

GOVERNMENT COLLEGE ROPAR

(Affiliated To Punjabi University, Patiala)



Criterion 3

Research, Innovations and Extension

3.3.1 Number of research papers published per teacher in the Journals notified on UGC care list during the last five years:

INDEX

Year 2018-2019

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1	Gurmat Sangeet ka mansik Aarogayta Main Mahatav Journal-Mental health ISSN 2394-5303	Dr. Harjas Kaur	1-9

Year 2019-2020

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2	Manvia Vikas main Matr Bhasha or sangeet ka yogdan Journal-Ajanta ISSN 2277-5730	Dr. Harjas Kaur	10-15
3	Plant growth-regulating molecules as thermo protectants: functional relevance and prospects for improving heat tolerance in food crops Journal of Experimental Botany doi:101093/xb/erz333	Shikha Chaudhary	16-41

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4	Identification and characterization of contrasting genotypes/cultivars for developing heat tolerance in agricultural crops: current status and prospects Journal- Frontiers In Plant Science Doi:10.33879/fpls.2020.587264	Shikha Chaudhary	42-75
5	COMMUNALISM AND NATIONAL INTEGRATION Journal- Kala Sarovar ISSN:0975-4520	Dr. Harpreet Kaur	76-80

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6	'Omics' approaches in developing combined drought and heat tolerance in food crops Journal- Plant Cell Reports Doi.org/10.1007/s00299-021-02742-0	Shikha Chaudhary	81-121
7	Impact of classical music on Film music Journal-Ideal ISSN 2319-359X	Dr. Harjus Kaur	122-129

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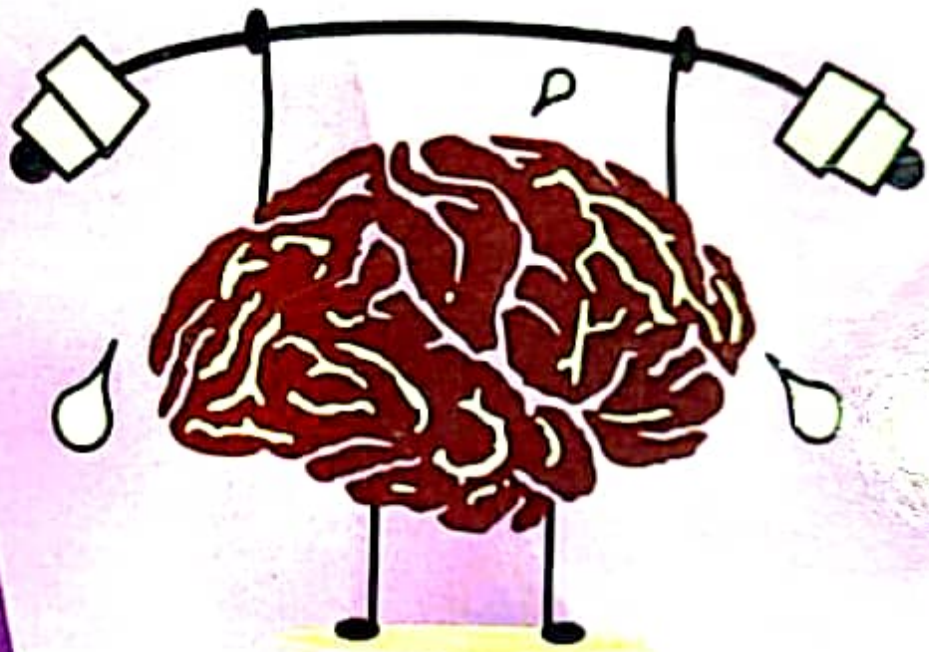
8	Bolpur se birandanban tak bhatkati ik lady ke sangrass ki katha Journal-Printing Area ISSN: 2394-5303	Dr. Kanchan	130-136
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ISSN 2394-5303



प्रिदिमागरियाँ
Special Issue

Mental Health



: Editor :
Prof Dinesh Jaronde



Harshwardhan

आंतरराष्ट्रीय बहुभाषिक शोध पत्रिका

प्रिंटिंग एरिया

Printing Area International Interdisciplinary Research
Journal in Marathi, Hindi & English Languages

Special issue

Mental Health

Editor

Prof. Dinesh Jaronde



Reg No.U74120 MH2013 PTC 251205

Harshwardhan Publication Pvt.Ltd.

At Post Limhaganesh, Tq Dist Beed

Pin-431126 (Maharashtra) Cell 07588057695, 09850203295

harshwardhanpubli@gmail.com, vidyawarta@gmail.com

All Types Educational & Reference Book Publisher & Distributors www.vidyawarta.com

UGC Approved Jr.No.43053

Impact Factor 5.011 (IIJF)



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गुरमत संगीत का मानसिक आरोग्यता में महत्व

डॉ. हरजस कौर

ऐसोसीएट प्रोफ़ेसर, सरकारी कालेज रूपनगर, पंजाब

आरोग्य जीवन में भाव मन संतुष्ट, चिन्ता मुक्त, विकार अनुपालन, भटकना से दूर और मुख में आनन्दमयी जीना है। मन को आरोग्य बनाने में संगीत कला की अहम भूमिका है। गुरमत संगीत श्री गुरु ग्रंथ साहिब में निर्दिष्ट है। श्री गुरु ग्रंथ साहिब में अंकित वाणी मन को संबोधित है और मनुष्य को जीवन जीने की सही दिशा प्रदान करती है। संगीत में मन के लिए आश्चर्यजनक वातावरण के सृष्टि की क्षमता है। संगीत एक अद्वितीय शक्ति है जिसका गुरु साहिबान ने भी अपनी वाणी को संचारण करने हेतु प्रयोग किया। आरोग्य जीवन जीने के लिए वाणी भाव गुरमत और संगीत का मेल सोने पर सुहागे का काम करता है।

प्राचीन काल से ही संगीत मनुष्य आत्मा का भोजन रहा है, पर इसके साथ एक बड़ी कठिनाई यह आ रही थी कि समय समय पर गायक की तरफ से दिया गया ज्ञान इतने नीचे स्तर का था कि वह मनुष्य मन के वेग को सही पथ से हटा कर विकारों की तरफ ले जाता था विकारी व्यक्ति कभी भी समाज की रचनात्मक तौर पर सेवा नहीं कर सकता। गुरमत संगीत ने एक नई दात हमारे सामने रखी। यह संगीत हमारे मन को आध्यात्मिक आनंद देता है। गुरमत संगीत एक सच्ची विचार धारा हृदय में प्रवेश करवाता है, अपनी आंतरिक कमजोरियों के प्रति ज्ञान करवाता है और यह अपने अंदर देखने पर मजबूर करता है। फिर मनुष्य अपने आप की सफाई करता है अच्छे मार्ग पर चलता है और निरंकार के चरणों में लीन होता है। आधुनिक समय में ऐसा कोई

व्यक्ति नहीं है जिस को डॉक्टर के पास जाने से मुनने को नहीं मिलता कि टैन्शन छोड़ो, चिंता छोड़ो क्योंकि आज के समय में प्रत्येक मनुष्य किसी न किसी चिंता में व्यस्त है पर जो मनुष्य गुरुमत संगीत के साथ है उसके अंदर एक भाव है—

गावीअै सुणीअै मनि रखैअै भाउ॥

दुखु परिहरि मुखु परि लै जाइ॥

वह अपने जीवन के परम आनंद में रहता है यहाँ

नानक भगता सदा विगास॥

सुणिअै दुख पाप का नाम॥

की अवस्था बन जाती है।

यह गुरुमत संगीत की बहुत बड़ी देन है जो हमारी जिंदगी के अंदर गुरु साहिबान ने अमूल्य अमृत वाणी से हमारे सामने स्पष्ट कर दिया है। जब श्री गुरु नानक देव जी अमृत वाणी कर उताग करते थे तो सब से पहले भाई मर्दाना जी गुरुमत के संगीत का विछौना करते थे। गुरुमत संगीत के सजे हुए विछौने पर, सजी हुई सेज पर परमात्मा की वाणी का गायन किया जाता था।

गुरु साहिबान ने गुरुमत संगीत की अलग से भाषा हमें दी है। इसके साथ मनुष्य के रोग कट जाते हैं। मनुष्य की आत्मिक कमजोरी खत्म हो जाती है और वह नैसर्गिक जीवन भाव आरोग्य जीवन में विचरता है। एक निरोग जीवन ही परिवार की अच्छी रख रखाव कर सकता है। अच्छा नागरिक बन सकता है। वह संसार के प्रत्येक पहलु पर सफलता पा सकता है, क्योंकि उसके भीतर व्यक्तित्व आ जाता है जो इसको गिरे हुए कर्म करने नहीं देता, जिससे उसके आरोग्य जीवन पर बुरा प्रभाव नहीं पड़ता शायद आधुनिक मनुष्य दो तत्वों से ग्रस्त है, एक समय आने पर पाप कर लेता है, दूसरा समय बीत जाने पर पछतावा करता है पर गुरुमत संगीत के धारणी मनुष्य की जिन्दगी के साथ—साथ जहाँ गुरुमत चलती है वहाँ संगीत भी जिन्दगी के साथ चलता है। वह अपनी आनंदमयी अवस्था में रहता हुआ भी अपने परमात्मा के चरणों में जुड़ कर बुराई के काम नहीं करता, जिससे मन

में चिंता हो उसकी आरोग्य जीवन पर बुरा प्रभाव पड़े या विकार पैदा हो। इन सभी से बच कर अपना शरीर निरोग रखते हुए अपनी जीवन यात्रा पूरी करता हुआ 'गुरमति जनमत सवारि दरगाह चलिअर' की अवस्था में लीन हो जाता है।

गुरमत संगीत वाणी/शब्द प्रधान है, इसमें प्रत्येक विषय नहीं गाया जाता। दुनियावी संगीत जहाँ मुख देता है वहाँ निरंकार के लिए संगीत आत्मिक रोशनी देता है। इसकी माक्षी इतिहास भी देता है कि एक बार अकबर बादशाह ने तानसेन को संगीत सुनने के लिए कहा। संगीत का आनंद लेने पर बादशाह ने तानसेन को कहा कि अगर तू इतना अच्छा गाता है, तो गुरु कितना अच्छा गाता होगा। तानसेन ने कहा मेरा गुरु बहुत महान् संगीतकार है पर जब उनका मन करे तब ही वे संगीत को खुशी लेते हैं इस पर बादशाह ने तानसेन के गुरु स्वामी हरिदास जी के संगीत सुनने की इच्छा प्रगटाई और कितने दिन इंतजार के बाद आखिर स्वामी हरिदास जी का संगीत सुनने को मिला। स्वामी हरिदास जी के संगीत से मंत्रमुग्ध हो कर बादशाह अकबर ने कहा कि तानसेन जिस तरह तेरा गुरु संगीत की प्रस्तुति करता है, उस तरह से संगीत का आनंद नहीं दे सकता। क्या तेरे गुरु ने तुम्हें इस तरह की शिक्षा नहीं दी। तानसेन ने कहा बादशाह मेरे और मेरे गुरु स्वामी हरिदास जी में यही अन्तर है कि मैं अकबर बादशाह को खुश करने के लिए गायन करता हूँ पर मेरा गुरु उस परमात्मा की खुशी के लिए गायन करता है। गुरु साहिवान की तरफ से आध्यात्मिक आनंद प्रदान गुरमत संगीत हमारे लिए एक वरदान है गुरमति संगीत के धारणीय मनुष्य की जिन्दगी गुरमत औपधि संगीत से समन्वय है। गुरमत संगीत की व्यवहारिक परम्परा सिक्ख धर्म में आस्था रखने वाले लोगों के जीवन संग पूरी तरह जुड़ी हुई है, सिक्खी जीवन के आरम्भ (जन्म) से ले कर अंत (मौत) तक अलग-अलग रस्में, रीत शब्द कीर्तन से सुसज्जित है। जीवन की प्रत्येक घड़ी, प्रत्येक पल जहाँ उस परमात्मा के नाम में ध्यान लगाने और निरमोल कीर्तन द्वारा हरी जस का आदेश सिक्ख जगत को है वहाँ जीवन के प्रत्येक अवस्था पर वाणी से जीव

के उपदेश दिया गया है। भाव जीवन के जन्म के समय परमात्मा की तरफ से दी गई दात का भन्यवाद करने के लिए भन्यवाद/बख्शीश के शब्दों के सिवाय बच्चे के जन्म से संबंध रखने वाले शब्दों का व्यान किया जाता है वहाँ प्राणी के अकाल चलाने पर जब तक देह है मारु के शब्द, माय की वार गायन की जाती है और देह को दाह देने के बाद बडहंस राग की खास तौर पर अल्पाहुनीयां गायन करने की प्रथा है। श्री गुरु ग्रंथ साहिब की वाणी को सामाजिक जीवन के प्रसंग से देखें तो सहज रूप से ही पता लग जाता है कि गुरु साहिबान हमें हमारे संस्कृतिक जीवन का अध्यात्मिक बदल दे रहे हैं। इस तरह जीवन की प्रत्येक घटना और कार्य से संबंध हमें वाणी में से शब्द मिल जाते हैं जिनका निर्दिष्ट विधि और परम्परा अनुसार गायन किया जाता है। गुरुमत संगीत का यह नियम है कि खुशी और गमी की रस्य निर्दिष्ट शब्द कीर्तन से सम्पन्न की जाए। सो गुरुमत संगीत हमारी जिन्दगी के प्रत्येक मौके पर मार्ग दर्शक के तौर पर जीवन के समय—समय पर आई कठिनाईयों का सम्मान करने के लिए ढाल बन कर जिन्दगी को बढ़ावा देने और न्यारापन लाने में मदद करती है।

गरु साहिबान ने वाणी की सफल प्रस्तुति हेतु वाणी औषध राग को इनकी प्रकृति की अंतरीवी सम्मेल रसात्मक और भावात्मक पक्ष पर जोड़ने की कोशिश की है। वैरागमई मारु राग में परमात्मा से विछोड़े का वियोग, मिलन की इच्छा भरपूर वाणी की रचना की। खुशियों के बसंत राग में ऋतु और प्रभु मिलाप के चाव आदि का वर्णन है। श्री गुरु ग्रंथ साहिब में वाणी रचना के लिए रागों के साथ—साथ अनुकूल गायन शैलियों का भी ध्यान रखा गया है जो गुरुमत संगीत के प्रयोजन की सिद्धि लिए लाभकारी है। वाणी और संगीत भाव गुरुमत संगीत का संयुक्त और सम्मिलित रूप स्रोतों के मन को वशीभूत कर इसको आस—पास से तोड़ कर सुरात्मक संसार में प्रवेश करवाता है। इस आनंदमयी आत्मा शुद्धि अवस्था वाणी का साहित प्रवेश और बोद्ध आरोग्य जीवन जीने में गुरुमत संगीत एक मौलिक और अनूठा माडल है। संगीत आत्मा की खुराक तो है ही पर गुरुमत संगीत हमें काम,

क्रोध, लोभ, मोह, अहंकार इत्यादि विकारों में दूर कर मन को अध्यात्मिक तौर पर तंदुरुस्त बनाने के साथ-साथ तन की खूबखाय के लिए भी दिशा अनुदेश करती है।

घटि वसहि चरणरविंद गगना जपै गोपाल।

नानक सो प्रभु सिमरीअै तिगु देही कड पालि।^१

क्योंकि आधुनिक समय मनुष्य ही खुशी वर्दाशत कर सकता है और न ही गमी। गुरुमत हमें संसार में किस तरह विचरना है, की भी शिक्षा देती है। वाणी की प्रस्तुति माध्यम संगीत भाव गुरुमत संगीत मनुष्य को जीवन बिताने के लिए ही नहीं बल्कि आरोग्य जीवन जीने के लिए हमेशा अंग संग रहता है।

वाणी और वाणी की प्रस्तुति का मूल और केन्द्रीय नुक्ता सहज है। वाणी जहाँ शांत संतोष अवस्था में रहने के लिए प्रेरित करती है वहाँ वाणी की गायन प्रस्तुति में कला के दिखावटी प्रदर्शन आकर्षण और प्रलोभन का त्याग बुनियादी तौर पर महत्वपूर्ण है।

इकि गावत रहे मनि साटु न पाइ।

हउ मै विचि गवाए सु हरिगुन गाउ।^२

आपि गवाए सु हरिगुन गाउ।^३

सहजे गाविदा थाइ पवै।

विनु सहजै कथनी बादि।^४

गुरुमत संगीत की किसी भी शब्द कीर्तन प्रस्तुति में जब-जब शब्द की बाजाए राग/गायन का कलात्मक पक्ष प्रधान होगा तभी गुरुमत संगीत की यह प्रस्तुति अपने लक्ष्य से विछड़ जाएगी। गुरुमत संगीत का उद्देश्य कलात्मक आनन्द की प्राप्ति करना नहीं बल्कि वाणी से अध्यात्मिक आनंद और अध्यात्मिक बोध की प्राप्ति करना है।

गुरुमत संगीत में भिन्न-भिन्न कीर्तन शैलियाँ और रूपों से वाणी का गायन किया जाता है जो गुरुमत अनुसार जीवन जीना सिखाता है। इस कीर्तन प्रस्तुति में व्यापक संस्कृति का अध्यात्मिक संस्कृति बदल के तौर पर रूपान्तरण किया जाता है। जो मनुष्य गुरुमत संगीत के इस महान खजाने से अपना रिश्ता जोड़ लेता है उसके जीवन

में अभंग भिट जाता है। वह मालिक के चरणों में जुड जाता है। वह अध्यात्मिक आनंद में सकारात्मक जिन्दगी जीता है। इस तरह से हम यकीन से कह सकते हैं कि गुग्गत संगीत के बिना तन्दुरुस्त जीवन हरी भरी और संतोषजनक जिन्दगी की कल्पना करना भी सपना सा लगता है।

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(Journal No. 40776)

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Volume-VIII, Issue-II
April-June-2019
Marathi/English Part-II/Hindi

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डॉ. हरजस कौर

सहायक प्रोफेसर, सरकारी कालेज, रूपनगर।

कायनात में मनुष्य एक चेतन तथा भावुक प्राणी है। भाषा उसकी भावनाओं की अभिव्यक्ति का माध्यम है। जिस बोली में वह तोतली जुबान द्वारा कुछ बोलता और सीखता है। वह उसकी मातृ भाषा होती है। पहले से ही संगीत मनुष्य की भावपूर्ण अभिव्यक्ति का साधन रहा है। जब भाषाई चिन्ह भी विकसित नहीं हुए थे उस समय भी मानव लय और संगीतात्मक धुनों के द्वारा अपने इष्ट को रिझाता था। यह सारी प्रक्रिया में उसके हृदय और प्रकृति की अहम भूमिका है। उदाहरण के तौर पर जब हम किसी बच्चे को आवाज देते हैं तो वह उस आवाज के प्रति आकर्षित होता है। यदि हम चलचित्र देखते हैं तो यह प्रक्रिया हमारी आँखों द्वारा होती है, परन्तु आवाज के प्रति हमारा आकर्षण स्वभाविक है। भाषा की वर्णमाला 'क', 'ख', 'ग' को भी यदि संगीत के साथ बच्चों को सिखाया जाए तो बच्चा जल्दी सीखता है। जहाँ बालक भाषा कविता के रूप में सीखता है वहीं गाकर संगीत उसके मन में घर बना लेता है।

'देवां तोरीआं मावां पुत जे प्यारे।'

लालां बालिया देह मैं बँचड़ा।

मोहरां वंडदी आवां।'

संगीत की धुन पर लोरी गाई जाती है। भाषा और संगीत की कशिश द्वारा ही बालक नींद के सपने लेने लग जाता है। मातृ भाषा जहाँ बच्चे को आवश्यकताओं का अहसास करवाती है वहीं संगीत की सहायता से अपनी भावनाओं को प्रस्तुत करने में सहायक होती है। मातृ भाषा और संगीत दोनों साथ-साथ चलते हैं। कदम-कदम पर भाषा और संगीत द्वारा मनुष्य अपने विचारों का आदान-प्रदान करता है यदि कहा जाए तो मातृ भाषा मनुष्य की पहचान है और संगीत उसके जीवित रहने का साक्षी है इसलिए यह गलत नहीं है। मनुष्य प्रकृति का एक हिस्सा है। इसलिए प्रकृति में रो अकुरित संगीत जैसे नदियों की कलकलाहट, वृक्षों की पत्तियों की कड़कड़ाहट, पक्षियों की चहचहाट, भवरो की गुंजन घोड़ो का कूदना आदि भी इसके

साथ उत्सुकता दिखाता है। संगीत मानवीय हृदय के खीचाव का केन्द्र बिन्दू है। डॉ. रोजी श्रीवास्तव अनुसार "संगीत जीवन के ताने-बाने का वह धागा है जिसके बिना हम सत्य, वित और आनन्द को प्राप्त नहीं कर सकते हैं। संसार की सभी कलाओं तथा विद्याओं में संगीत का सर्वश्रेष्ठ स्थान है। संगीत एक मानसिक विमारी की एक औषधि है विश्व का नैतिक विधान है। विश्वनुमा सौन्दर्य प्रदान करता है। मानव मक्षिक में नए रंग भरता है तथा भावनाओं को रंगीन उडान देकर निराशा के आँगन में आनन्द की प्रभात प्रवाहित करता है। जीवन और उत्साह के अभिनव सपनों को पूरा करने का काम करता है। जब मनुष्य ने अपने आपको सामाजिक प्राणी की तरह विकसित किया तथा लोकचारी में संगीत को प्रचलित किया उस समय यह समाप्ति की भावना तहत लोक संगीत

बना। रीता धनकर के अनुसार "लोक संगीत 'लोक' और संगीत दो शब्दों के समेल से बना है। लोक का अर्थ है जन साधारण और संगीत का अर्थ गायन, वादन और नृत्य परन्तु जब हम विशेष रूप से भाषा, लोक गीत की बात करते हैं तो इसकी पहले व्यक्तिगत रूप में स्वीकार किया गया था।

जिसकी आवेग, सहज प्रकृति की प्रवृत्ति की तरह पेश किया जाता था। क्योंकि लोक मन का कोई भी गहरा प्रभाव लोक गीत की पहचान बना लेता है। धीरे-धीरे कोई कथा, कहानी, ऋतु, दृश्य के आधार पर रचनाएँ होती गईं परन्तु आरम्भिक रूप में अध्यात्म युक्त ही थी। जन साधारण की खुशहाली इसका उत्तम स्वरूप माना जाता है। डॉ. रश्मी नन्दा भी आरम्भ में इसको व्यक्तिगत स्वरूप मानते हुए लिखते हैं, 'आरम्भ में यह किसी एक व्यक्ति की रचना होती है, परन्तु समय के साथ यह एक जन जाति के जीवन में अलिखित अमर परम्परा बन कर समा जाती है। इस रचे गए संगीत में कई परिवर्तन आते हैं और यह अपने मूल रूप का सुरक्षित रखते हुए नित नए रंग प्रदान करता रहता है।

पंजाबी मातृ भाषा और जनजीवन संगीत पर आधारित है। मानव अपनी ही भाषा के माध्यम द्वारा संचारित वह संगीत मनुष्य के दिल की धड़कन में सहज रूप से बस जाता है। इसके संचार के लिए किसी खास किस्म की रश्मी सिखलाई की जरूरत नहीं पड़ती है परन्तु फिर भी यह जीवन को दिशा देने में समर्थ है।

मातृ भाषा यानि लोक गीत और लोक संगीत का समेल मानव जीवन को अपनी संस्कृति से जोड़ कर रखता है। उसकी जिन्दगी में मासुगियत मिलवर्तन और प्यार की झलक मिलती है। मातृ भाषा और संगीत संगीत का संयोग मानव जीवन संवेदनाओं की अभिव्यक्ति करने के साथ-साथ मानवी विकास के हर कदम पर पंजाब और पंजाबीयत की नुहार प्रस्तुत करता है। प्रेम, भक्ति, सुख-दुःख की मानवीय संवेदनाएं, मान-अपमान, मिलन, विरह, शक्ति-रिवाज लोक गीत के भाव के साधन बनते हैं। डॉ. राजवंत कौर पंजाबी लोकगीत को परिभाषित करते हुए लिखते हैं 'जिस रचना में किसी भी जाति की भावनाएं जिन्हें वह एकसार कर के लड़ी में पिरो कर हृदय से गाकर प्रकट करने, जिसको सुनकर प्रभावित हो उन्हें यह अपनी कथा लगे और उनकी भावनाओं में खुशी, गमी, प्यार, दर्द, आर्थिक, सामाजिक, सदाचार आदि पक्ष उनकी मातृ भाषा और पेश होने और वह रचना मौखिक रूप में पीढ़ी दर पीढ़ी अतीत से वर्तमान तक अपनी हो और उस में उस कार्य की संस्कृति के अवशेष प्रत्यक्ष रूप से नजर आते हैं। उसे को लोकगीत का नाम दिया जा सकता है। इस का आधार मनोविज्ञानिक होता है।'

संगीत मनुष्य मन को बाहरी तथा शारीरिक आकर्षण से अलग करके आनन्द की अवस्था तक पहुंचाती है। भाषा मन के भावों को अंदर तक समाने और बसाने की समर्था रखता है। यह हमारी इन्द्रियाई, सांसारिक और मानसिक रुचियों की तृप्ति करता है। जिसकी सपष्ट उदाहरण संगीत को आदिकाल से ही पंजाब में ऋत्रि मुनियों, मगतों ने ईलाही वाणी के गायन संगीत का केन्द्र होते थे क्योंकि घरों में निरा दिन ईश्वर की इस के नियम का पालन किया जाता था। क्योंकि यह कथा रूप में प्रचलित थी इसलिए यह लोक गीतों की नीव बनी माना जाता है कि लोक गीतों के रूप में यह कथाएं नैतिक जीवन के रूप में वैदिक काल के लोगों के जीवन का अंग था। अथर्ववेद में लोक संगीत का जिकर मिलता है कि धार्मिक संस्कारों के अलावा तत्कालीन समाज में संगीत का विशेष महत्व था। छोटे-छोटे दैनिक कार्यों में संगीत को शामिल किया जाता था। कामकाजी लोग अपने मनोरंजन और खुशी के लिए गीत गाते थे। इसका जिकर अथर्ववेद में उपलब्ध है। पंजाबी, इतिहास मिथिहास और परम्परा में

प्रभावित होता लोकगीत विन्न-विन्न रूपों में संगीतक शैली तैयार करता है जो विभिन्न-2 अवसरों पर अपने स्वरूप में दिखाई देते हैं। यह मुख्य रूप से रत्नी प्रधान रूपों में प्रचलित हुए। तुवी वाले, वार और काव्य-शैली आदि नित्य प्रयोग में ही नहीं बल्कि संस्कृतिक मेलों का गूगार बन कर रह गए। घड़ों या ढोलकी वाले गीतों में सुहाग, घोड़ी आदि के अलावा रत्नी अपने नित्य की उलझनों को तीक्ष्ण भावों के साथ-साथ हलकें व्यंग के माध्यम से भी प्रस्तुत करती है। ऊँचे स्वर वाले गीतों का

उहराव ही गीत के भाव के मध्य, प्राप्त एकाग्रता, गम्भीरता को प्रकट करने में सहायक है। इस लोक गीतों में सुहाग, घोड़ी, हेयरे आदि के अलावा गीत जीवन के बुनियादी संस्कार मानवी रिशतों, भावों के साथ सम्बन्धित होते हैं। पंजाबी मातृ भाषा में जन-जीवन के हर पहलु के साथ सम्बन्धित लोकगीत मिलते हैं। जो अलाहुणी, वेष या कीरने नाम द्वारा जाने जाते हैं। आधुनिक समय में मातृ भाषा में संजोए पंजाबी लोकगीतों को संस्कृति विज्ञान की दृष्टि से एक संस्कृति सृजन के तौर पर पहचानने की बहुत ही आवश्यकता महसूस हो रही थी। राजनीतिक कारणों के कारण भूगोलिक बढ़त गई। इस ग्लोबल गोंव वाली मिथ्य के मण्डीकरण के दस्तूर में क्या नई पीढ़ी अपनी विरासत लोक गीत खो देगी। यह सबसे बड़ा प्रश्न विन्ह है। इसके निवारण के लिए ऐसे सैमीनार सार्थक रूप में काम कर सकते हैं जो खोज पर आधारित तथ्यों को पाठक्रम में शामिल अध्यापन में लागू करवाया जा सके। पुराने लोगों की तरह सिर्फ हम लोकगीत ही नहीं नई पीढ़ी के हाथ में देंगे। हमारी जिम्मेदारी इस से भी ज्यादा बढ़ गई है। हमें लोक गीतों को ढूँढना सम्मालना पड़ेगा उसके निश्चित स्वरूप को पहचानना पड़ेगा। उसका अमीर परम्परागत इतिहास आज के विद्यार्थियों को पढ़ाना पड़ेगा और संस्कृति मेलों के आयोजन द्वारा उनकी पुर्न उन्नित करनी पड़ेगी। तभी हमारी अगली पीढ़ी मानवी संवेदनाओं की सुझवान पारखी बनेगी। उनके हाथों में लोक गीतों को पकड़ा कर हम उन्हें आधुनिक युग भयानक रोक अकैलेपन से बचा सकते हैं। इस तरह हमारे लोकगीत, हमारी बढ़ती उम्र की अशीश बना रहेगा। जैसे:-


फूलां विचों फूल हैगा, फूल नी गुलाव
इहनूं रब दीआं रखा, ऐथे प्यार बेहिसाव
शाला मानदा जवानीआं रहे नी पंजाव
मचे किकली असाडी जिवें मचे नी शवाव।

संदर्भ सूची

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REVIEW PAPER

Plant growth-regulating molecules as thermoprotectants: functional relevance and prospects for improving heat tolerance in food crops

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Received 28 March 2019; Editorial decision 8 July 2019; Accepted 9 July 2019

Editor: Christine Foyer, University of Birmingham, UK

Abstract

Among various abiotic stresses, heat stress is one of the most damaging, threatening plant productivity and survival all over the world. Warmer temperatures due to climatic anomalies above optimum growing temperatures have detrimental impacts on crop yield potential as well as plant distribution patterns. Heat stress affects overall plant metabolism in terms of physiology, biochemistry, and gene expression. Membrane damage, protein degradation, enzyme inactivation, and the accumulation of reactive oxygen species are some of the harmful effects of heat stress that cause injury to various cellular compartments. Although plants are equipped with various defense strategies to counteract these adversities, their defensive means are not sufficient to defend against the ever-rising temperatures. Hence, substantial yield losses have been observed in all crop species under heat stress. Here, we describe the involvement of various plant growth-regulators (PGRs) (hormones, polyamines, osmoprotectants, antioxidants, and other signaling molecules) in thermotolerance, through diverse cellular mechanisms that protect cells under heat stress. Several studies involving the exogenous application of PGRs to heat-stressed plants have demonstrated their role in imparting tolerance, suggesting the strong potential of these molecules in improving the performance of food crops grown under high temperature.

Keywords: Antioxidants, crosstalk, GABA, high temperature, hormones, osmolytes.

Introduction

Rising temperatures, as a result of changing climate, are a major concern to scientists and agriculturists worldwide (Hasanuzzaman *et al.*, 2013). The Inter-Governmental Panel on Climate Change (IPCC, 2014) reported that the world's temperature increased by 0.74 °C from 1906 to

2005 because of unabated emanation of greenhouse gases by anthropogenic exercises (IPCC, 2014). This trend is expected to persist, which will lead to catastrophic losses in crop productivity (Bita and Gerats, 2013; Sharma *et al.*, 2016). Estimated yield losses in India by 2100 range from

10% to 40% (Aggarwal, 2008). Moreover, abnormal spikes in day/night temperatures in several parts of the world are becoming more frequent, causing serious damage to several crops (Bita and Gerats, 2013).

'Heat stress is often defined as where temperatures are hot enough for sufficient time that they cause irreversible damage to plant function or development' (Hall, 1992). 'Increase in air temperature, even by one degree above a threshold level, is considered heat stress in plants' (Teixeira *et al.*, 2013). Heat stress directly affects plant physiology, biochemistry, and overall gene expression, involving alterations in membrane structure and function, tissue water content, and the composition of primary and secondary metabolites, proteins, and lipids. These resulting physiological, molecular, and biochemical changes impair normal plant growth and development (Wang *et al.*, 2018). There are several target sites of heat stress: the oxygen-evolving complex (OEC) and associated cofactors in PSII, carbon assimilation by Rubisco, and ATP-producing machinery. Heat stress disrupts electron transport, which enhances the production of reactive oxygen species (ROS) in chloroplasts and mitochondria that can seriously harm DNA and cause lipid peroxidation of the cell membrane leading to cell death (Hameed *et al.*, 2012; Asthir, 2015). Consequently, one of the plant defenses against heat stress is firmly related to the increased capacity for ROS scavenging and detoxification (Awasthi *et al.*, 2015). Thermotolerance might be attributed to better thermostability of the plasma membrane and lower levels of ROS generation (Chakraborty and Pradhan, 2011). To overcome heat stress, plants have various defensive components including the maintenance of membrane integrity, disposal of ROS through antioxidant production, accumulation of osmolytes, and up-regulation of heat shock protein (HSP) biosynthesis (Asthir, 2015; Awasthi *et al.*, 2015; Sehgal *et al.*, 2017). The response of field crops to heat stress varies depending on the timing and duration of exposure; the reproductive stage is the most sensitive growth stage (Prasad *et al.*, 2017). Studies have shown that development of male reproductive organs (i.e. male gametophytes) is the main factor deciding seed set during heat stress (X. Li *et al.*, 2015; Sage *et al.*, 2015; González-Schain *et al.*, 2016). The ideal and threshold temperatures for fulfilling reproductive success are crop dependent, beyond which the biochemical and physiological processes deciding seed set are affected, resulting in huge yield losses (Prasad *et al.*, 2015; Sage *et al.*, 2015; W. Shi *et al.*, 2015). Knowledge of heat sensitivity across plant developmental stages to calculate the portion of damage during the sensitive stages will help in the development of accurate genetic and molecular arbitrations to minimize the drastic effects of heat stress (Djanaguiraman *et al.*, 2014; Prasad *et al.*, 2017).

In response to heat stress, several plant growth-regulating molecules (plant growth regulators; PGRs) participate directly or indirectly to impart thermotolerance. These include phytohormones such as abscisic acid (ABA), auxin (indole-3-acetic acid; IAA), cytokinin (CK), ethylene, gibberellins (GA), brassinosteroids (BRs), jasmonic acid (JA), salicylic acid (SA), nitric oxide (NO) (Wani *et al.*, 2016), polyamines (PAs) (Asthir *et al.*, 2018), osmolytes (Alamri *et al.*, 2018), and antioxidants (Zhang *et al.*, 2018) (Table 1).

Damaging effects of heat stress on plants

Heat stress causes leaf scorching, leaf necrosis, leaf senescence, leaf abscission, reduced root and shoot growth, flower drop, and poor seed set (Zinn *et al.*, 2010). Under heat stress, cell membrane composition is altered by denaturation of plasma membrane proteins, which causes electrolyte leakage (Savchenko *et al.*, 2002). Photosynthesis is also very sensitive to high-temperature stress; high temperature modifies the photochemical reaction in thylakoid lamellae in chloroplasts and alters the OEC, resulting in modification of the electron acceptor site of PSII and a direct effect on photophosphorylation (L.J. Wang *et al.*, 2010). Severe heat stress inactivates enzymes and produces ROS, causing serious cellular injuries (Liu and Huang, 2000). Reproductive processes are highly sensitive to high temperature. Heat stress disrupts pollen formation, pollen viability, pollen germination, pollen tube formation, egg formation in the ovule, the normal position of the style and stigma, pollen receptivity by stigma, fertilization, endosperm formation, and embryo growth, resulting in impaired reproductive growth (Foolad, 2005). In response to heat stress, plant cells increase the production of some ROS-scavenging enzymes and activate several diverse antioxidants as a defense mechanism (Wahid *et al.*, 2007; Awasthi *et al.*, 2015). At the same time, plants produce endogenous compatible osmolytes such as Pro, glycine betaine (GB), and trehalose, which serve many functions including maintaining water relations, scavenging ROS, and protecting photosynthesis (Alamri *et al.*, 2018; Dawood and El-Awadi, 2018). Plants also produce phytohormones such as ABA, SA, JA, auxins, and CKs, which act as signaling molecules to induce the activation of many defense-related mechanisms, and other molecules to increase the level of thermotolerance. Exogenous treatment of heat-stressed plants with these substances has imparted heat tolerance in various food crops (Wahid *et al.*, 2007; Ahammed *et al.*, 2016). Increases in temperature also alter the stability, biosynthesis, concentration, and homeostasis of various growth-regulating molecules in different plant parts (Maestri *et al.*, 2002; Ahammed *et al.*, 2016), which result in cellular damage at various levels, but, at appropriate concentrations, they offer protection from heat stress.

Plants exposed to short-term temperature changes trigger various acclimation responses, while continuous alteration may trigger adaptation responses (Bahuguna and Jagdish, 2015). While several PGRs, including phytohormones, are activated in response to heat stress in various plant tissues to participate in diverse signaling mechanisms, their roles in the heat stress response are not fully understood; in particular, how they interact and participate in crosstalk to sense, defend, and impart thermotolerance. Here, we describe the role of various growth-regulating molecules in heat-stressed plants, along with the crosstalk among them, in synergistic and antagonistic mechanisms that confer cellular thermotolerance. Initially, we describe how heat stress is sensed by plants, resulting in the expression of different defensive molecules.

Thermosensors in plants

Temperature changes are sensed by all plant cells subjected to heat stress at the same time. At the cellular level, heat stress

Table 1. Various molecules involved in thermoprotection along with their functions

Molecule	Function
Auxin	<ul style="list-style-type: none"> Involved in cell growth and cell expansion, mainly produced in actively growing parts of the plant. Hypocotyl elongation in <i>Arabidopsis thaliana</i> seedling under heat stress (29 °C) (Gray <i>et al.</i>, 1998). Exogenous application promoted anther cell proliferation and reversed male sterility to improve male reproductive growth in barley when exposed to heat stress (33 °C; Sakata <i>et al.</i>, 2010). Mitigated the harmful effect of high temperature stress (35 °C for 6 h d⁻¹ for 4 d) in pea during flowering stage and enhanced yield (Abeyasingha, 2015).
Gibberellins	<ul style="list-style-type: none"> Play major roles in plant growth by cell elongation (Hedden and Thomas, 2012). GA by interacting with auxin and PIF4 helps in hypocotyl elongation in <i>Arabidopsis</i> under high temperature (29 °C; Stavang <i>et al.</i>, 2009). Promote flowering under heat stress (27 °C) by GA-mediated DELLA protein degradation in <i>Arabidopsis</i> (Kumar <i>et al.</i>, 2012). Exogenous treatment with 50 µM GA helps to promote seed germination and seedling growth of <i>Arabidopsis</i> under heat stress (3 h at 50 °C) (Alonso-Ramírez <i>et al.</i>, 2009). In <i>Arabidopsis</i> mutants for GA biosynthesis, its exogenous application restores deformities in reproductive function (Plackett <i>et al.</i>, 2012).
Cytokinins	<ul style="list-style-type: none"> Major role in the regulation of cell division, nucleic acid metabolism under stress conditions (Ha <i>et al.</i>, 2012). Maintenance of meristematic nature and nutrient mobilization in plant cells (Gupta and Rashotte, 2012). Enhance the rate of grain filling in rice by accelerating the rate of cell division in endosperm at early grain-filling stage and control the grain sink size (Zhang <i>et al.</i>, 2010) Improve the rate of stomatal conductance to facilitate transpiration under heat stress condition (Macková <i>et al.</i>, 2013). Help in various heat-responsive processes such as production of glycine-rich proteins and HSPs. CK treatment delayed leaf senescence under heat stress (35 °C) in creeping bentgrass (Xu and Huang, 2009). Exogenous treatment with (0.01 g l⁻¹) CK improved grain yield by enhancing stay-green characteristics under heat stress (37 °C and 33 °C) in wheat cultivars (Yang <i>et al.</i>, 2016).
Abscisic acid	<ul style="list-style-type: none"> Plays important role in seed germination, lateral root growth, seed development, seed dormancy, and transition from vegetative to reproductive phase (Sah <i>et al.</i>, 2016). Induced the expression of small heat shock factors (sHSFs), such as sHSP17.2, sHSP17.4, and sHSP26, under heat shock (42 °C at an interval 2 °C h⁻¹) (Hu <i>et al.</i>, 2010b) Rice plants on treatment with ABA (1, 10 and 100 µmol l⁻¹) maintained optimum starch level, soluble sugars, and non-structural carbohydrates under heat stress (39–41 °C from 09.00 h to 15. 00 h and 30 °C at night for 7 d) (Islam <i>et al.</i>, 2018). Its exogenous application of 10⁻⁵ M ABA to barley seedlings enhanced thermostability of thylakoids in barley seedling when exposed to 45 °C and 50 °C by reducing chlorophyll fluorescence (Ivanov <i>et al.</i>, 1992). Maintained higher activities of catalase (CAT), superoxide dismutase (SOD), ascorbate peroxidase (APX), and glutathione peroxidase (GPX) in maize seedlings on exposure to heat stress at 50 °C (Gong <i>et al.</i>, 1998).
γ-Aminobutyric acid	<ul style="list-style-type: none"> Role in signal transduction, maintenance of cytosolic pH, carbon and nitrogen metabolism and their transport, plant growth, and stress resistance in plants (Bown and Shelp, 1997; Bouché and Fromm, 2004). Regulates the production of osmolytes such as glycine betaine and proline in rice seedlings under heat stress (42 °C/37 °C) (Nayyar <i>et al.</i>, 2014). Exogenous application of 2 mM GABA in <i>Piper nigrum</i> enhanced the activities of antioxidant system under PEG-induced stress (Vijayakumari and Puthur, 2016).
Brassinosteroids	<ul style="list-style-type: none"> Similar to steroid hormones in animals, regulate cell division, cell elongation, seed germination, plant growth, flowering, and senescence (Khrpach <i>et al.</i>, 2003; Bajguz and Hayat, 2009). Enhanced activity of Rubisco and increased CO₂ assimilation in <i>Cucumis sativus</i> (Yu <i>et al.</i>, 2004) under heat stress. Exogenous application of 1 µM EBR helps in aggregation of HSPs which results in enhanced basic thermoerance in canola and tomato seedlings under heat treatment of 45 °C of varying length (Dhaubhadel <i>et al.</i>, 1999). Improve the chlorophyll concentration, stomatal conductance, quantum efficiency, and expression of antioxidants in <i>Cucumis melo</i> on exposure to heat stress (42 °C/32 °C; Y.P. Zhang <i>et al.</i>, 2014).
Salicylic acid	<ul style="list-style-type: none"> Phenolic plant growth regulator involved in plant responses such as water transport and nutrient uptake, stomatal conductance, and gaseous exchange (Yusuf <i>et al.</i>, 2013). Plays a key role in signal transduction involved in thermotolerance by increased endogenous and free SA in mustard under heat stress (Dat <i>et al.</i>, 1998a, b). Wheat plants exposed to 40 °C for 6 h daily, increased SA level, stimulated proline synthesis to improve osmotic potential and water uptake (Khan <i>et al.</i>, 2013). Its endogenous level in heat-stressed mungbean plant enhanced antioxidant enzyme activities to impart thermotolerance (Saleh <i>et al.</i>, 2007). Exogenous treatment increased plant dry matter, free proline accumulation, and soluble protein content under heat stress (42±2 °C) in cotton seedlings (Hameed and Ali, 2016).
Jasmonates	<ul style="list-style-type: none"> Play important role in plant growth regulation, involved in seed germination, root growth, sex determination in maize, leaf orientation, tuber formation, and fruit formation Yoshida <i>et al.</i>, 2009; Sharma and Laxmi, 2016). Exogenous treatment with 50 µM JA to grape seedlings activated antioxidant enzymes to prevent harmful effects of heat stress (42 °C: Qin and Lin, 2006). <p>1 µM JA exogenous treatment improved wheat coleoptile tolerance to heat stress(43 °C) by enhancing antioxidant activity (Karpets <i>et al.</i>, 2014).</p>

Table 1. *Continued*

Molecule	Function
Nitric oxide	<ul style="list-style-type: none"> Acts as a key player of cell signaling for many physiological processes, including stress tolerance in plants. Under heat stress, interacts with other signaling molecules such as MAPKs, cADP ribose, and phytohormones along with Ca²⁺ to prevent harmful effects on plants (Khan <i>et al.</i>, 2014; Asgher <i>et al.</i>, 2017). Increased endogenous NO production in dorsal epidermal cells and suspension cells of tobacco plant induce thermotolerance under heat stress (40 °C for 7 min) Exogenous treatment of NO improved thermotolerance by increasing the antioxidants in wheat (0.05–0.5 mM; El-Beltagi <i>et al.</i>, 2016), enhancing seed germination in lettuce (0.1–0.5 mM; Deng and Song, 2012). Prevents oxidative stress and ion leakage in rice on treatment with 0.001–0.02 mM NO (Song <i>et al.</i>, 2013).
Melatonin	<ul style="list-style-type: none"> Acts as strong growth modulator and rooting agent in plants (Hernández-Ruiz and Arnao, 2008; N. Zhang <i>et al.</i>, 2014) Exogenous melatonin prevented heat-induced (38/33 °C; day/night) growth inhibition, extended the duration of leaf senescence, and improved tiller number, cell membrane integrity, and photosynthetic efficiency in ryegrass (<i>Lolium perenne</i> L.; J. Zhang <i>et al.</i>, 2017). Foliar-sprayed melatonin (100 μmol l⁻¹) on maize (<i>Zea mays</i> L.) seedlings helped to enhance antioxidant enzyme activity and reduce the effect of oxidative stress (Ye <i>et al.</i>, 2016). Pre-treatment with melatonin (200 μM) reduced H₂O₂ content, increased proline content, and enhanced antioxidants in kiwifruit seedlings (Liang <i>et al.</i>, 2018).
Polyamines	<ul style="list-style-type: none"> Ubiquitous nitrogenous compounds present in all living cells meant for various cellular responses (Sengupta <i>et al.</i>, 2016). Exist in various forms—diamine (putrescine; Put), triamine (spermidine; Spd), and tetramine (spermine; Spm)—are the three most abundant PAs in plants. Under heat stress, an increase in conjugated and free PAs was reported in heat-tolerant cotton and rice plants along with enhanced PA biosynthetic enzymes during high-temperature stress (Evans and Malmberg, 1989; Cona <i>et al.</i>, 2006). Exogenous application imparts heat tolerance in mungbean (50 °C for 2 h; 1 mM Put; Basra <i>et al.</i>, 1997). Tomato supplied with 1 mM Spd increased expression of ethylene-related genes, PA biosynthesis genes under high temperature treatment (33/27 °C). In rice seedlings, exogenous treatment of 1 mM Spd ameliorated heat stress (42 °C, 48 h) induced damage, and enhanced activity of antioxidant enzymes for heat stress tolerance (Mostofa <i>et al.</i>, 2014).
Osmolytes	<ul style="list-style-type: none"> Play an important role in cellular osmoregulation and stabilization of proteins in plant cells (Hayat <i>et al.</i>, 2012).
Proline	<ul style="list-style-type: none"> Under heat stress, accumulation of free proline has been reported in many crops including tomato (Rivero <i>et al.</i>, 2004), mulberry (<i>Morus alba</i>; Chaitanaya, 2001), cotton (De Ronde <i>et al.</i>, 2000), cabbage and Chinese cabbage (<i>Brassica oleracea</i>; Hossain <i>et al.</i>, 1995), and apple (<i>Malus domestica</i> Borkh.; Park <i>et al.</i>, 2001).
Glycine betaine	<ul style="list-style-type: none"> Sugarcane, nodal buds soaked in 20 mM proline as well as glycine betaine improved the accumulation of soluble sugars, free proline, glycine betaine, K⁺ and Ca²⁺ contents under heat stress (42 °C) to overcome its harmful effects. Acts as a compatible solute and inhibits ROS accumulation under heat stress (Chen and Murata, 2002). Endogenous biosynthesis or exogenous application of glycine betaine has stabilizing effect on photosynthetic membranes under heat stress in plants (Allakhverdiev <i>et al.</i>, 1996). Exogenous treatment with 20 mM glycine betaine promoted seed germination and yield due to improved shoot water content in barley seedlings (Wahid and Shabbir, 2005). Tomato seeds supplemented with 0.1, 1, or 5 mM glycine betaine improved seed germination and seedling growth under high temperature (34 °C) (Li <i>et al.</i>, 2011).
Antioxidants	<ul style="list-style-type: none"> Ascorbic acid is an important antioxidant molecule; plays an important role in scavenging ROS (Smirnof, 2000).
Ascorbic acid	<ul style="list-style-type: none"> Also act as a major signaling molecule for oxidative stress in plant cells (Akram <i>et al.</i>, 2017)
Glutathione	<ul style="list-style-type: none"> Exogenous application with (50 μM) ascorbic acid imparted heat stress tolerance in mungbean under heat stress 40/30 °C and 45/35 °C; day/night temperatures; Kumar <i>et al.</i>, 2011) GSH is a non-enzymatic, low molecular weight antioxidant molecule which participates in ROS detoxification in stressed conditions by interacting with plant hormones and signaling molecules (Hasanuzzaman <i>et al.</i>, 2017). Pre-treatment of mungbean seedlings with 0.1 mM GSH improved physiological performance as well as antioxidant defense systems during heat shock (42 °C; Nahar <i>et al.</i>, 2015).

perception and signaling involve the same stress response system throughout the plant (Mittler *et al.*, 2012; Hasanuzzaman *et al.*, 2013). Plants have developed an incredible capacity to detect the slightest fluctuations in temperature. Different pathways, regulatory systems, and cellular compartments are associated with inducing thermotolerance in plants (Bita and Gerats, 2013; Asthir, 2015; Awasthi *et al.*, 2015) (Fig. 1). Plants have a wide range of thermosensors for detecting absolute and steady changes in seasonal and diurnal temperatures. In plant cells, the macromolecules (membranes, nucleic acids, and protein

complexes) can simultaneously perceive heat stimuli from their surroundings (Richter *et al.*, 2010) and act as thermosensors, through reversible changes such as increasing fluidity of the plasma membrane, fractional melting of nucleic acids, and protein misfolding. These high-temperature-responsive sensors have the potential to sense stimuli precisely, followed by different heat stress responses, depending on the extent of alteration. In addition, they can differentially activate signaling pathways to up-regulate a large number of heat stress response genes and gene networks (Mittler *et al.*, 2012).

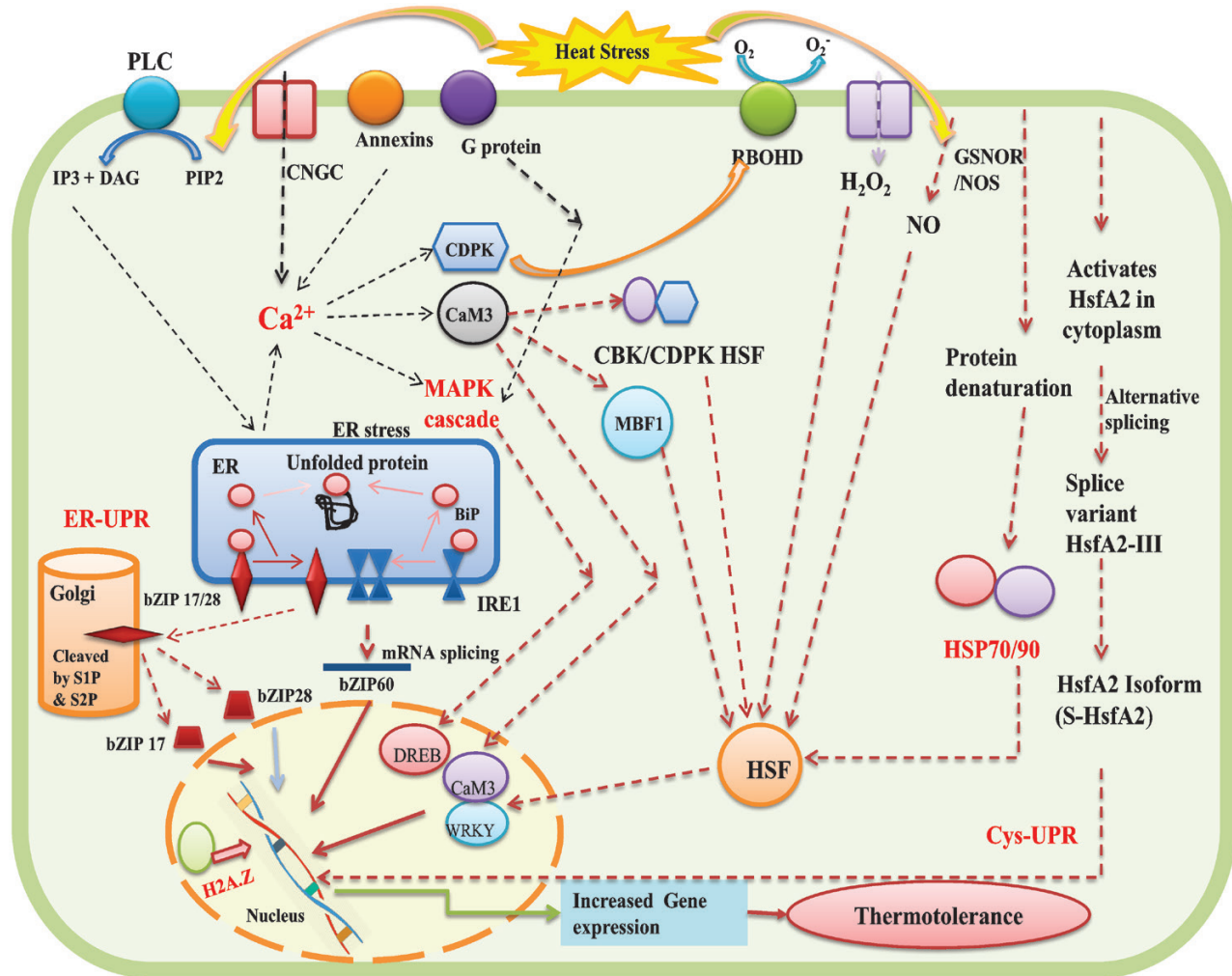


Fig. 1. Heat stress sensing and signaling in plants. The plasma membrane and endoplasmic reticulum both participate actively in the plant heat stress response. High-temperature stress alters membrane composition as well as function. The membrane-localized RBOHD is regulated by cAMP activated by the calcium-permeable channel CNGC6 that mediates calcium influx. Other membrane components such as PIPK, PLD, and PLC sense changes in the state of membranes and activate the lipid signaling molecules PIP₂, PA, and IP₃, respectively. These molecules are further phosphorylated to IP₆ and IP₃ and mediate the release of calcium from the ER. RBOHD initiates a rapid increase in hydrogen peroxide (H₂O₂) and induces the ROS/redox signaling pathway along with MAPK HSFs and MBF1c–HSFA3–DREB2A during the heat stress response. MAPK HSFs also regulate the expression of CAT, hence maintaining the ROS level. Accumulated calcium further binds to CaM3 and activates CBK3/PP7 as well as TFs of the heat stress response, such as HSFs and WRKY39. The heat sensors associated with the ER-UPR consist of bZIP28 (spliced in the Golgi) and IRE1 (splicing bZIP60 mRNA). The FAD2 and FAD3 in the ER are crucial components in regulating membrane fluidity during the heat stress response. Several TFs may enter the nucleus to activate genes related to defense to impart thermotolerance in plants. Abbreviations: RBOHD, respiratory burst oxidase homolog D; CNGC6, cyclic nucleotide-gated ion channel; PIPK, phosphatidylinositol-4-phosphate 5-kinase; PLD, PM-localized phospholipase D; PLC, PM-localized phospholipase C; PIP2, phosphatidylinositol-4,5-bisphosphate; IP₃, inositol 1,4,5-triphosphate; ER, endoplasmic reticulum; ROS, reactive oxygen species; MAPK, mitogen-activated protein kinases; HSF, heat shock factor; MBF1c, multiprotein bridging factor; DREB2A, dehydration response element-binding factor 2A; CAT, catalase; CaM3, calmodulins; CBK3, calmodulin-binding protein kinase 3; PP7, phosphatase; WRKY, amino acid sequence; ER-UPR, endoplasmic reticulum unfolded protein response; bZIP28, basic leucine zipper; IRE1, inositol-requiring enzyme; FAD2, fatty acid desaturase 2; FAD3, (fatty acid desaturase 3; HSR, heat shock response, TF, transcription factor.

The heat stress response involves various cellular compartments and regulatory pathways, and is triggered by four thermosensors (Fig. 1): (i) cyclic nucleotide-gated calcium channels (CNGCs) that lead to inward calcium flux (Saidi *et al.*, 2009); (ii) a histone sensor in the nucleus (Kumar and Wigge, 2010); (iii) unfolded protein sensors in the endoplasmic reticulum (ER-UPRs) (Che *et al.*, 2010; Deng *et al.*, 2011); and (iv) unfolded protein sensors in the cytosol (Cyt-UPRs) (Sugio *et al.*, 2009). Heat sensors (CNGCs, ER-UPRs, and Cyt-UPRs) are activated in response to high temperatures, triggering various signaling pathways through numerous kinases as well as transcriptional regulators of the heat

stress response, such as heat shock factors (HSFs), MBF1c (multiprotein bridging factor), and RBOHD (respiratory burst oxidase homolog D) (Rasul *et al.*, 2017). Many secondary messengers such as NO, hydrogen peroxide (H₂O₂), and Ca²⁺ ions are significantly important in heat stress signaling pathways (Pandey *et al.*, 2015; Rasul *et al.*, 2017). The heat signal is amplified by numerous pathways that merge into the final activation of heat stress-responsive genes, elevation of HSPs, and the onset of cellular thermotolerance (Mittler *et al.*, 2011). The activation of different pathways may be tissue specific and vary between vegetative and reproductive tissues (Mittler *et al.*, 2012).

The cell membrane is considered an important sensor for high temperature as it senses temperature variations and transduces them into the nucleus where the transcriptome is rehabilitated (Conde *et al.*, 2011; Fig. 1). Membrane composition plays an important role in controlling the calcium-dependent heat-sensing signaling pathway (Saidi *et al.*, 2009). Heat stress activates Ca^{2+} channels in the membrane, causing the influx of Ca^{2+} into plant cells (Hofmann, 2009). Membrane alteration due to heat stress stimulates many heat-responsive regulatory mechanisms (Rasul *et al.*, 2017). Inside the cell, Ca^{2+} communicates and negotiates multiple signaling cascades by activating CaM3 (calmodulins) and CDPKs (calcium-dependent protein kinases) (Sajid *et al.*, 2018). CDPKs are further initiated by MBF1C that acts as its co-activator to stimulate the expression of antioxidant enzymes under heat stress (Qu *et al.*, 2013). In turn, CDPK stimulates RBOHD and MAPK (mitogen-activated protein kinase) cascades (Suzuki *et al.*, 2011) (Fig. 1). These MAPKs (MAPK3 and MAPK6) play a crucial role in the heat stress response by regulating the expressions of HsfA2 (heat-stress transcription factor A2) and HSPs (Wang and Huang, 2017). All these activated genes act downstream of the Ca^{2+} signaling cascades; hence, Ca^{2+} acts as a key node in the expression of HSFs and HSPs under heat stress (Sajid *et al.*, 2018). Inside the nucleus, Ca^{2+} or MAPK-activated HsfA2c stimulates the expression of HSP genes such as Hsp18, Hsp70, and Hsp90 (Wang and Huang, 2017). Calmodulin activation by Ca^{2+} also induces the expression of some HSPs through signal transduction mechanisms (Wang and Huang, 2017; Fig. 1).

In the cytosol, HsfA2 is a key regulator in the response to heat stress, as reported in *Arabidopsis thaliana* (Wang and Huang, 2017). It serves as a regulatory amplifier of a subset of genes for the heat stress response. HsfA2 is regulated by alternative splicing to form splice variant HsfA2-III, which further encodes the HsfA2 isoform (S-HsfA2) that binds to a heat shock element, resulting in the transcription of HSP genes and other heat-inducible genes (Liu *et al.*, 2013) (Fig. 1). Heat stress-responsive machinery in plants includes HSPs, transcription factors (TFs), and important enzymes (Qu *et al.*, 2013). On exposure to very high temperature, overexpression of HSFs causes downstream activation of heat stress-responsive genes (Saidi *et al.*, 2011). Elevated levels of HSPs are produced in response to heat stress and are the key players in the heat shock response (Lindquist, 1986). HSPs are molecular chaperones involved in protecting misfolded proteins from irreversible aggregation. Functionally, there are seven classes of HSPs, and the predominant form is molecular chaperonins. The five major types of molecular chaperonins are Hsp60s, Hsp70s, Hsp90s, Hsp100s, and small heat shock proteins (sHsps) (Richter *et al.*, 2010).

The ER plays an important role in protein synthesis, folding, processing, and exportation. In addition, the ER has a role in lipid metabolism. The ER secretory pathway is responsible for the passage of more than a third of total protein via the ER lumen (Fragkostefanakis *et al.*, 2016; Niu and Xiang, 2018). ER homeostasis is highly sensitive to abiotic stress, leading to the production of misfolded and denatured proteins, which is known as ER stress (Walter and Ron, 2011; Niu and Xiang, 2018). The basic mechanism behind ER stress tolerance is

known as the unfolded protein response (UPR), which involves the identification of unfolded or misfolded proteins and the activation of some TFs, foldases, and chaperones. Plants have two primary heat stress signaling pathways that are reported to sense ER stress. One pathway is initiated by membrane-linked TFs (the basic leucine zipper TFs, i.e. bZIP17 and bZIP28), and the other includes the RNA splicing factor (inositol-requiring enzyme IRE1) (Liu and Howell, 2016) (Fig. 1). Heat-induced ER stress is specifically sensed by bZIP28 and translocated into Golgi bodies where its TF domain can be cleaved by proteolytic processing on the cytosolic side. The portion containing TFs subsequently enters the nucleus to initiate the expression of stress-related genes. In the case of the RNA splicing factor-mediated heat stress response, IRE1 is activated by its interaction with unfolded proteins to locate and recognize the mRNA of bZIP60 to be spliced. After splicing, its products penetrate the nucleus to trigger the expression of UPR genes (Deng *et al.*, 2011; Liu and Howell, 2016; Niu and Xiang, 2018). These sensing mechanisms eventually lead to the activation and expression of genes related to several molecules involved in defense, including phytohormones, antioxidants, heat stress proteins, osmolytes, and amino acids (Wahid *et al.*, 2007).

Roles of plant growth-regulating molecules in thermotolerance

Thermotolerance in plants is an inherent developmental system that is a vital component of the survival mechanism (Bahuguna and Jagadish, 2015). Thermotolerance consists of basal and acquired thermotolerance. The basal thermotolerance is an inherent ability for the plants to survive on exposure to temperatures above the optimal for growth, while acquired thermotolerance refers to the ability to cope with lethal high temperatures after acclimatization to mild temperatures (Clarke *et al.*, 2004). Basal thermotolerance is reported to involve SA, JA, and ethylene signaling pathways, and scavenging systems for ROS (Miller *et al.*, 2008; Clarke *et al.*, 2009). On the other hand, the acquired thermotolerance involves HSFs and HSPs; the former are primary regulators for the expression of HSP genes. Diverse types of signaling molecules such as SA, ethylene, ABA, H_2O_2 , calcium, and phospholipids are found to participate in acquired thermotolerance (Liu *et al.*, 2015a). The expression of HSFs and HSPs is regulated by these molecules, which assist in preventing oxidative damage to the heat-stressed cells (Song *et al.*, 2012).

Responses to heat stress are mainly related to altered production and translocation of various PGRs, including phytohormones that ultimately affect the production potential of the plants. An array of studies has provided strong evidence on the involvement of these molecules in response to heat stress (Peleg and Blumwald, 2011; Ahammed *et al.*, 2015; Xia *et al.*, 2015). A diverse group of PGRs play an important role in stress defense responses, and their signaling pathways are complexly interconnected to promote an efficient stress response (Fig. 2). It is important to understand the complex network of interactions among various PGRs to improve our knowledge of plant resistance mechanisms (Xia *et al.*, 2015). Most of the

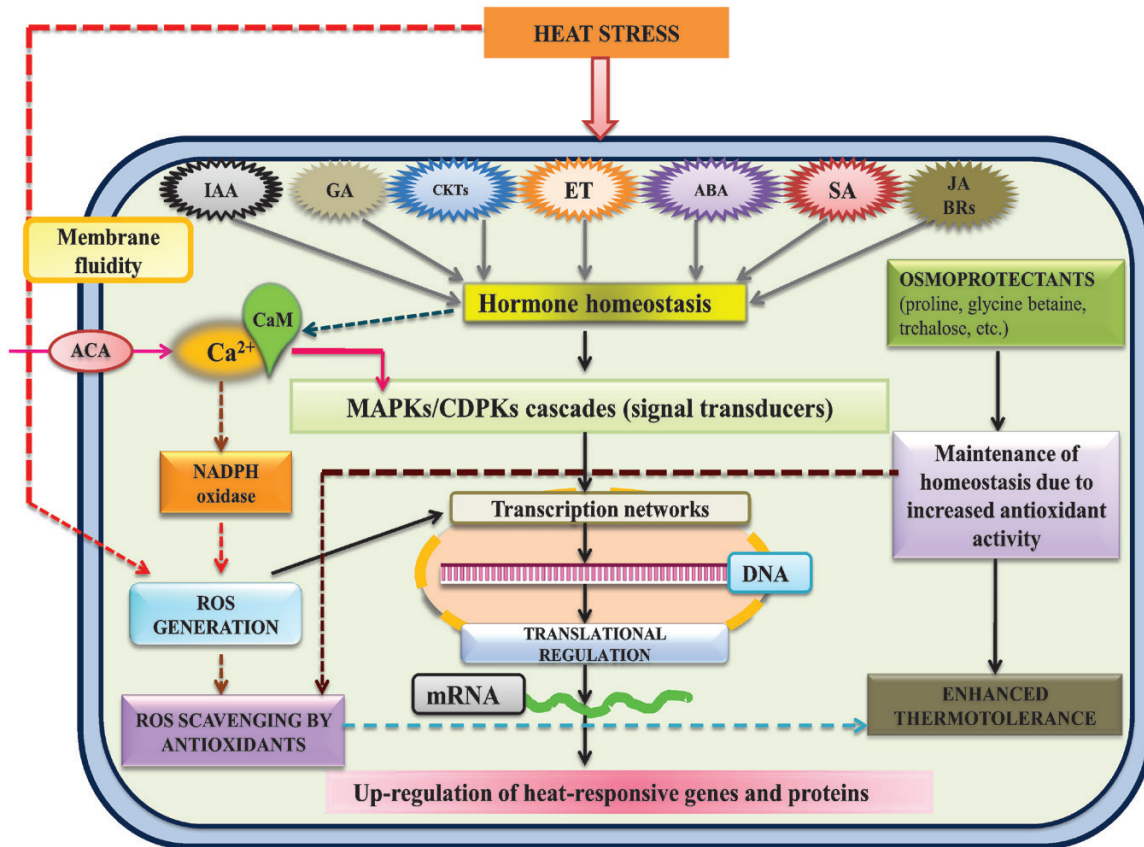


Fig. 2. Proposed mechanism of phytohormones, osmoprotectants, and antioxidants in thermotolerance in plants. Heat stress increases membrane fluidity and leads to the generation of reactive oxygen species (ROS) in plants. Phytohormones, especially auxins (as IAA), gibberellins (GA), cytokinins (CTKs), abscisic acid (ABA), ethylene (ET), salicylic acid (SA), jasmonic acid (JA), and brassinosteroids (BRs) along with other signaling molecules induce the mitogen-activated protein kinase (MAPK)/CDPK (calcium-dependent protein kinase) cascade leading to the up-regulation of different transcription networks, which further result in the expression of specific heat-responsive genes and elevation of antioxidants providing heat stress resilience. High temperature also activates the plasma membrane calcium channels that cause calcium influx. Calcium ions after binding with calmodulins initiate MAPK/CDPK cascades, up-regulating transcription networks to impart thermotolerance. Some osmoprotectants such as proline, glycine betaine, and trehalose also alleviate the harmful effects of heat stress by osmoregulation and ROS detoxification via enhanced expression of antioxidants.

PGRs reported to protect plants from heat-induced injuries act either individually or together to coordinate defense responses to heat stress (Xia *et al.*, 2015; Fig. 2). Generally, they respond quickly by altering gene expression during the stress period by either preventing or enhancing the degeneration of transcriptional activators via the ubiquitin–proteasome system (Santner *et al.*, 2009). Hence, the negative effects of extreme temperatures can be mitigated by developing novel heat-tolerant lines with improved thermotolerance through the implication of PGRs at the genetic level (Zhou *et al.*, 2014). Altering PGR levels through exogenous application or breeding techniques, at appropriate concentrations without harmful effects, may assist in the management of heat stress responses and to sustain crop production in the era of climate change (Ahmed *et al.*, 2015). Considering these aspects, the expression of genes related to PGRs in a stage- and tissue-specific manner is essential for initiating heat tolerance, and this targeted modulation of the desired hormone pool offers better efficacy for regulating heat stress responses in plants (Macková *et al.*, 2013). All major PGRs—auxins, GAs, CKs, ABA, ethylene, SA, JA and BRs—play a crucial role in high-temperature tolerance in plants (Zhou *et al.*, 2014; Xia *et al.*, 2015; Ahmed *et al.*, 2016; Fig. 2). While considerable progress has been made in

deciphering the molecular mechanisms related to heat perception, the signaling mechanisms related to various PGRs under heat stress remain unclear and require further investigation (Ahmed *et al.*, 2016). The role of various phytohormones in regulating reproductive growth and seed filling has been recently described (Ozga *et al.*, 2017), and thus will not be part of this review. Our focus here is on the role of various molecules, especially phytohormones, involved in the heat response, and their potential involvement in thermoprotection, mainly in vegetative components, though studies on their involvement in reproductive components have also been cited. It is pertinent to mention here that the endogenous concentrations of phytohormones may vary in a stage-specific manner, and so do their effects. Moreover, the effects of exogenous application of various molecules having a role in thermoprotection may also differ, depending upon their concentration, as well as the growth stage of the plants.

Auxins

The role of auxins in the heat stress response has recently attracted attention, and there is some strong experimental evidence regarding their role in thermoprotection. Exposure

to mild heat stress rapidly increased auxin accumulation and stimulated the *YUCCA* (flavin-containing monooxygenase) gene in *Arabidopsis* (Sharma *et al.*, 2015). Auxins have been implicated in cell division and elongation; this function was also noticed in heat-stressed (29 °C) *A. thaliana* seedlings, compared with those grown at 20 °C. A dramatic hypocotyl elongation was noticed under heat stress, which was not observed in mutants defective for auxin response and transport. On the other hand, mutants deficient in GA and ABA biosynthesis or in ethylene response were unaffected. Moreover, an increase in the endogenous IAA level was observed in heat-stressed plants, suggesting that high temperature enhanced the auxin levels, resulting in increased elongation of hypocotyls (Gray *et al.*, 1998; Table 1). The transcripts of auxin biosynthetic

genes *YUCCA8* and *YUCCA9* were up-regulated more in cotyledons than in hypocotyls, suggesting that cotyledons are the main auxin source under high-temperature stress, which is subsequently mobilized to hypocotyls. This observation has been validated using an inhibitor of polar transport of auxin [naphthaleneacetic acid (NAA)] to demonstrate that auxin transport from the cotyledons (main site of auxin synthesis) to the hypocotyls is inhibited (de Wit *et al.*, 2014). Hypocotyl elongation under mild heat stress involves TFs such as helix-loop-helix TFs and PHYTOHORMONE INTERACTING FACTOR 4 (PIF4) (Koini *et al.*, 2009) (Fig. 3), which regulate auxin synthesis and probably maintain appropriate cellular levels. Moreover, *pif4* mutants were unable to elongate when exposed to 28 °C as compared with control (20 °C) (Franklin

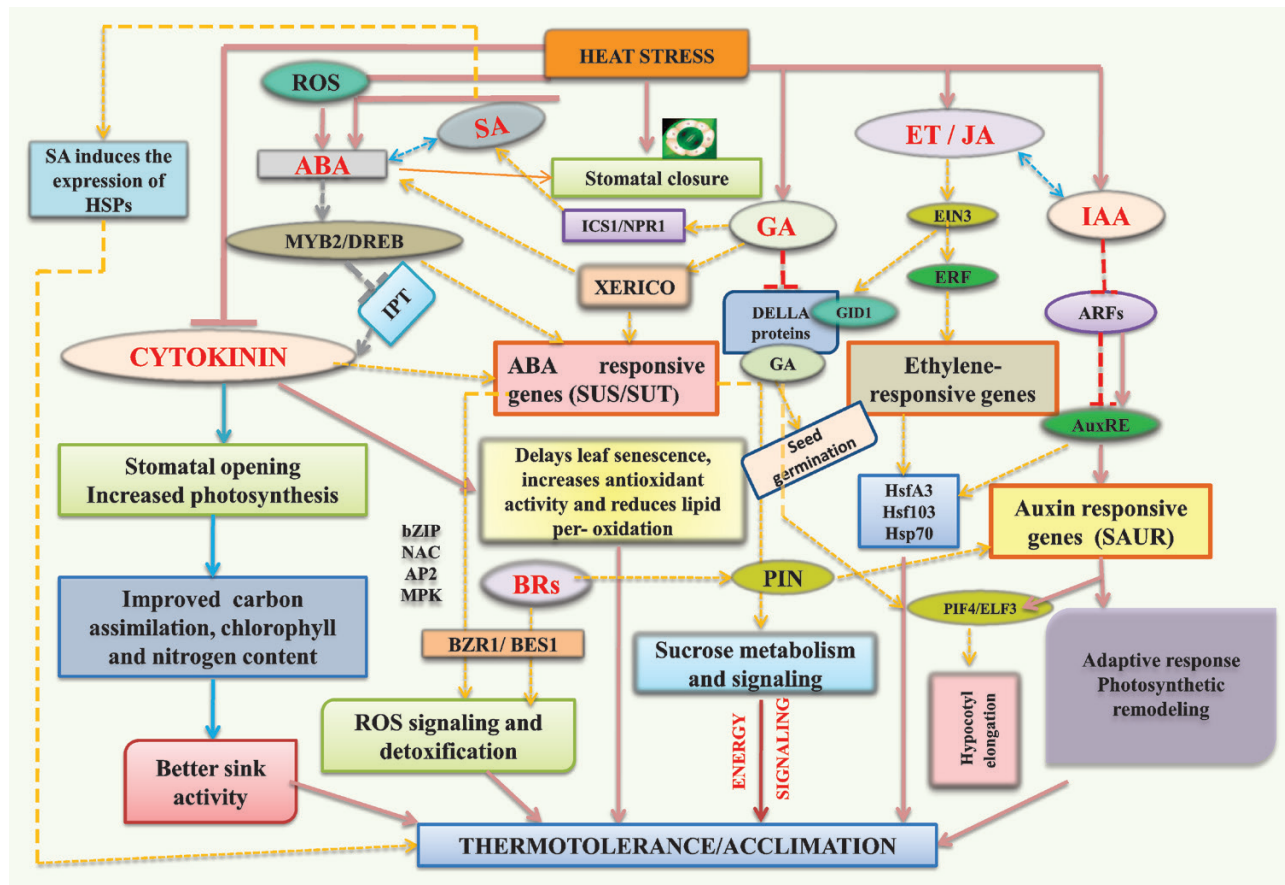


Fig. 3. Possible mechanism of hormonal crosstalk under heat stress, resulting in thermotolerance. Heat stress leads to the excessive production of ROS in plants. ABA is generally associated with a wide range of stress signals that alter all growth and development processes during heat stress. Beside ABA, other phytohormones such as CK, GA, IAA, ET, JA, and BRs have a significant role in heat stress tolerance in plants. These phytohormones act either synergistically or antagonistically in heat stress signaling events in plants. ABA is the key regulator of stomatal functioning and induces stomatal closure to prevent water loss under heat stress, whereas CK stimulates stomatal opening that increases photosynthetic efficiency and improves carbon assimilation and sink activity due to better gaseous exchange. CK also delays leaf senescence and reduces lipid peroxidation by enhancing antioxidant activity to confer thermotolerance. ABA inhibits CK production by blocking one or two steps in IPT synthesis (a key enzyme of the CK biosynthetic pathway) and stimulates the expression of BR-responsive genes (BZR1/BES1) that help in ROS scavenging. ABA also enhances sugar metabolism and signaling, and stimulates carbohydrate transportation to spikelets, which is highly beneficial for plants to withstand heat stress. Both GA and ABA have antagonistic effects during high-temperature stress; ABA represses seed germination while GA stimulates germination and activates SA biosynthetic genes (ICS1/NPR1) to induce the expression of HSPs to prevent protein folding/denaturation, and hence provides heat resilience in plants. Similarly, auxin imparts thermotolerance by inducing hypocotyl elongation and photosynthetic remodeling via up-regulating some auxin-responsive genes (SAUR, PIF4/ELF3). These genes are also activated by BR, ET, and JA. Likewise, ET and JA act together to provide thermal acclimation via up-regulating some heat shock factors (HSF3/HSF101/HSP70). Together, this creates an intricate web of hormonal interactions under heat stress to induce heat stress responses in plants. Abbreviations: ROS, reactive oxygen species; ABA, abscisic acid; CK, cytokinin; GA, gibberellic acid; IAA, indole acetic acid; ET, ethylene; JA, jasmonic acid; BR, brassinosteroid; SA, salicylic acid; IPT, isopentenyl transferase; BZR1, brassinazole resistant1; BES1, BRI1-EMS-SUPPRESSOR 1; ICS1, isochlorismate synthase 1; NPR1, non-expressor of pathogenesis resistance (PR) genes; SAUR, small auxin up RNAs; PIF4, phytochrome-interacting factor 4; ELF3, early floweringing 3; HSF, heat shock factor; HSP, heat shock protein.

et al., 2011). PIF4 regulates the expression of a *SMALL AUXIN UP RNA (SAUR)* genes to induce hypocotyl elongation (Box *et al.*, 2015).

Auxin also interacts with HSPs to regulate thermotolerance in heat-stressed plants, as observed in *Arabidopsis* (Wang *et al.*, 2016). Under heat stress, HSP90 acts as a major molecular chaperone and is involved in the heat stress-induced auxin-mediated hypocotyl growth response in *Arabidopsis*. The auxin receptor TIR1 (TRANSPORT INHIBITOR RESPONSE 1) interacts with HSP90; HSP90–SGT1 (SUPPRESSOR OF G2 ALLELE SKP1), a protein implicated in the auxin response chaperone system, regulates thermotolerance in plants (Han and Hwang, 2018). HSP90 and SGT1 are thought to be an important link between high temperature and auxin signaling to regulate growth with respect to rising temperature (Wang *et al.*, 2016). Auxins have been implicated in imparting thermotolerance to reproductive components (anthers) (Oshino *et al.*, 2011). Under heat stress, endogenous levels of auxin declined significantly in developing anthers and panicles of *Hordeum vulgare* (barley) and *Arabidopsis* under heat stress due to the repression of auxin synthesis genes (*YUCCA2* and *YUCCA6*) (Oshino *et al.*, 2011). Exogenous application of auxins (10^{-5} M IAA was applied just prior to the high-temperature treatment at the five-leaf stage) under heat stress promoted anther cell proliferation and reversed male sterility to enhance reproductive growth (Sakata *et al.*, 2010; Oshino *et al.*, 2011; Table 1). Treatment of field pea with 4-Cl-IAA (1×10^{-6} M) or the auxin analog 4-methylindole-3-acetic acid, before the onset of primary flowering, partly mitigated the adverse effects of moderate heat stress (35 °C for 6 h d^{-1} for 4 d) on seed yield in field pea (Abeyasingha, 2015). Field-grown tomato plants treated with different concentrations (15, 45, and 75 ppm) of 4-chlorophenoxyacetic acid (4-CPA) showed significant improvement in fruit set and yield (Baliyan *et al.*, 2013).

Gibberellins

GAs function primarily to enhance growth in nearly all plant organs by stimulating cell elongation and, sometimes, cell division (Hedden and Thomas, 2012). Hence, reduction in growth under a stress environment is attained by decreasing the bioactive GA level (Hedden and Thomas, 2012). The reduction in GA levels results in accumulation of DELLA proteins, which enhance the stress tolerance by inhibiting growth (Hedden and Thomas, 2012). A few studies have verified the role of GAs in the heat stress response. For instance, stem elongation is a well-known adaptation to heat stress; suppression of GA biosynthesis inhibited hypocotyl elongation in *Arabidopsis* under heat stress (Stavang *et al.*, 2009). A strong molecular interaction between auxins, GAs, PIF4, and hypocotyl elongation under heat stress has been shown (Stavang *et al.*, 2009; Fig. 3). GA interacts with PIF4, which is a key signaling molecule under heat stress (Stavang *et al.*, 2009; Yamashino *et al.*, 2013). High temperature increases the receptiveness of the PIF4-binding site at the FT (flowering locus T) promoter to release H2A.Z nucleosomes (Bahuguna and Jagadish, 2015). Heat stress increases the flowering rate, which depends on the functioning of florigen; under heat stress, PIF4 activates

the FT promoter that controls floral transition. GA-mediated DELLA protein degradation stimulates the activity of PIF4, while it activates the FT promoter, which may be the mechanism through which GA promotes flowering under heat stress (Kumar *et al.*, 2012). Studies involving the exogenous application of GA validated its role in the acquisition of heat tolerance. For example, in *A. thaliana*, 50 μ M GA alleviated the inhibition of growth due to heat stress by improving germination and seedling growth (Alonso-Ramírez *et al.*, 2009). The role of GA was further evidenced by overexpressing *GASA4* from *Fagus sylvatica* in *Arabidopsis*, which improved heat tolerance by altering the expression of SA and pathogenesis-related genes [*ISOCHORISMATE SYNTHASE1 (ICS1)* and *NON-EXPRESSOR OF PATHOGENESIS-RELATED GENES 1 (NPR1)*]. This also increased SA accumulation in *Arabidopsis* under heat stress, suggesting that GA improves seed germination and seedling growth under high temperature by modulating SA biosynthesis and signaling pathways to induce thermotolerance (Alonso-Ramírez *et al.*, 2009; Table 1). In barley and radish, application of 900 μ M GA protected the seedlings of these plant species from heat stress (35 °C and 38 °C, respectively). The plants treated with GA attained better germination and growth of seedlings (Cavusoglu and Kabar, 2007). The heat-stressed (35 °C) seeds of kiwifruit (*Actinidia deliciosa* Chev. cv. Hayward) showed improved germination with GA₃ (2000, 4000, and 6000 ppm concentrations) (Çelik *et al.*, 2006). At the reproductive stage, maintenance of appropriate GA levels is critical since the mutants for GA biosynthesis in *Arabidopsis* produced deformed stamens and anthers that prevented the production of normal mature pollen grains (Plackett *et al.*, 2012; Regnault *et al.*, 2014), but could be restored by exogenous application of GA, thus validating its role in reproductive function (Plackett *et al.*, 2012). The role of GAs in regulating pollen development and function under heat stress needs to be explored further.

Cytokinins

CKs have a major role in the regulation of cell division, nucleic acid metabolism, and the interaction between roots and shoots, especially under stress conditions (Banowitz *et al.*, 1999; Ha *et al.*, 2012). In plant abiotic stress tolerance, CKs have a key role in the promotion of cell division, maintenance of the meristematic nature of cells, increasing redox potentials during abiotic stress, and the regulation of nutrient mobilization (Werner *et al.*, 2010; Gupta and Rashotte, 2012). Higher levels of zeatin (Z) and zeatin riboside (ZR) in rice grains enhanced the grain-filling rate during early and middle grain-filling stages, when grown under a field environment (Yang *et al.*, 2000; Zhang *et al.*, 2010). CKs in rice grains accelerated the rate of cell division in endosperm at early grain-filling stages and regulated the grain sink size, when grown in field conditions (Zhang *et al.*, 2010).

Leaf cooling is vital under heat stress, which occurs by increasing the rate of transpiration and maintaining stomatal function under heat stress. CKs play a critical role in enhancing stomatal conductance to facilitate transpiration in response to heat stress. Genetically modified tobacco plants overexpressing

the *CYTOKININ OXIDASE/DEHYDROGENASE 1* (*CKX1*) gene of *A. thaliana* had slower stomatal movement, which maintained an appropriate leaf temperature (Macková *et al.*, 2013). In the same study, overexpression of the *CKX1* precursor gene in roots, using the *WRKY6* promoter, improved resistance to heat and drought stress in tobacco plants (Macková *et al.*, 2013).

CKs also direct various heat-responsive processes such as the production of glycine-rich proteins and HSPs (Zwack and Rashotte, 2015). High accumulation of CK was correlated with heat tolerance in *Passiflora edulis* (Sobol *et al.*, 2014). Induced expression of the cytokinin-synthesizing gene *ISOPENTENYLTRANSFERASE (IPT)* increased endogenous cytokinin levels to impart thermotolerance in creeping bentgrass (*Agrostis capillaries*; Xu and Huang, 2009; Fig. 3). In creeping bentgrass, a CK treatment [0.01, 0.1, 1, and 10 μmol of ZR, injected into the 0–5 cm root zone on the day before heat stress (0 d) and 14 d after] delayed leaf senescence and enhanced resistance to high-temperature stress by activating the antioxidants and decreasing lipid peroxidation (Liu and Huang, 2000). In other studies, CK has helped to maintain chlorophyll levels and hence photosynthetic ability in *Triticum aestivum* (wheat; Zavaleta-Mancera *et al.*, 2007), *Zea mays* (maize; He and Jin, 1999), and *H. vulgare* (barley; Yaronskaya *et al.*, 2006). Treatment of broccoli florets with 6-benzylaminopurine (6-BA; 200 mg l^{-1}) decreased chlorophyllase levels and hindered chlorophyll degradation, while exogenous treatment of 6-BA on two field-grown wheat cultivars (Wennong 6 and Jimai 20) improved grain yield by enhancing stay-green characteristics under heat stress (Xu *et al.*, 2012; Yang *et al.*, 2016; Table 1).

CKs respond to environmental cues in plants and this is believed to be related to its role in maintaining the overall hormonal balance and interactions with other hormones such as ABA, ethylene, JA, and SA, which are directly involved in abiotic stress responses (Hare *et al.*, 1997; Thu *et al.*, 2017). The crosstalk among auxins, CKs, GAs, ABA, and ethylene is important for the whole plant as well as organ-specific adaptation and growth responses under abiotic stress. When plants are confronted with growth-limiting conditions, stress hormones such as ethylene and ABA retard growth by changing auxin, GA, and CK activity in a tissue-dependent manner (Wolters and Jürgens, 2009; Peleg and Blumwald, 2011). CKs also interact with other growth regulators such as SA and BRs to activate many physiological processes under heat stress (Peleg and Blumwald, 2011). Complex crosstalk and interactions have been observed between CKs and ABA under heat stress (Wang *et al.*, 2011; Ha *et al.*, 2012). It is assumed that CKs and ABA work antagonistically in various physiological and developmental events, as well as in response to different environmental stresses (Catala *et al.*, 2007; Fig. 3). Interestingly, heat stress markedly reduced ZR content in wheat kernels, while IAA, GA, and ABA contents increased (Yang *et al.*, 2016). In rice under heat stress, exogenous application of melatonin significantly increased CK and melatonin levels but reduced ABA levels (J. Zhang *et al.*, 2017). In the same study, the exogenous melatonin treatment up-regulated CK biosynthetic genes and their corresponding TFs, and down-regulated ABA-responsive genes (J. Zhang *et al.*, 2017). These studies indicated the vital

role of CKs in regulating chlorophyll concentration and grain growth under heat stress.

Abscisic acid

Among plant hormones, ABA is the essential regulator of environmental stress responses and coordinates with several other functions, enabling plants to combat various stresses (Wani and Kumar, 2015). ABA plays a critical role in developmental processes such as seed germination, seedling growth, lateral root formation, seed development, seed dormancy, and the transition from vegetative to reproductive phase under stress (Sah *et al.*, 2016) in a concentration-dependent manner. Generally, HSPs and antioxidant systems mediate ABA signaling to enhance thermotolerance in plants. However, sugar metabolism and signaling also play essential roles in thermal acclimation in the presence of ABA (Islam *et al.*, 2018; Fig. 3). In maize leaves under heat stress, ABA induced (100 μM) the expression of small heat shock factors (sHSFs), such as sHSP17.2, sHSP17.4, and sHSP26 (Hu *et al.*, 2010b). The interaction of ABA with HSP70 mitigated the harmful effects of heat stress on enzymes and proteins via preventing their misfolding and proteolysis (Hu *et al.*, 2010a; C. Li *et al.*, 2015). Similarly, in rice spikelets at the pollen mother cell meiosis stage, ABA (1, 10, and 100 $\mu\text{mol l}^{-1}$) significantly increased the expression of *HSP24.1* and *HSP71.1* genes, especially *HSP24.1* (Islam *et al.*, 2018), and prevented pollen abortion by mediating sucrose metabolism in the heat stress environment.

Stomatal regulation is also a common adaptive approach in the response to heat stress. High temperature rapidly increases endogenous ABA content to improve water balance and strengthen thermal acclimation in plants by mediating stomatal closure and inducing antioxidant ability (Hu *et al.*, 2010a; Hsieh *et al.*, 2013), as reported in cucumber and rice leaves (Gong *et al.*, 1998; Tang *et al.*, 2008). Stomatal closure can be regulated by controlling endogenous ABA levels; for example, tobacco plants increased stomatal conductance possibly due to enhanced catabolism of ABA (Macková *et al.*, 2013). A transient rise in temperature beyond the optimum level initially enhanced transpiration to reduce leaf temperature; however, increased transpiration eventually results in water deficit that induces ABA synthesis for stomatal closure (Macková *et al.*, 2013). Hence, maintaining appropriate ABA levels is pivotal to regulate stomatal controls to attain leaf cooling under heat stress.

The effects of ABA differ according to the stage of the plants, depending upon its endogenous concentration. For example, heat stress inhibited seed germination in *A. thaliana* by increasing endogenous ABA levels (Toh *et al.*, 2008), suggesting the inhibitory role of this hormone in germinating seeds. Increased ABA levels in imbibed seeds is achieved by up-regulation of ABA biosynthetic genes such as *ABA1/ZEP*, *NCED2*, *NCED5*, and *NCED9*, while lower levels of GA are maintained by suppression of GA 20-oxidase genes, *GA20ox1*, *GA20ox2*, and *GA20ox3*, and GA 3-oxidase genes in Arabidopsis (Toh *et al.*, 2008). Furthermore, ABA-deficient *aba2-2* mutant seeds showed increased expression of GA synthesis genes but suppressed expression of the GA negative regulator gene *SPINDLY (SPY)* upon exposure to heat stress,

indicating that ABA levels are important for controlling GA levels in seeds under high temperature (Toh *et al.*, 2008), and thus affecting seed germination. Appropriate relative concentrations of ABA/GA appear to be more important, rather than their absolute concentrations, in seeds germinating under heat stress. In contrast, ABA induced heat resistance in pea leaves, as a result of acclimation at 38 °C, and affected the genes and enzymes related to lipid metabolism, including phosphatidylinositol-4,5-bisphosphate (PIP2)–phospholipase C (PLC) enzyme activity, which has a vital role in signaling (Liu *et al.*, 2006). Another study in cultured grape cells and leaves also showed the involvement of ABA in inducing heat tolerance (Abass and Rajashekar, 1993). Heat acclimation at 38 °C and 36 °C, respectively, increased endogenous ABA levels, suggesting its putative role in thermotolerance (Abass and Rajashekar, 1993). Moreover, exogenous application of ABA (9.5 µM or 7.6 µM) to cultured cells significantly improved thermotolerance in grapes (Abass and Rajashekar, 1993). Similarly, application of 75 µM ABA in *Bromus inermis* cell suspensions induced the expression of ABA-responsive proteins to impart thermotolerance (Robertson *et al.*, 1994). In another study, exogenous application of 10⁻⁵ M ABA to barley seedlings at 45 °C and 50 °C reduced heat-induced chlorophyll fluorescence and enhanced the thermostability of thylakoids (Ivanov *et al.*, 1992). In maize, various concentrations of ABA (0.2, 0.3, and 0.5 mM) maintained higher activities of antioxidant enzymes including catalase (CAT), superoxide dismutase (SOD), ascorbate peroxidase (APX), and glutathione peroxidase (GPX) under heat stress (Gong *et al.*, 1998; Table 1). Kumar *et al.* (2012) showed that 2.5 µM ABA was sufficient to reduce oxidative damage in chickpea plants. In lucerne (alfalfa, *Medicago sativa* L.) genotypes contrasting in heat tolerance, a foliar application of ABA (0.1 mM) increased heat tolerance by reducing the damage to membranes, affecting stomatal conductance, and increased recovery in growth and leaf water potential (An *et al.*, 2014). ABA treatment also increased the performance of reproductive function and grain development in a heat stress environment. For instance, in tomato, under heat stress, the endogenous ABA level increased in the tolerant cultivar, but not in the sensitive cultivar. Moreover, exogenous ABA treatment improved pollen germination in a heat stress environment (Shengli *et al.*, 2005). Furthermore, ABA-treated rice plants maintained optimum levels of starch, soluble sugars, and non-structural carbohydrates under heat stress at the pollen mother cell meiosis stage (Islam *et al.*, 2018). Recently, Rezaul *et al.* (2019) showed that ABA treatment (100 µmol l⁻¹) of rice plants prior to heat stress (40 °C) reduced the impact of high temperature on pollen function, which was attributed to enhanced expression of HSPs and genes related to carbohydrate metabolism, sucrose transporters, and antioxidants. In developing wheat grains, under a heat stress environment, ABA was found to control starch biosynthesis. Exogenously applied ABA improved starch accumulation under heat stress by increasing the activity of glutamate-pyruvate transaminase and glutamate-oxaloacetate transaminase: the ABA concentration doubled in hormone-treated wheat plants, suggesting its role in thermoprotection (Asthir and Bhatia, 2014; Asthir, 2015). In wheat, *TaHsfC2a-B* genes induced by ABA and heat

were highly up-regulated during the grain-filling stage to confer heat tolerance (Hu *et al.*, 2018). Since ABA plays a crucial role in the thermal acclimation of plants, understanding the underlying mechanisms would be beneficial for breeding heat-resistant lines and developing new breeding techniques that compensate for heat damage (Islam *et al.*, 2018).

Brassinosteroids

BRs are an important class of plant hormones—similar to steroid hormones of animals—that regulate developmental processes such as cell division, cell elongation, seed germination, vegetative growth, flowering, reproductive growth, and senescence (Khripach *et al.*, 2003; Sasse, 2003; Bajguz and Hayat, 2009; Bari and Jones, 2009). The basic mechanisms behind these processes influenced by BRs are not clear. BRs are present in different plant parts including leaves, shoots, vascular cambium, roots, flower, pollen, fruits, and seeds (Bajguz and Hayat, 2009).

