

Crosstalk and trade-offs: Plant responses to climate change-associated abiotic and biotic stresses

Courtney Leisner¹, Neha Potnis², and Alvaro Sanz-Saez³

¹Auburn University Department of Biological Sciences

²Auburn University Department of Entomology and Plant Pathology

³Auburn University Department of Crop Soil and Environmental Sciences

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Abstract

As sessile organisms, plants are constantly challenged by a dynamic growing environment. This includes fluctuations in temperature, water availability, light levels, and atmospheric conditions. In concert with changes in abiotic conditions, plants experience changes in biotic stress pressures, including plant pathogens, viruses, and herbivores. Human-induced increases in atmospheric carbon dioxide (CO₂) levels have led to alterations in plant growth environments that challenge their productivity and nutritional quality. Additionally, it is predicted that climate change will alter the prevalence and virulence of plant pathogens, further challenging plant productivity. A knowledge gap exists in the complex interplay between plant responses to biotic and abiotic stress conditions. Closing this gap is crucial for developing climate resilient crops in the future. Here, we review the physiological responses of plants to elevated CO₂, temperature, tropospheric ozone (O₃), and drought conditions, as well as the interaction of these abiotic stress factors with plant pathogen pressure. Additionally, we describe the crosstalk and trade-offs involved in plant responses to both abiotic and biotic stress, and outline targets for future work to develop a more sustainable future food supply in light of future climate change.

Crosstalk and trade-offs: Plant responses to climate change-associated abiotic and biotic stresses

Courtney P. Leisner^{1*}, Neha Potnis², Alvaro Sanz-Saez³

¹Department of Biological Sciences, Auburn University, Auburn, AL 36849, USA

²Department of Entomology and Plant Pathology, Auburn University, Auburn, AL 36849, USA

³Department of Crop, Soil and Environmental Science, Auburn University, Auburn, AL 36849, USA; *Corresponding author: cpl0013@auburn.edu

ABSTRACT

As sessile organisms, plants are constantly challenged by a dynamic growing environment. This includes fluctuations in temperature, water availability, light levels, and atmospheric conditions. In concert with changes in abiotic conditions, plants experience changes in biotic stress pressures, including plant pathogens, viruses, and herbivores. Human-induced increases in atmospheric carbon dioxide (CO₂) levels have led to alterations in plant growth environments that challenge their productivity and nutritional quality. Additionally, it is predicted that climate change will alter the prevalence and virulence of plant pathogens, further challenging plant productivity. A knowledge gap exists in the complex interplay between plant responses to biotic and abiotic stress conditions. Closing this gap is crucial for developing climate resilient crops in the future. Here, we review the physiological responses of plants to elevated CO₂, temperature, tropospheric ozone (O₃), and

drought conditions, as well as the interaction of these abiotic stress factors with plant pathogen pressure. Additionally, we describe the crosstalk and trade-offs involved in plant responses to both abiotic and biotic stress, and outline targets for future work to develop a more sustainable future food supply in light of future climate change.

INTRODUCTION

Anthropogenic increases in fossil fuel emissions have led to atmospheric concentrations of carbon dioxide (CO₂) that are unprecedented for the last 800,000 years (IPCC, 2021). This has led to unequivocal warming of the global atmosphere, changes in precipitation patterns and extreme weather events, and increased sea level rise leading to coastal flooding (IPCC, 2021). Additionally, other changes in atmospheric constituents, such as the concentration of secondary air pollutants like tropospheric ozone (O₃), are also predicted to increase this century (IPCC, 2021). Global climate change will lead to more frequent and extreme heat waves, drought, waterlogging, and associated changes in soil moisture (IPCC, 2021). While the predicted negative impacts of global warming on agricultural productivity and the associated socioeconomic impact on food systems have been well reviewed (e.g., Cushman et al., 2022; Fisher et al., 2005; Hatfield et al., 2011; Vermeulen et al., 2012; Slattery & Ort, 2019), less is known about the significant interactions and trade-offs between and among different climate change-associated abiotic stresses on plant productivity (Rivero et al., 2022). For example, while global warming and associated changes in plant growing conditions have potential negative impacts on yield and productivity especially for the latter half of the 21st century (Challinor et al., 2014; Lobell et al., 2011), elevated CO₂ concentrations [CO₂] stimulates growth and harvestable grain production in C₃ crops (Ainsworth et al., 2008). This, however, comes at a cost of decreased nutritional content in major crop plants (Myers et al., 2014; Soares et al., 2019), but has also been shown to be ameliorated under elevated temperature (Kohler et al., 2019).

