Shabir Hussain Wani *Editor*

Disease Resistance in Crop Plants

Molecular, Genetic and Genomic Perspectives

Springer

Disease Resistance in Crop Plants

Shabir Hussain Wani
Editor

Disease Resistance in Crop Plants

Molecular, Genetic and Genomic Perspectives

Springer

Editor
Shabir Hussain Wani
Mountain Research Centre for Field Crops
Sher-e-Kashmir University of Agricultural
Sciences and Technology of Kashmir
Srinagar, Jammu and Kashmir, India

ISBN 978-3-030-20727-4 ISBN 978-3-030-20728-1 (eBook)
https://doi.org/10.1007/978-3-030-20728-1

© Springer Nature Switzerland AG 2019, Corrected Publication 2022
This work is subject to copyright. All rights are reserved by the Publisher, whether the whole or part of the material is concerned, specifically the rights of translation, reprinting, reuse of illustrations, recitation, broadcasting, reproduction on microfilms or in any other physical way, and transmission or information storage and retrieval, electronic adaptation, computer software, or by similar or dissimilar methodology now known or hereafter developed.
The use of general descriptive names, registered names, trademarks, service marks, etc. in this publication does not imply, even in the absence of a specific statement, that such names are exempt from the relevant protective laws and regulations and therefore free for general use.
The publisher, the authors, and the editors are safe to assume that the advice and information in this book are believed to be true and accurate at the date of publication. Neither the publisher nor the authors or the editors give a warranty, express or implied, with respect to the material contained herein or for any errors or omissions that may have been made. The publisher remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

This Springer imprint is published by the registered company Springer Nature Switzerland AG
The registered company address is: Gewerbestrasse 11, 6330 Cham, Switzerland

Dedication

Professor Robert McIntosh is an Australian scientist who has dedicated his life to wheat rusts and to the resistance genetics of wheat. Wheat researchers recognize him for the atlas of wheat rust resistance genes published jointly with Colin R. Wellings and Robert F. Park. Indeed, he is an inspirational figure not only for wheat researchers but also for researchers in other fields.

Prof. McIntosh rooted himself to Australian agriculture from his childhood. Growing up at Gloucester in New South Wales, he spent his early years on a dairy farm.

Prof. McIntosh has been closely associated with the University of Sydney through undergraduate and postgraduate studies (PhD, 1969) and later continuous service within the Plant Breeding Institute (PBI) for more than 60 years. He served as director of Rust Research within the PBI from 1980 to 2000.

Prof. McIntosh made significant contributions to wheat rust research. His pre-molecular era studies on chromosome location and genetic linkage in wheat resulted in the documentation of 7 leaf rust resistance genes, 14 stem rust resistance genes, and 2 stripe rust resistance genes. His research enabled the commercial deployment of white seeded varieties with leaf rust resistance gene Lr24 and stem rust resistance gene Sr24 in Australia where these genes remained effective in agriculture for a much longer period than elsewhere; indeed, Sr24 is still effective after almost 40 years. He led the early Australian research on stripe rust after the pathogen was introduced in 1979. His research explained sequential losses of chromosome 3R resistances in day length-insensitive 2D(2R)-substituted triticale cultivars. He has published more than 175 research papers in international and national journals and has coordinated and published the internationally accepted wheat gene catalogue for wheat from 1973.

Prof. McIntosh retired from his academic position in 2000, but he continues to work as an emeritus. He has been honored with several international fellowships including a Postdoctoral Fellowship at the Department of Genetics, University of Missouri, in

1969–1970; a Royal Society Fellowship at the Plant Breeding Institute, Cambridge, in 1977; and Visiting Professorships at Kansas State University in 1993 and Kyoto University in 2000–2001. He has also given lectures on host-pathogen relationships on multiple occasions at the International Maize and Wheat Improvement Centre (CIMMYT), Mexico (1987), and several institutions in China. He served on the External Advisory Committee of the Bill & Melinda Gates Foundation-supported international project "Durable Rust Resistance in Wheat (DRRW)" administered by Cornell University from 2007 to 2015 and was editor of various proceedings of the Borlaug Global Rust Initiative.

Prof. McIntosh has been recipient of many national and international honors for his work on wheat rust research, including Order of Australia (AO) in 2009. Other notable awards include the Farrer Memorial Medal for services to agriculture in 1976; Daniel McAlpine Memorial Lecture, Australasian Plant Pathology Society in 1985; Medal of the Australian Institute of Agricultural Science in 1987; Fellow of the Australian Institute of Agricultural Science in 1988; a Personal Chair in Cereal Genetics and Cytogenetics in 1993; Fellow of the Australian Academy of Science in 1993; J.C. Walker Memorial Lecture, University of Wisconsin, USA, in 1994; Fellow of the American Phytopathological Society, E.C. Stakman Award, University of Minnesota, St Paul, USA, in 2002; Centenary Medal, awarded by the Australian Government "For Service to Australian

Society and Science in Genetics" in 2003; "Wheat Warrior" Award from the Crawford Fund to mark the occasion of the CIMMYT Board Meeting in Canberra in 2010; Tian Fu Friendship Award, Sichuan Province, China, in 2016; and "The Norman" – awarded by the Borlaug Global Rust Initiative in 2018. He was an instructor for annual BGRI training workshops at Njoro, Kenya, from 2009 to 2018.

Prof. McIntosh is an effective teacher and mentor. Several postgraduate students completed their studies under his mentorship. He supervised or co-supervised nine postgraduate students. This book covers different aspects of disease resistance in crop plants including wheat and is dedicated to the contributions of Professor Robert McIntosh to the world wheat community.

Foreword

I am delighted to know that Dr. Shabir Hussain Wani has edited this volume entitled *Disease Resistance in Crop Plants: Molecular, Genetic and Genomic Perspectives* for the internationally reputed publisher Springer Nature. Recently, in 2016, he has successfully completed 1 year postdoctoral fellowship program at Michigan State University, USA, and worked on dissection of *Pythium* root rot resistance in soybean using molecular genetics approaches utilizing SNP markers. The outcome of this postdoc research came out in the form of a good publication in the journals *Genetics Society of America* and *G3: Genes, Genomes, Genetics*. He had a good experience to work in the area of plant biotechnology particularly molecular breeding approaches for the development of disease resistance in plants. I appreciate his enthusiasm and devotion for science, including research, teaching, and dissemination of scientific knowledge.

Yield losses caused by pathogens, animals, and weeds are altogether responsible for losses ranging between 20% and 40% of the global agricultural productivity. Nevertheless, it is estimated that 30 to 40% of harvests are lost each year throughout the production chain. Disease development in plants continues, having a great impact on these societies. Host plant resistance is largely the most promising control method for environmental, economic, and social reasons. Therefore, genes for resistance to diseases and pests may fairly be considered most imperative natural resources for global food security. The evolution of a next-generation phase of disease resistance research is proceeding, and both the public and private sectors are moving to exploit the novel tools and prospects offered by genetics and molecular biology. Maximum disease resistance traits are polygenic in nature and controlled by several genes positioned at putative quantitative trait loci (QTLs). Although quantitative disease resistance (QDR) is a durable and broad-spectrum form of resistance in plants, the identification of the genes responsible for QDR is an upcoming area of research. Furthermore, the sources of resistance are generally found in wild relatives or cultivars of less agronomic significance, so introgression of disease resistance traits into commercial crop varieties typically involves many generations of backcrossing to restore the promising genotype. Molecular marker-assisted breeding (MAB), still, facilitates the preselection of traits even prior to their expression. Most of the plant diseases involve a complex network assimilating manifold response pathways prompted by discrete pathogen molecular elements. By digging deep into the portrayal of the molecular signals necessary for pathogen identification and dissection of the cellular phenomenon that describes the utterance of resistance, it has opened new vistas for sustainable crop disease management. This edited volume by Dr. Wani includes recent advances in disease control for major food crops using the novel molecular and genetic techniques.

Dr. Wani has done an outstanding endeavor by editing this volume, including high-quality chapters from the international- as well as national-level experts in various research fields. The chapters included in this book are nicely written by potential scientists and researchers belonging to various developed and developing nations. This book describes the recent advances in plant disease management utilizing genetic and genomic approaches and their application in important agricultural crops like rice, wheat, maize, barley, pulses, etc. Recent techniques, like genome editing and genomic selection, and their importance and application in the development of disease-resistant crops have also been included. I congratulate Dr. Wani for unraveling this edited volume and hope that this will be a useful reference material for the researchers, student, and policy-makers.