Studies have shown that BR-induced heat stress resistance is closely related to increased synthesis of HSPs (Dhaubhadel *et al.*, 1999; Ogwenon *et al.*, 2008). At high temperature, plants gather highly ordered cytoplasmic complexes known as heat shock granules, which reportedly increase in BR-treated leaves relative to untreated leaves (Bajguz and Hayat, 2009). Moreover, increased BR levels can activate various antioxidants to minimize oxidative damage (Divi *et al.*, 2016; Sahmi *et al.*, 2016). In greenhouse-grown *Cucumis sativus*, under heat stress, BRs significantly enhanced the initial activity of Rubisco and increased the assimilation of CO₂ (Yu *et al.*, 2004). BR-treated canola (*Brassica napus*) and tomato (*Solanum lycopersicum*) seedlings increased their basic thermotolerance, which was associated with the aggregation of HSPs such as Hsp100, Hsp90, Hsp70, and low molecular weight HSPs (Bajguz and Hayat, 2009; Fig. 3). As a result, the BR-treated plants had better photosynthetic efficiency, pollen germination, and low pollen bursting. Another beneficial effect of BR treatment was an increase in fruit yield due to increased fruit numbers, as reported in tomato grown under heat stress (Singh and Shono, 2005). In heat-stressed (43 °C) wheat plants, BR application improved the protein concentration and cell ultrastructure of leaves (Kulaeva *et al.*, 1991). Exogenous treatment (through seed or leaves) with BR improved thermotolerance in *Brassica juncea*, grown under a field environment (Sandeep *et al.*, 2014; Table 1), and *Cucumis melo* (Y.P. Zhang *et al.*, 2014) by improving chlorophyll concentration, chlorophyll fluorescence, stomatal conductance, quantum efficiency, and the expression of antioxidants. Similarly, in tomato, BR treatment (as foliar spray) decreased oxidative damage (Zhou *et al.*, 2014) and membrane damage, and enhanced photosynthetic activity (Khan *et al.*, 2015). A recent study (Divi *et al.*, 2016) in *A. thaliana* revealed that the transcription factors HSF21 and HSF4 are the putative BRASSINAZOLE-RESISTANT1 (BZR1) targets imparting protection from heat stress. In addition, up-regulation of the genes *WRKY33*, *ACID PHOSPHATASE5 (ACP5)*, *BR-RESPONSIVE-RECEPTOR-LIKE KINASE (BRRLK)*, and *JACALIN-RELATED LECTIN1-3 (JAC-LEC)* in the BR treatment, under heat stress, might play a role in thermotolerance. Studies

are needed to assess the endogenous concentration of BR in normal and heat-stressed plants, and to probe their interaction with other hormones in conferring heat tolerance.

Salicylic acid

SA or *o*-hydroxybenzoic acid is a potential phenolic plant growth regulator involved in various responses such as water transport and nutrient uptake, chlorophyll and protein formation, stomatal conductance, and gaseous exchange (Fariduddin *et al.*, 2003; Vlot *et al.*, 2009; Yusuf *et al.*, 2013). It also regulates some other processes including Pro metabolism, GB production, and antioxidant defenses, improves plant water relations under stress condition, and protects plants against abiotic stress. Studies have shown that SA is directly or indirectly involved in high-temperature stress responses in plants (Nazar *et al.*, 2015). It has been reported that SA is highly beneficial for plant growth under both normal and stressed environments, as it modulates osmolytes and other metabolites to participate in thermoprotection (Khan *et al.*, 2015). SA plays a key role in the signal transduction process involved in thermotolerance, as evidenced by the increased endogenous free and bound SA in *Brassica campestris* (mustard) under a heat stress environment (Dat *et al.*, 1998b). In wheat, increased SA levels further stimulated Pro synthesis to increase osmotic potential, enabling plants to take up more water under heat stress (Khan *et al.*, 2013). A significant increase in endogenous SA levels in heat-stressed mungbean plants increased antioxidant enzyme (CAT, POD, SOD, etc.) activities to impart thermotolerance (Saleh *et al.*, 2007). Moreover, studies involving exogenous application of SA also validated its role in imparting heat tolerance in potato (Lopez-Delgado *et al.*, 1998), chickpea (Chakraborty and Tongden, 2005), and Kentucky bluegrass (He *et al.*, 2005). Various mechanisms through which SA can exert thermotolerance include increased activity in antioxidants such as SOD, CAT, POD, glutathione reductase (GR), and Rubisco as observed in wheat (Khan *et al.*, 2013; Y. Wang *et al.*, 2014; Table 1) and grapevines (L.J. Wang *et al.*, 2010). In cotton (*Gossypium hirsutum*), exogenous SA application increased plant dry matter, free Pro accumulation, and total soluble protein content under heat stress, relative to unstressed seedlings without SA treatment (Hameed and Ali, 2016). Similarly, SA application in rice induced phytohormones (auxins, GA₃, BRs, ABA, CK, and JA), antioxidant enzymes (SOD, POD, CAT, and APX), soluble sugars, and Pro (C.X. Zhang *et al.*, 2017; Fig. 3). Foliar spray of SA diminished heat stress-induced oxidative harm in Arabidopsis plants (Larkindale and Knight, 2002; Pál *et al.*, 2013, 2014) and chickpea (Chakraborty and Tongden, 2005). In grapes, SA sprayed exogenously on leaves induced long-term thermotolerance by improving the antioxidant system and Ca²⁺ homeostasis (Wang and Li, 2006). Chakraborty and Tongden (2005) induced thermotolerance in chickpea plants by applying a 0.1 mM foliar SA treatment, which increased antioxidant activity. In grapevines (*Vitis vinifera* L.), exogenous application of SA reduced the heat stress-induced altered CO₂ assimilation by maintaining a higher activity of Rubisco, which ensures PSII efficiency (L.J. Wang *et al.*, 2010). There are other instances where exogenous SA has enhanced

thermotolerance; some examples include Arabidopsis (Clarke *et al.*, 2009), mungbean (*Vigna radiata*; 1 mM; Saleh *et al.*, 2007), Indian mustard (10⁻⁵ M; Hayat *et al.*, 2009), wheat (0.5 mM; Khan *et al.*, 2013; Y. Wang *et al.*, 2014), cotton (0.5–1.5 mM; Hameed and Ali, 2016), and rice (50 mM; C.X. Zhang *et al.*, 2017). The mechanisms for SA-enhanced thermotolerance include activation of protein kinase, inhibition of D1 protein degradation (Zhao *et al.*, 2011), up-regulation of various antioxidants, improved photosynthetic activity, and changes in phytohormones such as ABA, GA₃, IAA, ZR, and JA (C.X. Zhang *et al.*, 2017; J. Zhang *et al.*, 2017).

Jasmonates

JA plays an important role in plant growth regulation involving seed germination, root growth, sex determination in maize, seedling development, leaf orientation, stamen and trichome differentiation, anthocyanin accumulation, tuber formation, fruit maturation, cell cycle regulation, and senescence (Zhang and Turner, 2008; Yoshida *et al.*, 2009; Sharma and Laxmi, 2016). JA helps in the activation of plant defense responses for both biotic and abiotic stresses, including high temperature, low temperature, salinity, and heavy metal stress (Tani *et al.*, 2008; Yan *et al.*, 2012; Samota *et al.*, 2017). JA acts as a signaling molecule to induce thermotolerance in many plants (Turner *et al.*, 2002; Clarke *et al.*, 2009). The key role of JA in response to temperature stress has been explored in detail (Sharma and Laxmi, 2016). JA is mainly involved in signal transmission under heat stress but also regulates growth, aging, floral development, and leaf abscission (Dar *et al.*, 2015). Further, JA induces the expression of HSPs, as well as other stress-related proteins or TFs under heat stress (Sharma and Laxmi, 2016). Several studies involving the exogenous application of JA have reported its mitigatory role in heat stress, for example in grapes (Wang and Li, 2006), Arabidopsis (Clarke *et al.*, 2009), and wheat (Karpets *et al.*, 2014).

Treatment of grape seedlings with 50 μM JA activated antioxidant enzymes to prevent the harmful effects of heat stress (42 °C: Wang and Li, 2006; Table 1). Exogenous application at low concentrations of methyl jasmonate (MeJA) maintained cellular stability in heat-stressed Arabidopsis plants, as demonstrated by low electrolyte leakage tests and maintenance of cellular viability (Clarke *et al.*, 2009). However, no evidence showed that thermotolerance involved MeJA in the expression of HSPs. Evidence of the role of JA in thermotolerance was observed from Arabidopsis mutants (*coi1-1*, *opr3*, and *jar1-1cpr5-1*) (Clarke *et al.*, 2009). In *Helianthus annuus*, seed treatment with JA (10⁻²–10⁻⁴ M) imparted heat tolerance by reducing membrane damage (Górník *et al.*, 2014). Similarly, in wheat, JA treatment improved coleoptile tolerance to heat stress by enhancing antioxidant activity (Karpets *et al.*, 2014). The mechanism by which JA confers protection from heat stress involves the activation of diverse antioxidants (Wang and Li, 2006) and stabilization of membranes (Clarke *et al.*, 2009). There is enough evidence that many WRKY genes are involved in abiotic stresses, including heat stress. Various WRKY TFs impart heat stress tolerance, including OsWRKY11 (Wu *et al.*, 2009), AtWRKY25 (Zhu *et al.*, 2009), and AtWRKY39

(Li *et al.*, 2010). The studies by Dang *et al.* (2013) revealed that *CaWRKY40* is transcriptionally triggered by the exogenous application of JA, which in turn influences the expression of downstream thermotolerance-associated genes.

Nitric oxide

NO is an inorganic free radical in living organisms that is considered a plant hormone and key player in cell signaling for many physiological processes, including stress tolerance in plants (Khan *et al.*, 2014; Oz *et al.*, 2015; Table 1). NO plays an important role in controlling physiological processes such as seed germination, growth, development, photosynthesis, and senescence, and responds to specific abiotic stress (Arc *et al.*, 2013; Fatma *et al.*, 2016; Asgher *et al.*, 2017). NO acts as an antioxidant, depending on its concentration and location in a plant cell or tissue (Lamattina *et al.*, 2003; Corpas *et al.*, 2007; Neill *et al.*, 2008). Many studies have shown the direct and indirect role of NO in plant stress tolerance pathways under drought and high-temperature stress (García-Mata and Lamattina, 2001; Benzarti *et al.*, 2008; Siddiqui *et al.*, 2011). In response to heat stress, plants produce NO to induce thermotolerance, which has been reported in various plants (Corpas *et al.*, 2011; Wendehenne, 2016). In tobacco, heat stress at 40 °C for 7 min significantly increased NO in dorsal epidermal cells and suspension cells (Gould *et al.*, 2003). In another study, pea plants exposed to 38 °C for 4 h reduced the amount of NO in leaves but had no effect on the activity of its biosynthetic enzymes (Corpas *et al.*, 2008). In *M. sativa* (alfalfa), a short heat stress increased NO production, which was negatively correlated with ethylene production (Leshem, 2012). The role of NO during extreme temperature stress might be to decrease ROS levels (Neill *et al.*, 2002, 2008). The relationship between NO formation and stress resistance is not clear, and significant variation has been observed in NO-controlled heat stress tolerance. Under heat stress, NO also interacts with other signaling molecules such as MAPKs, cADP ribose, Ca²⁺ (Khan *et al.*, 2015; Asgher *et al.*, 2017), and phytohormones such as ABA (Neill *et al.*, 2008; Song *et al.*, 2008; Wendehenne, 2016). These signaling molecules further induce the expression of certain protein kinases that initiate downstream gene expression (Parankusam *et al.*, 2017). This alteration in gene expression often stimulates a cascade of events such as antioxidant synthesis, overaccumulation of osmoprotectants, changes in plant metabolism, and up-regulation of HSPs to enhance survival under heat stress (Asgher *et al.*, 2017). NO improved thermotolerance by increasing the antioxidants in wheat (0.05–0.5 mM; El-Beltagi *et al.*, 2016; Table 1), enhancing seed germination in lettuce (0.1–0.5 mM; Deng and Song, 2012), up-regulating transcription of PSII core proteins in tall fescue (0.1 mM; Chen *et al.*, 2013), and reducing ion leakage and preventing oxidative stress in rice (0.001–0.02 mM; Song *et al.*, 2013; Singh *et al.*, 2016).

γ-Aminobutyric acid

γ-Aminobutyric acid (GABA) is a non-protein amino acid; its concentration is up-regulated to activate genes related to stress

tolerance including heat stress (Lancien and Roberts, 2006; Renault *et al.*, 2010). GABA plays a role in signal transduction, maintenance of cytosolic pH, carbon metabolism, nitrogen metabolism and its transport, plant growth, development, and plant resistance to abiotic stresses (Bown and Shelp, 1997; Bouché and Fromm, 2004; Roberts, 2007; Barbosa *et al.*, 2010; Li *et al.*, 2016). GABA can amplify stress stimuli, activate ethylene synthesis, and perform a variety of roles in stress-resistant mechanisms in plants (Kinnersley and Turano, 2000). External treatment with GABA initiates a stimulatory action in many plants (Baum *et al.*, 1996; Kinnersley and Turano, 2000; Roberts, 2007). In sunflower, exogenous treatment with GABA (for 12 h) increased expression of the ACC synthase enzyme of ethylene production, which increased ethylene content by 14-fold (Kathiresan *et al.*, 1997). GABA treatment can positively influence the growth, physiology, and various biochemical responses of plants to environmental cues such as drought and heat stress. For instance, in rice seedlings under heat stress, GABA regulated the production of osmolytes such as GB and Pro, increased leaf water content by accelerating the synthesis of osmolytes, and reduced damage caused by oxidative stress (Nayyar *et al.*, 2014; Table 1). In GABA-treated plants, osmotic adjustment is comparatively faster, and therefore, relative leaf water content (RLWC) is better maintained (Li *et al.*, 2016). In *Piper nigrum*, GABA enhanced the activity of various antioxidants, and their concentrations increased more quickly under polyethylene glycol (PEG)-induced stress than the untreated plants (Vijayakumari and Puthur, 2016). The role of GABA in heat tolerance has not been fully explored; in particular, its role in signaling and interaction with phytohormones is yet to be ascertained.

Melatonin

Melatonin is a derivative of indoleamine, present throughout the plant kingdom. It is an amphiphilic substance, so it can cross cell membranes effortlessly and enter subcellular compartments (Shida *et al.*, 1994). Various studies have shown that melatonin is a strong growth modulator and rooting agent (Hernández-Ruiz and Arnao, 2008; Chen *et al.*, 2009; Sarrou *et al.*, 2014; N. Zhang *et al.*, 2014). Besides its roles in plant growth modulation, melatonin plays an important role in plant stress tolerance. Recent reports showed the protective role of melatonin in high-temperature-mediated senescence of ryegrass (*Lolium perenne* L.) leaves (J. Zhang *et al.*, 2017). Melatonin prevented heat-induced growth inhibition, extended the duration of leaf senescence, repressed senescence-associated genes (*LpSAG12* and *LpH36*), and improved tiller number, cell membrane integrity, chlorophyll content, and photosynthetic efficiency (J. Zhang *et al.*, 2017; Table 1). Application of melatonin to ryegrass plants increased CK levels under heat stress (N. Zhang *et al.*, 2014), which might have contributed to the delay in leaf senescence. The levels of isopentenyladenine and *trans*-zeatin riboside, which decreased under heat stress, recovered in melatonin-treated plants, showing a positive interaction between endogenous levels of CKs and melatonin. In contrast, under optimum environmental conditions, the application of melatonin had no effect on CK levels. The level of two CK biosynthesis genes (*LpIPT2* and *LpOG1*) was induced

by melatonin when plants were exposed to heat stress. Also, two TFs, A-ARRs and B-ARRs, involved in the CK signaling pathways, decreased and increased, respectively (J. Zhang *et al.*, 2017). These studies demonstrate that the mitigation of heat stress by melatonin is the result of crosstalk between melatonin and CKs (J. Zhang *et al.*, 2017).

Various studies have shown that exogenous application of melatonin helps to enhance antioxidant enzyme performance and reduce the harmful effects of oxidative stress in maize plants grown under a rain-shelter in the field (Ye *et al.*, 2016), sunflower (Arora and Bhatla, 2017), tomato, apple (Wang *et al.*, 2013), grapes (Meng *et al.*, 2014), *Malus* species (C. Li *et al.*, 2015), and tomato seedlings (Liu *et al.*, 2015b; Table 1). Application of melatonin alleviated H₂O₂-mediated cell damage and increased plant growth and ROS content in bermuda grass (*Cynodon dactylon*) under heat stress (Chan and Shi, 2015). Exogenous application of melatonin caused induced expression of class A1 HSFs (HSFA1s) and HSP in Arabidopsis (H. Shi *et al.*, 2015), and improved seed germination and HSP contents. Further, melatonin enhanced expression of HSFA1s and HSP in *Phacelia tanacetifolia* (Tiryaki and Keles, 2012), regulated the ABA and CK pathways, enhanced photosynthesis in *L. perenne* (J. Zhang *et al.*, 2017), reduced H₂O₂ content, increased Pro content, and raised the antioxidants in kiwifruit seedlings under heat stress (Liang *et al.*, 2018). In heat-stressed tomato plants, endogenous melatonin was manipulated by up-regulation of the *N*-acetylserotonin methyltransferase (*ASMT*) gene, and exogenous melatonin reduced the levels of ubiquitinated and insoluble proteins and induced HSPs to prevent unfolding and denaturation of proteins (Xu *et al.*, 2016). Further studies are required to understand the functioning of these molecules under stress situations, especially its role in protecting heat-stressed plants, as well its interaction with other phytohormones.

Polyamines

PAs are ubiquitous nitrogenous compounds present in all living cells that affect various cellular responses (Igarashi and Kashiwagi, 2000; Zhao and Yang, 2008; Sengupta *et al.*, 2016). Various forms of PAs—diamine (putrescine; Put), triamine (spermidine; Spd), and tetramine (spermine; Spm)—are the three most abundant PAs in plants. Other types, including homospermine and cadaverine, are present in some plants (Sengupta *et al.*, 2016). Plants accumulate PAs in various parts during different developmental stages and when exposed to abiotic stress conditions. The biological action of PAs is attributed to their cationic nature, which facilitates cooperation with negatively charged biomolecules such as DNA, RNA, proteins, and phospholipids (Kaur-Sawhney *et al.*, 2003; Liu *et al.*, 2006; Pang *et al.*, 2007; Groppa and Benavides, 2008; Kusano *et al.*, 2008). Variations in the endogenous content of PAs have been broadly examined when plants are subjected to a single stress or a combination of stresses. Increased concentrations of PAs may be due to *de novo* synthesis and reduced degradation of PA pathways; however, the exact mechanism is not well known (Sengupta *et al.*, 2016). The role of Put in abiotic stress tolerance is of great importance, but its role in heat stress is not well

understood (Kakkar and Sawhney, 2002). Put, Spm, and Spd, and some unusual PAs (non-spermidine and non-spermine) have been reported in *Canavalia gladiata* (Matsuzaki *et al.*, 1990) and cultured calluses of a thermotolerant rice cultivar subjected to heat shock (45 °C, 30 min) (Roy and Ghosh, 1996). Their presence positively correlated with the activity of adenine decarboxylase (ADC), the enzyme involved in PA biosynthesis. Some other unusual PAs include thermospermine, homocaldopentamine, and homo-caldohexamine, which have been identified in thermotolerant alfalfa plants (Bagga *et al.*, 1997). Pollen grains and cell cultures of a cotton genotype accumulated caldine and thermine under high temperature (Kuehn *et al.*, 1990); their functional relevance in heat tolerance is yet to be investigated. A significant increase in conjugated and free PAs was reported in heat-tolerant cotton and rice plants along with enhanced PA biosynthetic and oxidizing enzymes during high-temperature stress (Evans and Malmberg, 1989; Cona *et al.*, 2006). Since *S*-adenosyl-*L*-methionine decarboxylase (SAMDC) is a key regulatory enzyme in the biosynthesis of PAs, increasing PA biosynthesis by manipulating the activity of this enzyme may prove beneficial for creating thermotolerant genotypes. Introgression of SAMDC DNA, isolated from yeast in transgenic tomato, produced high Spm and Spd levels and enhanced the activity of antioxidants under heat stress (Cheng *et al.*, 2009). In Arabidopsis, exposure to heat stress increased Spm, Put, and Spd contents, and also induced some HSPs (HSP101, HSP90, HSP70, and HSP17.6) (Sagor *et al.*, 2013) at the same time, suggesting a relationship between them.

There are several studies where exogenous application of PAs has imparted thermotolerance, involving diverse cellular mechanisms. For example, in mungbean (*Vigna radiata*; 50 °C for 2 h), 1 mM Put was found to protect the plants from heat stress; Basra *et al.*, 1997; Table 1). Similarly, in garden tomato (*S. lycopersicum*), Spd (1 mM) induced heat tolerance by increased expression of PA biosynthesis genes; and at the same time up-regulated ethylene-related and oxidation/reduction genes (Cheng *et al.*, 2012). In most instances, PAs were reported to confer heat tolerance by improving the expression of antioxidants. Cotton plants, supplied with 10 mM Put, increased their endogenous Put content (Bibi *et al.*, 2012) and showed improvement under heat stress. Wheat plants supplied with 10 μM Put had elevated activities of enzymatic and non-enzymatic antioxidants and reduced lipid peroxidation in roots and shoots (Asthir *et al.*, 2012), when grown under heat stress. Similarly, in another study, also in wheat, foliar spray of Put lowered the activities of IAA oxidase, POD, and polyphenol oxidase (PPO), and enhanced CAT and SOD efficiency under heat stress (Hassanein *et al.*, 2013). A similar situation was observed in soybean, where exogenous application of Put, Spd, and Spm (1 mM) improved growth, prevented membrane damage, and minimized oxidative injuries (Amooaghaie and Moghym, 2011). In beans too, pre-treatment with Spm and Spd inhibited peroxidase but amplified CAT activities (Velikova *et al.*, 2000) to reduce oxidative damage under heat stress. In Arabidopsis, exogenous treatment with 0.05 mM and 0.1 mM Spm reduced oxidative damage and increased chlorophyll content (Sagor *et al.*, 2013). Likewise, in rice, exogenous application of Spd ameliorated heat stress-induced damage and enhanced the

activities of antioxidant enzymes and concentrations of antioxidants (Mostofa *et al.*, 2014). In tomato, a different mechanism was noticed, where exogenous application of 4 mM Spd improved the heat stress tolerance in both heat-sensitive and heat-tolerant cultivars of tomato by enhancing tolerance to thermal degradation of pigment-protein complex structure and working of PSII (Murkowski, 2001). Wheat treated with Arg and Put (1.25 mM/2.5 mM) expressed heat tolerance by increasing the endogenous contents of Put, Spd, total PAs, total amino acids, and the ratio of essential to non-essential amino acids (Hassanein *et al.*, 2013). Thus, the mechanisms by which PAs confer heat tolerance are diverse and include stabilizing membranes (Minocha *et al.*, 2014), increasing antioxidant enzymes (Marco *et al.*, 2015), enhancing chlorophyll concentration (Liu *et al.*, 2016), stabilizing the photosynthetic apparatus (Murkowski, 2001), and restoring plant water status through osmoregulation (Nahar *et al.*, 2017).

Osmoprotectants

Osmolytes, such as Pro, are considered compatible with cellular functioning, since it does not interfere with cellular metabolism, even at higher concentrations (Sung *et al.*, 2003). Pro brings about osmoregulation (Jagels, 1983), oxidative stress mitigation, particularly by scavenging ROS (Mohanty and Matsyik, 2001; Takagi, 2008), and regulation of the NAD⁺/NADH ratio (as NAD⁺) produced during the synthesis of Pro (Verbruggen and Hermans, 2008) (Fig. 2). It also modulates the stabilization of proteins (Hayat *et al.*, 2012), enzymes, and biomembranes including the conservation of energy and amino acids for post-stress growth (Aspinall, 1981) and the stabilization of the double-stranded helical structure of DNA (Rajendrakumar *et al.*, 1997). Free Pro accumulation, as a consequence of heat stress, has been reported in many crops including tomato (Rivero *et al.*, 2004), mulberry (*Morus alba*; Chaitanaya *et al.*, 2001), cotton (De Ronde *et al.*, 2000), cabbage and Chinese cabbage (*Brassica oleracea*; Hossain *et al.*, 1995), apple (*Malus domestica* Borkh.; Park *et al.*, 2001), chickpea (Chakraborty and Tongden, 2005), wheat (Hasan *et al.*, 2007), French beans (*Phaseolus vulgaris* L.; Nagesh Babu and Devraj, 2008), and tobacco (Cvikrová *et al.*, 2012). In soybean, Pro concentration was higher in acclimated plants than in non-acclimated plants, and recovered faster to indicate the protective role of Pro under stress conditions (Yadegari *et al.*, 2007). Exogenous application of Pro (Table 1) to heat-stressed plants reduced membrane damage in grapevines (Ozden *et al.*, 2009), which was confirmed by Kaushal *et al.* (2011) in chickpea. The chickpea plants also had reduced oxidative injury, coupled with elevated levels of enzymatic (SOD, CAT, APX, and GR) and non-enzymatic [ascorbate (ASC) and glutathione (GSH)] antioxidants, indicating up-regulation of the antioxidant defense system and enhanced heat tolerance. In sugarcane, nodal buds soaked in 20 mM Pro as well as GB performed better under heat stress. The treatment also reduced H₂O₂ production and improved the accumulation of soluble sugars, free Pro, GB, and K⁺ and Ca²⁺ contents (Rasheed *et al.*, 2011). In barley leaves, exogenous application of Pro and GB increased PSII stability at high temperature (45 °C), with Pro more effective than GB (Oukarroum *et al.*, 2012), thus rendering the plants more heat tolerant.

GB plays an important role as a compatible solute under heat stress and has multiple mechanisms of action (Chen and Murata, 2002). It stabilizes the activities and structures of protein and enzyme complexes and sustains membrane integrity against the inhibitory impacts of salinity and temperature stresses (Sakamoto and Murata, 2000; Table 1). The biosynthesis of GB is stimulated under stressful conditions (Jagendorf and Takabe, 2001). Endogenous biosynthesis or exogenous application of GB has a stabilizing effect on photosynthetic membranes under heat stress (Allakhverdiev *et al.*, 1996). GB plays an important role in signaling, inhibition of water loss, stabilization of proteins, protection of enzymes and protein complexes from heat-induced destabilization, and as an energy source (Gorham, 1995; Chen and Murata, 2011). It also inhibits ROS accumulation (Chen and Murata, 2002, 2011), thus preventing oxidative damage (Fig. 2). *In vitro* studies have indicated that GB plays an important role in the protection of photosynthetic machinery by protecting the PSII complex (Allakhverdiev *et al.*, 1996), as reported in transgenic tobacco (Liang *et al.*, 1997); however, no reports are available on *in vivo* protection of photosynthesis against high-temperature stress. Under heat stress, high GB accumulation has been observed in various crops including maize (Quan *et al.*, 2004) and sugarcane (Wahid and Close, 2007), but there are many important crops such as rice, mustard, soybean, potato, tobacco, and Arabidopsis that do not accumulate GB, and are therefore potential targets for engineering GB biosynthesis (McCue and Hanson, 1990) to increase heat tolerance. High endogenous GB levels reduced the heat-induced ion leakage in barley (Wahid and Shabbir, 2005), and improved tolerance to drought and heat stress in wheat (G.P. Wang *et al.*, 2010), which correlated with enhanced photosynthesis and activation of enzymatic and non-enzymatic antioxidants to reduce the impact of oxidative stress. The involvement of GB in heat tolerance has been shown through exogenous application to heat-stressed plants. In barley seedlings, exogenous application of 20 mM GB promoted seed germination and yield due to improved shoot water content, compared with a marked reduction with no GB treatment (Wahid and Shabbir, 2005; Table 1). In tomato grown under heat stress, GB supplementation (0.1–5 mM) improved seed germination and seedling growth under high temperature (Li *et al.*, 2011); it protected PSII and increased yield due to increased carbon assimilation (Ashraf and Foolad, 2007).

Reactive oxygen species scavengers

ASC is an important antioxidant molecule, and a major substrate for the scavenging ROS (Smirnoff, 2000). The apoplasmic content of ASC is the major signaling molecule for oxidative stress, although its amount and exposure time characterize the general redox status of the cell (Akram *et al.*, 2017; Table 1). Exogenous application of ASC (50 μM) imparted high tolerance to heat stress (40/30 °C and 45/35 °C; day/night temperatures) in mungbean (Kumar *et al.*, 2011). Furthermore, ASC-treated plants had significant reductions in H₂O₂ and malondialdehyde (MDA) contents (Kumar *et al.*, 2011). Similar observations were made for strawberry (Ergin *et al.*, 2014) and rice plants (Zhang *et al.*, 2018), where the exogenous application of ASC increased antioxidant activities to mitigate heat-induced injuries. In a

recent study, the impact of ASC (5 mM) on three hormones (ABA, SA, and auxin) and some physiological parameters was measured in a maize cultivar under heat stress. ASC treatment increased chlorophyll content, relative leaf water content, and stomatal conductance, along with a significant reduction in SA level and increased auxin and ABA contents (Dinler *et al.*, 2014), suggesting that thermotolerance imparted by ASC might primarily involve the latter two hormones, though SA has an established role in this regard. Further studies are needed to determine the mechanism of interaction of ASC with phytohormones in protection from heat stress.

GSH is another non-enzymatic, low molecular weight antioxidant molecule that participates in ROS and methylglyoxal (MG) detoxification in stressed environments by interacting with hormones and other signaling molecules (Hasanuzzaman *et al.*, 2017; Table 1). Previous studies have shown its essential role in meristem development, pollen germination, pollen tube growth, embryo development (Pellny *et al.*, 2009; Zechmann *et al.*, 2011), and heavy metal detoxification (Dhankher *et al.*, 2002). The protective role of GSH under heat stress has been reported in fewer studies; the spatial and temporal changes in GSH pools and its role in redox signaling and defense processes are important in thermotolerance mechanisms (Szalai *et al.*, 2009). High GSH content imparted heat stress tolerance in maize at the seedling stage (Nieto-Sotelo and Ho, 1986). Similarly, increased total GSH content conferred thermotolerance in wheat, maize, and mungbean (Nieto-Sotelo and Ho, 1986; Dash and Mohanty, 2002; Nahar *et al.*, 2015). An elevated level of GSH in heat-stressed mustard seedlings was related to the efficient removal of H₂O₂ due to improved GR activity (Dat *et al.*, 1998a). Likewise, a significant rise in endogenous GSH level was observed in apple peel exposed to extreme temperatures and solar radiation, which helped in acclimating to heat stress (Zhang *et al.*, 2008). Pre-treatment of mungbean seedlings with 0.1 mM GSH improved physiological performance as well as antioxidant defense systems during heat shock (Nahar *et al.*, 2015; Table 1). The exogenous application of GSH provided significant thermotolerance (high root zone temperature) in cucumber seedlings by regulating photosynthesis, antioxidant activity, and osmolyte accumulation to improve physiological adaptation (Ding *et al.*, 2016). In a recent study, Kumar and Chattopadhyay (2018) revealed that GSH induced the expression of some HSP genes (*BiP3*, *HSP70B*, and *HSP90.1*) in Arabidopsis by activating the promoters of these genes to confer heat tolerance. As both GSH and ASC are promising candidates involved in antioxidant defense pathways during heat stress, significant efforts are needed to decipher their roles in thermotolerance, especially their interactive involvement with osmolytes, hormones, and HSPs.

Stress priming-induced heat tolerance, and thermoprotectants

Thermo-priming of plants can induce heat tolerance by establishing stress memory during the priming treatments. Such a type of induced thermotolerance reprograms the metabolic networks and assists in sustaining metabolic homeostasis under

heat stress. For instance, multiple heat priming of winter wheat seedlings improved thermotolerance at a later heat stress by increasing the subcellular levels of antioxidants (X. Wang *et al.*, 2014). Thermotolerance induced in wheat plants can even be remembered and inherited by the progeny (Zhang *et al.*, 2016). A recent study in wheat (Fan *et al.*, 2018) showed that heat priming at the time of stem elongation stage and booting significantly inhibited the damage to grain yield, resulting from heat stress during grain filling. Enhanced thermotolerance was associated with an increase in sucrose content as well as sucrose synthase activity in leaves; it also improved photosynthetic capacity, chlorophyll concentration, and stomatal conductance. At the same time, primed plants showed significantly less oxidative damage and up-regulated activities of antioxidants such as SOD and peroxidase (Fan *et al.*, 2018). It was also noticed that cross-treatments by other stresses also induced heat tolerance. For instance, the drought-primed plants of tall fescue (*Festuca arundinacea*) showed heat tolerance, which was attributed to maintenance of a higher leaf water content, chlorophyll content, and photochemical efficiency, and lower damage to membranes. At the same time, the accumulation of lipids (phospholipids and glycolipids) increased, which stabilized the membranes under subsequent heat stress (Zhang *et al.*, 2019). Several molecules were implicated in heat tolerance in thermo-primed Arabidopsis plants subsequently exposed to heat stress (Serrano *et al.*, 2019), which were categorized into carbohydrates (sucrose, raffinose family oligosaccharides, stachyose, galactinol, and raffinose), branched chain amino acids, tocopherols, osmolytes, and antioxidants. The primed plants showed significantly more expression of these molecules to improve thermotolerance. The molecular mechanisms involving genetic and epigenetic regulatory systems are reported to be involved in heat responses (Liu *et al.*, 2015a), which may have a role in establishing memory associated with stress priming (Avramova, 2015; Brzezinka *et al.*, 2016). Recently, alternative splicing, a post-transcriptional regulatory mechanism, has been reported to be involved in heat shock memory (Ling *et al.*, 2018) in heat-primed Arabidopsis plants. These studies indicated that priming with a non-lethal heat stress resulted in de-repression of splicing after subsequent exposure to stress, while a significant repression was noticed in non-primed plants, thereby linking splicing memory to thermotolerance. The types and role of phytohormones involved in stress memory during heat priming or acclimation, which confer thermoprotection at a later stage, need to be probed.

Crosstalk of PGRs under heat stress

Plants can sense small disturbances in the outer environment and trigger various signaling cascades in the cells that communicate with downstream signals transduced by various phytohormones (Dobrá *et al.*, 2015). Considering these mechanisms, phytohormones interplay by activating either a common transducer or a phosphorylation event (Fahad *et al.*, 2016). Due to the involvement of different phytohormones and signaling molecules in the heat stress response, crosstalk among them is a complicated process that requires deep

insight (Depuydt and Hardtke, 2011; Fig. 3). Signal transduction mechanisms initiate genetic modulations that directly influence the synthesis or action of other hormones, representing an additional way of hormonal crosstalk under heat stress (Xia *et al.*, 2015). The crosstalk among auxins, CKs, GA, ABA, and ethylene is important for the whole plant as well as organ-specific adaptation and growth responses under abiotic stress conditions. Auxin (IAA) and BRs may interact during heat stress; exogenous application of auxin enhanced expression of the BR-biosynthesizing gene *DWARF4*, indicating an important interaction between BR and auxin to control hypocotyl expansion in Arabidopsis under heat stress (Gray *et al.*, 1998; Maharjan and Choe, 2011). Similarly, IAA along with GA and BR plays an important role in controlling plant growth, particularly stem elongation during heat stress (Gollmack *et al.*, 2013). Previous data showed the direct link between the IAA, GA, PIF4, and stem elongation response under heat stress, with both GA and IAA stimulating the expression of the PIF4 gene to induce hypocotyl elongation under high temperature (Stavang *et al.*, 2009). In addition, GA participates in hormonal crosstalk to transduce environmental inputs and act antagonistically to ABA (Depuydt and Hardtke, 2011).

CK responds to environmental cues in plants and this is believed to be related to its role in maintaining the overall hormonal balance and its interaction with other hormones such as ABA, ethylene, JA, and SA, which are directly involved in abiotic stress responses (Hare *et al.*, 1997; Thu *et al.*, 2017). Complex crosstalk and interactions have been observed between CKs and ABA under heat stress (Wang *et al.*, 2011; Ha *et al.*, 2012). It is assumed that CKs and ABA work antagonistically in various physiological and developmental events, as well as in response to different environmental stresses (Catala *et al.*, 2007). Interestingly, wheat kernels under heat stress showed a marked reduction in ZR content, whereas IAA, GA, and ABA contents increased (Yang *et al.*, 2016). Likewise, exogenous application of melatonin to perennial ryegrass under heat stress significantly increased CK and melatonin levels, but reduced ABA levels (J. Zhang *et al.*, 2017). Cytokinin biosynthetic genes and their corresponding TFs were up-regulated by melatonin under heat stress, whereas ABA-responsive genes were down-regulated (J. Zhang *et al.*, 2017). CKs also interact with other growth regulators such as BR and SA to elicit many physiological processes under heat stress (Peleg and Blumwald, 2011). A recent study showed that expression of *IPT* (a gene responsible for CK biosynthesis) in tobacco and rice significantly altered gene expression related to hormone biosynthesis as well as regulation to impart thermotolerance (Peleg *et al.*, 2011). As mentioned earlier, heat stress during anthesis leads to major yield losses; in passion fruit (*Passiflora edulis*), flower abortion involves two phytohormones, CK and GA, which act differently in this situation, with GA stimulating flower abortion and CK application reducing flower abortion, to provide heat tolerance (Sobol *et al.*, 2014).

Stress hormones such as ethylene and ABA retard growth by changing auxin, GA, and CK activity in a tissue-dependent manner (Wolters and Jürgens, 2009; Peleg and Blumwald, 2011). Moreover, both ABA and ethylene act antagonistically to GA, and this crosstalk occurs at the DELLA protein level (Achard *et al.*, 2006; Wolters and Jürgens, 2009). ABA and ethylene seem to further interfere with this crosstalk to

restrict plant growth (Beaudoin *et al.*, 2000). ABA regulates stomatal behavior during stress periods; however, recent findings suggest that other hormones such as ethylene, CKs, JA, SA, BRs, and NO also control the opening and closing of stomata (Acharya and Assmann, 2009). Hormones, especially ABA, SA, JA, BRs, and NO, lead to stomatal closure, whereas IAA and CKs stimulate stomatal opening under heat and drought stress. Further, NO functions as a key mediator in the ABA-regulated signaling web to induce stomatal closure (Ribeiro *et al.*, 2009).

In Arabidopsis, high temperature inhibits germination by enhancing ABA levels that suppress both GA synthesis and translocation (Toh *et al.*, 2008). GA is also linked with SA, and exogenous application of GA in heat-stressed Arabidopsis stimulated seed germination and growth by regulating SA expression. GA₃ induces the expression of *ICS1* (isochorismate synthase 1) and *NPR1* [non-expressor of pathogenesis-resistance (PR) genes] involved in SA synthesis and action, respectively (Alonso-Ramírez *et al.*, 2009).

Similarly, ethylene and JA act together in response to environmental stimuli. The key precursor of ethylene signaling and response is the ERF (ethylene response factor), whose expression increases on exposure to heat stress (Müller and Munné-Bosch, 2015). The ERF binds with DRE (dehydration response element-binding factor) and induces expression of heat-responsive genes such as *HSF3*, *HSP101*, and *HSP70* to impart thermotolerance (Müller and Munné-Bosch, 2015). Ethylene and JA may act as antagonists to control heat stress responses; ethylene is a negative regulator of the heat stress response (Clarke *et al.*, 2009). Studies have indicated that the *ein2* mutant displayed thermotolerance, suggesting that the EIN2-regulated pathway negatively controls thermotolerance (Clarke *et al.*, 2009). Additionally, ethylene production was augmented by JA in a study on the wild type and *opr3* mutant (Sharma and Laxmi, 2016).

Other PGRs also communicate with phytohormones; for instance, the endogenous content of ASC promoted the biosynthesis of many hormones and signal transduction pathways in which hormones intervened in stressed environments (Pastori *et al.*, 2003). ASC intensity in tomato plants was correlated with gene activation concerned with hormone signaling, relative to ASC synthesis that in turn was reliant on oxidative status (Lima-Silva *et al.*, 2012). Sadak *et al.* (2013) observed that the endogenous concentrations of ASC and citric acid (2:1 ratio) enhanced the levels of IAA, GA, BRs, and zeatin, and reduced ABA content. In another study, Ye *et al.* (2012) observed a promising interaction between ASC and plant hormones in rice. Since ASC acts as a cofactor to synthesize ethylene and ABA (Barth *et al.*, 2006; Ye *et al.*, 2012; Zhang, 2013), the cellular ASC content via the interface with plant hormones controls a variety of signal transduction pathways to normalize growth and development (Pastori *et al.*, 2003). Thus, it is expected that the interaction between ASC and phytohormones establishes redox homeostasis and further developmental responses in plants under heat stress (Awasthi *et al.*, 2015).

Prospects and conclusions

The heat stress response is a complex phenomenon involving numerous cellular changes at several levels of organization, which prepare the cells for thermotolerance under mild stress conditions, yet these mechanisms may fail to function and

protect plants under severe heat conditions, resulting in cellular and plant death. Cellular changes involve various molecules with diverse roles in signaling and defense mechanisms to confer protection, including stabilizing cell membranes and organelles from oxidative damage, maintaining photosynthesis by stabilizing the reaction centers of the electron transport chain, protecting enzymes from denaturation, saving native proteins by producing chaperones, controlling stomatal conductance and water relations to regulate leaf temperature, and sustaining growth by up-regulating various growth-related molecules. Considering these diverse protective mechanisms, cells need to produce phytohormones, osmolytes, antioxidants, and stress-related proteins, which can interact with each other to reach an appropriate defensive state (basal or acquired thermotolerance). While there are several reports on changes in the expression of these molecules, the interactive mechanisms that impart thermoprotection remain elusive. Moreover, studies involving their intermutual effects are needed to identify the thermoprotective mechanisms. One of the ways to mitigate heat stress damage involves treatment of the plants at one stage or other with exogenous application of some molecules such as phytohormones, osmoprotectants, and ROS scavengers. Studies on their exogenous application have provided some strong evidence about the roles of these molecules in conferring heat tolerance; they are largely restricted to controlled environments, and need to be validated under realistic field environments. Moreover, it is highly challenging to find out their appropriate concentrations, duration of the treatment, and stage of the plant to be treated in order to achieve the desired results. For this purpose, each crop species requiring protection from heat stress needs to be tested for its response to diverse types of molecules implicated in thermoprotection. Furthermore, studies are needed to probe the finer mechanism and up-regulation of hormone-responsive genes involved in induction of heat tolerance. Establishing a common role for hormones in limiting heat-induced injuries may provide significant knowledge regarding the field application of these molecules as well as their implications in breeding programs (Macková *et al.*, 2013). Further investigations on genetic manipulation of these molecules in target crops are needed to validate their involvement in thermoprotection. A combination of treatments, which protect the leaves from heat-induced oxidative damage and save the flowers from abortion at the same time, would be vital to enhance the performance of the plants under heat stress. Considering the impacts of climate change, increase in temperature would be a primary issue, coupled with drought stress, affecting agriculture, which would require quick as well as long-term solutions involving several scientific disciplines. Many studies have shown successful management of heat stress involving exogenous application of thermoprotectants, described above, but largely under a laboratory environment, and to a limited extent in the field environment, which appears to limit their successful application. Further research would be needed to test these molecules, individually and in combination, under heat and drought environments, under a field environment, to extend their practical usage to improve stress tolerance in food crops.

Acknowledgements

HN is grateful for the financial assistance from DST-India (PURSE grant), CSIR (India), University of Western Australia, Australia, ICARDA, Morocco, and the World Vegetable Center, to carry out various experiments related to drought and heat stress at various stages of our research endeavors. OPD acknowledges the partial financial support from the Worldwide University Network (WUN) for the Climate Resiliency Open Partnership for Food Security (CROP-FS) consortium.

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Identification and Characterization of Contrasting Genotypes/Cultivars for Developing Heat Tolerance in Agricultural Crops: Current Status and Prospects

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OPEN ACCESS

Edited by:

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Specialty section:

This article was submitted to
Crop and Product Physiology,
a section of the journal
Frontiers in Plant Science

Received: 25 July 2020

Accepted: 14 September 2020

Published: 22 October 2020

Citation:

Chaudhary S, Devi P, Bhardwaj A, Jha UC, Sharma KD, Prasad PVV, Siddique KHM, Bindumadhava H, Kumar S and Nayyar H (2020) Identification and Characterization of Contrasting Genotypes/Cultivars for Developing Heat Tolerance in Agricultural Crops: Current Status and Prospects. *Front. Plant Sci.* 11:587264. doi: 10.3389/fpls.2020.587264

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Rising global temperatures due to climate change are affecting crop performance in several regions of the world. High temperatures affect plants at various organizational levels, primarily accelerating phenology to limit biomass production and shortening reproductive phase to curtail flower and fruit numbers, thus resulting in severe yield losses. Besides, heat stress also disrupts normal growth, development, cellular metabolism, and gene expression, which alters shoot and root structures, branching patterns, leaf surface and orientation, and anatomical, structural, and functional aspects of leaves and flowers. The reproductive growth stage is crucial in plants' life cycle, and susceptible to high temperatures, as reproductive processes are negatively impacted thus reducing crop yield. Genetic variation exists among genotypes of various crops to resist impacts of heat stress. Several screening studies have successfully phenotyped large populations of various crops to distinguish heat-tolerant and heat-sensitive genotypes using various traits, related to shoots (including leaves), flowers, fruits (pods, spikes, spikelets), and seeds (or grains), which have led to direct release of heat-tolerant cultivars in some cases (such as chickpea). In the present review, we discuss examples of contrasting genotypes for heat tolerance in different crops, involving many traits related to thermotolerance in leaves (membrane thermostability, photosynthetic efficiency, chlorophyll content, chlorophyll fluorescence, stomatal activity), flowers (pollen viability, pollen germination, fertilization, ovule viability), roots (architecture), biomolecules (antioxidants, osmolytes, phytohormones, heat-shock proteins, other stress proteins), and "omics" (phenomics, transcriptomics, genomics) approaches. The traits linked to heat tolerance can be introgressed into high yielding but heat-sensitive genotypes of crops to enhance their thermotolerance. Involving these traits will be useful for screening

contrasting genotypes and would pave the way for characterizing the underlying molecular mechanisms, which could be valuable for engineering plants with enhanced thermotolerance. Wherever possible, we discussed breeding and biotechnological approaches for using these traits to develop heat-tolerant genotypes of various food crops.

Keywords: heat-stress, crops, tolerance, agriculture, physiology

INTRODUCTION

The Earth's increasing average surface temperature due to climate change is proving to be stressful for all phases of plant growth and development, particularly in tropical and subtropical countries (Li B. et al., 2018). Among abiotic stresses, high temperature stress is a major factor disrupting plants' performance (Wahid et al., 2007). Each plant species has its own maximum, optimum and minimum temperatures, known as cardinal temperatures. Temperatures below or above these thresholds causes stress (Wahid et al., 2007). Above optimum (high-temperatures) affect plant's morphological, physiological, biochemical and molecular traits, which ultimately leads to poor growth and yields (Hasanuzzaman et al., 2013). The impact of high-temperature (heat) stress depends on intensity, timing, duration of stress and type of plant species (Wahid et al., 2007). Although all stages of plant development can be negatively impacted by heat stress, reproductive stages of crop are relatively more sensitive than vegetative stages (Prasad et al., 2008b, 2017). Heat stress during seed germination reduces germination percentage, seedling emergence, and radicle and plumule growth in germinated seedlings, resulting in abnormal seedlings with poor seedling vigor (Hasanuzzaman et al., 2013). At later vegetative stages, heat stress adversely affects photosynthesis, leaf area development leading to lower biomass production; whereas, stress during reproductive stages of development results in lower seed numbers and decrease seed size resulting in lower yields (Bita and Gerats, 2013; Prasad et al., 2017). Different crops and their genotypes vary in their heat sensitivity, the response is generally stage-and trait-specific, which can reveal mechanisms related to heat tolerance (Bita and Gerats, 2013; Prasad et al., 2017). Thus, genotypes having contrasting heat sensitivity have been identified in several crops (detailed below), that yielded vital information on various traits controlling heat tolerance (Figure 1).

IMPACT OF HEAT STRESS

Heat stress can have damaging effects (direct and indirect) on all stages of plant growth and development (Kaushal et al., 2016). Phenological stages differ in their sensitivity to heat stress, and vary between species and genotypes of same species. Various plant tissue injuries have been observed under heat stress, such as leaf and twig scorching, leaf, branch and stem chlorosis and necrosis, leaf senescence and abscission, root and shoot growth inhibition, flower drop, and fruit damage,

which consequently reduce plant productivity (Vollenweider and Günthardt-Goerg, 2005). Heat stress primarily affects the stability of plasma membranes, several proteins, cytoskeleton organization, and the efficiency of cell enzymatic reactions and creating metabolic disparity (Xu et al., 2006). Heat-stress-induced oxidative stress causes peroxidation of membrane lipids, proteins, and nucleic acids (Mittler et al., 2004). Due to reduced membrane stability, electrolyte leakage increases, which intensifies the membrane injuries (Wahid et al., 2007). Physiological processes, such as photosynthetic activity and sucrose metabolism, are highly sensitive to heat stress (Berry and Bjorkman, 1980). At the subcellular level, disruption of structural organization of thylakoids and loss of grana stacking in chloroplasts are the primary sites of heat injury (Sharkey, 2005), which lead to changes in electron transport to PSII (Lu and Zhang, 2000). Heat stress also damages PSII and inhibits its repair due to the generation of reactive oxygen species (ROS) (Allakhverdiev et al., 2008). Heat stress affects enzymes in Calvin cycle, including RuBisCo and RuBisCo activase (Camejo et al., 2005; HanumanthaRao et al., 2016; Bindumadhava et al., 2018), which hampers photosynthesis and photorespiration. Heat stress during reproductive stages adversely affects seed-set and yield in many food legumes, such as chickpea (*Cicer arietinum*) (Kaushal et al., 2013), mungbean (*Vigna radiata*) (Kaur et al., 2015; HanumanthaRao et al., 2016), peanut (*Arachis hypogaea*) (Prasad et al., 1999a,b) and lentil (*Lens culinaris*) (Bhandari et al., 2016) and cereals, such as wheat (Wahid et al., 2007; Prasad and Djanaguiraman, 2014), sorghum (*Sorghum bicolor*) (Prasad et al., 2015), barley (*Hordeum vulgare*) (Barnabás et al., 2008), and maize (*Zea mays*) (Kumar et al., 2012). During the reproductive stage, gametogenesis and fertilization are highly sensitive to heat stress, which impairs meiosis in both male and female organs, affects pollen germination and pollen tube growth, reduces ovule viability and ovule size, alters stigmatic and style positions, reduces stigma receptivity, disturbs fertilization processes, affects embryo fertilization, and impedes endosperm growth (Farooq et al., 2017; Prasad et al., 2017). Heat stress hastens the rate of grain filling, but reduces the duration of grain filling, as reported in wheat (Prasad et al., 2008a; Farooq et al., 2011), which may be due to direct effects of heat stress on the source-sink relationship that reduce photoassimilate supply to developing seeds (Calderini et al., 2006). The detrimental effects of heat stress can be alleviated by developing crop varieties with improved heat tolerance. The most popular approach used by many plant researchers has been screening a large population to identify contrasting genotypes for elucidating physiological, biochemical, and molecular mechanisms governing heat

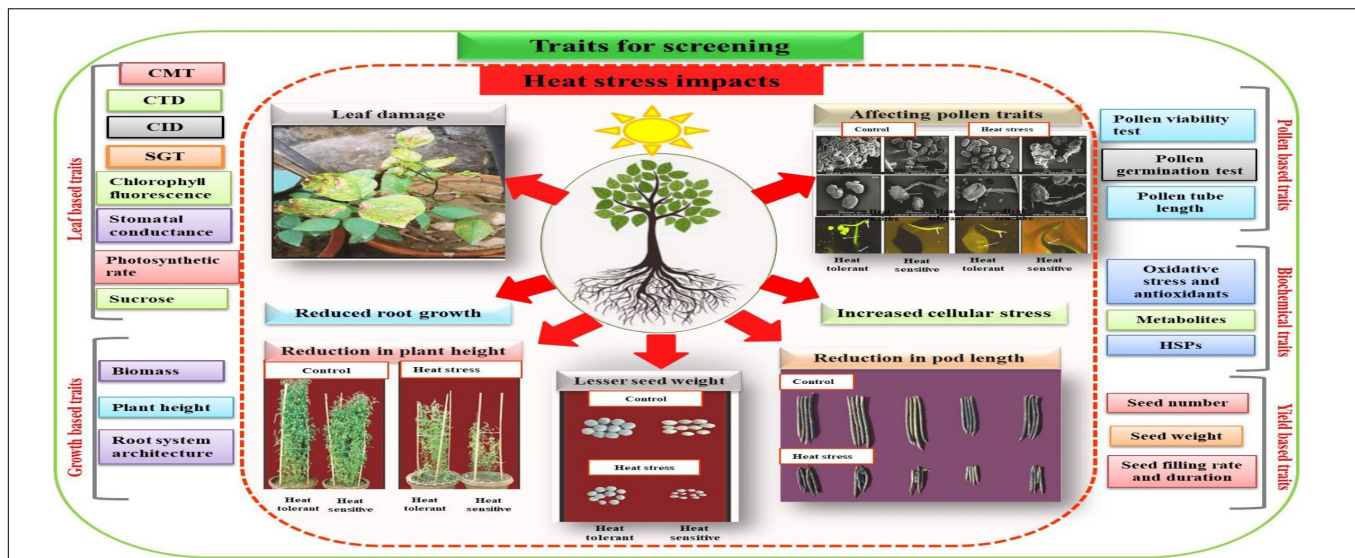


FIGURE 1 | Screening traits for developing heat tolerant genotypes. Different traits based on leaf, growth, pollen grains biochemical and yield can be used for the selection of genotypes. Cell membrane thermostability (CMT), canopy temperature depression (CTD), carbon isotope discrimination (CID), stay green trait (SGT), chlorophyll fluorescence, stomatal conductance, photosynthetic rate and sucrose are the traits that can be assessed from leaves. However growth pattern such as plant biomass, plant height, and RSA of different genotypes can also be compared for selection of contrasting genotypes. Similarly, reproductive wellness of genotypes can be checked by using pollen based traits such as pollen viability test, pollen germination test and pollen tube length. The mitigation of cellular stress by genotypes can be compared by analysis of oxidative stress damage (production of free radicals) and production of antioxidants, metabolites and heat shock proteins (HSPs) whereas yield based traits such as seed number, seed weight, seed filling rate and duration can also be employed for selection purpose.

tolerance. Understanding such mechanisms will pave the way for improving crop genotypes under heat stress. Here, we discuss how heat stress impacts traits related to stress tolerance in contrasting genotypes of various crops to provide further clues for breeders and agronomists for improving the selection of heat-tolerant genotypes across crop species. Heat stress is often accompanied by drought stress; the impacts of heat stress are worsened in drought-stressed plants, which are manifested in various organizational changes in plants (Sehgal et al., 2017), hence, wherever possible, we have also included some examples where genotypes of crops have been screened against combined heat and drought stress situations.

MECHANISMS GOVERNING THERMOTOLERANCE

Plants can endure two types of mechanisms to cope with heat stress: (1) basal thermotolerance (inherent ability of plant) and (2) acquired thermotolerance (induced by pre-exposure to higher but non-lethal temperatures) (Bokszczanin and Fragkostefanakis, 2013). Acquired thermotolerance has an important role to play in plant survival (Kotak et al., 2007). Hence, the heat stress response is a genetically controlled process that can be stimulated by mild or sub-lethal temperatures and further trigger the onset of heat-stress response in plants (Charng et al., 2006). The heat-stress response in plants is mainly conserved via cellular compartments and regulatory networks (Wahid et al., 2007). Plants have evolved various short-term acclimation mechanisms and long-term adaptations in response to heat stress. Short-term acclimation

mechanisms include leaf orientation, transpirational cooling, and changes in membrane lipid composition (Wahid et al., 2007). For longer term adaptations, plants activate heat-stress tolerance mechanisms, such as heat stress sensing through various sensors and regulating downstream signal transduction pathways (e.g., lipidome, metabolome, transcriptome, and proteome) to modify gene expression to ensure survival (Sung et al., 2003; Bokszczanin and Fragkostefanakis, 2013; Dang et al., 2013).

Major adaptive mechanisms that induce thermotolerance in plants include amplified production of thermoprotectants, such as secondary metabolites, compatible solutes, ROS scavenging mechanisms, and heat-shock proteins (HSPs) (Nakamoto and Hiyama, 1999; Sakamoto and Murata, 2002; Wahid et al., 2007; Mittler et al., 2012). During severe heat stress, ROS generated as a byproduct of aerobic metabolism negatively affect cellular metabolism, such as peroxidation of lipid membranes and damage to nucleic acids and proteins (Bita and Gerats, 2013). Plants activate enzymatic and non-enzymatic ROS scavenging systems to defend this ROS production. The main ROS scavenging enzymes are superoxide dismutase (SOD), catalase (CAT), peroxidase (POX), ascorbate peroxidase (APX), and glutathione reductase (GR), and the non-enzymatic systems include ascorbic acid (ASC) and glutathione (GSH) (Suzuki et al., 2012). Elevated levels of these antioxidants are crucial for imparting thermotolerance in plants (Awasthi et al., 2015). Thus, to cope with heat stress, plants synthesize and accumulate more stress proteins, including HSPs, which are well-defined molecular chaperones involved in protein folding, and proper aggregation, translocation, and degradation under normal and stress conditions, and essential for sustaining cellular stability

(Vierling, 1991). Five major families of HSPs/chaperones are HSP60, HSP70, HSP90, HSP100, and the small HSP (sHSP) family (Wang et al., 2004), which play an important role in the mitigation of heat-stress effects, especially protecting native proteins from denaturation. The accumulation of secondary metabolites, such as carotenoids, isoprenoids, and flavonoids, augments high-temperature stress tolerance by preventing peroxidase activity (Havaux, 1998; Loreto et al., 1998; Rivero et al., 2004). The accumulation of compatible solutes, *viz.* sugars (trehalose), sugar alcohols (polyols), proline, glycine betaine, tertiary, and quaternary ammonium compounds, also provides heat-stress tolerance in plants (Sakamoto and Murata, 2002). Due to their low molecular weight, these molecules can buffer the cellular redox potential under heat stress. Phytohormones, such as salicylic acid, abscisic acid, brassinosteroids, and polyamines, also play a significant role in providing thermotolerance to plants (Ahammed and Yu, 2016; Sharma et al., 2020).

GROWTH-BASED PARAMETERS

Most studies on contrasting genotypes have measured biomass, plant height, and root growth, with significant variations identified in various crops subjected to heat stress, either in laboratory or field experiments, which has resulted in using these traits to quantify the impact of heat stress. Some examples of the impacts of heat stress on these traits are described below.

Plant Height

Vegetative growth can be assessed as plant height to distinguish heat-stress tolerant genotypes (Debnath et al., 2016). In *Brassica juncea* L., high temperature (34°C) after the induction of flowering significantly affected plant height when grown in the field, declining by 18.9–30.5% (mean 22.3%), relative to the control. Genotypes BPR-538-10, NRCD-2, RH-0216 had lower heat susceptibility, based on plant height, than genotypes RGN193, NPJ112 and SKM531 (Chauhan et al., 2009). Heat stress (>40°C) reduced plant height in 20 maize genotypes in the field (Debnath et al., 2016), with the most heat-tolerant genotype (DTPYC9F119) declining by 2.31% compared with a 72.2% reduction in the most heat-sensitive genotype LM13. Assessment of five potato cultivars (L1: 84.194.30; L2:86.61.26; L3: 87HW13.7, L4: DG81-68, and L5: Desiree) under controlled environment of combined heat (30 + 1°C) and drought stress (PEG 8000) for 21 days revealed severe effects all the cultivars on plant height, when both the stresses were together, except L2 and L3 (Handayani and Watanabe, 2020).

Seedling growth could be a potentially useful trait for early screening against heat stress. For instance, in some tropical parts of Africa, surface temperatures of tropical soils at planting time can exceed 50°C for hours to restrict the germination and seedling growth (Setimela et al., 2007). Hence, seedling heat tolerance is critical for adequate crop establishment in the semi-arid tropics. In a study carried out on sorghum (*Sorghum bicolor*) in Zimbabwe, seedling tolerance was estimated as heat tolerance index (HTI; defined as a ratio of resumed coleoptile growth after a controlled heat shock, compared to normal

growth). Genetic parameters of HTI were assessed by crossing four sorghum lines having varying HTI, with three tester lines, and deriving F1, F2, F3, BC1, and BC11 families for generation means analysis. HTI was found to be highest (0.71) in Line IS20969 from Egypt, while an experimental line (290R), from the University of Nebraska, had the lowest at 0.51. The study revealed that additive and dominance effects contributed to coleoptile elongation under normal conditions, but only additive effects were significant in recovery growth. Epistatic effects were observed in both normal and heat-stressed environment. General combining ability (GCA) effects for HTI were highly marked in both conditions, but specific combining ability (SCA) effects were negligible. These results showed that it is achievable to enhance seedling heat tolerance and, thus, improve plant populations of sorghum in tropical areas where hot soil temperatures occur.

Root System Architecture

The structure, spatial, and temporal configuration of the plant root system is called root system architecture (RSA) (de Dorlodot et al., 2007). The organization of primary and secondary roots is determined by RSA at the macroscale (Smith and De Smet, 2012). Root microstructure, such as fine root hairs, root tips and their interactions with soil and soil microorganisms responsible for water and mineral uptake, is determined by RSA at the microscale (Wu et al., 2018). Most resources are heterogeneously distributed in the soil, and the spatial and temporal distribution of roots determines the crop's ability to exploit resources (Brussaard et al., 2007). Better understanding of RSA allows us to determine the impact of environmental conditions and management practices on crops, which can help to reduce the difference between genetic potential and actual average yields (Garnett et al., 2009; Judd et al., 2015; Ryan et al., 2016). RSA has a vital role in plant–soil–microbe interactions and resolves the crosstalk with beneficial soil microbes in the rhizosphere (Ryan et al., 2016).

Across fluctuating environments, RSA is an important characteristic for adaptability. Therefore, we can improve crop performance in terms of increased root traits, such as allocation, morphological, anatomical, or developmental plasticity (Sultan, 2000). There is a direct relationship between individual RSA plasticity and yield, which is related to more stable plant performance across changing environments in various species (Sadras, 2009; Niones et al., 2012, 2013). Root branching is important for improving the root surface area, enabling the plant to reach more distant reserves of water and nutrients and improve soil anchorage. In plants, heat stress generally reduces primary root length, lateral root density (number of lateral roots per unit primary root length) and angle of emergence of lateral roots from the primary root, but has little effect on average lateral root length (McMichael and Quisenberry, 1993; Nagel et al., 2009). Root growth has a lower optimal growing temperature than shoot growth and is thus more sensitive to rising temperatures (Huang and Gao, 2000; Xu and Huang, 2000). Plant heat tolerance is directly influenced by root morphological features. Among Kentucky bluegrass (*Poa pratensis*) cultivars, increased root number and root length contributed to variations in heat tolerance (Lehman and Engelke, 1993). Root phenotyping of 577 common bean (*Phaseolus vulgaris* L.) genotypes in

variable environments of heat, drought, and nutrient deficiency revealed significant relationships between seed yield and seedling basal root number, seedling adventitious root abundance, and seedling taproot length. Under heat stress, adventitious root number had a positive relationship (13%) with seed yield. Mesoamerican genotypes of common bean yielded higher than Andean genotypes under heat stress (Strock et al., 2019). In canola, heat stress reduced stem diameter by 8.4%, cross-sectional area by 17.3%, and aboveground biomass by 11.5% in two genotypes; genotype 13C204 (heat-sensitive) had smaller stem diameter, cross-sectional area, root length, root surface area, root biomass, and root volume than Invigor 5440 (heat-tolerant) (Wu et al., 2017). In another study, heat stress reduced lateral root elongation (−38%), number of axile roots (−30%), elongation rate of primary root (−26%), root dry weight (−39%), leaf water potential (−59%) and leaf area (19%) in heat-sensitive maize lines K64R, Ac7643, and Ac7729TZSRW when the temperature increased from 28 to 37°C. The heat-tolerant lines H16, CML444, and SC-Malawi were least affected by high temperature (Trachsel et al., 2010). In maize, screening of 10 genotypes for combined heat and drought stress (40°C/60%) revealed DK 6789, NT 6621 as tolerant and genotypes FH 988 and FH 1137 as sensitive on the basis of root tolerance indices (Ayub et al., 2020).

Biomass

Wheat seedlings grown for 7 days under normal conditions and then subjected to heat stress (42°C for 2 h) in a growth chamber revealed growth differences between genotypes (Gupta et al., 2013). In general, heat stress reduced growth (shoot/root dry weight and shoot/root length). Heat-tolerant genotypes (Raj-4037 and PBW590) retained more shoot and root length and dry weight than heat-sensitive genotypes (PBW502, DBW16, DBW17, WH1021, and PBW550) (Gupta et al., 2013). In a field experiment, heat stress (30/20°C) reduced wheat biomass, relative to optimum conditions (25/15°C), but heat-tolerant genotypes (MW-8, BW-4, and BW-3) maintained more biomass than heat-sensitive genotypes (MW-7, MW-6, and BW-5) (Rahman et al., 2009). Heat stress (> 32/20°C) significantly reduced chickpea biomass by 22–30%, relative to those grown under normal temperatures; heat stress had a smaller effect on the biomass of heat-tolerant genotypes (ICC15614 and ICCV92944) than heat-sensitive genotypes (ICC5912, ICC10685) (Kaushal et al., 2013). Similarly, in a field experiment on alfalfa (*Medicago sativa*), heat stress (38/35°C) reduced plant biomass, relative to the control (25°C), more so in heat-sensitive W1712 than heat-tolerant Bara310SC (Wassie et al., 2019). Field studies on lentil revealed that heat stress (> 32/20°C) significantly reduced plant biomass, relative to the control (Sita et al., 2017a); genotypes IG3263, IG2507, IG3297, IG3312, IGG3327, IG3330, IG3546, IG3745, IG4258, and FLIP2009 retained more biomass (termed heat-tolerant) than genotypes IG2519, IG2802, IG2506, IG2849, IG2821, IG2878, IG3326, IG3290, IG3973, IG3964, IG4242, DPL15, DP315, IG4221, and IG3568 (termed heat-sensitive). Likewise, heat stress (> 40/28°C) significantly reduced mungbean biomass (up to 76%), relative to the control (34/16°C) in the field, due to the inhibition of vegetative growth and acceleration in reproductive growth.

Genotypes EC693357, EC693358, EC693369, Harsha, and ML 1299 produced more biomass under heat stress (heat-tolerant) than genotypes EC693363, EC693361, KPS1, EC693370, and IPM02-3 (heat-sensitive) (Sharma et al., 2016). A study on potato (*Solanum tuberosum*) revealed that warmer temperatures (31/29°C) severely affected plant biomass in two genotypes—Norchip (heat-tolerant) and Up-to-date (heat-sensitive)—grown in controlled environment chambers (Lafta and Lorenzen, 1995). Both genotypes had similar total dry mass under controlled conditions (19/17°C), but heat stress (31/29°C) reduced total dry mass by up to 44% in Norchip and 72% in Up-to-date. Leaf, stem, shoot, and tuber dry and fresh weights followed the same trend under high temperature in both genotypes. At Niger, West Africa (ICRISAT Sahelian Centre research farm (13° 29' N, 2° 10' E; 221 m above sea level), field experiments were performed to evaluate heat tolerance of groundnut (*Arachis hypogaea* L.) using physiological traits identified in a yield model [crop growth rate (C), reproductive duration (Dr) and partitioning (p)]. After screening 625 diverse groundnut genotypes, under irrigation during the hottest months (February to May), 16 contrasting genotypes, selected on the basis of combination of high pod yield and partitioning coefficient, revealed that crop growth rate was a powerful factor affecting pod yield. Pod yield of most genotypes decreased by more than 50% because of heat stress (40°C) at the time of flowering and pod formation. The findings showed that estimates of p would be vital as a dependable selection criterion, compared to yield, for identification of heat tolerant genotypes. The breeders should explore strategies to maximize the crop growth rate and partitioning in genotypes growing under warm environments (Ntare et al., 2001). Under combined heat and drought (36/26°C without irrigation) stresses, Biomass was used as a trait for evaluation of 3 tomato cultivars (Arvento and two heat tolerant; LA1994 and LA2093) (Zhou et al., 2017) resulting in identification of “Areventro” cultivar as more tolerant than “LA1994” and “LA2093” genotypes (Zhou et al., 2017).

LEAF-BASED TRAITS

Heat stress causes serious leaf injuries, yellowing of leaves (chlorosis), tissue death (necrosis), especially tips and margins, wilting, and drying, resulting in severe loss of functionality (Wahid et al., 2007). Various traits have been used to assess heat damage, with genotypes contrasting for heat tolerance identified based on these traits.

Tissue Damage

Tissue damage can be assessed by measuring membrane damage based on electrolyte leakage, which is a reliable indicator of heat sensitivity in several crop species. The primary target of environmental stress is the cell membrane (Chen et al., 2014; Sita et al., 2017b). Heat stress loosens chemical bonds within the molecules of biological membranes by accelerating the kinetic energy and movement of molecules across membranes, which results in membrane fluidity by protein denaturation or increased unsaturated fatty acids (Savchenko et al., 2002). Under high temperature, protein denaturation, increased membrane

fluidity, and enzyme inactivation decreases protein synthesis and degradation, and alters membrane integrity (Howarth, 2005). The tertiary and quaternary structure of membrane proteins changes with heat stress and enhances membrane permeability, as evident from increased ionic leakage, which is an indicator of decreased cell membrane thermostability (CMT) (Wahid et al., 2007). Damage to leaf membranes occurs due to the direct effects of high temperature, photo-oxidation of chlorophyll pigments, impaired electron flow, inhibition of carbon fixation, and water loss from leaves. Damage to membranes impairs photo-assimilate production in leaves (Prasad et al., 2017). Under high temperature, the relationship between CMT and crop yield varies from plant to plant. CMT has been used as an indirect measure of heat stress tolerance in plant species, such as sorghum (Sullivan, 1997; Marcum, 1998), soybean (Martineau et al., 1979), potato and tomato (Chen et al., 1982), sorghum, wheat (Blum et al., 2001), cotton (Ashraf et al., 1994; Cottee et al., 2010), lentil (Sita et al., 2017a), chickpea (Kaushal et al., 2013), mungbean (Sharma et al., 2016), and barley (Wahid and Shabbir, 2005). Abro et al. (2015) identified several heat-tolerant cotton genotypes with high membrane thermostability at 50°C in the laboratory environment, which could be used for breeding purposes to develop heat-tolerant genotypes. During the late developmental phase of plants, membrane stability tends to decrease (Ahmad and Prasad, 2011). For breeding purposes, significant variations in membrane thermostability among genotypes could be used to improve selection (Hemantaranjan et al., 2014).

In wheat grown under high temperatures (45°C for 2 h), genotypes (Raj4037, PBW373) with high CMT (58.20, 55.43) during grain filling performed better than those (Raj4083, DBW16, PBW550) with low membrane thermostability (48.15, 50, 51.96). Under controlled conditions, membrane thermostability was maximum in WH1021 (64.13) and minimum in DBW16 (51.11) (Gupta et al., 2013). Similarly, CMT was markedly higher in heat-tolerant (56.83%) than heat-sensitive (31.43%) wheat genotypes during grain filling. Based on CMT, Bala and Sikder (2017) identified heat-tolerant wheat genotypes BAW-1143, BARI Gom-25, BARI Gom-26, and Prodig. At the seedling stage in wheat, CMT had a positive correlation with grain yield, grain weight (Saadalla et al., 1990), and biomass (Blum et al., 2001), indicating the effectiveness of this trait for assessing heat tolerance. In rice at 40°C, thermostability was closely related to crop yield potential (Maavimani and Saraswathi, 2014). In a comparative study of rice and maize grown under controlled high temperatures (40/35°C and 45/40°C), the rice genotypes (PR116, PR118) had greater electrolyte leakage (27.4–40.2%) than the maize genotypes (PMH1, PMH2) (19.2–26.2%) (Kumar et al., 2012). Similarly, among three rice cultivars, F60 and F733 were more heat-susceptible than F473 when grown at 40°C, with greater electrolyte leakage (20 and 15%) (Sanchez-Reinoso et al., 2014). Likewise, Yadav et al. (2014) used CMT as an effective screening parameters for selecting heat tolerant lines in Pearl millet. From the same study, the authors also identified H77/29-2 × CVJ-2-5-3-1-3 hybrid as heat tolerance based on seedling thermotolerance index. Under combined stresses (drought-42–45% of irrigated conditions) and heat

(> 32/20°C), the drought tolerant chickpea genotypes were found to tolerate the two stresses more effectively than heat tolerant genotypes. For instance, genotypes ICC1356 (drought-tolerant) showed less damage to membranes than genotype ICC3776 (drought-sensitive), when subjected to both the stresses (Awasthi et al., 2017).

In legumes, a few studies have identified heat-tolerant and heat-sensitive genotypes. Based on the membrane stability test, chickpea was most sensitive to heat stress, relative to other legumes such as pigeon pea, groundnut, and soybean (Devasirvatham et al., 2012). Contrasting chickpea genotypes exposed to high temperatures (40/30°C and 45/35°C) varied markedly, with heat-tolerant genotypes (ICCV07110, ICCV92944) showing less membrane damage (22.6, 20.6%) than heat-sensitive genotypes (ICC14183, ICC5912) (30.4, 33.3%) (Kumar et al., 2013). A similar test conducted at 37/27°C reported up to 25% electrolyte leakage in chickpea seedlings (Pareek et al., 2019). A heat-tolerant genotype (ICC1205) had low electrolyte leakage (13–14%), indicating better cell membrane integrity. Screening of cowpea genotypes exposed to heat stress also revealed less leaf electrolyte leakage (35.8–36.7%) in heat-tolerant genotypes (H36, H8-9, DLS99) during flowering and pod set than heat-susceptible genotypes (CB5, CB3, DLS127) (66.2–79%) (Ismail and Hall, 1999). In lentil, heat tolerance was related to less membrane damage (<20%) in heat-tolerant genotypes (IG2507, IG3263, IG3745, IG4258, and FLIP2009) than heat-sensitive genotypes (IG2821, IG2849, IG4242, IG3973, IG3964) (> 30%) at 38/28°C and 40/30°C in a controlled environment (Sita et al., 2017a). In another study, lentil genotypes (Ranjan, Moitree, 14-4-1, IC201710, and IC208329) were reported as heat-tolerant based on cell membrane stability under field and growth chamber studies at 34°C (Choudhury et al., 2012). Barghi et al. (2013) reported the highest CMT in genotype Qazvin (98.13%) and regarded it as heat-tolerant, whereas genotype B4400 (33.19%) had the lowest CMT (heat-sensitive). Under high temperature (38/35°C), screening of 15 *Medicago* cultivars for CMT identified Bara310SC and WL712 as heat-tolerant (24.07%) and heat-sensitive (53.2%) cultivars, respectively, having minimum and maximum electrolyte leakage, respectively (Wassie et al., 2019).

Cotton displays heat sensitivity at various growth stages. Cotton genotypes grown in a controlled environment under optimal conditions (35/21 ± 2°C) for 30 days and then exposed to high temperature (46/30 ± 2°C) at the reproductive stage, by gradually increasing temperature by 2°C per day, were screened for CMT—cultivars FH-900, MNH-552, CRIS-19, and Karishma emerged as relatively heat-tolerant (thermostable) and FH-634, CIM-448, HR109-RT, and CIM-443 as heat-susceptible (Rahman et al., 2004). In a similar study at > 32°C, cotton genotypes B557 and NIAB-78 showed minimum electrolyte leakage (<40%) and were regarded as tolerant compared to genotypes MNH-554, FH682 and FH900 which showed maximum electrolyte leakage (>50%) (Rana et al., 2011). Abro et al. (2015) reported cotton varieties NIA-80, NIA-81, NIA-83, NIA-84, NIA-M-30, NIA-M31, NIA-HM-48, NIA-HM-327, NIA-H-32, NIA-HM-2-1, NIA-Bt1, NIA-Bt2, NIA-Perkh, CRIS-342, CRIS-134, and

NIAB-111 and check variety Sadori as heat-tolerant using CMT as a screening parameter in both heat-stressed (44°C) and non-stressed (32°C) temperature regimes. Other similar studies where cotton genotypes were differentiated by CMT into heat-tolerant and heat-sensitive were conducted by Karademir et al. (2012); 15 genotypes; > 40°C) and Singh K. et al. (2018); 37 genotypes; > 40°C).

Likewise, in cucumber, contrasting genotypes were identified based on membrane stability under heat stress (40/32°C)—L3466 and Desi cucumber as heat-tolerant and Suyo Long and Poinsett as heat-sensitive (Ali et al., 2019). In tomato, 2 h exposure to high temperature (45°C) altered CMT more in heat-sensitive variety Campbell-28 (> 45%) than heat-tolerant variety Nagcarlang (<20%) (Camejo et al., 2005). In another study on 44 tomato lines, exposure to 44°C for 4 h after 1 week of vegetative stage increased electrolyte leakage in heat-sensitive genotypes (32.92 $\mu\text{mhos/cm}$) more than heat-tolerant genotypes (22.2 $\mu\text{mhos/cm}$) (Hameed et al., 2015). Similar studies have screened tomato genotypes for heat tolerance using membrane thermostability (Sangu et al., 2015; Alsamir et al., 2017). Thus, CMT is an effective trait for identifying stable and heat-tolerant genotypes.

Canopy Temperature Depression

At the whole crop level, leaf temperatures decrease below air temperature when water evaporates. Canopy temperature depression (CTD)—the difference between air temperature (T_a) and canopy temperature (T_c)—acts as an indirect measure of transpiration (Reynolds et al., 2001) and plant water status (Araus et al., 2003). A positive CTD value is observed when the canopy is cooler than the air ($\text{CTD} = T_a - T_c$) (Balota et al., 2008). CTD is a heritable trait that can be measured on cloudless days with an infrared thermometer (Reynolds et al., 1998). Plants transpire through open stomata to maintain canopy temperature in a metabolically comfortable range. Under stress, plants close their stomata for some period, which increases the canopy temperature (Kashiwagi et al., 2008). Canopy temperature is affected by soil water status, wind, evapotranspiration, cloudiness, conduction systems, plant metabolism, air temperature, relative humidity, and continuous radiation (Reynolds et al., 2001). To assess heat tolerance, many traits can be used as selection criteria, but, CTD is considered to be best as a single reading integrates scores of leaves (Reynolds et al., 1994, 1998; Fischer et al., 1998). Yield potential and the metabolic fitness of crop plants under specific environmental conditions are determined by CTD (Kumari et al., 2013). A study on barley revealed a strong link between epicuticular leaf wax QTL and CTD, and that wax load influences plant canopy temperature (Awika et al., 2017). Based on phenotypic variation, CTD can act as a desirable criterion for heat-tolerant genotype selection (Mason and Singh, 2014). CTD is a mechanism of heat escape and has a strong genetic correlation with yield (Reynolds et al., 2001). Heat-tolerant genotypes of wheat had higher CTD than heat-sensitive genotypes, indicating their greater ability to maintain a cooler canopy environment (Gare et al., 2018). In another study, the CTD value in wheat was correlated with heat resilience (Pradhan et al., 2012). In 102 durum wheat genotypes tested under late-sown conditions, CTD had a strong

positive correlation with days to maturity (Gautam et al., 2015), confirming that CTD is an effective selection criterion in plant breeding (Seema et al., 2014). Leaf area having more greenness and CTD are strongly interrelated in wheat and with grain yield, grain-filling duration, and biomass (Kumari et al., 2013). Stay-green genotypes have high CTD values due to transpirational cooling, resulting in lower canopy temperatures (Reynolds et al., 1994; Fischer et al., 1998). In stay-green lines, low CTD values delayed senescence (Kumari et al., 2013). Leaf width in wheat had a high correlation with canopy temperature under heat stress (Mohammadi et al., 2012). In durum wheat, CTD had a positive correlation with biological yield and spike number/m² at first spikelet emergence and 50% inflorescence stages. At three growth stages (first spikelet emergence, 50% inflorescence, and completion of anthesis), harvest index had a negative correlation with CTD (Bahar et al., 2008). Screening of Indian and CIMMYT wheat germplasm for the stay-green trait and CTD revealed higher CTD values in the stay-green genotypes due to transpirational cooling and lower canopy temperatures (Kumari et al., 2013). In wheat (*Triticum aestivum*), heat stress reduced CTD by 39.7% at the grain-filling stage (Joshi et al., 2016). Timely sown wheat had higher CTD than late-sown wheat (Saxena et al., 2016), with genotypes HD2932, HD2864, HD3095, HI8703, and HUW234 identified as heat-tolerant due to their higher net photosynthesis, relative water content, membrane stability index and CTD than the other tested genotypes (Saxena et al., 2016). Additional management factors, such as the use of farmyard manure and NPK, improved physiological traits (light interception, CTD, and flag leaf chlorophyll content) in wheat (Badaruddin et al., 1999). In seven rice varieties, CTD was closely related to stomatal conductance and leaf photosynthetic rate (Takai et al., 2010). Rice varieties Takanari and TUAT1-5-6a had lower leaf temperatures and higher stomatal conductance and leaf photosynthetic rates than the other varieties tested under cloudy conditions. Infrared thermography, as a simple method of evaluating varietal differences in stomatal conductance via CTD, is feasible even under cloudy conditions. In chickpea, water potential, osmotic pressure, relative leaf water content, and seed yield had a negative correlation with CTD (Sharma D. K. et al., 2015). Heat-tolerant chickpea genotypes ICCVs 95311, 98902, 07109, and 92944 had higher CTD than sensitive genotypes ICCVs 07116, 07117, and 14592, which had negative CTD values (Devasirvatham et al., 2015). In mungbean, CTD had a significant positive correlation with seed yield, and a negative correlation with root traits, such as lateral branch number and dry root weight (Raina et al., 2019). Greater pod number and pod to node ratio was associated with CTD in pea (Tafesse et al., 2019). In cotton, the involvement of CTD in heat tolerance was indicated (Cornish et al., 1991), with additive, dominance, and epistatic components involved in its inheritance (Khan et al., 2014). In another study on cotton, crop development stage had no effect on CTD, which was significantly correlated with seed yield (Karademir et al., 2018). Canopy temperature in cotton increased under combined heat and drought stress treatment (>36°C and 35% irrigation) (Carmo-Silva et al., 2012), as compared to control. Low canopy temperature was noticed in cotton cultivar Pima S-6 (S6),

which was reported as tolerant, unlike high canopy temperature in Monseratt Sea Island (MS), termed as sensitive, under combined stress.

Stomatal Conductance

Under heat stress, regulating the transpirational mechanisms is a possible strategy for selecting heat-tolerant varieties (Condon et al., 2007). As leaves open their stomata, the rate of gaseous exchange may create differences in stomatal behavior that can be recorded by a leaf porometer (Chandra et al., 2017; Priya et al., 2018). Fully opened stomata increase the diffusion of CO₂ and, at the same time, increase transpiration and photosynthetic efficiency in wheat (Condon et al., 2007). Consequently, stomatal regulation is an important factor that governs plant growth and survival. Therefore, stomatal conductance (g_s) is a useful trait for determining photosynthetic and transpiration rates. Stomatal conductance increases with rising temperature (Urban et al., 2017). Crawford et al. (2012) suggested that plants acclimatize to high temperatures by evaporating more water, thereby keeping their canopies cool despite the presence of fewer stomata. Similarly, semi-dwarf spring wheat cultivars had strong positive correlations between g_s and photosynthetic rate, cooler canopies and yield (Fischer et al., 1998). Heat-tolerant advanced cotton lines (e.g., Pima S-6) developed by Cornish et al. (1991) had higher stomatal conductance and photosynthetic rates under heat stress, which was possibly due to cooling effect of plants through stomata. The stomatal conductance of 50 cotton genotypes was measured under high temperature (45–50°C/20–30°C day/night) in a glasshouse, and identified five heat-tolerant genotypes (NIAB-111/2, BH-160, MNH-554, N-313, BH-163, Mutant-94) (Khan et al., 2008). Similarly, 41 wheat lines of different origin were screened for higher g_s , which was associated with heat tolerance (36/30°C for 1 week) (Sharma K. D. et al., 2015). Heat-tolerant genotypes with high g_s also had higher photosynthetic efficiency under severe heat stress; therefore, this trait acts as a useful genetic tool for developing heat tolerance. Stomatal conductance increased in heat-stressed tomato plants, relative to control conditions (Camejo et al., 2005). In another study, heat-tolerant tomato genotypes maintained higher stomatal conductance under stressed conditions (36/28°C), relative to the control (26/18°C). Further, heat stress severely affected stomatal anatomy and stomatal number in heat-sensitive genotypes, relative to heat-tolerant genotypes (Zhou et al., 2015).

Multiple screening parameters, including stomatal conductance, were used to screen 15 common bean genotypes for heat tolerance in a greenhouse chamber (Traub et al., 2018). Five genotypes—SB761, SB776, SB781, Jaguar, and TB1—were screened at three temperature regimes (35/30, 40/35, 45/40°C). Stomatal conductance increased with increasing temperature until 40/35°C—after which, it declined—genotype TB1 had the highest values for stomatal conductance. In mungbean genotypes, g_s increased up to 40/30°C but declined significantly under heat stress at 43/30°C and 45/32°C, contributing to a rise in leaf temperature (Kaur et al., 2015). In another study on mungbean, g_s was used to differentiate between heat-tolerant and heat-sensitive genotypes (Sharma et al., 2016). Using a similar approach, Sita et al. (2017a) identified heat-tolerant lentil

genotypes (IG2507, IG3263, IG3745, IG4258, and FLIP2009) on the basis of stomatal conductance, with g_s increasing with increasing temperature up to 38/28°C in heat-tolerant genotypes. Heat-tolerant genotypes also had higher g_s values under late-sown than normal-sown conditions; in contrast, heat-sensitive genotypes were unable to maintain higher g_s under heat stress. In chickpea, heat-tolerant (ICC1356, ICC15614) and heat-sensitive genotypes (ICC4567, ICC5912) genotypes were selected on the basis of leaf and seed traits (Awasthi et al., 2014)—heat-tolerant genotypes maintained higher stomatal conductance and photosynthetic function than heat-sensitive genotypes under similar conditions and produced more seed yield. Evaluation of three varieties of tomato (Nagcarlang, Hybrid 61 and Moskvich) against combined heat and drought stresses (25–45°C; 20% irrigation; 2 days), revealed that genotype Hybrid 61 performed better by maintaining higher stomatal conductance and having lower leaf temperature than other two varieties (Nankishore and Farrell, 2016), suggesting this trait to be useful even under stress combinations.

Carbon Isotope Discrimination (CID, $\Delta^{13}\text{C}$)

Carbon isotope discrimination has become an important tool for interpreting photosynthetic rate and water use efficiency (WUE) in plant species (Sheshshayee et al., 2003; Bindumadhava et al., 2011). ¹²C (98.89%) and ¹³C (1.11%) are the two stable carbon isotopes (non-radioactive) in the global carbon pool. Small but significant amount of ¹³C (heavy isotope) incorporated in the organic and inorganic matter during CO₂ fixation by carboxylating enzymes. These small differences in ¹³C abundance are expressed as Carbon isotope ratio and analyzed with isotope ratio mass spectrometer (IRMS) (Farquhar et al., 1989). Composition of carbon isotopes in plant tissue samples show photosynthetic ability governed by RuBisCO in mesophyll tissues (Bindumadhava et al., 2005, 2011, Impa et al., 2005). Lower values of CID represent lower stomatal conductance (limited diffusion of CO₂) and vice versa (Bindumadhava et al., 2011). Further, under high temperature, leaf water status declines due to reduced root hydraulic conductivity, resulting in stomatal closure (Hairat and Khurana, 2016). Therefore, lower CID values at high temperature can be ascribed to indicate declined root absorption and stomatal closure. In barley, carbon-13 discrimination is a useful indicator of high yield (Craufurd et al., 1999), and could be a sound screening parameter for identifying heat-tolerant genotypes. Heat-tolerant (C306, K7903) and heat-sensitive (HD2329) wheat genotypes were identified from CID values and other physiological traits. The heat-tolerant genotypes had higher mean CID values at high temperature (42°C) than the heat-sensitive genotypes. This study demonstrated that the heat-tolerant genotype maintained stomatal opening by accumulating osmolytes, such as proline, to maintain osmotic pressure for water absorption (Hairat and Khurana, 2016).

Photosynthetic Pigments

Heat stress negatively affects photosynthesis by decreasing leaf pigment content and damaging leaf ultrastructure. Chloroplasts

play a vital role in photosynthesis as one of the most heat-sensitive organelles (Krause and Santarius, 1975; Ogwen et al., 2008; Abdelmageed and Gruda, 2009). Decreases in total chlorophyll content and changes in the chlorophyll a/b ratio have been correlated with reductions in photosynthesis during heat stress, due to reduced “antenna (pigment units)” size and thus reduced light-harvesting (Blum, 1986; Harding et al., 1990; Shanmugam et al., 2013). The stay-green (SGR) trait, or delayed leaf senescence, is a crucial trait that allows plants to retain leaves in an active photosynthetic state under high temperature to maintain the assimilation process and increase crop yield (Gregersen et al., 2013; Kumari et al., 2013). Stay-green rice genotypes exhibited high photosynthetic activities under heat stress, resulting in high yields (Jagadish et al., 2015).

Chlorophyll content is an integrative trait that is correlated with stomatal conductance, photosynthetic rate, and transpiration (Del Blanco et al., 2000; Netto et al., 2005), and considered a good criterion for screening for heat-stress tolerance. In the current era of global climate change, introduction of the SGR trait is vital for developing heat-resistant cultivars (Kumari et al., 2013). The SGR trait has been linked to increased yield production in many crops under heat stress, including wheat, barley, rice, maize, and cowpea (Kumari et al., 2007; Borrell et al., 2014; Kobata et al., 2015; Gous et al., 2016; Abdelrahman et al., 2017). The stay-green trait has helped to identify heat-tolerant wheat cultivars that maintain yields at high temperatures (Vijayalakshmi et al., 2010). A significant correlation was detected between heat tolerance and the stay-green trait in 936 elite wheat genotypes (Kumari et al., 2007), suggesting that delayed senescence is an essential selection criterion for heat adaptability. The stay-green characteristic of wheat cultivar Mairaj-2008 was correlated with higher grain yield under heat stress than other lines that lacked the stay-green trait (Nawaz et al., 2013). Genotypes with delayed leaf senescence or stay-green traits have been associated with thermotolerance, due to the longer grain-filling period and thus higher yields, relative to genotypes lacking these traits (Reynolds et al., 1997; Vijayalakshmi et al., 2010). Delayed leaf senescence enhances the transpiration use efficiency, resulting in higher yields. Thus, the stay-green trait is beneficial for retaining active photosynthesis under heat stress (Bavei et al., 2011).

The stay-green trait was used to identify three promising heat-tolerant wheat genotypes [CB-367 (BB#2/PT//CC/INIA/3/ALD“S”), CB-333 (WL 711/3/KAL/BB//ALD “S”), and CB-335 (WL711/CROW “S”//ALD#1/CMH 77A)] based on maximum grain development and survival under heat stress (32°C for 4 weeks) (Rehman et al., 2009). Two recombinant inbred lines (RILs) of wheat, SB062 and SB003, were exposed to 7-day heat shocks (32.7/21.6°C day/night) in a growth chamber during the vegetative or reproductive stage. SB062 maintained leaf greenness for longer than SB003 under heat stress and identified as heat-tolerant; in addition, delayed leaf senescence appeared to play a role in maintaining grain size in SB062 under heat stress (Ullah and Chenu, 2019). Lu et al. (1997) suggested that higher stomatal conductance and photosynthetic rate are functionally important for higher heat tolerance and yields.

A high temperature (38/28°C) treatment for 6 days under controlled conditions in a greenhouse modified chlorophyll content in two contrasting maize genotypes; DTPYC9F119 maintained higher leaf chlorophyll content (identified as heat-stress tolerant) than K64R (identified as heat-stress susceptible) (Debnath et al., 2016; Singh et al., 2020). In another study, 12 barley genotypes were exposed to heat stress (> 40°C) for 107–119 days in the field—genotypes L3, L6, L8, and L10 had longer stay-green duration and higher yields under heat stress than the other genotypes. Fifteen cotton genotypes were screened for thermotolerance (40°C) in the field—genotypes AGC375 and AGC208 were identified as heat-tolerant based on their chlorophyll content (Karademir et al., 2012). In a similar study, cotton genotype Sicot 53 had higher thermotolerance than Sicala 45 (Cottee et al., 2007). In rice, cultivar N44 was identified as heat-tolerant (exposed to 38°C for 25 days in the field during the reproductive stage), with its higher chlorophyll content under heat stress than N-22 (Bahuguna et al., 2015).

Chlorophyll content was used to screen for heat tolerance in several lentil genotypes after exposure to heat stress (>32/20°C) in a growth chamber at the vegetative and reproductive stage. Heat-tolerant genotypes IG3263 and IG2507 had more chlorophyll than heat-sensitive genotypes IG4242 and IG3964, which was positively correlated with yield (Sita et al., 2017a). In chickpea, genotypes were selected for heat tolerance based on the SGR trait; plants were exposed to gradual increasing temperatures (2°C per day) from 27/18°C to 42/25°C day/night for 8 days in a growth chamber; at which time, genotype ICC16374 (heat-sensitive) had lower leaf chlorophyll content than JG14 (heat-tolerant) (Parankusam et al., 2017). Likewise, Kaushal et al. (2013) identified two heat-tolerant (ICC15614, ICCV92944) and two heat-sensitive (ICC10685, ICC5912) chickpea genotypes based on chlorophyll content, after exposure to heat stress (>32°C/20°C) in the field during reproductive development. The stay-green trait could be used as a morphological indicator for thermotolerance in tomato, as in wheat (Sharma D. K. et al., 2015; Zhou et al., 2015). The stay-green trait contributes to high yield in tomato exposed to heat stress (Zhou et al., 2015). Tomato’s ability to stay-green and maintain photosynthesis during heat stress at different developmental stages, especially anthesis, could be vital for reproductive growth and yield (Zhou et al., 2017). Heat-sensitive tomato genotypes do not stay-green under heat stress due to the decline in chlorophyll and carotenoid contents, and show early chlorosis and withered leaves (Vijayalakshmi et al., 2010; Zhou et al., 2015).

Chlorophyll Fluorescence

Chlorophyll fluorescence (F_v/F_m ratio) is a relatively sensitive indicator of direct or indirect effects of abiotic stress on photosynthesis (Schreiber and Bilger, 1993). The relationships between primary photosynthetic reactions and chlorophyll fluorescence are crucial as they provide information on the plant’s photosynthetic capability and its acclimation capacity under stressful environmental conditions (Lichtenthaler, 1987; Kalaji et al., 2018). Of the photosynthetic apparatus, photosystem II (PSII) is the most heat-labile cell structure (Vacha et al., 2007). As damage to PSII is often the first response when plants are

subjected to heat stress, PSII response studies can reveal the primary effects of heat stress on plants (Mathur et al., 2011; Van der Tol et al., 2014); measuring chlorophyll *a* fluorescence is an effective and non-invasive technique to identify damage to PSII efficiency (Baker and Rosenqvist, 2004; Baker, 2008). The ratio between variable fluorescence (F_v) and maximum fluorescence (F_m), or F_v/F_m , reflects the maximum quantum efficiency of PSII (Butler, 1978), and is one of the most heat-affected fluorescence parameters. A decline in F_v/F_m is frequently observed when plants are subjected to abiotic stress, including heat (Willits and Peet, 2001; Molina-Bravo et al., 2011; Sharma et al., 2012). There is a negative linear correlation between F_v/F_m and the maximum quantum yield of photosynthesis, when measured as O_2 evolution (Demmig and Björkman, 1987; Kao and Forseth, 1992) and CO_2 fixation (Ogren and Sjöstrom, 1990). Screening methodologies using chlorophyll fluorescence to detect and quantify damage in photosystem II (PSII) and thylakoid membranes in response to temperature stress have been used in several cereal crops, including barley (Rizza et al., 2011), wheat (Balouchi, 2010), maize (Sinsawat et al., 2004), legume crops [chickpea, groundnut, pigeon pea (*Cajanus cajan*), and soybean] (Srinivasan et al., 1996; Herzog and Chai-Arree, 2012), and horticultural crops, including strawberry (*Fragaria ananassa*) (Ledesma et al., 2004; Kadir et al., 2006), tomato (Willits and Peet, 2001), grapes (*Vitis vinifera*) (Kadir et al., 2007), and various tropical and subtropical fruits (Yamada et al., 1996; Weng and Lai, 2005). Therefore, chlorophyll fluorescence is a promising tool for detecting stress-induced injuries and thermotolerance (Méthy et al., 1994) but its successful implementation in crop breeding programs requires careful selection of suitable fluorescence parameters (Malaspina et al., 2014).