Even less is known about these interacting abiotic stress factors in perennial and specialty cropping systems (Leisner, 2020), and about crosstalk between abiotic and biotic stress signaling pathways (Fujita et al., 2006). While there are many unknowns related to the effects of climate change on pathogen spread, evidence indicates there will be enhanced reproductive potential and increased geographic spread of pathogens, which has the potential to lead to changes in disease dynamics and pathogen host ranges, raising concerns of increased disease outbreaks (Garret et al., 2006; Kissoudis et al., 2014). Combined biotic and abiotic stresses can lead to alterations in defense signaling pathways in plants, predisposing plants to increased susceptibility to endemic pathogens, but also potentially new pathogens. Here we briefly review the physiological responses of plants to climate-change related abiotic stress, outline the complex interplay of stress signaling pathways between abiotic and biotic stress pathways related to climate change, and highlight trade-offs and targets for future research efforts and work to enhance resilience in plant development and defense responses considering future climate change.

PHYSIOLOGICAL RESPONSES OF PLANTS TO ABIOTIC STRESS

2.1 Drought stress

Human-induced changes in the atmosphere have led to increasing incidence of drought in many areas of the world, such as Central and South America, Southeast Asia, and the Mediterranean basin (IPCC, 2021). The incidence of drought in these regions is expected to worsen in the future (IPCC, 2021). By 2020, 5 billion people will be living in water scarce regions where crop production will be threatened by drought (UN-DESA, 2011). As a result of an increasing population and intensification of agriculture in drought prone areas, water demand for agriculture will double by 2050, while freshwater resources are expected to drop by 50% (Gupta et al., 2020). Drought significantly decreases crop growth and yield, and in the past decade has produced a loss in crop income of approximately \$30 billion (Gupta et al., 2020). For example, the drought of summer 2012, is the most severe global drought recorded in recent years and caused \$18 billion in crop losses (Schnoor, 2012). This drought caused production losses in corn (*Zea mays*) (52%) and sorghum (*Sorghum bicolor*) (51%) (Lal et al., 2012) led to significant yield reductions of 24-26% for these crops (Schnoor, 2012). Water is crucial for human and plant survival, and its deficit limits plant growth, development, and

ultimately yield. Drought negatively affects plant growth from the cellular to the whole-plant level. This section will review the main effects of drought on plant physiological characteristics focusing on those that may be relevant for plant-biotic interactions.

With drought, the soil water potential decreases, leading to drop in root and leaf water potential (Liu et al., 2004). This drop in water potential is accompanied by tissue dehydration and loss in turgor (Reddy et al., 2004). To adapt to this lower water potential, plants tend to accumulate osmotolerant substances such as sugars, proline and other active amino acids that decrease the water potential in the cell allowing for retention of water (Roosens et al., 2002). The decrease in turgor is associated with a reduction in cell elongation and division. This results in stunted growth, observed as a reduction in leaf area and overall aboveground biomass (Farooq et al., 2009; Asrar & Elhindi, 2011).

At the leaf level, the cuticle is one barrier that protects the leaf from desiccation and limits water loss through the stomata. Drought increases cuticle thickness as an adaptation to reduce leaf transpiration (Bi et al., 2017). In fact, cultivars that show higher increases in cuticle thickness under drought are considered drought tolerant (Bi et al., 2017). Additionally, work in *Arabidopsis* has shown mutant lines (*aldh2c4*) with a 50% reduction in leaf cuticle thickness have higher water loss than wild type plants (Liu et al., 2022). Alterations in leaf thickness under drought stress also works to better regulate the balance between CO₂ acquisition and water loss (Li et al., 2021). For this reason, some species respond to drought by thickening their leaves while others become thinner (Wellstein et al., 2016).

As the soil dries and soil and plant water potential decreases, the hormone abscisic acid (ABA) is synthesized in roots and leaves, and consequently, the stomata close and transpiration is reduced (Buckley, 2019). Additional drought adaptations include reductions in total stomatal number and size (Casson & Gray, 2008; Pitaloka et al., 2022). It has been documented that rice mutants with decreased stomatal density and size show higher yield and water use efficiency due to a reduced transpiration without any yield penalty under drought (Pitaloka et al., 2022). As the stomata are one of the main points of entry of leaf pathogens, drought acts to decrease pathogen entry through the stomatal pore, making the interaction of pathogens and drought a key area of research for future climate resiliency in plants.

2.2 Elevated temperature stress

It is estimated that human activities have led to an approximate increase of 0.8°C to 1.3°C in global temperatures since pre-industrial levels, with a likely increase to 1.0°C to 2.0°C by mid-century given current rates of increase (IPCC, 2021). In addition to increases in mean temperature in most land and ocean regions, regional climates are also likely to see an increase in extreme heat events (IPCC, 2021). This is predicted to lead to a widespread and significant negative impact on crop yields if global warming exceeds 1.5 °C above pre-industrial levels (Battisti & Naylor, 2009; Hatfield & Prueger, 2015; Perkins et al., 2012; IPCC, 2021; Zhu et al., 2021). It is estimated that 3-12% of global crop yields will decline for every 1°C of warming for major global crops (soybean (*Glycine max*), rice (*Oryza sativa*), wheat (*Triticum aestivum*), and maize) (Zhao et al., 2017; Zhu et al., 2021). Temperature (along with daylength) also signal significant physiological transitions in plants, which is a major determinant of yield in grain crops (Ruiz-Vera et al., 2015; Zhu et al., 2018) and proper developmental timing in perennial cropping systems (Leisner, 2020).