G. P. Singh
Director, ICAR-IIWBR
Karnal, India

Contents

Chapter 1
RETRACTED CHAPTER: Impact of Biotic and Abiotic Stresses on Plants, and Their Responses

Bilal Ahmad, Aamir Raina, and Samiullah Khan

1.1 Introduction

In the present era of drastic climate changes such as global warming, erratic rainfall and depletion of arable land and water resources, plants encounter a diverse range of climate-induced biotic and abiotic stresses (Atkinson et al. 2013; Narsai et al. 2013; Prasch and Sonnewald 2013; Suzuki et al. 2014; Mahalingam 2015; Pandey et al. 2015; Ramegowda and Senthil-Kumar 2015). Stress may be defined as an adverse condition for plant growth and development, caused by either environmental or biological factors, or both. Under natural conditions, concurrent occurrence of two or more different types of stresses—such as drought and salinity, drought and heat are more detrimental to global crop production. Concurrent abiotic stresses are more destructive in disrupting plant metabolism and reducing yield than the same stresses occurring separately at different growth stages. Co-occurrence of drought and heat stress or drought and salinity stress during summer are examples of combined abiotic stresses. Abiotic stresses also play a central role in regulating outbreaks of pests, pathogens, insects and weeds (Coakley et al. 1999; Scherm and Coakley 2003; McDonald et al. 2009; Ziska et al. 2010; Peters et al. 2014). These

---

The original version of this chapter was retracted: The retraction note to this chapter is available at https://doi.org/10.1007/978-3-030-20728-1_12

B. Ahmad
Plant Physiology Laboratory, Department of Botany, Aligarh Muslim University,
Aligarh, India

A. Raina (✉) · S. Khan
Mutation Breeding Laboratory, Department of Botany, Aligarh Muslim University,
Aligarh, India

Botany Section, Women's College, Aligarh Muslim University, Aligarh, India

S. H. Wani (ed.), *Disease Resistance in Crop Plants*,
https://doi.org/10.1007/978-3-030-20728-1_1

stresses also influence plant–pest interactions by altering the physiological and adaptive responses of plants (Scherm and Coakley 2003). Because of their enhanced water use efficiency, weeds outcompete crops under abiotic stress (Patterson 1995; Ziska et al. 2010; Valerio et al. 2013). Abiotic stress has a massive impact on plant growth; consequently, it is responsible for huge losses in yield. The consequential growth reductions can reach upto 50% in most plant species (Wang et al. 2003). Daryanto et al. (2016) reported that the yield of maize is reduced by up to 40% and 21% reduction in the yield of wheat is also noted with a 40% water reduction. The cowpea yield is also decreased, and the extent of the reduction varies between 34% and 68%, depending on the developmental stage and drought stress (Farooq et al. 2017). In case of cowpea, which is an important crop in Africa, and source of food to the millions of farmers, the yield reduction can vary to a great extent depending on the developmental stage and the severity of drought stress. In 2002 it was estimated that soil salinity alone caused losses of more than US$11 billion annually and affected about 10% of the world's arable land, greatly influencing global food production and is considered as the main stress to influence the global crop productivity (Tanji 2002; Ahmad et al. 2019)

In addition to several combinations of abiotic stresses, plants also encounter multiple biotic stresses, commonly through pathogen or herbivore attack simultaneously or sequentially. Biotic stress is an additional threat and puts a great pressure on plant productivity (Mordecai 2011; Maron and Crone 2006; Maron and Kauffman 2006; Strauss and Zangerl 2002; Brown and Hovmoller 2002). A common case of combined biotic stresses is simultaneous attacks by bacterial and fungal pathogens on plants. For example, combined attacks by the bacterium *Xanthomonas arboricola* and fungal pathogens such as *Fusarium* spp., *Alternaria* spp., *Cladosporium* spp., *Colletotrichum* spp., or *Phomopsis* spp. cause brown apical necrosis of *Juglans regia* (Belisario et al. 2002). Plants are severely damaged by concurrent fungal, bacterial and viral infections, which lead to more severe disease symptoms than separate infections with these pathogens.

The impact of concurrent stresses on plants is determined by the types of interactions between various kinds of stress factors (Prasch and Sonnewald 2013; Choudhary et al. 2016). Therefore, the impact of concurrent stresses can be evaluated by understanding the underlying mechanisms of such interactions between various stress factors. Mittler (2006) and Suzuki et al. (2014) showed that the interactions between various stress factors can have either positive or negative effects on plant growth. Plants act in response to concurrent stresses by inducing the expression of diverse set of genes whose products such as secondary metabolites (phenolics) play critical roles in alleviating a broad range of stresses (Niakoo et al. 2019). Plants alter their responses to concurrent stress factors and reveal numerous distinctive responses, along with other general responses. Improved plant tolerance to concurrent stresses involves recognition of physiomorphological traits that are affected by these concurrent stresses. Bearing in mind the global occurrence and the influence of concurrent stresses on agricultural productivity, this chapter attempts to provide insights into the current understanding of stress combinations and improvement of physiomorphological traits to mitigate the effects of concurrent stresses. The significance of studies assessing the impact of concurrent stresses on plant growth is documented and additionally, some important and common examples of different, naturally occurring combinations of stresses are described.

1.1.1 Stress Combinations Occurring in Nature

Stresses are categorized as single, multiple individual, concurrent, and repetitive stresses, depending on the number of interacting factors. A single stress involves only one stress factor, whereas multiple individual stresses represent two or more stresses occurring without any overlap and concurrent stresses represent two or more stresses occurring simultaneously with a little overlap. In repetitive stresses, plants face a single stress or multiple stresses followed by recovery periods, which may be of shorter or longer duration. Several spells of hot days or multiple events of drought and heat stress may occur at different developmental stages of plants. The interactions between various stress factors may either enhance the tolerance capacity or predispose the plant toward a wide range of stresses. For example, drought facilitates the growth of *Macrophomina phaseolina* in the roots of *Sorghum bicolor* and results in a severe reduction in its productivity (Goudarzi et al. 2011). Likewise, the productivity of *Vitis vinifera* is reduced by the occurrence of concurrent drought and cold stress in North China (Su et al. 2015). Plants growing in hot and dry regions such as arid and semi-arid areas are often challenged by the onset of concurrent salinity and heat stress. In the Mediterranean region cold and light stresses are most prevalent and affect the growth and development of plants (Loreto and Bongi 1989). The frost durability of *Triticum aestivum* and the production of *Cicer arietinum* are significantly reduced by concurrent cold and ozone stresses and by concurrent salinity and ozone stresses, respectively (Barnes and Davison 1988; Welfare et al. 2002). Likewise, the combination of salinity and ozone stress plays a critical role in decreasing yield of chickpea and rice cultivars. As in the case of diverse concurrent abiotic stresses, plants are faced with the challenge of concurrent biotic stresses and are damaged more severely by the combinations of fungal and bacterial infections than by infections with these pathogens individually. Lamichhane and Venturi (2015) have documented the incidence of different concurrent biotic stresses and their impacts on plant growth and yield. Plants have evolved a perception network that enables them to perceive both biotic and abiotic stressors simultaneously and help them to mitigate the devastating impact of stresses. The effects of abiotic stresses such as drought or salinity may lead to either susceptibility or resistance of plants to biotic stresses such as powdery mildew, rust, and wilt depending on the timing and severity drought and/or salinity stress.