Heat-tolerant wheat lines with tolerance to high temperatures during grain filling had greater F_v/F_m ratios than heat-sensitive lines in warmer irrigated environments, which were linked to higher grain yield (Shefazadeh et al., 2012). The physiological state of thylakoid membranes, as determined by chlorophyll *a* fluorescence, identified heat-tolerant wheat cultivars with high chlorophyll fluorescence (Ristic et al., 2007). Various wheat lines were exposed to heat stress for 3 days at 40°C in controlled conditions; the lines having high chlorophyll fluorescence (F_v/F_m 0.836)—830, 1313, 1039, 1223—were less sensitive to heat in terms of growth and photosynthesis than the other lines, and were identified as heat-tolerant (Sharma et al., 2014). Similarly, genotypic variation for chlorophyll fluorescence parameters exists in rice under heat stress (29°C for 25 days at anthesis) in a growth chamber; N22 genotype maintained high F_v/F_m (0.75) under heat stress, and was identified as heat-tolerant, relative to the low F_v/F_m (0.70) in Vandana (Sailaja et al., 2015). Modified chlorophyll fluorescence imaging was used to screen 20 wild barley (*Hordeum spontaneum*) genotypes exposed to heat stress (45°C, 1 h) in growth chambers, and identified HOR10478 as the most heat-sensitive and HOR12818 as the most heat-tolerant genotypes (Jedmowski and Brüggemann, 2015). Oukarroum et al. (2016) also differentiated heat tolerance in 10 varieties of barley. After 2 weeks of growth, detached leaves were exposed to a short-term heat treatment at 45°C for 10 min in a growth chamber, which decreased chlorophyll fluorescence; notably, varieties Ig,

Im, and Tz had high chlorophyll fluorescence (heat-tolerant) and Ma, Ra and I_{gr} had low chlorophyll fluorescence (heat-sensitive).

In many legumes, chlorophyll fluorescence has been used to identify genotypes that tolerate heat stress. In lentil, photosynthetic efficiency was measured as PSII function (F_v/F_m ratio) in a natural environment by exposing plants to heat stress (above 32/20°C) during the reproductive stage. Heat-tolerant genotypes—IG2507, IG3263, IG3297, IG3312, IG3327, IG3546, IG3330, IG3745, IG4258, and FLIP2009—maintained high chlorophyll fluorescence (F_v/F_m 0.71) under heat stress, relative to heat-sensitive genotypes—IG2821, IG2849, IG4242, IG3973, IG3964—which had the lowest F_v/F_m values (0.58) (Sita et al., 2017a). Nine common bean lines were measured for changes in chlorophyll fluorescence under heat stress at flowering (2 h at 45°C) in a greenhouse; thermotolerant lines 83201007 and RRR46 had higher F_v/F_m values under heat stress than the heat-sensitive line Secuntsa (Petkova et al., 2009). In another study, 12 varieties and lines of common bean were exposed to 42°C in the field during the reproductive period; two genotypes (Ranit and Nerine) maintained F_v/F_m values at 42°C, relative to the controls at 26°C, and were considered heat-tolerant. These two genotypes also showed good productivity and quality and can be used as parental lines in bean breeding programs (Petkova et al., 2007). Likewise, 41 mungbean lines were grown outdoors and exposed to high temperatures (>40/28°C) during the reproductive stage; several promising heat-tolerant lines (EC693358, EC693357, EC693369, Harsha, and ML1299) were identified, with high F_v/F_m ratios (0.73–0.75 units) compared to sensitive lines (0.61–0.67 units), which would not only serve as useful donor/s for breeding programs, but also as suitable base plant source to gain insight into heat-stress-induced effects in cell metabolism (Sharma et al., 2016). In chickpea, heat stress (>30°C) in the field during the reproductive stage reduced F_v/F_m more (0.48, 0.41) in two heat-sensitive genotypes ICC10685 and ICC5912, than in two heat-tolerant genotypes ICC15614 and ICCV92944 (0.64, 0.60) (Kaushal et al., 2013; Awasthi et al., 2014). A field experiment conducted in two winter seasons at three locations with known differences in temperature in NE South Africa, involving four chickpea genotypes, showed that two genotypes, which were tolerant to heat stress had chlorophyll fluorescence (F_v/F_m) of 0.83–0.85 at the warmer site, while the two sensitive genotypes showed lower F_v/F_m of 0.78–0.80; these values correlated positively with grain yield. The two tolerant genotypes had higher photosynthetic rates, starch, sucrose and grain yield than the sensitive genotypes at the warmer site. The observation revealed that chlorophyll fluorescence and leaf carbohydrates are suitable tools for selection of heat tolerant chickpea genotypes under field conditions (Makonya et al., 2019). Screening of 15 alfalfa (*Medicago sativa* L.) genotypes by exposing seedlings to 38/35°C day/night for 7 days in a growth chamber identified Bara310SC (F_v/F_m 0.79) and WL712 (F_v/F_m < 0.79) as heat-tolerant and heat-sensitive cultivars, respectively (Wassie et al., 2019), showing that F_v/F_m is an effective tool for phenotyping contrasting genotypes for heat tolerance.

The heat susceptibilities of 67 tomato genotypes were evaluated in a climate chamber—the genotypes with higher F_v/F_m under heat stress (36/28°C for 4 days or 40°C for 7 h),

maintained their physiological status, relative to genotypes with lower F_v/F_m (Zhou et al., 2015). The two genotypes with the highest F_v/F_m ratios (heat-tolerant group; T1, T2; 0.82, 0.80 units) and two with the lowest F_v/F_m ratios (heat-sensitive group; S1 and S2; 0.74, 0.77 units) were selected for further study (Zhou et al., 2015). Another study screened wild genotypes and cultivars of tomato in a growth chamber at 33°C—wild tomato varieties Pe and Pr1 had the highest temperature stress tolerance with high F_v/F_m ratios (0.56, 0.58), while the cultivated species were more sensitive to temperature stress with lower F_v/F_m ratios (0.28, 0.38) (Zhou et al., 2018).

Chlorophyll fluorescence was used to screen cotton landraces—6-week-old cotton plants were subjected to heat stress at 45°C in a growth chamber to determine thermotolerance in terms of photosynthetic ability, independent of agronomic yield and productivity. Three genotypes (TX2287, TX2285, and TX761) maintained high photosynthetic efficiency (F_v/F_m 0.57), relative to sensitive genotype (F_v/F_m 0.46) (Wu et al., 2014). In another growth chamber study, a commercial set of eight cotton genotypes was screened for heat tolerance by subjecting to heat stress (>35°C); four genotypes (SG215BR, ST474, and DP444BG/RR) had relatively high F_v/F_m indicating that they suffered less from stress, while Sphinx and Acala Riata had low F_v/F_m , indicating temperature sensitivity (Bibi et al., 2004). In a related study, screening of 15 cotton genotypes for thermotolerance (40°C) in the field identified genotypes AGC375 and AGC208 as heat-tolerant, based on their superior chlorophyll fluorescence (Karademir et al., 2012). Imposing combined drought and heat stress significantly affected the photosynthetic efficiency of chickpea (*Cicer arietinum*) genotypes, in a study conducted in outdoor conditions at two different sowing times [November (<32–20°C at the time of reproductive stage; control) and in February (>32–20°C at the time of reproductive stage; heat stress during pod filling)], while drought was applied during both sowing times during pod filling (at ~75% podding) by withholding water until maturity. The photosynthetic efficiency (F_v/F_m) of the leaves decreased more in plants subjected to drought stress (54–74%) than to heat stress alone (9–46%) and the combined heat + drought stress treatment showed the greatest reduction in photosynthetic efficiency (68–83%), with the smallest reduction occurring in the drought-tolerant genotype (ICC8950), compared to drought- and heat sensitive genotypes (Awasthi et al., 2017).

Photosynthetic Rate

Heat stress affects plant characteristics such as the stay-green trait, chlorophyll content, and chlorophyll fluorescence, which influences the photosynthetic rate (Sharkey, 2005). Hence, photosynthetic rate can be used as a screening parameter for the selection of heat-tolerant genotypes. Variation in photosynthetic rate among plant species in response to heat stress has been well-documented. For example, a heat-shock treatment (45°C for 2 h at the fourth true leaf stage) reduced the net photosynthetic rate (P_n) of two tomato cultivars, more so in Campbell-28 (heat-sensitive) than wild Nagcarlang (heat-tolerant) (Camejo et al., 2005). High temperature deactivates RuBisCo, which could be involved in reducing photosynthetic

rate (Sharkey, 2005). Another study on tomato compared the P_n of one cultivated (Ly from *Solanum lycopersicum*) and six wild (Ha from *S. habrochaites*, Pe from *S. pennellii*, Pi1 and Pi2 from *S. pimpinellifolium*, Pr1 and Pr2 from *S. peruvianum*) genotypes grown at high temperature (33°C) in a growth chamber—Ly, Ha, Pi1, and Pi2 had lower P_n than the control, while Pe, Pr1, and Pr2 showed higher P_n indicating their heat tolerance (Zhou et al., 2018). Plants of the tomato cultivar “Liaoyuanduoli” grown in greenhouse exposed to heat stress (35°C after 15 DAS led to a significant change in photosynthetic apparatus as damage of chloroplast membrane and at the same time, the thylakoids loosely distributed with lesser grana, thus, changed chloroplast ultrastructure might have declined the P_n (Zhang et al., 2014). In rice, heat tolerant genotype (N22) could maintain photosynthetic activity for a longer time after anthesis and thus could produce higher grain weights, compared to heat-sensitive genotypes (IR20, IR53, IR46) (Gesch et al., 2003).

Soybean cultivars (IA3023 and KS4694) and PI lines (PI393540 and PI588026A) expressed heat tolerance and susceptibility with high and low P_n , respectively (Djanaguiraman et al., 2019). The soybean cultivars had less thylakoid membrane damage than the PI lines. In an earlier study on soybean genotype K03–2897, high-temperature stress (38/28°C) for 14 days at the flowering stage significantly decreased leaf P_n , due to anatomical and structural changes (increased thickness of palisade and spongy layers and lower epidermis) in cells and cell organelles, particularly damage to chloroplasts and mitochondria (Djanaguiraman and Prasad, 2010). Two heat-tolerant chickpea genotypes (Acc#RR-3, Acc#7) had higher P_n than two heat-sensitive genotypes (Acc#2, Acc#8) at high temperature (35/30°C), which may have been due to increased RuBisCo activity (Makonya et al., 2019). In another chickpea study, 56 genotypes were exposed to high temperatures in the field from the flowering stage to crop maturity (maximum temperatures 25–40°C)—the tolerant genotypes (PUSA1103, PUSA1003, KWR108, BGM408, BG240, PG95333, JG14, BG) had higher P_n than the sensitive genotypes (ICC1882, PUSA372, PUSA2024) (Kumar et al., 2017). Similarly, the response of four chickpea genotypes to a natural temperature gradient in the field at the flowering stage identified two heat-tolerant genotypes (Acc#RR-3, Acc#7) with high P_n and two heat-sensitive genotypes (Acc#2, Acc#8) with lower P_n ; these results were validated in a climate chamber experiment set at 30/25°C and 35/30°C (Makonya et al., 2019). Improvement of heat stress tolerance by stabilizing PSII system through introducing *IbOr* gene in transgenic potato (Goo et al., 2015), sweet potato (Kang et al., 2017), and in alfalfa (Wang et al., 2015) is worth mentioning. Heat, drought and their combination limited the Photosynthetic rate of lentil (*Lens culinaris* Medikus), particularly during reproductive growth and seed filling. In recent study eight lentil genotypes two drought-tolerant (DT; DPL53 and JL1), two drought-sensitive (DS; ILL 2150 and ILL 4345), two heat-tolerant (HT; 1G 2507 and 1G 4258) and two heat-sensitive (HS; 1G 3973 and 1G 3964) sown at the normal time (November), at the time of seed filling (30/20°C), or sown late (February) to impose heat stress (> 30/20°C (day/night) and drought maintained by water withheld (50% of field capacity) from the start of

seed filling to maturity. The photosynthetic rate (Pn) decreased significantly more under drought stress (33.4–56.6%) than heat stress (13.3–43%), as compared to the control plants. Under the combined stress, Pn declined more (57–82% reduction), less so in the heat and drought tolerant genotypes compared to sensitive (Sehgal et al., 2017).

Sucrose

Leaf photosynthates are largely transported to sink organs in the form of sucrose, and sucrose synthase (SS) is a key enzyme for sucrose to enter a variety of metabolic pathways (Lu et al., 2005). Down-regulation of SS indirectly inhibits carbohydrate production, eventually reducing yield and quality. Maintaining sucrose levels is vital during stressed conditions, which depend on its synthesis and hydrolysis. Heat-stressed plants had significant reductions in the activity of key enzymes—sucrose phosphate synthase (SPS) and SS—involved in sucrose synthesis. The availability of sucrose to reproductive organs is crucial for sustaining their function (Kaushal et al., 2013). Heat-tolerant genotypes are expected to stabilize the photosynthetic process better than heat-sensitive genotypes. Measuring sucrose concentrations reveals the photosynthetic status of plants under heat stress (Awasthi et al., 2014). A large core-collection of chickpea genotypes screened for heat tolerance (32/20°C) in a natural environment identified two heat-tolerant (ICC15614, ICCV92944) and two heat-sensitive (ICC10685, ICC5912) genotypes. The heat-sensitive genotypes had significantly greater inhibition of RuBisCo (carbon-fixing enzyme), SPS, and SS than the heat-tolerant genotypes, and thus produced less sucrose than the tolerant genotypes (Kaushal et al., 2013). Heat-sensitive genotypes produced far less leaf sucrose than heat-tolerant genotypes, which impaired its supply to developing reproductive organs (flowers, pods, and seeds) in sorghum (Prasad and Djanaguiraman, 2011), tomato (Li et al., 2012), and chickpea (Kaushal et al., 2013).

In wheat, heat-tolerant genotypes (PBW343 and C306) exposed to heat stress (>25°C) in the field had higher SS activity and thus higher sucrose contents in grain than heat-sensitive genotypes (PBW521, PBW522) (Bavita et al., 2012). Limitations in sucrose supply may disrupt the development and function of reproductive organs (Prasad and Djanaguiraman, 2011; Snider et al., 2011). In lentil, sucrose production is vital for leaf and anther function, and has been correlated with SPS activity in natural high-temperature environments (> 32/20°C). Heat-tolerant lentil genotypes (IG2507, IG3263, IG3297, IG3312, IG3327, IG3546, IG3330, IG3745, IG4258, and FLIP2009) produced more sucrose in their leaves (65–73%) and anthers (35–78%), than heat-sensitive genotypes (IG2821, IG2849, IG4242, IG3973, IG3964), which was associated with superior reproductive function and nodulation in tolerant genotypes (Sita et al., 2017a). Thus, heat stress negatively affects sucrose metabolism due to the inhibition of carbon fixation and assimilation (Awasthi et al., 2014). Sucrose concentrations in leaves and anthers and SS and SPS activities declined significantly in two mungbean genotypes (SML832 and SML668) exposed to heat stress (>40/25°C day/night) outdoors and in a controlled environment, more so in SML668 (heat-tolerant)

than SML832 (heat-susceptible) (Kaur et al., 2015). Tomato cultivars exposed to heat stress in growth chambers (31/25°C day/night) or greenhouses (32/26°C day/night) revealed four genotypes (FLA7516, Hazera3018, Hazera3042, and Saladate) as heat-tolerant with high sucrose contents in the mature pollen grains, and three genotypes (Grace, NC8288, and Hazera3017) as heat-sensitive, with 50% less sucrose than the tolerant genotypes (Firon et al., 2006).

Expression of the sucrose transporter gene, OsSUT1, is important for maintaining photo-assimilate supply to grains. In rice exposed to high-temperature stress (31/26°C) in a glasshouse, cultivar Genkitsukushi (heat-tolerant) had higher expression of OsSUT1 in stems than Tsukushiroman (heat-sensitive), indicating that sugar transport is more effective in Genkitsukushi than Tsukushiroman under heat stress, which improves grain quality (Miyazaki et al., 2013).

BIOCHEMICAL TRAITS

Heat sensitivity is linked to the expression of several cellular molecules, including antioxidants (Wilson et al., 2014), HSPs (Xu et al., 2011) osmolytes (Bitra and Gerats, 2013), and phytohormones (Sharma et al., 2020). These molecules assist cells to adapt, repair, and survive in adverse temperature environments; hence, measuring the extent of their expression in contrasting genotypes grown under heat stress might reveal mechanisms regulating the heat response.

Oxidative Stress and Antioxidants

Heat stress negatively affects cellular metabolism due to extensive ROS production that can severely damage lipids, proteins, and nucleic acids (Bitra and Gerats, 2013). Plants protect themselves from ROS production by activating enzymatic and non-enzymatic processes (Bitra and Gerats, 2013). The main ROS-scavenging enzymes are superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), ascorbate peroxidase (APX), and glutathione reductase (GR), and the non-enzymatic system includes ascorbic acid (ASC) and glutathione (GSH) (Suzuki et al., 2012). Genotypes can be selected based on their enzyme expression level, with more prominent activities among heat-tolerant than heat-sensitive genotypes (Kumar et al., 2013). Genotypes respond differently to heat stress due to variation in their antioxidant systems. Hence, this trait is useful for identifying heat-tolerant genotypes.

Two tomato cultivars differing in heat sensitivity (Sufen14, Jinlingmeiyu) were raised in a greenhouse in optimum temperature (26/18°C) and heat-stressed (38/30°C for 6 days with 2 days recovery). Jinlingmeiyu had lower activities of SOD, POD, APX, and MDA (malondialdehyde) and lower proline content than Sufen14, suggesting the involvement of these enzymes in imparting heat tolerance in Sufen14 (Zhou et al., 2019). Categorization of 50 *Brassica juncea* genotypes into tolerant, moderately tolerant and susceptible genotypes after exposure to 45°C was based on oxidative damage tolerant genotypes had less lipid peroxidation and higher POD, CAT, and GR activities than moderately tolerant and susceptible

genotypes (Wilson et al., 2014). In contrast, *Brassica juncea* seedlings grown under optimum (25°C) and high (45°C) temperatures had higher MDA and lipoxygenase (LOX) activities of antioxidants (SOD, CAT, POX, APX, and GR) in the thermosensitive genotype (NPJ-119) than the thermotolerant genotype (NRCDR-02) suggesting variations in the response of antioxidants, which might be stage- or plant-specific (Rani et al., 2012). Wheat genotypes were differentiated into heat-tolerant (C306), intermediate heat-tolerant (HD2285), and heat-sensitive genotype (HD2329) by subjecting them to heat stress (8 and 23 days after anthesis) by delaying the sowing time: C306 had higher relative water content, ASC, APO, CAT, and SOD and lower lipid peroxidation and H₂O₂ content than HD2285 and HD2329 (Sairam and Srivastava, 2000).

In chickpea plants raised under natural conditions and heat stressed at 50% flowering (30/20, 35/25, 40/30, and 45/35°C) in growth chambers, tolerant genotypes (ICCV07110, ICCV92944) had lower MDA concentration and H₂O₂ content than sensitive genotypes (ICC14183, ICC5912), which was attributed to their higher activity levels of APX, GR, and ASC (Kumar et al., 2013). Forty-one mungbean genotypes exposed to heat stress (>40/28°C) in the field revealed that heat-tolerant genotypes (EC693357, EC693358, EC693369, Harsha, and ML1299) suffered less oxidative damage (1.52–2.0-fold increase MDA; 1.59–1.96-fold increase H₂O₂) than sensitive genotypes (2.2–2.4-fold increase MDA; 2.21–2.93-fold H₂O₂) (Sharma et al., 2016). The heat-tolerant genotypes also significantly increased APX activity (by 1.48–1.77-fold), relative to susceptible genotypes (1.27–1.37-fold) and similar response was observed for GR activity. However, heat-tolerant and heat-sensitive genotypes had similar increases in CAT activity. Similarly, 38 lentil accessions screened for heat tolerance (>35/20°C) during the reproductive stage revealed less oxidative damage (MDA and H₂O₂ contents increased) and higher SOD, CAT, APX, and GR activities—involved in detoxification—in heat-tolerant genotypes (IG2507, IG3263, IG3745, IG4258 and FLIP2009) than heat-sensitive genotypes (IG2821, IG2849, IG4242, IG3973, IG3964 (Sita et al., 2017a). Concurrence of heat and drought stress will do more damage at the biochemical level. Oxidative damage and antioxidant mechanisms responding toward combined stress were reported in tomato cultivars. Two cultivars of tomato (CV1; Sufen14 and CV2; Jinlingmeiyu) were raised in green house conditions to compare the cultivar difference. Treatment (Heat stress-38/30°C, and drought stress-no irrigation) were given to 28 days old seedlings for six days. Significant increase in ROS such as H₂O₂ and O²⁻ were reported in both the cultivars than control (26/18°C). Their studies showed that CV2 had lower activity of enzymes—peroxidase, ascorbate peroxidase, superoxide dismutase, malondialdehyde (MDA) and proline content than CV1, under combined stress on day 6, clearly depicting cultivar differences with respect to antioxidant activity (Zhou et al., 2019).

Metabolites

Plant metabolites are low molecular weight compounds involved in stress tolerance. They play a crucial role in maintaining the redox homeostasis of cells and stabilizing cell membranes and proteins (Wahid et al., 2007) through

various intermediate/precursor compounds, such as compatible solutes, signaling agents, and antioxidants (Kaplan et al., 2004). Metabolites are categorized into primary and secondary metabolites. Primary metabolites that are specifically upregulated in response to abiotic stress are amino acids (proline), polyamines (spermidine, spermine, putrescine), carbohydrates (sucrose, hexoses, polyhydric alcohols), and glycine betaine. Similarly, secondary metabolites include phenolic compounds (flavonoids, isoflavonoids, anthocyanins), terpenoids (saponins, tocopherols), and nitrogen-containing metabolites (alkaloids and glucosinolates) (Rodziewicz et al., 2014). Under heat stress, plants restructure their metabolites to help the cells to maintain homeostasis via the production of stress-induced compounds (Serrano et al., 2019). Activation of heat-shock factors, such as HSF2 and HSF3, increases the level of metabolites such as galactinol and its derivatives in response to heat stress (Song et al., 2016). Therefore, metabolites may serve as a useful tool for selecting heat-tolerant varieties under high-temperature stress. Comparing heat-tolerant and heat-sensitive genotypes can identify metabolite markers that are constitutively expressed and allow selection of superior germplasm.

Seed metabolomic analysis performed on contrasting soybean genotypes (PI587982A, heat-tolerant; A5279 and DP3478, heat-sensitive) revealed 25 metabolites that differed between genotypes, including tocopherol isoforms, ascorbate precursors, flavonoids, two amino acids, and amino acid derivatives (Chebrolu et al., 2016). At 36°C, 10 flavonoids were more abundant in the seeds of the heat-tolerant genotype than the heat-sensitive genotypes, along with several tocopherols (major antioxidants). Moreover, the heat-tolerant genotype had higher levels of a precursor of L-ascorbic acid biosynthesis—gulono-1,4-lactone—than the heat-tolerant genotypes. Overexpression of these stress-induced compounds provides thermotolerance to soybean seeds, which ultimately perform better in terms of seed vigor, seed germination, seed weight, and oil content. Metabolomic analysis of rice spikelets in a heat-tolerant (N22) and heat-sensitive (Moroberekan) genotype revealed that N22 accumulated more metabolites than Moroberekan, including carbohydrates (glucose 6-phosphate, fructose 6-phosphate, glucose, maltose, and other sugars), compatible solutes, and amino acids (leucine, isoleucine, and valine). N22 had lower levels of trehalose, sugar phosphatases, malic acid, and galactaric acid than Moroberekan under heat stress (Li X. et al., 2015). In wheat, a comparative analysis of metabolites in transgenic wheat (PC₂₇ and PC₅) and its wild type (varying in heat sensitivity), exposed to heat stress (40°C for 4 h) during heading revealed 25 metabolites that were highly expressed in transgenic wheat, including proline, three sugar alcohols (inositol, mannitol, and xylitol), pyruvic acid, and other amino acids (glycine, alanine, serine, valine, and tyrosine) (Qi et al., 2017). The metabolite profiling approach is an effective way to accurately screen and select the best-performing genotypes.

Proline is a multifunctional amino acid with diverse roles in maintaining cellular redox balance by dissipating excess of reducing potential (Rivero et al., 2004). Proline levels are upregulated under stress conditions as its biosynthesis is an adaptive response to reduce excess NADPH produced in response

to the halt in CO₂ fixation in the Calvin cycle due to stomatal closure (Berry and Bjorkman, 1980). Moreover, under stress conditions, proline is involved in osmotic adjustment, ROS scavenging, and as an energy source. Therefore, high proline contents under high-temperature stress can be used to screen heat-tolerant genotypes. Twenty wheat genotypes were screened for heat tolerance by exposing them to 25 or 35°C, and measuring proline content and membrane damage (Ahmed and Hasan, 2011). Heat-tolerant genotypes (Bijoy, Sufi, Kanchan, Fang 60, BAW 1059, BL 1883, BL 1022, IVT 7, IVT 8, IVT 9, IVT 10, and BAW 917) had higher proline contents (>200%) and less membrane damage (<50%) than heat-sensitive genotypes (Shatabdi, PRODIP, BAW 1064, Gourab, Pavon 76, Sonara, Kalyansona, and IVT 6). Thirty-five-day-old seedlings of different cabbage cultivars, including Chinese cabbage and their hybrids, were exposed to two temperature regimes (25 or 35°C) at the flower bud stage and assessed for heat tolerance based on proline contents in stalks, flower buds, and leaves—heat-tolerant cultivars (Yoshin, Kenshin, and full white) had higher proline levels than heat-sensitive cultivars (YR Kinshun, Chihiri 70, and Large leaf) (Hossain et al., 1995). Six cotton cultivars (Sicala, Acala 1517-88, Molopo, Alpha, Delta Pine Acala90, and OR19) were tested for genetic variability against combined heat and drought stress. Stress treatment (Heat stress; 40°C without irrigation for 15 days) were imposed on 3 weeks old seedlings. Stress treatment were increased the proline content in all the genotypes but the accumulation was more in tolerant genotypes (Alpha, Delta Pine Acala90, and OR19) compared to sensitive genotypes (Sicala, Acala 1517-88, Molopo) (De Ronde et al., 2000).

Heat-Shock Proteins

During rapid heat stress, plants synthesize and accumulate specific proteins called heat-shock proteins (HSPs) (Howarth, 1991); this is a universal response to high-temperature stress in all organisms (Vierling, 1991). Heat-shock genes are upregulated during stress to encode HSPs which are vital for plant survival under such conditions (Chang et al., 2007). Three classes of HSPs are distinguished, according to molecular weight—HSP90, HSP70, and low molecular weight proteins. HSPs provide stress-related chaperone functions in plants under stress conditions (Reddy et al., 2010, 2016). Chaperones have a role in protein synthesis, maturation, targeting, degradation, renaturation, and membrane stabilization (Reddy et al., 2014, 2016). HSPs are located in the cytoplasm, nucleus, mitochondria, chloroplasts, and endoplasmic reticulum (Waters et al., 1996). Heat-stress transcription factors (HSFs), located in the cytoplasm in an inactive state, control HSP gene transcription and play a vital role in plant thermotolerance. Specific HSPs have been identified in response to high temperature, including HSP68 in the mitochondria of potato, maize, soybean, and barley (Neumann et al., 1994). The expression profiles of HSPs have been compared in plant species/genotypes contrasting in heat sensitivity. For instance, the higher heat tolerance of maize than wheat and rye at 42°C is correlated with the expression of five mitochondrial low molecular weight HSPs (28, 23, 22, 20, and 19 kDa), as opposed to only 20 kDa in wheat and rye (Korotaeva et al., 2001).

According to Sharma-Natu et al. (2010), HSP18 was upregulated in developing grains of heat-tolerant wheat exposed to 3.2–3.6°C higher temperatures than normal. In other studies, HSP100 increased with heat stress in a tolerant wheat variety (Sumesh et al., 2008). Similarly, HSP26 increased in heat-tolerant wheat genotypes (K7903, C306) at 42°C, relative to heat-sensitive genotypes (PBW343, HD2329) (Hairat and Khurana, 2016). At 42°C, the expression levels of five Hsps—Hsp26.7, Hsp23.2, Hsp17.9A, Hsp17.4, and Hsp16.9A—were upregulated in the heat-tolerant rice cultivar Co39, relative to the heat-sensitive rice cultivar Azucena, and regarded as biomarkers for screening rice cultivars for heat tolerance (Chen et al., 2014). At 40°C, potato cultivar Norchip synthesized small (sm) Hsps for longer than other cultivars. In Norchip and Desiree, an 18 kDa small (sm)HSP increased for up to 24 h, while in cultivars Russet Burbank and Atlantic, the levels started to decline after 4 and 12 h respectively (Ahn et al., 2004). Anthers of a heat-tolerant tomato cultivar had higher constitutive levels of HSP100 than a heat-sensitive cultivar (Pressman et al., 2007). In chickpea, HSP levels increased in genotype JG14 (heat-tolerant) more than genotype ICC16374 (Heat-sensitive) when exposed to 42/25°C at anthesis (Parankusam et al., 2017). Likewise, in peanut, the best-characterized aspect of acquired thermotolerance is HSP production, with ICGS76, COC038, and COC068 selected as heat-tolerant genotypes and COC812, COC166, Tamrun OL 02, and Spanco selected as heat-sensitive (Selvaraj et al., 2011). In another study, heat-tolerant peanut genotype ICGS 44 showed higher HSP expression throughout the stress period than heat-sensitive genotypes AK 159 and DRG 1 (Chakraborty et al., 2018). Comparison of expression of heat shock proteins in wheat cultivars (Katya and Sadovo) under combined heat and drought stress (40°C/56%) reported 100% elevation of HSP100 and HSP70 as compared to 60 and 10% elevation under individual drought and heat stress in tolerant cultivar Katya (Grigorova et al., 2011).

GENE/S EXPRESSION

Relatively few studies have been undertaken on changes in gene expression in contrasting genotypes under heat stress, but vital information has been garnered. In wheat, two contrasting genotypes—Chinese spring (heat-sensitive) and TAM107 (heat-tolerant)—were analyzed for changes in gene expression upon exposure to heat stress (40°C), using Affymetrix Barley 1 GeneChip, and expressed sequence tags. The analysis identified 6550 heat-responsive probe sets, accounting for 11% of the total probe sets (Qin et al., 2008). Heat-tolerant genotype (2199 probe set) had more heat-responsive probe sets than the heat-sensitive genotype (2084 probe set), which mainly belonged to HSPs, transcription factors, calcium and sugar signaling pathways, phytohormones biosynthesis and signaling, ribosomal proteins, RNA metabolism, and primary and secondary metabolites (Qin et al., 2008). In rice, contrasting genotypes N2219379 (heat-tolerant) and IR64 and N226264 (heat-susceptible) were compared for their heat response at 38°C using reproductive function and molecular

approaches (González-Schain et al., 2016). Heat stress impaired reproductive functions, such as pollen production, pollen number, anther dehiscence, pollen germination, and stigma receptivity, more so in the sensitive genotypes than the tolerant genotype (Devasirvatham et al., 2012). Eighteen heat-responsive genes, such as HSFA2a, OsFKBP62b, and OsHSP17.9A had higher upregulation in tolerant genotypes than sensitive genotype. Under heat stress, the expression of HSFA2a increased 268-, 15-, and 3.2-fold in N2219379 (heat-tolerant), N226264 (heat-sensitive), and IR64 (heat-sensitive), respectively and that of OsFKBP62b increased by 108-, 10-, and 3-fold in N2219379, N226264, and IR64, respectively (González-Schain et al., 2016). A study was conducted on 197 spring wheat genotypes from ICARDA at two different locations, one in Sudan (Wad Medani) and another one in Egypt (Sids), to identify single nucleotide polymorphism (SNP) markers association mapping. The study detected 111 significant marker-trait associations; the *w SNP_Ex_c12812_20324622* marker on chromosome 4A was significantly correlated with yield at both locations. Wheat genotypes carrying the cytosine base at the *w SNP_Ex_c12812_20324622* and *w SNP_Ex_c2526_4715978* markers produced more yield, compared to those carrying the alternative bases, by 15%, indicating the significance of involving these markers for marker-assisted selection in breeding programs to increase yield under heat stress. The best performing 20 high-yielding as well as heat-tolerant wheat genotypes, found in this study, have been distributed across Central and West Asia and North Africa (CWANA) and sub-Saharan Africa (SSA) for potential direct release and/or use as parents after local adaptation trials (Tadesse et al., 2019).

DNA methylation is one of the mechanisms of epigenetic modifications that plays a crucial role in imparting stress tolerance for various environmental stresses (Lukens and Zhan, 2007). A study on heat-tolerant (Huyou 2) and heat-sensitive (Fengyou 1) *Brassica napus* seedlings exposed to 45°C measured changes in DNA methylation levels and the cytosine methylation pattern using Methylation Sensitive Amplification Polymorphism (MSAP) analysis and RT-PCR (Gao et al., 2014). Under heat stress, percentage of methylated bands was 10.7% in Fengyou 1 (heat-sensitive) and 0.6% in Huyou 2 (heat-tolerant) (Gao et al., 2014). The cytosine methylation was also higher in the heat-sensitive genotype than the heat-tolerant genotype suggesting involvement of methylation to heat stress sensitivity. It has already been reported that superior crop genotypes avoid the methylation process (Gao et al., 2014). The effects of combined heat and drought stress on the gene expression in durum wheat (*Triticum turgidum subsp. durum*) cultivar “ofanto” were evaluated (Rampino et al., 2012). Plants were raised in the growth chamber and stress conditions were introduced at booting stage; heat stress- 30/22°C for 2 days, then raised to 34/24°C for following 2 days, 40/32°C for next one day and 42°C for last day and collected samples after 6 h of heat treatment, however, drought conditions were maintained at 28% field capacity. Gene expressions, analyzed through cDNA-AFLP studies, showed that combined stress down-regulated 92 genes and up-regulated 132 genes. Many of these genes reported to control the expression level of HSPs and dehydrins.

POLLEN-BASED TRAITS

In most plant species, reproductive tissues, mainly male gametophytes, are more sensitive to heat stress than female gametophytes (Djanaguiraman et al., 2018a), and the threshold temperature for imposing damage in these tissues is lower than that for vegetative tissues. Damage imposed by heat stress can occur pre- or post-pollination, which impair fertilization and ultimately reduce seed set (Prasad et al., 2008a, 2017; Prasad and Djanaguiraman, 2014; Sage et al., 2015). Pre-pollination events that are highly susceptible to high temperature are (1) meiosis I and meiosis II of the microspore mother cell (Young et al., 2004), (2) development and subsequent dissolution of the tapetum layer (Farooq et al., 2011), and (3) exine and intine formation (Nahar et al., 2016). Post-pollination events that are highly susceptible to heat stress are (1) pollen load (Prasad et al., 1999b, 2006), (2) pollen germination (Prasad et al., 2001), (3) pollen tube growth (Prasad et al., 2001), and (4) fertilization (Prasad et al., 2001; Barnabás et al., 2008; Hedhly, 2011; Sita et al., 2017b). The development of male gametophyte under high temperature is more susceptible than female gametophyte (Djanaguiraman et al., 2018a; Liu et al., 2019). However, in pearl millet (*Pennisetum glaucum*), the female gametophyte was more sensitive than male gametophyte (Djanaguiraman et al., 2018b). Several effects of heat stress on reproductive function have been reported. For instance, it reduced the fertility of the microgametophyte in *Brassica* (Rao et al., 1992), and impaired meiosis in the male gametophyte in tomato (*Lycopersicon esculentum*), which affected pollen germination and pollen tube growth (Firon et al., 2006). Shriveled pollen grains under high temperature may be why heat stress prevents starch accumulation in anther walls and pollen grains by disturbing the source-sink relationship that subsequently leads to lower levels of soluble sugars for their development (Pressman et al., 2002; Djanaguiraman et al., 2018a). Variation in contrasting genotypes of various pollen traits; could be used to identify and screen genotypes tolerant to high-temperature stress. For instance, 12 field-grown cultivars of *Brassica napus* L. were screened for heat tolerance based on pollen traits—pollen viability, pollen germination and pollen tube length—at 33.7°C (Singh et al., 2008). Pollen grains were placed on a germinating medium in Petri plates and artificially incubated by raising the temperature by 5°C at 5-hourly intervals from 10 to 35°C for 30 h before measuring the three pollen traits. As a result, the *Brassica* cultivars were divided into four groups—heat-tolerant (Kadore, ARC98007, NPZ0591RR, and DSV06200), moderately heat-tolerant (Plainsman, Kronos and DSV05102), moderately heat-susceptible (DSV05101 and KS4085), and heat-susceptible (KS4002, Ceres and KS3077). Thirty-four tomato genotypes were tested under field conditions in a normal (27.1/15.5°C) and summer (39.2/24.4°C) season for heat tolerance, which identified three heat-tolerant genotypes (Pusa Sadabahar, FLA-7171, and NDTVIR-60) with high pollen germination and pollen viability, relative to the heat-susceptible genotypes (Floradade and H-86) (Srivastava et al., 2012). In another study, 17 tomato genotypes were evaluated under heat stress (32/26°C) for thermotolerance on the basis of pollen traits (Paupière et al., 2017). The tomato plants were raised in a greenhouse (25/19°C), before being

moved to climate chambers when the first flower appeared for the subsequent heat treatment (32/26°C). Thermotolerant genotypes (LA2854, LA1478, and LA0417) had higher pollen viability and pollen numbers than thermosensitive genotypes (LA1719, LA1580, and SWEET4). Similarly, 18 rice (*Oryza sativa*) genotypes varying in heat sensitivity were raised in a greenhouse before being transferred to growth cabinets for high-temperature exposure during anthesis—30°C (control), and 35 and 38°C (heat stress). In this study, two experiments were conducted in two successive years, 1st year experiment involved 30°C (control), and 35°C and 38°C (heat stress) for 2 h on the onset of anthesis while 2nd year experiment involved the same set of conditions but heat stress exposure was raised to 6 h (Jagadish et al., 2008). A lower fertility percentage was noticed at 38°C for 6 h compared to 2 h. Genotype N22 had the highest spikelet fertility (86%) and was selected as highly tolerant, while Azucena and Moroberekan had <10% spikelet fertility, thus being the most susceptible genotypes (IR64, CG14); the observations correlated with superior pollen performance at high temperature (Jagadish et al., 2008). *In vitro* pollen germination and pollen tube growth were used to screen 14 cotton cultivars for heat tolerance by raising the temperature by 10°C at 5-hourly intervals from 10 to 50°C for 24 h under controlled environment (Liu et al., 2006). The study revealed that boll retention and boll number per plant were strongly correlated with pollen germination and pollen tube length. The genotypes were categorized into heat-tolerant (Sumian 16 and HLY11), moderately tolerant (JC108, Simian 3, Simian 4, and Lumian 584), moderately susceptible (Zhongmiansuo 12, Zhongmiansuo 41, Zhongmiansuo 9409, Xinyoumian 68, and Sumian 12), and susceptible (TS18, HLY15, and NuCOTN33B).

In legumes, heat stress exposure (47°C) to 44 soybean genotypes identified heat-tolerant (DG 5630RR), heat-intermediate (PI 471938), and heat-sensitive (Stewart III) genotypes based on pollen germination and pollen tube length (Salem et al., 2007). Similarly, heat-tolerant and heat-sensitive mungbean genotypes were identified based on pollen stainability (Suzuki et al., 2001). The plants were exposed to high temperatures (38/28°C) for 24 h in a growth chamber, with pollen stainability recorded on flowers that opened 8–11 days after heat treatment. The heat-tolerant genotype (Haibushi) had higher pollen stainability (60%) than heat-sensitive genotypes (<20%; Kentucky Wonder, Oregon, and Okinawa Local). Heat stress (43/30°C and 45/32°C) in mungbean affected pollen viability, pollen germination, and pollen tube length, more so in the heat-tolerant genotype (SML832) than the heat-sensitive genotype (SML668) in outdoor and controlled conditions (Kaur et al., 2015; Bindumadhava et al., 2018). Exposure of 45 mungbean genotypes to high temperature (42°C) during flowering in the field produced fewer and more shriveled pollen grains, and identified heat-tolerant genotypes (C693357, EC693358, EC693369, Harsha, and ML1299) with superior pollen traits (pollen germination, pollen viability) (Sharma et al., 2016). In chickpea, reproductive traits such as pollen viability, pollen germination, and pollen tube length were used to screen a large number of chickpea genotypes for heat tolerance by delaying sowing to expose plants to temperatures > 32/20°C

(day/night); a few tolerant (ICC15614, ICCV92944) and sensitive (ICC10685, ICC5912) genotypes were identified (Kaushal et al., 2013). Another study identified heat-tolerant and heat-sensitive chickpea genotypes using reproductive traits (Devasirvatham et al., 2013) by exposing plants to high temperature ($\geq 35^\circ\text{C}$). Pollen grains were more sensitive to high temperature than stigmas in both controlled and field conditions. Genotype ICC1205 was identified as heat-tolerant and ICC4567 as heat-sensitive, with a positive correlation between reproductive and yield traits. Lentil is sensitive to heat stress ($> 35^\circ\text{C}$), which adversely impairs pollen development and function, resulting in poor pod yields. Based on pollen traits, Kumar et al. (2016) identified heat-tolerant genotypes (FLIP2009-55L, IG2507, and IG4258) after screening 334 lentil accessions for heat tolerance under field conditions ($> 35/25^\circ\text{C}$), with a positive correlation between pollen viability and filled pods/plant. In another field study, heat stress ($> 35/25^\circ\text{C}$) reduced pollen viability in lentil by up to 78–83% (Sita et al., 2017b), with heat-tolerant genotypes (IG2507, IG3263, IG3745, IG4258, and FLIP2009) maintaining higher pollen germination (48–50%) than heat-sensitive genotypes (28–33%), which was positively correlated with yield. In soybean, exposure of cultivars (i.e., IA3023 and KS4694) and plant introduction lines (PI) lines (i.e., PI393540 and PI588026A) to heat stress (36.5–38.6°C) between gametogenesis and full bloom, as compared to control treatment (29.5–31.6°C; optimum temperature) revealed that the cultivars were more heat tolerant because of greater pollen germination and less distortion in pollen shapes (Djanaguiraman et al., 2019). Combined stress treatment damages the reproductive stages mainly pollen grains to a larger extent (Sehgal et al., 2017). Genetic variations among 38 cotton cultivars for heat and drought were assessed using reproductive and physiological traits. Among reproductive traits, pollen germination as well as pollen viability were tested at two temperature regimes (30 and 38°C) and cumulative heat and drought stress response (CHDSRI) using photosynthetic and reproductive traits was calculated. Based upon CHDSRI, 12 genotypes were categorized as heat and drought sensitive, 20 as intermediate and 6 genotypes as heat and drought tolerant (CT12214, MON11R124B2R2, UA48, MON11R112B2R2, PHY367WRF, and PX53221 1WRF) (Singh K. et al., 2018), which could be potentially used for breeding programs.

YIELD-BASED PARAMETERS

Heat stress adversely affects the reproductive and seed-filling stages, leading to severe reductions in crop yield and quality (Sehgal et al., 2018). Various studies have confirmed that the relative performance of plants in terms of yield under heat stress was suitable for selecting genotypes with heat-tolerance mechanisms/traits that can be used for crop improvement. Various traits linked to yield have been used to identify genotypes contrasting for heat tolerance.

Seed formation and seed filling is the last phase in the life cycle of seed plants. Heat stress drastically affects seed development and seed filling in many crop species, which consequently

increases the fraction of abnormal and shriveled seeds. Seed development starts from cell division; when seed cells are fully formed, storage reserves start to accumulate in the seed (Egli, 1998). The direct effect of heat stress is reportedly on the division and size of endosperm cells (Commuri and Jones, 1999), such that lower amounts of carbohydrates, proteins, lipids, and starch accumulate in developing seeds. Heat stress also accelerates the rate and duration of seed filling, resulting in more abnormal seeds, which reduces crop yield. Heat stress reduces seed yield by (i) reducing seed number, (ii) reducing seed weight, and (iii) accelerating the seed filling rate (Farooq et al., 2017; Prasad et al., 2017).

Seed Filling Rate and Duration

Heat stress hastens the seed filling rate and reduces the duration of seed filling. In cowpea, raising the temperature from 15.5 to 26.6°C shortened the seed filling duration by 14–21 days (Nielsen and Hall, 1985). Heat stress impaired the growth of the cotyledons, and reduced the number of endosperm cells and cell expansion in the embryo, which had a negative effect on photosynthate translocation in developing seeds and resulted in shriveled seeds in maize (Jones et al., 1985; Munier-Jolain and Ney, 1998). A heat-stressed environment (> 32/20°C) during seed development increased the seed filling rate in six chickpea genotypes, relative to the optimum temperature (Awasthi et al., 2014). The same study revealed that heat stress decreased the duration of seed filling more in heat-sensitive (ICC 4567) than heat-tolerant (ICC1356, ICC15614) genotypes. High temperature (25/20°C) reduced the duration of grain filling by 30% and increased the grain-filling rate by 20% in six wheat genotypes (G1, G2, G3, G4, G5, G6), relative to the control (20/15°C), more so in heat-sensitive (G6) than heat-tolerant (G4) genotypes (Yin et al., 2009).

Seed Number

Heat stress leads to poor pollination and fertilization, which reduces seed number. In faba bean (*Vicia faba* L), seed number declined with increasing temperature (Bishop et al., 2016). In mungbean, heat-tolerant genotype (SML 832) produced more seeds than heat-sensitive genotype (SML 668) under high temperature (45/32°C) in the field (Kaur et al., 2015). While testing 24 genotypes of common bean in the greenhouse under different temperature regimes (24/21°C, 27/24°C, 30/27°C, 33/30°C), 33/30°C was the most damaging to plants with respect to seed number and seeds/pod, with the reductions more prominent in heat-sensitive genotypes (–66%; A55, Labrador, Majestic, IJR) than heat-tolerant genotypes (–31%; Brio, Carson, G122, HB1880, HT38, Venture) (Rainey and Griffiths, 2005). Heat stress (36/27°C) reduced seed number/pod in 46 of 48 lines of cowpea (*Vigna unguiculata*) evaluated for heat tolerance in a greenhouse; two heat-tolerant lines (B89-600 and TN88-63) did not exhibit reduced seed numbers/pod (Ehlers and Hall, 1998). The average number of seeds/pod varied in the heat-sensitive genotypes (e.g., 3.3 in IT82E-60, 2.9 in Bambey 21 and 3.6 in IT84S-2049), while those of the heat-tolerant genotypes had 6.3 in B89-600 and 8.1 in TN88-63 compared to control values

(e.g., 11 in IT84S-2049, 9.6 in IT82E-60, 7.4 in B89-600 and 6.4 in TN88-63).

Seed Weight

Seed weight represents the ultimate yield of the crop; hence it has been reliably used as a trait to screen for heat tolerance (Sehgal et al., 2018). Chickpea yields declined when genotypes were exposed to various temperature ranges (35/25°C, 40/30°C, and 45/35°C) in a growth chamber, relative to the control (30/20°C) (Kumar et al., 2013). At 40/30°C, the seed weight of heat-sensitive genotypes (ICC14183, ICC5912) declined by 37–45% compared with heat-tolerant genotypes (ICCV07110, ICCV92944). At 45/35°C, heat-tolerant genotypes also experienced a decline in seed weight but heat-sensitive genotypes did not set any pods. Similarly, mungbean genotypes grown outdoors in April, with high temperatures (45/32°C) coinciding with reproductive phase, reduced seed weight by 48.3% in the heat-sensitive genotype (SML668) and 35.1% in the heat-tolerant genotype (SML832), relative to control (Sharma et al., 2016). Likewise, seed weight of lentil grown at high temperature (> 32/20°C) in field declined drastically compared to control plants (Bhandari et al., 2016), more so in heat-sensitive genotypes (–50%; LL699 and LL1122) than the heat-tolerant genotype (–33%; LL931). In common bean, heat stress (33/30°C) under field conditions was significant for the selection of heat-tolerant (Brio, Carson, G122, HB1880, HT38, Venture) and heat-sensitive genotypes (A55, Labrador, Majestic, IJR), based on seed weight. At this temperature, seed weight declined by 47% across genotypes, more so in heat-sensitive genotypes (–88%) than heat-tolerant genotypes (–25%) (Rainey and Griffiths, 2005). In cowpea, studies at two locations with varying temperatures (Coachella (41/25°C) and Riverside (36/17°C) assessed the effect of high temperature on the yield of contrasting genotypes (Ismail and Hall, 1999). Yield parameters such as seed weight and seeds/pod reduced drastically, as the temperature increased, however, heat-tolerant genotypes (H36, H8-9, DLS99) at higher temperature (41/25°C) retained more seed weight (193 mg/seed) than heat-sensitive genotypes (CB5, CB3, DLS127), which had smaller seeds with an average weight of 168 mg. Screening experiments on Pearl millet, conducted over a period of 3–4 years (2009–2012) at ICRISAT, India, involving 221 hybrid parental lines (both B- and R-lines), 53 germplasm accessions and 4 improved populations over 4-year period showed large genetic variability in seed set at daily maximum air-temperature of ≥ 42 °C during flowering. Five hybrid seed parents (ICMB 92777, ICMB 05666, ICMB 00333, ICMB 02333, and ICMB 03555) and a germplasm accession IP 19877 with 61–69% seed set as compared to 71% seed set in a heat tolerant commercial hybrid 9444 (used as a control) was identified. A comparative study on 23 hybrids and their parents for seed set at high air temperature (>42°C) showed heat tolerance as a dominant trait, indicating that heat tolerance in one parent would be ample to generate heat tolerant hybrids in pearl millet (Gupta et al., 2015). In sub-Saharan Africa, 24 elite durum wheat breeding lines and cultivars were tested for adaptation to warm environments at two stations: Kaedi, Mauritania and Fanaye, Senegal. Top grain yield was recorded at 5,330 kg ha⁻¹ and the average yield at 2,484 kg ha⁻¹. Biomass and spike

fertility (i.e., number of seeds produced per spike) were found to be the most vital adaptive traits to warm environments. The study showed three genotypes (“Bani Suef 5,” “DAWRyT118,” and “DAWRyT123”) as the most stable and high yielding; while the last two genotypes were the best performers (Sall et al., 2018).

Combined drought and heat stress were found to be greatly detrimental for production potential of crops. Thus, lentil genotypes were evaluated for their response to impacts of combined drought and heat stress (drought tolerant: DPL53 and drought sensitive: LL699) (Sehgal et al., 2019). The heat and drought (33/28°C with 50% field capacity) treatments were imposed to determine to effects on yield traits (seed filling duration, seed filling rate, seed number/plant, and seed weight/plant). Under combined stress, a decline in seed filling duration by 5.4–8.9 days, seed growth rate by 44–60.2%, seed number/plant by 35–48.7%, seed weight/plant by 47–59% compared to control. This reduction pattern was more drastic in heat sensitive genotype than heat tolerant genotype. A field experiment on 300 maize inbred lines test-crossed to CML539 was conducted at multiple locations (Tlaltizapán, México (18°41′ N, 99°07′ W, and 940 m asl), Kiboko, Kenya (2°21′ S, 37°72′ E, and 975 m asl), Chiredzi, Zimbabwe (21°01′ S, 31°34′ E, and 430 m asl), at the Nakhonsawan Field Crops Research Center in Takfa, Thailand (15°21′ N, 100°30′ E, and 87 m asl), and at the ICRISAT experimental station in Hyderabad, India) to evaluate their response to reproductive stage drought stress, heat stress, and combined drought and heat stress. The study identified few lines (notably La posta Sequia C7-F64-2-6-2-2 and DTpYC9-F46-1-2-1-2) having higher tolerance to drought and combined drought and heat stress. The findings indicated that tolerance to individual stresses was genetically distinct from tolerance to combined stresses. The assessment indicated that most of the current drought donors and key inbreds used in widely grown African hybrids were sensitive combined drought and heat stresses. The identified lines, as mentioned above, need to be introduced into breeding programs for maize (Cairns et al., 2013).

BREEDING FOR HEAT TOLERANCE INVOLVING CONTRASTING GENOTYPES

Breeding techniques remain one of the inexpensive and viable approaches for developing heat stress tolerance in crop plants (Priya et al., 2018). Field-based screening of crop gene pool and landraces for yield and heat stress tolerance in targeted environments is a way to develop heat tolerant genotypes in various crop plants (Craufurd et al., 1998; Hede et al., 1999; Ntare et al., 2001; Jagadish et al., 2008; Scafaro et al., 2010; Krishnamurthy et al., 2011; Dhanda and Munjal, 2012; Pradhan et al., 2012). The breeders also focus toward yield and yield-related traits under heat stress so that genotypes/progeny lines with higher yield under heat stress can be selected. Varieties possessing heat stress tolerance as well as higher yields will ensure adequate food to the world’s burgeoning population under global warming. To develop heat tolerant crop varieties, contrasting donor parents are crossed, progenies advanced using various

crop breeding strategies and desirable heat tolerant segregants are selected. Finally, heat tolerant homozygous lines are evaluated for yield and other useful agronomic traits under appropriate environments followed by possible release as a variety/ies. For transfer of heat tolerance to high yielding but heat sensitive mega crop varieties (varieties that occupy large area) from heat tolerant landraces or wild relatives, backcross breeding with recurrent parent remains an effective strategy as it allows for the recovery of the genome of recurrent parent, thereby traits of mega variety, with an addition of heat tolerance. To broaden the genetic base for heat tolerance, next generation breeding schemes viz., development of Multiparents Advanced Generation Intercross (MAGIC) and Nested Association Mapping (NAM) population are also receiving wider attention (Li H. et al., 2018).

Morpho-physiological and phenological traits could play an important role in contributing toward heat stress adaptation as these could act as surrogate traits for selecting heat tolerance (Reynolds et al., 2007). These physiological traits range from early phenology (Gaur et al., 2015), canopy temperature (Kumar et al., 2012; Mondal et al., 2013), chlorophyll fluorescence, chlorophyll content (Ristic et al., 2007; Kumar et al., 2013), cell membrane stability (Blum and Ebercon, 1981), stay green trait or delayed senescence (Thomas and Howarth, 2000; Ristic et al., 2007), pollen and pollen related traits (Devasirvatham et al., 2010; Kaushal et al., 2013; Djanaguiraman et al., 2018, Djanaguiraman et al., 2019) to water soluble carbohydrates in stem (Schittenhelm et al., 2020). The physiological trait-breeding has gained great attention for improving plant adaptation to heat stress in various crop plants especially in wheat (Reynolds et al., 2007; Reynolds and Langridge, 2016). A focus on selection of physiological traits that are correlated with yield either directly or indirectly could increase chances of accumulation of yield contributing genes thereby ensuring higher plant yield under heat stress (Reynolds and Langridge, 2016). In developing heat tolerance in wheat, the cross-species gene transfer system was used wherein three heat-tolerant accessions of *Aegilops tauschii* (wild genotype) were crossed with bread wheat (*Triticum aestivum* L.) cultivar “PBW 550” (Sehgal et al., 2011). The BC₁F₄ lines derived from these crosses that possessed improved cell membrane stability, TTC and chlorophyll retention under heat stress were selected (Sehgal et al., 2011). For winter sown crops, early phenology allows plants to escape heat stress (Bueckert et al., 2015). For such crops, selection for earliness could be an important option to develop crop varieties that escape heat stress thereby escaping the damage caused by heat. As reproductive processes are most vulnerable to heat stress, physiological screening of genotypes for two reproductive traits, i.e., better pollen viability and pollen germination under heat stress could lead to the identification of heat tolerant genotypes as stability of these two traits under heat stress will ensure better fertilization, adequate seed set and improved grain yield (Devasirvatham et al., 2013; Poli et al., 2013). Relying on higher pollen germination and better seed setting capability Nguyen et al. (2013) identified two sorghum R9403463–2-1 and IS8525 genotypes from a set of diverse sorghum genotypes originated from United States, Australia, Africa and Asia. Likewise, several promising genotypes viz., PI609489, AQL33/QL36; CCH2; IS

8525 (Singh V. et al., 2015) due to their better seed setting ability and Macia, BTx378, SC155 (Sunoj et al., 2017) having better pollen germination capability and maintaining high grain yield under heat stress were identified. Given the field screening of large set of germplasm and hybrid parental lines of Pearl millet under high temperature stress, a wide range of genetic variability for seed setting was noted in under high temperature stress (Gupta et al., 2015). Several parental lines viz., ICMB 92777, ICMB 05666, ICMB 00333 along with IP 19877 germplasm accession exhibited better seed setting under heat stress and thus could be used in developing heat tolerant hybrid Pearl millet (Gupta et al., 2015). Likewise, Jukanti et al. (2017) underscored the importance of CZH 233, CZP 9603, CZI 2011/5, and CZMS 21A genotypes due to their better seed setting higher capability of grain yield for developing superior Pearl millet genotypes under heat stress. Likewise, the potentiality of “Norchip” and “Désirée” potato cultivars in potato breeding program for improving genetic gain because of their better photo-assimilate transport from leaf to tuber under heat stress has been discussed (Basu and Minhas, 1991; Ahn et al., 2004).

Heat stress tolerance is a polygenic trait. Classical genetics was earlier used to identify the genetic bases of heat tolerance in various field and vegetable crops (Patel and Hall, 1988; Marfo and Hall, 1992; Gupta et al., 2015; Jha et al., 2019), this approach, however, could not completely explain the genetic nature of heat stress tolerance because of its multigenic nature (Upadhyaya et al., 2011). Subsequent advances in molecular marker technology has allowed identification and precise mapping of genes/QTLs governing heat stress tolerance several crops such as rice (Gui-lian et al., 2009; Lei et al., 2013; Wei et al., 2013; Li M. et al., 2018), maize (Inghelandt et al., 2019), wheat (Mason et al., 2010; Pinto et al., 2010; Paliwal et al., 2012; Lopes-Caitar et al., 2013; Sharma et al., 2017), chickpea (Paul et al., 2018), cowpea (Pottorff et al., 2014), *Brassica* (Branham et al., 2017) and tomato (Wen et al., 2019). Marker assisted selection can be used to transfer heat tolerant QTLs/genomic region to the elite but heat stress sensitive genotypes if genetic maps with sufficient marker density are available (see Jha et al., 2014). The approach has been successfully employed in rice (Ye et al., 2012; Shirasawa et al., 2013), wheat (Pinto et al., 2010; Bennett et al., 2012; Bonneau et al., 2013) and tomato (Grilli et al., 2007) to transfer QTLs governing heat tolerance. Considering potato, Trapero-Mozos et al. (2017) discussed the scope of introgression of *HSc70* allelic variant contributing toward enhancing yield under heat stress into high yielding potato cultivars through marker assisted breeding for improving heat tolerance in potato. Advent of improved sequencing technologies that allow faster sequencing of genomes at lower costs led to generation of profuse SNP markers that enabled genome-wide association studies (GWAS) for elucidating novel genomic regions controlling heat stress tolerance. GWAS for identifying heat stress tolerance genomic regions have been conducted in rice (Lafarge et al., 2017), maize (Yuan et al., 2019), wheat (Maulana et al., 2018), barley (Cantalapiedra et al., 2017), pea (Tafesse et al., 2020), chickpea (Thudi et al., 2014; Jha et al., 2018; Varshney et al., 2019), and in *Brassica* (Rahaman et al., 2018).

TRANSCRIPTOMICS

Previously cDNA-AFLP and microarrays were employed for identifying heat tolerance genes in various crop plants (Bita et al., 2011; Johnson et al., 2014). After the advent of crop-specific gene chips, microarrays became the method of choice for estimating changes in gene expression upon exposure to abiotic stress e.g., Gene Chip wheat genome array in wheat (Qin et al., 2008), Affymetrix GeneChip® Tomato Genome Array in tomato (Frank et al., 2009), Affymetrix 22K Barley 1 Gene Chip microarray in barley (Mangelsen et al., 2011) and *Brassica* 95k EST microarray in *Brassica* (Yu et al., 2014). Microarray-based analysis by Johnson et al. (2014) provided insights into various genes involved in heat tolerance in sorghum. Major revolution in our understanding of genes involved in heat stress tolerance occurred after the advent of modern DNA sequencing technologies that allowed sequencing of whole transcriptomes, a technique called transcriptomics/transcriptome sequencing/whole genome transcriptome sequencing/whole genome expression profiling. Transcriptomics allowed identification of various heat tolerant candidate genes with greater precision in rice (González-Schain et al., 2016; Mangrauthia et al., 2016; Fang et al., 2018), wheat (Liu et al., 2015), maize (Shi et al., 2017), chickpea (Agarwal et al., 2016), and soybean (Gillman et al., 2019). Transcriptome analysis of contrasting heat tolerant and sensitive lines led to identification of 35 differentially expressed transcripts between the contrasting rice lines, 21 of which were functionally validated (Liao et al., 2015). The study suggested involvement in oxidation-reduction, metabolic activity, defense response and photosynthesis activity in heat tolerance (Liao et al., 2015). Zhao et al. (2018) explored several *Hsp20* family genes involved in heat stress response across the whole genome in potato. A total of 14 *Hsp20* genes displaying up-regulatory role under heat stress in potato was confirmed through real-time quantitative PCR. RNA-seq analysis of maize seedling treated with heat stress unveiled myriads of up and down regulated genes related to photosynthesis, protein synthesis and biosynthesis of various metabolites including zeatin, brassinosteroids (Frey et al., 2015; Shi et al., 2017). Further, Zhao et al. (2019) unearthed the involvement of 5,400 non-additive genes specific to heat stress through transcriptome analysis of parental lines and F₁ hybrid maize seedlings under heat stress conditions. RNA-seq technology not only identified the genes for heat tolerance but also the non-coding RNAs that were involved in regulating heat stress responses in various crops (Wang et al., 2011; Xin et al., 2011; Yu et al., 2013; Mangrauthia et al., 2017).

PROTEOMICS

Gene expression enhanced our understanding of mechanisms of heat stress tolerance significantly, however, gene transcripts do not directly influence plants' responses to stresses. Instead the proteins/enzymes, the gene products, modify plants' metabolite pool in response to external stimulus. To understand better, the mechanisms of stress tolerance, studies of the proteome, i.e., entire set of proteins in a cell or organ were initiated. Prior to

TABLE 1 | Few selective heat-tolerant genotypes identified for various crops involving various traits (details in the text).

Crop	Traits used	Screening method	Promising heat-tolerant genotypes	Country	References
1. Cereals					
Barley (<i>Hordeum vulgare</i> L.)	Stay green trait	Field experiments (> 40°C)	L6 and L8 and L3 and L10	Iran	Bavei et al., 2011
	Chlorophyll fluorescence	Growth chamber (45°C)	Ig, Im, and Tz	North Africa	Oukarroum et al., 2016
Wheat (<i>Triticum aestivum</i> L.)	Stay green trait	Field experiments (32°C)	CB367(BB#2/PT//CC/INIA/3/ALD"S," CB = 333(WL711/3/KAL/BB//ALD"S"and CB335(WL711/CROW"S"//ALD#1/CMH7 7A.917/3/Hi666PVN"S")	Pakistan	Rehman et al., 2009
	Canopy temperature depression	Field experiment (41°C)	HD 2932, HD 2864, HD 3095, HI 8703, HUW 234	India	Saxena et al., 2016
Rice (<i>Oryza sativa</i> L.)	Pollen-based	Growth cabinets (35°C, 38°C)	N22	United Kingdom	Jagadish et al., 2008
	Cell membrane thermostability	Phytotron (40°C)	F473	America	Sanchez-Reinoso et al., 2014
Maize (<i>Zea mays</i> L.)	Plant height	Field experiments (> 40°C)	DTPYC9F119	India	Debnath et al., 2016
	Root system architecture	Growth chamber (37°C)	H16, CML444, SC-Malavi	United States	Trachsel et al., 2010
2. Legumes					
Chickpea (<i>Cicer arietinum</i>)	Photosynthetic rate	Field environment (25 to 40°C)	Pusa 1103, Pusa 1003, KWR 108, BGM 408, BG 240, PG 95333, JG 14, BG	India	Kumar et al., 2017
	Cell membrane thermostability	Growth chamber (40–45°C)	ICCV07110, ICCV92944, ICC1205	India	Kumar et al., 2013
Lentil (<i>Lens culinaris</i> Medik.)	Biomass	Field study (> 32/20°C)	IG2507, IG3263, IG3745, IG4258, and FLIP2009	India	Sita et al., 2017a
	Stomatal conductance				
	Chlorophyll fluorescence				
	Chlorophyll content				
	Sucrose				
	Oxidative stress and antioxidants				
	Cell membrane thermostability	Growth chamber (34°C)	FLIP2009, Ranjan, Moitree, 14-4-1, IC201710, IC208329	India	Choudhury et al., 2012
Mungbean (<i>Vigna radiata</i> L.)	Pollen-based Biomass	Field experiments (> 40/28°C)	EC693357, EC693358, EC693369, Harsha, and ML 1299	India	Sharma et al., 2016
	Chlorophyll fluorescence				
	Oxidative stress and antioxidants				
Common bean (<i>Phaseolus vulgaris</i> L.),	Chlorophyll fluorescence	Growth chamber (42°C)	<i>Ranit</i> and <i>Nerine RS</i>	Bulgaria	Petkova et al., 2007
	Seed weight	Field conditions (27/24°C, 30/27°C, and 33/30°C)	Brio, Carson, G122, HB1880, HT38, Venture	Switzerland	Rainey and Griffiths, 2005
	Seed number				
Alfalfa (<i>Medicago sativa</i>)	Biomass Chlorophyll fluorescence	Greenhouse and growth incubators (38/35°C)	Bara310SC	China	Wassie et al., 2019
Soybeans (<i>Glycine max</i> L. Merr.)	Cell membrane thermostability				
	Photosynthetic rate	Field experiments (36.5–38.6°C)	IA3023 and KS4694	United States	Djanaguiraman et al., 2019
	Metabolites	Lab experiments (36°C/24°C; 46/26°C)	PI587982A	South America	Chebrolu et al., 2016
Cowpea (<i>Vigna unguiculata</i> L. Walp)	Seed weight	Field studies (41/25°C)	H36, H8-9, DLS99	United States	Ismail and Hall, 1999
	Seed number	Greenhouse conditions, (36/27°C)	B89-600 and TN88-63	United States	Ehlers and Hall, 1998
3. Oil seed crops					
Indian Mustard (<i>Brassica juncea</i> L)	Plant height	Field conditions (34°C)	BPR-538-10, NRCDR-2, RH-0216	India	Chauhan et al., 2009
Canola (<i>Brassica napus</i>)	Pollen-based	Field studies (10–35°C)	Kadore, ARC98007, NPZ0591RR, and DSV06200	United States	Singh et al., 2008
	Root system architecture	Growth chamber (32°C)	Invigor 5440	Canada	Wu et al., 2017
Peanut (<i>Arachis hypogaea</i> L.),	Carbon isotope discrimination	Polytunnels (40/28°C)	Spanish botanical type	United Kingdom	Craufurd et al., 1999
Peanut (<i>Arachis hypogaea</i>)	Heat shock proteins	Controlled environment (50°C)	ICGS 76, COC038, COC068, COC050, COC041	United States	Selvaraj et al., 2011

(Continued)

TABLE 1 | Continued

Crop	Traits used	Screening method	Promising heat-tolerant genotypes	Country	References
Cotton (<i>Gossypium hirsutum</i> L.)	Cell membrane thermostability	Field conditions (>44°C)	NIA-80, NIA-81, NIA-83, NIA-84, NIA-M-30, NIA-M31, NIA-HM-48, NIA-HM-327, NIA-H-32, NIA-HM-2-1, NIA-Bt1, NIA-Bt2, NIA-Perkh, CRIS-342, CRIS-134, NIAB-111 and check variety Sadori	Pakistan	Abro et al., 2015
	Chlorophyll fluorescence	Green house (30 and 40°C)	DP393, VH260 and DP 210 B2RF	Africa	Van der Westhuizen et al., 2020
4. Vegetable crops					
Potato (<i>Solanum tuberosum</i> L.)	Heat shock proteins	Growth chamber (40°C)	Norchip, Desiree	Baltimore	Ahn et al., 2004
Tomato (<i>Solanum lycopersicum</i> L.)	Pollen-based	Field conditions (39.24/24.42°C)	Pusa Sadabahar, FLA-7171, NDTV-60	Japan	Srivastava et al., 2012
	Sucrose	Growth chambers (31/25°C) or Greenhouses (32/26°C)	FLA 7516, Hazera 3018, Hazera 3042, and Saladate	Israel/United States	Firon et al., 2006
Cabbage (<i>Brassica</i> species)	Metabolites	Control environment (25–35°C)	Yoshin, Kenshin and full white	Japan	Hossain et al., 1995
Cucumber (<i>Cucumis sativus</i> L.)	Cell membrane thermostability	Growth room (40/32°C)	L-3466, Desi Cucumber	Pakistan	Ali et al., 2019

proteomics, proteins suspected to play role in heat tolerance were analyzed by MALDI TOF MS/MS analysis, e.g., rice (Han et al., 2009; Jagadish et al., 2010; Liao et al., 2014). Further advances in proteomics strengthen our understanding of identification of the proteins that confer thermotolerance in plants. Proteomics analysis of two contrasting rice genotypes, N22 (tolerant) and Gharib (sensitive), showed that heat tolerance of N22 was due to higher capability of mediating renaturation of stress damaged proteins, higher efficiency in repairing ribosomal protein, higher upregulation of proteins involved in calcium signaling and phytohormone synthesis and protein modifications under high night temperature at early grain filling stage (Shi et al., 2013). The functional role of proteins that contribute to heat tolerance ranges from oxidation-reduction, cellular metabolic activity to defense responses (Lu et al., 2017; Zhang et al., 2017). In this context, Zhang et al. (2017) identified various proteins by analysis of grains of contrasting heat tolerant rice lines by employing isobaric tags for relative and absolute quantitation (iTRAQ) methods (Zhang et al., 2017). Similarly, by employing iTRAQ technique, Lu et al. (2017) identified 258 heat responsive proteins from wheat leaf, most of which were involved in chlorophyll synthesis, carbon fixation and redox regulation under heat stress. Various proteins such as HSP, those related to anti-oxidant mechanism, and glycolysis were involved in adaption of grape to heat stress as revealed through iTRAQ analysis (Liu et al., 2014). Proteomics analysis of ethylene pre-treated tomato pollen by LC-MS/MS suggested that various proteins help in protecting pollen development and function through higher abundance of protein synthesis and upregulating stress protecting proteins that maintain cellular redox state under heat stress (Jegadeesan et al., 2018). Proteomics analysis by 2-DE technique allowed identification of important heat shock proteins viz., HSP26, HSP16.9, and unknown HSP/Chaperonin contributing to heat

stress tolerance in maize (Abou-Deif et al., 2019). Considering contributory role of proteins adapting roots under heat stress, Valdes-Lopez et al. (2016) reported the involvement of both up and down regulatory proteins contributing to heat tolerance in soybean root. Recently, proteomics analysis deduced that protein phosphorylation and protein acetylation could regulate heat tolerance by modulating photosynthesis protein in grape (Liu et al., 2019). The proteins involved in heat tolerance elucidated through proteomics analysis could serve as biomarkers for identifying heat tolerant cultivars in various crop plants. Participatory role of miR156 targeting SPL transcription factor in *A. thaliana* (Stief et al., 2014), miR160, miR166, and miR167 in wheat and barley (Xin et al., 2010), IbmiR397 targeting *laccase gene* in sweet potato (Yu et al., 2020) controlling heat stress response are worth mentioning.

METABOLOMICS

Metabolomics, the study of metabolites in a cell or organ, enhance our understanding of novel metabolites that contribute to plant adaptation to heat stress (Bokszczanin and Frągkostefanakis, 2013). Metabolomics have unraveled the key metabolites ranging from sugars, proteins and lipids participating in key biological processes to anti-oxidants and defense molecules in response to heat stress (Li T. et al., 2015; Chebroul et al., 2016; Muhlemann et al., 2018; Salvi et al., 2018). Metabolomics at specific plant stages viz., seed germination, vegetative, reproductive, grain formation and grain filling have broadened our understanding of metabolites involved in heat stress responses at different development stages (Wang et al., 2015; Mangrauthia et al., 2016; Spicher et al., 2016; Templer et al., 2017; Muhlemann et al., 2018; Qu et al., 2018; Thomason et al., 2018). Metabolomics

provided novel insights into the role of various lipids viz., plastidic glycerolipids, oxidized glycerolipids in regulating heat stress responses in wheat leaves (Narayanan et al., 2016), that of α -tocopherol and plastoquinone in maintaining the photosynthesis apparatus in tomato under heat stress (Spicher et al., 2016) and that of galactinol in minimizing excessive ROS activity in chickpea under heat stress (Salvi et al., 2018). Metabolomics also emphasized the role of sugars in anthers such as glucose-6-P, fructose-6-P, glucose, maltose and *myo*-inositol in improving heat stress acclimation in N22 (heat-tolerant) rice genotype (Li X. et al., 2015). Likewise, the ameliorative role of various anti-oxidant phenolic compounds viz., flavonoids, flavonols, tocopherols in heat tolerance by preventing ROS mediated negative effect on pollen tube germination in tomato (Muhlemann et al., 2018) and also during seed development in soybean (Chebrolu et al., 2016) are other examples of the use of metabolomics in improving knowledge of heat stress tolerance mechanisms. At post anthesis stage, metabolites viz., drummondol, anthranilate appear to regulate heat stress response in wheat flag leaves (Thomason et al., 2018). The studies pinpoint that metabolomics along with system biology approaches could significantly enhance our understanding of various metabolites produced in response to heat stress (Janni et al., 2020) and would be a vital tool to develop heat tolerant crops in agriculture.

CONCLUSION AND FUTURE PERSPECTIVES

The past few decades have seen considerable developments in genetics, biochemical, genomics, transcriptomics, proteomics and metabolomics approaches to enhance the understanding of heat stress tolerance. However, basal thermotolerance remains the major tool to develop agronomically superior heat tolerant cultivars for agricultural crops. Basal thermotolerance is primarily evaluated by exposing small or large sets of germplasm (accessions, cultivars, wild relatives) under controlled (laboratory, screen/greenhouse) or natural field environments to stressful temperatures. These tests have identified several sources of heat tolerance in various crop gene pools and landraces, which may act as potential candidates/donors of heat stress tolerance for developing heat tolerant cultivars using conventional or modern breeding approaches (Table 1). In some instances, heat tolerant genotypes have been directly released as cultivars (as in Chickpea) owing to their agronomic superiority. In addition to heat stress tolerance, contrasting genotypes are also being evaluated for diverse traits related to phenology, growth, physiology and biochemistry, genes, and reproductive biology. Of the several traits being evaluated for heat stress tolerance in crops, the majority of studies have indicated pollen function to be highly sensitive to heat stress, thus making it one of the vital selection traits for heat tolerance. Evaluation of thousands of germplasm or progeny lines for several traits associated with heat tolerance in a short span of time is needed to fasten the breeding for heat tolerance. High-throughput phenotyping that allows choosing important traits as selection criteria for heat tolerance can

facilitate identification of genotypes for heat stress tolerance as well as other desirable agronomic traits in a short span of time but high throughput phenotyping requires high investment and is available with only a few laboratories around the world. In addition to it, remote sensing tools (UAVs with spectral and thermal imaging camera) can be effectively deployed under realistic field environments to screen thousands of germplasm or progeny lines.

Plant heat tolerance being a quantitative trait is highly influenced by $G \times E$ interactions and genetic inheritance of heat tolerance remains challenging. Large scale DNA-based marker development during the last decade led to mapping of QTLs linked to heat tolerance in various crops (Jha et al., 2014; Janni et al., 2020). Advances in sequencing technologies especially, next generation sequencing (NGS), genotyping by sequencing (GBS), and other high throughput genotyping platforms have facilitated narrowing down of the heat tolerance QTL regions for analysis of candidate genes (Xu et al., 2017; Kilasi et al., 2018; Inghelandt et al., 2019; Tadesse et al., 2019). Given the huge number of novel SNPs developed recently and GWAS in large set of global crop germplasm, it became possible to identify novel haplotypes/genomic regions controlling heat tolerance (Paul et al., 2018; Varshney et al., 2019; Khan et al., 2020; Weckwerth et al., 2020) and allowed for the assessment of genetic diversity at nucleotide-scale. High throughput phenotyping coupled with advanced imaging devices, unmanned vehicles and machine learning, deep learning approaches and molecular genetics tools can further enhance the accuracy of selection of genomic regions associated with heat tolerance. The developments in marker and sequencing technologies are expected to allow genome wide marker profiling facilitating genomic selection for heat tolerance (Tricker et al., 2018; Inghelandt et al., 2019) and thus, rapid breeding for the development of varieties with novel genetic combinations. Similarly, advances in proteomics, transcriptomics and metabolomics will further unravel the complexity of heat stress tolerance in crops by identifying missing links in the current information. A combination of these approaches could allow for the quantifying of plant heat stress responses, spatially and temporally, at a large scale, thus narrowing the “genotype-phenotype gap” (Fahlgren et al., 2015; Singh A. et al., 2015; Singh A. K. et al., 2018; Pinto et al., 2016). Corresponding to breeding approaches, current developments in the spatial and temporal expressions of engineered genes or pathway engineering by the targeted editing of genomes using CRISPR-Cas technology can be used for development of heat tolerant designer crops. A better knowledge of plant cellular mechanisms associated with heat tolerance and increased yields would be vital to drive essential gains in crop improvement, which can be greatly assisted by exploring the genetic diversity in heat tolerance, and put into practice by genome-scale breeding, precisely done gene engineering and better agronomic management practices.

AUTHOR CONTRIBUTIONS

HN conceived the outline. All authors contributed in preparing various sections of this manuscript.

ACKNOWLEDGMENTS

Contribution no. 21-068-J from Kansas Agricultural Experiment Station. HN is thankful to DST (India; PURSE grant), DBT (India), CSIR (India), World Vegetable Center (at ICRISAT), University of Western Australia, Australia,

International Center for Agricultural Research in Dry Areas (ICARDA), Morocco, for supporting the research by funding, Indian Institute of Pulses Research, Kanpur, Punjab Agricultural University, Ludhiana, for providing the germplasm from time to time. PD is thankful to CSIR (India) for fellowship during the course of this study.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The reviewer PK declared a past co-authorship with one of the authors KS to the handling editor.

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Kala Sarovar

UGC CARE Group - I Journal
ISSN : 0975-4520

CERTIFICATE OF PUBLICATION

This is to certify the paper Entitled

COMMUNALISM AND NATIONAL INTEGRATION

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University Grants Commission

Approved Journal

Published in

Vol-24 No.03(B) July-September 2021

Kala Sarovar

ISSN : 0975-4520

UGC Care Group 1 Journal



COMMUNALISM AND NATIONAL INTEGRATION

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National Integration is a problem of great significance for a multi-racial and multi-religious country like India. To get the independence from colonial rule, people joined their hands together in spite of various communal and cultural differences. When they got independence, they become aware of their primordial loyalties e.g. religion, caste, language etc. Integration is an inter group activity which is never complete. National Integration is a combination of two words: National and Integration. National stands for characteristic features of a nation and integration means combining parts into a whole or bringing them together¹. National Integration is not a house which could be built by mortar and bricks. It is not an industrial plan too which could be discussed and implemented by experts. Integration on the contrary, is a thought which must go into the hearts of all the people. It is a consciousness which must awaken the people at large². Integration implies unification and consolidation of a community with the objective of ensuring maximum well being of largest number of its member also developing its distinctive personality to make its own contribution to the mankind and world civilization. It implies provision of education, better, economy, social, political and moral status³.

When India became independent the national leader faced various problems. The Leaders gave priority to national integration. Leader believed in the application of democratic methods to achieve national integration of the people and created unity among them. Ever since independence integrity of Indian nation came to be challenged. There are various hindrances in the way of national integration like language, communalism, regionalism, ethnic, religious, caste conflicts etc. Mrs. Indira Gandhi former P.M. of India, remarked that the greatest threat to integration came from communalism. She appealed to all political parties to treat the problem of National integration as a national and not a political issue.

The word "Communal" is derived from the word 'commune' striking the meaning of a feeling of oneness or consciousness or friendliness. In India, the word communal means mistrust, hatred, rivalry etc. among the people of different religions. It is characterized by tension or conflict between culturally distinct, but geographically mixed communities⁵. Before the advent of the British rule in India, the Hindus and Muslims lived amicably. Communalism is not a new concept, although it has its own roots from Britishers time. Communal problem was the legacy of british rule. The British Govt. adopted a policy of divide and rule with a view to drive wedge between the Hindus and the Muslims⁶. Communalism literally means that "It is the belief because a group of people follow a particular religion they have as result common social political and economic interest⁷. Each individual being born in a community naturally has a closer connection or relationship to the community members their customs and practices. To loves that community and think of the welfare of that community is branded as being communal.

Communalism has been treated as a negative concept and seen in opposition to nationalism in pre independence as well as post independence India. The partition of India on communal lines has led people to associate it with Hindu-Muslim rivalry though it is not confined to these two communities⁸.

India is a land of minorities where there is an acute problem of communalism which has led to

thousands communal riots in the country⁹. These are various communal incidents in India like 1984, Sikh riots, Kanpur in Utter Pradesh and riots in Gujrat, Babri Masjid/Ram Janambhumi, are the major examples before us. The communal attacks in Gujarat shows that the slow poison of communalism is spreading through Indian society and threatening to tear apart our multi-religious and multi cultural nation. The decision of the VHP- a constituent of the Sangh parivar to construct a Ram Mandir at the site of Babri Masjid which was demolished by them in violation of the commitment given by their leaders before the honourable High Court where the title of the disputed land was being contested. This was done to whip up the communal sentiments for electoral gains. The need to pursue the Hindutva agenda more aggressively was felt and stressed by the constituents of the Parivar particularly the VHP for electoral consideration¹⁰.

The Gujarat communal massacres and violence that followed shortly thereafter were also carried out according to carefully prepared plans. The Gujarat violence was therefore part of the larger plan of communal politics. The burning alive of men, women and children, the selective looting and burning of shops and homes and call for economic boycott of persons belonging to minority community, which were barbaric and were nothing less than genocide. For the first time in our history a state government has displayed a thoroughly communal approach colluding with the attackers and justifying their actions¹¹. The barbaric events of Gujarat must now serve as a last warning of what is in store for our country if the politics of communalism remains unchallenged. Communalism is no longer only a vehicle to capture votes and come to power.

Causes of Communalism

- The presence of communal parties & organization like Hindu Maha sabha is one of the main cause of communalism in India. They not only represent particular communities but also thrive on communal politics. To achieve their inner objectives they often create communal tensions among the people.
- The communal groups present among certain religions also create tension among the people as their ideologies always differ. They do not look at economic perspective but they want their presence felt among the society.
- Economic rivalry between small sections of communities also flares communalism in the society. It certain section of society economically suppressed tries to rise up, is also taken in bad taste by large section of society belonging to different religion.
- Another cause which has also lead to communalism is the partial behaviour of law enforcement agencies.
- We cannot ignore the historical communal legacy which was adopted by British to curb the rising tide of nationalism in India. For this they encouraged the muslim community to establish their own educational institution.
- Chauvnmism Shown by particular religious groups also add to the fire of communalism. Hindus considering India their homeland and floating the idea of Muslims to leave India and go to Pakistan also add tension in the Society.
- Caste based politics also help perpetuating the communal differences. For taking votes religion is always main agenda among politics parties.

Suggestion or preventive measures to curb Communalism:-

The communalism of society is being done at a time when people of all religions are facing problems of poverty, unemployment, lack of access to education and health and decline in values, communal division, caste and Gender oppression. People's movement against these problems can be successful only if we accept the need for complete separation of religion from politics and preventive measures should be adopted to eradicate communal violence.

- Communal harmony should also be made a compulsory syllabi in schools and colleges so that the citizens are fully sensitized to this problem from the childhood.
- Banning communal organization and imposing community fire in the riot affected areas are considered the two important remedies of the problem.
- Instructions to T.V. and media to avoid of coverage of news and views likely to promote communal prejudice.
- Severe punishments like life imprisonment for instigating communal riots and death sentence for committing communal violence must be prescribed in the law.
- Educational institutions should serve as 'agencies' to extend this message to all the communities. These institutions should encourage the celebrations of festivals among various communities.
- The communalization of civil society also needs to be checked because it leads to more communal riots and violence.
- Communal press should be banned and legal action can be taken against commercial writers.
- Preventive measure includes educative efforts to inculcate among the people mutual respect and tolerance towards all the religions.
- Communalization of the state and of the political elite in power has to be checked because it leads to inaction against communalism.
- Every community which prevailed in society should learn to separate religion from politics.
- Communal parties should be banned and peace keeping samities should be appointed.
- There should be special courts to try cases of communal violence so that those who are indulge in them may be punished.
- An anti-riot force with substantial minority representation should be set up.
- Strict watch must be kept on places of religious worship and they should not be allowed to be used by communal elements.
- Political parties must look to the citizens not as voters but as people and people must consider each other belonging to same nation and be compassionate with each other and also part of humanity in the interest of communal harmony.

To control the communalism we need other alternative ideology to neutralize the communal ideologies. Secularism provides such ideological weapons to fight with communalism. The progress of the country depends upon the communal harmony and brotherhood among the inmates of that country. The lack of economic growth, ill health, services, deteriorated system of education and ill device infrastructure is the cause of communal tension. If the above said ill-bred functions are curtailed and the youth are adjusted and given employment then the menace of communalism

does not come into the fore and the ill devised ideas of the politicians would not pollute the minds of the innocent people as all would be busy in the field of work. A principled state policy of secularism may or may not immediately stop Hindu-Muslim riots today but it will at least prevent to some extent, communalism of every aspect of society. Absence of communalism leads to National Integration.

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'Omics' approaches in developing combined drought and heat tolerance in food crops

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Received: 24 March 2021 / Accepted: 24 June 2021

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Abstract

Global climate change will significantly increase the intensity and frequency of hot, dry days. The simultaneous occurrence of drought and heat stress is also likely to increase, influencing various agronomic characteristics, such as biomass and other growth traits, phenology, and yield-contributing traits, of various crops. At the same time, vital physiological traits will be seriously disrupted, including leaf water content, canopy temperature depression, membrane stability, photosynthesis, and related attributes such as chlorophyll content, stomatal conductance, and chlorophyll fluorescence. Several metabolic processes contributing to general growth and development will be restricted, along with the production of reactive oxygen species (ROS) that negatively affect cellular homeostasis. Plants have adaptive defense strategies, such as ROS-scavenging mechanisms, osmolyte production, secondary metabolite modulation, and different phytohormones, which can help distinguish tolerant crop genotypes. Understanding plant responses to combined drought/heat stress at various organizational levels is vital for developing stress-resilient crops. Elucidating the genomic, proteomic, and metabolic responses of various crops, particularly tolerant genotypes, to identify tolerance mechanisms will markedly enhance the continuing efforts to introduce combined drought/heat stress tolerance. Besides agronomic management, genetic engineering and molecular breeding approaches have great potential in this direction.

Keywords Water stress · High temperature · Cereals · Legumes · Genomics · Proteomics · Metabolomics

Introduction

Rising annual mean temperatures, modified precipitation patterns, and emerging drought stress in many regions affect agriculture at the global level by limiting crop yield potential (Awasthi et al. 2014). Drought and heat stress are two key factors confining crop productivity (Barnabás et al. 2008). Drought stress occurs when plant available water is very low, exposing plants to unfavorable growth conditions (Zhu 2001; Egert and Tevini 2002). Heat stress is often defined as the increase in temperature beyond a threshold level for an extended period that may cause irreversible damage and inhibit plant growth and development (Wahid 2007; Bitá and Gerats 2013). Drought often occurs with heat, especially during summer (Lamaoui et al. 2018), causing severe damage to plants (Sehgal et al. 2018). Decades of research have significantly improved our understanding of how plants encounter drought or heat stress individually in the field, and how these stresses affect plant growth and development (Rennenberg et al. 2006; Fahad et al. 2017a, b; Lamaoui

Communicated by Manzer H. Siddiqui.

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et al. 2018). With the frequency of combined drought/heat stress estimated to increase due to climate change (IPCC 2014), it is vital to study the effects of this stress combination to enhance the tolerance of various crops and minimize yield losses.

Most studies in the last decade have focused on crop responses to a single stress (Chew and Halliday 2011; Siddiqui et al. 2015). However, crops are often subjected to a combination of stresses in the field (Mittler 2006; Suzuki et al. 2014; Mahalingam and Bregitzer 2019; Qaseem et al. 2019a, b). Drought and heat stress are interlinked, with the combined stress causing more crop losses than individual stresses (Shah and Paulsen 2003; Dreesen et al. 2012). The effect of combined drought/heat stress has been studied in model plants and crops at different developmental stages at the agronomic (Mahrookashani et al. 2017; Lawas et al. 2018a), physiological (Pradhan et al. 2012; Mahrookashani et al. 2017), molecular (Rizhsky et al. 2002; Zhou et al. 2016), and metabolic (Rizhsky et al. 2004; Templer et al. 2017; Lawas et al. 2019) levels. In nature, combined drought/heat stress results in a unique plant response that differs from individual stresses (Zandalinas et al. 2018). The extent of plant damage depends on the severity and duration of the stresses and the growth stage exposed to the stresses. Crop plants at the reproductive stage are more susceptible to combined drought/heat stress than individual stresses (Barnabás et al. 2008; Zandalinas et al. 2016). Studies have also reported cultivar-specific responses, enabling the identification of cultivars with superior tolerance to combined drought/heat stress (Awasthi et al. 2017; Athar et al. 2019; Zhou et al. 2020). In general, combined drought/heat stress adversely affects plant phenology and physiology, including growth, chlorophyll content, leaf photosynthesis, grain number, spikelet fertility, grain-filling duration, and grain yield (Shah and Paulsen 2003; Barnabás et al. 2008; Prasad et al. 2011; Perdomo et al. 2017; Sehgal et al. 2018).

Combined drought/heat stress can severely affect the yield of staple food crops, including legumes such as soybean (*Glycine max*), chickpea (*Cicer arietinum*) and lentil (*Lens culinaris*) (Awasthi et al. 2014; Sehgal et al. 2017) and cereals such as wheat (*Triticum aestivum* L.) (Prasad et al. 2011), maize (*Zea mays* L.) (Cairns et al. 2013) and rice (*Oryza sativa* L.) (Lawas et al. 2018b). The yield losses are mainly attributed to changes in plant water balance (Machado and Paulsen 2001) and disruptions in photosynthesis (Rizhsky et al. 2002), sucrose metabolism and carbohydrate assimilation (Awasthi et al. 2014), increased oxidative damage, and impaired nitrogen metabolism and fixation (Trachsel et al. 2016). Crop plants such as maize and wheat, which tolerate heat or drought as individual stresses, do not necessarily

endure combined drought/heat stress (Cairns et al. 2013; Qaseem et al. 2019a, b).

It is important to understand the various plant mechanisms at different organizational levels, including growth, physiology, metabolites (metabolomics), proteins (proteomics), and genes (genomics), to develop strategies for designing crops with superior tolerance to drought and heat stress. Understanding crop responses, especially at the 'omics' level, will enhance the quality and meaning of the derived biological information to develop stress-resilient cultivars. Here, we present updated information on how various traits involving growth, physiology, genes, proteins, and metabolites are affected in various crops under combined drought/heat stress. We then identify various strategies for developing crops resilient to combined drought/heat stress. The general effects of combined drought/heat stress at various organizational levels are presented in Fig. 1.

Growth

Growth can be assessed using various vegetative traits, including plant height, branching, leaf area, and biomass. Combined drought/heat stress reduces plant growth, accelerates senescence, and causes premature death, relative to heat or drought stress alone (Machado and Paulsen 2001) in various crops. For example, combined drought/heat stress decreased plant height and biomass in lentil (*Lens culinaris*; Sehgal et al. 2017; Rajendran et al. 2020), maize (Athar et al. 2019), potato (*Solanum tuberosum* L.; Handayani and Watanabe 2020), *Sorghum bicolor* (Machado and Paulsen 2001) and wheat (*Triticum aestivum*; Farooq et al. 2017; Qaseem et al. 2019a, b) (Table 1). Combined drought/heat stress severely inhibited various growth traits (leaf area, leaf number, stomatal dimensions) in 21-day-old tomato (*Solanum lycopersicum*) seedlings (Zhou et al. 2017) and adult plants (Zhou et al. 2019). Similarly, combined stress reduced plant height and biomass in chickpea (Awasthi et al. 2014, 2017), shoot dry weight in faba bean (Siddiqui et al. 2015), common bean (Seidel et al. 2016), maize (Cairns et al. 2013), and barley (Mahalingam and Bregitzer 2019). Rapid leaf senescence was reported in wheat and sorghum (Machado and Paulsen 2001) exposed to combined drought/heat stress. Combined drought/heat stress accelerated leaf senescence, leaf rolling, and cuticular wax deposition and decreased plant growth (Machado and Paulsen 2001). These findings indicate that combined drought/heat stress seriously affects various growth-related traits, compared to individual stresses, which can be used to evaluate contrasting crop genotypes for selection/screening for resilience to combined drought/heat stress. For instance, in a recent study, 162 lentil (*Lens culinaris* Medikus) accessions screened for tolerance to heat stress and combined drought/heat stress at two field

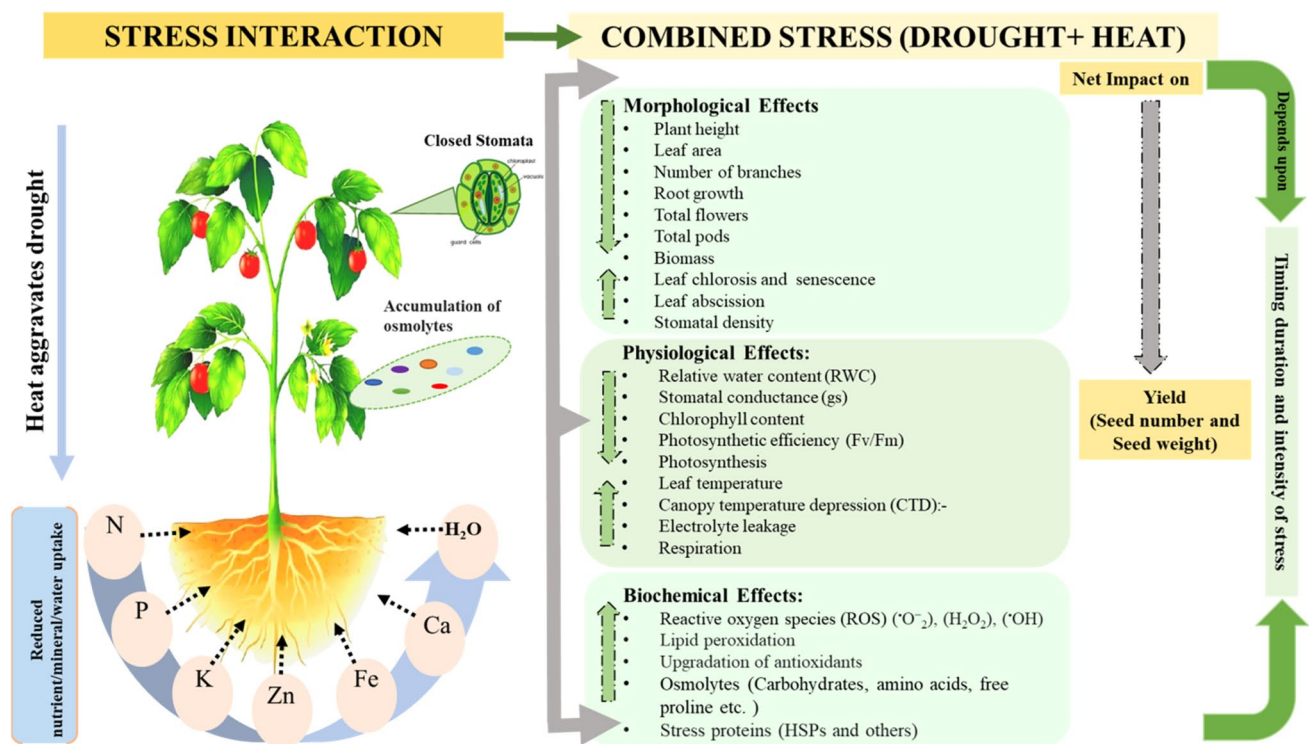


Fig. 1 Simultaneous occurrence of drought and heat stress significantly affects the various traits (morphological, physiological, biochemical and genes) of the plants. Severity of stress depends on the timing, duration and intensity of stress. Visible damages in the plants include reduction in plant height, leaf area, number of branches, root growth, total flowers, pods and biomass, acceleration of leaf senescence, chlorosis and stomatal density. At physiological level, relative

leaf water content, stomatal conductance, chlorophyll concentration and photosynthetic traits decrease canopy temperature depression, electrolyte leakage, respiration and oxidative stress increase. Plants adapt themselves under such conditions by modulating the expressions of antioxidants, osmolytes, antioxidants and stress proteins. All these traits synergistically affect the yield and resulted in major agronomic losses

locations in Morocco revealed that plant height, biomass, and the number of primary, secondary and tertiary branches per plant could serve as vital indicators for combined stress tolerance (Rajendran et al. 2020).