Due to this importance, much work has been done to understand the physiological response of crop plants to elevated temperatures (for review see Hatfield & Prueger, 2015; Moore et al., 2021; Zhu et al., 2021). This work has illustrated key impacts of elevated temperature on photosynthesis (Moore et al., 2021), growth, development, and other biochemical and physiological processes (Hatfield & Prueger, 2015; Zhu et al., 2021). From these reviews we enumerate a few key impacts of elevated temperature on photosynthesis (Moore et al., 2021). First, C₃ crop plants are sensitive to elevated temperature impacts on photosynthetic enzymes involved in carbon assimilation. This is due to a decline in specificity of the key carboxylation enzyme Rubisco (Ribulose-1,5- biphosphate carboxylase/oxygenase), deactivating the enzyme under supra-optimal temperatures (Moore et al., 2021). Second, regulation of Rubisco activity by Rubisco activase is another possible area of improvement of plant photosynthetic responses to high temperatures, as manipulation of

the thermostability of Rubisco activase at higher temperatures has been shown to increase photosynthetic thermotolerance in *Arabidopsis* and rice (Kurek et al., 2007; Kumar et al., 2009; Shivhare & Mueller-Cajar, 2017; Scafaro et al., 2016; Scafaro et al., 2019; Wang et al., 2010).

Third, plant photosynthetic responses to heat stress can be modulated through changes in stomatal density and size which in turn, affect rates of stomatal conductance, which is a key control point for gas exchange between the leaf interior and the atmosphere (Moore et al., 2021). Elevated temperature also determines the air vapor pressure deficit, plant transpiration rate, and plant water status, all of which affect stomatal behavior and photosynthetic capacity (Moore et al., 2021). Work to improve stomatal anatomy and metabolism is underway to improve stomatal resilience to heat stress (Moore et al., 2021).

Fourth, elevated temperature can negatively impact photosynthetic capacity through alterations in source-sink relationships (Moore et al., 2021). Changes in the translocation of the products of photosynthesis (carbohydrates) determines source-sink relationships, and changes in this relationship can also affect the timing of vegetative and reproductive development, and ultimately affect yield. Previous work has found that structural changes in the phloem, along with changes in activity and gene expression of key enzymes involved in sucrose transport and metabolism effect source-sink relationship in plants exposed to heat stress (Moore et al., 2021), and are future targets for developing heat-resistant cultivars of plants. Finally, increased temperature has also been shown to cause denaturation of proteins and inhibition of protein synthesis, degradation of chlorophyll, changes in membrane fluidity and permeability, and alterations in respiration and cell death (Zhu et al., 2021), all of which directly affect plant photosynthesis, growth, development, and productivity.

The ultimate impact of elevated temperature on plant growth and development is also dictated by the timing of temperature stress during a plant's life cycle (Hatfield & Prueger, 2015). Generally, vegetative development has a higher temperature optimum than reproductive development, but a range of acceptable maximum and minimum temperatures for growth and temperature extremes exist (Hatfield & Prueger, 2015; Zhu et al., 2021). Elevated temperatures during vegetative growth leads to accelerated development in non-perennial crops, which can decrease yield potential by reducing vegetative growth and decreasing the duration of reproductive growth (Hatfield & Prueger, 2015). Additionally, elevated temperature can significantly negatively affect reproductive structures, including impacts on pollen viability, fertilization, grain/fruit formation (CCSP, 2008; Hatfield et al., 2011), and chronic exposure to elevated temperatures during pollination can lead to decreased grain/fruit set and yield (Hatfield & Prueger, 2015).

Previous work suggests crop plants that exhibit variation in flowering times during the day may be more resilient to future elevated temperatures, as flowering at cooler times of the day would be beneficial (Caviness & Fagala, 1973; Sha et al., 2011; Sheehy et al., 2005; Wiebbecke et al., 2012). Additionally, the length of anthesis has a strong correlation with crop sensitivity to temperature extremes, as exhibited in the range of anthesis times in maize, rice, sorghum, soybean, peanuts (*Arachis hypogaea*), and cotton (*Gossypium hirsutum*), with longer anthesis times potentially leading to more resilience to extreme heat events (Hatfield & Prueger, 2015). Taken together, these impacts on plant growth and development may cause declines in yield in annual crop plants but are dependent on CO₂ emission scenarios and crops evaluated (Hatfield et al., 2011; Lobell et al., 2011; Schlenker & Roberts, 2009). Further work is needed to understand the complex interaction of elevated CO₂ and temperature, crop genetics, biotic stresses, and adaptive management strategies on yield loss estimates (Hatfield & Prueger, 2015). Furthermore, precise evaluations of maximum and minimum temperature, atmospheric water vapor demand and duration of heat stress in both annual and perennial plants is needed to gain a more complete understanding of temperature impacts on plant productivity (Hatfield & Prueger, 2015; Leisner, 2020).