1.1.2 Impact of Stress Combinations on Plant Physiology and Development

The nature of the interactions between the stressors and the duration of stress exposure can lead to a series of effects on the plant growth, development overall yield. The nature of the interactions between stressors also determines the extent of the influence on crop productivity. For instance, abiotic–abiotic stresses such as concurrent drought and heat stress can lead to a greater reduction in the crop yield due to increased soil water evaporation. Mittler (2006) noted that the synergistic effect of drought and heat stress on the physiological aspects of plant growth lead to substantial reduction in crop yield and Stuart et al. (1984) reported that weeds outcompete crops because of their efficient water use ability during concurrent drought and heat stress. These concurrent stresses cause substantial drop in the leaf water potential and transpiration rate, which eventually result in increased leaf and canopy temperature particularly in tropical and subtropical environments (Turner et al. 2001; Simoes-Araujo et al. 2003). Several workers have reported that concurrent stress induced increase in the transpiration rate affects vital physiological processes in plants. Drought and heat stress greatly impact nutrient relations, consequently retarding growth by limiting the nutrient mobility through diffusion, and also lead to reductions in the mass, number and growth of roots (Barber 1995; Wahid et al. 2007; Huang et al. 2012). Drought and heat stress alter photopigments and damage thylakoid membranes, usually leading to either reduced chlorophyll biosynthesis and increased chlorophyll degradation or combined effects of both processes (Anjum et al. 2011; Dutta et al. 2009). The damage due to these concurrent stresses affects light reactions occurring in the thylakoid lumen and light-dependent chemical reactions taking place in the stroma. Camejo et al. (2005) reported that photosystem II is very sensitive to concurrent stresses, and its activity is significantly altered or even reduced to zero under severe heat stress. In the event of concurrent abiotic–biotic stresses such as heat and pathogen stress, heat stress promotes the growth of pathogens and leads to occurrence of a wide range of bacterial and fungal diseases such as wilt in tomato (caused by *Ralstonia solanacearum*), seedling blight and bacterial fruit blotch of cucurbits (caused by *Acidovorax avenae*), and panicle blight in rice (caused by *Burkholderia glumae*) (Kudela 2009). Ladanyi and Horvath (2010) reported that heat stress negatively influences the growth and development of plants but promotes pathogen growth and reproduction. In addition to the promotive effects on pathogen growth, heat stress favors the growth of various vectors, thereby facilitating the occurrence of vector borne diseases. Another example of concurrent biotic–abiotic stresses is salinity and pathogen stress. Salinity influences the virulence of pathogens, the physiology of plants and the activity of microbes in the soil (Triky-Dotan et al. 2005). Daami-Remadi et al. (2009) reported that salinity causes more sporulation in fungi and leads to severe *Fusarium* wilt in tomato.

Concurrent abiotic–abiotic or abiotic–biotic stresses do not necessarily affect plant growth and development negatively, as one stress may enhance plant tolerance to the other stress. Some concurrent stresses counteract the effects of one another and eventually result in a net neutral or positive effect on plant growth; therefore, the yield is not always reduced. The yield of *Medicago truncatula* (alfalfa) was improved under concurrent drought and ozone stress as compared with individual drought and ozone stress (Puckette et al. 2007) The improved yield was attributed to enhanced tolerance of the alfalfa plants towards this stress combination. Similarly, concurrent salt and heat stresses led to an improved yield of *Solanum lycopersicum* in comparison with individual salt and heat stresses, and attributed this increase in yield to the improved tolerance of tomato plants towards concurrent salt and heat stresses (Rivero et al. 2014).

1.1.3 Complex Interactions in Stress Combinations

Unlike simple interactions in the aforementioned stress combinations, some stress combinations interact in a complex manner and have variable effects on plants. Examples are the effects of concurrent heat–pathogen and concurrent drought–pathogen stress combinations on *T. aestivum* and *Avena sativa* (oats). Coakley et al. (1999) reported that exposure of *T. aestivum* and *A. sativa* to heat stress facilitates growth and reproduction of *Puccinia* spp., thereby increasing their susceptibility to more severe infection. However, in *Cynodon dactylon* (Bermuda grass) the same stress enhances tolerance to a wide range of rust diseases. Heat–pathogen and drought–pathogen interactions are considered agroeconomically important stress combinations. Pautasso et al. (2012) and Garrett et al. (2006) reviewed the influences of concurrent heat and pathogen interactions on plants. Plant interactions with concurrent drought and pathogen stress have been well investigated in cases of abiotic and biotic stress combinations (Carter et al. 2009; Király et al. 2008; Mayek-Perez et al. 2002; McElrone et al. 2003; Ramegowda et al. 2013; Sharma et al. 2007; Wang et al. 2009; Xu et al. 2008). Here we emphasize the effects of abiotic and biotic stress combinations on plants, with special reference to drought and pathogen stress combination.

1.2 Potential Traits for Genotype Screening for Combined Drought and Pathogen Stress Tolerance

1.2.1 Root System Architecture

The spatial configuration of the root system is referred to as the root system architecture (RSA). The genetic control of the RSA and its relationship to increased productivity under stress is well documented in a wide range of crops, especially cereals. Roots play vital roles in crop production by facilitating water and nutrient uptake, forming symbiotic associations with fungi and bacteria, providing anchorage and serving as storage organs. Additionally, they serve as the main interface for interactions between the plants and various stress factors, and they play a vital role in mitigating the devastating impacts of stress on plant growth and development. The types of interactions that occur between roots and stress factors are determined by the organization and structure of the roots such as their length and density. Resistance to drought stress in rice varieties is linked to increased root length density (RLD) and a wide root diameter. Allah et al. (2010) reported that drought-resistant rice varieties had a greater RLD, which promoted access to the moisture available in the deeper layers of the soil. Under drought stress, maize with a greater RLD and fewer lateral roots showed a higher photosynthetic rate, a more favorable plant water status and greater stomatal conduction than maize with a lesser RLD and more lateral roots. Zhan et al. (2015) reported that the presence of fewer but longer lateral roots led to good use of water available in the deeper layers of the soil by virtue of enhanced rooting, thereby helping the plant to perform better under drought stress (Lynch et al. 2014). The RSA also plays a critical role in reducing pathogen infection in plants. Higginbotham et al. (2004) reported that *T. aestivum* lines with increased root length were less vulnerable to fungal infection with *Pythium debaryanum* and *Pythium ultimum*. Berta et al. (2005) reported that the fungal pathogen *Rhizoctonia solani* decreased root length, root branching and root tips which eventually impaired water absorption from deeper layers of the soil. Hence, it can be concluded that pathogen infection could be reduced to a great extent by increasing the RLD. The RSA plays a key role in crop plant's responses to drought stress and pathogen attack; however, drought and pathogen stress often occur concurrently in field conditions, which leads to greater damage to plants due to complete disruption of the RSA. For instance, in a study of chickpea plants exposed to concurrent drought and infection with the pathogen *Ralstonia solanacearum*, plants that faced progressive drought with 2 and 4 days of *R. solanacearum* infection were categorized as experiencing short-duration (SD) and long-duration (LD) stress stresses, respectively. The study revealed that SD combined stress reduced the growth and reproduction of the pathogen, but there was no significant change in LD combined stress (Sinha et al. 2017). Dryden and Van Alfen (1984) reported stunted growth of *Phaseolus vulgaris* under concurrent stresses caused by drought and the pathogen *Fusarium solani*. The reduced growth was attributed to root rot caused by the pathogen, thereby limiting acquisition of water from deeper layers of the soil. Concurrent drought and pathogen stress are often reported to decrease plant size, leaf area, hydraulic conductance and photosynthetic and transpiration rates (Pennypacker et al. 1991; Abd El-Rahim et al. 1998; Choi et al. 2013).

The timing of pathogen attacks and the onset of drought affect plant growth in different ways, as seen in *S. lycopersicum* infected with *Phytophthora parasitica*. A pathogen attack during drought stress resulted in greater damage as evidenced by decreased root numbers and root mass, with a greater proportion of brown roots and lower fresh weight than those seen with a pathogen attack followed by drought stress. Schroth and Hildebrand (1964) and Duniway (1977) also reported that root rot disease is more severe in plants exposed to concurrent drought and pathogen stress. They attributed the severity of infection to drought-induced increased release of root exudates such as alanine, proline, pentose, and glucose, which serve as nutrients for the growth of soilborne pathogens. Apart from increased exudate release, pathogens also induce changes in the composition of root exudates, and this has been reported in tomato roots infected with *Fusarium oxysporum*. The pathogen attack induced greater release of succinic acid and restricted the release of citric acid, whereas in uninfected plants, such a trend in the release of exudates was not found (Kamilova et al. 2006).

Several researchers have reported contradictory findings of no correlation between drought and the severity of pathogen infection. Balota et al. (2005) found that *Gaeumannomyces graminis* infection in *Triticum* had similar effects under low and severe drought stresses. Likewise, infection of *T. aestivum* cultivars with *Pythium irregulare* and *R. solani* did not result in any change in root lesions under drought stress versus well-watered conditions (Aldahadha 2012). The RLD gets affected and that impairs water acquisition under combined drought and pathogen stress. The RLD is high in plants that show tolerance to concurrent drought and pathogen stress. Taking the vital role of the RLD into consideration, these traits offer a basis for screening for varieties with tolerance to combined drought and pathogen stress.