Root system architecture

Root system architecture (RSA) is an important plant agronomic trait assisting plant development and the acquisition of available soil nutrients and water (Koevoets et al. 2016; Morris et al. 2017). RSA plays a pivotal role in improving plant adaptation and plasticity under various stresses, especially water scarcity (Ye et al. 2018). Drought affects root function by altering cell water permeability and influencing root growth and RSA (Fahad et al. 2017a, b), as reported in several plant species, including wheat (Fang et al. 2017), maize (Li et al. 2015a, b), rice (Cairns et al. 2004), and chickpea (Kashiwagi et al. 2005). Root function is inhibited due to alterations in hydraulics (cell water permeability), which disrupts mineral uptake (Garg 2003). Plants exposed to mild drought can increase primary root growth to move

into deeper layers or enhance the surface area of shallow roots, and change RSA to absorb more water and nutrients (Lynch and Brown 2001; Fahad et al. 2017a, b).

Heat stress inhibits root proliferation, in terms of number, mass and growth, as reported for canola (Wu et al. 2017) and maize (Trachsel et al. 2010), which eventually restricts water and nutrient transport to shoots (Huang et al. 2012). In warmer environments, plant water requirements increase due to water loss from evapotranspiration and reduced water uptake by roots, resulting in water deficit stress (Heckathorn et al. 2013). Water uptake occurs either through aquaporins (Cabañero et al. 2004) or the plasma membrane involving diffusion (Maurel et al. 2015). Heat stress inhibits the expression of aquaporins and increases membrane rigidity to decrease water uptake (Iglesias-Acosta et al. 2010; Ionenko et al. 2010). Root growth is inhibited in warmer environments, reducing macro- and micro-element uptake in tomato (Giri et al. 2017), and maize hybrids (Hussain et al. 2019a, b).

There are relatively few studies on the effect of combined drought/heat stress on RSA. Under combined drought/heat stress, a deeper root system provides more tolerance than

Table 1 Summary of experimental details and genotypes of various crops in response to combined drought and heat stress

Trait	Crop	Growth condition	Stress treatment stage	Genotypes studied	References
Growth	Lentil	Field conditions; HS: > 32 °C; DS: withholding at flowering initiation stage onward	Reproductive stage	162 germplasm accessions	
	Wheat	Glasshouse; HS: > 32 °C; DS: 35% WHC	Throughout growing season	Mairaj-2008, C-591, Uqab-2000, BARS-2009, Dharabi-2011, Chakwal-50 Sehr-2006, Shafaq-2006, Fsd-2008, Lasani-2008	Farooq et al. (2017)
	Wheat and sorghum	Glasshouse; HS: 36/30 °C; DS: 30% WHC	Pre-anthesis to maturity	108 advance wheat lines	Qaseem et al. (2019a, b)
	Tomato	Growth chamber; HS: 35/30 and 40/3 °C; DS: withholding water for 14 d Climate chamber; HS: 32/26 °C; DS: without irrigation for 5 d	Reproductive stage	cv. Len, cv. C305	Machado and Paulsen (2001)
	Maize	Greenhouse; HS: 38 °C; DS: 50% FC for 15 d	Seedling stage	Arvento, LA1994, LA2093	Zhou et al. (2017)
	Potato	Climate chamber; HS: 30 ± 1 °C; DS: 40–60% FC for 21 d	Reproductive stage	Xida 889, Xida 319	Athar et al. (2019)
	Chickpea	Field; HS: < 32 – 20 °C; DS: WHC for 7 d	Vegetative stage	Breeding lines (L1: 84.194.30; L2: 86.61.26; L3: 87HW13.7, L4: DG81-68)	Handayani and Watanabe (2020)
	Barley	Growth chamber; HS: 36 °C; DS: 18% FC for 4 d	Seed filling stage	ICC1356, ICC15614, ICC4567, ICC5912, ICC8950, ICC3776	Awasthi et al. (2014)
	Kentucky bluegrass	Growth chamber; HS: 35/30 °C; DS: 17% FC for 35 d	Vegetative stage	18 varieties	Mahalingam and Bregitzer (2019)
					Jiang and Huang (2000)

Table 1 (continued)

Trait	Crop	Growth condition	Stress treatment stage	Genotypes studied	References
RWC	Tea	Field; HS: > 40/30 °C for 50 d	Vegetative stage	Longyan, Xianglin 78, Xianglin 16	Wang et al. (2015)
	Grasses tall fescue and ryegrass	Growth chamber; HS: 35/30 °C; DS: withholding water for 35 d	35 d after planting	Mustang, Bright-star (II)	Jiang and Huang (2001a, b)
	Wheat	Growth chamber; HS: 32/24 °C, DS: water withdrawal for 5 d	Reproductive stage	Plainsman V, Cappelle Desprez	Fabián et al. (2019)
	Wheat and sorghum	Glasshouse; HS: 36/30 °C, DS: 30% FC	Heading to maturity	108 advance wheat lines	Qaseem et al. (2019a, b)
		Growth chamber; HS: 25/20, 35/30, and 40/35 °C, DS: water withdrawal for 14 d	Vegetative stage	cv. Len, cv. C305	Machado and Paulsen (2001)
	Potato	Climate chamber; HS: 30 ± 1 °C; DS: 40–60% FC for 21 d	Vegetative stage	Breeding lines (L1: 84.194.30; L2: 86.61.26; L3: 87HW 13.7, and L4: DG81-68)	Handayani and Watanabe (2020)
	Tomato	Growth chamber; HS: 45 °C; DS: 60% FC for 24 h	Vegetative stage		Raja et al. (2020)
		Growth chamber; HS: 38/30 °C; DS: without irrigation for 6 d	Vegetative stage	Sufen No. 14 as CV1; Jinlingmeiyu as CV2	Zhou et al. (2019)
	<i>Nonelia insignis</i>	Climate chamber; HS: 25, 40 and 50 °C; DS: withholding water for 6 d	Vegetative stage		Zheng et al. (2019)

Table 1 (continued)

Trait	Crop	Growth condition	Stress treatment stage	Genotypes studied	References
Chlorophyll content	Chickpea	Field; HS: 50 °C; DS: withholding water	Seed filling to maturity	ICC1356, ICC15614, ICC4567, ICC5912, ICC8950, ICC3776	Awasthi et al. (2017)
	Wheat	Field; HS: 31/18 °C and 34/22 °C, drought stress withholding water for 18 d Glasshouse; HS: 36/30 °C, DS: 30% FC Glasshouse; HS: > 32 °C; DS: 35% WHC	Heading to maturity Pre-anthesis to maturity	Pavon-76 and Seri-82 108 advance wheat lines	Prasad et al. (2011) Qaseem et al. (2019a, b)
	Lentil	Field study; HS: > 32 °C; DS: 50% WHC	Throughout growing season Seed filling to maturity	Mairaj-2008, C-591, Uqab-2000, BARS-2009, Dharabi-2011, Chakwal-50, Sehr-2006, Shafaq-2006, Fsd-2008, Lasami-2008 DPL53, JL1, ILL 2150, ILL 4345), 1G 2507, 1G 4258, 1G 3973, 1G 3964	Farooq et al. (2017) Sehgal et al. (2017)
	Tomato	Greenhouse; HS: 25–45 °C; DS: 20% FC for 14 d Climate chamber; HS: 32/26 °C; DS: without irrigation for 5 d Growth chamber; HS: 45 °C; DS: 60% FC for 24 h	Four-leaf stage Seedling stage Vegetative stage	Nagariang, Hybrid 61 and Moskvich Arvento, LA1994 and LA2093	Nankishore and Farrell (2016) Zhou et al. (2017) Raja et al. (2020)
	Potato	Climate chamber; HS: 30 ± 1 °C; DS: 40–60% FC for 21 d	Vegetative stage	Breeding lines (L1: 84.194.30; L2: 86.61.26; L3: 87HW13.7, and L4: DG81-68)	Handayani and Watanabe (2020)

Table 1 (continued)

Trait	Crop	Growth condition	Stress treatment stage	Genotypes studied	References
Cell membrane thermostability	Lentil	Field conditions; HS: > 30/20 °C; DS: 50% FC	Seed filling to maturity	IG 2507, IG 4258, DPL53, JL1, ILL 2150, ILL 4345, IG 3973, IG 3964	Sehgal et al. (2017)
	Kentucky bluegrass	Green house; HS: 37/26 °C; DS: withholding water for 21 d	Vegetative stages	Penncross	Liu et al. (2008)
Photosynthesis	Chickpea	Field conditions; HS: > 32/20 °C; DS: 54–57% field capacity for 7 d	Seed filling stage	ICC1356, ICC15614, ICC4567, ICC5912, ICC8950, ICC3776	Awasthi et al. (2014)
	Maize	Field conditions; HS: > 32/20 °C; DS: till RLWC 45–50%	Seed filling to maturity	ICC1356, ICC15614, ICC4567, ICC5912, ICC8950, ICC3776	Awasthi et al. (2017)
	Lucerne	Greenhouse; HS: 38/30 °C; DS: 50% for 15 d	Tasseling stage	Xida 889, Xida 319	Hussain et al. (2019a, b)
Photosynthesis	Wheat	Growth chamber; HS: 38 °C for 72 h; DS: 10–20% FC for 72 h	Seedling stage		An et al. (2014)
	Wheat	Growth chamber; HS: 40 °C for 5 h; DS: withholding water for 7 d	Seedling stage	Katya, Sadovo	Grigorova et al. (2011a, b)
	Tall fescue and perennial ryegrass	Glasshouse; HS: 36/30 °C, DS: 30% FC	Pre-anthesis stages to maturity	108 wheat lines	Qaseem et al. (2019a, b)
	Wheat	Greenhouse; HS: 40 °C for 4 h; DS: till RLWC 78–82% for 6–7 d	Flowering stage	T6, WT	Wang et al. (2010)
Photosynthesis	Arabidopsis	Growth chamber; HS: 35/30 °C, DS: withholding water for 35 d	35 d after planting		Jiang and Huang (2001a, b)
	Wheat	Climate chamber; HS: 38/30 °C; DS: 45% FC	32 d after sowing		Zinta et al. (2014)
Photosynthesis	Wheat	Greenhouse; HS: 40 °C for 4 h; DS: till RLWC 78–82% for 6–7 d	Flowering stage	T6, WT	Wang et al. (2010)
	Wheat	Glasshouse; HS: 36/30 °C; DS: 30% FC	Pre-anthesis to maturity	108 wheat lines	Qaseem et al. (2019a, b)
	Wheat	Growth chamber; HS: 31/18 °C and 34/22 °C, DS: withholding water for 18 d	Heading stage	Seri-82, Pavon 76	Prasad et al. (2011)
Photosynthesis	Wheat	Phytotron; HS: 35 °C; DS: 40–45% FC	12 d after heading	Mv Makaroni, Bankuti 1201, Fatima 2, Mv Mambo, Mv Mariska, G K Othalom	Balla et al. (2006)

Table 1 (continued)

Trait	Crop	Growth condition	Stress treatment stage	Genotypes studied	References
	Tobacco	Growth chamber; HS: 37 °C for 1 h, 40 °C for 6 h; DS: RLWC 65–70%	Vegetative stage	Xanthi-nc NN	Rizhsky et al. (2002)
	Poplar	Greenhouse; HS: 40 °C, DS: no watering for 0, 6, 12, 24, or 48 h	60 days after planting		Li et al. (2014)
	Tomato	Greenhouse; HS: 25–45 °C; DS: 20% FC for 14 d Greenhouse; HS: 32/26 °C; DS: without irrigation for 5 d	Vegetative stage Seedling stage	Hybrid 61, Nagcarlang, Moskvich Arvento, LA 1994, LA 2093	Nankishore and Farrell (2016) Zhou et al. (2017)
	Lucerne	Growth chamber; HS: 35/30 °C; DS: no irrigation for 12 h Growth chamber; HS: 38 °C for 72 h; DS: 10–20% FC for 72 h	27-day-old plants Seedling stage	LA 2093, OuBei AS 801, Aohan	Zhou et al. (2020) An et al. (2014)
	Barley	Greenhouse; HS: 36 °C; DS: 100 ml water for 4 d	Heading stage	Crystal, Garnet Bowman, Conrad	Mahalingam and Breigitzer (2019)
	Chickpea	Field conditions; HS: > 32/20 °C; DS: till RLWC 45–50%	Seed filling to maturity	ICC1356, ICC15614, ICC4567, ICC5912, ICC8950, ICC3776	Awasthi et al. (2017)
	Lentil	Field conditions; HS: > 30/20 °C; DS: 50% FC	Seed filling stage	IG 2507, IG 4258, DPL53, JLI, ILL 2150, ILL 4345, IG 3973, IG 3964	Sehgal et al. (2017)
	Mustard	Growth chamber; HS: 33/26 °C; DS: 30% FC for 7 d	Three-leaf stage	Variety Fenja	Diksaityt et al. (2019)
	Maize	Greenhouse; HS: 38/30 °C; DS: 50% for 15 d	Tasseling stage	Xida 319, Xida 889	Hussain et al. (2019a, b)

Table 1 (continued)

Trait	Crop	Growth condition	Stress treatment stage	Genotypes studied	References
Stomatal conductance	Tomato	Greenhouse; HS: 25–45 °C, DS: 20% FC for 14 d	Four-leaf stage	Nagcarlang, Hybrid 61, Moskvich	Nankishore and Farrell (2016)
	Cotton	Field studies, HS: > 35 °C; DS: 35% FC for 2.5 months	Vegetative stage	Monseratt Sea Island (MS), Pima 32 (P32), Pima S-6 (S6), Pima S-7 (S7)	Carmo-Silva et al. (2012)
	Lentil	Field conditions, HS: > 33/28 °C; DS: 50% FC	Seed filling to maturity	DPL 53, DS LL699	Sehgal et al. (2017)
	Desert grass	Greenhouse, HS: 37 °C; DS: 50% FC for 5 and 10 d	3-month-old plants		Alhaithloul (2019)
	Tall fescue	Growth chamber; HS: 30/25 °C and DS: 50% FC for 28 d	Vegetative stage		Yu et al. (2012)
Chlorophyll fluorescence	Wheat	Growth chamber studies; HS: 35/20 °C, DS: 40–45% for 15 d	12 d after heading (for 15 days)	Plainsman V, Fatima 2, Mv Mamb6, Mv Mariska, Maris Huntsman, Bdnkuti 1201, Bezostaya 1, Mv Magma, Mv 15, and GK Othalom, the spelt variety Frankenkorn, Mv Makaro	Balla et al. (2006)
	Tomato	Greenhouse, HS: 25–45 °C, DS: 20% FC for 14 d	Four-leaf stage	Nagcarlang, Hybrid 61, Moskvich	Nankishore and Farrell (2016)
	Chickpea	Field studies; HS: > 32/20 °C, DS: 42–45%	Seed filling to maturity	ICC4567, ICC5912, ICC8950, ICC3776	Awasthi et al. (2017)
	Wild barley	Climate chamber studies; HT: 42 °C, DS: –2.5 MPa	Two-leaf stage for three weeks		Jedrnowski et al. (2015)
	Lentil	Field studies; HS: 33/28 °C, DS: 50% FC from seed filling to maturity	Seed filling stage	DPL 53, LL699	Sehgal et al. (2019)
	Rice	Field studies; HS: 36.4–37.8 °C; DS: water withheld for 14 d	Anthesis stage	ADT 43, TKM9, N22	Kumar et al. (2014)

Table 1 (continued)

Trait	Crop	Growth condition	Stress treatment stage	Genotypes studied	References
Canopy temperature depression	Cotton	Field studies; HS: > 35 °C, DS: 35% FC for 2.5 months	Vegetative stage	Monseratt Sea Island (MS), Pima 32 (P32), Pima S-6 (S6), Pima S-7 (S7)	Carmo-silva et al. (2012)
	Tomato	Greenhouse; HS: 25–45 °C, DS: 20% FC for 14 d	Four-leaf stage	Nagcarlang, Hybrid 61, Moskvich	Nankishore and Farrell (2016)
	Chickpea	Field studies; HS: > 32/20 °C, DS: 42–45%	Seed filling to maturity	ICC4567, ICC5912, ICC8950, ICC3776	Awasthi et al. (2017)
	Wheat	Glasshouse; HS: 36/30 °C, DS: 30% FC	Pre-anthesis to maturity	108 advanced wheat lines	Qaseem et al. (2019a, b)
	Durum wheat	Growth chamber; HS: 37/27 °C, DS: 12% FC	Booting stage	DBA Aurora, L2, L1, WID 802, L5, L4, DBA Spes, EGA Bellaroi, L3, L6	Liu et al. (2019)
	Maize	Greenhouse studies; HS: 38/30 °C, DS: 50% FC	Tasseling stage for 15 d	Xida889, Xida319	Hussain et al. (2019a, b)
	Rice	Growth chamber; HS: 30/27 °C, DS: water withheld for 14 d	Reproductive stage	N/A, WAT 1395-B-24-2, WITA 4, WAB923-B-6-AL1, WAB 569-35-1-1-1-HB, WAB 880-1-38-20-28-P1-HB, Zong geng	Mukamuhirwa et al. (2019)
	Canola	Greenhouse studies; HS: 29 °C, DS: 30% FC	Bolting to final harvest	N99-508	Elferjani and Soolanayakana-hally (2018)
	Soybean	Greenhouse conditions; HS: 38/26 and 42/28 °C, DS: 2.5 MPa	Vegetative and reproductive stages	JS 97-52, EC 538828	Jumrani and Bhattia (2018)

Table 1 (continued)

Trait	Crop	Growth condition	Stress treatment stage	Genotypes studied	References
ROS and antioxidants	Poplar	Greenhouse; HS: 40 °C, DS: no watering for 0, 6, 12, 24, or 48 h	60 d after planting		Li et al. (2014)
	Chickpea	Field conditions; HS: > 32/20 °C; DS: till RLWC 45–50%	Seed filling to maturity	ICC1356, ICC15614, ICC4567, ICC5912, ICC8950, ICC3776	Awasthi et al. (2017)
	Cotton	Growth chamber; HS: 30–45 °C (1 °C/15 min); DS: 40% PEG 6000 for 10 d	Three-week-old seedlings	Nazilli 84-S, M-503	Sekmen et al. (2014)
	Tobacco	Growth chamber; HS: 40 °C for 2 h; DS: withholding water for 10 d	Six-week-old plants	M51 and 35S:P5CSF129A	Cvikrova et al. (2013)
	Tomato	Growth chamber; HS: 45 °C for 24 h; DS: withholding water for 10 d until RWC decreased to 60%	Seedling stage		Raja et al. (2020)
	Bread wheat	Field conditions; HS: > 35 °C; DS: 50% FC	Reproductive stage		Sattar et al. (2020)
Carbohydrate metabolism	Chickpea	Field conditions; HS: > 32/20 °C; DS: 54–57% FC for 7 d	Seed filling stage	ICC1356, ICC15614, ICC4567, ICC5912, ICC8950, ICC3776	Awasthi et al. (2014)
	Tomato	Greenhouse; HS: 32/26 °C; DS: without irrigation for 5 d	Seedling stage	Arvento, LA 1994, LA 2093	Zhou et al. (2017)
Osmolytes and amino acid	Rice	Greenhouse; HS: 35 °C; DS: 35–40% FC for 12 d	Anthesis		Hanif et al. (2020)
	Bread wheat	Field conditions; HS: > 35 °C; DS: 50% FC	Reproductive stage		Sattar et al. (2020)
		Glass house; HS: 36/30 °C; DS: 30% FC	Pre-anthesis to maturity	108 wheat lines	Qaseem et al. (2019a, b)

Table 1 (continued)

Trait	Crop	Growth condition	Stress treatment stage	Genotypes studied	References
Yield	Lentil	Field studies, HS: 33/28 °C, DS: 50% FC	Seed filling to maturity	DPL 53, LL699	Sehgal et al. (2019)
	Chickpea	Field studies; HS: > 32/20 °C, DS: 42–45% FC	Seed filling to maturity	ICC4567, ICC5912, ICC8950, ICC3776	Awasthi et al. (2017)
	Wheat	Glass house; HS: 36/30 °C, DS: 30% FC Growth chamber studies; HS: 37/27 °C, DS: 12% FC at 5, 15, 25, 35, 45 d after anthesis Greenhouse studies; HS: 38/30 °C, DS: 50% FC	Pre-anthesis to maturity Booting stage Tasseling stage for 15 d	108 advanced wheat lines DBA Aurora, L2, L1, WID 802, L5, L4, DBA Spes, EGA Bellaroi, L3, L6 Xida889, Xida319	Qaseem et al. (2019a, b) Liu et al. (2019) Hussain et al. (2019a, b)
	Maize	Greenhouse studies; HS: 38/30 °C, DS: 50% FC	Tasseling stage for 15 d	Xida889, Xida319	Hussain et al. (2019a, b)
	Rice	Growth chamber; HS: 30/27 °C, DS: water withheld for 14 d	Reproductive stage	N/A, WAT 1395-B-24-2, WITA 4, WAB923-B-6-ALI, WAB 569-35-1-1-1-HB, WAB 880-1-38-20-28-PI-HB, Zong geng	Mukamuhirwa et al. (2019)
	Canola	Greenhouse studies; HS: 29 °C, DS: 30% FC	Bolting to final harvest	N99-508	Elferjani and Soolanayakana-hally (2018)
	Soybean	Greenhouse conditions; HS: 38/26 and 42/28 °C; DS: 2.5 MPa for vegetative stage at four-leaf stage and reproductive stage at seed filling stage	Vegetative and reproductive stages	JS 97-52, EC 538828	Jumrani and Bhatia (2018)

DS drought stress; HS heat stress; WHC water-holding capacity; FC field capacity; ROS reactive oxygen species; RWC relative water content

shallow roots (Jiang and Huang 2001a, b; Vescio et al. 2021). A deeper root system has great potential for improving crop tolerance to combined drought/heat stress. Vescio et al. (2021) adopted a distinct approach for studying growth and morphological parameters of different root types (primary, primary lateral, and seminal roots) in maize seedlings under combined heat (32 °C) and drought (30% field capacity) stress. The maize root system modifies specific root types to tackle combined drought/heat stress. Among the 11 traits studied for primary roots, branching density, root length ratio, root mass ratio, and tissue density increased under combined stress. Among primary lateral roots, morphological traits such as length, surface area, fitness, root length ratio, and average length increased compared to the control. Seminal roots were less affected than the other root types, with only fresh weight decreasing compared to the control. Similar studies have been reported in grasses, which could provide useful insights into the potential responses of crops to combined drought/heat stress. For example, tall fescue (*Festuca arundinacea* L.) and perennial ryegrass (*Lolium perenne* L.) exposed to heat (35 °C day/30 °C night) and drought (induced by withholding irrigation) in growth chambers for 35 days drastically reduced root dry weight in all the soil layers (0–20, 20–40, and 40–60 cm) but to a greater extent in 0–20 cm, and reduced root viability more than heat stress alone (Jiang and Huang 2001a, b). Tall fescue had more root viability and root dry weight in all soil layers than perennial ryegrass, which would help to withdraw more water, favor transpirational cooling, and maintain higher photosynthetic activity (Jiang and Huang 2001a, b). Bonos and Murphy (1999) reported that tolerant cultivars of Kentucky bluegrass produced 19% and 65% more roots in the 15–30 cm and 30–40 cm soil layers and had a 5 °C cooler canopy temperature than sensitive cultivars under combined drought/heat stress. These root behaviors are important in combating the effects of combined drought/heat stress and need to be addressed and integrated into breeding approaches to develop tolerant varieties.

Phenology

Phenology is a good indicator of stress sensitivity in crops (Sabagh et al. 2020); however, there are few reports on the effect of combined drought/heat stress on this trait. In chickpea grown in the field, combined drought/heat stress markedly reduced days to podding and maturity and flowering and podding durations, especially in heat- and drought-sensitive genotypes (Awasthi et al. 2017). In a glasshouse study on wheat genotypes, heat stress reduced days to anthesis (DA) and days to maturity (DM) by 16% and 20%, respectively, while drought stress reduced DA and DM by 10% and 14%, respectively, and combined stress reduced DA and DM

by 25% and 31%, respectively (Qaseem et al. 2019a, b). In a field study on lentil, combined drought/heat stress markedly reduced flowering and podding durations and DM (Sehgal et al. 2017). A more recent study on lentil reported that combined drought/heat stress reduced crop duration more than individual stresses (Rajendran et al. 2020). In maize (*Zea mays* L.), combined drought/heat stress significantly reduced average DA, relative to drought alone (Kumar et al. 2020). Thus, the greater inhibition of yield traits under combined drought/heat stress can be attributed to accelerated phenology, which can decrease flower, pod, and seed numbers, and may serve as vital selection criteria for combined stress tolerance.

Reproductive processes

Timing of the stress during different developmental stages is critical. During flowering, pollen is particularly sensitive to heat stress, especially when combined with drought (Ruan et al. 2010; Jiang et al. 2019). Combined drought/heat stress during the reproductive stage is more detrimental to crop yields than the vegetative stage (Barnabás et al. 2008), particularly for male reproductive components (Cairns et al. 2013). There is emerging evidence of the sensitivity of female reproductive cell and organ development to heat or drought stress per se in sorghum (Jain et al. 2007), rice (Jagadish et al. 2010), maize (Djanaguiraman 2018), wheat (Prasad et al. 2011; Onyemaobi et al. 2017), tomato (Pan et al. 2018), and chickpea (Kaloki et al. 2019), with little information on the combined effect of these two stresses. According to a recent study in winter wheat, combined high temperature (32/24 °C) and water withdrawal for five days at gametogenesis altered plant phenology, reduced pollen viability, and modified pistil morphology and anatomy, which reduced fertility and yield in the sensitive genotype (Fábián et al. 2019). The inhibited functionality of female and male reproductive parts accounted for 34% and 66%, respectively (Fábián et al. 2019). These findings suggest that besides male functionality, stigma functionality and fertility are markedly affected under combined drought/heat stress contributing to flower abortion. Further research is needed on how this stress combination affects reproductive development and function in various crops.

Seed filling

The seed filling process is a critical growth stage in grain crops, and includes various biochemical processes related to leaf assimilation and the partitioning of carbohydrates, proteins, and lipids in developing seeds (Barnabás et al. 2008; Awasthi et al. 2014; Farooq et al. 2017; Sehgal et al.

2017). Seed filling relies on the transfer of current assimilates directly to seeds and their reallocation from vegetative reserve pools either pre- or post-anthesis (Yang and Zhang 2006). Seed filling processes and the accumulation of reserves in developing and maturing seeds are highly sensitive to environmental changes, impacting the qualitative and quantitative traits of the final yield (Yang and Zhang 2006). Carbohydrates (sucrose, starch, and soluble sugars) are the primary component of seeds. Sucrose is mainly exported to seeds from the leaves, with some synthesized in seeds (Weschke et al. 2000), which is metabolized into glucose and fructose; glucose is involved in starch formation through various seed enzymes. Drought and heat stress can obstruct the accumulation of various seed constituents, fundamentally starch and proteins (Behboudian et al. 2001; Asthir et al. 2012; Farooq et al. 2017), by inhibiting enzymatic processes of starch (Ahmadi and Baker 2001) and protein (Triboi et al. 2003) synthesis. For example, in lentil seeds, heat stress inhibited the enzymes related to sucrose and starch metabolism (Sehgal et al. 2017), which could further limit sucrose import into seeds. Sucrose and starch synthesis enzymes are also sensitive to combined drought/heat stress in the seeds of other plants. For instance, in wheat exposed to combined drought/heat stress, the rate of transport of non-structural carbohydrates in endosperm tissue diminishes severely (Wardlaw 2002; Plaut et al. 2004). Combined drought/heat stress severely reduced starch accumulation and thus starch synthesizing enzymes, relative to individual stresses, in chickpea (Awasthi et al. 2014) and lentil (Sehgal et al. 2017), resulting in shriveled seeds. Increased β -amylase activity has been reported under high temperature (Kaplan et al. 2006), decreasing starch reserves. However, the reducing sugars produced due to increased amylase activity during stress can assist plants to adapt to environmental stresses (Anderson and Kohorn 2001).

Plant hormones, such as abscisic acid and cytokinins, play an important role in regulating seed filling (Brenner and Cheikh 1995). These phytohormones are involved in determining sink size and strength and the ability of seeds to accumulate biomass (Thakur et al. 2010). For example, auxins, gibberellins, and abscisic acid mediate cell division, enlarge endosperm cells, and regulate the direction and rate of assimilate flow from source to sink tissues (Hansen and Grossmann 2000). No studies have assessed the endogenous levels of phytohormones in seeds of plants subjected to combined drought/heat stress to identify the biochemical mechanisms affecting seed filling.

Yield

Yield traits, mainly seed number, seed weight, and seed filling, are the most affected traits in various crop species in response to combined drought/heat stress. Even a short period of combined drought/heat stress during the reproductive stage adversely affects crop yields (Sehgal et al. 2018). For example, yield losses of up to 50% were reported in wheat exposed to combined drought/heat stress (Lamaoui et al. 2018). Combined drought/heat stress (36/30 °C; 30% field capacity) applied in the glasshouse from heading to maturity in wheat decreased grain yield by 56%, grain number/spike by 40%, harvest index by 41%, spikelet number/spike by 20%, and spike length by 30%, relative to the control (Qaseem et al. 2019a, b; Table 1). In Australian durum wheat (*Triticum turgidum*), grain yield declined by 39% under water deficit stress, 45.5% under heat stress, and 55% under combined heat and water deficit stress (Liu et al. 2019). In rice, combined drought/heat stress (30/27 °C; water withheld for two weeks) imposed at the seedling, tillering, or reproductive stage reduced yield to zero in all seven cultivars (Mukamuhirwa et al. 2019). Combined heat (38/30 °C) and drought (50% field capacity) stress severely reduced various yield traits (ears/plant, kernel rows/ear, kernels/ear, 100 kernel weight, grain yield/plant, and harvest index) in two maize hybrids (Xida889 and Xida319) (Hussain et al. 2019a, b).

In lentil, combined drought/heat stress (32/28 °C; 50% field capacity) from seed filling to maturity reduced seed size and quality in terms of seed starch reserves, storage protein, amino acids, and minerals, seed growth rate by 44–60.2%, seed number/plant by 35–48.7%, and seed weight by 47–59%, compared with control conditions (Sehgal et al. 2019). Similarly, in chickpea, combined drought/heat stress during seed filling decreased seed weight to 1.1–3.9 g/plant, relative to 5.3–6.0 g in the control (Awasthi et al. 2017). Elferjani and Soolanayakanahally (2018) evaluated the response of *Brassica napus* L. to high-temperature (29 °C) and water stress (30% field capacity), individually and combined, from flowering to seed development in a controlled greenhouse. Seed yields declined by 31%, 85%, and 89% for plants exposed to drought, heat, and their combination, respectively, relative to the well-watered control plants. Severe reductions in yield traits due to combined drought/heat stress during seed development indicate the critical sensitivity of this stage, which can be attributed to severe limitations in several cellular processes, especially related to the accumulation of various seed reserves.

Physiological traits

Leaf water status and stomatal conductance

Leaf water status, measured as relative leaf water content (RWC), is a valuable measure of plant water status in terms of the physiological consequences of cellular water deficit and is widely used for abiotic stress assessments (Zhou et al. 2017; Tani et al. 2019). Leaf RWC decreased rapidly under combined drought/heat stress in *Camellia oleifera* (Wang et al. 2015), tall fescue (*Festuca arundinacea* L.) and perennial ryegrass (*Lolium perenne* L.) (Jiang and Huang 2001a, b), wheat (Jiang and Huang 2001a, b; Qaseem et al. 2019a, b), sorghum (Machado and Paulsen 2001), potato (Handayani and Watanabe 2020), and tomato (Zhou et al. 2019; Raja et al. 2020) (Table 1). A reduction in RWC due to combined drought/heat stress is attributable to a rapid decline in stomatal conductance. During heat stress, plants open their stomata to cool their leaves by transpiration; when heat stress is combined with drought stress, plants keep their stomata closed to reduce water loss, and leaf temperatures remain high (Zhang et al. 2010). Under combined drought/heat stress, transpirational regulation and stomatal closure are possible survival strategies for plants; therefore, stomatal conductance is beneficial for assessing the effects of stress on plant water relations, carbon assimilation, and the ability to escape overheating (Nankishore and Farrell 2016). Differences in the gaseous exchange rate through stomata can be recorded by a leaf porometer (Chandra et al. 2017). Fully opened stomata increase CO₂ diffusion, thus increasing the transpiration rate and photosynthetic efficiency of plants (Condon et al. 2007). Therefore, stomatal conductance (g_s) is an important trait for determining the photosynthetic rate and connecting the global carbon cycle with carbon metabolism in plants. There is a linear relationship between stomatal conductance and temperature (Urban et al. 2017).

High stomatal conductance is correlated with high grain yield, which is a useful tool for the early identification of stress-tolerant genotypes. For instance, genetic variation in three tomato varieties (Nagcarlang, Hybrid 61, and Moskvich) under combined drought/heat stress (25–45 °C; 20% field capacity) was examined in a greenhouse. After two days of stress, Hybrid 61 had higher stomatal conductance and lower leaf temperature than the other two varieties (Nankishore and Farrell 2016). A study on cotton demonstrated that stomatal conductance is an informative indicator of genotypic differences in growth under combined drought/heat stress (> 35 °C; 35% water depletion; Carmo-Silva et al. 2012). Similarly, decreased photosynthetic efficiency due to a decline in stomatal conductance was noted in lentil genotypes exposed to combined drought/heat stress (33/28 °C; 50% field capacity) during seed filling in growth chambers

(Sehgal et al. 2019). Stomatal conductance declined in all of the genotypes, relative to control plants, but drought-tolerant genotypes maintained higher stomatal conductance (26%) than sensitive genotypes under combined drought/heat stress (Sehgal et al. 2019). Reductions in leaf water status and stomatal conductance were also reported in *Artemisia sieberi alba*, an important Mediterranean plant, under combined drought/heat stress (37 °C; 50% field capacity) in a greenhouse and tall fescue (*Festuca arundinacea* Schreb. cultivar Rembrandt) under combined stress (30/25 °C; 50% field capacity) in growth chambers (Yu et al. 2012). Thus, examining stomatal behavior under stress conditions is important because it captures the mechanisms regulating the plant water status in response to changing environmental conditions and can be used to assess stomatal acclimation. The stomatal conductance response under combined drought/heat stress deserves attention as it provides a mechanistic model linking it with other physiological traits.

Cell membrane thermostability

Plant cell membranes play a significant role in maintaining cell turgor pressure and physiological functions when subjected to various environmental stresses. Cell membrane stability has been used to differentiate plant tolerance and susceptibility to stresses (Blum and Ebercon 1981; Rahman et al. 2004). Electrolyte leakage has been used as a key parameter to estimate cell membrane stability (Hu et al. 2010). An increase in electrolyte leakage suggests that membrane injury has occurred (Blum and Ebercon 1981). Drought stress damages leaf tissue (cell membranes) more than heat stress, with the damage increasing manifold under combined drought/heat stress. Membrane injury can occur due to the direct impact of high temperature and increased water loss from leaf tissue, impaired lipid–protein configuration, leakage of essential ions, and damaged cellular function causing electrolyte leakage from the stressed tissue (Conde et al. 2011). For example, in lentil, membrane damage increased more under combined drought/heat stress (33–60%) than drought (21–40%) or heat (14–30%) stress alone (Sehgal et al. 2017). In chickpea, membrane damage increased more under combined drought/heat stress (1.5–2.5-fold) than drought (1.3–2.0-fold) or heat (1.2–1.8-fold) stress alone, with a greater impact on sensitive genotypes (Awasthi et al. 2017) (Table 1). Similarly, combined drought/heat stress markedly reduced membrane stability in chickpea (Kumar et al. 2012; Awasthi et al. 2014), lucerne (An et al. 2014), sunflower and maize (Killi et al. 2017), Kentucky bluegrass (*Poa pratensis* L.) (Liu et al. 2008), and wheat (Grigороva et al. 2011a, b; Qaseem et al. 2019a). Membrane stability has been used extensively for assessing stress tolerance; thus, relatively heat-tolerant genotypes showed less membrane damage than heat-sensitive genotypes of lentil

(Sehgal et al. 2018) and chickpea (Awasthi et al. 2017). Heat-tolerant wheat cultivars had better membrane stability than susceptible cultivars under combined drought/heat stress (Liu et al. 2008). A drought-tolerant lucerne genotype (AS801) had less membrane damage than a sensitive genotype (An et al. 2014). For perennial ryegrass (*Poa pratensis* L.) and tall fescue (*Festuca arundinacea* L.), electrolyte leakage was more severe and earlier under combined drought/heat stress than individual stresses. Tall fescue had more membrane damage than perennial ryegrass and hence exhibited better tolerance to combined stress by maintaining higher photosynthetic rate, chlorophyll fluorescence (F_v/F_m), leaf RWC, cell membrane stability, and root growth, and lower electrolyte leakage than perennial ryegrass (Jiang and Huang 2001a, b).

A major cause of membrane damage is the generation of oxidative stress, which can be measured as malondialdehyde (MDA), a product of lipid peroxidation and hydrogen peroxide. The extent of lipid peroxidation has been used to assess the level of free radical damage to cell membranes (Scandalios 1993). The hydroxyl-free radical attacks unsaturated fatty acids of lipids to induce lipid peroxidation, resulting in membrane damage (Okuda et al. 1991). Under combined drought/heat stress, intense membrane damage was linked to increased oxidative stress in sensitive genotypes of chickpea (Awasthi et al. 2017) and maize (Hussain et al. 2019a, b). Electrolyte leakage indicates a characteristic pattern of cellular membrane damage under stress, as most stresses target cell membranes in the first instance. Therefore, it is generally accepted that maintaining membrane stability and integrity under stress conditions is a major component of stress tolerance. Various plant responses under stress, including antioxidant enzyme synthesis (Liu and Huang 2000; Sreenivasulu et al. 2000), membrane acyl lipid concentrations (Lauriano et al. 2000), water use efficiency (França et al. 2000; Saelim and Zwiazek 2000), stomatal resistance, osmotic potential, and leaf rolling index (Premachandra et al. 1989), are correlated with electrolyte leakage. Therefore, electrolyte leakage or cell membrane thermostability is a valuable criterion for identifying stress-resistant cultivars in various plant species (Leopold et al. 1981; Stevanović et al. 1997) and a promising trait for selection against combined drought/heat stress.

Canopy temperature depression

Canopy temperature depression (CTD) is the variation between air temperature (T_a) and canopy temperature (T_c), which acts as an indirect measure of transpiration (Reynolds et al. 2001). A positive CTD value occurs when the canopy is cooler than the air ($CTD = T_a - T_c$). Under combined drought/heat stress, soil moisture does not adequately keep up with transpiration demands, decreasing stomatal conductance and increasing canopy temperature (Balota et al.

2008), thus increasing the CTD value. CTD is associated with increased water supply to plants due to deeper RSA (Pinto and Reynolds 2015). Some studies have reported a positive relationship between cooler canopy temperature and yield traits; for example, in wheat (Bahar et al. 2008), cotton (Carmo-Silva et al. 2012) and tomato (Nankishore and Farrell 2016). Therefore, CTD can be a strong measure for selecting better-performing genotypes under stress. For instance, in cotton, canopy temperature increased under combined drought/heat stress (> 36 °C; 35% irrigation), relative to the control; Pima S-6 (low T_c) and Monseratt Sea Island (high T_c) were identified as tolerant and sensitive genotypes, respectively, based on comparative CTD values (Carmo-Silva et al. 2012). Under combined drought/heat stress (25–42 °C; 20% field capacity), tolerant tomato cultivar ‘Hybrid 61’ had a lower canopy temperature than sensitive cultivar ‘Nagcarlang’ (Nankishore and Farrell 2016). CTD is easy to measure with an infrared thermometer. It is a vital indicator of plant responses to heat (Kumari et al. 2013) and drought (Pinto and Reynolds 2015) (Table 1) and should be explored further, along with stomatal conductance or transpiration, under combined stress environments for development as a screening marker.

Chlorophyll and chlorophyll fluorescence

Drought and heat stress can induce leaf senescence, resulting in chlorophyll degradation and disorganization of photosynthetic apparatus (Matile et al. 1999), which hampers crop yield. Chlorophyll is the main pigment for photosynthesis and is most sensitive to high temperatures (Berry and Bjorkman 1980) and drought stress (Oneto et al. 2016). High temperature destroys chlorophyll and damages plants by reducing the acceptance of light quanta (Zafar et al. 2017). A study on genotypic variation in chickpea revealed that plants exposed to combined drought/heat stress lost more chlorophyll than those under drought or heat stress alone, more so in heat-sensitive (ICC4567, ICC5912) and drought-sensitive (ICC3776) genotypes than heat-tolerant (ICC1356, ICC15614) and drought-tolerant (ICC8950) genotypes (Awasthi et al. 2017). Similarly, chlorophyll concentrations declined more in plants exposed to combined drought/heat stress than individual stresses in wheat (Prasad et al. 2011; Farooq et al. 2017; Qaseem et al. 2019a), lentil (Sehgal et al. 2017), and tomato (Duan et al. 2017; Raja et al. 2020). Combined drought/heat stress (25–45 °C; 20% field capacity) reduced chlorophyll content less in a tolerant tomato genotype (Hybrid 61) than moderately sensitive (Nagcarlang) and sensitive (Moskvich) genotypes (Nankishore and Farrell 2016) (Table 1). Plants with the stay-green character filled grains better under stress conditions than those without stay-green (Hörtensteiner 2009; Farooq et al. 2009, Farooq et al. 2011). Being

an easy trait to measure, stay-green can be used to evaluate stress tolerance among large populations of crop plants under combined drought/heat stress.

Reduced chlorophyll inhibits chlorophyll fluorescence (F_v/F_m ratio), reflecting photosynthetic efficiency in terms of photosystem II (PSII) function and other downstream electron acceptors. PSII is the most labile portion of the photosynthetic apparatus and easily undergoes light-induced damage in heat and drought-stressed plants (Maxwell and Johnson 2000; Killi et al. 2020). The D1 protein in the PSII reaction center is more sensitive to heat and drought stress than other core proteins. PSII is a reaction center for harvesting light energy to yield energy currency (ATP) and reducing power (NADPH) through non-cyclic photophosphorylation in the thylakoids and is associated with the oxygen-evolving complex to release O_2 and protons (H^+) (Taiz and Zeiger 1991). Therefore, a plant's photosynthetic efficiency can be accurately measured using the F_v/F_m ratio, with a decreasing value indicating a non-functional PSII system and photoinhibition. Chlorophyll fluorescence (F_v/F_m) values typically range from 0.75–0.80 and are linearly related to quantum yield (Kitajima and Butler 1975). Besides light-induced damage, ROS generation can damage the PSII reaction center (Guidi et al. 2019). Combined drought/heat stress affect chlorophyll fluorescence in various crops, reducing or even stopping PSII activity due to the reduced concentration of photosynthetic pigments. For example, combined drought/heat stress (35/20 °C; 40–45% field capacity) applied 12 days after heading for 15 days significantly reduced chlorophyll fluorescence values in 12 wheat varieties raised in the phytotron; GK-Othalom, Frankenkorn, and MV-Makaroni had higher chlorophyll fluorescence values and thus higher grain yields than the other varieties (Balla et al. 2006), suggesting a positive association between the two traits. Similarly, combined drought/heat stress significantly reduced chlorophyll fluorescence values in tomato (Nankishore and Farrell 2016), chickpea (Awasthi et al. 2017), wild barley (*Hordeum spontaneum*; Jedmowski et al. 2015), lentil (Sehgal et al. 2019), and rice (Kumar et al. 2014), and thus yields. Chlorophyll fluorescence has been used to distinguish genotypes resilient to combined drought/heat stress in crops, including wheat (Balla et al. 2006), chickpea (Awasthi et al. 2017), and rice (Kumar et al. 2014), demonstrating that chlorophyll fluorescence is a reliable method for assessing the pattern of inhibition of photosynthetic electron transport. Photosynthetic traits, such as chlorophyll content and chlorophyll fluorescence, can be measured to estimate the effect of stresses on growth and yield and positively correlate with the carbon exchange rate. The studies mentioned above showed that chlorophyll content and chlorophyll fluorescence values vary significantly between tolerant and sensitive genotypes, indicating their importance as selection traits during early plant

growth (Jedmowski et al. 2015). Therefore, these traits offer valuable insight into the physiological responses of different genotypes under combined stress.

Photosynthesis

Abiotic stresses profoundly affect photosynthesis, one of the primary processes determining crop yield (Liu and Huang 2008). Photosynthesis is inhibited by impaired electron transport and reduced PSII and RuBisCo activity (Lawlor and Cornic 2002). Drought stress reduces photosynthesis by decreasing CO_2 availability due to increased resistance to CO_2 diffusion from the atmosphere to leaves or sub-stomatal cavity to carboxylation sites (Flexas et al. 2007). Heat stress decreases photosynthesis by altering electron transport capacity (Zafar et al. 2018). Combined drought/heat stress limits CO_2 availability by closing stomata and decreasing the CO_2/O_2 ratio in chloroplasts (Foyer and Noctor 2000). The reduction in CO_2 solubility and reduced RuBisCo affinity increases photorespiration, relative to photosynthesis, as the temperature increases (Jordan and Ogren 1984). Drought and heat stress can also damage photosynthetic components in plants by overproducing ROS (Hussain et al. 2019a, b). The effects of combined drought/heat stress on photosynthesis vary depending on plant species— C_4 plants maintain a higher photosynthetic rate at high temperature than C_3 plants due to effective CO_2 concentrations within bundle sheath cells and suppressed photorespiration. Photosynthesis and growth in C_3 crops are directly affected more by water deficit and temperature than C_4 crops (Crafts-Brander and Salvucci, 2002).

Combined drought/heat stress inhibited photosynthetic activity by destabilizing RuBisCo and damaging PSII (Nishiyama and Murata 2014) in chickpea (Awasthi et al. 2017). In *Arabidopsis*, combined drought/heat stress (38/30 °C; soil RWC 45%) at 32 days after sowing reduced photosynthesis by 54% and 62% after 4 and 8 days of stress exposure, respectively (Zinta et al. 2014). Similarly, this stress combination suppressed photosynthesis, enhanced respiration, closed stomata, and increased leaf temperature in tobacco (Rizhsky et al. 2002). Combined drought/heat stress decreased photosynthetic activity and enhanced ROS production in *Populus yunnanensis* (Li et al. 2014) and severely reduced PSII efficiency in *Festuca arundinacea* and *Lolium perenne* (Jiang and Huang 2001a, b). The stresses, when imposed together, can reduce photosynthesis; the subsequent dilution of sucrose in wheat spikelets was associated with floret abortion (Barnabás et al. 2008). Combined drought/heat stress in rice suppressed photosynthetic gene expression and increased the demand for sugars by inducing transcripts encoding enzymes that catalyze reactions in glycolysis and the pentose phosphate pathway (Lawas et al. 2018a, b). Other studies have shown the adverse effects of combined

drought/heat stress on various photosynthetic traits in various crops, including wheat (Balla et al. 2006; Wang et al. 2010; Qaseem et al. 2019a, b), tomato (Zhou et al. 2017), *Medicago* (An et al. 2014), tobacco (Rizhsky et al. 2002), chickpea (Awasthi et al. 2017), barley (Mahalingam and Breigitzer 2019), lentil (Sehgal et al. 2017), *Brassica* (Diksaity et al. 2019) maize (Hussain et al. 2019a, b), and cotton (Loka et al. 2020). Stress-induced stomatal or non-stomatal limitations reduce photosynthetic performance (Athar and Ashraf 2005; Rahnama et al. 2010; Taiz and Zeiger 2010). Using photosynthetic capacity as a selection criterion is possible because it positively affects plant growth under stress conditions. Understanding photosynthetic responses to fluctuating environments could improve model predictions of dynamic photosynthesis.

Carbohydrate metabolism

Drought and heat stress can reduce photosynthesis, curbing sucrose production in leaves and subsequent transport to flowers and grains (Awasthi et al. 2014). Disruption in sugar metabolism was attributed to floral abortion in wheat spikelets (Barnabás et al. 2008) (Table 1). Combined drought/heat stress adversely affects metabolic and assimilate transfer processes necessary for seed filling in chickpea (Awasthi et al. 2014), such as the accumulation of seed reserves due to the impact on enzyme activity. Combined drought/heat stress in chickpea during seed filling reduced starch concentrations in leaves by 44% due to decreased starch phosphorylase activity, and inhibited the activities of starch hydrolyzing (β -amylase), sucrose-synthesizing (sucrose synthase), and hydrolyzing (acid invertase) enzymes (Awasthi et al. 2014). In tomato, combined drought/heat stress decreased sucrose content in leaves due to decreases in photosynthetic rate and photosynthetic gain (Zhou et al. 2017). Sucrose is cleaved by invertases (Sturm and Tang 1999); in maize, the activity of vacuolar and cell-wall-bound acid invertases predominates during kernel development (Weschke et al. 2000), which decreases during drought stress (Zinselmeier et al. 1999; Andersen et al. 2002), with parallel reductions in ovary growth and hexoses. In rice, sugar metabolism is a crucial metabolic and transcriptional component differentiating floral organ tolerance or susceptibility to combined drought/heat stress. The carbohydrates, trehalose, fructose-6-P, and galactaric acid, declined markedly in a stress-tolerant rice cultivar (N22) exposed to combined drought/heat stress (Li et al. 2015a, b). In lentil, combined drought/heat stress reduced sucrose and starch concentrations, more so in drought-sensitive than drought-tolerant genotypes (Sehgal et al. 2017). Similarly, other studies have revealed that the enzymes related to sucrose and starch synthesis and seed metabolism are sensitive to drought (e.g., sorghum; Bing et al. 2014) and heat stress [e.g., maize (Wilhelm

et al. 1999), wheat (Liu et al. 2011)]. Identifying the target enzymes related to carbohydrate accumulation in seeds is vital for understanding and improving seed filling in a combined stress environment.

Osmolytes

Plants survive combined drought/heat stress by changing their metabolism to favor osmolytes and secondary metabolites synthesis that promotes stress tolerance (Alhaithloul et al. 2020) (Table 1). Plants affected by drought and heat stress accumulate compatible solutes, such as proline, glycine betaine, and soluble sugars, which play a role in osmotic adjustment to maintain water status and protect leaf cells. Increased production of these osmoprotectants decreases ROS production and reduces leaf senescence (Hanif et al. 2020). Proline is part of numerous stress signaling pathways involved in stress adaptation (Qaseem et al. 2019a). Moreover, proline stabilizes membranes, sub-cellular structures, and cellular redox potential by destroying free radicals (Kishor et al. 2005). Proline plays a vital role in combating stress by scavenging ROS from cells without interfering with normal biological processes (Parvaiz and Satyawati 2008). Proline accumulation mitigates cytoplasmic acidosis and maintains the NADP⁺/NAD⁺ ratio (Alhaithloul et al. 2020). Increases in glycine betaine and proline can maintain RuBisCo activity and prevent photoinhibition (Parry et al. 2013). In tomato, combined drought/heat stress increased osmolyte accumulation (Qaseem et al. 2019b). In *Mentha piperita* and *Catharanthus roseus*, significant amounts of proline, glycine betaine, sugars, inositol, and mannitol accumulated in response to combined drought/heat stress (Alhaithloul et al. 2020). A connection between foliar proline accumulation and yield stability in heat- and drought-prone field environments was reported in barley (Singh et al. 1972) and wheat (Qaseem et al. 2019b; Sattar et al. 2020). In contrast, production of total soluble proteins, glycine betaine, and leaf proline declined in wheat under combined drought/heat stress (Hanif et al. 2020), causing an imbalance between antioxidants/osmoprotectants and oxidative stress, as reported in another study in wheat (Wang et al. 2014). Exogenous proline application to rice plants exposed to combined drought/heat stress upregulated enzymatic antioxidant activities [including superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT)] and total soluble proteins, leaf proline, and glycine betaine contents, and curtailed lipid peroxidation, which increased chlorophyll content and yield (Hanif et al. 2020), thus validating proline's role in conferring stress tolerance.

Glycine betaine plays an important role in enhancing plant tolerance to drought and heat stress (Sakamoto and Murata 2002; Yang et al. 2007; Khan et al. 2009). Glycine betaine can attenuate the effects of heat stress by disrupting

and repairing PSII during photoinhibition and protecting it from heat-induced injuries (Allakhverdiev and Murata 2004; Allakhverdiev et al. 1996; Allakhverdiev et al. 2007). Over-accumulation of glycine betaine can enhance PSII tolerance and ATPase activities under drought and heat stress, alone or in combination, and protect chloroplast and thylakoid structures from damage, increasing photosynthesis; the underlying mechanisms could be enhanced antioxidant activity and water status (Wang et al. 2010).

Sugars are osmolytes that display hormone-like activities and function as primary messengers in signaling (Alhailoul et al. 2020). Accumulated sugars in stressed plants serve as an energy source for stress recovery, signal transduction, and osmoprotection (Rosa et al. 2009). Drought or heat stress enhanced the accumulation of sugars in chickpea, more so in drought- or heat-tolerant genotypes, respectively (Awasthi et al. 2014). In contrast, combined drought/heat stress decreased sugar concentrations, more so in heat-sensitive genotypes (Awasthi et al. 2014), which was associated with more stress damage.

There is little information on osmolytes turnover in plants facing combined drought/heat stress; further studies are needed to correlate their accumulation with combined stress tolerance.

Oxidative damage and antioxidants

Drought and heat stress increase ROS concentrations manifold (Sehgal et al. 2017), causing membrane lipid peroxidation and damaging proteins and RNA and DNA molecules (Mittler 2002). ROS are mainly produced by NADPH oxidases (termed respiratory burst oxidase homologs; RBOHs) in apoplasts and some oxidases and peroxidases in chloroplasts, mitochondria, peroxisomes, and possibly other cellular compartments via different pathways (Suzuki et al. 2011; Vaahtera et al. 2014; Gilroy et al. 2016; Mignolet-Spruyt et al. 2016). Continual ROS production (metabolically or for signaling purposes) and detoxification involving diverse antioxidants occurs in all cellular compartments and is controlled by ROS gene expression (Mittler et al. 2004). Tomato plants exposed to combined drought/heat stress accumulated more malondialdehyde (an indicator of lipid peroxidation in membranes) and hydrogen peroxide than the controls (Raja et al. 2020). Antioxidant enzymes—SOD, ascorbate peroxidase (APX), catalase (CAT), and glutathione reductase (GR)—increased two- to three-fold in tomato under combined drought/heat stress, while non-enzymatic antioxidants—ascorbic acid (AsA) and reduced glutathione (GSH)—only increased one- to two-fold (Baxter et al. 2014; Raja et al. 2020) (Table 1). Some distinct variations have been reported in response to individual and combined stresses. For instance, in *Populus yunnanensis*, combined drought/heat stress decreased photosynthetic

activity and enhanced ROS production more than individual stresses (Li et al. 2014). Drought stress-induced detoxification enzymes, such as CAT and glutathione peroxidase (GPX), heat stress-induced cytosolic (APX), and thioredoxin peroxidase (TPX), and combined stress induced the expression of transcripts encoding alternative oxidase (AOX), GPX, GR, copper/zinc SOD (Cu/Zn-SOD), and glutathione S-transferase (GST) (Raja et al. 2020). Combined drought/heat stress caused more oxidative damage than individual stresses, as observed in birdsfoot trefoil (*Lotus corniculatus*) (Sainz et al. 2010), cotton (Sekmen et al. 2014), and purslane (*Portulaca oleracea* L.) (Jin et al. 2015). Drought and heat stress, alone or combined, significantly increased oxidative stress in chickpea, measured as the increase in malondialdehyde (MDA) and H₂O₂ contents in leaves and seeds, more so under combined stress, suggesting an intensification of damage; at the same time, antioxidant expression declined (Awasthi et al. 2017). In bread wheat, combined drought/heat stress increased SOD and ascorbate peroxidase (APX) activity by 54% and 55%, respectively, relative to the control (Sattar et al. 2020). Removal of H₂O₂ by APX, SOD, and CAT is vital for plants to tolerate combined drought/heat stress (Koussevitzky et al. 2008). Tolerance to combined drought/heat stress was associated with increased CAT activities in chickpea (Awasthi et al. 2017) and APX and GR in cotton (Sekmen et al. 2014). The induction of ROS detoxification enzymes is a common response among plant species to combined drought/heat stress, indicating that a higher antioxidant capacity is associated with stress tolerance (Zandalinas et al. 2018). There are large differences in the pattern of expression of various antioxidants in response to combined drought/heat stress, suggesting variations in the antioxidative adaptive mechanisms in diverse crop plants, which can be used as reliable markers of stress tolerance.

Strategies for improving combined drought heat stress tolerance in crops

Various strategies are available for improving crop tolerance to combined drought/heat stress, including agronomic, plant breeding, and ‘omics’ approaches. The following sections discuss these strategies and incorporate examples from various crops that could serve as a benchmark for developing crops that tolerate combined drought/heat stress.

Crop genetic resources act as reservoirs for combined drought/heat stress tolerance

Improving crop performance under combined drought/heat stress is an important research area for stabilizing yields and ensuring food security under increasing global drought and heat stress. Identifying crop germplasm with superior yield

and combined drought/heat tolerance is urgently needed to ensure global food security. Continuing efforts by plant breeders that explore, evaluate, and identify potential genotypes with combined drought/heat stress tolerance in test environments is the cornerstone for crop improvement (Chen et al. 2012; Cairns et al. 2013; Hamidou et al. 2013; Awasthi et al. 2014). Thus, the germplasm of various crop species has been screened for resilience to combined drought/heat stress, and promising genetic sources of tolerance have been identified.

Evaluation of selected maize varieties and inbred lines in hot, dry environments identified B76 as the most tolerant genotype of combined drought/heat stress due to its inherent ability to maintain higher relative water content, lower membrane injury, and superior yield than the other genotypes (Chen et al. 2012). An evaluation of 300 inbred maize lines in eastern and southern Africa—important maize-growing areas where drought and heat stress co-occur—revealed significant genetic variability for yield and yield-related traits for combined drought/heat tolerance (Cairns et al. 2013). Subsequent rigorous screening identified Posta Sequia C7-F6-42-6-2-2 and DTPYC9-F46-1-2-1-2 as the best genotypes for increasing genetic gain in maize breeding programs in combined drought- and heat-prone regions in Africa (Cairns et al. 2013). A three-year study assessed drought-tolerant hybrid maize genotypes to identify combined drought/heat tolerance in Kano State, Nigeria; M1227-17, M0826-3, and M1124-18 had promising results under combined stress (Meseke et al. 2018) and could be used as the base material for transferring combined tolerance into other elite breeding lines to sustain maize yields in regions that frequently experience combined drought/heat stress. Hossain et al. (2012) reported two barley genotypes (Zernograd.770 and Nutans) and one wheat genotype (Line4) as potential sources of combined drought/heat tolerance. An assessment of various phenological traits and yield attributes in 180 diverse elite wheat genotypes under drought and heat stress, alone and combined, revealed several promising lines for drought or heat tolerance; however, only two genotypes (ESWYT_116 and EBWYT_529) had superior yield performance under combined stress (Qaseem et al. 2019b). In groundnut, significant genetic variability for pod and hull yields and harvest index traits was captured in 268 genotypes tested under combined water stress and high-temperature stress, with the best performers being ICG10053, ICG862, ICG 6646 (Table 2; Hamidou et al. 2013). Similarly, lentil genotypes ILL 7835, ILL 6075, ILL 6362, ILL 7814 had superior performance based on stress tolerance indices associated with yield traits under combined drought/heat stress (El-haddad et al. 2020).

As landraces and crop wild relatives act as natural reservoirs for abiotic stress tolerance, Jumrani and Bhatia (2018) revealed that soybean accession EC 538828 retained more

pods/plant and yield than accession JS-97-52 under combined drought/heat stress. In an earlier study, Sapra and Anaele (1991) identified soybean genotypes, PI 408.155, PI 423.827B, PI 423.759, and Pershing, as promising sources of drought and heat stress tolerance. In wheat, synthetic hexaploid wheat, ALTAR 84/AO'S', could be incorporated in wheat breeding to develop combined drought/heat tolerance as it retained more chlorophyll and better grain yields in the field than other genotypes (Pradhan et al. 2012). In addition to directly selecting genotypes with superior yield performance, other physiological, biochemical, and reproductive parameters could be important for selecting genotypes as donor parents to transfer these traits to improve genetic gain and adaptation under combined drought/heat stress. Among five tested maize genotypes under drought and heat stress, Pioneer 31G70 could be a potential donor for combined drought/heat tolerance because it performed better in terms of photosynthesis, leaf water potential, and cell membrane injury (Kebede et al. 2012). Likewise, two N22 rice accessions showed combined drought/heat tolerance with improved anther dehiscence, pollen germination, and spikelet fertility in the field, relative to IR64 and Apo Moroberekan (Rang et al. 2011). The M-503 cotton cultivar expressed higher combined drought/heat tolerance than other cultivars due to its enhanced antioxidant defense mechanisms that induced higher CAT and POX activity and osmolyte (i.e., proline) accumulation (Sekmen et al. 2014). Maize genotype Xida 899 alleviated oxidative stress-mediated damage and induced antioxidant mechanisms to maintain proper photosynthesis and other essential physiological activities under combined drought/heat stress (Hussain et al. 2019a, b). Likewise, chickpea genotype ICC8950 increased the activity of RuBisCo and starch- and sucrose-synthesizing enzymes and improved other physiological and yield parameters (relative water content, membrane injury, and grain filling) under combined drought/heat stress (Awasthi et al. 2014).

Thus, a systematic screening of wild relatives, landraces, pre-bred lines, and unutilized germplasm reserved in global gene banks needs immediate attention to identify and transfer stress 'adaptive alleles' into elite crop cultivars for sustaining yield under combined drought/heat stress.

Genomics approaches involving bi-parental QTL mapping and genome-wide association for delineating underlying QTL/genomic regions controlling combined drought/heat tolerance

Combined drought/heat tolerance is a complex trait, which is inherited quantitatively and greatly influenced by the G×E effect. Clarifying its genetic basis may shed light on the common genetic determinants controlling combined drought/heat stress tolerance in crop plants. Given the

Table 2 List of crop genotypes exhibiting combined drought and heat stress tolerance

Crop	Name of genotype	Traits contributing combined tolerance	Country/place reported from	References
Rice	N22	Spikelet fertility, anther dehiscence, higher in vivo pollen germination	IRRI, Philippines	Rang et al. (2011), Jagadish et al. (2011), Li et al. (2015a, b)
Wheat	<i>Aegilops geniculata</i>	Physiological and yield and yield-related traits		Zaharieva et al. (2001)
	TAM107	Yield and yield-related traits	Wheat Genetics Resource Center, Kansas	Qin et al. (2008)
	Katya	High heat shock protein expression		Grigorova et al. (2011a, b)
	ALTAR 84/AO'S', ALTAR 84/ <i>Aegilops tauschii</i> Coss. (WX 193)	Physiological and yield and yield-related traits	Department of Agronomy, Kansas State University, Manhattan, Kansas, USA	Pradhan et al. (2012)
	ESWYT_116, EBWYT_529	Yield and yield-related traits	National Agriculture Research Center (NARC) Islamabad, Pakistan	Qaseem et al. (2019a)
Maize	Line4'	Yield and yield-related traits	South-eastern Russia	Hossain et al. (2012)
	Haurani*2/ <i>T. urartu</i> derivatives	Phenological traits and yield-related traits	Tessaout, Morocco, Wed Medani, Sudan	Aberkane et al. (2020)
	B76	Yield and yield-related traits	USDA, Lubbock, Texas	Chen et al. (2012)
	Pioneer 31G70	Physiological and yield and yield-related traits	Jamie Whitten Delta States Research Center, Stoneville, MS, UDSA-ARS	Kebede et al. (2012)
	La Posta Sequia C7-F64-2-6-2-2, DTPYC9-F46-1-2-1-2	Yield traits		Cairns et al. (2013)
	M1227-17, M0826-3, M1124-18	Yield	Kadawa, Kano State in Nigeria	Meseka et al. (2018)
	Xida 889	High ant-oxidant defense system and higher photosynthetic capacity	Southwest University, Chongqing, China	Hussain et al. (2019a, b)
Barley	GH-4859, TZm-1353	Yield traits	Ikenne, Nigeria	Nelimer et al. (2019)
	SBCC073	High yield	Spain	Cantalapiedra et al. (2017)
	Arta	Morphological adaptation and maintenance of photosynthesis	Syrian	Rollins et al. (2013)
Chickpea	Zernograd.770, Nutans	Yield and yield-related traits	South-eastern Russia	Hossain et al. (2012)
	ICC8950	Physiological, biochemical and yield-related traits	Panjab University, Chandigarh, India	Awasthi et al. (2014)
	ICC8950	High antioxidant defense capacity and high seed yield	Panjab University, Chandigarh, India	Awasthi et al. (2017)
Lentil	ILL 7835	Heat tolerance index		El-haddad et al. (2020)
Ground nut	ICG10053, ICG862, ICG 6646, ICG10950, 55-437, ICG6022, ICG6813, ICG8285, ICG12509, ICG12921	Yield and yield-related traits	ICRISAT Sahelian Centre (ISC) in Sadore, Niger	Hamidou et al. (2013)
Soybean	PI 408.155, PI 423.827B, PI 423.759, Pershing	Germination	Alabama A&M University Research Station	Sapra and Anaele (1991)
	EC 538828	Yield and yield-related traits	ICAR-Indian Institute of Soybean Research, Indore	Jumrani and Bhatia (2018)
Potato	L1 (84.194.30)	Various physiological traits	University of Tsukuba, Japan	Handayani and Watanabe (2020)
Tomato	Hybrid 61	Physiological traits		Nankishore and Farrell (2016)
Cotton	M-503	High antioxidant capacity	Nazilli Cotton Research Institute (NCRI) (Nazilli, Aydın, Turkey)	Sekmen et al. (2014)

unprecedented technical advancements, copious genomic resources are available to dissect traits of agricultural importance and abiotic stresses in various crop plants. Biparental QTL mapping and genome-wide association studies (GWAS) have been used to elucidate QTL/genomic regions/haplotypes related to combined drought/heat tolerance in various crops (Pinto et al. 2010; Templer et al. 2017; Sukumaran et al. 2018; Li et al. 2019). However, identified QTLs attributing combined drought/heat tolerance are limited. Biparental QTL mapping in wheat using the Seri×Babax cross identified several QTL on the 1B-a, 2B-a, 3B-b, 4A-a, 4B-b, and 7A-a linkage groups that contribute to yield, yield-related, and other important physiological traits (canopy temperature, chlorophyll content, and NDVI) under water and heat stress (Pinto et al. 2010). Another study in wheat, using a RAC875×Kukri doubled haploid population, identified QTL on the 2B, 3B-2, and 7A-2 linkage groups that control canopy temperature, NDVI, and yield traits under drought or heat stress alone (Bennett et al. 2012). Subsequent advancements in array-based genotyping platforms in various crop plants have enabled the precise mapping of complex traits. In this context, DArTseq and Illumina bead chip 90K array-based SNP genotyping of RILs developed from a SYN-D×Weebil1 wheat cross pinpointed five QTL hotspots related to yield and yield-related traits under drought, heat, and combined stresses (Liu et al. 2019). The authors also underpinned two important *NST1-like protein* genes and the *TPR15* stress-responsive candidate gene underlying the *QYLD-6D.1* QTL on 6D attributing to yield under combined drought/heat stress. However, the number and resolution of combined drought/heat-tolerant QTL identified through bi-parental QTL mapping remains low.

Further, the availability of high-throughput SNP markers has enabled GWAS to decipher a plethora of significant marker-trait associations (MTAs) controlling combined drought/heat tolerance across the whole genome in a large set of diverse plant accessions (Sukumaran et al. 2018; Yuan et al. 2019). Relying on this approach, genome-wide scanning of a large panel of 208 durum wheat identified 93 MTAs on chromosomes 2A, 4A, 4B, 5B, 7A, and 7B contributing to various phenological, physiological, and yield and yield-related traits under combined drought/heat stress (Sukumaran et al. 2018). Qaseem et al. (2019a) identified 60 MTAs for various phenological and yield-related traits and 29 MTAs for stress tolerance indices, such as the tolerance index (TOL) and stress tolerance index (STI), by performing GWAS on 192 diverse sets of wheat germplasm (see Table 3). IACX203 (67.24 cM) and wsnp_Ex_c18372_27196625 were two important markers attributed to STI, demonstrating 21.2% of the phenotypic variance explained (PVE). Likewise, RFL_Contig854_2253 on 3A was significantly attributed to TOL, clarifying 23.7% of the PVE (Qaseem et al. 2019a). In an earlier study, the same

research group obtained two IAAV8258 and wsnp_Ex_c7168_12311649, two markers residing on chromosome 5A exhibiting significant associations with traits under heat, drought, and combined stresses (Qaseem et al. 2018). Similarly, Schmidt et al. (2020) obtained QTL on chromosome 3B under combined drought/heat stress using GWAS on a panel of 315 spring wheat accessions overlapped with QTL related to tiller number, as reported by Qaseem et al. (2018). The QTL controlling grain weight under combined drought/heat stress found on chromosome 3B, 5B, and the long arm of chromosome (Schmidt et al. 2020) coincided with the QTL contributing to harvest index (Garcia et al. 2019) under combined stress. Emphasizing grain yield and yield-related traits, Li et al. (2019) identified 295 significant MTAs using GWAS on a set of 277 wheat accessions evaluated across 30 locations with a 660K SNP array under normal, drought, heat, and combined stresses. Two important candidate genes, *TraesCS6A02G124100* and *TraesCS6D02G114400*, contributing to grain yield under multiple stress were identified, which can be used to improve grain yield under combined drought/heat stress in wheat (Li et al. 2019). Considering maize, a single SNP and haplotype-based GWAS analysis on a panel of 300 maize genotypes revealed several MTAs related to phenological and yield-related traits under combined drought/heat stress (Yuan et al. 2019). Among the various candidate genes identified, *GRMZM2G151863* ‘encoding GDT1-like protein’ had a significant association with grain yield, and ‘WRKY DNA-binding protein’ gene *GRMZM2G076657* had a significant association with the anther–silking interval under combined drought/heat stress (Yuan et al. 2019). Recent advances in metabolomic platforms have provided insight into metabolic QTL (mQTL) that attenuate plant adaptation under abiotic stresses, including combined drought/heat stress, at the metabolic level (Riedelsheimer et al. 2012; Wen et al. 2015; Templer et al. 2017). Thus, to explore mQTL attributing to plant adaptation in barley under combined drought/heat stress, Illumina iSelect 9K array-based genotyping and comprehensive metabolite-based phenotyping data from 81 barley genotypes under control, drought, and combined drought/heat stress was investigated, uncovering 13 mQTL related to glutathione, succinate, and γ -tocopherol content contributing to antioxidant and ROS scavenging activity on chromosomes 3H, 5H, and 7H (Templer et al. 2017).

Hence, ‘metabolomics-assisted QTL’ breeding encompassing mQTL and metabolomics—GWAS will shed new light on improving traits under combined drought/heat stress (Raza 2020). Furthermore, GWAS based on SNP/structural variations derived from whole-genome resequencing (WGRS) of global crop germplasm delineated several genomic regions/haplotypes controlling various complex traits, including adaptive loci contributing to combined drought/heat tolerance (Bohra et al. 2020). Based on this

Table 3 List of QTLs contributing to combined drought and heat stress tolerance

Crop	QTLs/significant MTAs	Mapping population/ panel size	Approach used	Trait	Type of marker	LG	PVE%	References
Wheat	<i>QGwt.ara-3B.3</i> , <i>QGwt.ara-4A.1</i> , <i>QGwP.ara-4A</i> , <i>QGwP.ara-6A</i> , <i>QGwt.ara-6B.6</i> , <i>QGwt.ara-7B.6</i>	315 spring wheat	GWAS	Biomass, spike number, grain weight, grain number, harvest index	SNP	3B, 4A, 5B, 6A, 6B, 7B	3.6–21.2	Schmidt et al. (2020)
	17 stress QTLs	Seri/Babax RIL, 167	Biparental QTL mapping	Thousand grain weight, Normalized difference vegetative index, chlorophyll content, canopy temperature, grain number	SSR, AFLP, DArT	1B-a, 2B-a, 3B-b, 4A-a, 4B-b, 7A-a		Pinto et al. (2010)
	Leaf rolling, plant height, and chlorophyll content QTLs	SeriM82 × Babax RIL, 167	Biparental QTL mapping	Leaf rolling, plant height, chlorophyll	SSR, AFLP, DArT	4B, 1B, 2B, 1D-a		Tahmasebi et al. (2016)
	<i>Q.Flw.ara-2B</i> , <i>Q.Yld.ara-3B-2</i> , <i>Q.Ctsg.ara-3B-2</i> , <i>Q.Yld.ara-3D</i> , <i>Q.Ctneg.ara-3B-2</i> , <i>Q.Eet.ara-7A-2</i>	RAC875/Kukri doubled haploid	Biparental QTL mapping	Flag width leaf, yield, canopy temperature, canopy temperature vegetative	DArT, SSR	2B, 3B-2, 7A-2		Bennett et al. (2012)
	43 MQTLs co-localized for both drought and heat stress				SNP			Acuña-Galindo et al. (2015)
	35 QTLs under combined drought and heat stress and 8 common QTLs	SYN-D × Weebill 1 RIL, 276	Biparental QTL mapping	Grain number, thousand grain weight, days to heading, plant height, canopy temperature during vegetative and grain-filling stages	SNP	2A, 7B, 6D	7.9–36.1	Liu et al. (2019)
	<i>QTGW-2A.1</i> , <i>QGN-2A.1</i> , <i>QDTH-6D.1</i> , <i>QDTH-7B.2</i> , <i>QPH-5B.1</i> , <i>QCTvg-6D.1</i> , <i>QCTlg-6D.1</i> , <i>QWAX-2A.1</i>							
	under combined stress for more than one location							

Table 3 (continued)

Crop	QTLs/significant MTAs	Mapping population/ panel size	Approach used	Trait	Type of marker	LG	PVE%	References
	60 significant MTAs for various traits, 29 significant MTAs for stress tolerance index	192 diverse bread wheat lines	GWAS	Days to maturity, flag leaf width, grain yield, tiller/plant, harvest index, plant height, spike length, spikelet/spike	SNP	1A, 2D, 2B, 3A, 3D, 4A, 4B, 7B, 7D	19–29	Qaseem et al. (2019b)
	93 significant MTAs for various traits	208 lines of durum wheat	GWAS	Yield, thousand grain weight, days to anthesis, plant height, grain number/m ² , NDVI at grain filling stage	SNP	2A, 4A, 4B, 5B, 7A and 7B		Sukumaran et al. (2018)
	28 significant MTAs	277	GWAS	Grain yield, grain no./main spike, thousand kernel weight	SNP	2B		Li et al. (2019)
Barley	<i>i_SCRI_RS_146010</i> , <i>i_SCRI_RS_144776</i> , <i>i_SCRI_RS_138723</i> , <i>i_SCRI_RS_138723</i> , <i>i_SCRI_RS_169826</i> , <i>i_SCRI_RS_103377</i> , <i>i_SCRI_RS_195226</i> , <i>i_SCRI_RS_144696</i> , <i>i_SCRI_RS_158873</i> , <i>i_SCRI_RS_200107</i> , <i>i_SCRI_RS_4520</i>	81	GWAS	Glutathione, starch, glycine, succinate, α -tocopherol, γ -Tocopherol	SNP	2H, 3 h, 5H, 6H and 7 h		Templer et al. (2017)
Maize	44 significant MTAs and <i>GRMZM2G076657</i> , <i>GRMZM2G151863</i> candidate genes	300	GWAS	Anthesis date, anthesis silking interval, grain yield	SNP		8–19.7	Yuan et al. (2019)

SNP single nucleotide polymorphism; SSR simple sequence repeat; AFLP amplified fragment length polymorphism, *DArT* diversity arrays technology; *LG* linkage group; *PVE* phenotypic variance explained; *GWAS* Genome Wide Association Study

WGRS-based GWAS analysis, Varshney et al. (2019) identified 262 MTAs and some important candidate genes (*TIC*, *REF6*, *aspartic protease*, *cc-NBS-LRR*, *RGA3*) contributing to drought and heat stress in a set of 429 chickpea accessions. Thus, underpinning candidate gene(s) controlling combined drought/heat tolerance could provide the impetus for developing stress tolerant genotypes. In parallel, these QTL/haplotypes carrying various physiological traits and grain yield traits contributing to plant adaptation under combined drought/heat tolerance could be targeted for transfer into high yielding yet combined drought/heat-sensitive crop genotypes.

Transcriptomics for discovering novel/common regulatory candidate gene(s) controlling combined drought/heat tolerance

Understanding the molecular response of plants exposed to frequently occurring combined drought/heat stress is critical for improving plant yields (Barnabás et al. 2008). Plants respond by rapidly reprogramming transcription networks and alternative splicing upon receiving external stimuli of combined drought/heat stress (Liu et al. 2018). Several transcription factors and co-regulators involved in establishing transcription networks for plant adaptation to various abiotic stresses have been reported. Some studies have suggested that plant responses to combined water and heat stress at the molecular level differ from those of individual stresses (Suzuki et al. 2014; Zandalinas et al. 2018), but there is limited information available to confirm this suggestion (Tricker et al. 2018). Transcriptomics—an important functional genomics approach—could involve the dynamic expression of various gene(s) to decipher underlying candidate gene(s) controlling various abiotic stresses (Sakuma et al. 2006) and offer insight into novel/common candidate gene(s), gene networks, and signaling molecules associated with various pathways governing heat, drought, and combined stresses in plants. This approach could also offer insight into the expression of unique gene combinations or common genes and gene networks expressed under combined drought/heat stress or individual stresses that allow plants to acclimate under stress conditions (Shaar-Moshe et al. 2017; Cantalapiedra et al. 2017; Liu et al. 2018). Thus, transcriptomics could be used to inquire about the gene(s)/regulatory gene networks involved in various cellular metabolic pathways controlling osmoregulation, detoxification or minimizing ROS activity, expression of phytohormones, to mediate combined drought/heat tolerance in plants (Aprile et al. 2013; Liu et al. 2015; Kumazaki and Suzuki 2019; Sun et al. 2020).

Before the advent of RNA sequencing (RNA-seq) technology, microarray-based transcriptomic analysis was instrumental in unraveling candidate gene(s) and deciphering their

plausible function of various abiotic stresses, including drought and heat stress. This technique offered preliminary insight into several differentially expressed genes (DEGs) in two durum wheat cultivars, Cappelli and Ofanto, exposed to combined drought/heat stress (Aprile et al. 2013) (see Table 4). A plethora of genes involved in the fatty acid β -oxidation pathway, valine catabolism, heat shock factors, glyoxylate cycle, and senescence were upregulated under heat stress, and genes involved in proline synthesis, HSPs, dehydrins, stomata closure, chromatin condensation, and signal transduction were upregulated under drought stress in wheat (Aprile et al. 2013). Microarray analysis revealed 896 upregulatory (e.g., *OST1*, *TCH2*, *CPK16*, and *CIPK9*, *spermidine synthase (SPDS1)*, and *S-adenosylmethionine decarboxylase (SAMDC)*) and 1147 downregulatory genes (e.g., transcription factors *MYB61* and *BZIP6*) in sorghum under combined drought/heat stress (Johnson et al. 2014).

The subsequent arrival of high-throughput RNA-seq technology deepened our understanding of various candidate genes involved in combined drought/heat tolerance in bread wheat. Deep transcriptome analysis of genotype TAM107 exposed to heat, drought, and combined stresses resulted in a myriad of DEGs, including upregulated and downregulated genes (Liu et al. 2015). However, the gene expression pattern under combined drought/heat stress differed from those under individual drought or heat stress. The regulated genes belonged to various transcription factors (*NAC*, *AP2/ERF*, *DREB*, *MYB*, *WRKY*, and *HSF*) controlling the downstream target genes/gene networks involved in various stress-responsive hormone signaling pathways (Liu et al. 2015). Likewise, transcriptome analysis of *Agrotis stolonifera* revealed a set of 670 and 812 common upregulated and downregulated genes under drought and heat stress, respectively (Xu and Huang 2018). The commonly upregulated genes under drought and heat stress were associated with oxylipin and proline synthesis, while the commonly downregulated genes were associated with thiamine biosynthesis and calcium-sensing receptors, providing insight into the combined drought/heat tolerance mechanism in *Agrotis stolonifera*. Several common upregulated genes related to the antioxidant mechanism and encoding HSPs were identified through transcriptome profiling of *Phoenix dactylifera*, exposed to heat, drought, and combined stresses, revealing that increased activation of antioxidants and HSPs is common in plants adapting to drought and heat stress (Safronov et al. 2017). The protection of photosynthetic reaction centers under combined drought/heat stress by increasing the accumulation of transcripts encoding reaction center proteins (D1 and D2) in PSII of *sid2-1* mutant plants deficient in *ICS1* encoding salicylic acid and phyloquinone in *Arabidopsis* is noteworthy (Kumazaki and Suzuki 2019). Likewise, Pacbio transcriptome sequencing of pearl millet exposed to drought and heat stress, alone or combined, revealed the

Table 4 List of various plant regulatory genes expressed under combined drought and heat stress

Crop	Name of genotype	Gene up/down regulated	Function	Technique	References
Arabidopsis	Columbia-0	<i>ICS1</i>	In <i>sid2-1</i> mutant deficient in <i>ICS1</i> displayed higher protection of photosynthetic apparatus	qPCR	Kumazaki and Suzuki (2019)
<i>Agrostis stolonifera</i>	Penncross	670 upregulated and 812 downregulated genes	Oxylipin biosynthetic process, proline biosynthetic process, thiamine metabolic process, calcium-sensing receptor	Illumina, San Diego, CA	Xu and Huang (2018)
Rice	N22, Moroberekan	Upregulation of <i>CSA</i> and downregulation of sucrose transporter gene <i>SUT3</i> under combined stress in Moroberekan, upregulation of monosaccharide transporter gene (<i>MT8</i>) and cell wall invertase (<i>INV4</i>) in N22	Helps in regulating sugar metabolism	qRT-PCR, microarray	Li et al. (2015a, b)
Barley	SBCC073, Scarlett	<i>CCA1/LHY</i> TF	Upregulation of <i>CCA1/LHY</i> TF, enhanced polyamines accumulation, higher expression of genes related to carbon fixation metabolism and anti-oxidant enzymes	Illumina HiSeq2000	Cantalapiedra et al. (2017)
Pearl millet	Tifteaf 3	315 TFs, 128 TRs, 6920 genes, 6484 DEGs	Glycerophospholipid metabolic pathway, photosynthetic proteins ROS scavenging, encoding HSPs	Illumina platform	Sun et al. (2020)
<i>Phoenix dactylifera</i>		<i>UDP glucose 4-epimerase</i> genes, <i>PDACT_KE332624.1_G000480</i> , <i>PDACT_KE332831.1_G001110</i> differentially expressed	Increased galactose content, higher wax biosynthetic process, increased proline content, enriched ABA regulatory elements	Illumina HiSeq 1000	Safronov et al. (2017)
Sorghum	R16	896 upregulated and 1147 downregulated genes, MYB78 and ATAF1, chaperones, including unique heat shock proteins (HSPs)	Encodes HSPs, chaperone activity, polyamine biosynthesis	Microarrays	Johnson et al. (2014)
Tomato	Jinlingmeiyu	<i>SODCC.5</i> , <i>SCL6</i> , <i>GRF3</i> , <i>GRF4</i> , <i>GRF8</i> , <i>HSP22.7</i> , <i>ARF17</i>	Scavenger enzyme of ROS, plant hormone signal transduction, carbonate dehydratase activity	Illumina, San Diego, USA	Zhou et al. (2020)
Watermelon		<i>ClatHsp40-15</i> , <i>ClatHsp40-96</i> , <i>ClatHsp60-09</i> , <i>ClatHsp60-15</i> , <i>ClatHsp70-07</i> , <i>ClatHsp70-10</i> , <i>ClatHsp90-04</i> , <i>ClatHsp90-05</i> , <i>ClatHsp100-67</i>	Protect plant protein from misfolding/act as molecular chaperone under combined stress	qRT-PCR	Altunoglu et al. (2019)
Wheat	TAM107		HSFs and DREBs involved in combined drought and heat stress tolerance	HiSeq2000	Liu et al. (2015)
	Ofianto, Cappelli	3084 differentially expressed probe sets	Chromatin condensation, stomatal closure, fatty acid β -oxidation pathway, glyoxylate cycle, senescence	qRT-PCR, Affymetrix GeneChip	Aprile et al. (2013)

differential expression of a myriad of transcription factors and transcription regulators, including 6920 DEGs under heat stress, 6484 DEGs under drought stress, and 1881 common DEGs under combined drought/heat stress (Sun et al. 2020). The authors suggested that the identified DEGs were related to photosynthetic proteins involved in conferring heat tolerance, the glycerophospholipid metabolic pathway involved in water stress tolerance, amino acid metabolism, encoding ROS-scavenging enzymes, and HSPs and ABA signaling. This study also established the differential regulation of various genes under drought and heat stress, suggesting that plants select different genes in response to different stresses (Sun et al. 2020).

Furthermore, NGS-based deep RNA-seq technology can unearth underlying novel regulatory non-coding RNAs, including miRNAs and long non-coding RNAs, across the genome that control tolerance to various abiotic stresses in plants. Deep transcriptome sequencing of tomato leaf exposed to combined drought/heat stress identified 11 conserved and 26 novel miRNAs. At the same time, the upregulation and downregulation of several candidate gene(s) targeted by various miRNAs (*ARF8* targeted by sly-miR167h_mdm and sly-miR167a-5p_ath; *Solyc02g086820.3.1* targeted by PC-326-3p; *GRF3* and *GRF4* targeted by miR396) (Zhou et al. 2020) was also revealed. Further advancements, particularly in bioinformatic analysis, could identify underlying novel candidate gene(s) and non-coding regulatory RNAs with their precise function in response to combined drought/heat stress.

Proteome dynamics offer insight into proteins that enable plants to adapt under combined drought/heat stress

Proteome analysis increases our understanding of various proteins produced in response to abiotic stress, including drought, heat, and their combination, allowing plants to adjust. However, our understanding of various proteins contributing to combined drought/heat stress is limited. Various proteins obtained in response to combined drought/heat stress enable plant acclimation by protecting cellular proteins from misfolding, contributing to cellular detoxification, improving photosynthesis, lipid metabolism, amino acid synthesis (Grigorova et al. 2011a, b; Rollins et al. 2013; Ashoub et al. 2015). Among the various stress-responsive proteins, HSPs have a critical role in mediating plant abiotic stress tolerance (Wang et al. 2004; Kotak et al. 2007). Higher expression of HSPs and defense-related proteins under combined drought/heat stress than individual stresses has been reported in wheat (Grigorova et al. 2011a, b), rice (Jagadish et al. 2011), and tobacco (Rizhsky et al. 2002), further supported in a comparative study of wheat under drought, heat, and combined stresses (Grigorova et al.

2011a). Higher abundance of smHSPs, HSP70, and HSP100 occurred under combined drought/heat stress (Grigorova et al. 2011a), with HSP70, HSP90, HSP100, and smHSP18 abundant in *Arabidopsis* and tobacco (Rizhsky et al. 2002, 2004) and HSPs (16.9 and 17.4 kDa). Comparative proteomics analysis of wild barley exposed to drought, heat, and combined stresses revealed the regulation of several proteins providing plant adaptation—proteins contributing to detoxification (GST, tocopherol cyclase), amino acid synthesis, lipid metabolism, and HSPs—were upregulated under drought stress, HSP70 and HSP90 were upregulated under heat stress, and HSPs were upregulated, and photosynthetic apparatus proteins (ATP synthase and RuBisCo activase) were downregulated under combined stress (Ashoub et al. 2015). Several unique proteins with unknown functions were also noted under combined stress (Ashoub et al. 2015). Rollins et al. (2013) reported no significant change in proteins or plant performance in Arta and Keel barley genotypes under drought stress; however, the combined drought/heat stress significantly altered the expression of proteins and inhibited photosynthesis. Under heat stress and combined drought/heat stress, upregulation of proteins contributing to detoxification (Lhcb3, PsbO, PsbP, RuBisCo activase B, glycolytic proteins, chaperones) ultimately mediated plant adaptation to the stress in barley (Rollins et al. 2013). In soybean, some proteins (stromal 70 kDa heat shock-related protein, ribulose biphosphate carboxylase small chain, and carbonic anhydrase 1) were downregulated in genotype Surge but upregulated in genotype Davison under combined drought/heat stress (Das et al. 2016). Proteomics analysis of maize under heat, drought, and combined stresses using multiplex iTRAQ-based quantitative proteomics and the LC-MS/MS method revealed several differentially expressed proteins (Zhao et al. 2016). Of these, chaperone proteins, proteases, ethylene-responsive proteins, and ripening-related proteins provided the basis for adaptation plasticity to combined drought/heat stress in maize (Zhao et al. 2016). Thus, proteomics analysis reveals differentially expressed proteins, including known and novel proteins, in response to combined drought/heat stress. Increasing our understanding of these proteins and their accurate functions mediating combined drought/heat tolerance could assist in developing stress tolerance in crop plants.

Metabolomics for linking phenotypic responses under combined drought/heat stress

Metabolomics is an emerging robust approach for offering mechanistic insight into how metabolic reprogramming assists plants to acclimate in response to various abiotic stresses, including combined drought/heat stress (Li et al. 2015a, b; Alseekh and Fernie 2018). Gaining insight into the complexity of various abiotic stress responses cannot

be resolved at the proteome and transcriptome levels alone. Thus, metabolomics enriches our current understanding of plant responses to combined drought/heat stress by disentangling complex gene networks, functional gene pathways, and information related to stress-responsive metabolites that could serve as metabolic biomarkers for screening abiotic stress-tolerant crop plants (Li et al. 2015a, b).

A myriad of metabolites, including various amino acids, sugars, organic acids, fatty acids, and other derivative compounds, evoking different responses to drought, heat, and combined stresses have been identified through advances in metabolomic platforms (Obata et al. 2015; Zinta et al. 2018; Lawas et al. 2019; Janni et al. 2020). These differentially expressed metabolites in response to combined stress activate defense mechanisms to protect cellular activity, minimize ROS activity, enhance HSP activity, and induce regulatory TF genes and hormonal signaling. A large-scale metabolomic study in maize leaf exposed to heat, drought, and combined stresses revealed changes in numerous amino acids (tryptophan, proline, alanine, valine, isoleucine, glycine, serine, etc.), sugars (maltose, myoinositol, galactinol), and organic acids (glycerate, threonate) that enabled plants to adapt under stress (Obata et al. 2015). The authors suggested that most of the metabolic changes due to combined drought/heat stress were similar to the sum of those from individual drought or heat stress. A series of metabolic alterations, especially in various sugars, amino acids, and fatty acids, were captured in *Arabidopsis* grown under combined drought/heat stress in an enhanced CO₂ environment (Zinta et al. 2018). For carbohydrates, starch levels declined due to an increase in amylase activity. For amino acids, elevated activities of pyrroline-5-carboxylate synthase and pyrroline-5-carboxylate reductase contributed to proline synthesis and the upregulation of threonine synthase, indicating that diverse defense molecules are activated under combined drought/heat stress. Increased abundance of saturated fatty acids and reduced synthesis of unsaturated fatty acids would reduce membrane damage from oxidative stress under heat stress (Zinta et al. 2018). In rice, a combined metabolomics and transcriptomics analysis of floral organs, including anthers and pistils, of genotype Moroberekan (heat-sensitive) and genotype N22 (heat-tolerant) under normal, drought, heat, and combined stresses revealed that sugar metabolism is the major determining factor mediating sensitivity to combined drought/heat stress in Moroberekan due to the higher expression of ‘carbon starved anther’ genes (Li et al. 2015a, b). In contrast, N22 displayed increased expression of MST8 sugar transporter and cell wall invertase genes to mediate high sink strength. Comprehensive metabolome profiling of flag leaves, spikelets, and developing seeds of contrasting rice genotypes (N22, Dular, and Anjali) using gas chromatography–mass spectrometry (GC–MS) under drought, heat, and combined

stresses revealed up to 60 metabolites (including various amino acids, sugars, alcohols, and acids) specific to organ, cultivar, or stress (Lawas et al. 2019). Increased accumulation of isocitric, glycerol-3-P, and galactaric acids occurred during flower, spikelet, and seed development in N22 and Dular cultivars, which are more drought tolerant than Anjali (Lawas et al. 2019). Elevated glucose, fructose, 1-ketose, and raffinose levels occurred in flowers and spikelets of N22 and Dular. Increased accumulation of polyamines, putrescine, ornithine, and spermidine occurred in Anjali (sensitive to combined drought/heat stress) during flower and spikelet development; however, these compounds were absent in N22 and Dular. Increased abundance of glutamic acid, arbutin, and vanillic acid occurred in flag leaves of N22 (combined drought- and heat-tolerant cultivar) during flowering and grain filling (Lawas et al. 2019).

The metabolites obtained in response to combined drought/heat stress could be used as biomarkers for developing rice cultivars that tolerate combined drought/heat stress. Plants that recruit novel metabolic mechanisms under combined drought/heat stress may differ when subjected to these stresses alone. Despite metabolomic efforts to decipher diverse novel metabolites in response to combined stress, various signaling pathways and complex gene networks need to be resolved using a system biology approach and robust bioinformatics tools. Metabolomics studies are mostly undertaken on plants grown indoors or in growth chambers. Future studies in the field are needed to gain a realistic picture of the differentially expressed metabolites produced under various stress conditions, including combined drought/heat stress (Raza 2020).