2.3 Elevated tropospheric O₃ stress

Tropospheric O₃ is a harmful secondary air pollutant that negatively affects crop productivity through both direct oxidative damage to plant cells, and through its role as a greenhouse gas and subsequent contribution to global warming (Ainsworth, 2017). Tropospheric O₃ concentrations ([O₃]) have more than doubled since

pre-industrial times (Monks et al., 2015) and while there is spatial heterogeneity in global tropospheric $[O_3]$, O_3 levels remain high in major agricultural growing regions during the crop-growing season (Ainsworth, 2017). It is estimated that on a global scale, O_3 pollution has led to a 2-15% decrease in yield for crops such as wheat, rice, maize, and soybean (Avnery et al., 2011; Van Dingenen et al., 2009).

Plant uptake of O_3 occurs through both stomatal and non-stomatal pathways (soil and cuticular deposition), with the primary form of O_3 entry occurring through the leaf stomata (Ainsworth, 2017). Upon entry into the intercellular air space of leaves O_3 reacts to produce reactive oxygen species (ROS), leading to cellular damage (Ahlfors et al., 2009; Grimes et al., 1983; Heath, 1987). Perception, signaling and detoxification of O_3 and ROS has been well reviewed (Ainsworth et al., 2012; Ainsworth, 2017; Vainonen & Kangasjarvi, 2015), and includes altered redox balance, increases in cytosolic calcium, mitogen-activated protein kinase (MAPK) signaling cascades, and altered expression of genes involved in hormone and antioxidant metabolism, respiration, and photosynthesis (Ainsworth, 2017).

The physiological response of plant responses to O_3 and their agronomic consequences have also been previously reviewed (for list see Ainsworth, 2017; Montes et al., 2022), and demonstrate chronic elevated $[O_3]$ decrease photosynthesis and stomatal conductance in C_3 plants, and increase rates of respiration (Morgan et al., 2003; Ainsworth, 2008; Feng et al., 2008). Additionally, decreased photosynthetic rates are associated with a decrease in photosynthetic proteins, pigment, and nitrogen (N) content, and increased rates of respiration are associated with changes in leaf antioxidant balance (Dutilleul et al., 2003). These reductions in plant primary metabolism can lead to reduction in plant growth rates, leaf area and biomass accumulation (both aboveground and belowground) (Morgan et al., 2003; Ainsworth, 2008; Feng et al., 2008).

As with other abiotic stresses, the timing of O_3 stress can play a role in the overall impact on plant productivity; O_3 can directly impact reproductive development in plants (Black et al., 2000; Leisner & Ainsworth, 2012) and O_3 exposure during reproductive development can lead to a greater reduction in photosynthesis than during vegetative development in some plants (Morgan et al., 2003; Ainsworth, 2008; Feng et al., 2008). Overall, O_3 impacts plants at the community, whole plant, leaf, and cellular level and can lead to reductions in crop yield and overall biomass accumulation (Ainsworth et al., 2012). While there is significant within-species variation in O_3 tolerance in crops (Ainsworth, 2017; Booker et al., 2009), future work is needed to see successful gains in breeding and biotechnological approaches to improving resiliency to O_3 in crops.

2.4 Elevated atmospheric CO_2

Anthropogenic CO_2 emissions have increased the atmospheric $[CO_2]$ since the beginning of the industrial revolution, with the global concentration increasing from 340 ppm in 1980 to 417 ppm in February of 2022 (GML-NOAA, 2022). If CO_2 emissions are maintained, the Representative Concentration Pathway model (RCP) 8.5 predicts that atmospheric $[CO_2]$ could reach between 550-600 ppm by 2050 (IPCC, 2021). Therefore, it is important to understand the effects of elevated CO_2 on crop physiology, yield and its interaction with other abiotic factors as well as biotic stresses such as crop diseases. The effects of elevated CO_2 at the crop, plant and genetic level have been widely studied before (for review see Ainsworth & Rogers, 2007; Ainsworth & Long, 2020) but a better understanding of the interactive effects of CO_2 with other abiotic and biotic stress is needed.