Modern genetic tools have identified quantitative trait loci (QTLs) linked to the RSA under drought stress (Comas et al. 2013). For instance, one QTL known as root-abscisic acid 1 (ABA1) is linked to root branching and root mass (Giuliani et al. 2005). While working on *Arabidopsis thaliana*, Fitz Gerald et al. (2006) and Xiong et al. (2006) reported another QTL that was associated with abscisic acid–stimulated inhibition of lateral root growth. Therefore, to accomplish the development of drought-resistant and pathogen-resistant plants, a broader study is needed to screen QTLs linked to effective and efficient RSA.

1.2.2 Leaf Pubescence

Under drought or normal conditions the transpiration rate plays a central role in the plant response to a stress stimulus. The traits that affect the rate of transpiration include leaf characteristics such as the leaf area, root-to-leaf ratio, leaf orientation, leaf shape, leaf thickness, and distribution of stomata. Among these, the important factors are the leaf surface characteristics (pubescence/glabrousness). The presence and pattern of hairs (trichomes) on the leaf surface and their density are controlled by both the genotype and the habitat of the plants. Trichomes are modified epidermal cells, which may be branched or unbranched, and glandular or nonglandular, depending on the plant species. Plants show wide variations in the density and pattern of trichomes as a response to mitigate the impacts of combined drought and pathogen stress (Ehleringer et al. 1976; Wagner 1991; Wagner et al. 2004). The trichomes facilitate foliar absorption of water and play a vital role in maintaining leaf hydration in plants found in semiarid climates. In *Arabidopsis* a drought tolerance mutant named cap binding protein 20 (*cbp20*) revealed more trichomes and lower stomatal conductance than control plants (Papp et al. 2004; Jäger et al. 2011). Research on *Phlomis fruticosa* (Jerusalem sage) and *Hedera helix* (ivy) exposed to drought stress revealed that they maintain a low water potential by absorbing dew droplets via their trichomes, unlike plants without trichomes (Grammatikopoulos and Manetas 1994). Additionally, the photosynthetic rate of pubescent leaves was greater than that of glabrous leaves under drought conditions (Grammatikopoulos and Manetas 1994). Roy et al. (1999) reported that *Sinapis arvensis* (wild mustard) subjected to drought stress produced more trichomes than unstressed plants.

Lai et al. (2000) reported that glandular trichomes also resist the spread of pathogen infection by releasing oxidative enzymes, as is evident in *Solanum tuberosum* infected with *Phytophthora infestans*. Furthermore, trichomes reduce the relative humidity of the leaf surface, thereby making the conditions unfavorable for fungal spore germination (Lai et al. 2000). Secretion of T-phylloplanins from the glandular trichomes of tobacco inhibited the growth and reproduction of *Peronospora tabacina* (the causal agent of blue mold disease) in comparison with mock inoculated plants (Kroumova et al. 2007; Nguyen et al. 2016). It was concluded that trichomes can also prevent the spread of infection by release of antifungal components. Armstrong-Cho and Gossen (2005) reported that trichome exudates in chickpea are capable of preventing the spread of infection with *Ascochyta rabiei* (the causal agent of ascochyta blight). The inhibition of the growth and reproduction of *A. rabiei* was found to be exudate concentration dependent, and a lower concentration promoted the infection. The number of nonglandular trichomes was found to be increased in *Hordeum vulgare* exposed to concurrent drought and pathogen stress, in comparison with control plants (Liu and Liu 2016). Furthermore, it can be concluded that concurrent drought and pathogen stress tolerance is directly correlated with the number and kind of trichomes present all over the leaf surface. Ehleringer et al. (1976) stated that both glandular and nonglandular trichomes release antimicrobial components, which thereby serve as the first line of defense against pathogens. Monier and Lindow (2003) reported contradictory findings and reported that trichomes promoted the growth and reproduction of *Pseudomonas syringae*. They attributed this to the retention of water by the trichomes and suggested that exudates released from the broken cuticle at the base of the trichomes might favor microbial growth. Calo et al. (2006) reported that in *A. thaliana*, a mutant designated as *gl1* (*GLABROUS1*) had lower trichome density and increased resistance to *Botrytis cinerea*, whereas another mutant designated as *try* (*TRYPTYCHON*) had higher trichome density and decreased resistance.

Further studies need to be undertaken to fully understand the role of trichomes in pathogen infection. Under concurrent drought and pathogen stress, the roles of glandular trichomes and their exudates in cases where trichomes enhance pathogen growth need to be studied. Gene-mapping studies have screened and isolated leaf pubescence–linked QTLs in many plants, including *Gossypium hirsutum* and *A. thaliana* (Lacape and Nguyen 2005; Bloomer et al. 2014). It can be assumed that increased numbers of trichomes play a critical role in enhancing the tolerance to concurrent drought and pathogen stress, and trichomes can be considered a potential morphophysiological trait conferring tolerance to this stress combination. Isolation of QTLs that govern the number, density, and antimicrobial exudates of trichomes can enable plant breeders to create varieties with better tolerance to concurrent abiotic–biotic stresses. Moreover, it is useful to explore the genes and biochemical pathways that regulate the density and secretions of trichomes, which can be suitably modified to confer tolerance to combined stresses.

1.2.3 Leaf Water Potential and Leaf Turgidity

Under concurrent drought and pathogen stress, plants reveal wide variations in their leaf water potential and leaf turgidity which could be attributable to increases in hydraulic resistance and cell turgor loss (Paul and Ayres 1984; Yan et al. 2017). An alteration in the leaf water potential is directly correlated with soil moisture and is also influenced by pathogen stress, which can disrupt or even devastate the plant's vascular system. Concurrent drought and pathogen stress negatively affect the traits that play a role in maintenance of the leaf water potential and leaf turgidity—for instance, stomatal closure in response to drought stress reported by several workers. Some pathogens may decrease the plant water content even under sufficient soil moisture conditions, as seen in *P. vulgaris* infected with *Uromyces phaseoli* (the causal agent of leaf rust), which releases toxins that inhibit stomatal closure and lead to increased water loss. This further reduces the leaf water potential and leaf turgidity of plants under drought stress (Duniway and Durbin 1971), which indicates that pathogen attack can influence drought tolerance. McElrone et al. (2003) reported that the leaf water potential and leaf turgidity can be considered a physiological parameter for evaluation of the plant water status under concurrent stresses. They investigated the influences of separate and concurrent stresses caused by drought and the pathogen *Xylella fastidiosa* (the causal agent of bacterial leaf scorch) on the leaf water potential of Virginia creeper (*Parthenocissus quinquefolia*). A low water potential and less leaf turgidity was found in plants exposed to these stresses concurrently, causing more severe scorch symptoms than those seen in plants that faced separate drought and pathogen stress. The decreased hydraulic conductance and increased embolism in response to infection could be attributable to low water potential less leaf turgidity. Likewise, Burman and Lodha (1996), while studying the impacts of concurrent drought and *M. phaseolina* stress in cowpea (*Vigna unguiculata*), found drastic decreases in the leaf water potential, leaf turgidity, and transpiration rate under combined stress. Similarly, Paul and Ayres (1984) reported a decreased leaf water potential in *Senecio vulgaris* (groundsel) subjected to concurrent drought and infection with *Puccinia lagenophorae* (the causal agent of rust). They attributed the reduced leaf water potential to cuticle breakdown stimulated by the infection and its subsequent sporulation. Similarly, Mayek-Perez et al. (2002) reported a high transpiration rate, reduced water potential and low stomatal resistance in *P. vulgaris* subjected to simultaneous drought and *M. phaseolina* stress. Drought stress caused the plants to synthesize carbohydrates, which promoted the growth and reproduction of *M. phaseolina*. Moreover, it was found that resistant varieties maintained a higher leaf water potential than susceptible varieties. Contradictory results were reported by Pennypacker et al. (1991) in alfalfa exposed to concurrent drought and *Verticillium albo-atrum* (the causal agent of wilt stress), revealing a high leaf water potential than that seen in drought-stressed plants. Hence, it can be concluded that the impacts of concurrent drought and pathogen stress may have different influences on the leaf water potential and leaf turgidity depending on the type of plant and the type of pathogen.

The QTLs that govern the regulation of the leaf water potential have been identified in several plants. Bernier et al. (2009) and Shamsudin et al. (2016) identified a QTL in rice plants, designated as *qDTY12.1*, that regulates the leaf water potential under drought stress. Identification of QTLs associated with the xylem diameter and xylem pit anatomy can be used to explore molecular pathways and provide greater understanding of the mechanisms that confer tolerance to concurrent drought and pathogen infection. Pouzoulet et al. (2014) reported that xylem vessel dimensions play a vital role in conferring tolerance to vascular pathogen infection. *V. vinifera* genotypes with a smaller xylem diameter were found to be less affected by fungal vascular wilt pathogens. Hence, the plant water potential can be used as a potential morphophysiological trait to screen plants for resistance to concurrent drought and pathogen infection.