Genetic engineering, a powerful functional genomics approach for combined drought- and heat-tolerant crops

Genetic engineering approaches are used extensively for deciphering the function of various stress-responsive gene(s). How these genes confer stress tolerance has been explored in various plant species in the last two decades using this approach. The transgenic approach could be used to introduce/pyramid combined drought/heat tolerance in crop plants to sustain plant adaptation and improve yield under the challenging global climate changes. The introduction of various regulatory gene(s), ranging from *NAC*, *WRKY*, *DREB*, *ERF*, *MYB*, and *AVP1* to *OsSIZ1* that either upregulate or downregulate downstream target genes through genetic engineering can enhance abiotic stress tolerance in crop plants (El-Esawi and Alayafi 2019). Overexpression of transgenic cytokinin oxidase/dehydrogenase *CKX1* gene in *Nicotiana tabacum* L. increased combined drought/heat tolerance by increasing root system, enhancing stomatal conductance, and inducing the proline biosynthetic gene

P5CSA playing a critical role in osmoprotection (Macková et al. 2013). *NAC* (*NAM*, *ATAF1/2*, and *CUC2*) is a well-recognized element involved in regulating various genes and gene networks related to abiotic stress tolerance (Puranik et al. 2012). Fang et al. (2015) reported overexpression of the *SNAC3* gene in rice, which mediated combined drought/heat tolerance by inhibiting target genes (*LOC_Os02g02400*, *LOC_Os04g14680*, *LOC_Os02g34810*) (see Table 5) involved in excessive ROS activity and minimizing electrolyte leakage under combined stress. In transgenic rice, minimal ROS production, low electrolyte leakage, and enhanced grain yield resulted from overexpression of *OsRab7* under combined water and elevated temperature stress (El-Esawi and Alayafi 2019). Increased activity of antioxidant enzyme peroxidases and catalase, reduced electrolyte leakage and decreased malondialdehyde and hydrogen peroxide contents occurred in transgenic wheat overexpressing the *AtWRKY30* gene, relative to their wild-type counterparts, indicating the role of this gene in drought and heat tolerance in wheat (El-Esawi et al. 2019).

Casaretto et al. (2016) reported that enhanced activation of ROS-scavenging activity, upregulation of several genes related to stress hormone signaling, HSPs and chaperonins, and cell wall development due to overexpression of the *OsMYB5* gene increased combined drought/heat stress tolerance in transgenic maize. Likewise, overexpression of the rice *SUMO E3* ligase *OsSIZ1* gene conferred water and heat stress tolerance in creeping bentgrass (Li et al. 2013), cotton (Mishra et al. 2017) and *Arabidopsis* (Mishra et al. 2017). The significant role of *Arabidopsis* vacuolar pyrophosphatase gene *AVP1* mediating multiple abiotic stresses, including drought and salinity tolerance, has been established in *Arabidopsis* (Gaxiola et al. 2001; Li et al. 2005), cotton (Pasapula et al. 2011), and peanut (Qin et al. 2013). Co-overexpression of *OsSIZ1* and *AVP1* genes conferred combined drought/heat tolerance in *Arabidopsis* (Esmaeili et al. 2019). Similarly, co-overexpression of *OsSIZ1* and *AVP1* genes enhanced fiber yield in transgenic cotton, relative to the wild type, by upregulating cell wall synthesis, antioxidative metabolism, and HSP genes under combined drought/heat stress (Esmaeili et al. 2021). Co-overexpression of *AVP1* and *Larrea Rubisco activase (RCA)* gene in transgenic *Arabidopsis* aided in combined drought/heat tolerance by minimizing the effect on photosynthetic processes, increasing root length, and enhancing seed yield, relative to the wild type (Wijewardene et al. 2020). Genetically engineered wheat and *Arabidopsis* had increased tolerance to combined drought/heat stress due to overexpression of the phosphoenolpyruvate carboxylase kinase-related gene, enhancing the expression of *ABI3* (ABA signaling) and *HSP17.6A* genes (Zang et al. 2018). These transgenic plants also had lower electrolyte leakage and water loss than their wild-type counterparts.

Several transcriptional co-activators, e.g., *multi-protein bridging factor1c (MBF1c)*, contribute to abiotic stress tolerance in various plants (Suzuki et al. 2005). In this context, combined water and heat stress tolerance in transgenic *Arabidopsis* occurred due to the overexpression of *MBF1c*, which enhanced ethylene activity (Suzuki et al. 2005). Collectively, the transgenic approach could be valuable for manipulating various regulatory genes and genes related to activating antioxidant mechanisms and HSPs, accumulating osmolytes, and protecting photosynthetic apparatus under combined drought/heat stress.

Augmentation of CRISPR/Cas9-based genome editing technology has been used to incorporate heat stress tolerance by manipulating *NAC* TF in rice (Liu et al. 2020) and *BZR1* TF in tomato (Yin et al. 2018) and modulating *YODA* and *HSP90.1* in *Arabidopsis* (Samakovli et al. 2020). Examples of improved drought stress tolerance using CRISPR/Ca9 mediated technology include engineering of *AREB1/ABF2* regulating ABA in *Arabidopsis* (Roca Paixão et al. 2019), *ARGOS8* regulating ethylene in maize (Shi et al. 2017), and *OsNAC14* regulating ABA biosynthesis in rice (Shim et al. 2018). However, the potential of this technique has not yet been harnessed for developing combined drought/heat tolerance in plants. This powerful technology could be used to manipulate specific regulatory gene(s)/multiple genes/haplotypes controlling combined drought/heat tolerance with greater precision for designing future climate-resilient crops.

Concluding remarks and future directions

Under the changing global climate, combined drought/heat stress episodes are increasing in agricultural areas and becoming a significant global challenge for food security. Crop responses to combined stress differ from those of individual stresses. However, combined drought/heat stress significantly affects key physiological, morphological, biochemical, and molecular processes, resulting in serious yield losses for many crops (see details in Cohen et al. 2020).

Screening crop germplasm is an affordable and viable option for identifying crop genotypes tolerant to this combination. Exploring various landraces and gene pools could further identify adaptive traits contributing to plant adaptation to combined stresses (Mickelbart et al. 2015). The introduction of novel genetic variants/beneficial alleles contributing to combined drought/heat tolerance through pre-breeding activity needs urgent attention (Kilian et al. 2021). Traditional QTLs mapping, GWAS, and WGRS approaches could elucidate the underlying QTLs/genetic determinants/haplotypes stress tolerance across the whole genome (Templer et al. 2017; Sukumaran et al. 2018; Yuan et al. 2019). These genomic regions could be transferred into elite crop cultivars using genomic-assisted breeding.

Table 5 List of trans-genes showing combined drought and heat stress tolerance in plants

Crop	Genotype	Gene transferred from	Name of regulatory gene/gene	Tolerance mechanism	Method used	References
Arabidopsis	Columbia	Wheat	Multiprotein bridging factor 1c (<i>MBF1c</i>)	Promoting ethylene-response signal transduction pathway	Agrobacterium-mediated	Suzuki et al. (2005)
			<i>TaWRKY33</i>	Enhanced germination rate and root growth		He et al. (2016)
	Col-0	Wheat	<i>TaPEPKR2</i>	Reduced electrolyte leakage	<i>Agrobacterium tumefaciens</i>	Zang et al. (2018)
<i>Agrostis stolonifera</i> L.	Penn A-4	Rice and <i>Arabidopsis</i>	Overexpression of <i>AVP1/OsSIZ1</i>	<i>AVP1/OsSIZ1</i> co-overexpressing plants	Agrobacterium-mediated	Esmaili et al. (2019)
			Overexpression of <i>OsSIZ1</i>	Plants produce > 160% more seeds than the wild type		Wijewardene et al. (2020)
			Overexpression of <i>OsSIZ1</i>	628 and 1067 DEGs were upregulated		
Cotton	C312	Rice	<i>AVP1/RCA</i> co-overexpressing	Ribulose-1,5-bisphosphate carboxylase/oxygenase (<i>RuBisCo</i>) activase gene helps maintain higher photosynthetic activity under heat stress	Agrobacterium-mediated	Li et al. (2013)
			Overexpression of <i>OsSIZ1</i>	<i>AVP1</i> helps increase root growth and drought tolerance		
			Overexpression of <i>OsSIZ1</i>	Robust root growth, water retention and cell membrane integrity		Mishra et al. (2017)
Maize	SRG200	Rice	Overexpression of <i>OsSIZ1</i> and <i>AVP1</i> genes	Higher upregulation of <i>RD22</i> , <i>HSFB2B</i> , <i>HSP70</i> , <i>HSP90</i> , <i>NCED3</i> , <i>RAB18</i> , <i>SOD</i> , <i>CESA8</i> , <i>XTH6</i>	Agrobacterium-mediated	Esmaili et al. (2019)
			Overexpression of <i>OsMYB55</i>	Reduced leaf damage, higher plant biomass		Casaretto et al. (2016)

Table 5 (continued)

Crop	Genotype	Gene transferred from	Name of regulatory gene/gene	Tolerance mechanism	Method used	References
Rice	Giza 177	Rice	Overexpression of <i>OsRab7</i>	Higher proline accumulation and antioxidant activity Upregulation of <i>OsCATA</i> , <i>OsCATB</i> , <i>OsAPX2</i> , <i>OsSOD</i> - <i>Cu/Zn</i> genes Upregulation of <i>OsLEA3</i> , <i>OsRD29A</i> , <i>OsSNAC1</i> , <i>OsSNAC2</i> , <i>OsDREB2A</i> , <i>OsDREB2B</i> , <i>OsRAB16A</i> , <i>OsRAB16C</i>	<i>Agrobacterium tumefaciens</i>	El-Esawi and Alayafi (2019)
	Zhonghua 11	Rice	<i>SNAC3</i> (<i>ONAC003</i> , <i>LOC_Os01g09550</i>)	Enhanced expression of ROS-scavenging genes, lower H ₂ O ₂ and malondialdehyde (MDA) production and lower electrolyte leakage	Agrobacterium-mediated	Fang et al. (2015)
	Nipponbare	Rice	<i>OsHSP50.2</i>	Lower electrolyte leakage, high antioxidant activity, low chlorophyll loss	Agrobacterium-mediated	Xiang et al. (2018)
Tobacco	Samsun NN	<i>Arabidopsis thaliana</i>	<i>CKX1</i> gene	Enlarged root system, lower leaf temperature, higher stomatal conductance, higher expression of <i>ERD10B</i> and <i>P5CSA</i>		Macková et al. (2013)
		Tobacco	<i>NHSP70-1</i>	Drought-stress tolerance and thermos-protection	Particle gun bombardment	Cho and Choi (2009)
Wheat	Liaochun10	Wheat	<i>TaPEPKR2</i>	Reduced electrolyte leakage	<i>Agrobacterium tumefaciens</i>	Zang et al. (2018)

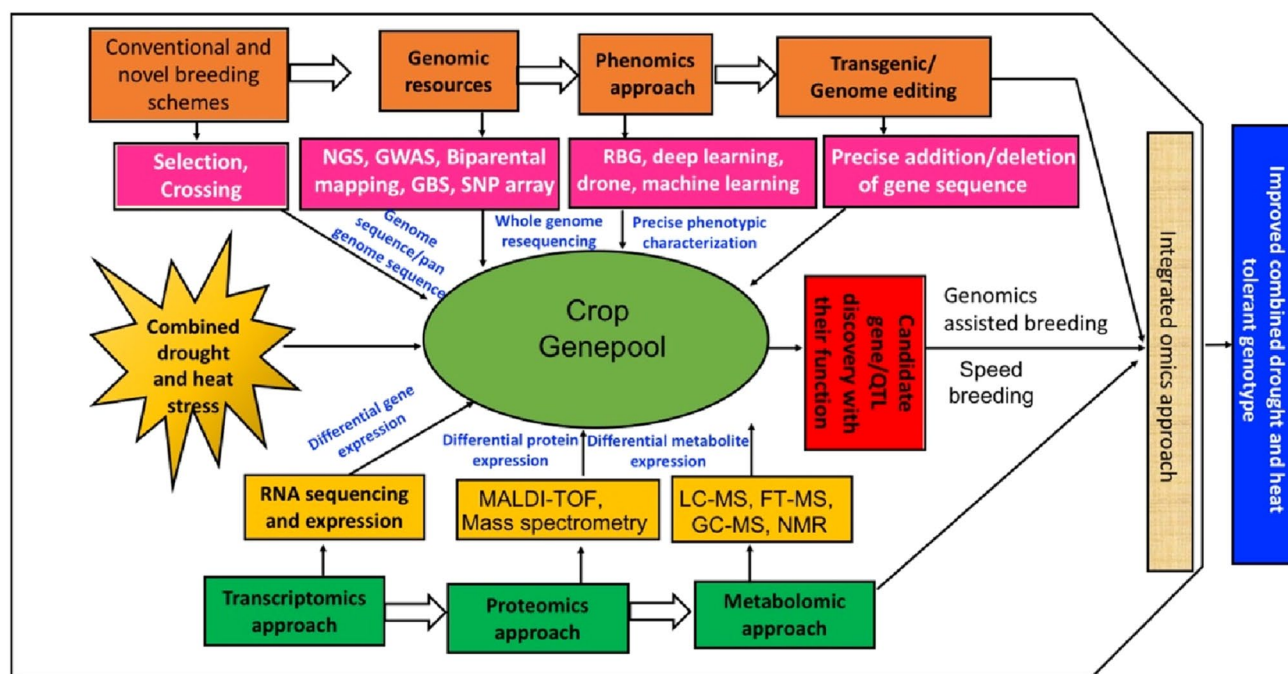


Fig. 2 Improving combined drought and heat tolerance in crop plant through integrated ‘omics’ approach. Among the omics approaches, genomics can be deployed to unveil the possible candidate gene(s) governing combined drought and heat tolerance through bi-parental, genome wide association studies mapping and resequencing of large crop germplasm. Transcriptomic, proteomic and metabolomic approaches could greatly inform us the functional role of various gene(s)/QTLs and their complex networks controlling combined drought and heat tolerance in plant at phenotypic level. In parallel, transgenic and genome editing could help us in designing combined drought and heat tolerant by base addition/deletion in targeted

genomic region with great precision. Besides, emerging speed breeding and novel breeding approach could enhance the crop breeding cycle. Thus, integration of all these omics approach and novel breeding tools could improve crop performance under combined drought and heat stress. *GWAS* genome-wide association study; *GBS* genotyping-by-sequencing; *NGS* next generation sequencing; *SNP* single nucleotide polymorphism; *RGB* Red–Green–Blue; *MALDI-TOF* matrix-assisted laser desorption/ionization-time of flight; *LC-MS* liquid chromatography–mass spectrometry; *FT-MS* Fourier transform mass spectrometry; *GC-MS* gas chromatography–mass spectrometry; *NMR* nuclear magnetic resonance

Advances in functional genomics, including transcriptomics, proteomics, and metabolomics, could shed light on possible candidate gene(s), gene networks, signaling molecules, candidate proteins, and metabolites contributing to combined stress tolerance (Zhao et al. 2016; Zandalinas et al. 2018; Lawas et al. 2019). However, phenotyping combined stress tolerance remains challenging due to its complex genetic inheritance and high $G \times E$ interaction. Therefore, the use of various emerging phenomics facilities, machine learning, and deep learning approaches will be crucial for improving our understanding of combined stress response in target environments (Singh et al. 2018).

Robust genetic engineering techniques and emerging CRISPR/cas9-based genome editing technologies could allow us to tailor crops tolerant to combined drought/heat stress through genome editing of targeted regions controlling stress tolerance. A holistic approach encompassing plant breeding, physiology, molecular biology, and various ‘omics’ is needed to ensure global food security under the increasing prevalence of combined stress environments (see Fig. 2). Scientists in the plant ‘omics’ community should

investigate crop stress responses in the field, as they are more valuable than laboratory-only studies, to improve our understanding of the complex stress tolerance mechanisms to accelerate the development of stress-tolerant cultivars.

Acknowledgements AB, PD, AR, and SC thank CSIR for providing fellowships to conduct the research work. HN is thankful to DST, UGC, DBT, UWA (Australia), ICARDA (Morocco), IIPR (Kanpur), PAU (Ludhiana), and World Vegetable Center for supporting the research work. Contribution number 21-341-J from Kansas Agricultural Experiment Station.

Author contribution statement HN and UJ conceived the idea; UJ, AB, PD, AR, and SC compiled the information. The other authors equally participated in editing and shaping the manuscript.

Declarations

Conflict of interest The authors declare no competing interests.

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**Peer Reviewed Refereed
and UGC Listed
Journal No. 47026**



**ISSN 2319 - 359X
AN INTERNATIONAL MULTIDISCIPLINARY
HALF YEARLY RESEARCH JOURNAL**

IDEAL

Volume - X, Issue - II,
March - August - 2022
English / Marathi & Hindi Part - II

Impact Factor /
Indexing
2020 - 6.008
www.sjifactor.com

**Ajanta
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ज्ञान-विज्ञान विमुक्तये

IMPACT FACTOR / INDEXING
2020 - 6.008
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❖ EDITOR ❖

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❖ PUBLISHED BY ❖



Ajanta Prakashan

Aurangabad. (M.S.)

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3. Impact of Classical Music on Film Music

Dr. Harjas Kaur

Associate Professor, HOD Music Vocal, Govt. College Ropar.

1. Introduction

Hindi film songs have been featured in Hindi cinema since Ardeshir Irani's first audio film *Alam Ara* (1931) featuring seven songs. This was closely followed by *Shirheen Farhad* (1931) by Jamshedji Framji Madan, also Madan, who had 42 songs composed in the style of opera, and later *Indra Sabha* who had a sequence of up to 69 songs. However, the trend dropped and subsequent films usually appeared between six and ten songs in each production (Gopal and Moorti, 2008). Since the founding of Indian cinema in 1931, music with song numbers has become a common feature in Indian cinema (Morcom, 2007). During the first few years, Hindi cinema had produced various films that could be easily distinguished by genres such as "historicals", "mythologicals", "devotional," fantasy "etc. (Gopal and Moorti, 2008). Hindi song was an important feature of traditional Hindi cinema, among other things, that another post-liberation cinema, such as the Satyajit Ray films, discarded song and dance in its attempt to break away from traditional cinema. Bollywood music found inspiration in the sources many traditional ones such as *Ramleela*, *nautanki*, concert and *Parsi theater*, as well as Western, Pakistan, and other Indic music subcultures (Mehta and Pandharipanda, 2010).

2. Indian Classical Music

Indian classical music has been a tradition for centuries. Ancient Indian music has evolved into two distinct branches. One is from North India called *Hindustani* and the other from South India is *Carnatic*. *Hindustani* culture is found in *Kashmir*, *Punjab*, and *Bengal*. In *Pakistan* and *Bangladesh*, culture has been weakened for the past half century in those countries. *Carnatic* is found mainly in the four southern states of *Karnataka*, *Andhra Pradesh*, *Tamil Nadu* and *Kerala*. *Hindustani* and *Carantic* are very similar to each other in form and specific categories such as development, or design category. The lyrics are different from *Carantic* music but the overall structure is the same. New historical and cultural studies have shown that Indian music developed through complex interactions between different peoples practicing different cultures and cultures.

Classical music is known for its impact, beauty and sense of beauty within the film. Since millions of films prefer *Classic* music over modern sounds, it is safe to say that the impact of

Classical music is hard to beat. Classical music is music written or created by a composer and recorded in a musical text. Classical music follows ancient musical traditions established from Western cultures, rather than traditional, jazz or popular culture. People often think of Classical music as 'old' music. This is because about 1750 to 1830, Classical musical forms such as symphony, concerto, and sonata were produced. As an important part of the film, many directors turned to Classical music in their movies. This can be for a variety of reasons, such as: (a) Representing a particular era, (b) Arousal (either romantic, sad, scared, angry or happy), and (c) With a shocking effect on horror or entertaining movies.

3. Impact and Influence of classical music on movies and songs

Classical music is known for its impact, beauty and sense of beauty within the film. Since millions of films prefer Classic music over modern sounds, it is safe to say that the impact of Classical music is hard to beat. Indian classical music has formed the basis of many Indian film songs over the decades and remains an important foundation for music directors across the country. Famous composers such as Naushad and Khayyam to Shankar-Jaikishan and R.D. Burman, based on their timeless pieces on ancient Indian raagas. Songs such as 'Radha ki tune bansuri churayi' and 'Jhanak jhanak tori baaje' on Raag Darbaari are some of the highlights.

4. Classical Bollywood Music

In the post-independence era when Hindi became a national language that enhanced nationalism in films that gave the impression of a united nation, Bollywood music served as a unifying factor. It incorporates a variety of styles from a variety of cultures - both Hindustani and Carnatic Classical, religious and traditional music, film music saw the effects of international music from Latin to Chinese to reggae. In time, Indian films became more and more popular around the world, especially with their music collection.

While Playback music became the heartbeat of Indian cinema, the performers and music directors became a major part of the films, from a variety of backgrounds. Some were highly trained, some were traditional, and some were self-taught. Some of the most notable music directors are S.D. Burman, Naushad, Khaiyyam and R.D. Burman, while the most prominent musicians who dominated the genre were Lata Mangeshkar, Mohammad Rafi, Manna De, Asha Bhosle, Kishore Kumar most.

Vedabala (2016) reported that any music originates in the community and develops with the changing of its realities. Embrace the new and adjusted existing ones from time to time. This process of acceptance and rejection makes any kind of art last longer. India is known for its rich musical heritage worldwide. There are many types and types of music. Among the most revered are classical Indian music, be it Hindustani or Carnatic. Music represents an exemplary standard

with a long set pattern or style based on long-term developed techniques. Other technological innovations that have influenced classical music are the development of archiving / archiving technologies, virtual music classes and online music availability. Music, one of the most inseparable things in society, cannot be kept from changing the realities of time. It has accepted the unpleasant things and rejected the desirable in the various stages of its evolution. Conflicts can be addressed by maintaining a balance between custom and tradition. Technology mixed with traditional values can be a complete advantage to an old music center.

Indian film music from the early 20th century to the 1960s had a profound effect on Indian Classical Music featuring a large number of scales (Ragas) and Rhythm patterns (Talas) which are their distinguishing features. Most of the composers have chosen the famous Raga such as 'Assavari', 'Bilawal', 'Kalyan', 'Kafi', 'Bhairav' and 'Khamaj' while in some places the raga is as rare as 'Nayaki', 'Kirwani', 'Shivaranjani', 'Megh' was also used. Naushad Saheb is regarded as the forerunner of his contemporaries introducing classical music and folklore to film music thus giving it many ratings that reached the peak of popularity in the 1940s, 50s and 60s. He created some of the most talented musicians. For Pakeezah his skills in orchestral and background music were excellent, as he used the many catchy 'Thumris' and Lataji's beautiful 'Aaps' in a strange way that created a beautiful mix of rhythm and music. "Ek shahenshah ne banwa ke haseen" in the film 'Taj Mahal' based on 'Raga lalit' was good morning music, while "Man tarapat hari darasan" bhajan titled 'Raga Malkauns' is still popular among the masses.

The 1970s and early 1980s were the era of Khayyam Saheb who provided memorable music, his compilation 'Dil Cheez kya hai' in 'Raga Bihag' took place as Ashaji's memorable play in Umrao Jaan by Muzaffar Ali. In the early 80s and 90s, Pt. Hari Prasad Chaurasia the famous flute and Santoor maestro Pt. Shiv Kumar Sharma has teamed up as the Shiv-Hari team, nominated three times for the Filmfare award. In 'Silsila' one of their main hits includes ancient 'Raga Pahadi' songs, with folk tunes, which delight their listeners. Classical Duo has definitely left a challenge for future Bollywood artists to maintain standards. Over time, about a quarter of the songs composed by music directors Shankar-Jaikishan (1953-71), Kalyanji-Anandji (1960-81), RD Burman (1971-81), AR Rahman (1992-2013, and Pritam). Chakraborty (2004-2013) was influenced by new genres of music, which combined to form Bollywood music. A.R. Rehman combined elements of Hindustani and Carnatic music with Qawwali styles and classical Western and electronic music to create unique timbre, forms and instruments, thus attracting his international audience.

Hindustani Classical music is one of the many genres of art music with its roots especially regional cultures. Ancient Indian music is derived from the Vedic books of Hinduism

and ancient Natyashastra, an ancient Sanskrit text on the working art of the Great Sage Bharat Muni. The folkloric songs Geet Gawai have their origins in gaths sung by sutas or traditional artists from the early Vedic period. In Rig Veda, gathas are ritualistic songs and are often recited not only to create a sense of humor but also to combine interesting, spelling and magnetic forces during marriage.

Hindustani Classical music in its purest form is hard to reach for the general public. So the great sangeet Gurus borrowed from traditional folk music and created timeless music that is easily accessible and easy to appreciate and famous for its sweetness. It is for this reason that such beautiful forms of humanity were associated with the 12 months of the year and provided beautiful and tangible songs such as Dadra, Chaiti, Kajri, Thumri, etc.

Film songs such as Baiju Bawra, Pakeezah, Nadiya Ke Paar Dilip Kumar's 1948's, Barsaat - Hawa mein dta jaye mora lal dupata... Madhumati and other contemporary artists such as Dabang, Bunty aur Babli or Bol Bacchan (Chalao na nainon se ban re) really eternal hits.

5. Cultural Impact

The Indian film, with its feature film, has not only spread throughout Indian society, but has also been instrumental in spreading Indian culture throughout the world. For example in Britain, Hindi film songs are heard in restaurants and cafes and restaurants. British actress Sudha Bhuchar has transformed the smash hit Hindi film, Hum Aapke Hain Koun to the hit music "Fourteen Songs" which was well received by the British audience. Filmmaker Baz Luhrmann acknowledged the impact of Hindi cinema on his production of Moulin Rouge by inserting the number "Hindi Sad Diamonds" based on the film's song "Chamma Chamma" composed by Anu Malik (Conrich and Tincknell, 2007). In Greece the genre of indoprepi emerged in Hindi film music while in Indonesia Dangdut artists such as Ellya Khadam, Rhoma Irama reworked Hindi songs for Indonesian audiences (David, 2008). In Nigeria bandiri music - a combination of Sufi style and Bollywood style music - has become quite popular among Hausa youths (Gopal and Moorti, 2008).

6. Conclusion

Music plays a vital role in films. Music helps the audience to capture the spirit of various scenes, and this helps the audience to better understand the plot. By incorporating music into a film, it is possible to evoke emotion in the characters of a film or film so that the audience can share what the characters are experiencing. When music is played along with the film, the audience can see through both the sight and the hearing. The aim is therefore to show Indian classical music is the legacy of everything that has influenced other songs and emerged over the centuries in the form of music.

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ISSN: 2394 5303

Impact
Factor
8.012(IJIF)

Printing Area[®]
Peer-Reviewed International Journal

February 2022
Issue-86, Vol-02

01

आंतरराष्ट्रीय बहुभाषिक शोध पत्रिका

प्रिंटिंग एरिया

Printing Area International Interdisciplinary Research
Journal in Marathi, Hindi & English Languages

February 2022, Issue-86, Vol-02

Editor

Dr. Babu g. Gholap

(M.A.Mar.& Pol.Sci.,B.Ed.Ph.D.NET.)

“Printed by: Harshwardhan Publication Pvt.Ltd. Published by Ghodke Archana
Rajendra & Printed & published at Harshwardhan Publication Pvt.Ltd.,At.Post.
Limbaganesh Dist,Beed -431122 (Maharashtra) and Editor Dr. Gholap Babu Ganpat.”

Reg.No.U74120 MH2013 PTC 251205



Harshwardhan Publication Pvt.Ltd.
At.Post.Limbaganesh,Tq.Dist.Beed
Pin-431126 (Maharashtra) Cell:07588057695,09850203295
harshwardhanpubli@gmail.com, vidyawarta@gmail.com

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डॉ. कंचन

सहायक प्रोफेसर,

सरकारी कॉलेज, रोपड़ (पंजाब)

औरत ने जन्म दिया मर्दों को

मर्दों ने उसे बाजार दिया...

साहिर लुधियानवी

सृष्टि के प्रत्येक समाज में स्त्री-तत्व की भूमिका एवं महत्व सर्वोपरि रहा है। किसी भी समाज की उत्पत्ति, विकास एवं संस्कार में स्त्री प्रमुख स्तंभ बनकर दृढ़ता, जिम्मेदारी एवं आत्मसमर्पण से खड़ी रही है। अति-यथार्थवादी एवं घोर-पदार्थवादी वर्तमान विखण्डित प्रवृत्त समाज एवं व्यक्ति के लिए स्त्री ही एक मात्र संबल है जो उसे विखराव, एकाकीपन और अजनबीपन के गर्त से निकाल सकती है, क्योंकि स्त्री में वात्सल्य है, श्रद्धा है। वह सृष्टि है, जननी है। अपने आदि रूप में वह प्रकृति है। लेकिन, साहिर लुधियानवी की उपरिलिखित पंक्तियाँ इंगित करती हैं कि समाज की निर्माता स्त्री के वात्सल्य, सेवा-श्रद्धा-भाव एवं आत्मसमर्पित हृदय को पुरुष-समाज ने ठगा है। स्त्री के ईश्वरीय-तुल्य महत्व को ठुकराकर समाज ने उसे विवशता की बेड़ियों में जकड़ दिया है। समाज द्वारा उसकी विवशता का लाभ उठाकर उसे बाजार में ला कर खड़ा कर दिया गया है। यह समाज का स्त्री के प्रति सबसे घृणित एवं अमानवीय कुकृत्य है। सम्पूर्ण समर्पण के पश्चात् भी स्त्री ने अपनी यात्रा में जो कुछ झेला है उसका वर्णन एवं मंथन करना भी एक भयंकर मानसिक पीड़ा से गुजरना है। इससे गुजरने का मादा बहुत कम लेखक/लेखिकाओं में होता है। इस विषय में कुसुम अंसल का उपन्यास 'तापसी'

विशेष रूप से उल्लेखनीय है। इस उपन्यास में नारी के तमाम उम्र के दर्द, जीवन के प्रत्येक पड़ाव पर छले जाने की पीड़ा और संघर्ष, शारीरिक और मानसिक उत्पीड़न को झेलने का चित्रण बखूबी मिलता है। उपन्यास की नायिका तापसी है। उसके जीवनवृत्त को केन्द्र में रखकर ही लेखिका ने औपन्यासिक-कथा का ताना-बाना बुना है तथा उसके माध्यम से ही विधवा आश्रमों की आढ़ लेकर प्रफुल्लित हो रहे दुराचार के अड्डे एवं उसमें नरक-तुल्य जीवन जी रही स्त्रियों की दशा को रूपायित किया गया है।

उपन्यास की नायिका तापसी बंगाल के बोलपुर से है। तापसी एक वेश्या की बेटी है, जिसकी माँ को उसके ही भाई ने अपने ताड़ी के व्यसन के कारण सोनागाच्छी में बेच दिया और फिर सत्रह की आयु में विवाह का झांसा देकर वह तापसी को भी बेच देता है। विवाह और पति जैसे शब्दों के मायने क्या हैं? तापसी कभी नहीं समझ पाती। पैसे लेकर उसे एक ऐसे व्यक्ति के पल्ले बांध दिया जाता है, जो अपनी शारीरिक असमर्थताओं की सारी झुंझलाहट व कुण्ठा तापसी के शरीर पर उतारता है, जैसे उसे शारीरिक-मानसिक उत्पीड़न देना नरेन मजूमदार का अपना सुख बन गया हो। तापसी के द्वारा पीड़ा से सनी स्त्री की मानसिकता को चित्रित करती हुई लेखिका लिखती है—अंधेरे में पसरा बदबू का भभका, अंधेरे में उसके शरीर को कचोटते पत्थर जैसे हाथ, गालों को दबोचते बदबूदार दोंत, साड़ी, वह, अनावृत दूसरा शरीर—वही थी जो निरन्तर हार रही थी और मजूमदार का दवाइयां खाता व्यक्तित्व जीत रहा था। हर रात उसके दूध का गुलाबी रंग, पुड़ियों का सत्व पिया हुआ पदार्थ और शरीरों की उठा-पटक, अंधेरे के गुच्छों में गहराती काँटेदार खाई और फिर झल्लाते मजूमदार का बेतहाशा मारना और समझना कि वह विजेता था, विजेता रहेगा—और—मजूमदार ही बात-बात में उस सारी रकम का भारीपन गिना जाता था, जो उससे शादी के लिए जतिन दा ने उससे ली थी और वह जो खाल काका ने ताड़ी के फेनिल प्रवाह में बहा दी थी। बेजुबान का क्रय तो होना ही था, ..सौदेबाजी...बाजार का नियम जो था? उपन्यास की नायिका जैसे ही और

अधिक अत्याचार न सह कर विद्रोह कर उठ खड़ी हुई उसका पति बीमारियों के कारण कमजोर पड़ता गया और मर गया। परन्तु, स्त्री की विडम्बना है कि वह किन्हीं भी परिस्थितियों में स्वतंत्र नहीं हो सकती। परम्पराएँ, संस्कार, समाज, संस्थाएँ, व्यक्ति आदि अनेक हैं जो उसे स्वतंत्र व्यक्तित्व में देखना ही नहीं चाहता। इसलिए नरेन के मरने के पश्चात् भी तापसी की मानसिक परिस्थितियों में कोई बदलाव नहीं आता। बल्कि वह और अधिक दयनीय परिस्थितियों में पहुँच जाती है। सुहाग तो था भी नहीं। फिर भी वैधव्य ओढ़ना पड़ा मुझे। सारे नाते रिश्तेदार, सब पैसे के थे और किसी के पैसे पर मेरा कोई अधिकार नहीं था।² तापसी के विधवा होते ही समाज उसे निष्कासित कर देता है। तापसी जैसी विधवाओं के लिए समाज ने कुछ एक स्थान निर्धारित किए हैं, जहाँ पहुँच वे अपने शेष जीवन को समाज से विमुख गुमनामी से काट सकती हैं। ऐसे स्थानों को समाज ने विधवा—आश्रम या धार्मिक स्थान के रूप में स्थापित किया है। ये स्थान समाज से पीड़ित स्त्रियों को एक बेहतर जीवन—विकल्प देने के लिए निर्माण किए गए हैं। परन्तु लेखिका का मानना है कि इन संस्थाओं ने तापसी जैसी स्त्रियों के पुनर्वास में कोई सकारात्मक भूमिका अदा नहीं की है, अपितु उनके कष्टों में और अधिक वृद्धि हुई है।

लेखिका ने तापसी के माध्यम से वर्तमान में धर्म की आड़ लेकर चल रहे विधवा आश्रमों में बढ़ती वेश्यावृत्ति को उपन्यास में विशेष रूप से स्थान दिया है। इस विषय में लेखिका उपन्यास की भूमिका में लिखती हैं— मुझे लगता है आज के तीर्थ अपना गंतव्य, अपनी भव्यता, कलात्मकता, यहाँ तक कि अपनी आत्मा भी खो चुके हैं।— आज का तीर्थ छीने झपटने का तीर्थ है, जो एक नकारात्मक भावावेश या नेगेटिव इमोशंस ही हमें पकड़ाता है। और आश्रम? जहाँ षड्यंत्र रचे जाते हैं, एक प्लैनिंग चलती है और जिसके बंद दरवाजों के भीतर सैल्फिश और मैनीप्यूलैटेड संसार की संरचना होती है। उनके विध्वंसकारी चक्रव्यूह में फंसकर कोई भी विधवा स्त्री अपनी मनुष्यता खो देने को विवश है।³ तापसी के माध्यम से लेखिका ने स्त्री हित में कार्यरत इन संस्थाओं को स्त्री—अस्तित्व

एवं संरचना के लिए अव्यवहारिक घोषित किया है। तापसी का अंतस बार—बार इन धर्मयुक्त संस्थाओं के ढाँचे के विपक्ष में खड़ा हुआ जात होता है। लेखिका के अनुरूप अवश्य ही विधवा स्त्रियों के पुनर्वास का यह परम्परात्मक ढाँचा स्त्री—स्वभाव के अनुकूल नहीं है। तापसी के माध्यम से लेखिका बयान करती है कि स्त्री हित में भारतीय समाज की यह संरचना उसके लिए बाहरी शोषण से कहीं अधिक पीड़ादायक है। इसलिए आश्रम में पहुँचने के पश्चात् तापसी कहती है कि — विधवा होने की नियति ! इतना बड़ा स्थानान्तरण।⁴ विधवा आश्रमों के धार्मिक माहौल पर तापसी का स्त्री—हृदय बार—बार विपक्षी होकर प्रश्न करता है। हर बार उसके प्रश्न अधिक से अधिक तार्किक एवं पैसे होते जाते हैं। भगवान हर समय अपना नाम ही क्यों सुनना चाहते हैं? उसे आश्चर्य हुआ। वह भी इन सब अकेली छुटी हुई परित्यक्ता, दुखियारी टूटी खण्डित विधवाओं के मुँह से? आश्रम में तापसी को केवल मानसिक रूप से ही पड़ताड़ित नहीं होना पड़ता अपितु प्रत्येक प्रकार से उसका शोषण होता है। तापसी ही नहीं बल्कि अनेक विधवा पात्रा हैं जिनके माध्यम से लेखिका ने इस व्यवस्था की विभीषिका को उजागर किया है। लेखिका के द्वारा प्रस्तुत विधवा—आश्रम के विवरण को पढ़कर ऐसा लगता है कि यह कोई नायक प्रधान रचना न होकर समाजगत संरचना के यथार्थ को बयान करने वाली कृति है। लेखिका ने अनेक ऐसी विधवा पात्रों को इस हिस्से में स्थान दिया है, जिन्हें समाज ने निष्कासित कर दिया है। उपन्यास की पात्रा वृंदा अपनी टेडी टांगों वाली बेटी के साथ विधवा आश्रम में रहती है। जहाँ उसे पर्याप्त भोजन भी नहीं मिलता, तब बेटी की टेडी टांगों का इलाज कैसे होता? अपनी लाचार बेटी के लिए बेबस वशंदा हाथ—पैर मारती है। वह कभी बेटी के लिए मंदिर से फल और मिठाई चुराती है, तो कभी कम्बल, ताबीज, तेल आदि छोटी—छोटी चीजों के लिए अपनी देह बेचती है। मुफ्त में दिया तेल?..या फिर रात सो ली उसके साथ? तेरी खिड़की खुली थी।⁵ उपन्यास की पात्र गउरी दासी भी इन्हीं परिस्थितियों का शिकार होती है। वह खुलना (वर्तमान बंगलादेश) की रहने वाली है।

भूख और गरीबी में, अनेक पुरुषों के हाथों छूटती—बिकती जैसे—तैसे वृंदावन विधवा आश्रम पहुँचती है। परन्तु यहाँ भी उसे यौन शोषण का शिकार होना पड़ता है। आश्रमों में बहुत मिट्टी खराब हुई मेरी। कभी कहीं रही कभी कहीं। मथुरा के एक आश्रम में तो खुले आम वेश्यावृत्ति चलती थी। मैं भी मजबूर कर दी गई थी।' लेखिका का मानना है कि इन भाग्यहीनों का समाज में कोई भी नहीं है। इनके हित में न कोई संस्था है, न ही कोई नियम—कानून है। बल्कि कानून के रखवाले तो इनके सबसे बड़े भक्षक हैं। उपन्यास में कोई भी पीड़ित पात्रा न्याय हेतु पुलिस के पास नहीं जाना चाहती। बल्कि उनका मानना है कि — पुलिस। वे क्या इंसान होते हैं? उनकी हवस का सामना करना तो और भी दूभर हो गया था।' उपन्यास की नायिका भी अपने पर हुए अत्याचार के विरुद्ध न्याय की गुहार लगाने हेतु पुलिसवालों के पास जाना चाहती है, परन्तु गाँव की युवती उसे समझाते हुए रोकती है — याद है आपको, कुछ ही महीने पहले यहाँ पास ही किसी गाँव में एक औरत को निर्वस्त्र करके शहर में धुमाया गया था, क्योंकि वह गाँव के गुण्डों के विरोध में घर की नौखट छोड़ कर पुलिस से मदद माँग रही थी। पुलिस ने उसकी टॉग तोड़ दी, इसलिए कि उसका यह साहस नाकाबिले बरदाशत था तमाम आदमी जात के लिए कि, भारत की भरती पर मदों के आमने—सामने होकर एक अदना—सी औरत अपने अधिकार की बात करे, सिर उठाये, यही नहीं, कानूनी लड़ाई लड़ने का दुस्साहस कर बैठे।'

लेखिका ने तापसी जैसी स्त्रियों के यौग—शोषण को ही वाणी नहीं दी बल्कि उनके अकेलेपन को भी बयान किया है। उपन्यास की नायिका तापसी जिसके पास परिवार के नाम पर सिर्फ रखाल काका (जिसने उसे बेच दिया था) ही है, जो पत्थरों की मूर्तियां गढ़ने में मशगूल तापसी की तमाम इच्छाओं से अलग—थलग एक स्वार्थपूर्ण संवेदनविहीन संसार में जीता है। तापसी का कोई नहीं है, जो उसके आन्तरिक सौन्दर्य एवं द्रव्य को पहचान सकें। तापसी हमेशा अपने एकाकीपन के विषय में सोचती रहती है। वस नितान्त अकेलेपन। पानी में बहती मछली जैसा अकेलेपन, कोई क्यों

होता है इतना अकेला? तापसी के अतिरिक्त लेखिका ने वृंदा, नूराबाई, गउरी दासी आदि स्त्री पात्रों के आन्तरिक द्वंद्व एवं एकाकीपन को भी अभिव्यक्ति दी है। ऐसी नारियां जो भूख और गरीबी में दर—दर की ठोकरे खातीं विधवा आश्रमों में पनाह लेती हैं, परन्तु वहाँ भी वे जीवन जीने नहीं उसे ढोने को अभिशप्त है। भयावह सूनेपन, अकेलेपन की शिकार ये स्त्रियाँ मौत की ओर खामोशी से बढ़ रही हैं। विधवा नूराबाई जिसके पति को लकवा मार गया, उसे अपने चार बच्चों का पेट भरने के लिए एक सौ पचास रुपये और दो किलो कोदों (अनाज) के लिए पहले अपनी आठ साल की संजू को गिरवी रखना पड़ता है और फिर एक—एक करके सब बच्चे गिरवी चले जाते हैं। बच्चे कहाँ गए उसे नहीं पता? पति मर गया और नूराबाई भक्के खाती, रोती, कलपती विधवा आश्रम पहुँच गई। लेखिका ने उसके अकेलेपन को बेहद संजीदगी से प्रस्तुत किया है। हर रात कमरे के कोने में रोती थी नूराबाई। कमरे का वह कोना गवाह था, उसके अकेलेपन का, उसके फड़फड़ाने अस्तित्व का जो यहाँ जी रहा था, साँभ ले रहा था। क्योंकि भूख उनकी जिंदगी का बहुत बड़ा सच, जो आंगुओं के गोलेपन से भी अधिक लिसलिसा था।'

भ्यातव्य है कि पश्चिमी आवाहवा ने जहाँ हमारी सभ्यता—संस्कृति, जीवन के प्रत्येक पक्ष को प्रभावित किया है, वहीं हमारे परिवारों की नींव माने जाने वाले स्त्री—पुरुष के परम्पर संबंधों पर भी चोट की है। आज का युवा वर्ग विवाह करने के पक्ष में नहीं है। उसकी कामवृत्तियों ने संस्कारों एवं परम्पराओं के बंधन तोड़ दिए हैं, जिसके परिणाम स्वरूप समलैंगिक सम्बन्धों में वृद्धि होने लगी है। इन परिस्थितियों के उभार में स्त्री और पुरुष दोनों ने गति पकड़ी है। कहना गलत न होगा कि इन परिस्थितियों के पीछे दोनों ही (स्त्री—पुरुष) जिम्मेदार हैं। हां, अधिक जिम्मेदार कौन है यह शोध का विषय अवश्य है। इन परिस्थितियों के उभार में भारतीय सामाजिक संरचना को भी कठघरे में खड़ा किया जाना लाजिमी है। चूँकि, प्रारम्भ से ही भारतीय पारिवारिक संरचना पितृसत्तात्मक रही है। परिवार में पिता, भाई, पति की छवि ने स्त्री को अवश्य ही

नकारात्मक बहाव दिया है। स्त्री, पुरुष की सत्ता एवं अधिकार की बेड़ियों को तोड़ना चाहती है, वह स्वतंत्र होना चाहती है। स्त्री-पुरुष के मध्य एक अविश्वास का भाव तीव्र हुआ है। वर्तमान पीढ़ी विवाह नामक संस्था से घबराने लगी है। सत्ता, अधिकार, स्वतंत्र अस्तित्व आदि के विद्रोह एवं अहं में स्त्री के समलैंगिक सम्बन्ध गति से पनपने लगे हैं। दूसरी तरफ स्त्री के दिनों-दिन विद्रोही होते स्वभाव तथा स्त्री हित में सक्रिय सामाजिक संस्थाओं के पुरुष विरोधी रवैये ने पुरुष को आतंकित किया है। अविश्वास के माहौल में पुरुषों में भी समलैंगिक सम्बन्ध बढ़े हैं। विवेच्य उपन्यास में लेखिका ने जबरन समलैंगिक संबंध बनाने या यौग-शोषण करने का चित्रण भी किया है। उपन्यास की पात्रा बरौता जो अपने पति के दोनों हाथ दर्राँत से चीरकर भाग आई है और सात वर्षों से विधवा आश्रम में रह रही है, वह आश्रम में आने वाली प्रत्येक लड़की के साथ जबरन यौग-संबंध बनाती है। बरौता का शिकार बन चुकी तापसी की मानसिक स्थिति भयावह है। उसका शरीर बरौता के व्यवहार से टूट गया है। उसे एक स्त्री के द्वारा इस प्रकार का कृत्य करना पुरुष से भी अधिक पीड़ादायक अनुभूत होता है। उसे महसूस होता है कि इतनी मानसिक पीड़ा तो उसके बीमार पति ने भी नहीं दी थी। अवश्य ही एक स्त्री दूसरी स्त्री से संवेदनात्मक व्यवहार की उम्मीद रखती है। परन्तु जब स्त्री ही स्त्री के अस्तित्व, मान-सम्मान को रौंदती है तो निश्चय ही पीड़ा अधिक होती है। अवश्य ही तापसी के माध्यम से लेखिका ने इस विषय को उजागर किया है। एक काली औरत उस पर झुकी थी। उसके कपडे शरीर से दूर जा पड़े थे। निर्वस्त्र उस तगड़ी औरत का शरीर उस पर किसी प्रेतात्मा-सा तना था। वह चीखती रही, चिल्लाती रही, आसपास की औरतें तमाशा देखती रहीं— काली औरत के दाँत—उसके सारे शरीर पर कालिख—सी पोत गये थे। औरत ने औरत को इस स्थिति तक पहुँचा दिया था जहाँ उसकी समूची शक्ति और उसका कमजोर विद्रोह उसे बेहोशी की स्थिति तक छोड़ कर चला गया था।¹²

लेखिका ने प्रस्तुत उपन्यास में इस विषय में दो अन्य स्त्री पात्रों की सृजना की है — अम्बिका देवी और जयमाला, जो आर्थिक-सम्पन्नता के लिए स्त्री होने हुए भी स्त्री के आत्मसम्मान पर चोंट करती हैं। 'श्री गंधा कृष्ण विधवा-आश्रम' की संचालिका अम्बिका

देवी आश्रम की गरीब व बेबस स्त्रियों को डंडों से पीटती है और आश्रम को मिले दान (कम्बल, बर्तन, खाने-पीने का सामान, चौक इत्यादि) से अपने ही बैंक बैलेंस में वृद्धि करती है। विधवा-सेवा का ढोंग रचकर 'सोशल वर्कर' के पुरस्कारों को एकत्रित करती है। जयमाला सोशल वर्कर के एवज में तापसी जैसी विधवा पीड़ितों को उज्ज्वल भविष्य के सब्जबाग दिखाती है। पढ़ाई-लिखाई, विदेशी स्कॉलरशिप और पासपोर्ट इत्यादि का झाँसा देकर उनका मानसिक एवं शारीरिक शोषण करती है। जयमाला और उसका परिवार तापसी के प्रति अत्यधिक उदारता इसलिए दिखाता है, क्योंकि जयमाला के लिए तापसी केवल एक प्रोडक्ट थी, एक मामूली-सा जिस्म जिसकी किडनी धोखे से लेकर उसे अपनी भतीजी वसुन्धरा की जान बचानी थी। इस विषय में तापसी को उसकी सहेली सूचित करती है— उन्हें कोई और नहीं मिला था डोनेट करने के लिए, इसलिए तुझे ही बनाया है बलि का बकरा।¹³ जीवन के प्रत्येक पड़ाव पर विश्वासघात को सहन करती तापसी जीवन से निराश हो जाती है। उसके भीतर जीवन हेतु सूक्ष्मातिसूक्ष्म विश्वास का अंत हो जाता है। वह अपनी जीवन-लीला बंगाल की रेल की पटरियों पर समाप्त कर लेती है। किसकी लाश है ? यह कुछ अता-पता? शिनाख्त, नहीं। अखबार से ढकी खून से लथपथ तापसी।¹⁴

दरअसल लेखिका ने भारतीय परिवेश में स्त्री के प्रति सामाजिक ढाँचे की अन्यायपूर्ण एवं अमानवीय दृष्टि को उजागर किया है। स्त्री के संबंध में भारतीय समाज दृष्टिगत एवं ढाँचागत दोनों स्तर पर सटीक दिशा में कार्यरत् नहीं है। इस पूरे ताने-बाने के चलते स्त्रियों को प्रत्येक स्तर पर शोषित होना ही पड़ेगा। वह कभी परिवार की जिम्मेदारियों के नाम पर शोषण का शिकार बनती रहेगी है तो कभी अपने सपने पूरे करने की इच्छा के एवज में छली जाती रहेगी। भले ही स्त्री मुक्ति आन्दोलन के प्रभावों-दवाबों को कारण सुधारवादी-उदारवादी-संशोधनवादी मेकअप जरूर हुआ परन्तु उससे न परिधि पर स्त्री की स्थिति (सामाजिक-आर्थिक-राजनीतिक..) बदली और न अन्य संकट कम हुए। शिक्षा और आर्थिक स्वतन्त्रता के आधार पर, नारी मुक्ति का सपना देखने-दिखाने वाले सिद्धान्तों को ही लकवा मार गया। महिलाओं की समस्या पहले से अधिक गम्भीर और जटिल हो गई है। शोषण दोहरा। जिम्मेवारी दोगुनी। अधिकार शून्य।¹⁵

निष्कर्षतः विवेच्य उपन्यास बंगाल (बालपुर) से वृंदावन की गलियों, मंदिरों एवं आश्रमों में भटकती तापसी के संघर्ष व व्यथा को ही नहीं दिखाता अपितु तापसी के साथ-साथ संपूर्ण विश्व पटल पर प्रत्येक उस स्त्री की व्यथा को भी रूपायित करता है जो इन परिस्थितियों का शिकार होती है। नायिका के मन में ताउम्र बहती प्रश्नों की वैतरणी हर उस स्त्री के प्रश्नों की वैतरणी है जिसके उत्तर पुरुषवादी समाज के पास नहीं हैं। निसदेह २१वी. सदी में नारी कल्याण हेतु रास्ते दिखाए जा रहे हैं, सिद्धांत बनाए जा रहे हैं परन्तु विडम्बना यही है परिवार, समाज व सरकारें उन रास्तों को व्यावहारिक रूप नहीं दे पा रही हैं। नारी विकास व सुरक्षा हेतु आन्दोलन शुरू होते ही दम तोड़ देते हैं, क्योंकि जब किसी नारी के साथ कुछ अप्रिय घटित हो जाए तो उसे लज्जा के नाम पर जग-जाहिर नहीं होने दिया जाता। हमारा समाज उस परित्यक्ता को ही कटघरे में ला खड़ा करता है। सभ्यता के इस पड़ाव पर पहुँच कर भी स्त्री-जीवन की असंख्य कहानियाँ हमें भारतीय समाज पर शंका की दृष्टि से देखने के लिए विवश करती हैं। लेखिका का प्रहार भारतीय समाज की मंशा पर है, जो उसकी आत्मा को झंकझोर देने का मादा रखता है।

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बच्चों के परवरिश पर माता-पिता के व्यवहार का प्रभाव

Dr. Madhuri Kumari
LNMU Darbhanga, Bihar

वर्तमान समय में यह देखने में आता है कि पारिवारिक संबंधों का हास हो रहा है। संबंधों में स्थिरता घट रही है और परिवर्तनशीलता बढ़ रही है। आज बालक माता-पिता से अधिक महत्व अपने समूह के साथियों तथा परिवार के अन्य सदस्यों को देता है। किशोर-बालक और बालिका परिवार से तालमेल नहीं बैठा पा रहे हैं। इन दोषपूर्ण संबंधों का प्रमुख कारण माता-पिता की व्यवहार, बाल पोषण की गलत विधियाँ एवं अधिकारवादिता प्रभुत्व आदि है। अच्छे पारिवारिक सम्बन्धों की आधारशिला रखने के लिये आवश्यक है कि माता-पिता केवल बच्चों की शारीरिक आवश्यकताओं की ही पूर्ति करे अपितु मानसिक और संवेगात्मक आवश्यकताओं की संतुष्टि पर भी पर्याप्त ध्यान दें किन्तु यदि किसी कारणवश माता-पिता अपने बच्चों की उपेक्षा व तिरस्कार करते हैं तो बच्चों भावनात्मक संतुलन बिगड़ जाता है और संबंधों में करवाहट आने लगती है। पारिवारिक संबंध अच्छे न होने पर बालक सामाजिक समायोजन में असफल हो जाता है। 'माता-पिता को चाहिये कि वे प्रत्येक आयु स्तर पर अपने बालको की भावनाओं को समझे, न तो बहुत अधिक लाड़-प्यार करें नही उपेक्षापूर्ण व्यवहार करें। बच्चे का न तो अधिक नियंत्रण

esj[lsu gh v f/kd Lor ar kn& माता-पिता यदि ये देखे कि बालक के व्यवहारों में बदलाव आ रहा है तो लापरवाही न बरतें तुरंत कारण जानने का प्रयास करें। यदि माता-पिता के किसी व्यवहार के कारण बालक की भावनाओं को ठेस पहुँची है तो उसे स्वीकारें तथा

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Approaches Toward Developing Heat and Drought Tolerance in Mungbean

10

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Abstract

The projected rise in the global temperature and water scarcity will increase the frequency and intensity of heat and drought stresses. Agriculture is the main sector that is severely affected by these stresses and going to threaten global food security. Mungbean is the major summer-season food legume and of paramount importance because of its protein-rich seeds and have the ability to restore soil fertility. But these stresses adversely affect the overall growth and development of this crop as revealed through altered morphology, physiology, enzymatic activities, and eventually declined its quality as well as quantity. Reproductive stage is extensively studied and more susceptible toward heat stress as various processes such as pollen germination, pollen load, pollen tube growth, stigma receptivity, ovule fertility, and seed filling are reduced to a much extent leading to poor yield. The present review summarizes the effects of heat and drought stress on the vegetative, reproductive growth, physiological functions, and cellular

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U. C Jha et al. (eds.), *Developing Climate Resilient Grain and Forage Legumes*,
https://doi.org/10.1007/978-981-16-9848-4_10

activities of mungbean. Furthermore, defense mechanisms employed by the plants that comprise elevated productions of HSPs, antioxidants, osmolytes, and secondary metabolites are also considered. Based upon such responses of the plants, various approaches, which can be employed by the breeders for developing stress-tolerant varieties comprise physiological, biochemical, molecular traits, and agronomic strategies. These approaches would prove to be valuable for getting insights into the physiological and molecular mechanisms governing heat and drought tolerance and will pave the way for engineering the plants.

Keywords

Mungbean · Heat stress · Drought stress · Climate resilience · QTL

10.1 Introduction

Mungbean or green gram (*Vigna radiata* L. wilczek) is grown on almost seven million hectares of land worldwide (Abid et al. 2018). *Vigna radiata* is the most widely distributed of the six Asiatic *Vigna* species (Dahiya et al. 2015). It is an important grain legume and cash crop that is widely farmed in South, East, and Southeast Asia as well as in South America and sub-Saharan Africa (Akhtar et al. 2015). Due to its photo-insensitivity and short duration, it can be used in a variety of intensive cropping techniques (Dahiya et al. 2015; Sehrawat et al. 2013). The crop is indigenous to India (Ardalani et al. 2015) and its seeds and sprouts are widely utilized as a fresh salad, vegetable, or staple meal not just in Asian countries but also in the Western world (Sehrawat et al. 2013). Around six million hectares of land are grown for the mungbean crop worldwide, accounting for around 8.5% of total pulse area (Chand et al. 2018). Mungbean is high in easily digestible proteins, carbs, fibers, minerals, vitamins, antioxidants, and other phytonutrients, making it a good candidate for malnutrition mitigation. The crop has a yield potential of roughly 2 tonnes per hectare, with average productivity of about 0.5 tonnes per hectare (Sehrawat et al. 2013). Mungbean is more heat and drought tolerant than other pulse crops, but it is still affected by severe abiotic stresses like low or high temperatures, insufficient or excessive water, high salinity, and low soil fertility (Reddy 2009).

Spring (February/March), summer (March/April), and kharif (June/July) are the three main seasons for mungbean cultivation on the Asian continent (Basu et al. 2019). When grown in rainfed areas, seedlings are exposed to water stress due to decreased water supplies throughout these months. Water scarcity causes stress in plants at any stage (Dias et al. 2010). Due to a predicted increase in the occurrence of water shortfalls, the global drought-restricted zone is expanding, posing a threat to mungbean crop production worldwide (Nair et al. 2019). For the growth of mungbean, sufficient water availability is more important than any other environmental trigger (Sehrawat et al. 2013). Water scarcity in the seedling stage makes it difficult to produce healthy seedlings and reduces overall productivity (Dahiya et al.

2015). Mungbean (*Vigna radiata* L. Wilczek) is also a unique source of protein supplement with a plethora of medicinal properties and is a climate-friendly crop (Chikukura et al. 2017). The plant is an annual legume of the Fabaceae family that plays a critical role in nutrition in all developing countries (Pratap et al. 2016). Thus, during the last few decades, there has been an increase in attempts to develop and expand the production of this pulse crop (Bazaz et al. 2016). Consuming mung beans in combination with cereals tends to improve the protein quality, as these grains are fairly high in sulfur-containing amino acids (Fang et al. 2017) and provide a cost-effective source of easily digestible protein for vegetarians. As a result, mungbean may sometimes be referred to as “poor man’s meat” (Hall 1992). Mungbean has also been claimed to be suitable for youngsters due to its decreased flatulence and hypoallergenic qualities (Dahiya et al. 2015; Ali et al. 2018).

The crop is usually grown in the summer and fall at an optimal temperature range of 27–30 °C and is primarily cultivated in dry and semiarid tropics at elevations <2000 m (Singh et al. 2017). However, the high degree of fluctuation in climatic conditions, such as rising temperatures and uncertain water scarcity situations, is restricting mungbean productivity during its cropping season (Singh et al. 2017). Heat stress is one of the primary issues influencing mungbean crop production during summers in the current global climatic condition (Martinez et al. 2012). Hence, the primary goal of mungbean breeders is to boost the genetic potential of genotypes under conditions of heat stress (Mariani and Ferrante 2017).

Numerous varieties have been produced that are resistant/tolerant to abiotic (drought, salinity, and heat) stresses (Mariani and Ferrante 2017). Drought and heat are some of the most critical threats gaining considerable attention from farmers and researchers due to their major influence on agriculture (Ashraf and Foolad 2007). The situation is worsening due to erratic changes in the nature of the environment and escalated frequency of global climate change; henceforth, it is imperious to secure food supplies for the future by increasing the survivability of important agricultural crop plants (Joshi et al. 2016). Due to their restricted genetic base, these types become prone to stressors, and their average production has remained nearly constant over the last few decades (Hanif and Wahid 2018). However, Mungbean wild relatives can be used to increase genetic diversity and to introduce beneficial characteristics into cultivated mungbean lines (Jiang et al. 2015). There is an urgent need for extensive study of genetic resources, cytological, genetic, genomic, and tissue culture research to elevate this critical crop’s vertical and horizontal base to that of other key legumes (Nair et al. 2019). In comparison to other legume crops, the publications on the development of transgenic mungbean demonstrate a lack of an efficient plant genetic transformation methodology compatible with in vitro regeneration. Heat and drought stress often occur simultaneously, and due to global climate change, this kind of phenomenon occurs more frequently and severely, which poses detrimental effects on plants (Nahar et al. 2015). Hence, it is critical to incorporate novel technologies like transgenics approaches, genome editing, conventional breeding, and embryo rescue procedures to enhance its productivity under heat and drought stress conditions (Devasirvatham

et al. 2012). However, little research has been done on this issue, which should be expanded to allow for greater use of wild mungbean species.

10.2 Various Traits for Heat Stress Tolerance in Mungbean

10.2.1 Morpho-Physiological Trait Variations for Improving Heat Tolerance

Heat stress is frequently associated with drought, high solar irradiation, and high wind velocity, and the combination of these conditions can exacerbate damage even in adequately watered plants (Hall 1992). A plethora of research has established mungbean's great susceptibility to rising temperatures (Teixeira et al. 2013; Jha et al. 2017).

High-temperature stress has a detrimental effect on plant growth and development as well as on a variety of physiological activities (HanumanthaRao et al. 2016). For example, extended exposure to high temperatures may cause mungbean seeds (*Phaseolus aureus* Roxb.) to lose vigor, impairing seedling emergence and establishment (Devasirvatham et al. 2012; Kumar et al. 2011). Photosynthetic rate, which is determined by leaf area and dry matter production, is related to the number of pods and seeds. With increased leaf area, the percentage of solar radiation intercepted and the rate of dry matter synthesis enhanced (Hamid et al. 1981). Temperatures above 45 °C, which occur frequently throughout the flowering cycle, can cause flower abortion and production losses. Sharma et al. (2016) used Temperature Induction Response (TIR) and physiological screening methodologies at the seedling and whole plant levels to assess the influence of high temperature on different mungbean lines for vegetative and reproductive performance. The most promising tolerant lines were chosen for further study at the plant level. These lines were evaluated for growth and yield features at two sowings: normal sowing (NS), where day/night temperatures throughout the reproductive stage were between 40 and 28 °C, and late sowing (LS), where temperatures were higher (>40/28 °C). Leaf rolling and chlorosis were observed on the leaves of LS plants and hastened phenology resulted in a significant reduction in leaf area, biomass, flowers, and pods. Intriguingly, the length of flowering and podding was also reduced (Sharma et al. 2016).

High-temperature treatment (50 °C for 10, 20, 30 min) dramatically lowered seed germination and vigor index in mungbean (Piramila et al. 2012). Furthermore, high temperatures, particularly those more than 40/30 °C (max/min), impede growth and produce chlorosis in mungbean (Kumar et al. 2011). This is connected with a drop in leaf hydration status and increased oxidative stress, which has been observed to be alleviated by exogenous ascorbic acid treatment (Kumar et al. 2011). Sharma et al. (2016) also discovered heat-induced leaf blistering, leaf rolling, and chlorosis in mungbean plants. Other effects of heat stress on mungbean included leaf curving, leaf withering, leaf yellowing and blackening, plant height reduction, and decreased leaf, branch, and biomass numbers (Kaur et al. 2015). Heat stress also reduces the

photosynthetic ability and crop productivity; however, the genetic reason for this is unknown and needs detailed insight in the future (Biswash et al. 2014).

10.2.1.1 Reproductive and Yield Traits for Heat Stress Tolerance

Although plants have the natural ability to maintain their metabolism and vegetative development under a wide range of temperature regimes, reproductive growth showed a significant sensitivity to warmer temperatures (Abou-Shleel 2014). Rawson and Craven (1979) conducted extensive research on the effects of high temperatures on blooming in several mungbean genotypes exposed to lengthy photoperiods and high mean temperatures (24–28 °C).

Extreme temperatures cause late flowering, tissue damage in male and female reproductive structures, and flower and pod abortion (Young et al. 2004; Zinn et al. 2010; Firon et al. 2012; Djanaguiraman et al. 2013). Increased temperature also affects the shape of anther and pollen, reduces pollen content, retards their dehiscence, and may result in full male sterility (Awasthi et al. 2015; Djanaguiraman et al. 2013). This modification in the anther dehiscence and pollen release process is frequently caused by high relative humidity during periods of heat stress (Bansal et al. 2014; Jiang et al. 2015). In comparison to female gametophytic tissue, elevated temperatures have a greater detrimental effect on male gametophytic development, affecting pollen germination, viability, and pollen tube elongation (Jiang et al. 2015). Across all stages of pollen development, the formation of meiocytes and microspores showed greater sensitivity to heat, as demonstrated in a variety of experiments on various crop species (Monterroso and Wien 1990; Ahmed et al. 1992; Devasirvatham et al. 2012). As a result of these irregularities in anther and pollen formation, pollination and fertilization events are disrupted, significantly reducing fruit and pod set (Bita and Gerats 2013). The assessment of pollen thermotolerance and the reaction to heat stress is a critical topic for plant geneticists, agronomists, and biologists interested in improving current germplasm (Mittler et al. 2012; Devasirvatham et al. 2012).

High temperatures (>40 °C) have a direct effect on flower maintenance and pod development in mungbean, accounting for up to 79% of flower shedding (Kumari and Verma 1983). In a similar investigation, flower preservation under heat stress was examined in 77 mutants produced from NM 92 and 51 recombinants derived from three crossings, namely, VC1482C NM92, VC1560D NM92, and NM98 VC3902A (Khattak et al. 2006). No genotype was completely resistant to flower shedding, although NM 92 was susceptible to the same feature under conditions of extreme heat (>40 °C) (Khattak et al. 2006). Additionally, shedding was detected only in opened flowers and not in pods at any developmental stage; further humidity changes had no influence on floral shedding (Khattak et al. 2006). Similarly, the detrimental effects of heat stress (45/25 °C) on two mungbean cultivars (SML 832 and SML 668) were evaluated, with a particular emphasis on the reproductive stage (Kaur et al. 2015). Their findings indicated that temperatures greater than 35/25 °C, 43/30 °C, 45/32 °C (day/night) were severely detrimental to reproductive activities and also had a significant effect on the crop's potential output (Kaur et al. 2015). In mungbean, high temperatures during the early phases of development and

reproduction have a detrimental effect on seed yield, owing to pollen viability, reduced fertilization, and complete flower shedding (Kaur et al. 2015). Thus, screening and selection of mungbean genotypes capable of withstanding high temperatures throughout reproductive phases are critical for increasing the crop's growth and output (Singh and Singh 2011). Alagupalamuthirsolai et al. (2015) also investigated reproductive heat stress in 20 high-yielding mungbean cultivars using stress indices, yield-contributing attributes, and growing degree days ($^{\circ}\text{C}$) and found that all genotypes exhibited significant variance in yield traits under heat stress.

Recently, a study was done to determine the effect of heat stress on the vegetative and reproductive functions of 41 mungbean genotypes grown under managed growth circumstances (Sharma et al. 2016). We identified a few selective heat-tolerant mungbean lines that can be used in future breeding projects (Sharma et al. 2016). Another study examined the variation in response of 28 mungbean genotypes to heat stress ($45/30^{\circ}\text{C}$ NAc-HT, unacclimated), particularly during the reproductive stage, and to pre-acclimation of different genotypes to elevated temperatures of $35/28^{\circ}\text{C}$ (Ac-HT, acclimated) prior to exposing them to high temperatures. The total pollen count was dramatically reduced from $88/\text{mm}^2$ in CON ($28^{\circ}\text{C}/24^{\circ}\text{C}$, control) to $50/\text{mm}^2$ in Ac-HT and $40/\text{mm}^2$ in NAc-HT plants, with evident genotypic variation, implying that acclimated plants (Ac-HT) maintained a greater pollen number and viability than non-acclimated plants (NAc-HT) (Patriyawaty et al. 2018).

Terminal heat stress is a typical problem with mungbean in India, particularly during the spring/summer season (HanumanthaRao et al. 2016). During the early growth period, high temperatures, greater than 40°C , result in a significant reduction in yield potential due to reduced fertilization, pollen sterility, and a rapid rate of flower shedding (HanumanthaRao et al. 2016). Rainey and Griffiths (2005) demonstrated that the abscission of reproductive structures was the primary determinant of yield in a variety of annual grain legumes when subjected to heat stress. Very little research has been conducted on the effects of heat stress on mungbean, particularly on the reproductive stage (Devasirvatham et al. 2012). Therefore, to boost mungbean productivity under heat stress conditions, it is critical to characterize the genetic variation for heat tolerance in the core germplasm and to investigate the mechanisms underlying this crop's heat sensitivity (Devasirvatham et al. 2012; Kumar et al. 2011). On the basis of grain yield in normal and heat stress conditions, eight heat indices were calculated. Under both normal and heat stress conditions, the highest significant positive correlations were established between mean productivity, geometric mean productivity, stress tolerance index, and yield indices. SML 1186, NDM 12-308, IPM 02-4, and Smrat genotypes were identified as having a high stress index score and could be used in mungbean breeding efforts to introduce and produce heat-tolerant promising varieties (Ahmad et al. 2021).

Furthermore, to boost mungbean growth and productivity, genotypes that can endure high temperatures during reproductive stages must be screened and selected (Singh and Singh 2011).

10.2.2 Biochemical Traits Modulating Heat Tolerance

The mungbean (*Vigna radiata* L. Wilczek) is one of the most significant crops in the world (Kumar et al. 2013; Farooq et al. 2017). It has a production potential of around 2000 kg per hectare; however, productivity is only 842 kg per hectare (BBS 2016). The ideal temperature for mungbean yield is between 28 °C and 30 °C (Poehlman 1991). Applying heat stress during the flowering period allows partitioning to the pods and seed development. Following a period of 15 days of stress, the data were collected on seed production and quality at maturity, as well as physiological and biochemical parameters were also evaluated (Hanif and Wahid 2018). According to their report, high temperature resulted in a significant increase in H₂O₂ and MDA levels as well as a decrease in net photosynthesis, stomatal conductance, and water content (Hanif and Wahid 2018). Similarly, a significant decrease in sucrose concentration was observed in the leaves and anthers, along with a decrease in the activities of sucrose-synthesizing enzymes (sucrose synthase, sucrose phosphate synthase) and hydrolyzing enzymes (acid invertase) due to heat stress, which could be a critical factor affecting reproductive function and yield attributes (Kaur et al. 2015). In another study, an increase in MDA content was noticed in seedlings treated with deadly temperature (40 °C) at any harvest but decreased when seedlings were pretreated with 40 °C prior to lethal stress (Mansoor and Naqvi 2013). Furthermore, there was a variable response of antioxidant enzyme activity among different genotypes. POD and SOD activities increased under stress in all genotypes except NM 20-21, whereas APX activity increased in all genotypes. However, CAT activity decreased under stress for NM 19-19 and 121-123 but increased for NM 20-21 and NCM 89. Under heat stress, NM 19-19 had a low MDA concentration and elevated antioxidant enzymes, indicating that it was the most thermotolerant genotype. However, elevated MDA levels and low antioxidant enzyme activity were found in NM 20-21, suggesting that it is the least thermotolerant genotype (Mansoor and Naqvi 2013). In another study, heat stress has caused significant accumulation of H₂O₂ and MDA that decreased stomatal conductance and water use efficiency, chlorophyll a and b, and total chlorophylls and net photosynthesis in the sensitive varieties while increased carotenoids contents in the tolerant varieties (Hanif and Wahid 2018).

10.2.3 Multi-Omics Approaches to Understand Heat Tolerance in Mungbean

10.2.3.1 Genomics Approaches

Mungbean is a quantitative short-day legume grown across varied locations, environments, and seasons (Ohama et al. 2017). The crop has inherent intrinsic tolerance mechanisms to cope with different environmental stressors (Pratap et al. 2016). Despite its wide growth and cultivation, it is exposed to high temperatures and also faces photo-thermoperiod sensitivity. Considerable efforts have been made toward the development of input-responsive, high-yielding, disease-resistant, and

short-duration varieties of mungbean in the past three to four decades (Priya et al. 2020). However, breeding techniques for heat stress resistance have largely remained untouched, consequently posing serious constraints to mungbean production (Pratap et al. 2016). In the current era, the advancements in “omics” technologies, particularly genomics, proteomics, metabolomics, and transcriptomics, have enabled unbiased and direct monitoring of the factors affecting Mungbean growth and yield in response to environmental constraints (Naveed et al. 2015). Omics tool is proving highly beneficial in deciphering the complex molecular mechanisms underlying plant growth, development, and their interactions with the environment, which ultimately determine the nutritional value, yield potential (Raina et al. 2016), and the agricultural inputs of crop. Substantial genetic and genomic resources of mungbean are available now, which can be exploited for the development of climate-resilient cultivars (Varshney et al. 2014). Different climate-smart traits can be incorporated in mungbean through current advancements in breeding techniques which will help them to adapt to varied climates and perform well across environments (Varshney et al. 2014).

At the present scenario of global warming and changing climate, breeders and plant researchers are working on the foundational work of implementation of genomic technologies (Yadav et al. 2010). The World Vegetable Centre and the Australian National Mungbean Improvement Program have dramatically increased the yields, reliability, and sustainability of mungbean crops worldwide through conventional breeding programs (Varshney et al. 2014). The genome sequencing of diverse sets of mungbean germplasm aims at quantifying the genetic diversity present among the world’s mungbean gene pool collection and to decipher genes associated with agronomically beneficial traits (Kajla et al. 2015).

The World Vegetable Center (AVRDC) has created a mungbean mini-core set, which comprises a significant fraction of the variety in the WorldVeg gene bank for this species (HanumanthaRao et al. 2016). This site contains a significant genetic resource for identifying new features that can be used in breeding programs in the future. There have been a variety of breeding procedures used to increase genetic variability in green gram, but hybridization and induction of mutations are seen to be the most promising for selecting acceptable variants from a segregating population (Kalaji et al. 2016). To generate varieties with pyramided traits, combining traditional breeding methods with molecular breeding technologies is beneficial (Nair et al. 2019). With the increasing availability of genomic technologies and resources for legumes, a more complete and in-depth genome mapping of green gram is critical for genetic improvement (Pratap et al. 2015). Systematic efforts must be made to investigate the physiological and biochemical regulation of biotic and abiotic stresses, as well as the entire profile of genes, proteins, and metabolites that confer resistance/tolerance, so that they can be modified to generate improved mungbean cultivars (Nair et al. 2019). Furthermore, by linking the sequence and phenotyping data regions of the genome associated with beneficial traits, the photosynthetic pathways, and water-use efficiency can be targeted (Kaushal et al. 2016). Once identified, these pathways can be manipulated directly using genome-editing tools, hence reducing current breeding efforts by more than half (Nair et al. 2019). As

abiotic stressors pose an extensive and immediate risk, these technologies and plant scientists needed to address the present issues in detail.

10.2.4 Exploring Gene Families and Transcriptional Factors as Heat Responsive Markers

To address the challenge of the hidden hunger and to ensure the nutritional security of future generations as proposed by the FAO (Food and Agriculture Organization), pulse production must be doubled by 2050; however, various environmental stressors are confronting this goal (Mannur et al. 2019; Kim et al. 2015). Among all environmental challenges, heat stress has the broadest and most far-reaching influence on legumes and is affecting agricultural crops more frequently and more severely (Hatfield and Prueger 2015). With the introduction of various physiological, molecular, and genetic bases of heat stress tolerance mechanisms, cultivated plants have gained a major attention for intense research on how they can tolerate or avoid heat stress through natural genetic variation or by using DNA technologies, mutational breeding, or genome editing to create new variations (Sgobba et al. 2015). Since past few decades, the identification of Hsf genes in many species has greatly increased our knowledge of the molecular mechanisms of plant developmental and defense processes (Guo et al. 2016; Wang et al. 2016). As mungbean is an economically important legume crop of the world, the emergence of its genetic database allows functional analysis of mungbean genes (Kang et al. 2014). Mungbean's genetic diversity has been conserved in various germplasm collection units globally. The major collection centers are developed in China, India, Philippines, Taiwan, and the United States (Liu et al. 2017) and by using genetic diversity at these centers genetic base of mungbean cultivars can be enlarged. Generally, screening of large collections for required traits is economically as well logistically challenging for mungbean breeders (Priya et al. 2020). The establishment of subsets of large germplasm collections can make screening more practical, but this procedure is laborious and costly (Schafleitner et al. 2015). In a recent study, 24 VrHsf genes were identified in mungbean and their characteristics were investigated using the mungbean genome database. Chromosome location analysis showed that out of 11 mungbean chromosomes, VrHsf genes are located on 8 and 7 duplicated gene pairs had formed between them. Furthermore, transcriptional patterns of VrHsf genes varied among different tissues, suggesting their involvement in plant growth and development. Identified multiple stress-related cis-elements in promoter regions of VrHsf and they observed that the expression of maximum VrHsf genes was influenced by different stress conditions, indicating their potential role in stress resilience pathways (Priya et al. 2020). Currently, the WRKY transcription factors are gaining importance for genomic and functional studies due to their seminal participation in plant growth, development, metabolism, and in the governance of multiple stress-defensive pathways. The recent release of draft genome sequences of Mung bean (*Vigna radiata*) has paved the way for the characterization of WRKY gene family in this crop. The genome-wide analysis of WRKY

transcription factors in mungbean led to the identification of two WRKY TFs (Vradi05g21980 Vradi0158s00480) for heat, drought, and osmotic stress tolerance (Zandalinas et al. 2018).

Regardless of the immense economic importance of the mungbean crop, the genomic studies and transcriptional analysis of this crop are still inadequate and need detailed insight to develop heat resilience under stressful environmental conditions.

10.2.5 Agronomic Approaches to Understand Heat Tolerance in Mungbean

Despite all of the efforts to improve green gram cultivars, the crop's yield potential remains poor due to biotic and abiotic causes (Mariani and Ferrante 2017). Poor yield potentiality, indeterminate growth, asynchronous maturity, low harvest index, faulty plant type, low partitioning efficiency, small seed size, and vulnerability to biotic and abiotic stressors are the key restrictions (Keatinge et al. 2011). As a leguminous crop, mungbean (*Vigna radiata*) may replenish soil fertility, prevent land degradation, and boost crop productivity and livestock raising while preserving the ecosystem (Priya et al. 2020). Cultivation of such dual-purpose leguminous crops improves overall productivity, conserves natural resources, and aids in generating greater output from the agricultural system (Fedoroff et al. 2010).

Seeding time and plant population are two of the most important factors contributing to lower pulse production. Managerial methods must be adjusted in the shifting scenario of abiotic and biotic stress to ensure greater crop output (Wang et al. 2015). The agro-ecological conditions play an important influence in determining when to plant. Planting time is critical, as it has a substantial impact on growth, development, and output (Waraich et al. 2012; Osakabe et al. 2014; Rasheed et al. 2016). The best time to plant mungbean depends on the cultivar (Sakata et al. 2010). As planting timings differ greatly among cultivars, precise planting schedules must be followed to achieve maximum output. Furthermore, due to an increase in grain weight and other production features, early sowing may also improve final yield and biomass production in mungbean (Sun et al. 2014). Due to the shortened growth cycle caused by late seeding, the interception of radiations was reduced, resulting in a drop in total dry matter accumulation and, as a result, inferior yields (Rasheed et al. 2011). To have a good yield, you need to pick the right cultivar and seed it at the right time (Reardon and Qaderi 2017). Mungbean cultivars respond to sowing dates and growing seasons in different ways. As a result, various kinds of mungbean cultivars should have different optimal planting dates (Reddy 2009). Sowing at the right times after identifying high-yielding cultivars can result in higher yields (Ahmad et al. 2021). Variable planting schedules resulted in considerable changes in mungbean seed production, according to the authors (Ahmad et al. 2015). Improving agronomic management systems and cultivation techniques may further prove promising in mechanized management and increasing yield potential (Chauhan and Williams 2018).

10.2.5.1 Drought Stress and Mungbean

Water stress is mainly caused by uneven rainfall, ground water shortage, or high soil salinity, and this situation becomes severe in many parts of the world including all arid and semiarid regions (Fathi and Tari 2016). The effects of drought range from morphological to molecular levels and influence all phenological stages of plant growth (Farooq et al. 2009). Drought stress is characterized by the cessation of various physiological processes like growth, development, and cell metabolism, eventually affecting the economic yield and productivity of crops (Yuriko et al. 2014). The first notable symptom of water scarcity is impaired seedling germination and poor stand establishment as reported in pea (Okcu et al. 2005). The main consequences of drought are wilting of leaves due to loss of turgor pressure, exhaltated solute concentrations in the cytosol, consequently inhibiting growth and reproductive functions (Ranawake et al. 2011). In fact, under severe water scarcity, ion uptake and transport get impaired along with a decrease in leaf area, cell wall lignifications, and increased root shoot ratio of grain (Farooq et al. 2009). Drought stress also triggers a decrease in leaf water potential, which acts as an important hydraulic signal for stomatal closure to prevent further loss via transpiration (Chai et al. 2016). Some other consequences of limited water supply are early switching to reproductive stage, reduction in fresh and dry matter production, due to diminished photosynthetic efficiency (Sheoran and Saini 1996). Water stress during the reproduction and grain-filling stage is more detrimental and usually results in a significant loss in grain yield. Pre-anthesis drought also leads to pollen sterility and hampers flowering and seed filling in plants (Jaleel et al. 2009). It also results in decreased intake of carbon dioxide, which reduces carboxylation and directs more electrons to form ROS (reactive oxygen species) which in turn damages the photosynthetic apparatus and promotes photoinhibition (Farooq et al. 2009). The major symptom of the degradation of the photosynthetic machinery in plants is the development of chlorosis.

Plants often confront adverse drought conditions, which significantly depend on plant genetics as well as the duration and severity of drought. In response to water deficit in plants, stomatal closure occurs often triggered by phytohormones ABA to avoid further loss via transpiration, which regulates the cell metabolism by inducing expression of various stress-related genes (Fathi and Tari 2016). Acclimation of plants to drought stress is an interrelated cross-talk between molecular and physiological events, including changes in plant growth structure, accumulation of various organic and inorganic osmolytes, improved antioxidant defense activity, and reduced transpiration (Anjum et al. 2011). Due to the exaggerated vulnerability of plants to drought stress in a scenario of climate change, it is crucial to understand the morphological and physiological adaptations of plants to cope with these adverse situations (Farooq et al. 2011).

In developing nations, grain legumes constitute a major source of dietary protein as a means to provide food security and nutrition. Among grain legumes, mungbean is an important pulse crop having a short life span and is more sensitive to drought stress mainly at the reproductive stage (flower initiation and pod set), leading to reduced productivity and yield.

10.2.5.2 Morpho-Physiological Traits for Drought Tolerance in Mungbean

Plants exhibit continuous growth throughout their lives that are accomplished through processes like cell division, cell enlargement, and cell differentiation (Farooq et al. 2009). The establishment of these processes mainly depends upon the turgor pressure of cell and underwater stress, they are reduced to a larger extent affecting the overall growth of plant (Taiz and Zeiger 1991). Deficit water supply poses negative effects at any growth and development stage of the plant. Water stress during early stages reduces germination and stand establishment due to lesser water uptake and reduced water potential during the imbibition phase of germination, impaired enzyme activity, and reduced energy supply (Farooq et al. 2011). Drought critically affects the growth and development of plants with a considerable reduction in biomass accumulation and crop growth rate. Plant growth under drought stress can be restricted at various levels, most studied are seed germination, plant height, leaf area, and crop growth (Ranawake et al. 2011; Aslam et al. 2013a, b; Saima et al. 2018). Reduction in growth parameters under drought stress was reported in many crops like chickpea (Talebi et al. 2013); sunflower (Kiani et al. 2007); and barley (McMaster and Wilhelm 2003). Various effects of drought on growth traits of mungbean crops are discussed below.

10.2.6 Seed Germination

Saima et al. (2018) reported effects of drought stress that include reduction in seed germination and shoot length in 10 days old seedlings in all the seven hybrids of *Vigna radiata* along with increasing PEG-induced drought stress (5% and 10%), whereas root growth increased with increasing drought stress.

Early growth stages of 17 mungbean genotypes were evaluated for drought tolerance at the seedling stage by Aslam et al. (2013a, b). Germination percentage, root/shoot length, root/shoot ratio, shoot weight, and stem diameter were studied at different moisture levels (80%, 50%, and 30% field capacity). They reported that all the reported traits decrease with an increase in drought stress except root/shoot ratio.

10.2.6.1 Plant Height and Biomass

Other growth traits like plant height and shoot weight were measured in the three mungbean varieties (Kamway-1, VC-2010, and King) by Ahmad et al. (2015). Experiments were divided into four sets of irrigation, that is, I₁, I₂, I₃, and I₄ that irrigated at third, fifth, seventh, and ninth day, respectively, and by controlling the amount of water in each set. Plant height and shoot weight varied among the genotypes and also with the irrigation set. These traits were declined along with increasing drought stress, which clearly represents the effects of drought on the growth of mungbean genotypes. Ranawake et al. (2011) reported the response of mungbean genotypes for drought stress by imposing stress at three different stages (3WAP, 6WAP, and 8 WAP). Growth traits like average plant height, average number of leaves, average dry matter weight of root/shoot, average number of lateral

roots, and average length of taproot were studied on the Harsha mungbean variety. They noted that drought stress imposed at 3 weeks after planting (Vegetative stage) and 6 WAP (reproductive stage) caused more damage to growth and crop yield than 8WAP (Podding stage). Therefore, it is recommended that mungbean be planted in such a way that drought stress ought not to coincide with 6WAP (reproductive stage).

Studies by Uddin et al. (2013) revealed similar findings that drought stress hampers the mungbean growth rate significantly. Morphological attributes including plant height, leaf area, shoot dry weight showed the lowest performance when no irrigation was applied to the crop compared to control. All above-mentioned studies imply that drought stress has retarding effect on the crop phenology involving traits like plant height, number of leaves, leaf area, and dry weight of shoots that are directly linked with low yield.

10.2.6.2 Chlorophyll Content

Drought stress environment hampers the process of photosynthesis by decreasing the concentration of various photosynthetic pigments. Degradation of pigment might be due to swelling of chloroplast membrane, distortion of lamellae, and vesiculation of lamellae (Baroowa and Gogoi 2012). Studies by Batra et al. (2014) recorded drought-induced damage by withholding water for 4 days on the chlorophyll content of three varieties of mungbean; RMG 268, K-851, and Anand. Gradual decline in total chlorophyll content up to 57% in Anand, 54% in K-851, and 39% in Anand when compared to control. These deformities further curtail the capturing of photons to the PSII by damaging D1 core protein and reducing the electron transfer. Uprety and Bhatia 1989, also reported comparable results in the three mungbean varieties; PS16, P105, Pusa Baisakhi having reduced total chlorophyll content. Higher reduction pattern recorded in Pusa Baisakhi and minimum in P105 reported during the flowering stage. Baroowa and Gogoi 2013 noted a positive correlation between soil moisture, total chlorophyll, and chlorophyll index. The rate of decline in chlorophyll content was rapid during prolonged drought stress (withholding water for 20 days).

10.2.6.3 Photosynthetic Rate (Pn)

Moderate and severe drought decreases photosynthesis rate by 25% and 50%, respectively, reported in the mungbean genotypes by Moradi et al. (2008). This reduction was accompanied by a decrease in stomatal conductance since the stomatal closure limits CO₂ availability to the mesophyll of leaves. Furthermore, they reported that drought stress imposes severe effects on the reproductive stage indicating 37% lower photosynthetic rate when compared to vegetative stage. More studies on the photosynthetic rate in mungbean genotypes demonstrate that Pn varied significantly at vegetative, pod setting, and pod filling stages. Photosynthetic rate increases with the advancement of crop stage under control but significantly decline on the application of drought treatment in all the mungbean varieties (Naresh et al. 2013). Hamid et al. assess the impacts of water stress imposed at different growth stages; pre-flowering, flowering, and pod development. Water deficits have more prominent effects in terms of photosynthesis rate, leaf area, leaf

growth, dry matter accumulation during the flowering phase compared to podding stage. A reduction in yield by 6% has been reported in water-stressed plants compared to well-watered plants. Yield loss is mainly caused by inhibition of photosynthetic rate as well as lower dry matter accumulation.

10.2.6.4 Stomatal Conductance

Drought stress negatively affects photosynthesis as well as gas exchange traits that target the assimilation capacity of plants. Loss over stomatal regulation during water-deficit conditions may be responsible for a decline in assimilation capacity reported in mungbean crop (Moradi et al. 2008). The effects of severity of drought stress on different growth stages (vegetative and reproductive) of mungbean were recorded by Moradi et al. (2008). Water deficit during the vegetative and reproductive growth stage reduces stomatal conductance and transpiration rate. But the greatest effects of severe drought stress on these traits were recorded during the reproductive stage. Zarifinia et al. (2012) recorded similar observations on the mungbean genotypes that drought stress significantly reduces the stomatal conductance. Their study provided two drought-tolerant genotypes; Partow and Indian heap based on physiological traits involving stomatal conductance.

10.2.6.5 Chlorophyll Fluorescence

Chlorophyll fluorescence is the measurement of photosystem II activity and to understand the photosynthetic mechanisms. It further provides an indicator that how plants respond under environmental fluctuations. This technique gained major attention due to its use for the selection of desirable plant traits related to genetic and physiological responses for crop improvement. Responses of mungbean genotypes under drought stress were also recorded using this trait are discussed below.

Response of mungbean plants recorded at vegetative (S_2) and reproductive stage (S_3) for drought stress by Allahmoradi et al. (2011). Their results showed that drought stress reduces vegetative growth significantly as compared to the reproductive stage. A study of chlorophyll fluorescence showed a significant difference between S_2 with S_3 and S_1 (Control). Furthermore, PS II activity in S_1 and S_3 fall in a normal range but in S_2 it was out of the normal range (Allahmoradi et al. 2011). Batra et al. 2014 study the effects of drought stress on different mungbean varieties (RMG 268, K-851, and Anand) by analyzing their chlorophyll fluorescence. Their results indicated that drought stress hinders PS II activity and energy transfer by altering D1 protein of thylakoid protein. Variety RMG 268 and K-851 were more tolerant to drought stress than Anand variety judged by PS II activity.

10.2.7 Relative Water Content (RWC)

It is an important measure of the physiological water status of plants indicating leaf hydration and leaf water deficit. Maintaining water potential is important for the plant cell because it has a crucial role in maintaining all vital cellular activities. Thus an understanding of the effects of drought on leaf water relations is imperative for

classifying the mechanism of drought tolerance of a plant. Therefore, it is a reliable trait for assessing the drought tolerance of plants (Chowdhury et al. 2017). Various studies conducted on mungbean are discussed below.

Effects of water deficit were examined in three mungbean varieties (PS 16, P105, and Pusa Baisakhi) by withholding irrigation at pre-flowering, flowering, post-flowering, and pod development stage (25, 35, 45, and 55 days after sowing, respectively). Relative water content was declined in all the three mungbean genotypes however the depression was less in variety P105 at pre-flowering, flowering, post-flowering stage. In contrast variety, Pusa Baisakhi exhibit maximum reduction at these stages, clearly pointing to their susceptibility toward drought stress (Uprety and Bhatia 1989).

Field studies of Bangar et al. (2019) also showed that RWC of mungbean leaves was significantly affected by drought. They screened total 25 varieties of mungbean and selected few drought-tolerant varieties (*Vigna sublobata*, MCV-1, PLM-32, LGG-407, LGG-450, TM-96-2, and Sattya) based on RWC along with other physiological traits. Drought stress significantly affects the RWC in the vegetative stage compared to the reproductive stage further decreasing pattern was more prominent in the sensitive genotypes. The lowest percentage decrease (1.5–1.82%) was recorded in tolerant genotypes (*V. sublobata* and MCV-1) and the highest percentage decrease (16.6–19.52%) noted in sensitive genotypes (PDM 139 and TARM-1).

Similarly, studies by Nazran et al. (2019) on the mungbean varieties indicate that severity of drought stress decreases leaf water content. Genotypic differences in mungbean demonstrate that BARI Mung-6 genotype maintains the maximum RWC (66.14%) while BU mug 2 genotype had the minimum RWC (55.21%).

10.2.7.1 Leaf Water Potential

Leaf water potential (LWP) and osmotic adjustment (OA) are the important traits that can be used as selection criteria for improving drought tolerance. Maintaining leaf water potential under water-deficit conditions is important for cellular activities. It is further associated with dehydration avoidance mechanisms that how plant cells manage to assess water through adjusting the osmolyte concentrations (Jongdee et al. 2002). Comparison of LWP in the mungbean varieties needs to be crucial for screening drought tolerance.

LWP of mungbean varieties was negatively affected by drought stress treatment reported in the studies of Nazran et al. (2019). Their studies showed that the highest water potential was reported in well-watered plants (−0.67 to −0.55 MPa) and it gradually decreases with the severity of drought stress (−1.64 to −1.13 MPa at 50–60% field capacity). Moreover, BARI Mung-6 variety of mungbean maintains higher water potential even at low field capacity (50–60%) and is categorized as drought stress-tolerant in terms of physiological adaptations.

In another study on mungbean, water stress significantly reduces the LWP throughout the growing period and majorly during flowering and post-flowering stages (Uprety and Bhatia 1989).

10.2.8 Biochemical Traits for Drought Tolerance in Mungbean

10.2.8.1 Oxidative Stress and Anti-oxidants

Under normal growth conditions, most of the cellular components of the plant exhibit constant homeostasis. But the exposure to drought stress imbalanced this homeostasis by reducing antioxidant production as a result of which greater production of ROS is obvious. The imbalance between ROS generation and their detoxification disrupts the redox control thus damaging the major biomolecules like carbohydrates, lipids, proteins, nucleic acids, and enzymatic activities (Hasanuzzaman et al. 2012). Water-deficit conditions make the protoplasm more viscous, denature proteins, and halting the activities of Calvin cycle enzymes. Inactivation of Calvin cycle enzymes resulted in shifting toward photorespiration, the main cycle for ROS production. Damage to PS II and lipid peroxidation are other reasons for ROS production. Oxidative stress was measured in terms of production of MDA accumulation, increased H_2O_2 . To endure oxidative stress damage, plants attain well-organized enzymatic and nonenzymatic systems. Enzymatic antioxidants in plants are superoxide dismutase (SOD), catalase (CAT), glutathione reductase (GR), ascorbate reductase (APX), and glutathione peroxidase (GPX). Among non-enzymatic anti-oxidants glutathione (GSH), ascorbic acid (ASA), tocopherol, alkaloids, and phenolic compounds are well recognized in plants. Improvement in antioxidant activities is effective in providing tolerance to plants against drought stress. It has been reported through various studies that higher levels of antioxidants help in reducing ROS-induced damage, thus improving drought tolerance.

Sengupta et al. (2013) studied the drought-induced ROS damage and significant production of antioxidants in the mungbean roots. Drought stress exposure (by withholding water for three (D3) and 6 days (D6) at the vegetative stage; 30 days old plant) lead to the gradual increment in H_2O_2 and MDA content. Non-enzymatic antioxidant GSH and ASA also showed progressive increase under drought stress treatment. Their content increased slightly in the D3 but significantly higher content (twofold) recorded on D6. Hence, root responses toward drought stress are crucial to understanding that further provide some interdependence mechanisms with photosynthetic performance and plant water status. Yin et al. (2015) recorded the responses of mungbean genotypes to polyethylene glycol-induced drought stress. Three concentrations of PEG 6000 were used as 5%, 10%, and 20% to impose drought stress at the flowering period. Drought stress caused a significant increase in the levels of O_2^- and MDA with decreasing water potential. In contrast, activities of enzymatic antioxidants such as SOD and POX increased in all the drought stress treatments. Drought stress hampered photosynthetic function and enhanced the oxidative stress measured in terms of lipid peroxidation and H_2O_2 . Drought stress-induced oxidative stress reduces the pools of GSH and ASA. Maintenance of content of non-enzymatic antioxidants increases the resistance of mungbean genotypes as reported in the studies of Anjum et al. (2015).