As a substrate of photosynthesis, elevated concentrations of atmospheric CO_2 increase photosynthesis of C_3 plants between 20 to 45% by saturating Rubisco and decreasing photorespiration (Ainsworth & Rogers, 2007; Leakey et al., 2009; Walker et al., 2016). Of these, C_3 legume crops such as soybean, peanut, and peas (*Pisum sativum*) have higher photosynthetic rates than other C_3 crops due to the benefits of biological nitrogen fixation on plant N and sugar metabolic status (Ainsworth & Rogers, 2007; Sanz-Saez et al., 2015). In C_4 plants, however, elevated CO_2 does not increase photosynthesis directly as they already possess a CO_2 concentration mechanism that saturates Rubisco and avoids photorespiration (Leakey et al., 2009). For that reason, C_4 crops such as maize, sorghum and other C_4 grasses such as *Panicum coloratum* only show higher photosynthetic rates when grown under elevated CO_2 when also exposed to drought stress. This is a result of reduced transpiration that allows the crops to save more water in the soil and maintain higher

photosynthetic rates during drought (Leakey et al., 2009).

The major function of stomata is to maximize CO₂ fixation while minimizing water loss. As atmospheric [CO₂] increase, the intercellular CO₂ concentration in C₃ and C₄ plants increases as well, and therefore plants respond by decreasing both stomatal aperture and stomatal density, resulting in lower water loss at the leaf level (Leakey et al., 2009; Ainsworth & Long, 2020). This decrease in stomatal conductance translates to a decrease in canopy evapotranspiration that results in increased soil moisture content (Leakey et al., 2009). In some cases, however, elevated [CO₂] stimulate leaf growth and canopy expansion and therefore canopy transpiration is increased (Gray et al., 2016; Parvin et al., 2019). These factors need to be taken in account when studying the interaction with diseases as a reduced stomatal conductance and number could limit the entrance of leaf pathogens and reduce disease severity (Eastburn et al., 2011).

Under elevated [CO₂], plants tend to produce more sugars due to increased photosynthetic rates (Ainsworth et al., 2004). Feedback inhibition occurs if plants are not able to distribute those sugars from the sources (leaves) to the sink organs (roots, flowers developing seeds) at the same pace that sugars are assimilated, which in turn, inhibits the expression of photosynthetic genes and limits photosynthesis (Ainsworth et al., 2004). This photosynthetic limitation at elevated [CO₂] produced by a sink limitation is more common in crops that produce more leaves (sources) and not as many seeds (sinks), as reproductive organs are stronger carbon (C) sinks. This has been demonstrated in wheat, where cultivars with higher harvest index (produce more seeds) were more responsive to elevated [CO₂] than cultivars that produced more vegetative biomass (Aranjuelo et al., 2013). Additionally, this increase in carbohydrate content is followed by a reduction in the assimilation of N (Rubio-Asensio & Bloom, 2017; Bloom et al., 2020; Adavi & Shathee, 2021) that, combined, results in a dilution of the N content in all plant tissues and an increase in the C/N ratio that could affect disease growth (Ainsworth & Long, 2004).

Due to a reduction of the transpiration stream and the dilution effect produced by an increase in carbohydrate concentration in seeds and leaves, mineral concentrations tend to decrease at elevated [CO₂] (McGrath & Lobell, 2013; Myers et al., 2014; Ebi & Loladze, 2019; Loladze et al., 2019; Ebi et al., 2021). The decrease of micronutrients like iron (Fe), zinc (Zn), and selenium (Se) is significant, as they are essential nutrients for human nutrition and its deficiency in diets affects more than 2 billion people in the world (Ebi & Loladze, 2019; Loladze et al., 2019; Ebi et al., 2021). This decrease in nutrient concentration due to a reduced transpiration at elevated [CO₂] can be significant for other nutrients that are important for the integrity of membranes and cell walls such as silicone, calcium (Ca) and boron (B), as it could facilitate the infection of some pathogens.

The stimulation of photosynthesis at elevated [CO₂] usually results in biomass and yield increases in C₃ plants (Bishop et al., 2014; Sanz-Saez et al., 2017; Hu et al., 2022). The magnitude of the positive effect depends on the crop species and the interactions between biotic and abiotic factors (Ainsworth & Long, 2020). However, genotypic variation in the biomass and yield response to elevated [CO₂] has been found in several crops under controlled and open environments (Aranjuelo et al., 2013; Bishop et al., 2014; Sanz-Saez et al., 2017). Additionally, under elevated [CO₂], leaf area is stimulated, and the canopy closes earlier in the season and is denser than at ambient [CO₂] (Srinivasan et al., 2017; Sanz-Saez et al., 2017). A canopy that closes earlier in the season and is denser could produce a more humid microclimate that favors the appearance of diseases.