1.2.4 Cuticular Wax and Composition of Cuticlar Layer

Cuticular wax and composition of cuticlar layer is of paramount importance in conferring tolerance to concurrent drought stress and pathogen invasion. Kim et al. (2007) reported that *Sesamum indicum* (sesame) exposed to drought stress produced higher-density cuticular wax than unstressed plants. In response to these combined stresses, plants show wide variations in cuticular wax composition (Marcell and Beattie 2002; Kosma et al. 2009). The cuticular layer serves as a physical barrier to pathogen infection, as it is hydrophobic in nature and lacks any moisture content (Martin 1964). Several workers have documented the vital role of the cuticular layer in conferring resistance to drought and pathogen stress. Kosma et al. (2009) reported that exposure of *Arabidopsis* plants to drought stress induced an increase in the concentration of the cuticular wax components, resulting in increased wax deposition in stressed plants. Hameed et al. (2002) reported that the thickness of the cuticular layer is determined by drought stress, and it can also determine the resistance to drought stress, as observed in drought-resistant *T. aestivum* plants, which possessed a thicker cuticle than susceptible plants. Marcell and Beattie (2002) subjected control and glossy mutants of *Zea mays* (*gl4*) to *Clavibacter michiganensis* (the causal agent of leaf blight and Goss's wilt in maize). They found that control plants were less affected, with fewer bacterial colonies present on their leaf surfaces than on those of the *gl4* mutants, which exhibited a thin cuticular layer due to a modified wax biosynthetic pathway. The greater sporulation of the pathogen may have been attributable to increased nutrient and water exudation through the weak cuticular layer, eventually favoring greater pathogen growth in the *gl4* mutants. Jenks et al. (1994), while working on mutants of *S. bicolor*, reported that bloomless (*bm*) mutants exhibited a thin cuticular layer and were more susceptible to infection with *Setosphaeria turcica* (the causal agent of leaf blight) than control plants. Furthermore, the transpiration rate was higher in the *bm* mutant plants than in the control plants. This apparently reflects the fact that the cuticular wax thickness can be employed to identify plants tolerant to *Exserohilum turcicum*. However, the importance of cuticular wax under concurrent stresses is yet to be studied. A detailed study of the pathways that alter the structure and composition of the cuticle layer may be useful in exploring targets that can be manipulated to provide plants with enhanced resistance to concurrent drought and pathogen stress. In rice plants, Srinivasan et al. (2008) have identified a QTL on chromosome 8 for epicuticular wax, the leaf transpiration rate, and the harvest index, colocated with QTLs associated with shoot- and root-related drought tolerance traits. Considering the significance of cuticular wax and composition of cuticular layer in conferring tolerance to pathogen invasion, isolation of QTLs associated with wax content and disease tolerance need to pay a wider attention. Therefore, cuticular wax and composition of cuticular layer may be considered a potential trait that can be used to screen plants for tolerance to concurrent drought and pathogen infection.

1.2.5 *Canopy Temperature*

Tolerance to drought and pathogen stress can be evaluated by measuring the canopy temperature (Gonzalez-Dugo et al. 2005). In response to concurrent drought and pathogen infection, plants alter their transpiration rate, thereby changing their canopy temperature to sustain growth. Under drought and pathogen stress the canopy temperature varies between leaves, as stress-induced drooping and curling of leaves cause differences in reflection of radiation (Jackson 1986). The canopy temperature plays a major role in plant growth under drought stress, as it has been observed that wheat plants under drought stress have a higher canopy temperature and a lower yield than well-watered plants (Blum et al. 1989). Moreover, it was reported that plants that had a lower canopy temperature were drought resistant, whereas plants with a higher canopy temperature were susceptible to drought stress (Blum et al. 1989). Plants that maintain a high canopy temperature under drought stress conditions have a lower plant water status and thus are less adapted to drought stress (Blum 2009). The significance of the canopy temperature in preventing pathogen infection was also reported by Eyal and Blum (1989). In comparison with control plants, the canopy temperature of wheat plants infected with *Mycosphaerella graminicola* (the causal agent of *Septoria tritici* blotch) was high, and the increase in canopy temperature was directly linked to the severity of the disease. The canopy temperature of *T. aestivum* plants infected with *M. graminicola* could be positively correlated with the occurrence of the disease, as infected plants had a higher canopy temperature. The rise in canopy temperature could be attributable to cuticular layer damage caused by pathogen invasion. Therefore, assessment of the canopy temperature could be helpful in identifying infected and uninfected plants (Eyal and Blum 1989). Pinter et al. (1979) and Dow et al. (1988) studied alterations in the canopy temperature in *Beta vulgaris* (sugar beet) subjected to concurrent drought and pathogen infection. They reported that sugar beet has a high canopy temperature under concurrent drought and infection with *Pythium aphanidermatum* (the causal agent of root rot). The sudden rise in the canopy temperature could be attributable to pathogen-induced root damage, hampering water uptake and causing a reduction in the plant water potential. Likewise, *Cucumis sativus* (cucumber) infected with the pathogen *Pseudoperonospora cubensis* (the causal agent of downy mildew) showed a higher canopy temperature than control plants (Oerke et al. 2006). Pinter et al. (1979) reported a raised canopy temperature in *Gossypium* spp. infected with *Phymatotrichum omnivorum* (the causal agent of *Phymatotrichum* root rot) under drought stress. Similarly, under concurrent drought and infection with *M. phaseolina* (the causal agent of charcoal rot infection), a raised leaf temperature and reduced stomatal resistance were noted in *P. vulgaris* (Mayek-Perez et al. 2002). Hence, as the canopy temperature shows significant variations under concurrent drought and pathogen infection, it can be considered a potential trait for evaluation of the concurrent drought and pathogen tolerance of plants. Infrared thermometers can be employed for measurement of the canopy temperature; thereby, screening for plant tolerance to concurrent drought and pathogen infection can be done.

1.3 Role of Genomics in Developing Crops with Combined Drought and Pathogen Stress Tolerance

A few important molecular studies have recently been employed to elucidate the molecular responses of plants to combined drought and pathogen stress. These studies have not only shed light on plant defense mechanisms against combined stresses but also revealed some potential candidates for improvement of plant tolerance to combined stresses. Some of the important candidate genes identified so far are methionine gamma lyase (*AtMGL*, a methionine homeostasis gene), rapid alkalinization factor-like 8 (*AtRALFL8*, involved in cell wall remodeling), and azelaic acid induced 1 (*AZI1*, which functions in systemic plant immunity) (Atkinson et al. 2013). Tolerance to combined drought and pathogen stress is also contributed by genes involved in cross talk between the drought-associated and pathogen infection–associated signaling pathways. The roles of proline and polyamine metabolism in combined drought and pathogen stress tolerance in *A. thaliana* and *V. vinifera* have also been indicated by some studies (Hatmi et al. 2015; Gupta et al. 2016). The identified candidate genes can be suitably modulated to confer enhanced tolerance to these combined stresses. The modification can be done by genome editing using tools such as the CRISPR/Cas9 [clustered regularly interspaced short palindromic repeats and CRISPR-associated protein 9] system. CRISPR/Cas9 can also be used to modulate the transcription of the genes of interest by guiding catalytically inactive dead Cas9 (dCas9) or dCas9 fused with transcriptional repressors/activators to the promoter of a gene. Further research in this direction using the different functional genomic approaches can thus help to reveal the responses of plants to combined drought and pathogen stress.