10.2.8.2 Osmotic Adjustment

To survive under water deficit conditions, one common approach endorsed by plants is the accumulation of osmolytes or compatible solutes. Osmolytes are low molecular weight, small organic compounds synthesized by plants in the cytosol, chloroplast, and other cellular organelles having a role in the protection of cellular components against dehydration (Hasanuzzaman et al. 2019). Osmolytes mainly include proline, glycine betaine, polyamines, and sugar alcohols (Ashraf and Foolad 2007). They not only help in maintaining cell turgor but are also involved in improving ROS scavenging mechanisms, therefore buffering the cellular redox potential (Anjum et al. 2017). Therefore, it is a protective mechanism involving the accumulation of compatible osmolytes in plants to prevent cellular dehydration which maintains cell water status by cell integrity, leaf water adjustment, and osmotic adjustment (Blum 2005). Osmotic adjustment is a means by which plants adapt to water stress by the active accumulation of solutes in the cell sap and as a result of solute accumulation, the osmotic potential of the cell decreases, therefore helping in withdrawing more water from surrounding and maintaining turgor of cell (Ludlow and Muchow 1990). Due to this osmotic adjustment, all cytoplasmic activities occur normally and, in this way, help plants to perform better in terms of growth, photosynthesis, and assimilate partitioning (Subbarao et al. 2000). Among all protective osmolytes, free proline is an important beneficial solute allowing plants to increase cellular osmolarity during drought (Ashraf and Foolad 2007).

Studies by Bangar et al. (2019), reported the proline content in 25 mungbean varieties at two development stages; vegetative and reproductive stage. Proline content significantly increases in both developmental stages. The percentage increase ranged from 6.5% to 80.2% during the vegetative stage and 9.6–118.3% during the reproductive stage over the control. Further, significant variations in the proline content were recorded in all 25 varieties. Similar findings were recorded from the studies of Bhardwaj et al. (2018) that drought stress significantly increases the proline content in all the seven mungbean genotypes. However genotypes ‘IPM99–125’ accumulate highest (62%) while the lowest content was recorded in genotype “Pratap” (42%) under both the development stages. Higher proline accumulation maintains to provide maximum cell osmoprotection, thus sustaining the vital cellular activities under water deficit conditions.

10.2.8.3 Yield Traits for Drought Tolerance in Mungbean

Abovementioned effects of water scarcity are reduced plant growth and biomass accumulation altered photosynthetic efficiency, low stomatal conductance, and weaker source-sink activities. Poor performances of all these traits merged to induce severe yield losses. The magnitude of reduction in grain yield depends on the intensity and duration of stress. Drought impedes productivity at all the growth stages but its occurrence during reproduction and grain development stages are more crucial and results in significant yield fall (Farooq et al. 2017). Drought-induced yield losses were reported in cereal crops like wheat by 34% (Saeidi and Abdoli 2015); maize by 59–90% (Kamara et al. 2003); and leguminous crops like Chickpea by 45–69% (Nayyar et al. 2006), cowpea by 34–66% (Ahmed and Suliman 2010);

lentil by 24% (Allahmoradi et al. 2013) and soybean by 42% (Maleki et al. 2013). Effects of drought stress on the yield of mungbean crop were discussed in detail in this review.

Ranawake et al. (2011) evaluated the effects of drought stress imposed at different growth stages (3WAP, 6WAP, 8WAP) on yield traits like average number of pods and average grain weight. Water stress affects the grain yield at 6 WAP (flowering stage) more severely because plants were failed to initiate reproductive processes resulting in no net yield. While drought stress imposed at 8WAP (podding stage) cause comparatively less damage indicating that crop should be planted in such a way that the reproductive phase should not coincide with drought stress. Ahmad et al. (2015) also reported that drought stress affects the yield of mungbean genotypes. The reduction pattern varies with the irrigation interval (3, 5, 7, and 9) and amount of irrigation. Seed yield (kg/h) declined in all the treatments, but more reduction was observed under irrigation interval of 9 days with the lowest number and amount of irrigation. Seed yield declined from 1146 to 78 kg/ha in this treatment clearly demonstrating that water deficiency hampered the yield components. Kumar and Sharma (2009) recorded the genotypic differences in mungbean and noted that drought stress affects the seed yield by affecting dry matter partitioning. Tolerant mungbean genotypes exhibit high yield and it is correlated with higher RWC which promotes more dry matter partitioning.

10.2.9 Genomics of Drought Tolerance in Mungbean

A high-throughput platform for genotyping in association with sequencing technologies allowed the access of genetic linkage maps and quantitative trait loci (QTL) mapping of the traits related to drought tolerance (Jha et al. 2020). Isolation of drought-responsive genes and detection of QTLs studies are limited in mungbean. However the study of Liu et al. 2017 identified novel genetic elements in the mungbean providing drought tolerance. They identified 58 QTLs in the 11 linkage groups ((LG 1–11) using 313 markers. These QTLs were associated with plant height, leaf area, biomass, RWC, days to first flowering, and yield traits. Sixteen QTLs were detected for plant height associated with linkage group LG 04, LG05, and LG08. Similarly, 8 QTLs for biomass involving LG02, LG03, LG04, LG06, and LG08, 6 QTLs for RWC on LG04, LG08 and LG10, 12 QTLs for leaf area in LG02, LG03, LG04, LG08, and LG11, 8 QTLs for days to flowering in LG04 and 4 QTLs for seed yield in LG01, LG04, and LG08. Few studies reported on Genome-wide association identification of transcription factors in the mungbean genotypes to gain more insights into the molecular mechanisms governing drought tolerance. Labbo et al. (2018) identified 71 AP2/ERF (APETALA 2/Ethylene-responsive element factor binding protein) transcription factors and classified them into AP2 (16), ERF (22), RAV (2), DREB (30). Among them, DREB genes played a critical role in drought tolerance. Five DREB genes (*VrDREB 5*, *VrDREB12*, *VrDREB13*, *VrDREB22*, *VrDREB30*) exhibit higher expression under drought stress and might be considered excellent candidates for improving drought tolerance in mungbean genotypes. Genome-wide analyses of genes related to sucrose nonfermenting-1-

related protein kinase 2 family (SnRK2) were characterized in mungbean that is known to play important role in osmotic stress. 8 SnRK2 genes were reported named as *VrSnRK2.1*, *VrSnRK2.2a*, *VrSnRK 2.2b*, *VrSnRK 2.2c*, *VrSnRK 2.3*, *VrSnRK 2.4*, *VrSnRK 2.5*, *VrSnRK 2.6a*, *VrSnRK 2.6b*, *VrSnRK 2.6c*, *VrSnRK2.7* and *VrSnRK2.8*. Expression of these genes induced by drought stress indicates its importance in drought tolerance. Moreover gene *VrSnRK 2.6c* exhibit higher expressions among all the genes illustrating its critical role under drought stress tolerance (Fatima et al. 2020).

10.2.9.1 Agronomic Approaches to Combat Drought Stress

Various approaches have been developed from time to time to achieve stress tolerance in plants. Nowadays, seed priming methods are extensively used as an emerging technology to raise stress-tolerant plants. Seed priming evokes physiological, biochemical, and cellular processes in the plant that prepares them to respond to stress conditions instantly (Lal et al. 2018). It has been reported through various studies that seed priming improves the seedling emergence, seed establishment, growth traits, and yield traits under drought stress in wheat (Hussain et al. 2018); maize (Nada and Hamza 2019); chickpea (Shariatmadari et al. 2017); and sorghum (Sheykhbaglou et al. 2014). Through these studies, it is clear that seed priming improves the drought tolerance in the plant through enhanced antioxidant activities, accumulation of osmolytes, and better nutrient uptake. Case study on seed priming in mungbean to exclude drought stress effects discussed in this review.

Studies by Jisha and Puthur (2016) recorded that seed priming of β -amino butyric acid (BABA) (0.5, 1, 1.5, 2, 2.5 mM) in mungbean genotypes (Pusa Ratna, Pusa 9531, Pusa Vishal) alleviate the drought stress effects. Primed seeds exhibit higher chlorophyll fluorescence, mitochondria activity, photosynthetic activity, and seedling growth parameters (shoot length, shoot fresh and dry weight). Moreover, primed seeds have reduced MDA content, increased accumulation of proline content, total carbohydrate, total proline, nitrate reductase activity, and activity of antioxidant enzymes like SOD and guaiacol peroxidase. Similarly, seed priming with polyamines (put+spd + spm) improves the drought tolerance in mungbean genotypes by decreasing the membrane damage, increasing the proline content, soluble proteins, and soluble sugars. Hence, treated mungbean genotypes resulted in improved growth and yield under drought stress (Sadeghipour 2019).

Besides conventional plant breeding and transgenic approaches, the application of plant growth-promoting rhizobacteria (PGPR) and arbuscular mycorrhiza (AM) proved to be useful for improving drought tolerance in mungbean crops (Sarma and Saikia 2014; Habibzadeh et al. 2014). PRPR is a group of bacteria that are found in the rhizosphere mainly at root surfaces and in association with roots that promote the establishment of various interactions that benefit the plant growth directly or indirectly. They are widely studied because of their potential use as bio-fertilizer (Kumari and Chakraborty 2017). In a similar way mycorrhiza is a symbiotic association between fungus and plant that forms a beneficial relationship between soil and plant that increases the water absorption as well as nutrient uptake through mycorrhizal hypha (Habibzadeh et al. 2014). Studies have confirmed that inoculation of various plant species with such micro-organisms leads to the

improvement of root system architecture that enhances the ability of the plant with better adaptation to stress condition (Sarma and Saikia 2014).

Elevated production of ROS scavenging enzymes, cellular osmolytes, and upregulation of genes associated with drought tolerance like Dehydration Responsive Element Binding protein (DREB2A) catalase (CAT1) and dehydrin, were reported in the mungbean plants when inoculated with arbuscular mycorrhizal fungi (*Glomus mosseae*, *G. intraradices*) (Habibzadeh et al. 2014). In another study, mungbean genotype; AU-M4 (overproducing mutant of PGPR) has significant drought tolerance. This mutant has enhanced ACC deaminase activity, IAA production, and inorganic phosphate solubilization compared to the wild strains. Therefore, express superior tolerance under drought stress in terms of higher plant biomass, proline accumulation, water content, and lower osmotic stress injury. Inoculation with osmoprotectant rhizobacteria isolates (A124-K and Ver5-K) produced glycine betaine that improved mungbean tolerance to drought stress (Maryani et al. 2018). Hence, to lessen the effects of drought stress, the use of PGPR and AM will be employed to ensure sufficient growth and yield of crop plants (Kumari et al. 2016).

10.3 Conclusion

To meet future food demands, plant stress tolerance must be improved. Plants express a wide range of responses to heat and drought stresses which are mostly represented by a variety of modifications in the overall growth of plant (Zhou et al. 2017). These stresses significantly affect morphological, physiological biochemical, and molecular processes resulting in major yield losses (Sehgal et al. 2018). Almost every plant process is affected by these stresses, from membrane stability, enzymatic activity, at a cellular level and decreased transpiration, stomatal conductance, and photosynthetic rate at the physiological level (Hussain et al. 2019). To minimize the damages plants have evolved various adaptive mechanisms and activated various signaling pathways for upregulation of antioxidants and accumulation of compatible solutes (Fahad et al. 2017). Aforementioned traits have successfully identified heat tolerance in mungbean crops which may provide useful information to the plant breeders. Various new technologies have been developed for assessing physiological, biochemical, and molecular traits for getting insight into the mechanisms governing heat tolerance (Chen et al. 2019). However commercial applications of these techniques are limited and require further field trials. Advances in Omics technique including genomics, transcriptomics, proteomics, and metabolomics could provide possible candidate genes, proteins, and metabolites contributing to stress tolerance (Zhou et al. 2017). Molecular breeding methods like QTLs and GWAS could also reveal the stress tolerance governing genes (Priya et al. 2019a, b). Therefore, concerted efforts are needed to enhance the efficiency of breeding programs for the rapid development of varieties with improved adaptation to heat, drought, and combined stresses and other desired traits (Fig. 10.1).

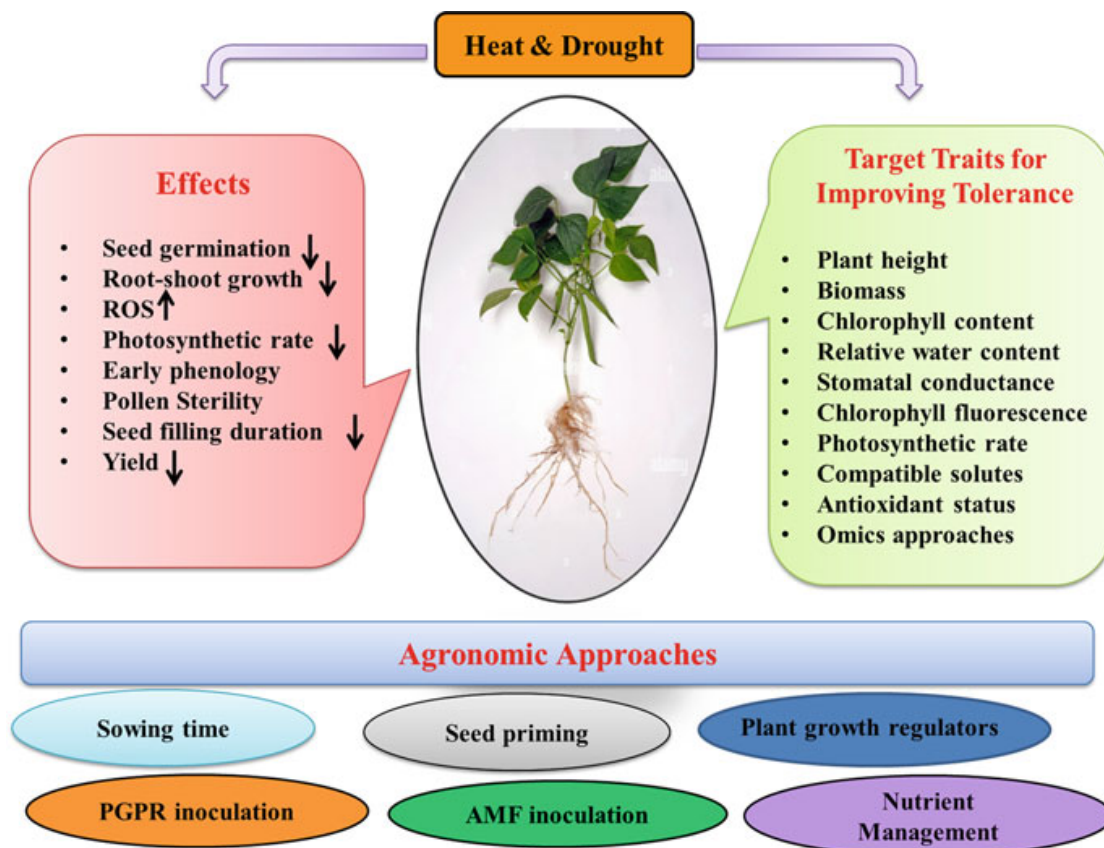


Fig. 10.1 Heat and drought stress has various negative effects on the plant performance. Overall life cycle starting from seed germination, root-shoot growth, photosynthesis, reproductive growth and seed filling stages are affected very badly leading to poor yield. But plants showed various adaptation responses under stress conditions which can be helpful to identify the underlying tolerance mechanisms and producing stress resilient varieties. Such target sites for improving plant tolerance are growth traits like plant height and biomass, morpho-physiological traits like chlorophyll content, relative water content, stomatal conductance, chlorophyll fluorescence, photosynthetic rate and biochemical traits like production of compatible solutes and antioxidants. Agronomic approaches like seed priming, sowing time, application of plant growth regulators, nutrient management, PGPR and AMF inoculation can also be employed to get better yield under stress conditions

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OPEN ACCESS

EDITED BY

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SPECIALTY SECTION

This article was submitted to
Plant Bioinformatics,
a section of the journal
Frontiers in Plant Science

RECEIVED 13 September 2022

ACCEPTED 07 November 2022

PUBLISHED 21 November 2022

CITATION

Chaudhary S, Jha UC, Paul PJ,
Prasad PVV, Sharma KD, Kumar S,
Gupta DS, Sharma P, Singh S,
Siddique KHM and Nayyar H (2022)
Assessing the heat sensitivity of
Urdbean (*Vigna mungo* L. Hepper)
genotypes involving physiological,
reproductive and yield traits under
field and controlled environment.
Front. Plant Sci. 13:1042999.
doi: 10.3389/fpls.2022.1042999

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Assessing the heat sensitivity of Urdbean (*Vigna mungo* L. Hepper) genotypes involving physiological, reproductive and yield traits under field and controlled environment

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The rising temperatures are seriously impacting the food crops, including urdbean; hence efforts are needed to identify the sources of heat tolerance in such crops to ensure global food security. In the present study, urdbean genotypes were evaluated for heat tolerance under natural outdoor for two consecutive years (2018, 2019) and subsequently in the controlled environment of the growth chamber to identify high temperature tolerant lines. The genotypes were assessed involving few physiological traits (membrane damage, chlorophyll, photosynthetic efficiency, stomatal conductance, lipid peroxidation), reproductive traits (pollen germination % and pollen viability %) and yield related traits (total number of pods plant⁻¹, total seeds plant⁻¹, single seed weight and seed yield plant⁻¹). Based upon these tested traits, PantU31, Mash114, UTTARA and IPU18-04 genotypes were identified as promising genotypes for both years under heat stress condition. Further confirming heat tolerance, all these four tolerant and four sensitive genotypes were tested under controlled environment under growth chamber condition. All these four genotypes PantU31, Mash114, UTTARA and IPU18-04 showed high chlorophyll content, photosynthetic efficiency, stomatal conductance, leaf area, pods plant⁻¹, total seeds plant⁻¹ and low reduction in pollen germination % and pollen viability under stress heat stress condition. Moreover, yield and yield related traits viz., pods plant⁻¹, seeds plant⁻¹, single seed weight and seed yield plant⁻¹ showed very strong positive correlation with

pollen germination and pollen viability except electrolyte leakage and malondialdehyde content. Thus, these genotypes could be potentially used as donors for transferring heat tolerance trait to the elite yet heat-sensitive urdbean cultivars.

KEYWORDS

urdbean, heat stress, genetic variability, physiological traits, biochemical traits

1 Introduction

Due to global climate change projections, heat waves are predicted to expand in many regions of the world imposing a huge threat to the agricultural security (Riaz et al., 2021). Variability around the optimum temperature is going to surge that will affect the complete life cycle or phenology of the plant (Chaturvedi et al., 2021). Continuously rising temperature (heat stress) has wide range of impacts on the overall morphology, anatomy and physiology of the plants (Chen et al., 2014). At sub-cellular levels, these impacts can be assessed using various biochemical and molecular approaches. Although heat stress has the potential to affect all the stages of plant but some stages are more vulnerable to heat stress; reproductive or seed filling stages are highly affected due to heat stress (Allakhverdiev et al., 2008; Hedhly, 2011). Moreover, the effects of high temperature are plant species- and stage- specific, the severity further depends on the duration and intensity of stress (Li et al., 2018). Various reports have suggested that heat stress disturbs the morphology of the plant by reducing its plant height, leaf area and root architecture (Chaudhary et al., 2020). At the cellular level, heat stress leads to protein denaturation, enzyme inactivation, membrane damage, exaggerate ROS generation, loss in water status and cellular viability. In leaves, photosynthetic machinery is reported as most sensitive to high temperature (Wahid et al., 2007; Bitá and Gerats, 2013). Loss of chlorophyll content, denaturation of D1 protein of photosystem II and reduced carbon metabolism are mainly responsible for reducing photosynthetic rate (Allakhverdiev et al., 2008). Of the reproductive organ development stages; male gametophyte development and seed filling processes are reported to be extremely sensitive to even a few degree rise in temperature that can result in substantial yield loss (Hedhly, 2011). Impaired transport of sucrose to the developing reproductive organs under heat stress may restrict the flower development that brings out more flower abortion, pod abortion and shrivelled seeds (Bhandari et al., 2016). Plant responds to such damages by reprogramming and activating various mechanisms related to production of antioxidants, phytohormones, osmolytes, primary and secondary metabolites to ensure their survival (Chebrolu

et al., 2016; Sharma et al., 2016; Jha et al., 2022). Therefore, correlation of crop phenology with temperature fluctuations is crucial for the better understanding of the impacts and defence strategies employed by plants for its adaptation.

Urdbean (*Vigna mungo* L. Hepper) is an important summer season food legume, cultivated mostly in many tropical and subtropical countries of Asia, Africa, America, and Australia (Joshi and Rao, 2017). Optimum temperature for its proper growth and development is 25–35°C and being a temperature sensitive crop, its yield is drastically reduced under high temperature exceeding 35°C (Anitha et al., 2016; Sen Gupta et al., 2021). Very little reports are available about the heat stress impacts as well as defence responses, especially at reproductive stage of this crop (Sen Gupta et al., 2021). It is vital to identify and characterise heat tolerant urdbean genotypes as well as to find out some leaf and pollen-based traits and mechanisms underlying heat tolerance. Heat tolerant urdbean genotypes can increase the cultivation of this food legume in summer season as well at warmer locations to extend its cultivation status. Thus, the aim of the present study was to screen selective number of genotypes of urdbean to heat stress in 2 successive years under outdoor environment to identify heat tolerant genotypes, followed by their validation and characterisation under controlled environment of the growth chamber involving some leaf and pollen-based traits.

2 Methodology

2.1 Field and growth chamber experiments

Urdbean genotypes (26) were procured from Indian Institute of Pulse Research, Kanpur, India and Punjab Agricultural University, Ludhiana, India (Supplementary Table S1). These genotypes were assessed for their heat tolerance under outdoor environment and controlled conditions of the growth chamber at the Department of Botany, Panjab University, Chandigarh, India. Urdbean seeds were raised in pots (8L capacity) containing a mixture of soil, sand, farmyard manure

[2:1:1 (v/v)] and Tri-calcium phosphate fertilizer 10 mg kg⁻¹. Seeds were soaked in distilled water overnight (12 h) and subsequently inoculated with suitable strain of *Rhizobia* before sowing. There were 5 pots genotype⁻¹ and each pot had 5 seeds that were thinned to 3 plants pot⁻¹ after emergence for their proper growth. Plants were fully irrigated daily (twice; morning and evening) to avoid any water paucity. Plants were arranged in a randomized complete block design. Meteorological data (daily temperature and relative humidity) from date of sowing to harvesting was recorded throughout the entire cropping season (Supplementary Figure S1). To evaluate the effects of heat stress against the control temperature, crop was sown twice during cropping season and for two subsequent years (Summers of 2018, 2019) (i) during the normal conditions (control), in the last week of March 2018, when the day/night temperatures (<35/25°C) were optimum for the plant's growth and ii) in the last week of April, to expose the plants to heat stress (>40/30°C). (Supplementary Figure S1, Supplementary Table S2). The plants after harvest were recorded for number of pods, seeds, seed yield plant⁻¹ and single seed weight.

For validation of the results, a subsequent study was conducted in the growth chamber under the controlled conditions on some selected contrasting genotypes (4 heat-tolerant and 4 heat-sensitive genotypes, 5 pots genotype⁻¹ having 2 plants pot⁻¹). These plants were initially raised in the outdoor natural environment to achieve full vegetative growth (Average temperature <35/25°C; average RH 61/41%; Max/min) and were subsequently transferred to growth chamber at the onset of bud stage for further analysis. To avoid any kind of heat shock situation, temperature was gradually raised (2°C per day) up to 42/32°C. The plants were maintained at this temperature up to maturity. Simultaneously, the control plants were maintained at 35/25°C.

After 10d of heat stress, fully expanded leaves at 2nd and 3rd positions from the topmost youngest leaf were from control and heat-stressed environments were evaluated for various physiological traits *viz.* SPAD chlorophyll content, chlorophyll fluorescence (Fv/Fm), electrolyte leakage (to assess membrane damage), stomatal conductance, leaf area, relative leaf water content, and malondialdehyde (MDA). The reproductive traits (pollen viability and pollen germination) were tested from flowers after 5d exposure to heat stress. All these traits were further correlated with yield traits like total number of pods plant⁻¹, total number of seeds plant⁻¹, total seed yield plant⁻¹, single seed weight.

2.2 Physiological, reproductive and yield traits

To assess the effects of heat stress on the plant growth and yield, various traits were studied; data were taken from three plants in triplicates genotype⁻¹, pooled and averaged. Mean values of replicates are presented through tables and figures.

2.3 Physiological traits

2.3.1 Chlorophyll content

Chlorophyll content (SPAD value) was measured using Apogee-SPAD meter and its readings were taken between 10.00 and 11.00 h of a fully expanded tagged leaf on alternative days at full vegetative and reproductive stage from 30 DAS (days after sowing) (Devi et al., 2022).

2.3.2 Chlorophyll fluorescence

PS II activity/stability or photosynthetic efficiency was measured as chlorophyll fluorescence. Readings were taken between 10.00-11.00 h of a fully expanded leaf using the dark adapted test of modulated chlorophyll fluorometer OS1-FL (Opti-Sciences, Tyngsboro, MA, United States) (Sharma et al., 2016).

2.3.3 Electrolyte leakage

Stress injury to leaves was measured as electrolyte leakage. Fresh leaves (1.0 g) were collected and washed three times with deionised water to remove surface adhering electrolytes. Plant tissue was placed in closed vials containing 10 ml of deionised water and incubated it for 25°C on a rotary shaker for 24 h; the electrical conductivity of the solution (L₁) was checked using a conductivity meter (ELICO CM 180, Hyderabad, India). Then the final conductivity (L₂) was measured after heating samples in a water bath at 120°C for 20 min (Lutts et al., 1996). Electrolyte leakage was calculated as (L₁/L₂) × 100. The electrolyte leakage was expressed as electrical conductivity in μmhos g⁻¹ DW.

2.3.4 Stomatal conductance

Stomatal conductance was measured from a fully expanded leaf using a portable leaf porometer (model SC1 Decagon Devices, Pullman, WA, United States) at 11.00 h and was expressed as m molm⁻²s⁻¹ (Awasthi et al., 2014).

2.3.5 Leaf area

Area of fully expanded tagged leaves was determined using a measurement scale and multiplied with a 'leaf factor' (method derived from urdbean from the ratio of actual and measured leaf area of many types of leaves from top to bottom of a plant) (Sharma et al., 2016).

2.3.6 Relative leaf water content

RLWC was measured by the method of Barrs and Weatherley (1962). Fresh leaves were collected and were washed three times to remove any kind of debris. After drying with blotters, they were weighed (fresh weight, FW) and then floated in the distilled water in a petri dish. After 2 h, leaves were taken out of petri dish, reweighed and surface dried with blotters. Leaves were then oven-dried at 110°C for 24h and again weighed for dry weight (DW). Final values for relative leaf water content was calculated as (FW-DW)/(TW-DW) × 100.

2.3.7 Malondialdehyde content

Lipid peroxidation of the cell membrane was measured as malondialdehyde (MDA) content (Heath and Packer, 1968). One hundred mg fresh leaf tissue was extracted in 10 mL of 0.1% trichloroacetic acid (TCA). The homogenate was centrifuged at 15,000 rpm for 5 min. Supernatant was used as extract. Afterward, 4 mL of 0.5% thiobarbituric acid (in 20% trichloroacetic acid) was added to a 1-ml of the supernatant. This mixture was heated at 95°C for 30 minutes followed by immediate cooling in ice bath. Re-centrifugation of this mixture was performed again at 10,000 rpm for 10 min and the absorbance of the supernatant was taken at 532 nm. Values were expressed as nmol g^{-1} DW.

2.4 Reproductive traits

For evaluating reproductive function, flowers were collected 5 days after exposure to heat stress and assessed for following traits.

2.4.1 Pollen germination

For testing pollen germination, pollen grain samples were taken in three replicates and each replicate consisted of five flowers genotype⁻¹ (Brewbaker and Kwack, 1963). Pollen grains were collected and immersed in few drops of pollen germinating medium (10% sucrose, 990 mM potassium nitrate (pH 6.5), 1.64 mM boric acid, 812 mM magnesium sulphate and 1.3 mM calcium nitrate) (Kaushal et al., 2013).

2.4.2 Pollen viability

Around 100 pollen grains were tested for the pollen viability with 0.5% acetocarmine/Alexander stain per genotype in three replicates. Selection of viable pollen grains was made on the basis of size (fully expanded), shape (triangular or spherical) and concentration of stain taken by them. Pollen grains were collected from freshly opened flowers and were pooled and checked for their viability (Kaushal et al., 2013).

2.5 Yield traits

For obtaining yield data, three plants genotype⁻¹ in three replications (9 plants genotype⁻¹) were harvested at maturity, wrapped in paper bags and dried in an oven at 65°C for at least three days. After drying, the total number of pods and seeds, total seed weight and single seed weight plant⁻¹ were calculated (Sharma et al., 2016).

2.6 Statistical analyses

Urdbean plants were grown in outdoor environment for 2 consecutive years as well as under controlled environment of the

growth chamber using RCBD. The analysis of data for computing standard errors and least significant differences ($P < 0.05$) was performed using 2-factorial (temperature \times genotypes) design using OPSTAT statistical software (CCS, HAU, Hisar, India). Genotypic correlation, heritability were analysed by using GenStat 15 software. The Euclidean dissimilarity matrix was constructed involving all the genotypes and traits, and were clustered using Ward's method (Patterson and Thompson, 1971). The principal component analysis was done using the R package factoextra, and heat map analysis was performed according to Babicki et al. (2016).

3 Results

3.1 Physiological traits

3.1.1 Electrolyte leakage

Electrolyte leakage (EL%) is one of the important physiological traits measuring membrane damage used for screening heat stress tolerant genotypes in plants. Heat stress significantly ($P < 0.01$) damaged the membranes (Supplementary Figure S2, Supplementary Table S3). EL increased by 49 and 51% in heat-stressed plants, compared to controls, in the first and second years, respectively. Based on this trait, Mash 114 (18.5%, 17.73%), PantU31(21.77%, 20.8%), UTTARA (21.43%, 20.73%), IPU18-04 (18.17%, 19.73%) genotypes revealed low value for EL % under heat stress environment for both years. However, the genotypes IPU 18-6 (25.13%, 26.9%), Mash 218 (26.47%, 26%), SuG1153 (26.23%, 26.9%) exhibited high value for EL% under heat stress environment for both years suggesting their heat stress sensitivity. The high heritability values (82.6% and 86.85, for first and second years, respectively) for this trait were noted under heat stress see Table 1.

3.1.2 Stomatal conductance

Stomatal conductance (gS) varied significantly ($P < 0.01$) across the genotypes in plants exposed to high temperature (Supplementary Figure S3, Supplementary Table S3). As a result of high temperature, gS decreased by 12 and 15% over control in 1st and 2nd year, respectively. Under heat stress environment, Mash 114 (45.6, 40.47) and Pant G 31(43.9, 46.53) genotypes showed high value for stomatal conductance in both years. Regarding heritability for gS, 96.5% (during the first year) and 95.2% (during second year) heritability values were noted (Table 1).

3.1.3 Chlorophyll content

A significant genetic variation ($P < 0.01$) was noticed in chlorophyll content among the genotypes under heat stress (Supplementary Figure S4, Supplementary Table S3). The range of leaf chlorophyll content was noted to be 11.4-19.8 mg g⁻¹ FW during the first year and 12.3- 21.3 mg g⁻¹ FW during

TABLE 1 General statistics of various traits in urdbean genotypes under heat stress environment.

	Heritability	CV%	Mean	Range
Heat stress 1 st year				
Chlorophyll content	85.5	8.1	15.1	11.4-19.8
chlorophyll fluorescence	90.1	5.3	0.53	0.41-0.61
Electrolyte leakage%	82.6	7.3	24.2	18.2-28
Leaf area	83.7	6.6	18.4	13.9-21.4
Stomatal conductance	96.5	8.1	28.9	22.3-45.6
Pods plant ⁻¹	98.5	13.8	5.72	2.4-15
Seeds plant ⁻¹	99.4	11.2	21.03	6.2-62
Seed yield plant ⁻¹	99.2	19	0.64	0.11-2.7
Single seed weight	92.2	12.1	0.03	0.02-0.04
Heat stress 2 nd year				
Chlorophyll content	92.7	7.6	15.7	12.3-21.3
Chlorophyll fluorescence	97.3	2.9	0.54	0.44-0.66
Electrolyte leakage%	86.8	6.7	24.4	17.3-27.7
Leaf area	89.8	6.1	17.6	14.7-20.6
Pods plant ⁻¹	99	11.3	6.16	2.8-15.9
Stomatal conductance	95.2	8.6	30	25.5-46.5
Seeds plant ⁻¹	99.6	9.4	22	5.3-71
Seed yield plant ⁻¹	99.6	15	0.73	0.16-2.03
Single seed weight	94.5	10.1	0.03	0.02-0.04
Growth chamber heat stress				
Chlorophyll content	94.5	7.5	16.35	13.27-19.67
chlorophyll fluorescence	98.8	3.7	0.54	0.42-0.66
Electrolyte leakage%	96.2	4.5	24.5	20.27-28.03
Leaf area	94.5	7.5	16.35	13.27- 19.67
Malondialdehyde	98.8	5.3	27.75	19.3-33.97
Pollen germination %	99.4	6.8	36.7	15.3-54.17
Pollen viability%	98.8	6.7	43.24	24.5-61.20
Relative water content	99.3	2.9	63.66	49.57- 79.1
Stomatal conductance	99.1	5.5	25.03	14.37-33.7
Seeds plant ⁻¹	99.4	9.1	29	4-52
Seed yield plant ⁻¹	99.5	10.6	1.26	0.15- 2.38
Single seed weight	98.7	7.4	0.03	0.02-0.04
Pods plant ⁻¹	99.4	9.1	8.79	2.7-14.73

second year under heat stress environment. An average reduction of 22 and 30% was observed due to heat stress, relative to controls, in 1st and 2nd year, respectively. High value for chlorophyll content was observed in Mash 114 (19.67, 18.97), PantG31 (19.77, 20.47), UTTARA (17, 20.4) genotypes under heat stress environment for both the years. This trait also showed high heritability (85.5% and 92.7% for 1st and 2nd years, respectively) and could be vital for selecting heat tolerant urdbean lines (Table 1).

3.1.4 Chlorophyll fluorescence

Significant genetic variability for chlorophyll fluorescence (ChlF) (Fv/Fm) was noted under heat stress environment (P<0.01) (Supplementary Figure S5, Supplementary Table S3).

Mean value for Fv/Fm was noted to be 0.53 during the first year and 0.54 during second year under heat stress environment. Heat stress caused about 28% reduction over control in both the years. The genotypes Mash 114 (0.61, 0.66), PantU31 (0.61, 0.65), UTTARA (0.6, 0.65) showed high value for ChlF under heat stress for both years. Heritability for this trait was noted to be 90.1% and 97.3% during the first year and second year, respectively (Table 1).

3.1.5 Leaf area

Significant genetic variation (P<0.01) was noted in leaf area (LA) among the tested genotypes under hot environment for both years (Supplementary Figure S6, Supplementary Table S3). LA decreased by 23 and 28% in heat-stressed plants, over

controls, in the 1st and 2nd years, respectively. Substantial genetic variability for this trait was noted under heat stress environment ranging from 13.9-21.4 cm² (during the first year) and 14.7-20.6 cm² (during second year). High heritability (83.7%) recorded during the first year and 89.8% during second year, suggested that this trait could be used for screening heat tolerance in urdbean (Table 1).

3.2 Yield and yield-related traits

Significant (P<0.01) genetic variability for pods plant⁻¹ (Figure 1) seeds plant⁻¹ (Figure 2), seed yield plant⁻¹ (Figure 3) and single seed weight (Figure 4) were recorded under heat stress environment for both years (Supplementary Table S3).

Under high temperature, maximum pods plant⁻¹ decreased by 82.4 and 83.7%, maximum seeds plant⁻¹ by 94.7 and 94.3%, maximum seed yield plant⁻¹ by 91.5 and 95.2% and single seed weight by 26 and 32% over the respective controls in 1st and 2nd year, respectively. The UTTARA genotype retained highest pod number plant⁻¹ (15, 16) followed by PantU31(15,15), IPU18-04 (14,16) under heat stress environment for both years. For seeds

plant⁻¹ trait, Mash114 (63, 66), UTTARA (63, 71) and IPU18-04 (62, 63) showed promising results under heat stress environment for both years. Likewise, Mash114 (47.7%, 41.6%), IPU18-04 (43.34%, 48.9%), UTTARA (57.39%, 38%), and PantU31 (55.45%, 28.7%) showed lower reduction percentage for seed yield plant⁻¹ for both years, and thus could be highly heat tolerant genotypes. Under heat stress environment, high heritability with 98.5%, 99.4% and 99.2% was noted for pods plant⁻¹, seeds plant⁻¹ and seed yield plant⁻¹, respectively during the first year. Similarly, these traits showed high heritability under hot environment during second year also (Table 1).

3.3 Validation of selected heat tolerant and heat-sensitive Urdbean genotypes in growth chamber

Significant genetic variability for the various evaluated traits was recorded in twenty-six selected urdbean genotypes under normal and heat stress condition in both years (Supplementary Table S3). Based on the various physiological and yield and yield related parameters, the following genotypes Mash 114, PantU31,

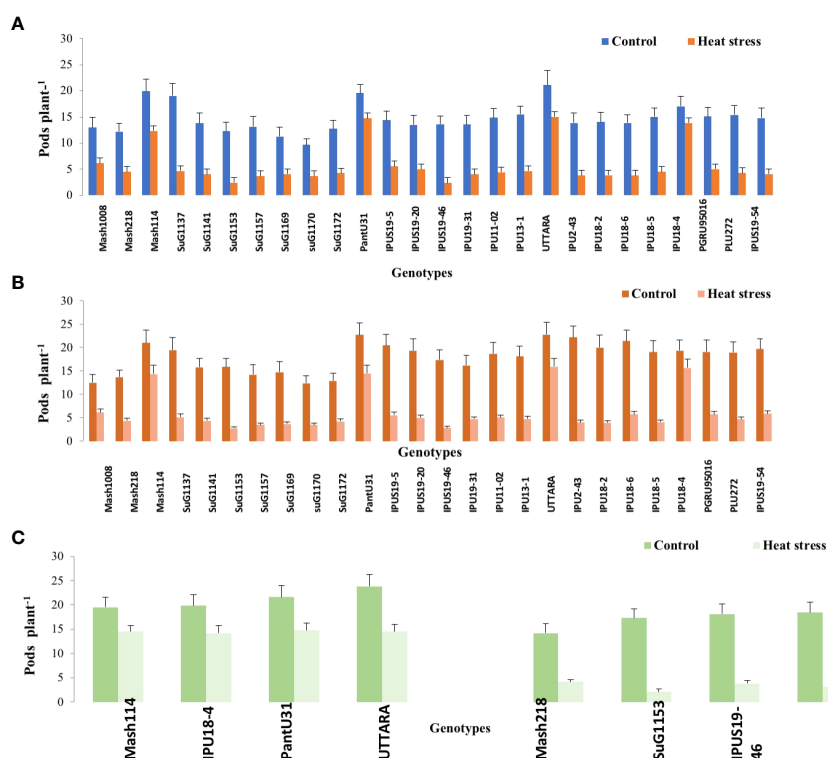


FIGURE 1 Pod number plant⁻¹ of Urdbean genotypes under control (normal-sown; Control) and heat stress environment during 2018 (A), 2019 (B) and in controlled environment of growth chamber (GC; C). LSD values (P < 0.05); genotype × treatment: 2.6 (2018), 3.1 (2019), 3.46 (GC). Values are means + SE. (n = 3).

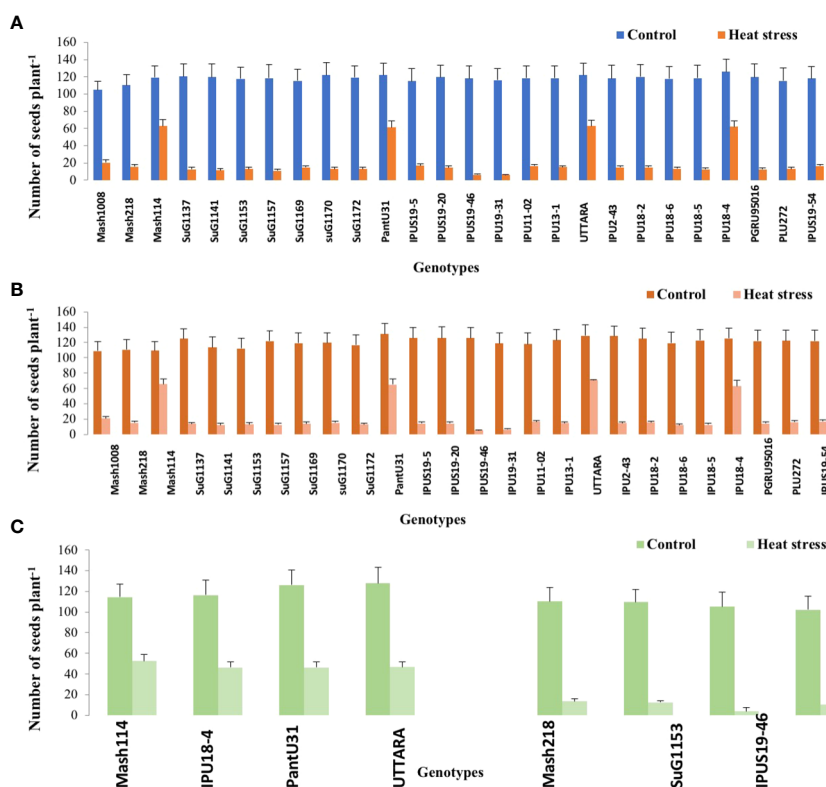


FIGURE 2

Seed number plant⁻¹ of Urdbean genotypes under control (normal-sown; Control) and heat stress environment during 2018 (A), 2019 (B) and in controlled environment of growth chamber (C; GC). LSD values ($P < 0.05$); genotype \times treatment: 6.9 (2018), 7.5 (2019), 12.1 (GC). Values are means \pm SE. ($n = 3$).

IPU18-04 and UTTARA were identified to be heat tolerant for both years under hot environment. Contrastingly, Mash 118, SuG1153, IPU18-5, IPU5(19-46) were identified to be highly sensitive to heat stress for both years.

To validate the response of selected heat tolerant and sensitive genotypes, a selected set of 4 heat tolerant and 4 heat-sensitive urdbean genotypes among the 26 genotypes were examined under growth chamber subjecting them to normal and heat stress treatments, separately. Among these selected 4 heat tolerant genotypes, Mash114 and IPU18-04 revealed high tolerance to heat stress, evidenced by high number of pods plant⁻¹ (14.5, 14.2), high seed number plant⁻¹ (52.5, 46.5) and high efficiency of various physiological traits (chlorophyll content (Supplementary Figure S4), chlorophyll fluorescence (Supplementary Figure S5), stomatal conductance (Supplementary Figure S6), low electrolyte leakage (Supplementary Figure S2), and low malondialdehyde content (Supplementary Figure S7) and reproductive traits [high pollen germination (57.4%, 52.5%) and viability percentage (61.2%, 57.1%)] under heat stress environment (see Supplementary Figure S7).

However, among the heat-sensitive genotypes, IPU5-(19-46) and IPU-18-5 showed high heat stress sensitivity, evidenced by

high reduction of yield and yield-related traits as well as physiological and reproductive traits.

3.4 Correlation analysis

Pod number plant⁻¹ showed significant positive correlations with traits-chlorophyll content, chlorophyll fluorescence, leaf area and stomatal conductance-directly contributing to photosynthesis process whereas significant and negative association of electrolyte leakage (EL) percentage was noticed (Table 2). EL also showed negative correlation with traits (chlorophyll content, chlorophyll fluorescence, leaf area and stomatal conductance), yield traits such as pods plant⁻¹, seeds plant⁻¹, single seed weight and seed yield plant⁻¹ under heat stress environment during both the years.

In urdbean plants grown under growth chamber condition, subjected to heat stress, electrolyte leakage and malondialdehyde (an indicator of oxidative stress) showed highly significant negative correlation with all the physiological traits viz., chlorophyll content, chlorophyll fluorescence, stomatal conductance, relative water content, leaf area, pollen

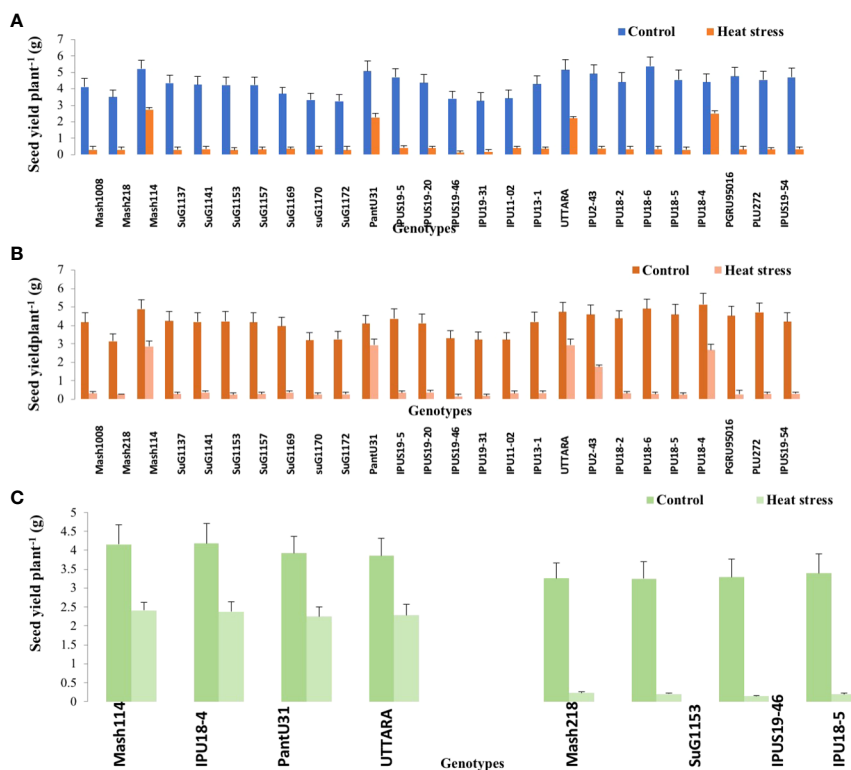


FIGURE 3 Seed yield plant⁻¹ of Urdbean genotypes under control (normal-sown; Control) and heat stress environment during 2018 (A), 2019 (B) and in controlled environment of growth chamber (C; GC). LSD values (P < 0.05); genotype × treatment: 1.3 (2018), 1.5 (2019), 1.3 (GC). Values are means + SE. (n = 3).

germination % and pollen viability % and yield traits viz. pods plant⁻¹, seed yield plant⁻¹ (Table 2).

High and significant positive correlation of pollen germination % and pollen viability % were noticed with all the traits except electrolyte leakage and malondialdehyde. Likewise, stomatal conductance and RLWC also exhibited high and positive correlation with all the traits except electrolyte leakage and malondialdehyde. The yield and yield related traits viz., pods plant⁻¹, seeds plant⁻¹, single seed weight and seed yield plant⁻¹ showed very strong positive correlation with pollen germination and pollen viability (Table 2) suggesting these traits as vital for screening heat tolerant urdbean genotypes.

3.5 PCA analysis

During the first year, under heat stress environment, PCA analysis (Figure 5) revealed five principal components correlated to 9 traits accounted for 96.5% of total variability. The individual contribution of each component was 76.8%, 6.84%, 5.18%, 4.23% and 3.38%. Analysis of factor loadings of the traits in the retained PCs suggested that seed yield plant⁻¹ (SPY) (13.76), seeds plant⁻¹

(SPP) (13.45) and pods plant⁻¹; PPP (13.12) contributed most positively. In PC2, leaf area (LA) contributed most positively. The trait chlorophyll fluorescence (ChlF) (58.47), chlorophyll (Chl) (76.45) and electrolyte leakage (EL%) (45.1) had highest contribution to PC3, PC4 and PC5, respectively.

Likewise, during second year, PCA analysis (Figure 6) indicated five principal components correlating to 9 traits contributed 97.9% to the total variability. The individual contribution of each component was 81.2%, 9.3%, 3.62%, 2.51% and 1.29%. PPP (12.6) had the highest contribution to PC1. Likewise, LA (50.69) contributed with highest positive value to PC2. EL% (57.38), ChlF (40.18) and Chl (53.1) had highest positive contribution to PC3, PC4 and PC5, respectively.

Under growth chamber, PCA analysis (Figure 7) suggested five PCAs attributing to 13 traits contributing 99.8% to the total variability. The individual contribution of each component was PC1 (97.5%), PC2 (1.03%), PC3 (0.64%), PC4 (0.35%) and PC5 (0.30%). Chlorophyll content (7.81) had the highest contribution to PC1, while single seed weight (32.58) had the highest contribution to PC2. Electrolyte leakage (30.42%) had the highest contribution to PC3 and stomatal conductance (42.09) had the highest contribution to PC4. Seeds plant⁻¹ (32.98) had the highest contribution to PC5.

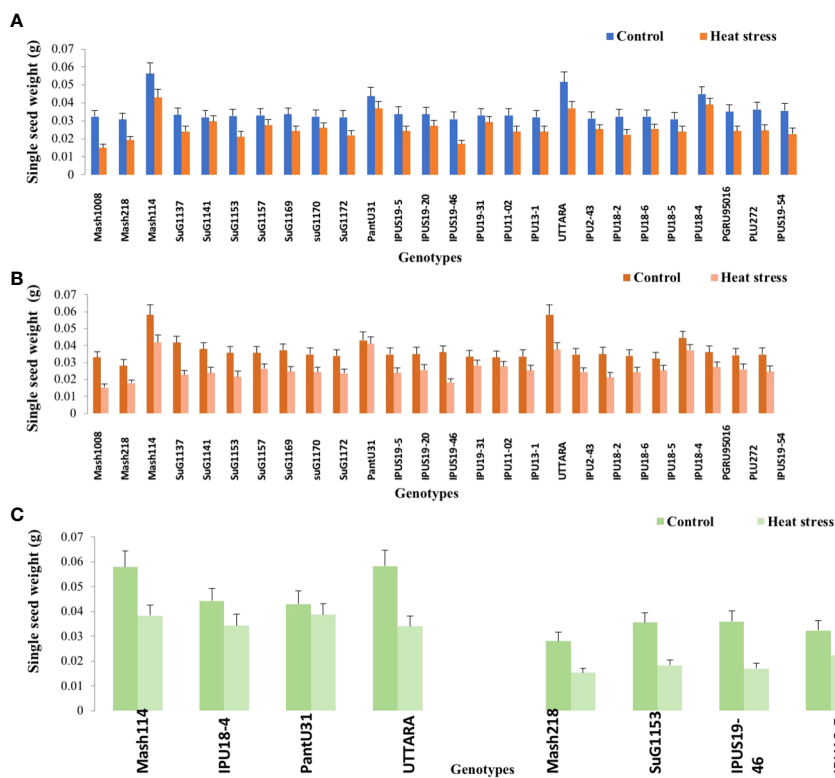


FIGURE 4 Single seed weight of Urdbean genotypes under control (normal-sown; Control) and heat stress environment during 2018 (A), 2019 (B) and in controlled environment of growth chamber (C;GC). LSD values ($P < 0.05$); genotype \times treatment: 0.0023 (2018), 0.0021 (2019), 0.0018 (GC). Values are means + SE. ($n = 3$).

TABLE 2 Correlation coefficients of various traits with yield traits in plants under heat stress environment.

Trait	Outdoor environment (2018)		Outdoor environment (2019)		Growth Chamber	
	Number of Pods Plant ⁻¹	Seed yield plant ⁻¹	Number of Pods Plant ⁻¹	Seed yield plant ⁻¹	Number of Pods Plant ⁻¹	Seed yield plant ⁻¹
Electrolyte leakage %	-0.71**	-0.76**	-0.73**	-0.73**	-0.96**	-0.98**
Chlorophyll	0.71**	0.72**	0.80**	0.73**	0.98**	0.99**
Chlorophyll fluorescence	0.68**	0.70**	0.87**	0.82**	0.99**	0.99**
Stomatal Conductance	0.91**	0.95**	0.97**	0.95**	0.98**	0.98**
Leaf area	0.70**	0.67**	0.60**	0.54**	0.98**	0.99**
Malondialdehyde					-0.98**	-0.98**
Pollen viability					0.98**	0.97**
Pollen germination					0.96**	0.99**
Number of Pods Plant ⁻¹	1	0.96**	1	0.95**	1	0.99**
Seed yield plant ⁻¹	0.96**	1	0.92**	1	0.99**	1
Seeds plant ⁻¹	0.98**	0.99**	0.98**	0.95**	0.98**	0.99**
Single seed weight	0.81**	0.88**	0.86**	0.85**	0.98**	0.97**

** denotes significant at 1%.

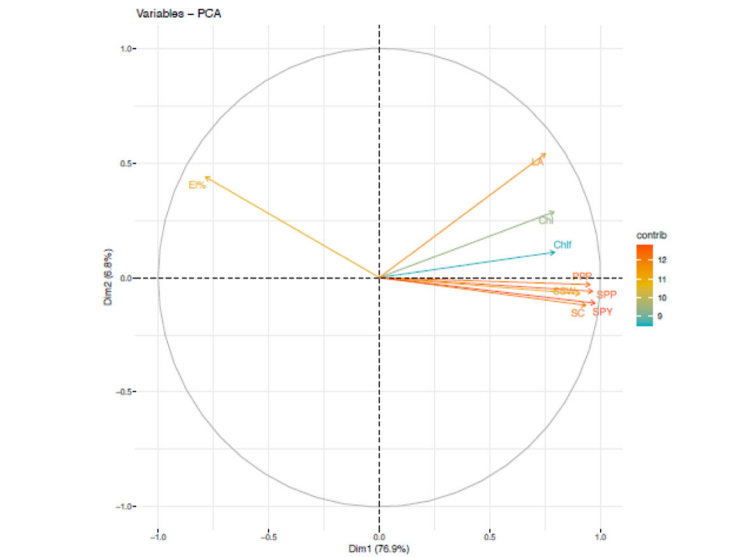


FIGURE 5 Principal component analysis (PCA) of various traits in Urdbean genotypes under heat stress in the year 2018.

3.6 Clustering and identifying heat tolerant Urdbean genotypes based on outdoor experiments

Based on the heat map analysis considering all the physiological and yield-related traits evaluated during the first year in all, the 26 genotypes revealed three major clusters.

Regarding first year, Cluster 1 contained all the highly heat tolerant genotypes, including IPU18-04(43.34%), Mash 114 (47.7%), UTTARA (IPU94-1) (57.39%), and PantU31 (55.45%) (Figure 8) relying on low reduction of seed yield plant⁻¹ (SYP) compared under non-stress and heat stress conditions. The heat-sensitive genotypes viz., Mash218 (91.35% SYP reduction), IPU5 (96.79% SYP reduction),

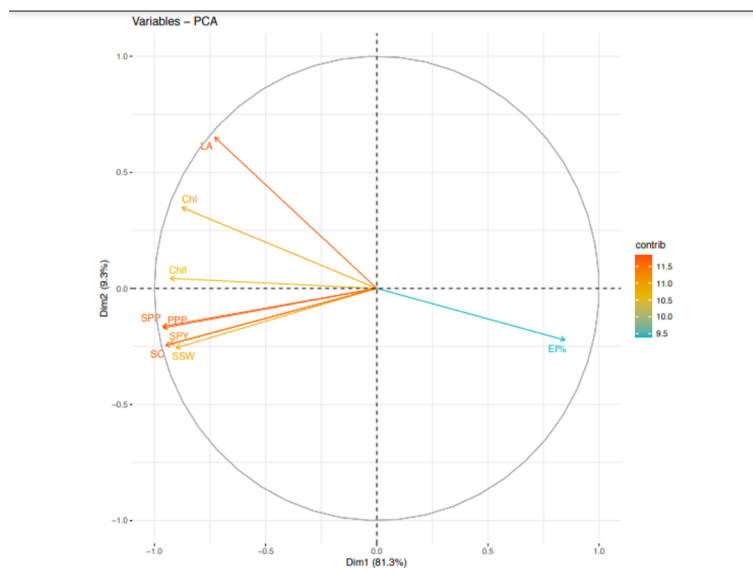


FIGURE 6 Principal component analysis (PCA) of various traits in urdbean genotypes under heat stress in the year 2019.

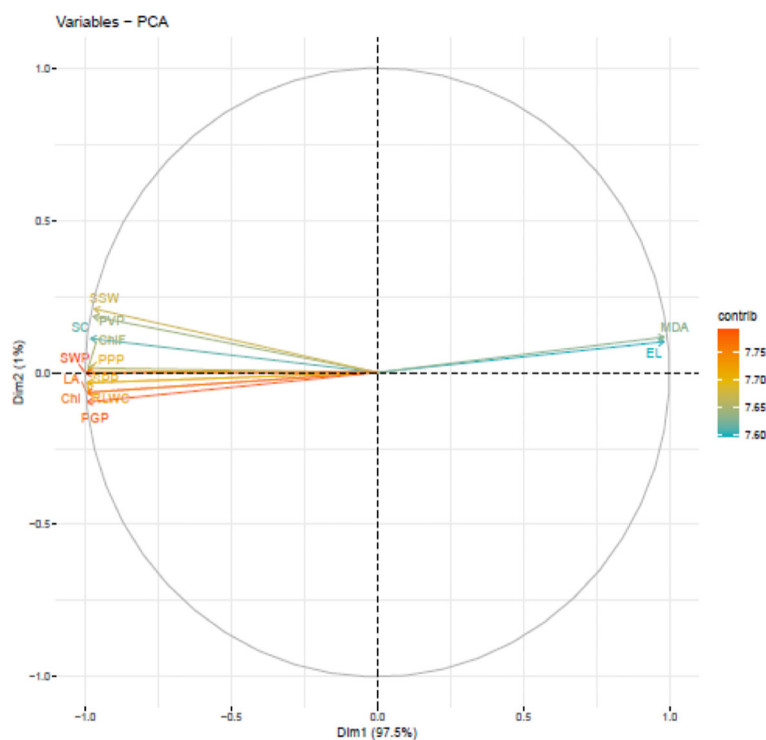


FIGURE 7
Principal component analysis (PCA) of various traits in urdbean genotypes under heat stress in a growth chamber.

IPU18-5(93.40% SYP reduction) remained in second cluster. The 3rd cluster had genotypes such as IPU 11-02 (88.45% SYP reduction), SuG1170 (89.79% SYP reduction), SuG1169 (90.235 SYP reduction), Mash 1008 (92.6% SYP reduction)

Likewise, during second year, the heat map also divided the genotypes into three clusters (Figure 9). The first cluster contained the highly heat tolerant genotypes viz., Mash 114 (41.6% SYP reduction), PantU31 (28.7% SYP reduction), IPU18-04 (48.35% SYP reduction) and UTTARA (38% SYP reduction). In the second cluster, all the heat-sensitive genotypes such as Mash 218 (91.5% SYP reduction), SuG1153 (94.1% SYP reduction), IPU18-5 (94.8% SYP reduction) and IPU5 (95.2% SYP reduction) were placed. Other genotypes, for example, IPU2-43 (62.1% SYP reduction), IPU-11-02 (90.3% SYP reduction), and SuG1169 (90.8% SYP reduction) were found in third cluster.

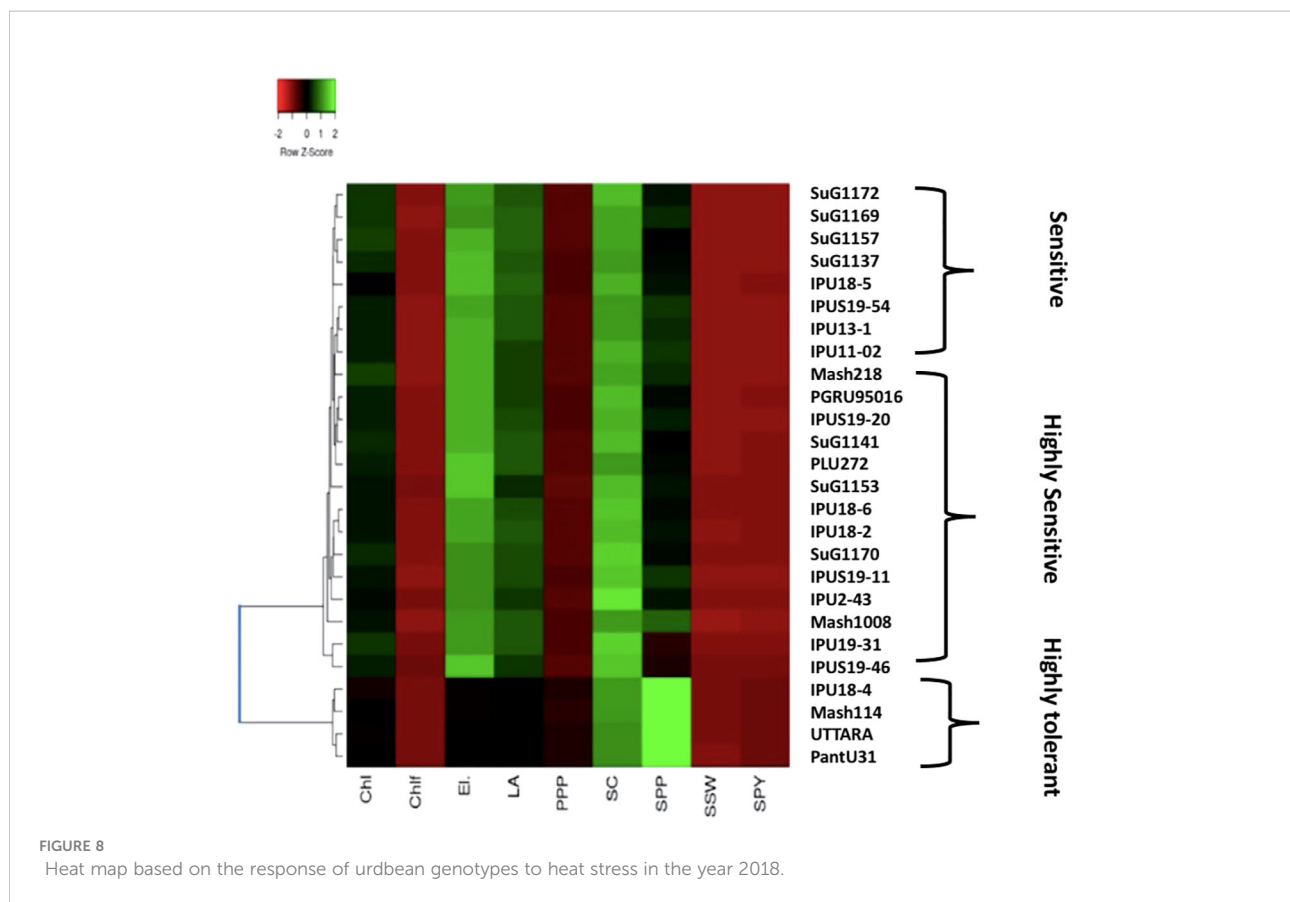
The cluster analysis of the selected genotypes evaluated for various traits under growth chamber condition resulted in two major clusters (Figure 10). The first cluster contained all the four heat-sensitive genotypes such as IPU18-5, IPU5, SuG1153, and Mash 218, whereas the second cluster contained all the heat tolerant genotypes UTTARA, PantU31, IPU18-04, and Mash114.

Various symptoms of heat stress on urdbean at vegetative and reproductive growth are shown in Figures 11 and 12.

4 Discussion

Increasing frequency of heat stress events poses serious challenges in all the plant growth stages, especially, reproductive stage, resulting in significant yield loss in various crop plants, including urdbean (Jha et al., 2014; Jha et al., 2017; Chaudhary et al., 2020; Chaudhary et al., 2022). Thus, assessing urdbean's genetic variability for phenological, morpho-physiological, biochemical and yield and yield related traits is one of the prime objectives for developing heat tolerant climate resilient urdbean genotypes.

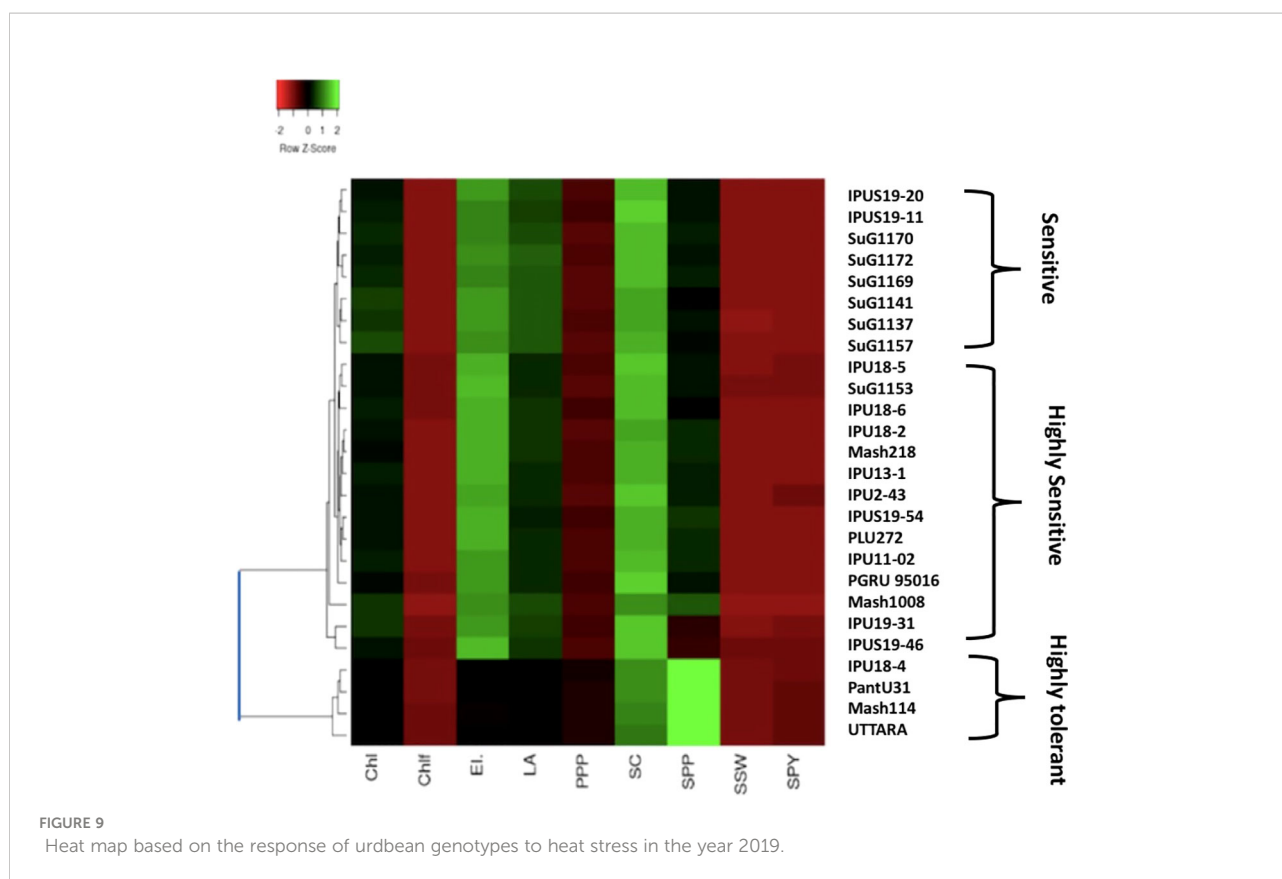
A selected set of 26 urdbean genotype were examined for heat stress tolerance by growing them under non-stress and heat stress under field condition and under controlled growth chamber conditions. Wide range of genetic variability for various physiological, biochemical and yield and yield related traits was observed. Thus, some genotypes showing promising results based on the physiological traits such as chlorophyll content, chlorophyll fluorescence, and yield traits like high pod setting plant⁻¹ and high seed yield plant⁻¹ under heat stress environment were identified and validated for heat tolerance under controlled high temperature environment. These urdbean genotypes could be a precious resource for heat tolerance. Further, the tolerant urdbean genotypes could be potentially used for investigating the genetic control of heat tolerance in urdbean.



Among the various physiological traits for assessing heat stress response at vegetative stage during photosynthesis, measuring chlorophyll content, electrolyte leakage, stomatal conductance and photosystem II function are essential parameters for selecting heat tolerant genotypes (Srinivasan et al., 1996; Sita et al., 2017; Bhandari et al., 2020; Devi et al., 2022). Chlorophyll is the main photosynthetic pigment, assists in capturing light energy and enables in photosynthesis process (Wang et al., 2018). Heat stress causes reduction in Chl content resulting in leaf senescence (Kim and Nam, 2007). Improved retention of Chl content under heat stress could be an indication of heat stress tolerance. Thus, genetic variability for Chl content could be useful for selecting heat tolerant genotypes. Heat tolerance based on membrane stability measured by electrolyte/ion leakage is an important trait for selecting genotypes for heat tolerance (Bajji et al., 2002). Under high temperature stress, the genotypes showing low electrolyte leakage indicate stable cell membrane stability and thus are considered heat tolerant. Likewise, stomatal conductance and transpiration cooling are important traits for assessing heat tolerance in plants. Leaf cooling is a vital heat stress avoidance mechanism (Deva et al., 2020) thus, enhanced stomatal conductance and transpiration cooling could help plants to conduct photosynthesis process under high temperature stress

(Porch and Hall, 2013). Thus, genotypes with high stomatal conductance could be heat tolerant. In the current study, Mash114, UTTARA, PantU31 genotypes showed high chlorophyll content, high stomatal conductance, low electrolyte leakage and high Fv/Fm value under heat stress, both under field and growth chamber condition, indicating their heat stress tolerance. Similar findings were reported in chickpea (Devi et al., 2022), lentil (Srinivasan et al., 1996; Delahunty et al., 2015; Sita et al., 2017; Sehgal et al., 2019; Bhandari et al., 2020) and pea (McDonald and Paulsen, 1997) under heat stress.

Of all the growth stages, reproductive stage is the most sensitive stage affected by negative impact of heat stress (Zinn et al., 2010). High temperature stress causes anomalies and malfunction in reproductive processes ranging from reduction in pollen germination (PGP) percentage, pollen viability percentage (PVP), malformation in ovule to inhibition in fertilization process in various crops, including rice (Xu et al., 2021), wheat (Ullah et al., 2022), chickpea (Bhandari et al., 2020; Devi et al., 2022), common bean (Silva et al., 2019; Soltani et al., 2019) and tomato (Gonzalo et al., 2021). High PGP and PVP values are indicators of efficient reproductive function leading to high pod and seed setting resulting in improved yield under heat stress (Firon et al., 2006; Pham et al., 2020). Sufficient range of



genetic variability for PGP (15.4%-57.4%), PVP (24.5%-61.2%) was noted under heat stress in the present study, providing scope for selection and developing heat tolerant urbean genotypes. Based on these traits, Mash114 and PantU31 genotypes could be promisingly used as donor parents for improving heat tolerance in urbean. Screening of heat tolerance relying on PGP and PVP has been reported in rice (Zhang et al., 2018), wheat (Bheemanahalli et al., 2019), chickpea (Devi et al., 2022), lentil (Barghi et al., 2013), common bean (Silva et al., 2019; Vargas et al., 2021), tomato (Pham et al., 2020) and sorghum (Djanaguiraman et al., 2018).

Emphasizing on yield and yield-related parameters such as pods plant⁻¹, significant genetic variability ranging from (2.43-15.07 during the first year) and (2.77-15.9 during second year), for seed yield plant⁻¹ (0.11-2.73g during the first year) and (0.16-2.93g during the second year) and for total seeds plant⁻¹ (6.2-62.9 during the first year) and (6.7-71.2 during the second year) under heat stress was recorded. Thus, genotypes with high pod setting, high seed yield plant⁻¹ and high seed number plant⁻¹ under heat stress environment could be promisingly selected as heat tolerant genotypes. Based on these traits, Mash114, PantU31, UTTARA and IPU18-04 were selected as heat tolerant urbean genotypes. Similarly, in previous studies, based on these yield traits, genotypes “40-10,” “Naparnyk,” and “CDC Meadow” in pea (Jiang et al., 2020), G122, PI

163120, Cornell 503 in common bean (Shonnard and Gepts, 1994; Rainey and Griffiths, 2005a), ICC1205, ICC15614, GNG469, GNG1488, GNG1499, and GNG1969 in chickpea (Devasirvatham et al., 2013), B89-200 and TN88-63 in cowpea (Ehlers and Hall, 1998), 72578, 70548, 71457 and 73838 in lentil (Delahunty et al., 2015) and 55-437 and 796 in groundnut (Ntare et al., 2001) were identified to be heat tolerant.

Correlation studies indicated that electrolyte leakage trait had highly negative association with all the physiological (except MDA) and yield and yield-related traits under heat stress condition, indicating genotypes having high value for electrolyte leakage are highly heat-sensitive genotypes. However, other physiological traits viz., chlorophyll content, chlorophyll fluorescence, relative water content stomatal conductance showing high and positive association with yield and yield related traits viz., seed yield plant⁻¹, total seeds plant⁻¹ and single seed weight indicated that selection of urbean genotypes with high chlorophyll content, enhanced stomatal conductance and high relative water content under heat stress could be highly heat tolerant. Positive association of chlorophyll content, stomatal conductance trait related to photosynthesis process with yield and yield-related traits ranging from seed yield plant⁻¹, pod number plant⁻¹ and single seed weight under heat stress has been reported in chickpea (Devi et al., 2022), lentil (Sita et al., 2017), and common bean (Petkova et al., 2007).

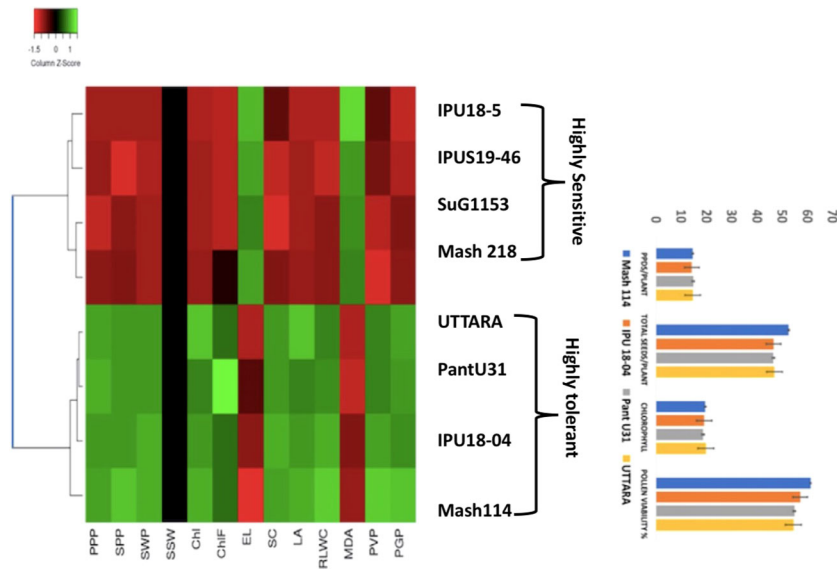


FIGURE 10 Heat map based on the response of urbean genotypes to heat stress in a growth chamber.



FIGURE 11 Morphological effects of heat stress on Urdbean plants; plant height under control environment (A), reduced plant height under heat stress (HS) environment (B), healthy leaves under control environment (C), scorching of leaves under HS (D), chlorosis in the HS (E), Leaf senescence and abscission in the HS (F).

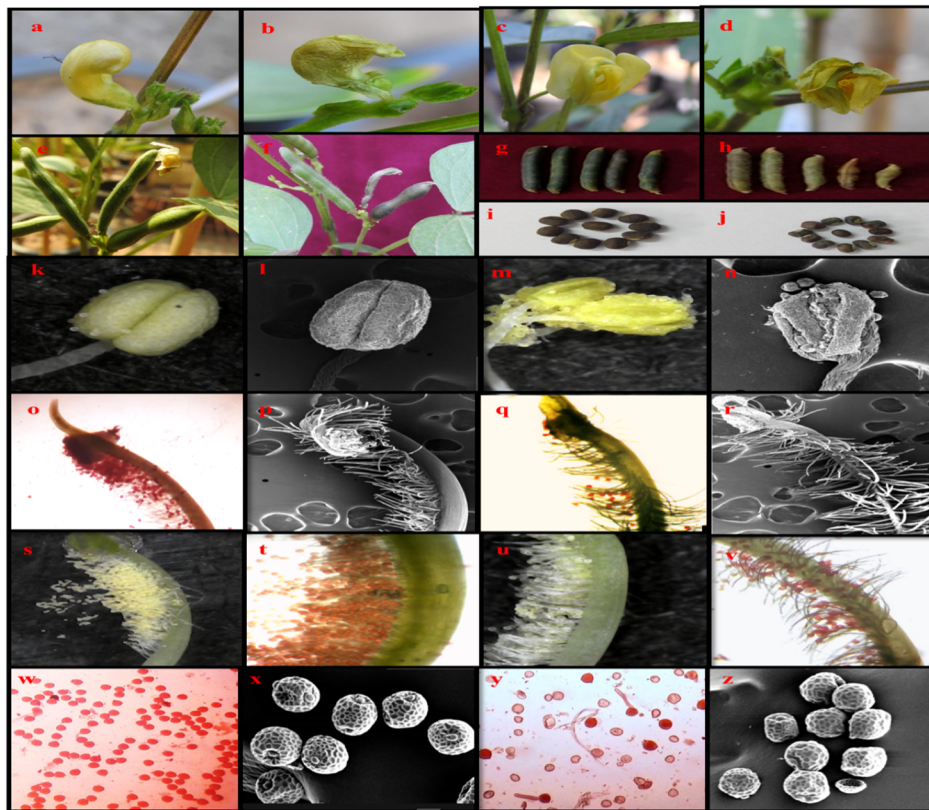


FIGURE 12

Urdbean plants showing various distinctive impacts on it are the reproductive phase when raised under control and heat stress environment. Plants grown under control temperature have healthy bud (A) healthy flower (C) filled pods (egg), normal seeds (I) compact anther (K, L) receptive stigma (O, P) higher pollen load (S, T) and possess viable pollen grains (W, X). However, plants raised under heat stress conditions have more frequency of aborted buds (B) aborted flowers (D) unfilled and aborted pods (F, H) shrivelled seeds (J) distorted anther (M, N) non-receptive stigma (Q, R) less pollen load (U, V) and non-viable pollen grains (Y, Z) healthy flower bud (A) aborted flower bud (B) healthy flower (C) aborted flower (D) healthy pods (E) aborted pod (F) normal pod length (G) reduced pod length (H) healthy seeds (G) shrivelled seeds (H) healthy anther under stereo-microscope (I) healthy anther under SEM (J) distorted anther.

Studies conducted in controlled high temperature environment of growth chamber revealed PGP and PVP to be highly correlated with pods plant⁻¹ and could be used as vital indicators of heat tolerance. Earlier studies have also indicated that these traits could be used for selecting heat tolerant genotypes in chickpea (Devi et al., 2022), common bean (Rainey and Griffiths, 2005), lentil (Sehgal et al., 2019) and tomato (Gonzalo et al., 2021).

High heritability of various morpho-physiological, yield and yield related traits could be of great importance for selecting these traits for screening of heat tolerant genotypes in various crops. High heritability for chlorophyll content, stomatal conductance, seed yield plant⁻¹, pods plant⁻¹, single seed weight, as noticed in the present study has also been noted in heat tolerant chickpea (Jha et al., 2019; Devi et al., 2022), rice (Enzi et al., 2022), tomato (Panthee et al., 2018), wheat (Rebetzke et al., 2013) under high temperature environment.

5 Conclusion

Heat stress related events are becoming serious constraints for crop yield including urdbean thus, causing great concern for global food security. Harnessing the genetic variability for various morpho-physiological and yield and yield related traits existing across the crop gene pool could be one of the important approaches for developing heat tolerant crop cultivars including urdbean. A wide range of genetic variability for various morpho-physiological and yield and yield related traits were captured for a selected 26 urdbean genotypes under both non-stress and heat stress environment for consecutive two years. A selected four heat tolerant and four heat-sensitive genotypes were further validated for their heat stress response under controlled growth chamber condition. Based on the results obtained from both outdoor and controlled growth chamber conditions, yield and yield related traits viz., pods plant⁻¹, seeds plant⁻¹, single seed

weight and seed yield plant⁻¹ showed strong positive correlation with chlorophyll, chlorophyll fluorescence, and stomatal conductance. Similarly, these yield traits had very strong correlation with reproductive traits, pollen germination and pollen viability except electrolyte leakage and malondialdehyde content. These results indicated selection for high pollen germination % and high pollen viability % and yield and yield related traits could assist in selecting heat tolerant urdbean genotypes. Thus, the candidate genotypes PantU31, Mash114, UTTARA and IPU18-04 exhibiting high pod setting and high seed yield plant⁻¹ under heat stress imposed under outdoor and growth chamber environment could be potentially used as heat tolerant donor parents for future urdbean breeding programme. Further, these genotypes can be assessed for their heat tolerance across the multiple locations for confirming their heat tolerance based on various locations.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding authors.

Author contributions

SC conducted the experiment. UJ and PJP helped in analysis and writing part of the manuscript. SS and DS contributed in providing the urdbean lines. KS and SK assisted in conducting the biochemical analyses. HN conceived the idea and helped in writing the manuscript. KHMS helped in writing part of the manuscript and edited the manuscript. All authors contributed to the article and approved the submitted version.

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Acknowledgments

SC thanks CSIR for project fellowship and CSIR-UGC for providing a doctoral research fellowship during her course study. The corresponding author HN is thankful to DST (FIST and PURSE), UGC, DBT, CSIR, India, The University of Western Australia (Australia), IIPR (Kanpur, India), PAU (Ludhiana, India), for supporting the research work at various times.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fpls.2022.1042999/full#supplementary-material>

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Physiological and Molecular Approaches for Developing Thermotolerance in Vegetable Crops: A Growth, Yield and Sustenance Perspective

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OPEN ACCESS

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Specialty section:

This article was submitted to
Crop and Product Physiology,
a section of the journal
Frontiers in Plant Science

Received: 18 February 2022

Accepted: 17 May 2022

Published: 28 June 2022

Citation:

Chaudhary S, Devi P,
HanumanthaRao B, Jha UC,
Sharma KD, Prasad PVV, Kumar S,
Siddique KHM and Nayyar H (2022)
Physiological and Molecular
Approaches for Developing
Thermotolerance in Vegetable Crops:
A Growth, Yield and Sustenance
Perspective.
Front. Plant Sci. 13:878498.
doi: 10.3389/fpls.2022.878498

Vegetables are a distinct collection of plant-based foods that vary in nutritional diversity and form an important part of the healthy diet of the human being. Besides providing basic nutrition, they have great potential for boosting human health. The balanced consumption of vegetables is highly recommended for supplementing the human body with better nutrition density, dietary fiber, minerals, vitamins, and bioactive compounds. However, the production and quality of fresh vegetables are influenced directly or indirectly by exposure to high temperatures or heat stress (HS). A decline in quality traits and harvestable yield are the most common effects of HS among vegetable crops. Heat-induced morphological damage, such as poor vegetative growth, leaf tip burning, and rib discoloration in leafy vegetables and sunburn, decreased fruit size, fruit/pod abortion, and unfilled fruit/pods in beans, are common, often rendering vegetable cultivation unprofitable. Further studies to trace down the possible physiological and biochemical effects associated with crop failure reveal that the key factors include membrane damage, photosynthetic inhibition, oxidative stress, and damage to reproductive tissues, which may be the key factors governing heat-induced crop failure. The reproductive stage of plants has extensively been studied for HS-induced abnormalities. Plant reproduction is more sensitive to HS than the vegetative stages, and affects various reproductive processes like pollen germination, pollen load, pollen tube growth, stigma receptivity, ovule fertility and, seed filling, resulting in poorer yields. Hence, sound and robust adaptation and mitigation strategies are needed to overcome the adverse impacts of HS at the morphological, physiological, and biochemical levels to ensure the productivity and quality of vegetable crops. Physiological traits such as the stay-green trait, canopy temperature depression, cell membrane thermostability, chlorophyll fluorescence, relative water content, increased reproductive fertility, fruit numbers, and

fruit size are important for developing better yielding heat-tolerant varieties/cultivars. Moreover, various molecular approaches such as omics, molecular breeding, and transgenics, have been proved to be useful in enhancing/incorporating tolerance and can be potential tools for developing heat-tolerant varieties/cultivars. Further, these approaches will provide insights into the physiological and molecular mechanisms that govern thermotolerance and pave the way for engineering “designer” vegetable crops for better health and nutritional security. Besides these approaches, agronomic methods are also important for adaptation, escape and mitigation of HS protect and improve yields.

Keywords: high temperature, vegetables, heat, environment, climate change

INTRODUCTION

Vegetables are parts of plants cultivated worldwide for consumption as flowers (e.g., cauliflower, broccoli), fruits (e.g., okra, tomato, cucumber, capsicum), leaves (e.g., spinach, lettuce, brassica, cabbage), tubers (e.g., potato, sweet potato), pods and seeds (e.g., common bean, chickpea, broad bean, mungbean, peas) (Peet and Wolfe, 2000). Vegetables contain secondary metabolites with bioactive properties, including carotenoids (e.g., carrots, pepper, tomato, spinach), polyphenols (e.g., tomato, cabbage), glucosinolates (e.g., brassica), saponins (e.g., beans, pea), and terpenes (e.g., carrots, tomato) (Crozier et al., 2006). These bioactive compounds are metabolic intermediates of primary metabolic processes, which are not essential for plant growth but are used in plant defense responses and plant-insect interactions and can stimulate human health. Clearly, vegetables are an important part of the human diet as they replenish our body with various nutrients, including vitamins, dietary minerals, fibers, proteins, antioxidants, carbohydrates, small amounts of fat, and phytochemicals with anticarcinogenic, antiviral, antifungal, and antibacterial properties (Osagie and Eka, 1998; Teng et al., 2021). While not a major energy source, vegetables nourish our bodies with much-needed minerals and vitamins. According to Food and Agriculture Organization (FAO) statistics, vegetables are the source of dietary requirements about 60% of vitamin A and 90% of vitamin C (Gruda, 2005). Vegetables can earn extra income for farmers as they are seasonal plants with higher yields per hectare than staple crops (Abewoy, 2018). The market value of vegetables is assessed by their quality; FAO and WHO provide many quality attributes for grading vegetables, e.g., color, size, shape, texture, aroma, shelf life, and storability (Gruda, 2005). Vegetables are categorized into two groups according to their growing season; warm-season vegetables include capsicum, common bean, cucumber, cowpea, okra, tomato, and mungbean (Peet and Wolfe, 2000), while cool-season vegetables include brassica, broad bean, broccoli, cabbage, cauliflower, lettuce, radish, spinach, soybean, pea, and potato (Peet and Wolfe, 2000) (Table 1).

Like other crops, vegetables are also affected by environmental changes that can render vegetable cultivation unprofitable. Abiotic stresses, mainly the high temperature (heat stress, HS), severely limit crop quantity, quality, nutritional status, and production (Boote et al., 2005; Aleem et al., 2021). High temperatures affect the overall growth and development

of vegetable crops by altering morphology, physiology, and enzymatic activities. Heat stress (HS) accelerates phenology, shortening the vegetative and reproductive stages. HS reduces vegetable quality, such as changing the color and texture of fruits (e.g., cucumber, pepper, and tomato) (Zipelevish et al., 2000). In general, HS affects morphological, physiological, and biochemical processes of the plant by hampering photosynthetic activity, source-sink relationship, and altered enzymatic activities (Bita and Gerats, 2013; Janni et al., 2020). The quality of vegetables is also impacted by HS, through a change in color and texture of fruit (e.g., cucumber, pepper, and tomato) (Zipelevish et al., 2000). HS also affects the nutritional status of vegetables; for instance, reducing lycopene in tomato (Gross, 1991) and β -carotene in spinach and lettuce (Oyama et al., 1999) and increasing nitrate levels to harmful levels for human consumption.

Due to climate change, in most regions of the world, rising temperatures will decrease quantity and quality of vegetables crops. Studies of Waithaka et al. (2013) suggested that changes in the climate (increased temperatures) will also provide avenues to grow crops in areas where they could not be grown previously. Climate change scenarios further suggest that development of crop and cultivar choice—especially for water-limited or high-temperature areas—will be an important strategy to have adequate yields under changing climate (Thomas et al., 2007). Hence, targeted studies are needed to assess the impact of high-temperature stress on the growth, yield, and quality (taste, flavor, color, nutritional content) of vegetable crops, with suitable agronomic strategies, developed to create heat-tolerant cultivars or mitigate HS.

HEAT STRESS AND VEGETABLES

High temperatures adversely impact plant growth and development (Hasanuzzaman et al., 2013). The constantly rising average surface temperature due to global warming is stressful for all plant growth and development phases, limiting metabolism and productivity, particularly in tropical and subtropical countries (Li et al., 2018). According to the newly released sixth assessment report of IPCC (2021), temperature during the twenty-first century is likely to increase by 1.5°C of warming within just the next two decades, and by 4.5°C, depending on the rate of greenhouse gas emissions. As plants are sedentary

TABLE 1 | Threshold temperature for some vegetable crops at different stages of plant development.

Crop	Family	Threshold temperature (°C)	Response	References
Cool season vegetables				
Vegetative stage				
Broccoli (<i>Brassica oleracea</i> var. <i>italica</i>)	Brassicaceae	30°C	Reduced growth and development	Hatfield and Prueger, 2015
Cabbage (<i>Brassica oleracea</i> var. <i>capitata</i>)	Brassicaceae	30°C	Reduced growth and development	Warland et al., 2006
Cauliflower (<i>Brassica oleracea</i> var. <i>botrytis</i>)	Brassicaceae	25°C	Reduced leaf growth	Lin et al., 2015
Reproductive stage				
Brassica (<i>Brassica napus</i>)	Brassicaceae	29°C	Reduction in flower number	Morrison and Stewart, 2002
Broad bean (<i>Vicia faba</i>)	Fabaceae	30/22°C	Accelerate Floral development	Bishop et al., 2016
Broccoli (<i>Brassica oleracea</i> var. <i>italica</i>)	Brassicaceae	35°C	Arrest of inflorescence development	Björkman and Pearson, 1998
Seed filling/maturity stage				
Chickpea (<i>Cicer arietinum</i> L.)	Fabaceae	30°C	Reduced yield	Summerfield and Wien, 1980
Lettuce (<i>Lactuca sativa</i>)	Asteraceae	24°C	Reduced yield	Jenni, 2005
Pea (<i>Pisum sativum</i>)	Fabaceae	25.6°C	Reduced yield	Pumphrey and Ramig, 1990
Potato (<i>Solanum tuberosum</i>)	Solanaceae	30/20°C	Reduced yield	Hancock et al., 2014
Warm season vegetables				
Vegetative stage				
Cucumber (<i>Cucumis sativus</i>)	Cucurbitaceae	38°C	Impede growth and development	Yu et al., 2022
Okra (<i>Abelmoschus esculentus</i>)	Malvaceae	35°C	Decreased leaf size	Hayamanesh, 2018
Reproductive stage				
Capsicum (<i>Capsicum annuum</i> L.)	Solanaceae	33°C	Inhibition of fertilization or early fruit development	Erickson and Markhart, 2002
Common bean (<i>Phaseolus vulgaris</i>)	Fabaceae	34/24°C	Reduced pollen viability	Boote et al., 2005
Soybean (<i>Glycine max</i>)	Fabaceae	26/20°C	Delay flowering and distort pod development	Nahar et al., 2016
Tomato (<i>Lycopersicon esculentum</i>)	Solanaceae	32/26°C	Abnormalities in male and female reproductive tissues	Peet et al., 1998
Seed filling/maturity stage				
Cowpea (<i>Vigna unguiculata</i>)	Fabaceae	36/27°C	Reduced yield	Craufurd et al., 1998
Okra (<i>Abelmoschus esculentus</i>)	Malvaceae	35°C	Reduced yield	Hayamanesh, 2018

organisms, they acclimate to HS by using avoidance mechanisms or programmed cell death (Mittler et al., 2012; Singh, 2013; Zhang T. et al., 2020). Each vegetable crop has temperature threshold for its growth and development; HS will occur beyond the upper threshold for temperature (Wahid et al., 2007; Prasad et al., 2008, 2017). HS impedes photosynthesis through reduced carbon assimilation, ATP reduction, and oxidative damage to chloroplasts, with simultaneous reductions in dry matter accumulation and yield (Sharkey, 2005; Farooq et al., 2011). HS

adversely affects vegetative and reproductive plant parts (Bita and Gerats, 2013); thus, the impact of HS varies depending on the developmental stage and crop species (Prasad et al., 2017; Li et al., 2018) (Table 2).

IMPACT ON VEGETATIVE GROWTH

Moderate high temperatures stimulate early vegetative growth and accelerate physiological maturity (Nahar et al., 2015).

TABLE 2 | Noticeable symptoms of heat stress in some vegetable crops.

Crop species	Symptoms	References
Cabbage (<i>Brassica oleracea</i> var. <i>capitata</i>)	Loosening or bolting of heads, smaller and tighter heads, rough leaf texture	Chang et al., 2016
Capsicum (<i>Capsicum annuum</i>)	Sun scald, yellowing and wilting	Moretti et al., 2010
Cauliflower (<i>Brassica oleracea</i> var. <i>botrytis</i>)	Leafy and uneven heads, puffy buds, yellow eyes and leaves, narrow leaves and hollow stems	Lin et al., 2015
Common bean (<i>Phaseolus vulgaris</i>)	High fiber in pods, brown and reddish spots in pods	Moretti et al., 2010
Lettuce (<i>Lactuca sativa</i>)	Tip burn, bolting, loose puffy heads, decreases β -carotene content	Han et al., 2013
Potato (<i>Solanum tuberosum</i>)	Secondary growth and heat sprouting	Hancock et al., 2014
Spinach (<i>Spinacia oleracea</i>)	Reduced leaf area and shoots dry weight, reduces β -carotene content	Chitwood et al., 2016
Tomato (<i>Lycopersicon esculentum</i>)	Fruit cracking, sunscald, hampered lycopene synthesis, blossom end rot, internal white tissue, blotchy ripening,	Moretti et al., 2010

During seed germination, HS reduces germination percentage and seedling emergence, reduces radical and plumule growth in germinated seedlings, and causes abnormal seedlings and poor seedling vigor (Hasanuzzaman et al., 2013). At later stages of vegetative growth, HS reduces plant height, leaf area, and leaf, stem, pod, root, and total biomass (Kumar et al., 2013). Leafy vegetables require proper growth and development of vegetative parts for realizing only the yield but also the quality. In 45-day-old cabbage plants exposed to 40°C for 6, 12, 24, 48, or 72 h, HS caused loosening or bolting of heads, smaller and tighter heads, and rougher leaf texture (Chang et al., 2016). Likewise, in 30-day-old cauliflower plants exposed to 40°C for 6, 12, 24, 48, 72, or 96 h, HS caused uneven heads, puffy buds, yellow eyes, narrow leaves, reduced leaf growth, and reduced petiole-to-blade ratio (Lin et al., 2015). HS (34.5°C) further delayed the curd induction stage and decreased the chlorophyll content in cauliflower plants; effects were more distinct in heat susceptible genotypes where they were unable to develop curd at high temperature and continued their vegetative growth until temperature fall below 30°C (Aleem et al., 2021). Exposing 4- to 5-leaved lettuce seedlings to 42/37°C for 3 days reduced seedling germination and caused tip burn, rib discoloration, and bolting (Jenni and Yan, 2009; Han et al., 2013). In spinach exposed to 35°C for 21 days, HS decreased seed germination (Chitwood et al., 2016). In potato, high temperature (30–40°C) inhibited tuber development and blocked the tuberization signal (Reynolds and Ewing, 1989). Potato plants exposed to 30/20°C (day/night) for 1 week had reduced yields by 16% compared to plants grown at 22/16°C due to decreased carbon transport to the sink organ (Hancock et al., 2014). Further, reduced yield has been reported in 50 potato cultivars when exposed to heat stressed

conditions (35/28°C) than control conditions (22/18°C) (Zhang G. et al., 2020). Likewise, in 6–7-leaved radish seedlings exposed to 40°C for 12 and 24 h, HS affected fleshy taproot growth and development, reducing quality and yield (Zhang et al., 2013) (Figure 1).