CROSSTALK BETWEEN ABIOTIC AND BIOTIC STRESS

Plants respond to individual biotic or abiotic stresses or simultaneous challenge by biotic and abiotic stresses in a complex and unique manner at the physiological, transcriptional, and cellular levels (Suzuki et al., 2014; Zhang et al., 2022). Common responses of plants to abiotic stresses are stomatal closure, reduced photosynthesis, increased ROS scavenging activity, reduced leaf growth, and increased root length, as described above. In response to biotic stress, plants respond to challenges by bacterial, fungal, and viral pathogens or nematodes in different ways depending on the biotrophic or necrotrophic lifestyle of pathogens. Some commonly observed responses to these biotic stresses include stomata closure, reduced photosynthesis, production of ROS, phytoalexin production, and local cell death. Overlap in the regulatory networks that control plant

responses to both abiotic stress, pathogen recognition and defense therefore include ROS signaling, expression of plant hormones, changes in redox status and ion flux, and changes in cell wall integrity (Kissoudis et al., 2014; Rivero et al., 2022), indicating crosstalk and convergence of mechanisms to combat general stress (Walley et al., 2007; Atkinson & Urwin et al., 2012; Kissoudis et al., 2014).

With climate change comes the higher likelihood that plants might be challenged with simultaneous stressors in agricultural fields and accompanied variable levels of pathogen pressure, as changes in the growing environment (i.e., temperature, water availability) can affect plant disease epidemics and other plant-microbe interactions (Rivero et al., 2022). These combined stresses have the potential to pose an even greater threat to global food security and climate resilience than each stress alone (Rivero et al., 2022). Previous work has shown that susceptibility to hemibiotrophic or necrotrophic pathogens is increased under abiotic stress, while susceptibility to biotrophic pathogens is reduced when combined with abiotic stress (Saijo & Loo, 2019). Therefore, to engineer a more sustainable future food supply we need to understand how biotic and abiotic stress combinations act in combination. This includes understanding stress signaling crosstalk in plant signaling, gene expression, metabolism, and development. Below we summarize our current knowledge of crosstalk in signaling and plant metabolic pathways that occurs when plants are exposed to combined abiotic and biotic stresses. In the following section we outline trade-offs between plant responses to combined biotic and abiotic stress conditions with targets for future research efforts.

3. 1 Drought and plant biotic stress interactions

The interaction between drought and plant disease stress has been previously reviewed for a wide variety of crops and disease systems (Kissoudis et al., 2014; Pandey et al., 2015a,b; Zarratini et al., 2021). From these reviews it is apparent that the outcomes from plant biotic and drought stress interactions are going to depend on environmental conditions that may favor the establishment and spread of the disease, the type of microorganism's mode of infection and virulence, and impacts of drought on plant defense mechanisms (Kissoudis et al., 2014; Pandey et al., 2015a; Zarratini et al., 2021). Here we will review how drought can affect plant-pathogen interactions by studying the effect of drought on pathogen fitness on plant physiology which can affect the plant-pathogen interaction.

Many fungal and bacterial pathogens need high soil or leaf moisture levels to be able to survive in the plant surface and infect it. Many root fungal pathogens such as root rot (*Phytium* sp.; *Aphanomyces* sp.) and downy mildew (*Plasmopara* sp.) are reduced under drought conditions due to inadequate soil moisture (Pandey et al., 2015a). For example, the occurrence of root rot and downy mildew in sunflowers (*Helianthus annuus*) was less severe under drought conditions due to detrimental environmental conditions for the survival of the pathogens (Pandey et al., 2015a). Similarly, foliar bacterial and fungal diseases can be impeded by drought, as they favor high water content in the leaf apoplast, which is usually associated with high humidity (Freeman & Beattie, 2009). Additionally, it has been observed that drought can reduce the spread of fungal pathogens as rain is needed for the dispersal of fungal spores (Pandey et al., 2015a), as well as the incidence of many bacterial leaf spot diseases, as they reproduce by water-soaked lesions (Rudolph, 1984).

Drought, however, can also enhance the severity of some root diseases, such as the incidence of smut on cereals (*Urocystis agropyri*; Colhoun, 1973), charcoal stalk rot in sorghum (*Macrophomina phaseoli*; Pandey et al., 2015a) and root rot in safflower (*Phytophthora* sp.; Duniway, 1977). The increased infection and severity observed in these root fungal pathogens can be possibly related with a higher diffusibility of volatile fungal attractors emitted by roots in dry soils (Kerr, 1964; Pandey et al., 2015a). Drought stress can also increase herbivore performance, as seen in faba bean (*Vicia faba* minor L.), where yield was decreased when plants experienced both water stress and herbivory pressure from black bean aphids (*Aphis fabae*) (Raderschall et al., 2021). This could increase the infection of viruses that are transmitted by aphid vectors.