1.4 Conclusion and Future Perspectives

Plants grown under field conditions face a combination of different abiotic and biotic stresses and to mitigate the effects plats have evolved complex signalling pathways. The interactions between these stresses and their impacts on plants have been discussed here. The interactions between the two different types of stress conditions may either negatively or positively affect plant growth. For example, a coexisting drought can modulate the interaction of different pathogens and plants differently, leading to either suppression of pathogen growth or an increase in it. Therefore, it becomes very important to study the interaction between the two different types of stresses in order to better understand the net impact of stress combinations on plants. Several important diseases such as dry root rot, powdery mildew, and charcoal rot are significantly affected by concurrent drought conditions, and identification and development of superior cultivars can be done if a mechanistic understanding of the interactions between pathogen and drought stress is attained. Strategies for improving crop performance under combined drought and pathogen stress require deeper understanding. Attempts to understand the interactions have already commenced in the form of transcriptomic studies. Well-designed experiments involving simultaneous drought and pathogen stress on plants have also been undertaken, revealing some aspects of drought–pathogen interactions (Gupta et al. 2016; Sinha et al. 2016). Plant genotypes can be screened for traits such as their root system architecture, leaf water potential, leaf turgidity, leaf pubescence, and leaf cuticular waxes for identification of superior germplasm lines. To vividly assess the effects of different stress combinations on plants, it is imperative to design experiments that can reveal different aspects of interactions between the two different types of stresses. A well-considered stress imposition protocol that is not very different from stresses occurring under field conditions, complemented by relevant physiological assays and the recently evolved genomic tools, can help uncover the responses of plants to stress combinations. Understanding obtained from studies on plant responses to combined drought and pathogen stresses can be utilized by breeders and field pathologists to better analyze the performance of tolerant genotypes. Further development of crop simulation models involving a combination of drought and pathogen stress can help in disease forecasting in places where concurrence of the two stresses is prevalent. Thus, integrative efforts made by crop modeling experts, agronomists, field pathologists, breeders, physiologists, and molecular biologists can efficiently lead to development of combined-stress-tolerant crops that can perform well under field conditions.

References

Abd El-Rahim MF, Fahmy GM, Fahmy ZM (1998) Alterations in transpiration and stem vascular tissues of two maize cultivars under conditions of water stress and late wilt disease. Plant Pathol 47:216–223. https://doi.org/10.1046/j.1365-3059.1998.00211.x

Ahmad B, Raina A, Naikoo MI, Khan S (2019) Role of methyl jasmonates in salt stress tolerance in crop plants. In: Plant Signalling Molecules (Eds Khan MIR, Reddy PS, Ferrante A, Khan NA). Woodhead Publishing, Elsevier, Duxford, United Kingdom pp. 371–384. https://doi.org/10.1016/B978-0-12-816451-8.00023-X

Aldahadha AMA (2012) Effect of root diseases and drought on water use efficiency of wheat. Doctoral thesis, University of New England, Armidale

Allah AA, Shimaa A, Zayed B, Gohary AE (2010) The role of root system traits in the drought tolerance of rice (*Oryza sativa* L.). Int J Agric Biol Sci 1:83–87

Anjum SA, Wang LC, Farooq M, Hussain M, Xue LL, Zou CM (2011) Brassinolide application improves the drought tolerance in maize through modulation of enzymatic antioxidants and leaf gas exchange. J Agron Crop Sci 197:177–185. https://doi.org/10.111[illegible]1439-037X.2010.00459.x

Armstrong-Cho C, Gossen BD (2005) Impact of glandular hair exudates on infection of chickpea by *Ascochyta rabiei*. Can J Bot 83:22–27. https://doi.org/10.1139/[illegible]147

Atkinson NJ, Lilley CJ, Urwin PE (2013) Identification of genes involved in the response to simultaneous biotic and abiotic stress. Plant Physiol 162:2028–2041. https://doi.org/10.1104/pp.113.222372

Balota M, Rush CM, Payne WA, Lazar MD (2005) The effect of take-all disease on gas-exchange rates and biomass in two winter wheat lines with different drought response. Plant Soil 275:337–348. https://doi.org/10.1007/s11104-005-2680-y

Barber SA (1995) Soil nutrient bioavailability: a mechanistic approach., 2nd edn. Wiley, New York

Barnes JD, Davison AW (1988) The influence of ozone on the winter hardiness of Norway Spruce [*Picea abies* (L) Karst]. New Phytol [illegible]08:159–166. https://doi.org/10.1111/j.1469-8137.1988.tb03692.x

Belisario A, Maccaroni M, Corazza [illegible] Balmas V, Valier A (2002) Occurrence and etiology of brown apical necrosis on Persian (English) walnut fruit. Plant Dis 86:599–602. https://doi.org/10.1094/PHYTO-01-15-0029-R

Bernier J, Serraj R, Kumar A, [illegible]nuprasad R, Impa S, Veereshgowda RP, Oane R, Spaner D, Atlin G (2009) The large-effect drought-resistance QTL *qtl12.1* increases water uptake in upland rice. Field Crop Res 110(2):139–146

Berta G, Sampo [illegible] Gamalero E, Massa N, Lemanceau P (2005) Suppression of *Rhizoctonia* root-rot of tomato by *Glomus mossae* BEG12 and *Pseudomonas fluorescens* A6RI is associated with their effect on the pathogen growth and on the root morphogenesis. Eur J Plant Pathol 111:279–288. https://doi.org/10.1007/s10658-004-4585-7

Bloom[illegible]H, Lloyd AM, Symonds VV (2014) The genetic architecture of constitutive and induced trichome density in two new recombinant inbred line populations of *Arabidopsis thaliana*: phenotypic plasticity, epistasis, and bidirectional leaf damage response. BMC Plant Biol 14:119. https://doi.org/10.1186/1471-2229-14-11

Blum A (2009) Effective use of water (EUW) and not water-use efficiency (WUE) is the target of crop yield improvement under drought stress. Field Crop Res 112:119–123. https://doi.org/10.1016/j.fcr.2009.03.009

Blum A, Shpiler L, Golan G, Mayer J (1989) Yield stability and canopy temperature of wheat genotypes under drought-stress. Field Crop Res 22:289–296. https://doi.org/10.1016/0378-4290(89)90028-2

Brown JKM, Hovmoller MS (2002) Aerial dispersal of pathogens on the global and continental scales and its impact on plant disease. Science 297:537–541

Burman U, Lodha S (1996) *Macrophomina phaseolina* induced changes in plant water relations of resistant and susceptible cowpea genotypes. Indian Phytopathol 49:254–259

Calo L, García I, Gotor C, Romero LC (2006) Leaf hairs influence phytopathogenic fungus infection and confer an increased resistance when expressing a *Trichoderma* α-1,3-glucanase. J Exp Bot 57:3911–3920. https://doi.org/10.1093/jxb/erl155

Camejo D, Rodriguez P, Morales MA, Dell'amico JM, Torrecillas A, Alarcon JJ (2005) High temperature effects on photosynthetic activity of two tomato cultivars with different heat susceptibility. J Plant Physiol 162:281–289. https://doi.org/10.1016/j.jplph.2004.07.014

Carter AH, Chen XM, Garland-Campbell K, Kidwell KK (2009) Identifying QTL for high temperature adult-plant resistance to stripe rust (*Puccinia striiformis* f. sp. *tritici*) in the spring wheat (*Triticum aestivum* L.) cultivar 'Louise'. Theor Appl Genet 119:1119–1128

Choi HK, Alberto I, Francisco GS, Douglas C (2013) Water deficit modulates the response of *Vitis vinifera* to the Pierce's disease pathogen *Xylella fastidiosa*. Mol Plant-Microbe Interact 26:1–46. https://doi.org/10.1094/MPMI-09-12-0217-R

Choudhary A, Pandey P, Senthil-Kumar M (2016) Tailored responses to simultaneous drought stress and pathogen infection in plants. In: Hossain MA, Wani SH, Bhattacharjee S, Burritt DJ, Tran L-SP (eds) Drought stress tolerance in plants, vol Vol 1. Springer, Cham, pp 427–443. https://doi.org/10.1007/978-3-319-28899-4_18

Coakley SM, Scherm H, Chakraborty S (1999) Climate change and plant disease management. Annu Rev Phytopathol 37:399–426. https://doi.org/10.1146/annurev.phyto.37.1.399

Comas LH, Becker SR, Cruz VMV, Byrne PF, Dierig DA (2013) Root traits contributing to plant productivity under drought. Front Plant Sci 4:442. https://doi.org/10.3389/fpls.2013.00442

Daami-Remadi M, Souissi A, Oun HB, Mansour M, Nasraoui B (2009) Salinity effects on *Fusarium* wilt severity and tomato growth. Dyn Soil Dyn Plant 3:61–69

Daryanto S, Wang L, Jacinthe PA (2016) Global synthesis of drought effects on maize and wheat production. PLoS One 11:e0156362. https://doi.org/10.1371/journal.pone.0156362

Dow RL, Powell NL, Porter DM (1988) Effects of modification of the plant canopy environment on *Sclerotinia* blight of peanut. Peanut Sci 15:1–5. https://doi.org/10.3146/i0095-3679-15-1-1