IMPACT ON REPRODUCTIVE GROWTH

Reproductive stage is highly sensitive to HS; even a single degree increase for a few hours can be fatal for proper reproductive growth, contributing to poor yields (Prasad et al., 2017). However, studies on reproductive tissues are difficult to assess because gamete development and fertilization are major events that occur over short periods. Here, we categorize the effects of HS in vegetables during three stages of reproduction: pre-fertilization (flower bud initiation, flowering, male and female gametophyte development), fertilization (pollen dehiscence, pollination, pollen reception by stigma, pollen tube growth and fertilization), and post-fertilization events (fruit/pod set, seed development, seed filling) (Figure 2; Table 3).

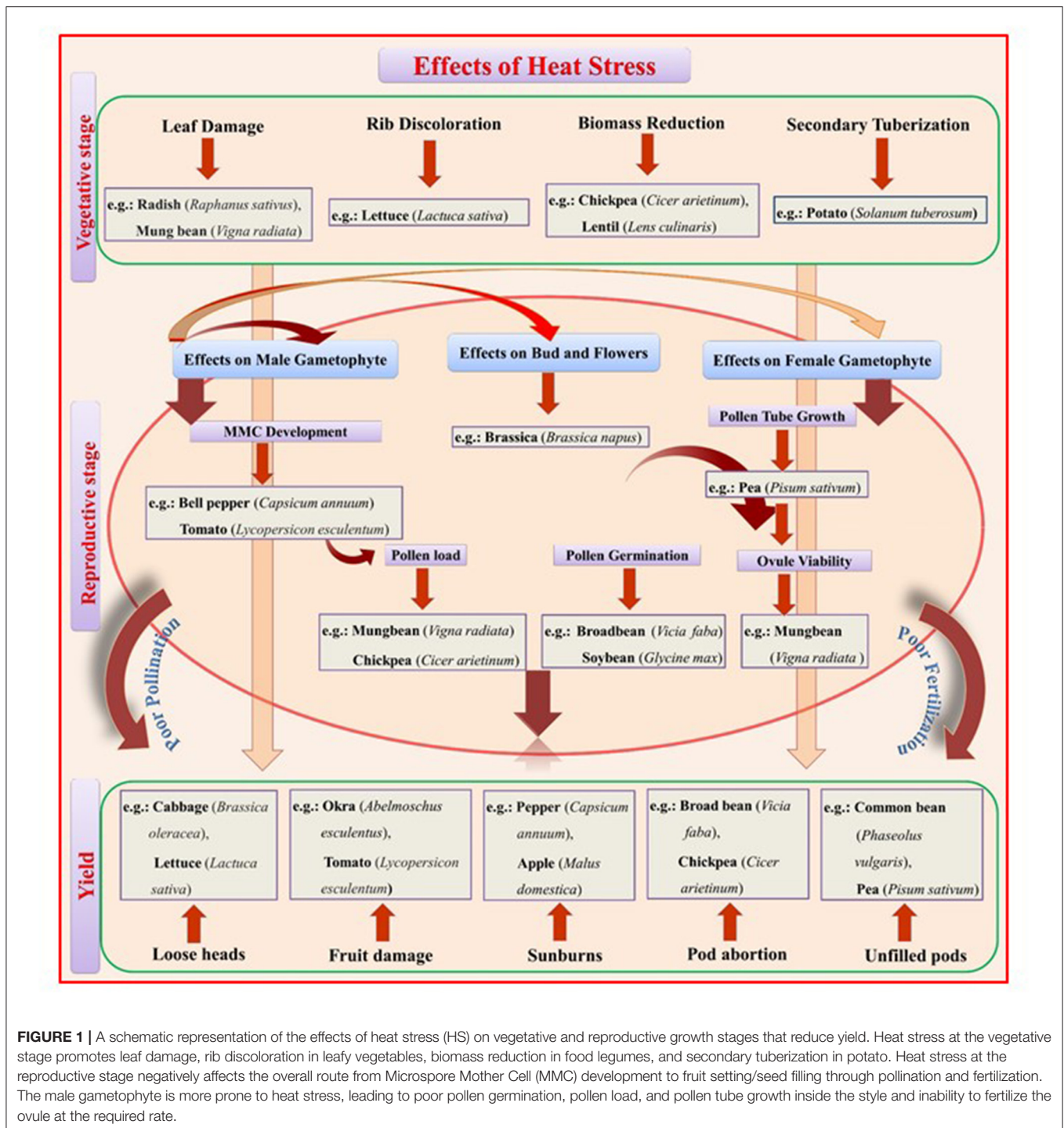
Pre-fertilization Events

Flower Bud Initiation

High-temperature stress causes flower bud abortion and abscission of reproductive organs in many crop species, including tomato (Levy et al., 1978; Pressman et al., 2002; Sato et al., 2002), common bean (Konsens et al., 1991), pea (Guilioni et al., 1997), brassica (Angadi et al., 2000), capsicum (Aloni et al., 2001; Erickson and Markhart, 2002), resulting in severe yield losses. Common bean grown at 32/27°C (from flowering to pod maturity) experienced greater abscission and drop of flower primordia (2–5 mm) and flower buds (>5 mm) than at 27/17°C (Konsens et al., 1991). In capsicum, high-temperature stress (33°C for 120 h) affected flower buds (<2.5 mm) and early pistil development less than stamen development, whereas buds (3–4 mm) during tetrad formation and dissolution were highly sensitive to elevated temperature, leading to pollen sterility (Erickson and Markhart, 2002). Flower and flower bud abscission also occurred in heat-stressed (35/15°C for 7 days at early stage) brassica species (Angadi et al., 2000). HS (32/28°C) severely affected flower initiation and development in tomato (Levy et al., 1978; Sato et al., 2002). HS (32/26°C for 8 days before anthesis) in capsicum reduced and altered sucrose mobilization and utilization by flower buds and flowers, resulting in fruit drop and abscission and thus reducing yield by 17% compared to normal sown (28/22°C) (Aloni et al., 2001).

Flowering

HS during flowering reduces flower numbers by damaging flower organs, reducing yield (Morrison and Stewart, 2002). HS also decreases the number of flowering branches and thus flower numbers per plant (Harsant et al., 2013). Damage to flower organs has been reported in many crops, including chickpea (Tickoo et al., 1996), common bean (Suzuki et al., 2001; Omae et al., 2012), and mungbean (Kaur et al., 2015). Early flowering and flower abortion are other impacts of HS, as reported in pea



(Guilioni et al., 1997), tomato (Sato et al., 2004), common bean (Omae et al., 2012), and mungbean (Sharma et al., 2016).

Male Gametophyte Development and Function

Threshold temperatures needed to impose damages in reproductive tissues are less than the one needed to cause injury to vegetative tissues. Male gametophytes are more sensitive to HS than female gametophytes, with lower threshold temperatures than vegetative tissues. HS damage can occur

pre-pollination or post-pollination, impairing fertilization and ultimately reducing seed set (Sage et al., 2015). Pre-pollination events that are highly susceptible to high temperature are (1) meiosis I and meiosis II of the microspore mother cell (Young et al., 2004), (2) development and subsequent dissolution of the tapetum layer (Farooq et al., 2017), and (3) exine and intine formation (Nahar et al., 2016). Post-pollination events affected by HS are (1) pollen load, (2) pollen germination, (3) pollen tube growth, and (4) fertilization (Hedhly et al., 2009; Sita et al., 2017).

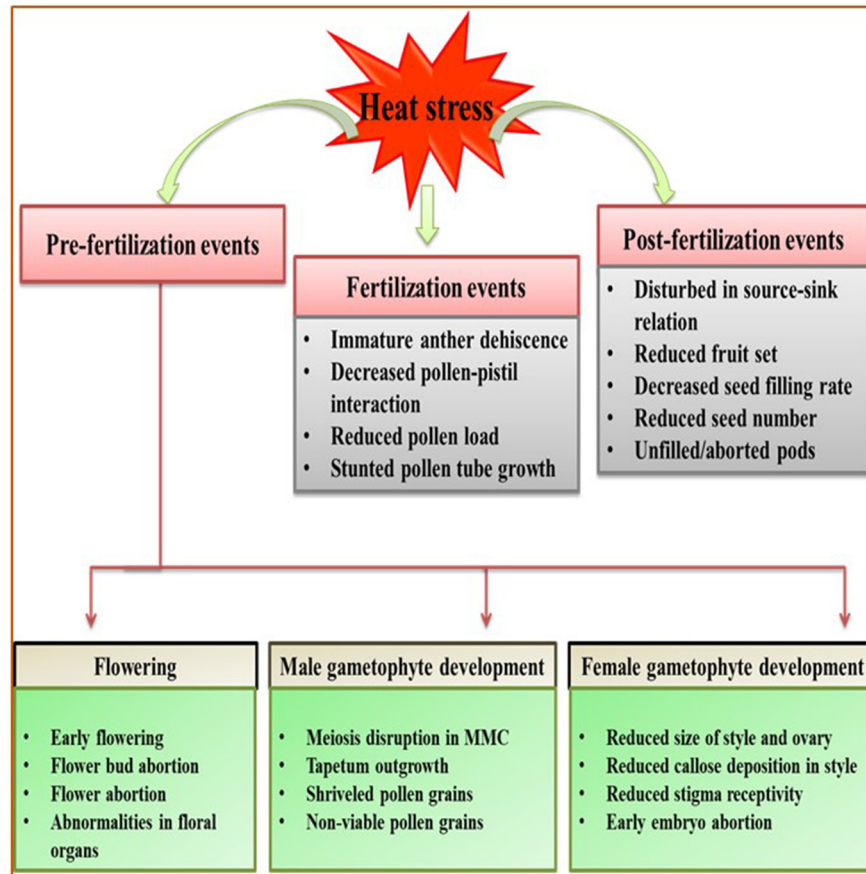


FIGURE 2 | Generalized overview of the effects of heat stress (HS) on the reproductive stage of plants, broadly categorized into three events: pre-fertilization, fertilization, and post-fertilization. Heat stress affects the flowering stage by promoting early flowering and flower bud/flower abortion. During male gametophyte development, heat stress disrupts meiosis and decreases tapetum growth, resulting in shriveled and non-viable pollen grains. During female gametophyte development, heat stress reduces style and ovary size and callose deposition, reduces stigma receptivity, and causes early embryo abortion. Moreover, immature dehiscence and malformed pollen grains result in poor pollination and fertilization. Heat stress during post-fertilization decreases the seed filling rate and disturb source-sink relations, potentially reducing yield manifold.

The sensitivity of male gametophytes to HS varies according to plant species (Li et al., 2018).

HS reduced fertility of microgametophytes in brassica (Rao et al., 1992) and impaired meiosis in tomato, damaging pollen germination and pollen tube growth (Foolad, 2005). In soybean, HS reduced pollen production, germination, tube elongation, and impaired pollen development (no apertures and disturbed exine ornamentation) (Salem et al., 2007; Nahar et al., 2016; Djanaguiraman et al., 2019). In capsicum, HS produced shrunken and empty microspores without an exine layer (Erickson and Markhart, 2002). Shriveled pollen grains under HS may be due to decreased starch accumulation in anther walls and pollen grains reducing soluble sugars for their development (Pressman et al., 2002).

Female Gametophyte Development and Function

Female gametophytes are relatively more tolerant to HS than male gametophytes (Hedhly, 2011). HS impairs megaspore

mother cell development by impeding meiosis, reducing pistil size, reducing stigma receptivity due to poor pollen adhesion, reducing stigmatic papillae for holding pollen grains, interrupting nutrient transport from style to pollen impeding pollen tube germination and growth, as noticed in chickpea (Kaushal et al., 2016), bean (Porch and Jahn, 2001) and cowpea (Ahmed et al., 1992). HS, reduced callose deposition in lentil styles (Bhandari et al., 2017), reduced the amount of attractants from ovule synergids cells that misguide the pollen tube (Saini et al., 1983) to severely affect the fertilization. Furthermore, HS damages the embryo sac and causes early embryo abortion, likely arresting fertilization; for instance, in tomato, HS exposure (40°C for 3 h) for 4 days before anthesis resulted in aborted embryos with degenerated eggs and synergids (Iwahori, 1965). Abnormalities in embryo sac development have also been observed in brassica, reducing seed set and yield (Polowick and Sawhney, 1988). HS also reduced ovule viability in common beans (Ormrod et al., 1967; Suzuki et al., 2001). Unlike, male

TABLE 3 | Effect of heat stress on reproductive tissues of some vegetable crops.

Crop	Heat stress	Effect	References
Brassica (<i>Brassica napus</i>)	35/23°C	Reduced <i>in-vitro</i> pollen germinability, pollen viability, and thinner pollen tubes with stunted & convoluted morphology.	Young et al., 2004
		Microspore and pollen development are sensitive to heat stress.	Sato et al., 2002
Bell pepper (<i>Capsicum annuum</i>)	33°C	Pollen development (during megaspore mother cell (MMC) meiosis) is greatly reduced. Reduced pollen viability, reduced anther dehiscence, reduced mature pollen grains, slightly swollen and deformed (affect pollen morphology) and without exine layer.	Erickson and Markhart, 2002
Broad bean (<i>Vicia faba</i>)	34/26°C	Pollen germination	Bishop et al., 2016
Broccoli (<i>Brassica oleracea</i> var. <i>italica</i>)	35°C	Arrested the development of flower buds	Björkman and Pearson, 1998
Chickpea (<i>Cicer arietinum</i> L.)	40/25°C	Pollen germination, pollen tube growth Pod set	Devasirvatham et al., 2013
Common bean (<i>Phaseolus vulgaris</i>)	33/27°C 33/29°C	Anther indehiscence and pollen sterility Degeneration of tapetal cells.	Gross and Kigel, 1994
Cowpea (<i>Vigna unguiculata</i>)	33/30°C	Another development	Ahmed et al., 1992
Mungbean (<i>Vigna radiata</i> L.)	>40/28°C	Reduced pollen viability, pollen germination, pollen load, stigma receptivity and ovule viability	Sharma et al., 2016
Okra (<i>Abelmoschus esculentus</i>)	45°C	Incomplete dehiscence, shrunken pollen, smaller anther sacs, reduced pollen number, pollen viability, and pollen germination.	Hayamanesh, 2018
Pea (<i>Pisum sativum</i>)	36/24°C	Decreased pollen germination, pollen tube growth, pod length, and seed number per pod.	Jiang et al., 2015
Soybean (<i>Glycine max</i>)	38/28°C	Decreased <i>in-vitro</i> pollen germination.	Djanaguiraman et al., 2013b
Tomato (<i>Lycopersicon esculentum</i>)	32/26°C	Reduced number of pollen grains, pollen viability, and pollen germination.	Sato et al., 2002
	31/25°C	Reduced number of pollen grains, pollen viability, and pollen germination.	Firon et al., 2006
	29°C	Decreased fruit number, fruit weight/plant and seed number/fruit	Peet et al., 1998

gametophyte, detailed impacts of HS on female gametophyte organs are, however, barely known. This may be because of the reason that female gametophyte is protected inside the ovary and sheltered and difficult to reach and dissect.

Fertilization

High-temperature stress (>30°C) negatively impacts male and female gametophyte development, leading to poor development and deformities of reproductive tissues, limiting the fertilization process in many plant species (Saini and Aspinall, 1982; Prasad et al., 2017). HS also reported to affect the flower pollination rate in tomato resulting in low fruit set with reduced lycopene content and fruit quality (Alsamir et al., 2021). Indehiscent anthers, non-viable pollen, and poor stigma receptivity are possible causes for fertilization failure and sterility imposition in many crops, including chickpea (Kumar et al., 2013), soybean (Board and Kahlon, 2011), mung bean (Kaur et al., 2015), tomato (Pressman et al., 2002), common bean (Porch and Jahn, 2001), and capsicum (Erickson and Markhart, 2002).

Post-fertilization Events

Fruit/Pod Set

High-temperature stress affects the proportion of flowers forming fruits (fruit set) (Prasad et al., 2000). HS (38/30°C)

markedly decreased fruit weight (51.6%), fruit diameter (25%), fruit length (30%), and seed number per fruit (57%) in sweet pepper compared with normal temperature (33/21°C) (Thuy and Kenji, 2015). Peet et al. (1998) reported that high temperature (29°C) decreased fruit number (10%), total fruit weight/plant (6.4%) and seed number/fruit (16.4%) in male fertile tomatoes compared to optimum temperature (25°C). The high temperature impaired pollen development and release, leading to reduced fruit set in male-fertile tomatoes compared with male-sterile lines. Similarly, fruit set and fruit size in tomato plants declined at 29/23°C compared to 24/18°C (Saha et al., 2010). HS seriously damaged fruit set in tomatoes exposed to 40°C for 4 h before anthesis and reduced the pollen germination from 79.5% (at 30/17°C) to 30% and pod set from 63% (at 30/17°C) to 14.9% (Rudich et al., 1977). In Common bean, high temperature (32/27°C) reduced the pod set from 17 to 97%, seed set by 39–98%, and seeds/pod by 42 to 73% compared to control temperature (22/17°C) (Gross and Kigel, 1994). Similar finding on bean plants exposed to even higher temperatures (40/30°C) had fewer filled pods, parthenocarpic pod development, sickle-shaped pods, reduced seed size, and fewer seeds/pod and total seeds than control condition (Prasad et al., 2002; Soltani et al., 2019). In peas, high temperature (32°C for 6 h) at the reproductive stage increased the abortion rate of reproductive

organs (flower buds and young pods) from 20 to 50% which reduce seed yield (Bueckert et al., 2015).

Seed Development and Seed Filling

Seed formation and seed filling are the last phases of the life cycle of seed plants; and, HS drastically affects seed development and the seed-filling phase, increasing the fraction of abnormal and shriveled seeds (Sehgal et al., 2018). In common bean, a linear relationship between temperature and grain weight was recorded resulting in a significant decrease in seed weight, i.e., 0.07 g per °C when temperature was raised beyond 31/21°C (Prasad et al., 2002). Seed development starts from cell division and, when seed cells are fully formed, storage reserves start to accumulate (Egli, 1998). Direct effects of HS on division and size of endosperm cells are well-documented (Commuri and Jones, 2001). Reduced division and size of endosperm cells results in accumulation of fewer carbohydrates, proteins, lipids, and starch accumulate in developing seeds. HS also accelerates the rate and duration of seed filling, resulting in abnormal seeds and significant yield losses (Farooq et al., 2017). Not only yields, HS affects seed quality characteristics, reducing seed number and size, degrading nutrient composition, and decreasing seed viability, through impaired nutrient uptake, assimilate partitioning, and translocation (Prasad et al., 2008). Starch, proteins, and lipids are the principal reserves transferred from the main plant to developing seeds (Alencar et al., 2012), but HS limits their synthesis and translocation during seed filling, affecting grain quality (Farooq et al., 2017), and could be due to decreased enzyme activity. The activity of starch synthesizing enzymes, such as starch synthase, sucrose synthase, and invertase, decrease under HS, as reported in pea (Smith and Denyer, 1992) and chickpea (Kaushal et al., 2013). Similarly, HS disrupts seed storage proteins, such as β -glycocynin and globulin 11S in soybean (Hashizume and Watanabe, 1979; Iwabuchi and Yamauchi, 1984), and sucrose-synthesizing enzymes and proteins that aid in sucrose translocation. Reduced sucrose synthase activity affects the sucrose and starch ratio, decreasing the transfer of soluble carbohydrates to developing ovules, as reported in pea (Jeuffroy et al., 1990) and cowpea (Ismail and Hall, 1999). Reduced crop duration and seed filling has been correlated with an inefficient light capture ability (canopy growth rate) in small plants, decreasing the photosynthetic rate and thus seed size, as reported in soybean (Board and Kahlon, 2011). Prasad et al. (2002) reported a linear relationship between temperature and grain weight in common bean, with seed weight decreasing by 0.07 g per °C at temperatures above 31/2.

PHYSIOLOGICAL ASPECTS AND CELLULAR FUNCTIONS UNDER HEAT STRESS

Membranes

HS disrupts the organization of the plasma membrane by increasing unsaturated fatty acids, thus making the membrane more fluid (Hofmann, 2009), and influencing the cellular functions by initiating a signal cascade (Firmansyah and Argosubekti, 2020; Hassan et al., 2021). HS also accelerates the

kinetic energy and movement of various molecules through the membrane. Further, protein denaturation and altered tertiary and quaternary structure of membrane proteins increase membrane fluidity (Savchenko et al., 2002). Thus, HS disturbs primary processes of plant-like photosynthesis and respiration due to increased permeability or solute leakage from cells (**Figure 3**). Therefore, cell membrane thermostability trait used to evaluate HS on plants and identify heat-tolerant and heat-sensitive genotypes; for example, in soybean (Martineau et al., 1979), potato (Chen et al., 1982), and cowpea (Ismail and Hall, 1999). The effectiveness of cell membrane thermostability assays depends on the tissue type and stress type used for plant adaptation. It is also unknown whether membrane thermostability is linked to other plant characteristics that confer heat tolerance, such as growth and yield.

Photosynthesis

Photosynthesis is highly sensitive to HS and photosynthetic activity reduces drastically under HS. Studies have detailed the affected photosynthetic mechanisms that ultimately reduce the photosynthetic capacity of plants (Berry and Bjorkman, 1980; Sharkey, 2005). Thylakoid reactions, Rubisco activity, and photosynthetic pigments are generally disturbed by HS. HS primarily affects the physical state and structure of the thylakoid membrane by triggering thylakoid leakiness and unstacking thylakoids, damaging the D1 protein of PSII (Sharkey, 2005). To counterbalance these reactions, zeaxanthin synthesis increases, affecting the normal state of thylakoids (Havaux, 1996). HS disturbs the electron flow between the two photosystems (PSI and PSII) and reduces the photosynthetic efficiency of plants. HS also accelerates the phosphorylation of light-harvesting complex (LHCII) and disconnects it from PSII core complex, thus decreasing its turnover rate, but increasing the turnover rate of PSI (Wise et al., 2004). HS dephosphorylates core proteins (D1, D2, and CP43), deactivating PSII (Yamamoto et al., 2016). HS alters the fluorescence induction parameters, measured as the Fv/Fm ratio; this ratio helps to determine the quantum efficiency of PSII and indicates the rate of linear electron flow and overall photosynthetic performance of plants (Jamil et al., 2007). HS decreased chlorophyll a fluorescence, PII quantum yield, photochemical quenching, and increased respiration rate in soybean (Djanaguiraman et al., 2013a).

Along with thylakoid reactions, HS triggers the deactivation of Rubisco (Crafts-Brandner and Salvucci, 2000). Rubisco being dual enzyme catalyses the carboxylation of ribulose-1,5-bisphosphate in the photosynthetic Calvin cycle and oxygenation in the photorespiratory pathway; the ratio between two reactions governs the photosynthetic efficiency of plant. But the elevated temperature inhibits the CO₂ fixation and increases the oxygenase activity and reduces photosynthetic rate (Crafts-Brandner and Salvucci, 2000). Rubisco activation is not only associated with pH and Mg²⁺ concentration of stroma but also with Rubisco activase (RA); an ATPase. RA induces the activation of the Rubisco by increasing the proportion of its active sites and brings conformational changes that allow CO₂ and Mg²⁺ for activation and carbamylation. High temperature can disturb the pH and Mg²⁺ concentration of

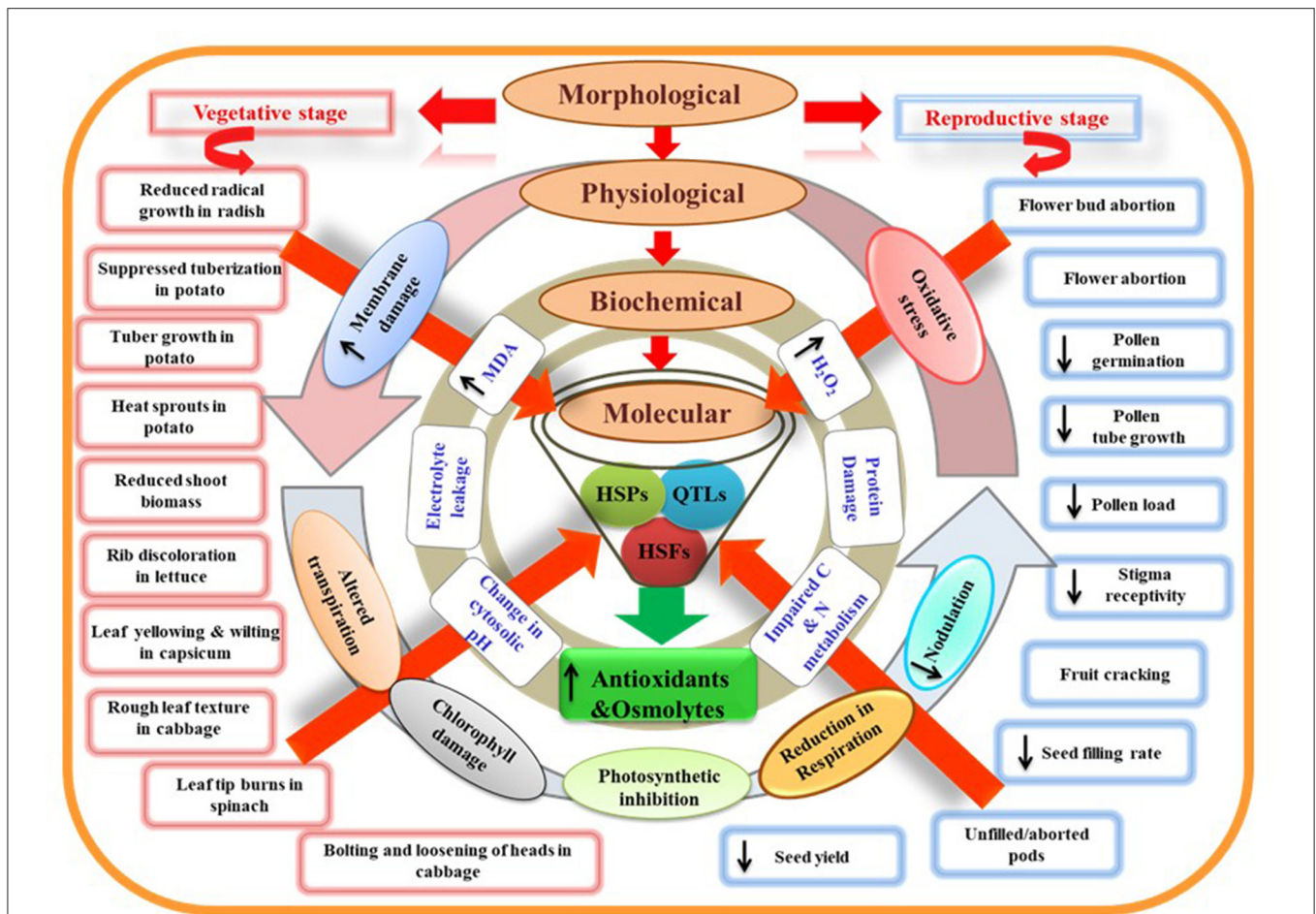


FIGURE 3 | Model representing morphological, physiological, biochemical, and molecular characteristics of plants under heat stress. Morphological damages at vegetative and reproductive stages can be visualized as direct measures of plant stress. At the physiological level, these damages are associated with leaky plasma membrane, altered transpiration, chlorophyll damage, reduced photosynthesis, respiration, and nodulation rate. Disturbed physiological processes can promote oxidative stress damage observed through stress indicators like increased *malondialdehyde* (MDA) and hydrogen peroxide (H_2O_2) content. Protein damage and impaired carbon and nitrogen metabolism due to impaired enzymatic activities further exaggerate stress levels at the biochemical level. Heat shock proteins (HSPs), heat shock factors (HSFs), and quantitative trait loci (QTLs) related to heat stress responses of plants may play a key role in the plant adaptation. HSPs and HSFs have a central role in regulating the activity of various genes that amplify the production of antioxidants and osmolytes and are helpful governing thermotolerance.

stroma, interfering with the carbamylation step of Rubisco activation (Weis, 1981a,b) and also caused RA dissociation because of its poor structural stability and heat labile nature (Demirevska-Kepova and Feller, 2004). Few reports have noticed that heat stress affects the photosynthesis through heat sensitivity of Rubisco and RA activity, for instance in tomato, heat stress ($40^{\circ}C$ for 8 h for 6 days to 3 weeks old plant) decreased the accumulation of Rubisco enzyme's isoforms (Parrotta et al., 2020), as in pea (Haldimann and Feller, 2005), potato (Cen and Sage, 2005) and spinach (Zhao Q. et al., 2018).

Pea plants exposed to HS reduced chlorophyll biosynthesis due to the destruction of various enzymes involved in biosynthetic pathways (Dutta et al., 2009; Aleem et al., 2021). HS decreased the activity of first enzyme of the biosynthetic pathway, 5-aminolevulinic acid dehydratase, in

cucumber (Tewari and Tripathy, 1998). Decreased chlorophyll content, Chl a/b ratio, and chlorophyll/carotenoid ratio have been reported in many crops under HS (Aien et al., 2011) (Table 4). Similarly, HS stress causes pre-mature leaf senescence in soybean leaves which results in decreased photosynthesis primarily due to decreased chlorophyll content, higher reactive oxygen species, lower antioxidants, and increased thylakoid membrane damage (Djanaguiraman and Prasad, 2010). HS increased ethylene production in leaves which was one of the reasons of premature leaf senescence in soybean (Djanaguiraman and Prasad, 2010). Detailed anatomical studies showed that HT stress significantly increased the thicknesses of the palisade and spongy layers and the lower epidermis (Djanaguiraman et al., 2013a). In addition, HT stress damaged the plasma membrane, chloroplast membrane, thylakoid membranes; mitochondrial membranes, cristae, and matrix were distorted which led

TABLE 4 | Effect of heat stress on photosynthesis in some vegetable crops.

Crop species	Temperature	Effect	References
Broad bean (<i>Vicia faba</i>)	42°C	Decreased content of Chl a, Chl b, and carotenoids	Hamada, 2001
Cabbage (<i>Brassica oleracea</i> var. <i>capitata</i>)	40°C	Decrease in F_v/F_m values and photosynthetic efficiency	Chang et al., 2016
Cauliflower (<i>Brassica oleracea</i> var. <i>botrytis</i>)	40°C	Significant reduction in chlorophyll fluorescence F_v/F_m Inhibition of CO ₂ fixation and damage to photosynthetic electron transport at site of PS II	Lin et al., 2015
Chickpea (<i>Cicer arietinum</i> L.)	40/30°C	Reduced chlorophyll content	Kaloki et al., 2019
Common bean (<i>Phaseolus vulgaris</i>)	45°C	Partially-reversible inactivation of PS-II and dissociation of light harvesting complex from reaction center of PS-II Destruction of PS-II reaction center and formation of quenching species	Costa et al., 2003
Cowpea (<i>Vigna unguiculata</i>)	30/25°C	Reduced rate of photosynthesis	McDonald and Paulsen, 1997
Cucumber (<i>Cucumis sativus</i> L.)	33–48°C	Decline in PS II activity and photochemical quenching Decreased net photosynthetic rate	Ding et al., 2016
Mungbean (<i>Vigna radiata</i>)	42°C >40/28°C	Chlorophyll biosynthesis Decline in PS II activity	Tewari and Tripathy, 1998 Sharma et al., 2016
Okra (<i>Abelmoschus esculentus</i>)	>39°C	Adverse effects on the photosynthetic apparatus	Hayamanesh, 2018
Pea (<i>Pisum sativum</i>)	>40°C	Decreased photosynthetic electron transport Complete suppression of photosynthetic electron transfer	Haldimann and Feller, 2005
Potato (<i>Solanum</i> spp.)	45°C 25°C	Decreased CO ₂ assimilation and O ₂ evolution Decreased photosynthetic rate Decreased Chl a+b and carotenoid content	Georgieva et al., 2000 Aien et al., 2011
Soybean (<i>Glycine max</i>)	38°C 38/30°C	Rapid and irreversible loss of PS II Decrease in leaf photosynthetic rate by 20.2% Significantly affects net photosynthesis and total chlorophyll content	Aien et al., 2011 Nahar et al., 2016
Spinach (<i>Spinacia oleracea</i>)	39/20°C 40°C	Severely damaged PSII site Inhibition of oxygen evolution Cleavage of D1 protein of PSII	Li et al., 2009 Yoshioka et al., 2006
Tomato (<i>Solanum lycopersicum</i>)	36/38°C	Decreased F_v/F_m values and PS II damage Decreased net photosynthetic rate Decreased chlorophyll content	Zhou et al., 2017

to decreased photosynthesis (Djanaguiraman et al., 2013a) (Figure 3).

Nitrogen Content, Fixation and Nodulation

Nitrogen is one of the main nutrients required by the plant for proper growth, development and productivity. It is the constituent of various important organic compounds like amino acids, proteins, nucleic acids, enzymes, and the chlorophyll molecule (Christophe et al., 2011). Nitrogen content in the plant measured as nitrate, ammonium ions, and proteins. Besides performing basic roles in plants, its metabolism is also very crucial for heat tolerance because it increases the osmolyte content and antioxidant enzyme activity (Ru et al., 2022). Studies have also shown their role in promoting the HSP production (Heckathorn et al., 1996). Osmolytes like proline and quaternary ammonium compounds, being nitrogen rich and

accumulate in plants under heat stress conditions (Rivero et al., 2004). Ammonium ion and proline accumulation confer heat tolerance to tomato and promoting higher biomass production (Rivero et al., 2004). During the reproductive period, nitrogen concentration successively increases when temperatures rise for example in pea, when high temperature occurs during or after flowering seed N concentration is increased (Larmure et al., 2005). Similarly, in soybean, seed N concentration increases during the reproductive period at temperature 40/30°C (Thomas et al., 2003). Increases in the accumulation of proteins; level of globulin protein storage causing a reduction of the albumin/globulin content in mature seeds (Hurkman et al., 2009). In pea, the final level of vicilin storage proteins was higher under heat stress (Bourgeois et al., 2009). However, in tomato roots, it has been reported that HS disturbs enzymes involve in nitrogen metabolism (nitrate and ammonium assimilation)

thereby decreasing total protein content and level of nutrient uptake and assimilation (Giri et al., 2017). Further, studies on the contrasting genotypes of brassica revealed that HS (40/30°C for 7 days) negatively affected the activities of nitrogen assimilation enzyme including Glutamate synthase (GOGAT), glutamine synthetase (GS), glutamate dehydrogenase (GDH), more in heat sensitive genotype (WS-6) as compared to heat tolerant genotype (WS-1). These enzymes help in possessing better photosynthetic nitrogen use efficiency (Yuan et al., 2017).

Symbiotic nitrogen fixation in leguminous crops depends on the presence of appropriate *Rhizobium* species in the vicinity of root zone, however, almost all processes starting from rhizobial survival to host infection and nitrogen fixation depend mainly on the environmental factors, such as soil temperature (Bordeleau and Prévost, 1994). High temperature interferes with almost all processes of symbiotic nitrogen fixation, directly as well as indirectly, soil temperature affects not only the rhizobial survival in the root zone but also the exchange of molecular signals between two symbiotic partners (Alexandre and Oliveira, 2013). Rhizobial strains have an optimum soil temperature (25–30°C) for their growth and nitrogen fixing ability and Rhizobia are greatly affected by high soil temperature. However, optimum temperature varies with the crop species, for instance, in soybean, weak rhizobia were formed at 40°C and no rhizobia were isolated at 45°C (Chen et al., 2002). HT interferes directly with nodule development as it hampers nodule development and increases nodule senescence (Aranjuelo et al., 2007). HS affects indirectly the nitrogen fixation by inhibiting the formation of root hairs, infection thread formation, reducing the nodulation sites, adherence between bacteria and root hair (bacterial infection), and bacteroid formation (Zahran, 1999; Hungria and Vargas, 2000; Alexandre and Oliveira, 2013).

Elevated temperature also affects nodule growth rate, nodule size, and nodule fixation ability, as reported for common bean exposed to HS (35 and 38°C/8 h/day) at the flowering stage (Hungria and Franco, 1993). Another study showed that at 47°C temperature no nodules were formed in common bean (Karanja and Wood, 1988). Studies have shown that nodulation ability varies inversely with temperature, and legume species differ in their temperature endurance; for instance, common bean is more sensitive to temperature stress than cowpea and soybean for nitrogen fixation (Piha and Munns, 1987). In cowpea, the optimum temperature for nodule growth and development is 30–36°C; temperatures above 40°C lead to fewer or no nodules (Day et al., 1978). In common bean, nodules that formed at high temperature ($\geq 35^\circ\text{C}$) were inefficient and unable to fix nitrogen (Hungria and Franco, 1993). Piha and Munns (1987) noted that nodules formed at 35°C were small and had low nitrogenase activity. The optimum temperature for nodule growth is 20°C for pea and 25–30°C for soybean (Michiels et al., 1994). HS decreased nodulation ability in mungbean (Sharma et al., 2016). In common bean, HS affected nitrogen fixation due to decreased activity of enzymes involved in nitrogen metabolism, such as dinitrogenase complex, glutamine synthetase (GS), and glutamine synthase (GOGAT), decreasing the concentration of ureids-N in nodules and xylem sap (Hungria and Kaschuk, 2014). Prasad et al. (2000) observed that high soil temperatures (35°C) significantly decreased number of nodules and nodule dry

weight per plant compared to optimum soil temperature (25°C) in peanut.

C:N ratio: Plant growth and defense are both fuelled by compounds synthesized from a common pool of carbon and nitrogen, implying the existence of a competition for carbon and nitrogen allocation to both metabolisms. The ratio of carbon to nitrogen (C: N) of an organ is often regarded as a convenient indicator of growth and quality. Almost a century ago, plant nutrition was considered a crucial factor in controlling flowering time. According to Klebs (1913), a high endogenous carbon: nitrogen ratio promotes flowering, while a low carbon: nitrogen ratio promotes vegetative growth. Inferred from the fact that (a) conditions favoring photosynthetic CO₂ fixation generally accelerate flowering and (b) high nitrogen intake (fertilizers) might delay or reduce reproductive development in some plants (Bernier et al., 1981). The flowering percentage increased when NH₄NO₃ concentration decreased from 16.5 to 8 g l⁻¹, in tomato plant (Dielen et al., 2001). Royer et al. (2013) revealed that C:N ratio in the pool of resources in the total plant, were correlated with the concentrations of diverse compounds of the primary and secondary metabolisms in young tomatoes. Under HS, Peet et al. (1997) found that in tomato plants, the carbon and nitrogen metabolism get imbalanced, and stem and petiole elongation consume too much nutrients, which in turn reduces the dry matter storage of the plant, affecting tomato quality and yield. Soil mixed with dry powder of *Sesbania* plant (leaves + tender stems; C: N ratio 15.4) plays effective role in enhancing resistance and resilience (stability) of soil microbial activity against heat stress (Kumar et al., 2014). Heat stress may accelerate leaf senescence and increase respiration rate which consequently decreases plant N and C availability for seeds and shorten the duration of seed filling period in soybean (Egli and Wardlaw, 1980). Thus, balanced C:N ratio plays an important role in plant physiological process. Similarly, Larmure et al., 2005 demonstrated that the lower seed N concentration in pea plant at the average temperature range (13–23°C) can be explained by prolonged duration of the seed-filling associated with the lower seed N concentration, higher C availability for the seeds. Because the rate of seed N accumulation per degree-day mainly depends on N availability to seed filling, the rate of N accumulation was higher at 25/20°C than at lower temperature. HS reduces seed size and modifies the C:N ratio in the period of seed formation in pea (Guilioni et al., 2003).

Antioxidants and Oxidative Stress

Severe HS generates ROS, such as hydrogen peroxide (H₂O₂) and superoxide radical (O₂⁻), as byproducts of the aerobic metabolism, which adversely affect cellular metabolism, such as lipid membrane peroxidation, and damage nucleic acids and proteins (Bita and Gerats, 2013). Plants respond to ROS production by activating enzymatic and non-enzymatic ROS scavenging systems (Bita and Gerats, 2013). The main ROS scavenging enzymes are superoxide dismutase (SOD), catalase (CAT), peroxidase (POX), ascorbate peroxidase (APX) glutathione reductase (GR), whereas non-enzymatic chemical are ascorbic acid (ASC) and glutathione (GSH) (Suzuki et al., 2012). SOD helps scavenge O₂⁻ whereas CAT and POX degrade H₂O₂. Elevated levels of these antioxidants are crucial in

imparting thermotolerance in plants (Awasthi et al., 2014). In soybean, ROS accumulation (mainly H_2O_2 and O_2^-) due to HS is associated with decreased enzyme activities of various antioxidants (Djanaguiraman et al., 2005, 2013a). Similarly, GR and CAT activities decreased in common bean under oxidative stress (Babu and Devaraj, 2008). Likewise, decreased APX and GR expression occurred in mungbean exposed to HS (Sharma et al., 2016). However, relationship between antioxidant enzymes and HS is far more complex in tomato where activity of SOD, APX increased and CAT activity decreased (Zhou et al., 2014). This complexity was also evident in capsicum where, NADPH oxidase and CAT activity increased at high temperature (Gulen et al., 2012). In chickpea, tolerant genotypes had higher SOD, CAT, APX, and GR activity than sensitive genotypes under HS (40/30°C and 45/35°C) (Kumar et al., 2013). Moderate HS increases the expression of various enzymatic antioxidants, while severe HS suppresses it (Wilson et al., 2014).

DEFENSE RESPONSES

In addition to antioxidants, plants endure HS by activating major defense mechanisms which are mainly comprised of increased production of heat shock proteins (HSPs) and compatible solutes (Sakamoto and Murata, 2002; Wahid et al., 2007; Mittler et al., 2012; Khan and Shahwar, 2020). HSPs are the molecular chaperones that protect the misfolded proteins from irreversible aggregation, sorting, translocation, and degradation, important for establishing cellular homeostasis in normal and stressed conditions (Vierling, 1991). There are five classes of HSPs categorized according to their molecular weight: HSP100, HSP90, HSP70, HSP60, and Small HSP (sHSP), and located in the cytoplasm as well as cellular organelles, nucleus, chloroplast, mitochondria, and endoplasmic reticulum (Wang et al., 2004). Different chaperone families though have a peculiar role but coordinate cellular homeostasis. Chaperones also maintain crosstalk with signaling molecules, antioxidants (ascorbate peroxidase), and osmolytes (trehalose, proline, glycine betaine) (Wang et al., 2004; Kang et al., 2022). Various reports have confirmed accumulation of all HSP families in different vegetables and food legumes under HS, with greater accumulation of sHSPs than other HSPs, as reported for spinach (Guy and Li, 1998), tomato (Preczewski et al., 2000), soybean (Ortiz and Cardemil, 2001), common bean and cowpea (Simões-Araújo et al., 2003), potato (Ahn et al., 2004), cabbage (Park et al., 2013), pea (Talalaiev and Korduym, 2014), faba bean (Kumar et al., 2015), capsicum (Li et al., 2015), chickpea (Meena et al., 2017), and broccoli (Lin et al., 2019). Accumulation of these proteins helps plants to re-establish homeostasis under HS conditions. Hence, the expression level of HSPs and HSFs could be manipulated genetically to improve heat tolerance ability. Overexpression of HSPs facilitates transformed cells to endure HS better than non-transformed cells (Grover et al., 2013); for instance, overexpression of sHSP (HSP21) in transgenic tomato imparts stable PSII, shielding photosynthesis from temperature-dependent oxidative stress and accumulating more carotenoids under HS (Neta-Sharir et al., 2005). Furthermore, overexpression of HSFs facilitates the expression of HSPs; for example, overexpression of HsFA1 in transgenic soybean enhanced the

expression of GmHSP70 leading to thermotolerance (45°C) (Zhu et al., 2006). Similarly, overexpression of transcription factor (CaWRKY40) enhanced thermotolerance in capsicum (Dang et al., 2013).

The role of various osmolytes, including proline and glycine betaine, in imparting heat tolerance is well-documented (Sakamoto and Murata, 2002). Osmolytes are low molecular weight compounds that can buffer cellular redox potential under HS. Proline is a well-studied osmolyte, concentration of which increases by several-fold under stress conditions. A heat-tolerant cabbage genotype accumulated more proline (and soluble sugars and antioxidants) than a sensitive genotype (Song et al., 2019). Similarly, Paul et al. (2014) even suggested using increased proline and soluble sugars in potato under HS can be used as markers for selecting heat-tolerant genotypes. Increasing HS gradually increased proline and soluble sugar contents in lettuce seedlings, indicating heat tolerance (Han et al., 2013). The role of proline in thermotolerance was also confirmed using exogenous proline applications. Kaushal et al. (2011) noted that exogenous treatment of proline induced thermotolerance in chickpea by protecting the enzymes involved in carbon and antioxidant metabolism. Glycine betaine is another compound that confers heat tolerance; Aien et al. (2011) suggested that glycine betaine imparts heat tolerance in potato genotypes under HS conditions.

Heat Avoidance

Heat avoidance through transpiration cooling is the best strategy adopted by plants to minimize the losses (Julia and Dingkuhn, 2013). Under moderately HS conditions, plants can accelerate growth to promote plant thermotolerance responses and architectural changes to move susceptible parts away from soil heat flow or to improve evaporative cooling (Havko et al., 2020). In soybean, tomato, or cabbage, moderately high ambient temperature induces hypocotyl elongation, and tomato displays leaf hyponasty (Quint et al., 2016; Casal and Balasubramanian, 2019; Vu et al., 2019). Pea canopies architecture and leaf type as traits of heat resistance can avoid heat and maintain a lower canopy temperature as leafed cultivars have greater leaf surface area and likely greater transpirational cooling, assuming soil moisture availability and an adequate root system (Tafesse et al., 2019). Another study showed that the leaf movement capacity in beans was shown to function in direct sunlight avoidance and benefited the plant by protecting it against photoinhibition and by maintaining leaf temperatures lower than the air temperature (Pastenes et al., 2004). Thus, as novel donors with higher heat tolerance or escape provides, there is ample evidence for systematic exploration of wild species and accessions (Prasad et al., 2017) for introducing these traits.

IDENTIFICATION OF TOLERANT GENOTYPES AND IMPROVING ADAPTATION AND MITIGATION TO HS

Physiological Approaches

Heat tolerance is a polygenic trait greatly influenced by environmental changes (Blum, 2018). HS effects are stage-specific, with the response at one stage differing from the

response at another. Breeders employ various techniques to minimize the impact of an unpredictable environment on crops. Conventional breeding is the oldest but most prevalent method, primarily based on selecting phenotypic plant characters (Acquaah, 2015). In recent decades, new techniques have emerged based on morpho-physiological plant characters merged with conventional breeding methods to screen superior varieties. These methods exploit inbuilt plant properties to cope with HS and assist in selecting heat-tolerant genotypes. Screening germplasm of various vegetable crops using various physiological traits linked to heat tolerance would be useful for breeding programs focused on developing HS tolerant genotypes. Although there are several methods or traits used for screening, some of the most common are discussed.

Stay-Green Assay

The stay-green character is the plant's ability to retain chlorophyll and remain green for longer to sustain photosynthesis, especially during seed filling (Thomas and Howarth, 2000). However, the adverse impacts of HS cause leaves structural changes and chlorophyll degradation and it ultimately induces premature, leaf senescence (Djanaguiraman and Prasad, 2010; Jha et al., 2014). Moreover, the onset of HS during seed filling affects various physiological processes, including increased leaf senescence (chlorophyll loss), altered source-sink relationship, and decreased assimilation of reserve food material in developing seeds, limiting plant yield (Luche et al., 2015). Therefore, delayed leaf senescence may be associated with heat tolerance, enabling plants to maintain their photosynthetic ability (Lim et al., 2007). High chlorophyll and carotenoid contents in leaves improve the photochemical efficiency of plants and reduces ROS concentration in plants such as tomato (Zhou et al., 2015) and pea (Tafesse, 2018).

In addition, the stay-green character positively correlates with canopy temperature depression. Stay-green genotypes have lower canopy temperatures due to transpirational cooling than non-stay-green genotypes (Kumari et al., 2013). In addition to these modifications, HS also causes plant morphological and architectural modifications like leaf hyponasty (measured through leaf angles), leaf petiole elongation, small and thin leaves, that are helpful for the plants to keep their canopies cool. For instance, the cucumber species have hyponastic leaves (Park et al., 2019) and reduced leaf size is found in potato (Tang et al., 2018) and capsicum species (Utami and Aryanti, 2021) under heat stress conditions. These processes involve various signaling cascades that mediate the developmental shaping for environment adaptation in plants (Gil and Park, 2019). This trait is also associated with grain yield and quality and abiotic stress tolerance (Kamal et al., 2019). Hence, the stay-green trait is essential for improving crop yield and useful for imparting heat tolerance (Joshi et al., 2007; Kusaba et al., 2013), and thus may be an important genetic trait for improving crop yield under HS.

Canopy Temperature Depression

Canopy temperature depression (CTD) is usually measured as the difference between air and canopy temperature, indicating the plant's ability to lower its foliar temperature by transpirational

cooling, as measured by an infrared thermometer. CTD also reflects plant water status and is influenced by the plant's ability to extract water and the transpiration difference between air and plant. Accordingly, CTD has been used to select heat-tolerant and drought-tolerant genotypes. Plants that can maintain cooler canopies during seed filling can tolerate high-temperature stress (Munjal and Rana, 2003). Heat-tolerant varieties of capsicum (Gajanayake et al., 2011) have been selected based on the stay-green trait. In soybean, there is a direct relationship between CTD, canopy greenness, photosynthetic rate, and yield (Kumar et al., 2017). Thus, the CTD trait can be used as a critical genetic trait for crop improvement aimed at increased yields at the vegetative stage.

Cell Membrane Thermostability

HS is amounts of sensed by cell membranes of leaf tissues, weakening cell membrane integrity/rigidity due to an increased degree of unsaturated fatty acids that increase membrane fluidity. This may change membrane permeability and disturb the selective transport of molecules across the membrane, affecting cellular homeostasis (Marcum, 1998). HS can directly affect membrane integrity through photochemical modifications during photosynthesis or ROS (Bita and Gerats, 2013). Cell membrane thermostability (CMT) can be evaluated with an electrolyte leakage test for screening crops for heat tolerance. The method is simple, quick, and inexpensive compared with whole-plant screening and can be used to assess plant tissue responses at the vegetative stage (Yeh and Lin, 2003). Electrolyte leakage is measured using a conductivity meter, with higher conductivity values indicating higher membrane damage (Nyarko et al., 2008). The CMT test has been used to screen heat-tolerant varieties of many crops, including soybean (Martineau et al., 1979), potato (Nagarajan and Bansal, 1986), cowpea (Ismail and Hall, 1999), cabbage (Nyarko et al., 2008), cauliflower (Aleem et al., 2021) chickpea (Kumar et al., 2013), mungbean (Sharma et al., 2016), and cucumber (Ali et al., 2019).

Chlorophyll Fluorescence

Chlorophyll fluorescence—expressed as the Fv/Fm ratio (Fv: variable fluorescence; Fm: maximum fluorescence)—is used to detect the state of PSII function in terms of the energy absorbed by PSII in chlorophyll and damage to photosynthetic apparatus by excess light *in vivo* (Maxwell and Johnson, 2000). Chlorophyll fluorescence is a rapid, reliable, and inexpensive procedure for predicting photosynthetic performance under HS. Reduced Fv/Fm values indicate damage to the light-harvesting complex (Moradpour et al., 2021). Chlorophyll fluorescence has been used to select heat-tolerant varieties of sweet pepper (Hanying et al., 2001), common bean (Stefanov et al., 2011), chickpea (Kaushal et al., 2013), mungbean (Kaur et al., 2015), tomato (Zhou et al., 2015; Poudyal et al., 2018), and okra (Hayamanesh, 2018). Makonya et al. (2019) showed that tolerant chickpea genotypes maintain higher Fv/Fm during HS than sensitive genotypes, and Fv/Fm positively correlates with grain yield in the field. Killi et al. (2020) reported the retention of PSII function at elevated temperature positively correlated with antioxidant

activity, confirming the applicability of this trait for selecting heat-tolerant varieties.

Relative Water Content

Relative water content indicates the hydration status of plants and reflects the balance between leaf water supply and transpiration rate. Hence, it can measure leaf water deficit and the degree of damage under HS (Mullan and Pietragalla, 2012). High transpiration increases water loss, which can cause tissue dehydration and wilting (Mazorra et al., 2002). Therefore, genotypes that can maintain turgid leaves will minimize HS effects and have numerous physiological advantages. Gowda et al. (2011) suggested using RWC as selection criteria for improving yield under HS. High temperature (40–42°C) at the vegetative and reproductive stage gradually reduced the RWC of capsicum genotypes, more so at the reproductive stage (Puneeth, 2018). RWC has been used to select heat-tolerant genotypes of mungbean (Sharma et al., 2016), capsicum (Puneeth, 2018), common bean (Chavez-Arias et al., 2018), lentil (Sita et al., 2017), tomato (Zhou et al., 2018), cucumber (Ali et al., 2019), and potato (Handayani and Watanabe, 2020) where genotypes with high RWC under HS were rated as heat tolerant.

Stomatal Conductance

Stomatal conductance measures the rate of carbon dioxide entering or water vapor exiting stomata. This change in transpiration rate facilitates changes in leaf temperature and water potential (Farquhar and Sharkey, 1982). Leaf stomatal conductance is often recognized as an important trait for evaluating differences in response to changing environments. It can be used to determine trait such as photosynthetic CO₂ uptake, leaf temperature, and water loss (Viale-Chabrand and Lawson, 2019). Decreased stomatal activity under a changing environment can significantly affect plant growth and biomass (Way and Percy, 2012). *In vivo* stomatal conductance can be measured with a steady-state leaf porometer and gas exchange. HS increases *in vivo* adaxial stomatal conductance relative to the control (Sharma et al., 2016). Low stomatal responses under stress can limit photosynthetic rate and cause unnecessary transpiration, decreasing plant water use efficiency and productivity (Matthews et al., 2018). This phenomenon has been used to select heat-tolerant genotypes of sweet pepper (Hanying et al., 2001); tomato (Camejo et al., 2005; Abdelmageed and Gruda, 2009), chickpea (Kaushal et al., 2013), and mungbean (Kaur et al., 2015). While many studies have successfully used one of the traits above to select heat-tolerant genotypes, combining multiple traits would reflect heat tolerance better than relying on a single trait.

Reproductive Function, Gamete Viability and Fruit-Set

Fruit yield in vegetable crops is a function of fruit numbers and fruit size. There is a strong and positive correlation between fruit-set and gamete viability (Prasad et al., 2017). Gamete functions (pollen and ovule) is the most important factor for fruit-set under HS. In tomato, fruit-set has been shown to correlate with pollen viability (Firon et al., 2006). In general, heat tolerant genotypes

maintain higher pollen viability compared to heat susceptible genotypes (Dane et al., 1991). Gamete functions depend on its viability, which can be evaluated by viability assays like staining, *in-vitro* and *in-vivo* germination of pollen, and ovule function. Genotypes are known to differ in gamete viability under HS stress. Singh et al. (2015) concluded from their research on tomato that traits like fruit-set and pollen viability could be used as a strategy to screen genotypes for HS. In general, the combination of gamete viability and fruit-set provide tolerance to HS (Paupière et al., 2017b; Pham et al., 2020). Similarly observations were also made on peppers (Aloni et al., 2001; Reddy and Kakani, 2007).

Cardinal temperatures (T_{min}, T_{opt}, and T_{max}) for pollen grain germination can be used to screen germplasm for HT stress tolerance. Results from *in-vitro* studies showed that genotypes varied in response to temperature for cardinal temperatures, and the differences in cardinal temperatures were mainly responsible for tolerance/susceptibility of genotypes to HT stress in soybean (Djanaguiraman et al., 2019) and peanut (Kakani et al., 2002). The genotypes having higher ceiling temperature (T_{max}) for pollen germination values tend to be HT tolerant in most cases. Cardinal temperature for pepper were different among susceptible and tolerant cultivars (Reddy and Kakani, 2007) and can be used to identify temperature tolerant or sustainable genotypes of pepper (Gajanayake et al., 2011). All the aforementioned traits based on leaf function are used collectively to select heat tolerant cultivars. Though many studies have successfully employed one trait for selection of heat tolerant genotypes, a combination of these traits reflects a better status of heat tolerance rather than relying on a single trait.

OMICS APPROACHES

Genomics

Various modern genome-based technologies can be used to introduce genetic variations for HS tolerance into plants. Under high-temperature stress, plants activate a complex chain of molecular responses, including heat-stress-responsive genes that control primary and secondary metabolism, transcription, translation, and lipid signaling, or protein modifications, including phosphorylation HS transcription factors (HSFs) that regulate differential expression of HSPs (Janni et al., 2020). HSPs and HSFs are key players in the acquisition of the HS response. HSFs are mainly involved in sensing and relaying the HS signal to activate the response (Mittler et al., 2012). Genome-wide associated studies (GWAS) have been conducted on a few vegetable crops to search for novel genes and transcription factors associated with heat tolerance. Genomic studies on cabbage (*Brassica rapa* ssp.) disclosed the role of differentially expressed long non-coding (lncRNAs), mRNAs, and microRNAs. Their expression is associated with phytohormones such as salicylic acid (SA) and brassinosteroids (BRs), possibly involved in heat tolerance. Of these, 25 lncRNAs were co-expressed with ten heat-responsive genes (Wang A. et al., 2019). NAC, a large family of transcription factors, was analyzed in cabbage; 188 genes were identified that play a major role in resistance to high-temperature stress (Ma et al., 2014). Analysis of the potato

Hsp 20 gene family revealed 48 putative Hsp20 (StHsp20) that accumulated under heat treatment. Different levels of these transcripts were upregulated during different HS exposures. The transcription of HSPs are regulated by HSFs that play an important role in imparting thermotolerance in plants (Zhao P. et al., 2018). Guo et al. (2015) characterized 35 putative Hsp 20 genes (CaHsp20) located on 12 chromosomes in thermotolerant (R9) and thermosensitive (B6) lines of pepper in four tissues (roots, stem, leaves, and flowers). Under high temperature stress (40°C), most of the CaHsp20 genes had higher expression in both lines, more so in the thermosensitive line. Chidambaranathan et al. (2018) identified 22 Hsfs in the desi (ICC4958) and kabuli (CDC Frontier) genomes of chickpea (15-day-old seedlings; heat treatment of 35 ± 2°C). Field analysis was undertaken to compare the expression pattern at the podding stage. HS at the seedling and pod development stages upregulated the expression of *CarHsfA2*, *A6a*, *A6c*, and *B2a*, indicating their role in conferring HS tolerance in chickpea. Yang et al. (2016) recorded 26 HSF (Sly HSF) genes in tomato, with HS (38°C) increasing the expression of most, especially SlyHSF-05/07/13/18/20/23/24. Expression of the SlyHSF-18 gene increased manifold compared to the control, indicating its strong response and correlation to high temperature sensitivity. Moreover, SlyHSF-02 was the main regulator for activating the heat response and acquiring thermotolerance in tomato.

Transcriptomics

Transcriptomics refers to the study of the transcriptome [entire set of transcripts (mRNA, tRNA, and rRNA, miRNA, siRNA, snRNA, snoRNA, and lncRNA)] expressed in a cell, tissue, organ, or organism. It represents all RNA synthesized, including protein-coding, non-coding, spliced, polyadenylated, and RNA-edited transcripts (Imadi et al., 2015). Transcriptomics reveals the molecular mechanism underlying the phenotype and explains how genes are expressed and interconnected (Jha et al., 2017). High throughput methods (microarray, RNA sequencing, RT-PCR) are used to analyze the expression level of multiple transcripts in different conditions. Several transcriptome studies in vegetable crops under HS have revealed the molecular basis for heat tolerance.

Transcriptome analysis in heat-stressed spinach (42°C for 15 days) revealed the expression of 4,145 transcripts (2,420 upregulated and 1,725 downregulated) in heat-tolerant and heat-sensitive genotypes (Guo et al., 2020). An enrichment analysis showed that the major metabolic difference between tolerant and sensitive genotypes was carbohydrate metabolism (Guo et al., 2020). Similarly, transcriptome analysis revealed 23,000–30,000 expressed genes in soybean seeds and differentially expressed genes (DEGs; 5–44% of expressed genes) (Gillman et al., 2019). The DEGs were measured at high temperature in mature, imbibed, and germinated seeds in a heat-tolerant (PI 587982A) and conventional high-yielding variety (S 99-11986), with 7,789 DEGs common between genotypes, 11,833 common between mature and imbibed seeds, and 13,344 common between imbibed and germinated seedlings (Gillman et al., 2019). In capsicum, seedling transcriptomics revealed 3,799 DEGs in R597 (heat-tolerant genotype) and 4,010 DEGs in S590 (heat-sensitive

genotype), related to hormones, HSPs, transcription factors, and calcium and kinase signaling (Li et al., 2015). Further, R597 had higher expression of transcription factors and hormone signaling genes than S590 (Li et al., 2015). Transcriptomic analysis of heat-tolerant PS-1 and heat-sensitive H-24 tomato genotypes under HS (40°C for 1 h) revealed upregulated genes associated with protease inhibitors, HSPs, and transcription factors, manifold higher in the tolerant genotype than the sensitive genotype (Sadder et al., 2014).

Proteomics

Proteomic analysis in heat-stressed radish leaves (advanced inbred line NAU-08Hr-10) revealed eleven differentially expressed proteins, of which four belonged to HSPs, four to energy and metabolism, two to redox homeostasis, and one to signal transduction (Zhang et al., 2013). Comparative proteome analysis of heat-tolerant (JG 14) and heat-sensitive (ICC16374) chickpea genotypes under HS during anthesis revealed that 482 heat-responsive proteins (related to photosynthesis, energy metabolism, and signaling molecules) were synthesized in higher amounts in the heat tolerant genotype compared to the sensitive genotype (Parankusam et al., 2017). Proteomics of spinach (50-day-old) exposed to 37/32°C for 24, 48, or 72 h identified heat-stress-responsive proteins in heat-tolerant (Sp75) and heat-sensitive (Sp73) lines (Li et al., 2019). The abundance pattern indicated that HS inhibited photosynthesis, initiated ROS scavenging pathways, and sped up carbohydrate and amino acid metabolism. A comparative proteomic study showed that heat-sensitive genotypes have a lower ability for photosynthetic adaptation, osmotic homeostasis, and antioxidant enzyme activities than heat-tolerant genotypes (Li et al., 2018). Ahsan et al. (2010) used a proteomics approach to study the tissue-specific protein expression pattern in heat-stressed soybean seedlings (40 ± 2°C for 12 h), identifying 61, 54, and 35 differentially expressed proteins in roots, leaves, and stem, respectively. Many of the proteins related to HSPs and the antioxidant system were upregulated.

Metabolomics

Recent metabolite profiling has focused on important metabolites that govern temperature stress tolerance (Guy et al., 2008). Wang J. et al. (2019) studied the metabolism of heat-tolerant (17CL30) and heat-sensitive (05S180) capsicum cultivars; the tolerant genotype accumulated 94 differentially accumulated metabolites (DEM) while the sensitive genotype accumulated 108 DEM. Both genotypes shared common metabolites, but they were more highly expressed in tolerant genotypes. Metabolite profiling of tomato anthers exposed to 38°C for 2 h revealed that flavonoids (alkaloids and flavonoids in young microspores) protect against HS (Paupière et al., 2017a,b). A metabolomics study on heat-stressed soybean seeds revealed 275 metabolites that comprised antioxidants, including ascorbate precursors, tocopherol, flavonoids, phenylpropanoids, which were more enriched in tolerant than sensitive genotypes (Chebrolu et al., 2016).

MOLECULAR BREEDING

Of late, molecular breeding has emerged as one of the important tools to identify progeny plants possessing the targeted genes/QTLs including the presence of several genes or ascertain the amount of genome of recurrent parent in a plant. Molecular breeding relies on molecular markers and hence the outcome, unlike the phenotyping, is not influenced by environmental factors. The molecular breeding has been exploited successfully in crop breeding and has led to the development of crop varieties possessing resistance to diseases or varieties with resistance genes pyramids (Janni et al., 2020). Molecular breeding methods to improve heat tolerance include (i) transfer of quantitative trait loci, (ii) marker-assisted selection. Other methods include marker assisted recurrent selection, marker-assisted pyramiding, and single nucleotide polymorphism. These methods pave the way for breeding stress tolerance in plants (Collard and Mackill, 2007). These methods pave the way for breeding stress tolerance in plants (Collard and Mackill, 2007).

Quantitative Trait Loci

QTL is a stretch of genomic regions on a chromosome that is linked to a quantitative trait. Usually, this stretch contains several genes and each QTL contribute partially to the trait in question; and hence, several QTLs together govern a trait. In molecular breeding, whole QTL is transferred to the recurrent parent utilizing markers flanking to the QTLs and sometimes using markers present within the QTL region. The exploitation of molecular breeding for QTLs transfers in breeding programs, a QTL must be well-defined and demonstrated to be linked to a particular trait (Collard and Mackill, 2009). Heat tolerance is a polygenic trait governed by several genes (Golam et al., 2012) and several QTLs. Unprecedented advances in genomics, especially molecular marker development, have identified numerous QTLs contributing to HS tolerance by dissecting various traits ranging from phenological, physiological, biochemical, reproductive biology to yield and yield-related traits (Lucas et al., 2013; Wen et al., 2019; Song et al., 2020; Jha et al., 2021; Vargas et al., 2021) in various vegetable crops, including bottle gourd (*Lagenaria siceraria*), cowpea (*Vigna unguiculata* [L.] Walp.), common bean, chickpea, chili, and tomato (Table 5). In broccoli (*Brassica oleracea* var. *italica*), five QTLs were identified under HS—QHT_C02, QHT_C03, QHT_C05, and QHT_C07 from the heat-tolerant parent and QHT_C09 from the heat-sensitive parent, with a positive epistatic co-relation between QHT_C03 and QHT_C05 for heat tolerance and APX activity was co-located with QHT_C03 (Branham et al., 2017). Likewise, QTLs such as QHT_C02, QHT_C05, and QHT_C09 were co-located with the AP2 gene governing floral development under HS (Aukerman and Sakai, 2003). Similarly, the meristem identity gene (TFL) was associated with QHT_C02 (Duclos and Björkman, 2008). Subsequently, two novel QTLs contributing to heat tolerance were uncovered by phenotypic evaluation of double haploid-based mapping population for two consecutive summer seasons and by employing QTL-seq approach in broccoli (Branham and Farnham, 2019). Recently, subjecting genome wide association (GWAS) study of one hundred forty two lines unearthed a total

of fifty seven significant marker trait associations for various physiological and yield related traits under heat stress in *Brassica rapa* (Chen et al., 2022). In tomato, Xu et al. (2017) mapped 13 QTLs for heat tolerance linked with reproductive traits, including pollen viability, pollen number, style protrusion, anther length, style length, flower per inflorescence, and inflorescence number. These QTLs showed additive effects and no epistatic interaction. Likewise, six QTLs linked to fruit set in tomato at high temperatures were identified (Grilli et al., 2007). Based on evaluating recombinant inbred lines and introgression lines developed from *Solanum lycopersicum* var. “MoneyMaker” × *S. pimpinellifolium* across multi environments under high temperature stress enabled in identification of 22 QTLs related to reproductive traits (flower number fruit number and fruit set proportion) on LG1, 2, 4, 6, 7, 10, and 11 explaining phenotypic variation from 4 to 13% (Gonzalo et al., 2020). In combination of phenotypic assessment of leaf cell membrane stability by applying heat stress in F₂ derived mapping population with QTL-seq approach in F₂ derived mapping population assisted in uncovering a total of seven QTLs *qHT1.1*, *qHT2.1*, *qHT2.2*, *qHT5.1*, *qHT6.1*, *qHT7.1*, and *qHT8.1* conferring heat tolerance in bottle gourd (Song et al., 2020). Likewise, employing conventional QTL mapping and QTL-seq analysis allowed in identifying a total of five major QTLs *qHII-1-1*, *qHII-1-2*, *qHII-1-3*, *qHII-2-1*, and *qCC-1-5* (*qREC-1-3*) related to heat injury index under heat stress in tomato (Wen et al., 2019). The authors performed the functional validation of the underlying selected four potential candidate genes *SlCathB2*, *SlGST*, *SlUBC5*, and *SlARG1*. To decipher genetic basis of heat tolerance in cucumber, QTL analysis of mapping population developed from “99281” (heat-tolerant) × “931” (heat-sensitive) population phenotypically evaluated during summer 2018, 2019, and 2020 allowed to identify one major QTL *qHT1.1* on LG1 (Liu et al., 2021). There were 98 genes underlying this QTL. Of these identified genes, expression of *Csa1G004990* candidate gene was higher in “99281” than “931” genotype rendering it heat tolerant. In order to shed light into the functional role of HSP20 contributing to heat tolerance, in *Cucurbita moschata*, genome wide bioinformatic analysis enabled in unveiling 33 HSP20 genes across the genome (Hu et al., 2021). Functional validation of CmoHSP20-7, 13, 18, 22, 26 and 32 genes indicated their possible role in heat tolerance in *Cucurbita moschata* (Hu et al., 2021).

In cowpea, five QTLs governing pod set at high temperature, namely Cht-1, Cht-2, Cht-3, Cht-4, and Cht-5, with CB 27 line of cowpea donating alleles for four QTLs (Cht-1, Cht-2, Cht-3, Cht-4) and IT82E-18 contributing alleles for Cht-5 (Lucas et al., 2013). Combinations of any of the four QTLs with Cht-5 positively correlated with heat tolerance in cowpea. Further, the presence of all five QTLs in the same line had the strongest positive correlation with heat tolerance (Lucas et al., 2013). Recently, four QTLs were identified in chickpea that conferred heat tolerance for filled pods (qfpod03_6), grain yield (qgy03_6), total seed number (qvs05_6), and pod set (q% podset08_6) using recombinant inbred lines produced from ICC 4567 (heat-sensitive) × ICC 15614 (heat-tolerant) lines (Paul et al., 2018). One QTL (qTBP5.2) was detected in lettuce, governing the tip-burn resistance trait, therefore beneficial in breeding programs

TABLE 5 | List of selected QTLs contributing to heat tolerance in vegetable crops.

Crop	Mapping population	Trait used	Name of gene/QTL	Type of marker	Linkage groups	Phenotypic variation	References
Bottle gourd (<i>Lagenaria siceraria</i>)	L1 × L6	Relative electrical conductivity	<i>qHT1.1, qHT2.1, qHT2.2, qHT5.1, qHT6.1, qHT7.1, and qHT8.1</i>	SNP	1, 2, 5, 6, 7, 8	–	Song et al., 2020
Cowpea (<i>Vigna unguiculata</i>)	CB27 × IT82E-18, RIL 141	–	<i>Cht-1, Cht-2, Cht-3, Cht-4, Cht-5</i>	SNP	2, 3, 6, 7, 10	11–18%	Lucas et al., 2013
	IT93K-503-1 × CB46, RIL 113; IT84S-2246 × TVu146, RIL 136	Seed coat browning	<i>Hbs-1, Hbs-2 and Hbs-3</i>	SNP	1, 3, 8	6–77%	Pottorff et al., 2014
Common bean (<i>Phaseolus vulgaris</i>)	IJR × AFR298, RIL	Reproductive trait and yield and yield traits	32 QTLs	SNP	1, 2, 3, 4, 5, 8, 9, 10	7.8–36%	Vargas et al., 2021
Chickpea (<i>Cicer arietinum</i>)	DCP 92-3 × ICCV92944 RIL(184)	Phenological, physiological and yield related traits	77 QTLs	SNP	LG1–LG8	5.9–43.5%	Jha et al., 2021
	DCP 92-3 × ICCV92944F2(206)	Phenological and physiological traits	2 QTLs	SSR	–	–	Jha et al., 2019
	ICC 4567 × ICC 15614, RILs(292)	Yield and yield traits	4 QTLs	SNP	CaLG05, CaLG06	–	Paul et al., 2018
	GPF2 × ILWC292, RIL	Phenological, physiological and yield related traits	28 + 23 QTLs	SNP	All LG groups except LG8	5.7–13.7%	Kushwah et al., 2021
Chili (<i>Capsicum annum</i>)	AVPP0702 × Kulai, backcross	Reproductive and yield trait	Hsp70 and sHsp gene	SSR	–	–	Usman et al., 2018
Tomato (<i>Lycopersicon esculentum</i>)	Nagcarlang × NCHS-1180 F2	Reproductive traits; viz., pollen viability, pollen number, style length, anther length; inflorescence number and flowers per inflorescence	<i>qPV11, qPN7, qSP1, qSP3, qAL1, qAL2, qAL7, qSL1, qSL2, qSL3, qFPI1 qIN1, qIN8</i>	SNP	1, 2, 3, 7, 8, 11	10.5–38.7%	Xu et al., 2017
	MAGIC population	Yield components, phenology and fruit quality	69 plasticity QTLs	SNP	–	–	Bineau et al., 2021
	LA1698 × LA2093	Relative electrical conductivity (REC), chlorophyll content (CC) and maximum photochemical quantum	5 major QTLs <i>qHll-1-1, qHll-1-2, qHll-1-3, qHll-2-1 and qCC-1-5 (qREC-1-3)</i>	SNP	1, 2	16.48%	Wen et al., 2019
	<i>Solanum lycopersicum</i> var. "MoneyMaker" × <i>S. pimpinellifolium</i> accession TO-937RIL and IL	Reproductive traits viz., flower number, fruit number per truss and percentage of fruit set, stigma exertion (SE), pollen viability (PV), tip burn	22 QTLs	SNP8K SNP SOLCAP Infinium chip	1, 2, 4, 6, 12	3.6–12.8%	Gonzalo et al., 2020

(Jenni et al., 2013). The information on genomes of crops is expanding rapidly. The sequencing coupled with resequencing will generate more information that will subsequently be used to gather detailed knowledge of QTLs and genomic bases of heat tolerance in crops. The closely-related crops share syntenic relationships and possess similar genomic regions with each other. In the forthcoming years, comparative genomic analysis and advancements in knowledge of molecular biology might

allow us to transfer heat tolerant regions from one crop to another, thereby expanding the repository of cold tolerance in crop plants.

MARKER-ASSISTED SELECTION

As mentioned earlier, phenotype-based selection is prone to environmental conditions sometimes leading to erroneous

conclusions especially if trait is complex and conferred by polygenes or QTLs. Under such circumstances, genotype-based selection is more effective, precise and fast as compared to phenotypic selection. Genotype-based selection rather than phenotype-based selection is possible using markers linked to gene of interest. Genotype-based selection utilizes DNA markers that are linked tightly to the gene(s) of interest (Collard and Mackill, 2007). For MAS, first step is to identify markers linked to the gene or QTL using either mapping populations or association mapping where a panel of genotypes is used to identify linked markers. Subsequently, these markers are used to ascertain transfer of the gene to the progeny populations. Different types of markers, such as RFLP (restricted fragment length polymorphism), AFLP (amplified fragment length polymorphism), SSR (single sequence repeat), and SNPs (single nucleotide polymorphisms), can be detected, and the amount of variation in each marker can be determined. Using this approach, gene mapping and identifying gene associations with particular traits are useful for genetic crop improvement (Ruane and Sonnino, 2007).

Paul et al. (2018) identified SNP markers linked to QTLs for heat tolerance traits (50% flowering, podding behavior, total filled pods, % pod set, total seed number, grain yield, biomass, harvest index, 100-seed weight) in chickpea RILs (heat-tolerant ICC 15614 × heat-sensitive ICC 4567). Composite interval mapping analysis affirmed two genomic regions (CaLG05 and CaLG06) with four QTLs (grain yield, total seed number, total filled pods, % pod set). A GWAS used 16,877 SNPs to identify marker-trait associations (MTA) in 135 diverse pea lines exposed to >28°C in the field to understand the genetic basis for heat tolerance (Gali et al., 2019). The study identified 32 MTAs and 48 candidate genes associated with various traits, including chlorophyll concentration, photochemical reflectance index, canopy temperature, reproductive stem length, internode length, pod number, with the potential for developing heat-tolerant cultivars (Tafesse et al., 2020). Lin et al. (2006) identified 14 RAPD markers linked to heat tolerance traits (flower number, fruit number, fruit set, yield) in tomato RILs derived from CL5915 (heat-tolerant) and L4422 (heat-sensitive) under HS. Developing heat tolerant *Capsicum annuum* through transferring heat shock protein encoding gene *Hsp70* and *sHsp* from AVPP0702 into Kulai an elite *C. annuum* cultivar by adopting marker assisted back crossing approach is notable illustration of marker assisted breeding for heat tolerance (Usman et al., 2018). Likewise, three non-synonymous SNPs identified in the *qHT2.1* major effect QTL in bottle gourd (Song et al., 2020) and non-synonymous SNP identified in the *QHT_C09.2* QTL regions in broccoli (Branham and Farnham, 2019) contributing to heat tolerance, which could be potentially used as candidate markers for screening heat tolerant bottle gourd and broccoli genotypes.

TRANSGENICS

Altering the genetic makeup of vegetable crops is a possible solution for developing crops that can grow and reproduce well under increasing temperatures. Plants have an inherent ability

to endure supra optimal temperatures (“basal thermotolerance” or “acquired tolerance to increasing temperature”) (Grover et al., 2013). The level of thermotolerance varies between plant species depending on their genetic makeup and specific expression of defense-related genes, however, levels of thermotolerance vary in different plant species again due to differences in genetic makeup of the plant species. Even within a species, genotypes differ for reaction (tolerance or sensitive) to HS owing to varying genetic makeup. Considerable number of genes/QTLs conferring tolerance to HS has been identified in vegetable crops and these genes/QTLs can be transferred from heat-tolerant genotypes to heat-sensitive genotypes using transgenic approaches to develop genetically modified heat tolerant crops. Genes expressed in heat-tolerant crops can be transferred to heat-sensitive crops using transgenic approaches to develop genetically modified heat-tolerant crops. Candidate genes for development of transgenics for heat tolerance are HSP, compatible osmolyte, and antioxidant levels, and detoxifying pathways (Parmar et al., 2017).

Manipulating HSPs

Many vegetable crops have been manipulated for increased expression of HSPs. For instance, in tomato, overexpression of trehalose-6-phosphate synthase/phosphatase (TPSP) gene derived from *Escherichia coli* increased the expression of HsfA1, HsfA2, and HsfB1, which was linked to escalating Hsp17.8, ER-sHsp and Mt-sHsp levels to impart heat tolerance (Lyu et al., 2018). Similarly, overexpression of small heat shock protein (CaHsp 25.9) improved thermotolerance in Capsicum transgenic lines (R9 and B6) under HS, decreasing MDA content and increasing proline and SOD content (Feng et al., 2019). In transgenic potato lines, overexpression of the A2 HSc70 (Heat-Shock Cognate) allele-maintained tuber yield at elevated temperature (Trapero-Mozos et al., 2018).

Manipulating Antioxidants

HS causes oxidative damage in plants; therefore, developing transgenics with enhanced antioxidative mechanisms may enhance thermotolerance in plants. Antioxidant mechanisms were manipulated in pea by incorporating heat shock factor gene (HsfA1d) from *Arabidopsis thaliana*. Under HS (42°C), transgenic pea plants had five-fold higher expression of HsfA1d than wild pea, decreasing H₂O₂ accumulation, and higher SOD and APX activities and proline content (Shah et al., 2020). Tang et al. (2006) developed transgenic potato plants (SSA plants) expressing Cu/Zn SOD and APX gene in chloroplasts under the control of a SWPA2. The transgenic plants had less damage induced by methyl viologen than non-transgenic plants. In the same study, photosynthetic activity decreased by 29% in non-transgenic plants but only 6% in transgenic plants under HS (42°C for 20 h). Overexpression of cytosolic APX (cAPX) in transgenic tomato (*Lycopersicon esculentum* cv. Zhongshu No. 5) under HS (40°C for 13 h) resulted in several-fold higher APX activity than wild plants, reducing electrolyte leakage (24% in A9 line and 52% in A16 line) compared with wild plants. Similarly, overexpression of cAPX in transgenic tomato increased tolerance HS (Wang et al., 2006).

Cross-Talk Between HSP and Redox Mechanism

Equilibrium between ROS generation and ROS scavenging is disturbed by the high temperature stress (Foyer and Noctor, 2005). One of the best strategies adopted by the plant cells is the production of HSPs on exposure to high temperature (Wang et al., 2004). HSPs positively affect thermotolerance by protecting ROS scavenging system and actively resulting in lower ROS concentration. HSPs also enable protein refolding, preventing aggregation of non-native proteins and stabilize polypeptides and membrane under stress conditions (Scarpecci et al., 2008). It is unclear whether there is specific interaction between HSPs and ROS scavenging machinery but ROS accumulation is reduced *via* HSP induced ROS scavenging activity. Hence the cross-talk between production of HSFs/HSPs and ROS scavenging activity play important role in acclimation (Kang et al., 2022). The communication between ROS and HSFs involve Mitogen Activated Protein Kinase (MAPK). ROS dependent phosphorylation can play vital role in HSF activation (Driedonks et al., 2015). MAPK3 and MAPK6 are the key players which are activated by H₂O₂ and further phosphorylate the HSFs, for instance in tomato, heat induced MAPK transduces the heat stress signal *via* HSFA3 (Link et al., 2002). Induction of heat shock transcription factors HsfA2 and HsfA4 is reported to be regulators of genes associated with ROS mitigation. HsfA4A is the principle candidate to function as H₂O₂ sensor (Scarpecci et al., 2008). At transcriptional level, HSPs are regulated by HSFs that bind to the conserved regulatory element of heat shock element (HSEs) and act as promoter for Hsp genes. Under stress conditions ROS mainly H₂O₂ functions as signal transduction molecule and cause HSF activation. ROS enhances the dissociation of HSP and HSF complex and promote the HSF trimerization and relocate the same to the nucleus leading to activation of the expression of HSPs and other heat responsive genes (Ul Haq et al., 2019) (Figure 4).

AGRONOMIC APPROACHES

By employing improved agronomic practices for different crops has improved crop yields. These practices include better soil, water, nutrient, weed, and pest management strategies, selection of varieties, and appropriate planting times and planting densities, and more and more (HanumanthaRao et al., 2016). Agronomic practices control soil temperature by minimizing the evaporation (Ferrante and Mariani, 2018) helping the cultivators with sustained water use, proper fertilizer use, and improved land maintenance, consequently improving crop quality and quantity. In addition, agronomic practice also helps with increased soil physical, chemical and microbial status. These help with water and nutrient availability and plant uptake. Agronomic practices for increasing vegetable crop yields that are efficient, cost-effective, and easily adaptable for HS management are described below.

Land preparation for planting involves tillage, seedbed shaping, and mulching. These practices depend on the soil type, physical and chemical properties. Sandy loam soils are

best for raising vegetables such as potato, cauliflower, lettuce, cabbage, and tomato. Tillage includes breaking up/loosening the soil by plow, favoring seed germination, and proper seedling growth. Tillage also helps control weeds, aerate soil, and bury the previous crop's residues; the tillage method varies between crops (Kladivko, 2001). However, the same benefits can be obtained with no-till or minimum tillage practices that minimizes soil disturbance and helps with building of soil organic carbon over time. Mulching is a process of covering the soil with chopped residues; it has many benefits, including reduced soil erosion and water loss, which maintain soil temperature (Mulumba and Lal, 2008). Use of conservation agricultural practices with minimum soil disturbance, grass mulch cover and crop rotations not only significantly increased yield of green pepper but also decreased irrigation water use and runoff, while increasing percolated water in the root zone (Belay et al., 2020). Similarly, improved yields of tomato, cucumber and bitter guard were observed under conservation agriculture (Paudel et al., 2020). Conservation agricultural practices in vegetable production systems has shown to increase soil organic matter and nutrients (Belay et al., 2022). Irrigation increases soil moisture, decreasing soil temperature (by 2°) compared to non-irrigated soil (Lobell and Bonfils, 2008). Water quality and supply varies according to soil type, crop (warm- or cool-season), and weather conditions. Generally, vegetable crops are irrigated at 4–6-day intervals during summer and 14–15-day intervals during winter to reduce the high-temperature effects. Many modern technologies for irrigation are available that minimize water use, such as drip or trickle irrigation and overhead micro-sprinklers.

Variety selection is a successful agronomic approach for achieving high yields under high-temperature stress. Selection characteristics include high yield, disease resistance, maturity group, and grain quality (Pedersen, 2003). Suitable crop genotypes need to be early maturing and high yielding to escape heat by completing their life cycle early and thus perform better under HS (Sekhon et al., 2010). Furthermore, shifting the sowing time (early or late) is another strategy to avoid HS and avoid heat induced yield reduction as has been reported in mungbean (up to 50%) and soybean where yield declined tremendously by delay in the sowing date (Coventry et al., 1993; Miah et al., 2009). The goal of selection of crop duration and time of planting is to avoid HS during sensitive stages of reproductive development. In contrast, late sowing has been used to screen large populations of chickpea (Gaur et al., 2013), mungbean (Sharma et al., 2016), and lentil (Sita et al., 2017) genotypes for heat tolerance, some of which have been released (e.g., chickpea ICCV 92944) (Gaur et al., 2013). Heat-tolerant varieties of some vegetable crops are listed in Table 6. Hence, determining the ideal sowing time and selection of heat tolerant varieties is crucial for growth, development, and yield of crops.

Nutrients/Thermo-Protectants

HS can be alleviated by exogenous application of nutrients or thermo-protectants as a seed pretreatment, foliar spray, or by fertilizer application *via* broadcasting, pellet placement, or band placement (Waraich et al., 2012; HanumanthaRao et al., 2016). Macro-nutrients such as N, P, K, Ca, and Mg are

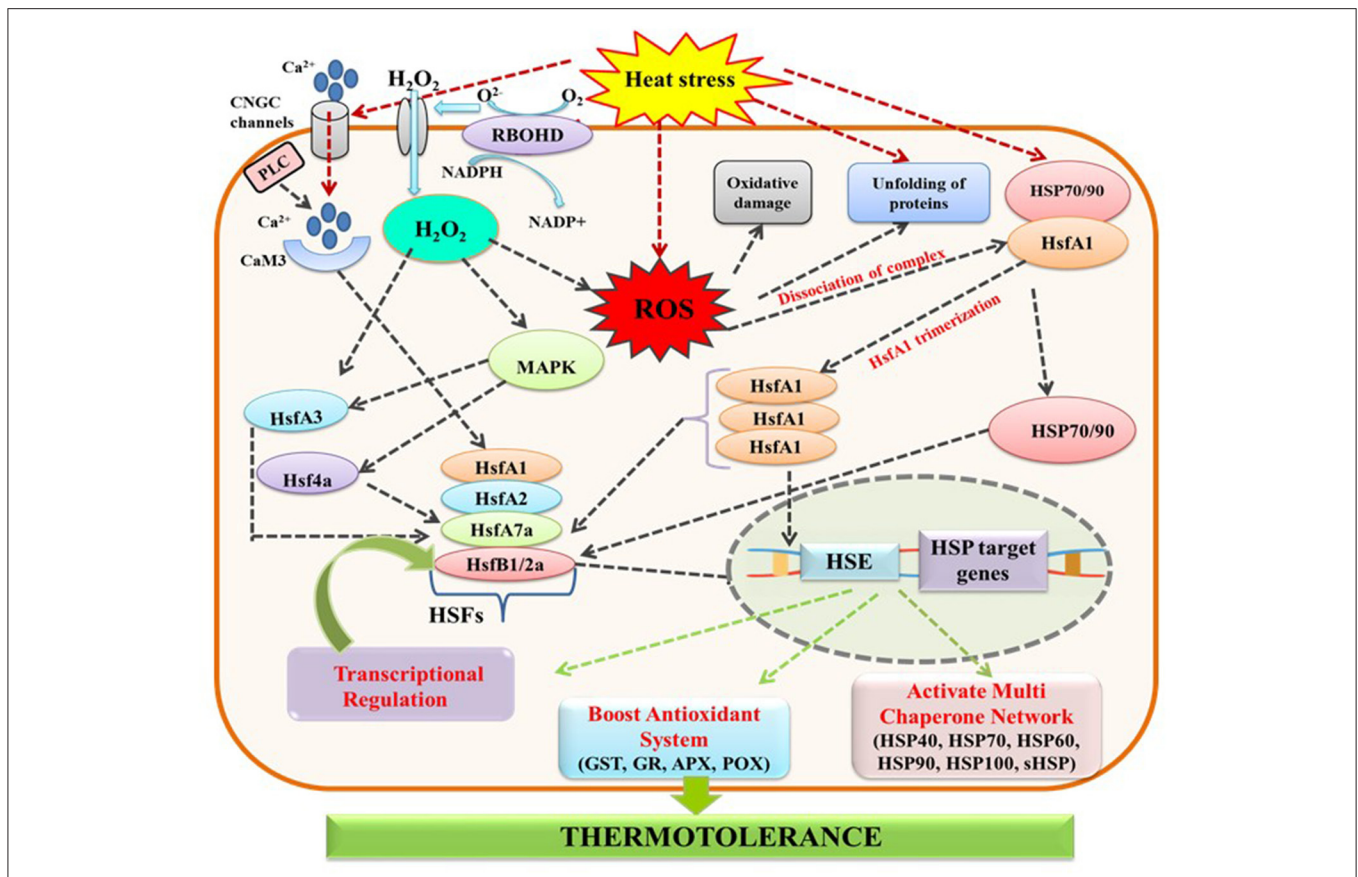


FIGURE 4 | Cross talk between HSPs and redox reaction: -Heat stress imposes damages to plant like increased membrane fluidity, unfolding of proteins, ROS production and dissociation of HSP70/90-HsfA1 complex. To endure HS, Plants activate various mechanisms to preserve their adaptation. First such mechanism is the activation of cyclic nucleotide gated calcium (CNGC) channels that result in the movement of Ca²⁺ ions in to cytoplasm and bind with Calmodulin Protein (CaM3) forming the Ca²⁺-CaM3 complex and help in the activation of Heat shock factors (HSFs). Second mechanism involves Phosphoinositol signaling pathway that also lead to the influx of more Ca²⁺ in to the cytoplasm and merge with Ca²⁺-CaM3 pathway. Another mechanism during HS is the activation of ROS signaling network by Respiratory Burst Oxidase Homolog D (RBOHD) that produce O₂⁻ which is converted in to H₂O₂ that is involved in the induction of HSFs activation. ROS like H₂O₂ also activate the HSFs complex through mitogen activated protein kinase (MAPK). On activation, HSFs move to the nucleus and activate HSE and HSP target genes. HS also lead to the dissociation, of HSP70/90-HsfA1 complex; on dissociation HsfA1 undergoes trimerization that further activates the HSFs complex in the cytosol and Heat shock element (HSE) in the nucleus. Their activation has many positive effects on the cellular metabolism like transcriptional regulation, activation of antioxidant system and multi chaperone network (HSP60, HSP70, HSP90, HSP100, and sHSP) that may lower down the ROS levels in the cell and help in achieving thermotolerance.

required by plants (>10 mM) and help maintain structural and functional integrity (Waraich et al., 2011). Nutrient deficiencies alter the levels of tolerance to abiotic stresses. During HS, N deficient plants were associated with increased lipid peroxidation, while N supplemented plants tolerated photo-oxidative damage (Kato et al., 2003). Likewise, K deficient plants had reduced translocation of photo-assimilates to the sink organ, whereas K application improved the translocation and utilization of photo-assimilates, maintained cell turgidity, and upregulated enzymatic activity under HS (Mengel et al., 2001; Cakmak, 2005), increasing yield by 1.9-fold in Capsicum and 2.4-fold in tomato (Waraich et al., 2012). Similarly, exogenous application of calcium (2 L/ha) increased lettuce production under HS (Almeida et al., 2016).

Micronutrients such as B and Mn also provide heat tolerance of plants by increasing antioxidant activity and

alleviating the damage induced by HS stress (Waraich et al., 2011). Other elements such as Se increased enzymatic activity and decreased membrane damage and ROS production in soybean (Djanaguiraman et al., 2005). Seed pretreatment and foliar application of thermoprotectant molecules such as proline, glycinebetaine, salicylic acid, spermidine, putrescine, GABA, ascorbic acid provides thermotolerance to crop plants (HanumanthaRao et al., 2016). For instance, exogenous application of proline mitigated HS effects in chickpea (Kaushal et al., 2011). Ascorbic acid application to mungbean seedlings under HS in a controlled environment improved seedling growth (Kumar et al., 2011). In cucumber, a 1 mM SA foliar spray provided heat tolerance by increasing CAT activity and thus reducing membrane damage and H₂O₂ levels (Shi et al., 2006). Similarly, Kaur et al. (2009) reported that exogenous application

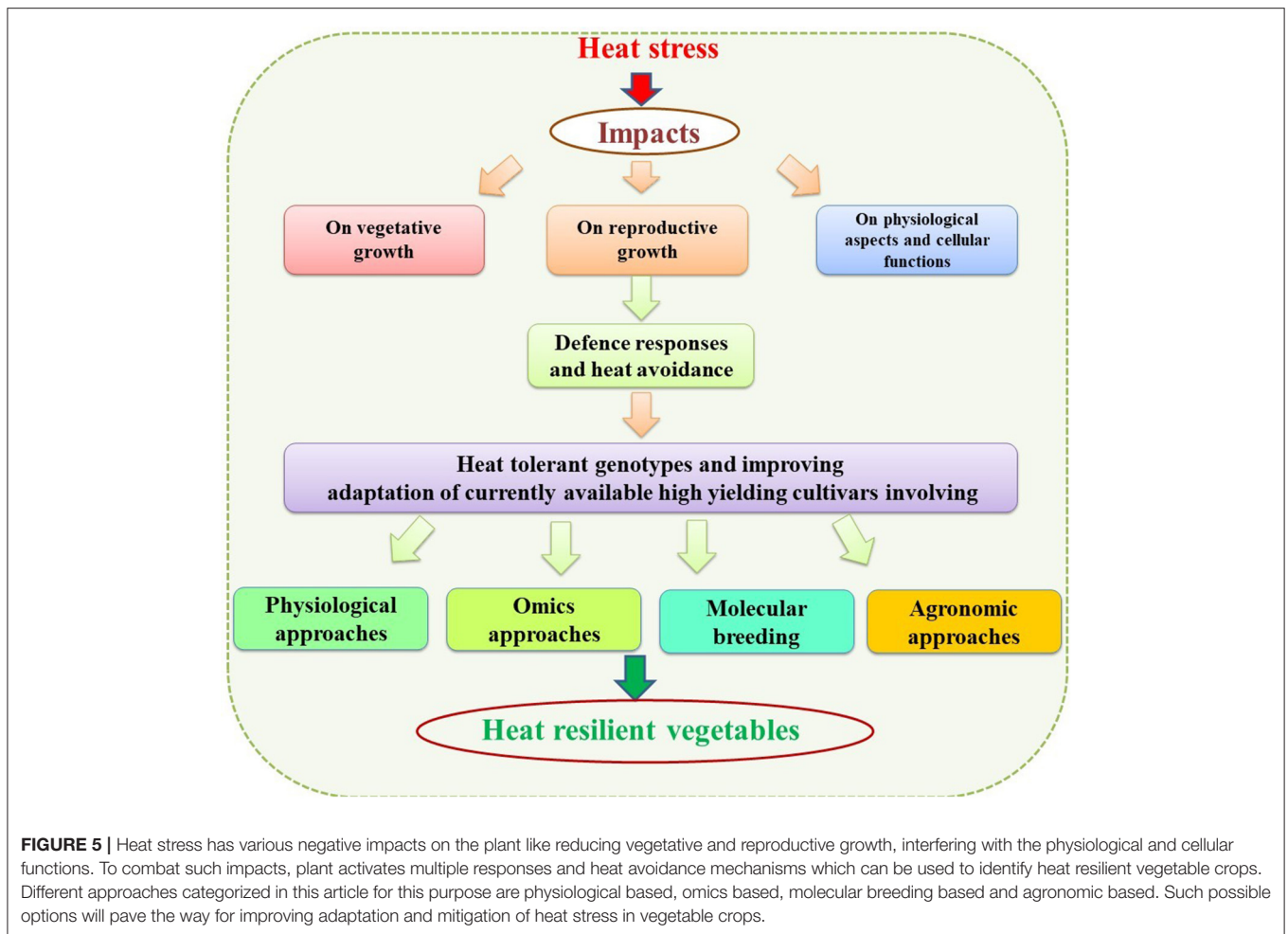
TABLE 6 | Heat-tolerant varieties of some vegetable crops.