Drought can also impair disease tolerance traits in plants, thereby limiting their defense mechanisms. Low levels of ROS have been related with the production of ABA in leaves and the regulation (closing) of stomatal opening and pathogen attack (Qi et al., 2018). ABA is a plant hormone that is synthesized during abiotic stress conditions, including water stress, and helps the plant to maintain its turgor and water potential by

closing stomata, accumulating osmotolerant solutes, and reducing leaf expansion at the expense of reduced growth (Kissoudis et al., 2014). ABA production under drought is of special interest as it downregulates the salicylic acid (SA) and jasmonic acid (JA) defense mechanisms against plant pathogens (Kissoudis et al., 2014; Pandey et al., 2015b). For example, drought induces the ABA signaling pathway, which downregulates Calmodulin-binding protein 60g (CBP60g) and Systemic Acquired Resistance Deficient 1 (SARD1). These two transcription factors are important nodes in the crosstalk since they are needed for SA production, required for suppression of pathogens (Choudhary & Senthil-Kumar, 2021), as well as for other defense related proteins. CBP60g plays a role early during defense response and SARD1 later during the infection (Wang et al., 2011). Additionally, drought stress has been shown to enhance the susceptibility of Arabidopsis to *Pseudomonas syringae* by increasing ABA signaling, which suppress SA-mediated defense responses (Mohr & Cahill, 2003, 2007; Choudhary & Senthil-Kumar, 2022).

Oxidative damage produced by ROS accumulation under severe drought can also produce membrane and cellular damage which results in plant solute leakage through the membrane, making plants vulnerable to more severe pathogen infection. For example, charcoal rot (*Macrophomina phaseolina*) can use osmotolerant amino acids, such as proline and asparagine, produced by common bean (*Phaseolus vulgaris*) to tolerate drought, and therefore exacerbate the severity of the infection and disease (Mayek-Perez et al., 2002; Ijaz et al., 2013).

As drought stress decreases the water potential of the whole soil-plant-atmosphere continuum, this can result in damage in the structure of the xylem, such as the pit membranes, which reduce xylem conductivity and transpiration (Ladjal et al., 2005; Hillabrand et al., 2016). This in turn can increase susceptibility of plants to disease, such as *Xylella fastidiosa* which causes Pierce's disease, as the bacteria has better access to the xylem when the pit membranes are damaged (Newman et al., 2003; Thorne et al., 2006).

Drought can also lead to improved disease tolerance traits in plants. Under drought, ABA-induced stomatal closure can lead to decreased pathogen infection, as seen with *P. syringae* (Melotto et al., 2006). ABA also stimulates pre-invasion defense mechanisms such as callose deposition in the phloem which reduces the spread of vascular pathogens such as *Phytophthora irregularis* (Adie et al., 2007). In addition, increased ABA levels during early drought have been shown to increase the resistance of *Nicotiana benthamiana* to white mold (*Sclerotinia sclerotiorum*) and tomato (*Solanum lycopersicum*) to gray mold (*Botrytis cinerea*) (Achuo et al., 2006; Ramegowda et al., 2013). Increased cuticle thickening caused by drought can also limit pathogen infection (Tang et al., 2007; Bi et al., 2017). Finally, pathogen stress can lead to improved plant responses to drought. Previous work has shown drought tolerance has been improved in plants exposed to RNA viruses (Xu et al., 2008) and Arabidopsis plants exposed to *Verticillium* spp. demonstrated enhanced tolerance to drought due to increased water flow from *de novo* xylem formation upon pathogen infection (Reusche et al., 2012).

3.2 Elevated temperature and plant biotic stress interactions

High temperature conditions, along with high humidity, can facilitate plant disease development by promoting pathogen growth, affecting the virulence in pathogens, and dampening plant disease resistance responses (Fujita et al., 2006; Desaint et al., 2020; Zarattini et al., 2021). High temperature has been shown to increase virulence of pathogens across diverse plant species (see reviews Cohen & Leach, 2020; Desaint et al., 2020; Zarattini et al., 2021). For example, resistance of rice to the fungal pathogen *Magnaporthe oryzae* is compromised when plants are pre-exposed to heat stress (Onaga et al., 2017), and barley (*Hordeum vulgare*) is more susceptible to powdery mildew disease (*Blumeria graminis* f. sp. *hordei*) when exposed to elevated temperature and CO₂ stress (Mikkelsen et al., 2015). This is also seen in Arabidopsis, where immunity is suppressed in plants exposed to high temperatures, decreasing resistance of Arabidopsis to *P. syringae* (Janda et al., 2019). Resistance to *Xanthomonas* in pepper (*Capsicum annum*) conferred by *bs5*, *bs6* resistance genes is compromised at elevated temperatures (Vallejos et al., 2010). Conversely, pathogen infection has the potential to compromise heat tolerance, as seen in *Tomato yellow leaf curl virus* (TYLCV) in tomatoes (Anfoka et al., 2016).