Dryden P, Van Alfen NK (1984) Soil moisture, root system density, and infection of roots of pinto beans by *Fusarium solani* f. sp. *phaseoli* under dryland conditions. Phytopathology 74:132–135. https://doi.org/10.1094/Phyto-74-132

Duniway J, Durbin R (1971) Detrimental effect of rust infection on the water relations of bean. Plant Physiol 48(1):69–72

Duniway JM (1977) Predisposing effect of water stress on the severity of Phytophthora root rot in safflower. Phytopathology 67:884–889. https://doi.org/10.1094/Phyto-67-884

Dutta S, Mohanty S, Tripathy BC (2009) Role of temperature stress on chloroplast biogenesis and protein import in pea. Plant Physiol 150:1050–1061. https://doi.org/10.1104/pp.109.137265

Ehleringer J, Björkman O, Mooney HA (1976) Leaf pubescence: effects on absorptance and photosynthesis in a desert shrub. Science 192(4237):376–377

Eyal Z, Blum A (1989) Canopy temperature as a correlative measure for assessing host response to *Septoria tritici* blotch of wheat. Plant Dis 73:468–471. https://doi.org/10.1094/PD-73-0468

Farooq M, Gogoi N, Barthakur S, Baroowa B, Bharadwaj N, Alghamdi SS, Siddique KH (2017) Drought stress in grain legumes during reproduction and grain filling. J Agron Crop Sci 203(2):81–102

Fitzgerald JN, Lehti-Shiu MD, Ingram PA, Deak KI, Biesiada T, Malamy JE (2006) Identification of quantitative trait loci that regulate *Arabidopsis* root system size and plasticity. Genetics 172:485–498. https://doi.org/10.1534/genetics.105.047555

Garrett KA, Dendy SP, Frank EE, Rouse MN, Travers SE (2006) Climate change effects on plant disease: genomes to ecosystems. Annu Rev Phytopathol 44:489–509. https://doi.org/10.1146/annurev.phyto.44.070505.143420

Giuliani S, Sanguineti MC, Tuberosa R, Bellotti M, Salvi S, Landi P (2005) *Root-ABA1*, a major constitutive QTL, affects maize root architecture and leaf ABA concentration at different water regimes. J Exp Bot 56:3061–3070. https://doi.org/10.1093/jxb/eri303

Gonzalez-Dugo MP, Moran MS, Mateos L, Bryant R (2005) Canopy temperature variability as an indicator of crop water stress severity. Irrig Sci 24:233–240. https://doi.org/10.1007/s00271-005-0022-8

Goudarzi S, Banihashemi Z, Maftoun M (2011) Effect of salt and water stress on root infection by *Macrophomina phaseolina* and ion composition in shoot in sorghum. Iran J Plant Pathol 47:69–83

Grammatikopoulos G, Manetas Y (1994) Direct absorption of water by hairy leaves of *Phlomis fruticosa* and its contribution to drought avoidance. Can J Bot 72(12):1805–1811

Gupta A, Dixit SK, Senthil-Kumar M (2016) Drought stress predominantly endures *Arabidopsis thaliana* to *Pseudomonas syringae* infection. Front Plant Sci 7:808

Hameed M, Mansoor U, Ashraf M, Rao AUR (2002) Variation in leaf anatomy in wheat germplasm from varying drought-hit habitats. Int J Agric Biol 4:12–16

Hatmi S, Gruau C, Trotel-Aziz P, Villaume S, Rabenoelina F, Baillieul F et al (2015) Drought stress tolerance in grapevine involves activation of polyamine oxidation contributing to improved immune response and low susceptibility to *Botrytis cinerea*. J Exp Bot 66:775–787. https://doi.org/10.1093/jxb/eru436

Higginbotham RW, Paulitz TC, Kidwell KK (2004) Virulence of *Pythium* species isolated from wheat fields in eastern Washington. Plant Dis 88:1021–1026. https://doi.org/10.1094/PDIS.2004.88.9.1021

Huang B, Rachmilevitch S, Xu J (2012) Root carbon and protein metabolism associated with heat tolerance. J Exp Bot 63:3455–3465. https://doi.org/10.1093/jxb/ers003

Jackson RD (1986) Remote sensing of biotic and abiotic plant stress. Annu Rev Phytopathol 24:265–287. https://doi.org/10.1146/annurev.py.24.090186.001405

Jäger K, Fábián A, Tompa G, Deák C, Höhn M, Olmedilla A, Barnabás B, Papp I (2011) New phenotypes of the drought-tolerant *cbp20 Arabidopsis thaliana* mutant have changed epidermal morphology. Plant Biol 13(1):78–84

Jenks MA, Joly RJ, Peters PJ, Rich PJ, Axtell JD, Ashworth EN (1994) Chemically induced cuticle mutation affecting epidermal conductance to water vapor and disease susceptibility in *Sorghum bicolor* (L.) Moench. Plant Physiol 105:1239–1245. https://doi.org/10.1104/pp.105.4.1239

Kamilova F, Kravchenko LV, Shaposhnikov AI, Makarova N, Lugtenberg B (2006) Effects of the tomato pathogen *Fusarium oxysporum* f. sp *radicis-lycopersici* and of the biocontrol bacterium *Pseudomonas fluorescens* WCS365 on the composition of organic acids and sugars in tomato root exudate. Mol Plant Microbe Interact 19:1121–1126. https://doi.org/10.1094/MPMI-19-1121

Kim KS, Park SH, Jenks MA (2007) Changes in leaf cuticular waxes of sesame (*Sesamum indicum* L.) plants exposed to water deficit. J Plant Physiol 164(9):1134–1143

Király L, Hafez YM, Fodor J, Király Z (2008) Suppression of tobacco mosaic virus–induced hypersensitive-type necrotization in tobacco at high temperature is associated with downregulation of NADPH oxidase and superoxide and stimulation of dehydroascorbate reductase. J Gen Virol 89:799–808

Kosma DK, Bourdenx B, Bernard A, Parsons EP, Lü S, Joubès J, Jenks MA (2009) The impact of water deficiency on leaf cuticle lipids of *Arabidopsis*. Plant Physiol 151(4):1918–1929

Kroumova AB, Shepherd RW, Wagner GJ (2007) Impacts of *T-phylloplanin* gene knockdown and of *Helianthus* and *Datura* phylloplanins on *Peronospora tabacina* spore germination and disease potential. Plant Physiol 144(4):1843–1851

Kůdela V (2009) Potential impact of climate change on geographic distribution of plant pathogenic bacteria in Central Europe. Plant Prot Sci 45:S27–S32

Lacape J-M, Nguyen TB (2005) Mapping quantitative trait loci associated with leaf and stem pubescence in cotton. J Hered 96:441–444. https://doi.org/10.1093/jhered/esi052

Ladanyi M, Horvath L (2010) A review of the potential climate change impact on insect populations—general and agricultural aspects. Appl Ecol Environ Res 8:143–152. https://doi.org/10.15666/aeer/0802_143151

Lai A, Cianciolo V, Chiavarini S, Sonnino A (2000) Effects of glandular trichomes on the development of *Phytophthora infestans* infection in potato (*S. tuberosum*). Euphytica 114:165–174. https://doi.org/10.1023/A:1003924318577

Lamichhane JR, Venturi V (2015) Synergisms between microbial pathogens in plant disease complexes: a growing trend. Front Plant Sci 6:385. https://doi.org/10.3389/fpls.2015.00385

Liu X, Liu C (2016) Effects of drought-stress on *Fusarium* crown rot development in barley. PLoS One 11(12):e0167304

Loreto F, Bongi G (1989) Combined low temperature–high light effect on gas-exchange properties of jojoba leaves. Plant Physiol 91:1580–1585. https://doi.org/10.1104/pp.91.4.1580

Lynch JP, Chimungu JG, Brown KM (2014) Root anatomical phenes associated with water acquisition from drying soil: targets for crop improvement. J Exp Bot 65:6155–6166. https://doi.org/10.1093/jxb/eru162

Mahalingam R (2015) Consideration of combined stress: a crucial paradigm for improving multiple stress tolerance in plants. In: Mahalingam R (ed) Combined stresses in plants. Springer International Publishing, Cham. https://doi.org/10.1007/978-3-319-07899-1_1