Crop	Trait indicating tolerance	Heat-tolerant varieties	References
Broad bean (<i>Vicia faba</i>)	Seed yield	C.52/1/1/1	Abdelmula and Abuanja, 2007
Broccoli (<i>Brassica oleracea</i> var. <i>italica</i>)		Gypsy and Packman	Farnham and Bjorkman, 2011
Cabbage (<i>Brassica oleracea</i> var. <i>capitata</i>)	Cell membrane thermostability	Sousyu	Chauhan and Senboku, 1996
Capsicum (<i>Capsicum annuum</i>)		ASVEG#1 Mr. Lee No. 3 selex, CCA-119A, Susan's Joy, CCA-3288	Fu et al., 1993 Dahal et al., 2006
Cauliflower (<i>Brassica oleracea</i> var. <i>botrytis</i>)		IIHR Sel.-3 IIHR316-1, IIHR371-1 and PusaMeghna	Devi et al., 2017 Devi et al., 2017
Chickpea (<i>Cicer arietinum</i>)		ICCV07110, ICCV92944	Kumar et al., 2013
Common bean (<i>Phaseolus vulgaris</i>)	Chlorophyll fluorescence	Ranit and Nerine RS	Petkova et al., 2007
Cowpea (<i>Vigna unguiculata</i>)		IIHR-19-1 IT93K-452-1, IT98K-1111-1, IT93K-693-2, IT97K-472-12, IT97K-472-25, IT97K819-43 and IT97K-499-38.	Muralidharan et al., 2016 Timko and Singh, 2008
Lettuce (<i>Lactuca sativa</i>)		S24 and S39	Han et al., 2013
Mungbean (<i>Vigna radiata</i>)	Seed yield	NFM-6-5 and NFM-12-14	Khattak et al., 2006
Okra (<i>Abelmoschus esculentus</i>)	Biomass, number of flowers, pods and seeds weight/plant	EC693357, EC693358, EC693369, Harsha and ML1299	Sharma et al., 2016
Potato (<i>Solanum tuberosum</i>)	Yield (fruit number)	L2-11 and L4-48	Hayamanesh, 2018
Pea (<i>Pisum sativum</i>)	Tuber yield and dry matter	HT/92-621 and HT/92-802	Minhas et al., 2001
Soybean (<i>Glycine max</i>)	Pollen traits	IIHR-1 and IIHR-8	Muralidharan et al., 2016
Spinach (<i>Spinacia oleracea</i>)	Pollen traits	45A-46	Alsajri et al., 2019
Tomato (<i>Lycopersicon esculentum</i>)	Seed germination	DG 5630RR Ozarka II, Donkey, Marabu, and Raccoon	Salem et al., 2007 Chitwood et al., 2016
		CL1131-0-043-0-6, CL6058-0-3-10-2-2-2 PusaSadabahar, PusaSheetal, Pusa Hybrid-1	Abdul-Baki, 1991* Devi et al., 2017

of SA (10 and 20 μ M) to heat-stressed brassica seedlings (40–55°C) improved CAT and POX activities. Pretreatment of SA to mungbean seedlings decreased lipid peroxidation and enhanced antioxidant activity, improving membrane stability (Saleh et al., 2007). In chickpea, a 100 μ M SA foliar spray to heat-stressed seedlings (46°C) increased proline content (Chakraborty and Tongden, 2005). Thus, exogenous SA application mitigates the harmful impacts of heat-induced damage by strengthening antioxidative pathways. Foliar spray of Se (8 μ M) to cucumber plants exposed to 40/30°C during flower initiation (35–75 DAS) decreased oxidative damage by stabilizing the antioxidative mechanism and increasing ROS scavenging (Balal et al., 2016).

Microorganisms Imparting Thermotolerance

In addition to other factors, plant-associated microorganisms, including plant-growth-promoting rhizobacteria, endophytic bacteria, and symbiotic fungi, play a significant role in imparting thermotolerance in plants (Grover et al., 2011). Many agriculturally important microbes have been discovered that colonize and promote plant growth and aid in nutrient and disease control through various direct and indirect methods (Singh et al., 2016). The interaction between microorganisms and host plants imparting stress tolerance is a complex process and polygenic in nature. Ali et al. (2009) discovered a thermotolerant



strain of *Pseudomonas* sp. AMK-P6 in sorghum that elicits HSPs synthesis under high-temperature stress, and improves biochemical activities by inducing the synthesis of osmolytes such as proline, sugars, amino acids, and chlorophyll. *Pseudomonas putida* NBRI0987, a thermotolerant strain (<math><40^{\circ}\text{C}</math>) was isolated from the chickpea rhizosphere (Srivastava et al., 2008). A recent study on different rhizobacterial strains of pigeon pea at high temperature (30, 40, 50°C) showed that S1p1 and S12p6 were the most promising strains for plant growth and development, stimulating auxin production, flavonoid production, and siderophore formation (Modi and Khanna, 2018). It would be worth evaluating the effectiveness of these microbes in vegetable crops for induction of thermotolerance.

Protected Cultivation

Growing vegetables in protected environments on small-scale farms using modern technologies has gained considerable attention for their high yields and quality and regular vegetable supply in the off-season (Sabir and Singh, 2013). Protected cultivation involves manipulating environmental factors such as temperature, humidity, light, water, and soil by designing suitable structures and following appropriate practices

(Wittwer and Castilla, 1995). The main practices for protected cultivation are row tunnels, polytunnels, and mulching, which are more beneficial than open-field cultivation with less demand for fertilizers, pesticides, and water (Choudhary et al., 2013). In tomato, using a fogging system for 20 min/h (between 10 a.m. and 4 p.m.) in a hot shade house (>37°C) obtained high fruit yields with fewer physiological disorders (Ro et al., 2021). A similar fogging system improved the antioxidant defense responses in tomato plants (Leyva et al., 2013). Related approaches have been used to cultivate cucumber, capsicum, and lettuce with high yields (Sabir and Singh, 2013).

CONCLUSIONS

Vegetables are a distinct collection of plant-based foods that vary in nutritional diversity and form an important part of healthy diets. They also have great potential for boosting human health. Exposure to high temperatures or HS can directly or indirectly influence the production and quality of fresh vegetables. Several heat-induced morphological damages, such as poor vegetative growth, leaf tip burning, rib discoloration in leafy vegetables, sun burned fruits, decreased fruit size; pod abortion,

and unfilled pods are common, which can render vegetable cultivation unprofitable. Key physiological and biochemical effects associated with crop failure include membrane damage, photosynthetic inhibition, oxidative stress, and reproductive tissue damage. Reproductive stage has extensively been studied and found to be more sensitive to HS as it directly affects yields by reducing processes like pollen germination, pollen load, pollen tube growth, stigma receptivity, ovule fertility, and seed filling, resulting in poorer yields. Hence, sound and robust adaptation strategies are needed to mitigate the adverse impacts of HS to ensure the productivity and quality of vegetable crops.

Most important strategy to manage HS is deployment of heat tolerant cultivars (Figure 5). Physiological traits, such as stay-green trait, canopy temperature depression, cell membrane thermostability, chlorophyll fluorescence, relative water content, and stomatal conductance, are especially important in developing high-yielding heat-tolerant varieties/cultivars. Molecular approaches like omics, molecular breeding and transgenics have the potential to enhancing heat tolerance either by transferring heat tolerant genes/QTLs to elite cultivars with the help of molecular markers or elucidating mechanisms of tolerance leading to identification of heat tolerance genes and transferring those across genera or families *via* genetic modifications. Besides these approaches, simple agronomic methods are also important for mitigating HS effects at the grassroots level. Therefore, developing heat-tolerant plant types

using physiological, molecular, and breeding-based techniques is essential for sustaining vegetable production systems and human health. Further, these approaches will offer insight into the physiological and molecular mechanisms that govern thermotolerance and pave the way for engineering 'designer' vegetable crops for better health and nutritional security.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding authors.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct, and intellectual contribution to the work and approved it for publication.

ACKNOWLEDGMENTS

SC and PD thank CSIR-UGC, India for providing their doctoral research fellowship. The corresponding author (HN) is thankful to DST, UGC, DBT, CSIR, India, UWA (Australia), ICARDA (Morocco), IIPR (Kanpur, India), PAU (Ludhiana, India), and World Vegetable Center (at ICRISAT) for supporting the research work at various times.

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Chapter · February 2023

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Harnessing Genetic Variation in Physiological and Molecular Traits to Improve Heat Tolerance in Food Legumes

2

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Abstract

Plant genetic variations provide opportunity to develop new and improved cultivars with desired characteristics, hence gaining major attention from the scientists and breeders all over the world. Harnessing genetic variability is the key factor in the adaptation of plants to ever-rising temperature. Nowadays, such characteristic traits among the population can be used to develop various heat-resilient crop varieties and have a profound effect on restoring the balance between climate change and agriculture. Genetic variations in physiological and

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P. Muthu Arjuna Samy et al. (eds.), *Legumes: Physiology and Molecular Biology of Abiotic Stress Tolerance*, https://doi.org/10.1007/978-981-19-5817-5_2

molecular **traits** proved to be the major components for breeding programs to augment the gene pool. With genetic variations, it is possible to identify the phenotypic variations governed either by a single gene or by many genes that will be helpful for mapping associated quantitative trait loci. Genetic variations can also be traced by examining various physiological traits of a crop plant like growth traits (biomass, plant height, and root growth), leaf traits (stomatal conductance, chlorophyll content, chlorophyll fluorescence, photosynthetic rate, membrane stability, sucrose content, and canopy temperature depression), and floral traits (mainly associated with male gametophyte). Yield traits can also display enormous variation, making it highly useful/reliable for screening purposes. Further, genetic variation at the biochemical level can be assessed by measuring the expression of enzymes (related to oxidative stress and antioxidants) and metabolites (both primary and secondary). Evaluating how genetic variation influences phenotype is the ultimate objective of genetics, and using omics approaches can improve the understanding of heat tolerance-governing mechanisms. Further, collecting molecular data at different levels of plant growth and development will help to accelerate our understanding of the mechanisms linking genotype to phenotype.

Keywords

Genetic variations · Physiological and molecular traits · Metabolites · Phenotype · Heat tolerance · Omics approaches

2.1 Introduction

The Earth's rising average surface temperature, possibly due to global warming, poses a significant threat to the production potential of plants (Bita and Gerats 2013). Temperature is one of the main factors affecting plant phenology and plays a significant role in plant species distribution around the globe (Li et al. 2018). All plant species have a threshold temperature for growth to reach their yield potential; temperatures beyond the threshold are stressful at all plant growth stages, affecting overall performance (Wahid et al. 2007). Heat stress is supraoptimal temperatures that cause irreversible damage to plants (Hasanuzzaman et al. 2013). The impact of heat stress depends on species, specific growth stage, and intensity and duration of the stress (Farooq et al. 2017; Li et al. 2018).

Heat stress affects all stages of plant growth, viz., (1) seed germination (decreases seed germination rate and seedling root and shoot lengths), (2) vegetative growth (decreases plant height, biomass production, and root growth), (3) leaf structure and function (damages membrane structure, increases canopy temperature, decreases stomatal conductance, chlorophyll fluorescence, photosynthetic rate, and sucrose metabolism), (4) reproductive traits (mainly male gametophyte), (5) cellular homeostasis (elevated reactive oxygen species production), and (6) yield (reduced seed number, seed weight, and seed-filling rate). The reproductive stage is much more

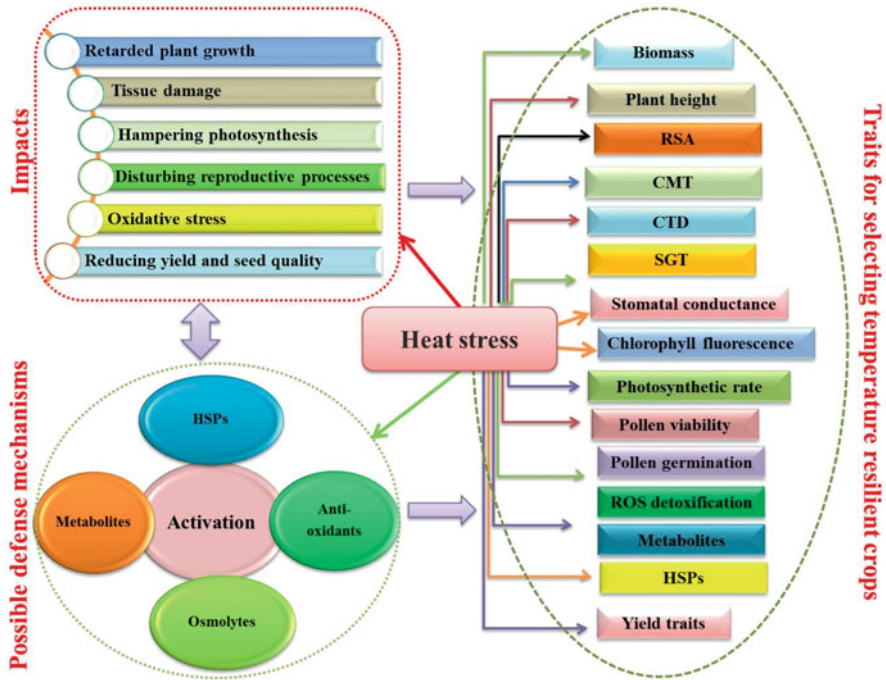


Fig. 2.1 Impacts, defense mechanisms against heat stress, and possible screening traits used for selecting temperature-resilient crops. High temperature adversely affects plant growth, causes tissue damage, and impairs vital processes such as photosynthesis, respiration, and reproduction. The injuries caused by heat stress lead to oxidative stress due to the production of reactive oxygen species, reducing crop yields. Plants implement various mechanisms to cope with heat stress, including antioxidant and metabolite production, accumulation and adjustment of compatible solutes, and most importantly chaperone (heat-stress proteins, HSPs) signaling and transcriptional activation. These mechanisms, regulated at the molecular level, enable plants to thrive under heat stress. Various growth traits [e.g., plant biomass, plant height, root system architecture (RSA)], leaf traits [e.g., cell membrane thermostability (CMT), canopy temperature depression (CTD)], stay-green trait (SGT), stomatal conductance, chlorophyll fluorescence, photosynthetic rate], reproductive traits (e.g., pollen viability, pollen germination), biochemical traits [e.g., reactive oxygen species (ROS) detoxification, various metabolites, HSP levels], and yield traits have been explored as heat-tolerance indicators for screening and breeding for heat tolerance

sensitive to heat stress than the vegetative stages, leading to lower seed weights and thus yield (Farooq et al. 2017). Plants are sessile organisms that can develop various adaptive mechanisms to endure heat waves, such as antioxidant production, synthesis of low-molecular-weight secondary metabolites, increasing heat-shock proteins (HSPs), and upregulating various transcription factors (Fig. 2.1). These endurance mechanisms vary between crop species, growth stage, and growth traits (Bita and Gerats 2013; Prasad et al. 2017).

2.2 Heat Stress and Legumes

Food legumes are an indispensable part of the human diet in developing countries. The major food legumes consumed worldwide are pea (*Pisum sativum* L.), chickpea (*Cicer arietinum* L.), common bean (*Phaseolus vulgaris* L.), lentil (*Lens culinaris* Medik.), mung bean/green gram (*Vigna radiata* L.), urdbean/black gram (*Vigna mungo* L.), and cowpea [*Vigna unguiculata* (L.) Walp.], and the major oilseed legumes include peanut (*Arachis hypogaea* L.) and soybean (*Glycine max* L.) (Maphosa and Jideani 2017). Due to their high nutritional value, legumes are ranked second after cereals. They are rich in protein (20–45%), carbohydrates (60%), dietary fiber (5–37%), and mineral matter (calcium, iron, potassium, phosphorus, copper, and zinc) with no cholesterol and low fat (Iqbal et al. 2006). Environmental factors, mainly rising temperatures, are major constraints on the growth and yield of food legumes. Heat stress adversely affects physiological and reproductive stages, resulting in poor seed yield and quality (Sita et al. 2017). Table 2.1 shows the threshold temperatures for commonly grown legumes in different regions of the world. Various studies have reported the impact of heat stress on seed germination, including poor emergence, germination percentage and radicle and plumule growth, and abnormal seedling vigor. For instance, chickpea germinated well at temperatures from 15 to 35 °C but poorly at temperatures above 40 °C (Kumari et al. 2018). Temperature beyond the threshold range showed lethal effects on the chickpea seedlings (Kumari et al. 2018). Similarly, a 50 °C heat treatment for 30 min significantly reduced seed germination, seed vigor, and seedling growth of dry black gram (Piramila et al. 2012).

Heat stress affects early vegetative growth, decreasing biomass accumulation and root growth and stunting plant height (Huang and Xu 2008; Kaushal et al. 2013).

Table 2.1 Threshold temperatures of few selective food legumes

Food legumes	Threshold temperature (°C)	References
Pulses		
Chickpea (<i>Cicer arietinum</i> L.)	16–27	Devasirvatham et al. (2013)
Common bean (<i>Phaseolus vulgaris</i> L.)	27–30	Rainey and Griffiths (2005)
Cowpea (<i>Vigna unguiculata</i> L.)	18–28	Craufurd et al. (1998)
Faba bean (<i>Vicia faba</i> L.)	22–23	Lavania et al. (2015)
Lentil (<i>Lens culinaris</i> Medik.)	18–30	Sita et al. (2017)
Mung bean (<i>Vigna radiata</i> L.)	28–30	Kaur et al. (2015)
Pea (<i>Pisum sativum</i> L.)	18–24	Jiang et al. (2015)
Urdbean/black gram (<i>Vigna mungo</i> L.)	30–35	Anitha et al. (2016)
Oilseeds		
Peanut (<i>Arachis hypogaea</i> L.)	22–28	Prasad et al. (1999)
Soybean (<i>Glycine max</i> L.)	20–26	Nahar et al. (2016)

Various studies have reported that heat stress inhibits physiological processes and cellular response activation, including decreased cellular membrane thermostability (Xu et al. 2006). Heat stress dramatically affects the photosynthetic process by disrupting chloroplast structures (thylakoid leakiness and grana stacking) and damaging the D1 protein of PSII due to the accumulation of reactive oxygen species (ROS) (Allakhverdiev et al. 2008; Sharkey 2005). Deactivation of the RuBisCo enzyme even at moderate–high temperatures further hampers photosynthesis (Allakhverdiev et al. 2008).

High temperatures significantly affect the reproductive phase, as reported in various food legumes, including mung bean (Kaur et al. 2015), chickpea (Kaushal et al. 2013), lentil (Bhandari et al. 2016; Sita et al. 2017), and peanut (Prasad et al. 1999). The main reproductive events affected by heat stress are male gametophyte development (meiosis in microspore mother cell, tapetum development in viable pollen, reduced pollen germination, reduced pollen tube growth), female gametophyte development (meiosis in the megaspore mother cell, tapetum development in viable eggs, altered stigmatic and style positions, reduced stigma receptivity), and fertilization (double fertilization and triple fusion) (Farooq et al. 2017; Prasad et al. 2017). Heat stress accelerates seed filling, inhibiting the accumulation of reserves in developing seeds, resulting in poor-quality seeds (Calderini et al. 2006) and reduced seed yields in food legumes such as chickpea (Awasthi et al. 2014) and lentil (Sehgal et al. 2018).

Understanding the impact of heat stress and the related mechanisms will help improve crop genotypes under heat stress. Therefore, identifying traits through extensive screening experiments related to heat tolerance is important for selecting better performing heat-tolerant genotypes of food legumes. This chapter identifies various traits in genotypes of various food legumes with different heat sensitivity/tolerance levels (Fig. 2.1) and offers insight into the overall traits and mechanisms used to select heat-tolerant genotypes.

2.3 Growth-Based Studies

High temperature adversely affects the growth and development of various legumes, restricting the growth cycle from emergence to seed set (Sehgal et al. 2018). Seed germination and seedling establishment, including root and shoot lengths and seedling vigor, are highly sensitive to high temperature. For instance, mung bean seedlings exposed to 45/35 °C had reduced growth (Kumar et al. 2011), and chickpea seedlings exposed to 40 °C for 96 h died (Kumari et al. 2018). Heat stress accelerates early vegetative growth, decreasing leaf number and dry matter accumulation (Tahir et al. 2008). Even moderate heat stress leads to rapid growth and development, resulting in shorter crop duration and less carbon assimilation over the plant's life cycle (Driedonks et al. 2016; Hatfield and Prueger 2015). Many studies have shown that disturbances in fundamental physiological processes, such as photosynthesis, respiration, water status, membrane stability, primary and secondary metabolites, and ROS generation, due to metabolic disparity resulted in

fewer and malformed plant parts (Wahid et al. 2007). Reduced vegetative growth also results from various anatomical and structural changes in cellular organelles, leading to necrosis, chlorosis, sunburn, senescence, and abscission of leaves, twigs, branches, and stems. Further, heat stress negatively affects plant architecture, including branching pattern, leaf area, internode elongation, and leaf/branch angles (Sabagh et al. 2020). The above studies indicate that several processes and molecules are involved in heat stress, reducing plant growth. Many studies have reported reduced vegetative growth in legumes, suggesting an interaction between potential yield and vegetative growth traits, for instance, in chickpea (Awasthi et al. 2014), common bean (Soltani et al. 2019; Yoldas and Esiyok 2009), faba bean (Siddiqui et al. 2015), lentil (Sita et al. 2017), mung bean (Kumar et al. 2011; Sharma et al. 2016), and soybean (Sabagh et al. 2020). Thus, the impact of heat stress on plant growth can be evaluated by assessing traits such as plant height, biomass, and root system architecture. Studies on contrasting genotypes revealed genetic variation in these traits in response to heat stress, which will help identify the mechanisms associated with heat tolerance in legumes.

2.3.1 Biomass

Biomass is an indicator of dry matter accumulation during plant growth, which is adversely affected by heat stress in various legumes (Sabagh et al. 2020). Several studies have revealed genetic variations in biomass accumulation in legumes under high temperatures. Thus, chickpea under heat stress ($>32/20$ °C) in a greenhouse had 22–30% less biomass than control plants (Kaushal et al. 2013). High temperature decreased biomass more in heat-sensitive chickpea genotypes (ICC5912, ICC10685) than heat-tolerant genotypes (ICC15614 and ICCV92944) (Kaushal et al. 2013). In another greenhouse study, heat stress (38/35 °C) decreased alfalfa (*Medicago sativa*) biomass, more so in heat-sensitive W1712 than heat-tolerant Bara310SC, compared to the control (25 °C) (Wassie et al. 2019). In the field, heat stress ($>32/20$ °C) significantly decreased lentil biomass (Sita et al. 2017). Genotypes IG3263, IG2507, IG3297, IG3312, IGG3327, IG3330, IG3546, IG3745, IG4258, and FLIP2009 retained the most biomass and were considered heat tolerant, while genotypes IG2519, IG2802, IG2506, IG2849, IG2821, IG2878, IG3326, IG3290, IG3973, IG3964, IG4242, DPL15, DP315, IG4221, and IG3568 were considered heat sensitive. High temperature ($>40/28$ °C) in the field significantly reduced (76%) plant biomass in 45 mung bean accessions from the World Vegetable Center, compared to control conditions (34/16 °C)—genotypes EC693357, EC693358, EC693369, Harsha, and ML 1299 retained the most biomass under heat stress and were considered heat tolerant, while genotypes EC693363, EC693361, KPS1, EC693370, and IPM02-3 retained the least biomass and were considered heat sensitive (Sharma et al. 2016).

2.3.2 Plant Height

Heat stress suppresses the overall vegetative growth of plants by affecting various growth-related mechanisms involving hormones and enzymes (Siddiqui et al. 2015). Plant height at different growth stages is a vital indicator of plant growth under stress situations and has been correlated with heat stress sensitivity (Prasad et al. 2008). A field study was undertaken to screen 12 Kabuli chickpea lines through delayed sowing for heat exposure (39.4 °C) (Mishra and Babbar 2014). Four chickpea lines—KAK2, JGK2, ICCV07311, and ICCV06301—were selected as heat tolerant based on plant height and other yield traits, with positive correlations between phenological traits (days to flowering, days to 50% flowering, maturity days, number of secondary branches, plant height) and yield traits (Mishra and Babbar 2014). Soybean genotypes (64) exposed to heat stress (40/32 °C; seedling stage for 20 days) varied in plant height—IREANE, CZ4898RY, CZ5242LL, CZ5375, ELLIS, 5N393R2, CZ4181, and 45A46 were categorized as heat tolerant, and 5115LL, S47-K5, S45-W9, 483C, 38R10, R01-416F, JTN-5110, S48RS53, and DG4825RR2/STS as heat sensitive, with the remainder categorized as moderately heat tolerant or moderately heat sensitive (Alsajri et al. 2019). Similarly, high temperature imposed on four common bean genotypes (Gima, Volare, Amboto, Nassan) by delaying normal sowing (late-sown) significantly reduced yields, relative to normal-sown plants, due to a shorter vegetative cycle, and genotypes Gima and Volare maintained taller plants than Amboto and Nassan (Yoldas and Esiyok 2009). In a greenhouse study, ten faba bean genotypes raised under high temperatures (HT1: 31 °C and HT2: 37 °C) had markedly reduced plant height compared to the control plants. Genotype C5 produced the tallest plants (heat tolerant), while Espan produced the shortest plants (heat sensitive) (Siddiqui et al. 2015).

2.3.3 Root System Architecture

Root system architecture (RSA) is the structure and spatial and temporal configuration of plant root systems (de Dorlodot et al. 2007). On a macroscale, RSA can determine the organization of the primary and secondary roots (Smith and De Smet 2012). On a microscale, RSA can determine root microstructures, such as fine root hairs and root tips and their interactions with soil and soil microorganisms responsible for water and mineral uptake (Wu et al. 2018). The spatial and temporal distribution of roots determines the crop's ability to exploit heterogeneously distributed soil resources (Brussaard et al. 2007). Heat stress directly affects plant roots by restricting carbohydrate transport from shoots to roots (Huang and Xu 2008). A comprehensive understanding of RSA helps us understand the effect of environmental conditions and management practices on crops, decreasing the deviation between potential and actual average yields (Garnett et al. 2009; Judd et al. 2015; Ryan et al. 2016). RSA plays an important role in plant–soil–microbe interactions and resolving the cross talk with beneficial soil microbes in the rhizosphere (Ryan et al. 2016).

Root architecture adapts to fluctuating environments. Therefore, we can improve crop performance by increasing root traits, such as root development allocation, and morphological, anatomical, or developmental plasticity (Sultan 2000). Thus, understanding the genetic and molecular mechanisms determining root phenotypic plasticity is necessary for effective selection and crop breeding efforts. Direct relationships between individual root architectural plasticity and yield have been reported across changing environments in various species (Niones et al. 2013; Sadras 2009). Root branching is important for improving soil anchorage and root surface area, enabling plants to reach more distant water reserves. In plants, high- and low-temperature stress generally reduces primary root length, lateral root density (number of lateral roots per unit primary root length), and emergence angle of lateral roots from the primary root, but does not affect the average lateral root length (McMichael and Quisenberry 1993; Nagel et al. 2009). Heat stress affects nutrient uptake due to a decline in root biomass and root hair surface area. In mung bean, high temperatures of 40/30 °C and 45/35 °C inhibited root growth by 13% and 23%, respectively (Kumar et al. 2011).

Root growth has lower optimal growth temperatures and is more sensitive to high temperatures than shoot growth (Huang and Gao 2000; Xu and Huang 2000). Some plant roots synthesize heat-shock proteins (HSPs) by ameliorating their working efficiency (Nieto-Sotelo et al. 2002). Root phenotyping of 577 common bean genotypes in variable heat environments revealed significant relationships between seed yield and seedling basal root number, seedling adventitious root abundance, and seedling taproot length (Strock et al. 2019). The Mesoamerican genotypes yielded higher than the Andean genotypes under heat stress (Strock et al. 2019). In another study, five chickpea genotypes were assessed for thermotolerance at 30, 35, and 40 °C using root length and root branching as criteria, which identified CSJD 884 and RSG 895 as heat tolerant and C 235 as heat sensitive (Kumari et al. 2018). The 40 °C treatment for 96 h negatively affected root branching in chickpea (Kumari et al. 2018).

Similarly, screening 48 lentil genotypes in a growth chamber at 34 °C using root length as one of the selection criteria identified Ranjan, Moitree, 14-4-1, IC 201710, and IC 208329 as heat tolerant (Choudhury et al. 2012). In another lentil study, heat-tolerant genotypes (IG2507, IG3263, IG3745, IG4258, and FLIP2009) had 1.8–22-fold more root nodulation than heat-sensitive genotypes (IG2821, IG2849, IG4242, IG3973, IG3964) under heat stress (>32/20 °C) (Sita et al. 2017).

2.4 Yield-Based Traits

Heat stress negatively impacts reproductive efficiencies and seed development stages, reducing crop yield and quality (Sehgal et al. 2018). Various studies have shown that the relative performance of plants in terms of yield under heat stress is useful for selecting genotypes for crop improvement programs (detailed below). Heat stress severely affects seed development and seed filling in many crop species, resulting in abnormal and shriveled seeds (Egli 1998). The direct effect of heat stress

on the sink potential of maturing seeds (Commuri and Jones 1999) disrupts cell division in the endosperm, decreases the number of starch granules, and reduces starch accumulation. Many screening studies under heat stress have included yield traits, such as seed number, seed weight, seed-filling rate, and duration (Farooq et al. 2017).

2.4.1 Seed Number

Heat stress disrupts pollination and fertilization events that directly curtail seed number. For instance, high temperature (45/32 °C) reduced seed number in mung bean genotypes relative to the control (34/16 °C), more so in heat-sensitive genotypes (EC693363, EC693361, KPS1, EC693370, and IPM02-3) than heat-tolerant genotypes (EC693357, EC693358, EC693369, Harsha, and ML 1299) (Sharma et al. 2016). Similarly, in a greenhouse study, the 33/30 °C treatment reduced pod number and seed number per pod the most in 24 common bean genotypes exposed to varying temperatures (24/21 °C, 27/24 °C, 30/27 °C, 33/30 °C), more so in heat-sensitive genotypes (−66%; A55, Labrador, Majestic, IJR) than heat-tolerant genotypes (−31%; Brio, Carson, G122, HB1880, HT38, Venture) (Rainey and Griffiths 2005). In another study, heat stress (36/27 °C) reduced seed number per pod in all but two cowpea lines (heat-tolerant B89-600 and TN88-63) evaluated for heat tolerance in a greenhouse (Ehlers and Hall 1998). In another greenhouse study, high temperature (38 °C) during the reproductive stage of 211 pea genotypes revealed HUDP-25, IPF-400, HFP-4, and DDR-56 as heat tolerant and VL-40, KPMR-615, DDR-61, and KPMR-557 as heat susceptible based on yield parameters; for example, heat-tolerant genotypes had more seeds per plant (35–197) than heat-sensitive genotypes (1–58) (Mohapatra et al. 2020).

2.4.2 Seed Weight

Seed weight is one of the major traits governing crop yield and is thus used as a screening trait in many studies to select heat-tolerant varieties. For example, chickpea exposed to different temperatures (35/25 °C, 40/30 °C, and 45/35 °C) in a growth chamber decreased seed weight at 40/30 °C by 37–45% in sensitive genotypes (ICC14183, ICC5912) relative to tolerant genotypes (ICCV07110, ICCV92944). However, higher temperature (45/35 °C) had a more severe effect, with fewer seeds in tolerant genotypes and no pod set in sensitive genotypes (Kumar et al. 2013). Similar findings were recorded in mung bean when high temperatures (45/32 °C) coincided with reproductive growth; seed weights declined by 48.3% in the sensitive genotype (SML668) and 35.1% in the tolerant genotype (SML832), relative to the control (Kaur et al. 2015). Likewise, seed weight of lentil plants exposed to high temperature (>32/20 °C) in the field declined, relative to control plants (Bhandari et al. 2016), more so in the heat-sensitive genotypes (−50%; LL699 and LL1122) than the heat-tolerant genotype (−33%; LL931).

In common bean, a high temperature of 33/30 °C was adequate for selecting heat-tolerant (Carson, G122, Brio, HB1880, HT38, Venture) and heat-sensitive genotypes (Labrador, A55, Majestic, IJR), based on seed weight trait in the field; seed weights decreased by 88% in heat-sensitive genotypes compared with 35% in heat-tolerant genotypes (Rainey and Griffiths 2005). Different location-based yield trials—Coachella (USA; 41/25 °C) and Riverside (USA; 36/17 °C)—were used to screen three groups of cowpea genotypes differing in heat sensitivity (Ismail and Hall 1999). Yield parameters, mainly seed weight, and seeds/pod, decreased significantly as the temperature increased. Tolerant genotypes (H36, H8-9, DLS99) retained more seed weight (193 mg/seed) at higher temperature (41/25 °C) than heat-sensitive genotypes (168 mg/seed; CB5, CB3, DLS127). Mohapatra et al. (2020) reported that heat stress reduced 25-seed weight in pea in heat-susceptible genotypes (VL-40, KPMR-615, DDR-61, KPMR-557) to a mean value of 4.13 g, while heat-tolerant genotypes (HUDP-25, IPF-400, HFP-4, DDR-56) had higher seed weights (4.60 g).

Heat stress accelerates the seed-filling rate but decreases the seed-filling duration. In cowpea, increasing the temperature from 15.5 to 26.6 °C increased the seed-filling duration by 14–21 days (Nielsen and Hall 1985). During seed development, heat stress (>32/20 °C) increased the seed-filling rate in six chickpea genotypes relative to the optimum temperature, and shortened the seed-filling duration, more so in heat-sensitive (ICC4567) than heat-tolerant (ICC1356, ICC15614) genotypes (Awasthi et al. 2014). Thus, reduced seed weight due to heat stress could be related to a decline in seed-filling processes (Sehgal et al. 2017).

2.5 Pollen Grain Traits

Pollen grains are sensitive to extreme temperatures from early pollen development to fertilization, including meiosis I and meiosis II of the microspore mother cell, early dissolution of the tapetum layer, anther dehiscence, pollen shedding, pollen viability, pollen germination, pollen tube growth, and fertilization (Barnabas et al. 2008; Hedhly 2011; Kumar et al. 2013). Observations on heat stress-induced arrest of male gametophyte development revealed the importance of starch accumulation during pollen development because it gives rise to carbohydrates at maturity (Raja et al. 2019). Heat stress prevents starch accumulation during pollen development, which possibly contributes to reduced pollen viability (Pressman et al. 2002). High temperature during anthesis leads to yield losses due to poor pollen traits such as pollen viability, pollen production, and pollen tube length in crop plants, including chickpea (Devasirvatham et al. 2012; Kaushal et al. 2013), common bean (Suzuki et al. 2001), mung bean (Kaur et al. 2015), lentil (Kumar et al. 2016; Sita et al. 2017), and soybean (Salem et al. 2007). Heat-tolerant and heat-sensitive common bean genotypes were identified based on pollen stainability—exposure to high temperature (>28 °C) for 8–11 days before anthesis decreased pollen stainability and increased flower abortion, reducing pod yield (Suzuki et al. 2001). Heat-sensitive genotypes (Kentucky Wonder, Oregon, and Okinawa Local) had <20% pollen

stainability, while the heat-tolerant genotype (Haibushi) had 60% pollen stainability under heat-stress conditions. Heat stress (43/30 °C and 45/32 °C) in mung bean adversely affected reproductive components, reducing pollen viability, pollen germination, and pollen tube length (Kaur et al. 2015), compared to the controls (>40/25 °C). Moreover, high temperature during microsporogenesis reduced pollen number and produced shriveled pollen grains, more so in the heat-sensitive genotype than the heat-tolerant genotype. Another field study exposed 45 mung bean genotypes to high temperature (42 °C) during the flowering stage (Sharma et al. 2016).

An *in vitro* pollen study revealed that heat-tolerant mung bean genotypes (C693357, EC693358, EC693369, Harsha, ML1299) had better pollen viability and pollen germination than sensitive genotypes (KPS1, EC693361, EC693363, EC693370, IPM02-3) (Sharma et al. 2016). Other pollen traits (pollen germination and pollen load) were used to screen chickpea, identifying heat-tolerant (ICC15614, ICCV92944) and -sensitive (ICC10685, ICC5912) genotypes (Kaushal et al. 2013). Another study identified tolerant and sensitive chickpea genotypes using pollen traits (Devasirvatham et al. 2013) under heat stress (≥ 35 °C); pollen grains were more sensitive to high temperature than stigmas, with genotype ICC1205 identified as heat tolerant and ICC4567 as heat sensitive. Kumar et al. (2016) screened 334 lentil accessions for heat tolerance under field conditions (>35/25 °C) and selected heat-tolerant genotypes (FLIP2009-55L, IG2507, and IG4258) based on pollen traits. Sita et al. (2017) revealed that high temperature (>32/20 °C) in the field reduced pollen viability to a greater extent than control (<32/20 °C), with higher pollen germination in heat-tolerant genotypes (48–50%; IG2507, IG3263, IG3745, IG4258, and FLIP2009) than heat-sensitive genotypes (28–33%).

Sixteen pea accessions were screened for heat tolerance by exposing plants to 45 °C for 2 h; the Ran1 line was selected as heat tolerant and R-Af-1, C-Af-2, and Cs-Af-3 as heat sensitive based on pollen traits (pollen viability, pollen germination, pollen tube growth) (Petkova et al. 2009). In another study, two pea cultivars were tested for their differential sensitivity to high temperature (27/18 °C, 30/18 °C, 33/18 °C, and 36/18 °C) based on *in vitro* pollen germination, pollen tube length, pollen surface morphology, and pollen wall structure; as a result, CDC Sage was classified as tolerant and CDC Golden as sensitive genotype based on its higher pollen germination and stable lipid composition in pollen than the heat-sensitive genotype at 36 °C (Jiang et al. 2015).

Pollen-based traits were also used to screen 44 soybean genotypes for heat tolerance at 38/30 °C (Salem et al. 2007). The total stress response index based on reproductive traits such as pollen germination and pollen tube length was used to categorize the genotypes. Three of these genotypes, heat tolerant (DG 5630RR), heat intermediate (PI 471938), and heat sensitive (Stewart III), were selected for pollen grain morphology; the heat-sensitive genotype had deformed pollen with reduced aperture. Based on the studies mentioned above, pollen grain structure and function could be used as a screening tool for heat tolerance in soybean (Salem et al. 2007).

2.6 Leaf-Based Parameters

2.6.1 Stomatal Conductance

Stomatal conductance is a measure of stomatal opening or the rate of passage of CO₂ entering and water vapor releasing through leaf stomata. Stomatal conductance is affected by many environmental factors, including high temperature. Stomatal conductance increases with increasing temperature to increase photosynthesis, which can help plants endure short heat waves (Urban et al. 2017). Moreover, plants acclimatize to high temperatures by evaporating more water, keeping their canopies cool despite the presence of fewer stomata (Crawford et al. 2012). Therefore, regulating stomatal conductance under high temperatures is a useful trait for screening contrasting genotypes. Stomatal conductance can be recorded with a leaf porometer and expressed in mmol m⁻² s⁻¹ (Priya et al. 2018). Heat-tolerant chickpea genotypes (ICC15614, ICCV92944) had higher stomatal conductance (265–271 mmol H₂O m⁻² s⁻¹) than heat-sensitive genotypes (ICC5912, ICC10685; 187–210 mmol H₂O m⁻² s⁻¹) under high temperatures (>32/20 °C) imposed by late sowing (Kaushal et al. 2013). Similarly, for late-sown mung bean genotypes, the heat-tolerant genotype (SML 868) had higher stomatal conductance (99 mmol m⁻² s⁻¹) than the heat-sensitive genotype (SML 668; 90 mmol m⁻² s⁻¹) (Kaur et al. 2015). In another study, five common bean genotypes (SB761, SB776, SB781, Jaguar, TB1) were screened in the greenhouse at three temperature regimes (35/30 °C, 40/35 °C, 45/40 °C); stomatal conductance in all genotypes increased with increasing temperature until 40/35 °C but declined at 45/40 °C except in genotype TB1, which was identified as heat tolerant (Traub et al. 2018). Similarly, Sita et al. (2017) identified heat-tolerant (IG2507, IG3263, IG3745, IG4258, FLIP2009) and heat-sensitive (IG2821, IG2849, IG4242, IG3973, IG3964) lentil genotypes based on stomatal conductance—the heat-tolerant genotypes had higher stomatal conductance values (390–497 mmol m⁻² s⁻¹) than heat-sensitive genotype (205–313 mmol m⁻² s⁻¹) in a late-sown environment.

2.6.2 Stay-Green Trait

Heat stress negatively affects photosynthesis by decreasing leaf pigment content and damaging leaf ultrastructure in heat-sensitive genotypes. Chloroplasts play a vital role in photosynthesis as one of the most heat-sensitive organelles (Abdelmageed and Gruda 2009; Krause and Santarius 1975). Decreased total chlorophyll content and changes in the chlorophyll a/b ratio have been correlated with reduced photosynthesis during heat stress due to reduced “antenna (pigment unit)” size that reduces light harvesting (Blum 1986; Harding et al. 1990; Shanmugam et al. 2013). Chlorophyll retention (chlorophyll content) is an integrative trait and is considered a good criterion for screening heat-stress tolerance in legume crops. For example, high-temperature (38/28 °C) stress for 14 days at the flowering stage in a growth chamber caused anatomical and structural changes, including damaged

plasma membrane, chloroplast membrane, and thylakoid membranes and reduced leaf photosynthetic rate, in the leaves of soybean genotype K 03-2897. Plant chlorophyll maintenance, also known as the stay-green (SGR) trait, is affected by high temperature. Understanding the physiological and molecular mechanisms of the stay-green trait is important for controlling photosynthetic ability (Abdelrahman et al. 2017). The SGR trait, or delayed leaf senescence (DLS), allows plants to retain leaves in an active photosynthetic state under high temperatures to maintain assimilation and increase crop yield (Gregersen et al. 2013; Kumari et al. 2013). Stay-green genotypes can carry out photosynthesis for longer than senescent types, often with yield benefits (Borrell et al. 2014). The development of contrasting F6 and F7 recombinant-inbred lines of cowpea for the DLS trait under heat stress revealed that the DLS trait increased plant survival and seed size under heat stress (Ismail et al. 2000). Of ten common bean genotypes, only BRS Expedito, FT-Taruma, and BAF071 had the stay-green trait, with higher initial chlorophyll *a* contents, less chlorophyll degradation, and higher grain yields under heat stress than the other genotypes (Schmit et al. 2019).

A field experiment screening 58 chickpea genotypes for high-temperature tolerance (25–40 °C) during the reproductive phase identified eight genotypes—Pusa 1103, Pusa 1003, KWR 108, BGM 408, BG 240, PG 95333, JG 14, and BG 1077—as heat tolerant, with higher chlorophyll contents than the heat-sensitive genotypes (ICC1882, PUSA 332, PUSA 112, RSG 803) (Kumar et al. 2017). Two heat-tolerant chickpea genotypes (ICC1356, ICC15614) maintained higher chlorophyll contents under heat stress (>32 °C/20 °C) in the field than two heat-sensitive genotypes (ICC4567, ICC5912) (Awasthi et al. 2017). In another study, chickpea genotypes were grown in the greenhouse to flowering (42 and 46 DAS) and then in a growth chamber under increasing temperatures (by 2 °C per day from 27/18 °C to 42/25 °C; day/night) for 8 days (anthesis), which revealed that genotype JG14 (heat tolerant) had higher total leaf chlorophyll content than genotype ICC16374 (heat sensitive) (Parankusam et al. 2017). Similarly, heat-tolerant chickpea genotypes Pusa-1103 and BGD-72 had significantly higher chlorophyll contents than heat-sensitive genotypes Pusa-256 and RSG-991 under high temperatures (25/35 °C) in wooden polyethylene chambers (Singh et al. 2018). Likewise, Kaushal et al. (2013) identified two heat-tolerant (ICC15614, ICCV92944) and two heat-sensitive (ICC10685, ICC5912) chickpea genotypes based on the chlorophyll content, after exposure to heat stress (>32/20 °C) in the field during reproductive development. A field study on lentils measured the stay-green trait as the loss of total chlorophyll (Chl) in leaves under high temperature (>32/20 °C) during the reproductive phase; heat-stressed plants had lower total chlorophyll concentrations than the control plants, and the heat-tolerant genotype (IG3263) retained more Chl than the heat-sensitive genotype (IG4242) (Sita et al. 2017). Similarly, lentil genotypes LL699 and LL931 (heat tolerant) retained more chlorophyll than genotype LL1122 (heat sensitive) in outdoor conditions (>32/23 °C), which was confirmed in a controlled environment with plants subjected to 33/15 °C or 35/20 °C during reproductive growth (Bhandari et al. 2016). Heat stress in the field (>30/20 °C) during reproductive growth and seed filling revealed two lentil heat-tolerant genotypes (1G 2507 and 1G 4258) with high

leaf chlorophyll concentrations and two heat-sensitive genotypes (1G 3973 and 1G 3964) with lower chlorophyll concentrations (Sehgal et al. 2017). In another study, common bean genotypes exposed to 32/25 °C at the V4 developmental stage identified two genotypes (Sacramento and NY-105) with high chlorophyll contents, indicating their high thermotolerance, relative to the thermosensitive genotype Redhawk with low chlorophyll content (Soltani et al. 2019). Likewise, in a heat-sensitive mung bean genotype (SML668), chlorophyll content declined, relative to the heat-tolerant genotype (SML832), grown under heat stress (43/30 °C and 45/32 °C) in outdoor late-sown conditions, contributing to an increase in leaf temperature (Kaur et al. 2015). Mung bean genotypes EC693357, EC693358, EC693369, Harsha, and ML 1299 produced more chlorophyll content under heat stress than genotypes EC693363, EC693361, KPS1, EC693370, and IPM02-3 (Sharma et al. 2016). Screening of ten faba bean genotypes for heat-stress tolerance (37 °C) revealed that genotype C5 tolerated high temperature by retaining more chlorophyll, while genotype Espan had less chlorophyll and was relatively more sensitive to heat stress (Siddiqui et al. 2015). In a recent study, 4-week-old seedlings of 15 alfalfa cultivars were exposed to heat treatment (38/35 °C) for 7 days in a growth incubator; genotypes Gibraltar, WL354HQ, Golden Queen, Siriver, WL712, and Sanditi had significantly lower Chl contents (heat sensitive) than genotypes Bara310SC, WL363HQ, WL656HQ, and Magna995 (heat tolerant) (Wassie et al. 2019).

2.6.3 Chlorophyll Fluorescence

Chlorophyll (Chl) fluorescence (F_v/F_m ratio) is used as an indicator of functional changes in photosynthetic apparatus under abiotic or biotic stress (Yamada et al. 1996). The relationships between essential photosynthetic responses and chlorophyll fluorescence are pivotal as they provide information on the plant's photosynthetic ability and acclimation limit under stress conditions (Kalaji et al. 2018; Lichtenthaler 1987). Chlorophyll fluorescence is a fast, nondestructive, and effective common tool for determining heat-stress responses as it can reveal damage before visible stress symptoms appear (Baker 2008; Méthy et al. 1994; Wilson and Greaves 1990). Of the photosynthetic apparatus, photosystem II (PSII) is the most heat-labile cell structure (Vacha et al. 2007). Since damage to PSII is often the first response of plants subjected to thermal stress (Mathur et al. 2011), measuring chlorophyll *a* fluorescence is an effective and noninvasive technique for identifying damage to PSII efficiency (Baker 2008; Baker and Rosenqvist 2004). The ratio between variable fluorescence (F_v) and maximum fluorescence (F_m), or F_v/F_m , reflects the maximum quantum efficiency of PSII (Butler 1978). When plants are exposed to abiotic stress, including thermal stress, F_v/F_m often declines (Molina-Bravo et al. 2011; Sharma et al. 2012; Willits and Peet 2001). Screening methodologies have used chlorophyll fluorescence to detect and quantify damage in PSII and thylakoid membranes in several legume crops under heat stress, including chickpea, groundnut, pigeon pea, and soybean (Herzog and Chai-Arree 2012; Srinivasan et al. 1996). Recent study assessed the response of four chickpea genotypes to a natural

temperature gradient during the reproductive stage in the field and a climate chamber using chlorophyll fluorescence. Field experiments were conducted over two winter seasons; two genotypes (Acc#RR-3, Acc#7) showed tolerance (F_v/F_m 0.83–0.85) and two (Acc#2, Acc#8) showed sensitivity (F_v/F_m 0.78–0.80) to heat stress. The field results were validated in the climate chamber experiment, where F_v/F_m declined more in the heat-sensitive (0.74–0.75 at 35/30 °C) than heat-tolerant (0.78–0.81 at 35/30 °C) genotypes when exposed to short-term heat treatments (30/25 °C and 35/30 °C) (Makonya et al. 2019). In another chickpea study, heat stress (>30 °C) in the field during the reproductive stage reduced F_v/F_m more in two heat-sensitive genotypes ICC10685 and ICC5912 (0.48, 0.41) than in two heat-tolerant genotypes ICC15614 and ICCV92944 (0.64, 0.60) (Awasthi et al. 2014; Kaushal et al. 2013). A similar study, where four contrasting chickpea genotypes—two heat tolerant (ICC1356, ICC15614) and two heat sensitive (ICC4567, ICC5912)—were analyzed in the field, revealed that the tolerant genotypes maintained higher chlorophyll fluorescence (F_v/F_m 0.60) on exposure to heat stress (>32/20 °C) than the sensitive genotypes (F_v/F_m 0.50) (Awasthi et al. 2017). In lentils, photosynthetic efficiency was measured as PSII function (F_v/F_m ratio) in the field by exposing plants to heat stress (>32/20 °C) during the reproductive stage. Heat-tolerant genotypes—IG2507, IG3263, IG3297, IG3312, IG3327, IG3546, IG3330, IG3745, IG4258, and FLIP2009—maintained higher chlorophyll fluorescence (F_v/F_m 0.71) under stress than heat-sensitive genotypes IG2821, IG2849, IG4242, IG3973, and IG3964 (F_v/F_m 0.58) (Sita et al. 2017). Similarly, two heat-tolerant lentil genotypes (1G 2507 and 1G 4258) exposed to heat stress (>25 °C) during reproductive growth and seed filling in the field had higher chlorophyll fluorescence (F_v/F_m 0.67) than two heat-sensitive genotypes (1G 3973 and 1G 3964; F_v/F_m 0.57) (Sehgal et al. 2017). Likewise, the screening of 41 mung bean lines grown outdoors and exposed to high temperatures (>40/28 °C) during the reproductive stage revealed several promising heat-tolerant lines (EC693358, EC693357, EC693369, Harsha, ML1299) with high F_v/F_m ratios (0.73–0.75) compared to sensitive lines (0.61–0.67), which could serve as useful donor/s for breeding programs and as a suitable base plant source to gain insight into heat stress-induced effects in cell metabolism (Sharma et al. 2016). Nine common bean lines were evaluated for changes in chlorophyll fluorescence under heat stress during flowering (45 °C for 2 h) in a greenhouse; thermotolerant lines 83201007 and RRR46 had higher F_v/F_m values under heat stress than the heat-sensitive line Secuntsa (Petkova et al. 2009). In another study, 12 varieties and lines of common bean were exposed to 42 °C in the field during the reproductive period; two genotypes (Ranit and Nerine) maintained their F_v/F_m values at 42 °C, relative to the controls at 26 °C, and were considered heat tolerant. These two genotypes also showed good productivity and quality and can be used as parental lines in bean breeding programs (Petkova et al. 2007). Screening of 15 alfalfa genotypes by exposing seedlings to 38/35 °C day/night for 7 days in a growth chamber identified Bara310SC (F_v/F_m 0.79) and WL712 (F_v/F_m <0.79) as heat-tolerant and heat-sensitive cultivars, respectively (Wassie et al. 2019), showing that F_v/F_m is an effective tool for phenotyping contrasting genotypes for heat tolerance.

2.6.4 Photosynthetic Rate

Heat stress affects the stay-green trait, chlorophyll content, and chlorophyll fluorescence, which affects RuBisCo activation, decreasing the photosynthetic rate (Salvucci Michael and Crafts-Brandner 2004; Sharkey 2005). Hence, photosynthetic rate can be used as a screening parameter for selecting heat-tolerant genotypes. Variation in photosynthetic rate among plant species in response to heat stress has been well documented. For example, the response of four chickpea genotypes to a natural temperature gradient in the field at the flowering stage identified two heat-tolerant genotypes (Acc#RR-3, Acc#7) with high P_n and two heat-sensitive genotypes (Acc#2, Acc#8) with lower P_n ; these results were validated in a climate chamber experiment set at 30/25 °C and 35/30 °C (Makonya et al. 2019). In another study, 56 chickpea genotypes were exposed to high temperatures in the field from flowering to crop maturity (maximum temperatures 25–40 °C)—the tolerant genotypes (PUSA1103, PUSA1003, KWR108, BGM408, BG240, PG95333, JG14, BG) had higher P_n than the sensitive genotypes (ICC1882, PUSA372, PUSA2024) (Kumar et al. 2017). In a similar study in lentil, two heat-tolerant (1G 2507 and 1G 4258) genotypes had higher photosynthetic rate (P_n) than two heat-sensitive (1G 3973 and 1G 3964) genotypes exposed to heat stress (>25 °C) in the field during reproductive growth and seed filling (Sehgal et al. 2017).

Soybean cultivars IA3023 and KS4694 and PI lines PI393540 and PI588026A expressed heat tolerance and susceptibility with high and low P_n , respectively (Djanaguiraman et al. 2019). The two cultivars had less thylakoid membrane damage than the PI lines. In an earlier study on soybean, genotype K 03-2897, exposed to high temperature (38/28 °C) in a growth chamber for 14 days at the flowering stage, significantly decreased P_n due to anatomical and structural changes (increased thickness of palisade and spongy layers and lower epidermis) in cells and cell organelles, particularly damage to chloroplasts and mitochondria (Djanaguiraman and Prasad 2010).

2.6.5 Sucrose

Leaf photosynthates are transported to sink organs primarily as sucrose, and sucrose synthase (SS) is a key enzyme for sucrose to enter various metabolic pathways (Calderini et al. 2006). Downregulation of SS indirectly inhibits carbohydrate production, eventually reducing yield and quality. Maintaining sucrose levels is vital during stressed conditions, which depend on its synthesis and hydrolysis. Heat-stressed plants had significantly lower activities of key enzymes—sucrose phosphate synthase (SPS) and SS—involved in sucrose synthesis than non-stressed plants. Sucrose availability to reproductive organs is crucial for sustaining their function (Kaushal et al. 2013). Heat-tolerant genotypes can stabilize the photosynthetic process better than heat-sensitive genotypes. Heat stress disturbs sucrose production in leaves and impairs its transportation to reproductive organs (Kaushal et al. 2013; Li et al. 2012). Limitations in sucrose supply to reproductive

organs, particularly under thermal stress, restrict flower development and function and pod and seed filling, reducing crop yield (Kaushal et al. 2013; Li et al. 2012). Measuring sucrose concentrations reveals the photosynthetic status of plants under heat stress (Awasthi et al. 2014). Sucrose synthase is strongly associated with heat tolerance in chickpea; heat-sensitive genotypes produced far less leaf sucrose than heat-tolerant genotypes, which impaired its supply to developing reproductive organs (flowers, pods, and seeds) in chickpea (Kaushal et al. 2013). Screening a large core collection of chickpea genotypes for heat tolerance (32/20 °C) in field condition identified two heat-tolerant (ICC15614, ICCV92944) and two heat-sensitive (ICC10685, ICC5912) genotypes. The heat-sensitive genotypes had significantly greater inhibition of RuBisCo (carbon-fixing enzyme), SPS, and SS than the heat-tolerant genotypes and thus produced less sucrose than the tolerant genotypes (Kaushal et al. 2013). Heat-sensitive (ICC16374) and heat-tolerant (JG14) chickpea genotypes exposed to gradually increasing temperatures (2 °C per day from 27/18 °C to 42/25 °C; day/night) for 8 days at anthesis in a growth chamber revealed greater sucrose synthase expression in JG14 than ICC16374 (Parankusam et al. 2017). Two tolerant chickpea genotypes (Acc#7 and Acc#RR-3) had higher starch contents and were relatively unaffected by heat-stress exposure compared to two heat-sensitive genotypes (Acc#2, Acc#8) at high temperature (35/30 °C) in a control chamber (Makonya et al. 2019). Therefore, an increased abundance of sucrose synthase in the tolerant genotype reasserted its potential role during heat-stress tolerance; this may ensure successful fertilization due to sustained pollen viability under heat stress, enhancing pod set and yield, as reported earlier for the tolerant genotype (ICC15614) (Krishnamurthy et al. 2011).

In lentil, sucrose production is vital for leaf and anther function and has been correlated with SPS activity in natural high-temperature environments (>32/20 °C). Heat-tolerant lentil genotypes (IG2507, IG3263, IG3297, IG3312, IG3327, IG3546, IG3330, IG3745, IG4258, FLIP2009) produced more sucrose in leaves (65–73%) and anthers (35–78%) than heat-sensitive genotypes (IG2821, IG2849, IG4242, IG3973, IG3964), which was associated with superior reproductive function and nodulation in tolerant genotypes (Sita et al. 2017). Limitations in sucrose supply may disrupt the development and function of reproductive organs (Prasad and Djanaguiraman 2011; Snider et al. 2011). In a similar study, two heat-tolerant (1G 2507 and 1G 4258) lentil genotypes exposed to heat stress (>25 °C) in the field had higher SS activity and thus higher sucrose contents in leaves and seeds than two heat-sensitive (1G 3973 and 1G 3964) genotypes (Sehgal et al. 2017). Thus, sucrose synthase in seeds and leaves is strongly correlated with seed yield; therefore, reductions in seed size and weight are attributed mainly to reductions in sucrose content.

Mung bean genotypes tested under heat stress (>40/25 °C day/night) during flowering and podding outdoors and in a controlled environment showed that two heat-tolerant genotypes (SML832 and SML668) had more sucrose than the heat-susceptible genotype (SML832). Thus, sucrose concentrations in leaves and anthers and SS and SPS activities declined significantly in sensitive genotypes under heat stress (Kaur et al. 2015). Exposure of common bean genotypes at the V4

developmental stage to heat treatment (32/25 °C) in a growth chamber significantly reduced leaf sucrose concentration in genotype Redhawk (most heat-sensitive genotype) and increased sugar contents in Sacramento (58%) and NY-105 (most heat tolerant) (Soltani et al. 2019).

2.6.6 Cell Membrane Thermostability

Under heat stress, protein denaturation, lipid liquefaction, and loss of membrane integrity are some of the chief physiological, biochemical, and molecular changes in plant metabolism (Gulen and Eris 2004). Most of the changes that appear during acclimation to heat stress are reversible, but death can occur if the stress is too intense (Saelim and Zwiazek 2000). Cell membranes are the principal target of environmental stresses, including heat stress (Chen et al. 2014; Sita et al. 2017). Protein denaturation and increased membrane fluidity, enzyme inactivation, decreased protein synthesis, protein degradation, and alterations in membrane integrity are documented injuries under heat stress (Howarth 2005). By accelerating the kinetic energy and movement of molecules across membranes, heat stress releases chemical bonds within the molecules of biological membranes, resulting in membrane fluidity by protein denaturation or increased unsaturated fatty acids (Savchenko et al. 2002). Decreased cell membrane thermostability or increased ionic leakage caused by the alteration of membrane protein structure is an important indicator of heat stress. The increased membrane fluidity caused by protein denaturation and increased unsaturated fatty acids in the membrane under high temperatures affect membrane structure and function (Wahid et al. 2007), causing symptoms, such as photooxidation of chlorophyll pigments, impaired electron flow, inhibited carbon fixation, and water loss from leaves (Prasad et al. 2017; Sharifi et al. 2012; Sita et al. 2017). The relationship between cell membrane thermostability (CMT) and crop yield changes from plant to plant under high temperatures. Ion leakage from plant tissues has been used as a membrane damage indicator in plants exposed to heat stress. Thus, CMT is an indirect indicator of heat-stress tolerance in legumes, such as soybean (Martineau et al. 1979), lentil (Sita et al. 2017), chickpea (Kaushal et al. 2013), and mung bean (Sharma et al. 2016). Membrane damage occurs under heat and cold stress, more so under heat stress, as reported for *Medicago* (Mo et al. 2011). Cell membrane thermostability (CMT) tends to decline during the late developmental phase of plants (Ahmad and Prasad 2011).

In addition to conventional breeding techniques, noticeable variations in membrane thermostability among genotypes, combined with biochemical and physiological screening methods, could be used to improve the selection for breeding objectives (Hemantaranjan et al. 2014). Membrane thermostability has been used to assess thermotolerance in many food crops worldwide. Depending on the growing season, electrolyte leakage in plants varies among tissues, organs, and growth stages and is affected by plant/tissue age, sampling organ, developmental stage, growing season, degree of hardening, and plant species. A significant positive relationship between CMT and yield was reported in sorghum (Sullivan and Ross 1979). In crop

plants such as barley (*Hordeum vulgare* L.), cotton (*Gossypium* spp.), sorghum, and cowpea, increased electrolyte leakage decreased membrane thermostability (Wahid et al. 2007; Wahid and Shabbir 2005). In leguminous crops, electrolyte leakage has been used to assess thermotolerance. For example, heat stress at 34 °C in lentil revealed genotypes Ranjan, Moitree, 14-4-1, IC201710, and IC208329 as heat tolerant and genotypes ICC201655, ICC201661, ICC201662, ICC201670, ICC201675, ICC201681, ICC201698, ICC201743, ICC201794, ICC248959, Asha, Sagardeep Local, and UP local as heat sensitive, based on cell membrane stability in field and growth chamber studies (Choudhury et al. 2012). In another study, lentil genotypes exposed to high temperature (45 °C) at the flowering stage revealed Qazvin and B4400 as heat-tolerant and -sensitive genotypes, with 98.13% and 33.19% CMT, respectively (Barghi et al. 2013). At 38/28 °C and 40/30 °C in a controlled environment, heat-tolerant lentil genotypes IG2507, IG3263, IG3745, IG4258, and FLIP2009 had less membrane damage (<20% electrolyte leakage) than heat-sensitive genotypes IG2821, IG2849, IG4242, IG3973, and IG3964 (>30%) (Sita et al. 2017).

Among various legumes (pigeon pea, peanut, chickpeas, and soybean), chickpea was the most sensitive to high temperature based on CMT (Devasirvatham et al. 2012). Heat-tolerant chickpea genotypes ICCV07110 and ICCV92944 had less membrane damage (22.6% and 20.6%) than heat-sensitive genotypes ICC14183 and ICC5912 (30.4% and 33.3%) under high temperatures of 40/30 °C and 45/35 °C (Kumar et al. 2013). In another study, high temperature (>32/20 °C) during the reproductive stage caused the most membrane damage in heat-sensitive chickpea genotypes ICC10685 (28.3%) and ICC5912 (26.3%) and the least membrane damage in heat-tolerant genotypes ICC15614 (17.3%) and ICCV 92944 (19.6%) (Kaushal et al. 2013). A gradual rise in temperature (42/25 °C) at anthesis for 8 days increased electrolyte leakage (EL) by 20–25% greater in heat-sensitive chickpea genotype ICC16374 compared to heat-tolerant genotype ICCV92944 (Parankusam et al. 2017). At 37/27 °C, electrolyte leakage increased by a maximum of 16–25% in chickpea genotypes (Pareek et al. 2019), with ICC1205 identified as heat tolerant (13–14%). Similarly, Dua et al. (2001) reported ICCV88, ICC512, and ICC513 as heat-tolerant chickpea genotypes under heat stress. Another study on six chickpea genotypes revealed DG36 (EL: 36.7%) and Pusa 372 (EL: 50.7%) as heat-tolerant and heat-sensitive genotypes, respectively, when exposed to high temperature (>38 °C) under field conditions, based on EL (Singh et al. 2004). Of 115 chickpea genotypes screened at high temperature (36.5 °C) in the field, GNG 663 and Pusa 244 were selected as heat tolerant and heat sensitive, with electrolyte leakage values of 23% and 50%, respectively (Kumar et al. 2012). Among 30 chickpea genotypes screened for heat tolerance (>30 °C), Pusa 240 and GG2 genotypes were identified as heat-tolerant and -sensitive genotypes, respectively, with minimum (45%) and maximum (69%) cell membrane injury (Kumar et al. 2013).

Screening of nine cowpea genotypes exposed to heat stress (33/20 °C) during flowering and pod revealed less leaf electrolyte leakage in heat-tolerant genotypes H36, H8-9, and DLS99 (35.8–36.7%) than heat-susceptible genotypes CB5, CB3, and DLS127 (66.2–79.0%) (Ismail and Hall 1999). In another study at high

temperature (38/30 °C), cell membrane injury was negatively correlated with yield in heat-tolerant (CB 27, Prima, UCR 193) and heat-sensitive genotypes (CB 5, CB 46) (Singh et al. 2010), with less membrane damage in heat-tolerant genotypes.

Screening of 15 *Medicago* cultivars at high temperature (38/35 °C) using membrane damage revealed “Bara310SC” and “WL712” as heat-tolerant and heat-sensitive genotypes with 24.07% and 53.2% electrolyte leakage, respectively (Wassie et al. 2019). Similarly, screening studies on 116 green gram genotypes at high temperature (45/25 °C) identified EC 3398889 and LGG460 as heat tolerant and heat sensitive, with minimum and maximum cell membrane damage, respectively (Basu et al. 2019). Gradual exposure to high temperature (35–50 °C) of 4-week-old three common bean genotype seedlings in a growth chamber revealed “local genotype” and “Ferasetsiz” as heat-sensitive genotypes, while “Balkız” was a relatively heat-sensitive genotype (Tokyol and Turhan 2019). Gross and Kigel (1994) used electrolyte leakage as a criterion for assessing heat tolerance at 32/28 °C during the reproductive stage and reported PI 271998 and BBL 47 as heat-tolerant and heat-sensitive genotypes in common bean, respectively. High-temperature studies (>40/28 °C) at the reproductive stage in mung bean showed high electrolyte leakage (21.8–23.6%) in heat-sensitive lines (EC 693363, EC 693361, EC 693370, KPS1, IPM02-3) compared to heat-tolerant lines (16.8–20.4%; EC693357, EC693358, EC693369, Harsha, ML1299) (Sharma et al. 2016). Another study on mung bean at high temperature (>35 °C) identified genotype MH 421 as heat tolerant and Basanti as heat sensitive, with low (34.88%) and high (41.34%) electrolyte leakage, respectively (Jha et al. 2015). Screening of ten faba bean genotypes exposed to heat stress (37 °C) 60 days after sowing revealed C5 as heat tolerant and Espan as heat sensitive, based on low (57.67%) and high (76%) membrane damage, respectively (Siddiqui et al. 2015).

2.6.7 Canopy Temperature Depression

Canopy temperature depression (CTD) is the plant canopy temperature deviation from the ambient temperature (Balota et al. 2007). At the whole-crop level, leaf temperature decreases below air temperature when water evaporates. CTD acts as an indirect measure of transpiration (Reynolds et al. 2001) and plant water status (Araus et al. 2003) and indicates the relative metabolic fitness of genotypes in a given environment (Reynolds 1997). CTD is a key trait for assessing the response of genotypes to low water usage, high temperature, and other stresses (Balota et al. 2007). At high temperatures, transpiration increases for some time, with plants using more water during growth due to more open stomata and lower CTD. A positive CTD value [i.e., difference between air temperature (T_a) and canopy temperature (T_c)] occurs when the canopy is cooler than the air ($CTD = T_a - T_c$) (Balota et al. 2008).

Canopy temperature depression is heritable and can be measured on cloudless days using an infrared thermometer (Reynolds et al. 1997). To maintain canopy temperature at a metabolically comfortable range, plants transpire through open

stomata. Plants close stomata during stress acclimation, increasing the canopy temperature (Kashiwagi et al. 2008). Canopy temperature can be affected by biological and environmental factors, such as soil water status, wind, evapotranspiration, cloudiness, conduction systems, plant metabolism, air temperature, relative humidity, and continuous radiations (Reynolds et al. 2001). Canopy temperature is an indicator of plant water status or the equilibrium between root water uptake and shoot transpiration (Berger et al. 2010). CTD can act as a desirable criterion for selecting heat-tolerant genotypes based on phenotypic variation (Mason and Singh 2014). It can be used to determine yield potential and metabolic fitness of crop plants under specific environmental conditions (Kumari et al. 2013). It acts as a mechanism of heat escape and is strongly correlated with yield (Reynolds et al. 2001); affected by many physiological factors, it is a strong trait for determining genotype fitness.

Epicuticular leaf wax QTL and CTD are strongly interlinked, with wax load affecting plant canopy temperature (Awika et al. 2017). Stay-green genotypes have high CTD values and thus low canopy temperature due to transpirational cooling under heat stress (Fischer et al. 1998; Reynolds et al. 1994). In chickpea, CTD is negatively correlated with water potential, osmotic pressure, relative leaf water content, and seed yield (Sharma et al. 2015). Differences in canopy temperature are not detectable in high-humidity environments because the effect of evaporative leaf cooling is negligible (de Souza et al. 2012). CTD has been successfully used to select for heat tolerance in various crop species, including legumes. For example, heat-tolerant chickpea genotypes ICCVs 95311, 98902, 07109, and 92944 had higher CTD values than sensitive genotypes ICCVs 07116, 07117, and 14592, which had negative CTD values (Devasirvatham et al. 2015). Another study screened 30 chickpea genotypes exposed to temperature >30 °C to reveal Pusa 240 as a heat-tolerant genotype due to its cooler canopy than other genotypes (Kumar et al. 2013). Similarly, screening chickpea genotypes subjected to 36.5 °C identified GNG 663 and Vaibhavaas as heat tolerant and heat sensitive, respectively, with CTD values of 4.8 °C (maximum) and 1.8 °C (minimum) (Kumar et al. 2012). In a screening study of 56 chickpea genotypes for heat tolerance (40 °C), CTD values ranged from 5.0 to 7.5 °C; eight genotypes (Pusa 1103, Pusa 1003, KWR 108, BGM 408, BG 240, PG 95333, JG 14, BG 1077) were identified as heat tolerant, with maximum CTD values compared to other genotypes (Kumar et al. 2017). In mung bean, seed yield positively correlated with CTD, while canopy temperature negatively correlated with root traits, such as the number of lateral branches and dry root weight (Raina et al. 2019). In another study, mung bean genotype MH 421 (CTD 5.78 °C) was selected as heat tolerant compared to Basanti (CTD 4.37 °C) when tested at high temperature (>35 °C) (Jha et al. 2015). In pea, CTD is affected by canopy structure, and increased pod number and pod-to-node ratio associated with CTD (Tafesse et al. 2019).

2.7 Biochemical Traits

2.7.1 Oxidative Stress and Antioxidants

Heat stress is a major environmental factor affecting vital metabolic processes in plants, hampering proper growth and development. Disturbances in these metabolic processes lead to ROS generation, such as hydrogen peroxide, hydroxyl radicals, and superoxides (Chakraborty and Pradhan 2011). ROS production damages cellular activity by inactivating enzymes, denaturing proteins, and damaging membranes and DNA. Plants shield such injuries by activating cascades of enzymatic activities, such as superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), ascorbate peroxidase (APX), and glutathione reductase (GR), and nonenzymatic activities, such as glutathione (GSH) and ascorbic acid (ASC) (Suzuki et al. 2012). The selection of contrasting genotypes based on the expression level of these antioxidants is effective in leguminous plants (Kumar et al. 2013). For example, chickpea genotypes raised under natural conditions until 50% flowering and then in a growth chamber for heat treatment (30/20 °C, 35/25 °C, 40/30 °C, and 45/35 °C) revealed that heat-tolerant genotypes (ICCV92944, ICCV07110) had lower H₂O₂ and MDA concentrations than sensitive genotypes (ICC5912, ICC14183). Tolerant genotypes face fewer injuries due to greater expression of antioxidants, such as APX and GR (Kumar et al. 2013). Similarly, 41 mung bean genotypes were screened, and contrasting genotypes were selected based on oxidative stress damage and antioxidant activity. Heat-tolerant genotypes (EC693357, EC693358, EC693369, Harsha, ML1299) experienced less oxidative damage (1.52–2.0-fold increase in MDA; 1.59–1.96-fold increase in H₂O₂) than sensitive genotypes (2.2–2.4-fold increase in MDA; 2.21–2.93-fold increase in H₂O₂) (Sharma et al. 2016). Moreover, heat-tolerant genotypes increased APX activity (by 1.48–1.77-fold) more than sensitive genotypes (1.27–1.37-fold). Likewise, of 38 lentil genotypes screened for heat tolerance (>35/20 °C) during the reproductive phase, heat-tolerant genotypes (IG2507, IG3263, IG3745, IG4258, FLIP2009) had less oxidative damage (MDA and H₂O₂ contents increased) and higher SOD, CAT, APX, and GR activities than heat-sensitive genotypes (IG2821, IG2849, IG4242, IG3973, IG3964) (Sita et al. 2017). In another study on lentil exposed to heat stress (30, 35, 40, 45, and 50 °C for 4 h) in plant growth chambers, SOD, CAT, and APOX activities initially increased in four heat-tolerant lentil varieties (IPL 81, IPL 406, Asha, Subrata) at 35, 40, and 45 °C but decreased at 50 °C, and decreased in heat-sensitive genotypes (Sehore and Lv) at all temperatures, except 30 °C (Chakraborty and Pradhan 2011). Further accumulation of carotenoids and ascorbate followed a similar trend, indicating the association of heat sensitivity with antioxidant expression.

2.7.2 Metabolites

Metabolite detection and quantification are an effective and powerful tool for selecting genotypes in response to environmental stresses (Bueno and Lopes

2020). Metabolites include low-molecular-weight compounds, including precursors and intermediate metabolic pathways, which are an indispensable part of plant metabolism, regulating vital biological processes and involved in stress tolerance (Wahid et al. 2007). The primary metabolites upregulated during abiotic stress are amino acids (proline), carbohydrates (sucrose, hexoses, polyhydric alcohols), polyamines (spermidine, spermine, putrescine), and glycine betaine. Correspondingly, secondary metabolites include terpenoids (saponins, tocopherols), phenolic compounds (flavonoids, isoflavonoids, anthocyanins), and nitrogen-containing metabolites (alkaloids and glucosinolates) (Rodziewicz et al. 2014). About one million specific metabolites varying in chemical structures, polarity, and physiochemical properties are present in the plant kingdom and can be analyzed through metabolomics profiling and metabolic fingerprinting. Due to heat stress, plants reshuffle their metabolites to sustain plant growth (Serrano et al. 2019). Metabolite production is regulated by genes; thus, the activation of heat-shock factors, mainly HSF2 and HSF3, increases metabolite content, such as galactinol (Song et al. 2016). Knowledge on metabolite production is important for developing metabolite markers to select heat-tolerant varieties.

Chebroly et al. (2016) raised heat-tolerant (04025-1-1-4-1-1) and heat-sensitive (DT97-4290) soybean genotypes in a growth chamber, which were maintained under control conditions (28/22 °C) until flowering. Heat stress [moderate (36/24 °C) and severe (42/26 °C)] was imposed from flowering to maturity, with metabolite profiling undertaken on harvested seeds. The seeds of genotypes collected at 42/26 °C were highly abnormal and small and had high nitrogen levels compared with the sensitive genotype. Two hundred and seventy-five metabolites were traced and compared for 36/24 °C and 28/22 °C; 83 metabolites (48 downregulated and 35 upregulated were differentially altered in tolerant than sensitive genotypes) significantly differed between genotypes at 36/24 °C, compared to 61 metabolites (−30 and +31 in tolerant than sensitive genotypes) at 28/22 °C. Most traced compounds were antioxidants belonging to tocopherol, terpenoid, and flavonoid precursors. The tolerant genotype had more gulono-1,4-lactones (precursor for ascorbic acid) than the sensitive genotype, which was attributed to its higher tolerance to heat stress and positively correlated with seed vigor, seed germination, seed weight, and oil content.

Proline is a multifunctional amino acid involved in plant growth and development that acts as a compatible osmolyte and ROS scavenger to regulate plant function in stressed environments (Szepesi and Szöllősi 2018). Under stress, proline has diverse roles, such as stabilizing membranes, proteins, subcellular structures, and energy sources, thus maintaining cellular homeostasis. Therefore, an increase in compatible solutes such as proline under stressful conditions is valuable for plants (Kaur and Asthir 2015). Leaf proline concentrations were measured in four chickpea genotypes varying in their sensitivity to high temperature (4.5 °C higher than the ambient temperature for 15 days); heat-treated genotypes had significant higher proline concentrations than the control, more so in Pusa 1103 and BGD-72 (tolerant genotypes) than Pusa 256 and Pusa 261 (sensitive genotypes) (Arunkumar et al. 2012). Similarly, a high-temperature treatment (45 °C for 8 h) on 6-day-old common

bean seedlings increased proline content compared to control plants (25 °C) (Babu and Devaraj 2008).

2.7.3 Heat-Shock Proteins

Heat-shock proteins are specific proteins accumulated during rapid heat stress. Heat-shock genes are upregulated for plant survival under heat stress and responsible for encoding HSPs (Chang et al. 2007). A sudden change in temperature increases HSP production (Wahid et al. 2007). In all organisms, HSP expression is a general response to high temperature (Vierling 1991). HSP90, HSP70, and low-molecular-weight proteins are three classes of proteins according to molecular weight. Under stress conditions, HSPs perform chaperone-like functions in protein synthesis, maturation, targeting, renaturation, and membrane stabilization (Reddy et al. 2010, 2016). HSPs also play a role in protein translation and translocation, perform proteolysis and protein folding, and reactivate denatured proteins (Zhang et al. 2005). Under heat stress, the expression of HSPs protects the machinery of protein biosynthesis (Miroshnichenko et al. 2005). Membrane lipid composition, membrane integrity osmoprotectants, and HSPs play important roles in heat tolerance (Blum 2018). HSPs are located mainly in the cytoplasm, nucleus, mitochondria, chloroplast, and endoplasmic reticulum (Waters et al. 1996). In plant species such as potato, maize, soybean, and barley, specific HSPs have been identified in mitochondria in response to high temperature (Neumann et al. 1994). HSPs maintain membrane stability and protect PSII from oxidative stress (Barua et al. 2003). In *Medicago truncatula*, the role of HSPs was determined by cloning and characterization (Li et al. 2016). The roots of some plants also synthesize HSPs to cope with heat stress (Nieto-Sotelo et al. 2002). The expression profiles of HSPs have been compared in plant species/genotypes contrasting in heat sensitivity. In a comparative study on cowpea and eight common bean varieties at 40 °C, cowpea showed more HSP expression than common bean and was thus more tolerant to high temperature. IPA 7 had the highest HSP expression of the eight common bean genotypes (Simões-Araújo et al. 2003).

In chickpea exposed to high temperature (42/25 °C) at anthesis, the levels of HSPs increased in genotype JG14 compared to ICC16374 (Parankusam et al. 2017). In another study, five chickpea genotypes were assessed for thermotolerance at 30, 35, and 40 °C, with CSJD 884 and RSG 895 identified as heat tolerant and C 235 as heat sensitive (Kumari et al. 2018). In peanut genotypes exposed to 50 °C for 30 min, ICGS 76, COC038, COC050, COC041, and COC068 were identified as heat tolerant and COC812, COC166, COC115, COC277, COC227, Tamrun OL 02, and Spanco as heat sensitive (Selvaraj et al. 2011). Heat-tolerant peanut genotype ICGS 44 had higher HSP expression than heat-sensitive genotypes AK 159 and DRG 1 under heat stress (45 °C) (Chakraborty et al. 2018). The level of thermotolerance positively correlated with HSP accumulation. Thirty varieties of pea seedlings exposed to high temperature (46–49 °C) in growth chambers for different time intervals (1–3 h) identified Acc#623 and Acc#476 as heat-tolerant and heat-sensitive

varieties, respectively, with Acc#623 having higher levels of HSP70, HSP90, and HSP104 than Acc#476 (Srikanthbabu et al. 2002). In soybean under 38/30 °C, cultivar PI 471938 had higher HSP expression (especially HSP70), conferring heat tolerance, than R95-1705 (Katam et al. 2020).

2.8 Genes for Heat Tolerance

Diverse genes have been identified using omics analyses (transcriptomics, genomics, and proteomics) in various plant species for heat resilience mechanisms; these genes are essential for developing stable cultivars (Singh et al. 2019). A lentil population was developed by crossing heat-tolerant (PDL-1 and PDL-2) and heat-sensitive (JL-3 and E-153) genotypes for molecular mapping and genetics studies (Singh et al. 2017). For this purpose, simple sequence repeat (SSR) marker analysis and QTL analysis were performed, using 495 SSR markers, which detected seven SSR markers and two QTLs—qHt_{ss} and qHt_{ps} were closely linked with SSR markers (PBA_LC_1507, PLC_105, PBA_LC_1288, LC_03, PBA_LC_1684, PBA_LC_1752, PBA_LC_1480). Further, SSR marker PBA_LC_1507 was closely linked to pod set and seedling survival trait. Another lentil study revealed genetic diversity for heat tolerance among 119 genotypes using SSR markers (Zhang et al. 2005). High-temperature stress was applied at the seedling (35/33 °C) and anthesis (35/20 °C) stages to study the effects on morphophysiological and reproductive traits of non-stressed and stressed plants in the field. A set of 209 alleles were identified using 35 SSR markers. Genotypes were clustered into nine groups based on SSR markers. Clusters 1 and 6 had significant variation, which could help produce better segregants for heat tolerance. The genotypes in clusters 2, 3, 4, 5, 7, 8, and 9 were moderately tolerant or moderately sensitive to heat stress. Significant differences among clusters were observed for seedling survivability, heat tolerance scores, membrane stability index, pollen viability, pollen germination, pod and seed set, and seed yield. The finding suggests that identifying the genetic distances between clusters will maximize their use for breeding heat-tolerant lentils. Results from the RT-PCR confirmed differential gene expression in heat-sensitive fescue genotype PI283316 and heat-tolerant genotype PI297901 (Zhang et al. 2005).

Similarly, in chickpea, phenotyping of RILs developed from a cross between ICC4567 (heat-sensitive) and ICC156614 (heat-tolerant) genotypes exhibited two genomic regions (CaLG05 and CaLG06) with four QTLs for the number of filled pods, seed number, grain yield, and pod set. Further, 25 genes responsible for heat tolerance were reported in these two genomic regions—five encoding HSPs and heat-shock transcription factors, three responsible for detoxifying ROS, five encoding proteins like farnesylated protein 6 and ethylene-responsive transcription factors, and all these genes collectively upregulating other genes like MYB4, AKH3, and RAN1 that are involved in the mitigation of heat stress in chickpea (Paul et al. 2018). Molecular characterization in mung bean genotype VC1973A revealed 24 *VrHsf* genes responsible for the synthesis of heat-shock transcription factors that mediate plant responses under heat stress, suggesting their potential role in

investigating mechanisms related to heat tolerance (Liu et al. 2019). Similarly, in a soybean study, 26 *GmHsf* genes coded for heat-shock transcription factors, with *GmHsf12*, *GmHsf28*, *GmHsf34*, *GmHsf35*, and *GmHsf47*, highly upregulated during heat stress (Chung et al. 2013).

2.9 Scope of Harnessing Germplasm for Designing Heat Tolerance

Harnessing crop germplasm variability is one of the cheapest and most environmentally friendly approaches for developing abiotic stress, including heat stress tolerance (Jha et al. 2014). Like other crops, substantial genetic variation has been harnessed to develop grain legumes that tolerate heat stress (Craufurd et al. 2003; Jha et al. 2017; Krishnamurthy et al. 2011). Several breeder-friendly techniques, such as field-based screening of grain legumes in targeted heat-stress environments, enabled the selection of potential heat-tolerant grain legumes in chickpea, soybean, common bean, pea, lentil, and cowpea. Based on the early phenology, an important heat stress, some important chickpea genotypes, viz., ICC 14346, ACC 316, and ACC 317, showing heat stress escape mechanisms have been reported (Canci and Toker 2009; Upadhyaya et al. 2011). Selection relying on yield and yield-related traits, such as high pod and seed set, low grain yield reduction, and maintaining high biomass, has been used to directly identify heat-tolerant lines, including ICC1205, ICC15614, BG256, and Vaibhav in chickpea (Devasirvatham et al. 2013; Gaur et al. 2012; Jha et al. 2015; Jumrani et al. 2018); G122, PI 163120, PI 271998, G122, A55, and Cornell 503 in common bean (Miklas et al. 2000; Rainey and Griffiths 2005; Shonnard and Gepts 1994); TN88-63, Tvu 4552, and Prima in cowpea (Nielsen and Hall 1985; Warrag and Hall 1983); 55-437, 796, 796, 55-437, ICG 1236, ICGV 86021, ICGV 87281, and ICGV 92121 in groundnut (Craufurd et al. 2003; Ntare et al. 2001); 72578, 70548, 71457, and 73838 in lentil (Delahunty et al. 2015); Dieng, IA3023, and KS4694 in soybean (Djanaguiraman et al. 2019; Puteh et al. 2013); C.52/1/1/1 and C.42 in faba bean (Abdelmula and Abuanja 2007); and JP-625, IARI-2877, PMR-38 II, EC-318760, EC-328758, and IARI-2904 in pea (Mohapatra et al. 2020). Similar studies based on various physiological parameters, including cell membrane stability, identified heat-tolerant ILC 482, Annegiri, and ICCV 10 in chickpea (Srinivasan et al. 1996), PI 271998 in common bean (Marsh et al. 1985), and SPT 06-07 in groundnut (Singh et al. 2016), and studies based on pollen germination and fertilization under heat stress identified heat-tolerant ICC 15614, ICCV 92944, and ICC1205 in chickpea (Devasirvatham et al. 2010; Kaushal et al. 2013), 55-437, ICG 1236, TMV 2, and ICGS 11 in groundnut (Kakani et al. 2002), DG 5630RR, NRC 7, and EC 538828 in soybean (Jumrani et al. 2018; Salem et al. 2007), and Haibushi in common bean (Tsukaguchi et al. 2003). In addition, studies based on superior yield performance and genotype \times genotype \times environment biplot analysis identified heat-tolerant ICC 4958, RVG 203, RVG 202, JAKI 9218, and JG 130 in chickpea (Jha et al. 2018, 2019), and studies based on several heat-stress tolerance indices identified heat-tolerant lines in soybean (Sapra and Anaele

1991), chickpea (Jha et al. 2018), and common bean (Porch 2006). Harnessing existing genetic variability in crop wild relatives and landraces should be considered to broaden the genetic base of grain legumes for higher heat tolerance in the future.

2.10 Genetics of Heat Tolerance

Classical genetics and quantitative genetics approaches, such as generation mean analysis and diallel analysis, provided preliminary information on heat-stress tolerance in chickpea (Jha et al. 2019), cowpea (Marfo and Hall 1992; Patel and Hall 1988), and common bean (Miklas et al. 2000; Rainey and Griffiths 2005) based on yield and yield-related traits under heat stress. However, this genetic information does not provide a complete picture of heat tolerance in these grain legumes, as this trait is governed by multigenes and highly influenced by $G \times E$ interactions (Upadhyaya et al. 2011).

2.11 Genomic Resources for Heat Tolerance

Unprecedented advances in genomic resource development have enabled the precise mapping of various traits of breeding importance, including heat-stress tolerance in various grain legume crops (Jha et al. 2021; Paul et al. 2018; Pottorff et al. 2014; Varshney et al. 2019). In parallel, the availability of reference genome sequences for major grain legumes has enriched the genomics resources in legume crops. Using a biparental mapping approach, several QTLs controlling heat-stress tolerance have been elucidated in chickpea (Jha et al. 2019; Paul et al. 2018), cowpea (Lucas et al. 2013; Pottorff et al. 2014), lentil (Singh et al. 2017), and pea (Huang et al. 2017). In chickpea, four important QTLs related to yield traits were identified on CaLG05 and CaLG06 from an ICC15614 \times ICC4567 RIL population under heat stress (Paul et al. 2018). Jha et al. (2021) reported that 37 major QTLs related to heat tolerance in chickpea were discovered. Five QTLs were elucidated in cowpea under heat stress (Lucas et al. 2013). Similarly, an evaluation of IT93K-503-1 \times CB46 and IT84S-2246 \times TVu14676 RIL populations identified three QTLs (*Hbs-1*, *Hbs-2*, and *Hbs-3*) contributing to heat tolerance in cowpea (Pottorff et al. 2014). Many QTLs contribute to phenological traits, such as days to flowering, with yield-related QTLs reported in pea under heat stress (Huang et al. 2017).

The availability of high-throughput SNP markers elucidated genomic regions controlling heat tolerance across the whole genome in a large set of chickpea germplasm using a genome-wide association mapping approach (Tafesse et al. 2020; Varshney et al. 2019). In this context, several marker-trait associations (MTAs) for various heat-stress traits have been deciphered in chickpea (Thudi et al. 2014; Varshney et al. 2019), pea (Tafesse et al. 2020), and common bean (López-Hernández and Cortés 2019). In whole genome resequencing derived SNP markers based GWAS analysis involving a large panel of chickpea germplasm, several significant MTAs for various physiological and yield traits were unveiled

under heat stress (Varshney et al., 2019). Likewise, Tafesse et al. (2020) identified several significant MTAs for chlorophyll content, photochemical reflectance index, canopy temperature, and pod number in pea under heat stress. In common bean, GWAS in 78 “geo-referenced” wild common bean accessions revealed several candidate genes (e.g., *MED23*, *MED25*, *HSFB1*, *HSP40*, *HSP20*, *phospholipase C*, *MBD9*, *PAP*) related to heat-stress tolerance (López-Hernández and Cortés 2019). These MTAs could be important in marker-assisted breeding for developing heat-tolerant grain legumes.

2.12 Transcriptomics for Unfolding Candidate Genes for Heat Tolerance

In the past decade, technical interventions in functional genomics, especially next-generation sequencing-based RNA-seq facility, have offered great insights into gaining function of candidate gene(s) controlling various complex traits, including heat stress in various grain legumes (Agarwal et al. 2016; Singh et al. 2019; Wang et al. 2018). Using the RNA-seq technique, *Ca_25811*, *Ca_23016*, *Ca_09743*, *Ca_17680*, and *Ca_25602* candidate genes were deciphered from heat-treated reproductive tissues of heat-tolerant and heat-sensitive chickpea genotypes (Agarwal et al. 2016). In soybean, RNA-seq analysis of contrasting genotypes treated with combined drought and heat stress revealed several differentially expressed genes, primarily involved in the defense response, photosynthesis, and metabolic processes (Wang et al. 2018). RNA-seq analysis of heat-treated soybean leaf tissue at the reproductive stage revealed a plethora of up- and down-regulatory differentially expressed genes and unearthed genes involved in flowering, oxidative stress, osmoregulation, HSPs, and ethylene biosynthesis (Xu et al. 2020). Transcriptional analysis of heat-treated soybean root tissue revealed numerous differentially expressed genes involved in regulating the heat-stress response (Valdés-López et al. 2016). In lentil, transcriptome analysis of contrasting heat-tolerant and heat-sensitive genotypes (PDL-2 and JL-3) revealed several genes encoding a WRKY transcription factor, DnaJ homolog subfamily B member 13, and 17.1 kDa class II heat-shock protein and cell wall (Singh et al. 2019). However, higher expression of NAC and WRKY transcription factor genes conferred heat tolerance in the PDL-2 genotype.

2.13 Proteomics and Metabolomics Resolving Gene Networks for Heat Tolerance in Grain Legumes

A proteomics approach could endow us with the whole landscape of proteins responding to various biotic and abiotic stresses (Ramalingam et al. 2015). A series of proteins contributing to switching on various complex signal transduction mechanisms and intricate gene networks associated with adapting the plant response to heat stress have been investigated (Rathi et al. 2016). However, the role of proteomics in mediating heat-stress tolerance remains limited in grain legumes.

Various types of HSPs, such as ClpB/HSP100 and VfHsp17.9-CII (Kumar et al. 2015), EF-Tu protein (Das et al. 2016), tissue-specific proteins (Ahsan et al. 2010), and early response to dehydration (ERD)-related proteins (ERD10 and ERD14) (Kovacs et al. 2008), act as chaperones, protecting cells from heat stress-related injuries. Similarly, heat stress increased HSP expression in chickpea genotype JG14 (Parankusam et al. 2017) and groundnut genotype ICGS 44 (Chakraborty et al. 2018). Further, Das et al. (2016) reported 25 proteins contributing to various cellular metabolic activities under heat stress in soybean. Furthermore, the participatory role of dehydrin-like proteins recovered from mitochondria and their plausible role in safeguarding mitochondrial membrane in yellow lupin under heat stress are worth noting (Rurek 2010). Valdés-López et al. (2016) reported 30 commonly up- and downregulated heat stress-responsive proteins involved in cell wall formation, amino acid and lipid biosynthesis, and ROS reduction in soybean.

Like proteomics, metabolomics is a robust approach for enriching our understanding of various primary and secondary metabolites produced in response to abiotic stresses, including heat stress (Janni et al. 2020; Ramalingam et al. 2015). Among the various metabolites, tocopherol and its isoforms, ascorbate, flavonoids, phenolic compounds, proline, polyamines, and glycine betaine help plants adjust to heat stress (Chebroly et al. 2016; Kaplan et al. 2004). For example, a heat-tolerant soybean genotype had a higher abundance of flavonoids and tocopherols acting as antioxidants than a heat-sensitive genotype (Chebroly et al. 2016). Further technical innovations and bioinformatic analysis of metabolomics-derived data could shed light on the complex gene network of heat-stress adaptation in grain legumes.

2.14 Conclusions

Increasing episodes of heat stress are becoming a serious issue worldwide, challenging the yield potential of various crops, including grain legumes. Harnessing genetic resources could be an important approach for sustaining legumes under rising temperatures. In addition to yield traits, incorporating various physiological traits could enable plants to adapt and sustain grain yield under heat stress (Reynolds and Langridge 2016).

As crop wild relatives are the reservoir of novel gene(s)/QTLs for various stress tolerance including heat-stress tolerance, introgression of heat-tolerance genomic region into elite legume cultivars using a pre-breeding approach could sustain legume yields under rising global temperatures (Chaudhary et al. 2020). Likewise, capitalizing on the various adaptive traits conferring heat tolerance from legume landraces could assist in developing grain legumes that tolerate heat stress. Furthermore, advances in grain legume genomics, especially molecular markers, and availability of grain legume genome assemblies have helped pinpoint heat-tolerance genomic regions in various legumes. Whole-genome resequencing efforts have also enabled the discovery of novel haplotypes controlling heat tolerance (Varshney et al. 2019). In parallel, progress in functional genomics, including RNA-seq-based transcriptomics, has enabled the discovery of underlying candidate gene

(s) involved in heat tolerance and putative functions (Agarwal et al. 2016; Singh et al. 2019; Wang et al. 2018). Additionally, advances in proteomics and metabolomics have uncovered various participatory proteins, especially HSPs and heat stress-responsive metabolites, and various novel signaling molecules in legumes (Chebrolu et al. 2016; Parankusam et al. 2017). Therefore, leveraging various breeding, physiological, and “omics” approaches combined with emerging “speed breeding,” genomic selection, and genome editing technology could help develop climate-resilient grain legumes to meet the increasing demand for plant-based dietary protein.

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