Marcell LM, Beattie GA (2002) Effect of leaf surface waxes on leaf colonization by *Pantoea agglomerans* and *Clavibacter michiganensis*. Mol Plant-Microbe Interact 15(12):1236–1244

Maron JL, Crone E (2006) Herbivory: effects on plant abundance, distribution and population growth. Proc R Soc B 273:2575–2584

Maron JL, Kauffman M (2006) Habitat-specific consumer impacts on plant population dynamics. Ecology 87:113–124

Martin JT (1964) Role of cuticle in the defense against plant disease. Annu Rev Phytopathol 2:81–100. https://doi.org/10.1146/annurev.py.02.090164.000501

Mayek-Perez N, Garcia-Espinosa R, Lopez-Castaneda C, Acosta-Gallegos JA, Simpson J (2002) Water relations, histopathology and growth of common bean (*Phaseolus vulgaris* L.) during pathogenesis of *Macrophomina phaseolina* under drought stress. Physiol Mol Plant Pathol 60:185–195. https://doi.org/10.1006/pmpp.2001.0388

McDonald A, Riha S, DiTommasob A, DeGaetanoa A (2009) Climate change and the geography of weed damage: analysis of US maize systems suggests the potential for significant range transformations. Agric Ecosyst Environ 130:131–140. https://doi.org/10.1016/j.agee.2008.12.007

McElrone AJ, Sherald JL, Forseth IN (2003) Interactive effects of water stress and xylem-limited bacterial infection on the water relations of a host vine. J Exp Bot 54(381):419–430

Mittler R (2006) Abiotic stress, the field environment and stress combination. Trends Plant Sci 11:15–19. https://doi.org/10.1016/j.tplants.2005.11.002

Monier JM, Lindow SE (2003) Differential survival of solitary and aggregated bacterial cells promotes aggregate formation on leaf surfaces. Proc Natl Acad Sci U S A 100:15977–15982. https://doi.org/10.1073/pnas.2436560100

Mordecai EA (2011) Pathogen impacts on plant communities: unifying theory, concepts, and empirical work. Ecol Monogr 81:429–441

Narsai R, Wang C, Chen J, Wu J, Shou H, Whelan J (2013) Antagonistic, overlapping and distinct responses to biotic stress in rice (*Oryza sativa*) and interactions with abiotic stress. BMC Genomics 14:93. https://doi.org/10.1186/1471-2164-14-93

Niakoo MI, Dar MI, Raghib F, Jaleel H, Ahmad B, Raina A, Khan FA, Naushin F (2019) Role and regulation of plants phenolics in abiotic stress tolerance: an overview. In: Plant Signalling Molecules (Eds Khan MIR, Reddy PS, Ferrante A, Khan NA). Woodhead Publishing, Elsevier, Duxford, United Kingdom pp. 157–168. https://doi.org/10.1016/B978-0-12-816451-8.00009-5

Nguyen TTX, Dehne H-W, Steiner U (2016) Maize leaf trichomes represent an entry point of infection for *Fusarium* species. Fungal Biol 120(8):895–903

Oerke E, Steiner U, Dehne H, Lindenthal M (2006) Thermal imaging of cucumber leaves affected by downy mildew and environmental conditions. J Exp Bot 57(9):2121–2132

Pandey P, Ramegowda V, Senthil-Kumar M (2015) Shared and unique responses of plants to multiple individual stresses and stress combinations: physiological and molecular mechanisms. Front Plant Sci 6:723

Papp I, Mur L, Dalmadi A, Dulai S, Koncz C (2004) A mutation in the cap binding protein 20 gene confers drought. Plant Mol Biol 55(5):679–686

Patterson DT (1995) Effects of environmental stress on weed/crop interaction. Weed Sci 43:483–490

Paul N, Ayres P (1984) Effects of rust and post-infection drought on photosynthesis, growth and water relations in groundsel. Plant Pathol 33(4):561–569

Pautasso M, Döring TF, Garbelotto M, Pellis L, Jeger MJ (2012) Impacts of climate change on plant diseases—opinions and trends. Eur J Plant Pathol 133:295–313. https://doi.org/10.1007/s10658-012-9936-1

Pennypacker B, Leath K, Hill R (1991) Impact of drought stress on the expression of resistance to *Verticillium albo-atrum* in alfalfa. Phytopathology 81(9):1014–1024

Peters K, Breitsameter L, Gerowitt B (2014) Impact of climate change on weeds in agriculture: a review. Agric Sustain Dev 34:707–721. https://doi.org/10.1007/s13593-014-0245-2

Pinter PJ, Stanghellini ME, Reginato RJ, Idso SB, Jenkins AD, Jackson RD (1979) Remote detection of biological stresses in plants with infrared thermometry. Science 205:585–586. https://doi.org/10.1126/science.2054406.585

Pouzoulet J, Pivovaroff AL, Santiago LS, Rolshausen PE (2014) Can vessel dimension explain tolerance toward fungal vascular wilt diseases in woody plants? Lessons from Dutch elm disease and esca disease in grapevine. Front Plant Sci 5:253. https://doi.org/10.3389/fpls.2[illegible]4.00253

Prasch CM, Sonnewald U (2013) Simultaneous application of heat, drought and virus to *Arabidopsis* plants reveals significant shifts in signaling networks. Plant Physiol 162(4): 1849–1866. https://doi.org/10.1104/pp.113.221044

Puckette MC, Weng H, Mahalingam R (2007) Physiological and biochemical responses to acute ozone-induced oxidative stress in *Medicago truncatula*. Plant Physiol Biochem 45:70–79. https://doi.org/10.1016/j.plaphy.200612.004

Ramegowda V, Senthil-Kumar M (2015) The interactive effects of simultaneous biotic and abiotic stresses on plants: mechanistic understanding from drought and pathogen combination. J Plant Physiol 176:47–54. https://doi.org/10.1016/j.jplph.2[illegible]1411.008

Ramegowda V, Senthil-Kumar M, Ishiga Y, Kaundal [illegible] Udayakumar M, Mysore KS (2013) Drought stress acclimation imparts tolerance to *Sclerotinia sclerotiorum* and *Pseudomonas syringae* in *Nicotiana benthamiana*. Int J Mol Sci 14:9497–9513

Rivero RM, Mestre TC, Mittler R, Rubio F, Garc[illegible]-Sanchez F, Martinez V (2014) The combined effect of salinity and heat reveals a specific physiological, biochemical and molecular response in tomato plants. Plant Cell Environ 37:1[illegible]59–1073. https://doi.org/10.1111/pce.12199

Roy BA, Stanton ML, Eppley SM (1999) Effects of environmental stress on leaf hair density and consequences for selection. J Evol Biol 12:1089–1103. https://doi.org/10.1046/j.1420-9101.1999.00107.x

Scherm H, Coakley SM (200[illegible]) Plant pathogens in a changing world. Australas Plant Pathol 32:157–165. https://doi.org/10.1071/AP03015

Schroth MN, Hildebrand DC (1964) Influence of plant exudates on root-infecting fungi. Annu Rev Phytopathol 2:101–132. https://doi.org/10.1146/annurev.py.02.090164.000533

Shamsudin NAA, S[illegible]amy BM, Ratnam W, Cruz MTS, Raman A, Kumar A (2016) Marker assisted pyramiding of drought yield QTLs into a popular Malaysian rice cultivar, MR219. BMC Genet 17(1):30

Sharm[illegible] RC, Duveiller E, Ortiz-Ferrara G (2007) Progress and challenge towards reducing wheat spot blotch threat in the Eastern Gangetic Plains of South Asia: is climate change already taking its toll? Field Crop Res 103:109–118

Si[illegible]es-Araujo JL, Rumjanek NG, and Margis-Pinheiro M (2003) Small heat shock proteins genes are differentially expressed in distinct varieties of common bean. Braz J Plant Physiol 15:33–41. https://doi.org/10.1590/S1677-04202003000100005

Sinha R, Gupta A, Senthil-Kumar M (2016) Understanding the impact of drought on foliar and xylem invading bacterial pathogen stress in chickpea. Front Plant Sci 7:902. https://doi.org/10.3389/fpls.2016.00902

Sinha R, Gupta A, Senthil-Kumar M (2017) "Concurrent drought stress and vascular pathogen infection induce common and distinct transcriptomic responses in chickpea." Frontiers in Plant Science 8(2017):333

Srinivasan S, Gomez SM, Kumar SS, Ganesh SK, Biji KR, Senthil A et al (2008) QTLs linked to leaf epicuticular wax, physio-morphological and plant production traits under drought