Virulence in pathogens can also be affected by high temperature stress. For example, the pathogen responsible for soft rot in potato crops (*Dickeya solani*) causes more severe symptoms in high temperatures due to an upregulation of genes in *D. solani* involved in biofilm production (Czajkowski et al., 2016). Temperature maximums have been observed however, beyond which pathogen virulence is decreased, as seen in the phytopathogenic bacterium *Pectobacterium carotovorum* which causes bacterial soft rot in a wide range plant species (Saha et al., 2015). Taken together, there is a complex interaction between environmental conditions affecting both host plant susceptibility to pathogen stress and the virulence of the pathogen. For additional review of heat-dependent plant immune mechanisms and pathogen thermosensory processes please see Desaint et al., (2020). The authors review plant-pathogen interactions under elevated temperature stress that have a negative, neutral, or positive effect on plant resistance,

Work has also been done to identify unique and overlapping responses in the plant transcriptome to singular and combined temperature and abiotic stress. A key point of interaction between high temperature and disease resistance is R protein stability (Fujita et al., 2006; Cohen & Leach, 2020). Previous work has shown that plant resistance is maintained or enhanced at high temperatures, as seen in expression of several R genes to wheat stem rust and bacterial blight, however the mechanism for this enhanced temperature-dependent resistance is not known (Cohen & Leach, 2020). Conversely, disease resistance mediated by receptor-like kinase (RLK)-type R genes are also compromised by high temperature, indicating the stability of RLK-type R proteins might also be decreased, weakening key components of defense signaling in plants (Fujita et al., 2006). Other common plant transcriptomic responses to combined heat and pathogen stress include activation of transcription factors, increased expression of stress responsive genes, and downregulation of photosynthetic and C metabolism genes (Desaint et al., 2020).

There is also an elaborate crosstalk between elevated temperature stress and plant hormone signaling. The activation of plant defense to biotic stress involves regulation of several phytohormone pathways, including SA, JA, and ethylene (ET) (Zarattini et al., 2021). For example, previous work has shown defense responses in Arabidopsis to *P. syringae* mediated by SA can increase under low temperatures (Li et al., 2020) but are compromised at elevated temperature (Wang et al., 2009; Huot et al., 2017; Janda et al., 2019). Resistance was compromised at elevated temperatures in Arabidopsis due to increased expression of genes that regulate SA, specifically JA signaling (Huot et al., 2017). When exposed to low temperature stress, however, SA-ET crosstalk regulates SA-dependent plant responses (Zarattini et al., 2021). This indicates there are complex temperature-phytohormone signaling interactions that lead to novel outcomes based on the treatment and pathosystem. Future work is needed to understand the synergistic outcomes from the combined stress, as the transcriptional and phytohormone response from the combined stress is often unpredictable and specific to different pathosystems (Cohen & Leach, 2020; Desaint et al., 2020; Zarattini et al., 2021).

3.3 Elevated $[O_3]$ and plant biotic stress interactions

Increased O_3 exposure has shown to have secondary impacts on plants by altering the incidence of pests or pathogens, or by mediating the ability of a plant to respond to these biotic pressures (Fuhrer, 2009; Eastburn et al., 2011). Plants exposed to elevated O_3 have been shown to be more prone to attacks by necrotrophic pathogens, root-rot fungi as well as insects such as bark beetles, while obligate biotrophic infections may be lessened on plants pre-exposed to elevated O_3 (Karnosky et al., 2002; Sandermann, 2000; Tiedemann & Firsching, 2000). These differential effects have been shown to stem from physiological differences (such as reduced net photosynthesis and premature ripening and senescence) and corresponding gene expression changes in the plant (different signaling pathways involved in responding to necrotrophic vs. biotrophic pathogens). Conclusions drawn for specific pests and disease interactions with elevated O_3 are controversial, however (Fuhrer, 2009), as responses can differ even within fungal genera. For example, wheat plants infected with leaf rust (*Puccinia recondita* sp. *tritici*) showed symptoms of O_3 damage earlier and with higher severity compared to plants without rust infection (Tiedemann & Firsching, 2000), whereas O_3 -fumigated plants showed resistance towards *Bipolaris* in barley (Plazek et al. 2000).

Changes in the leaf surface topography, and in turn, chemical composition, in response to O_3 , result in alterations in leaf wettability and solute retention (Karnosky et al., 2002). These alterations can influence

attachment of pathogens to the leaf surface. Leaf surface attachment and successful epiphytic colonization is a crucial step during pathogenesis of foliar bacterial pathogens (Lindow & Brandl 2003; Potnis et al., 2014). For example, studies involving the foliar bacterial pathogen *P. glycinea* on soybean exposed to elevated $[O_3]$ both pre- and post-inoculation showed reduced bacterial infection severity and a reduced number of lesions (Laurence & Wood, 1978), while there was no effect or protection against bacterial blight (*X. phaseoli*) on white bean (*P. vulgaris*) when plants were exposed to elevated $[O_3]$ (Temple & Bisessar, 1979). This indicates future work looking at O_3 impacts on specific plant-pathogen systems is needed to obtain a comprehensive view of plant resilience to future climate.

At the molecular level, the signaling pathways altered by elevated $[O_3]$ can influence the plant defense-growth trade-off/dilemma that plants face when attacked by the pathogen (Kangasjärvi et al., 1994; Eastburn et al. 2011). Plant defense signaling pathways in response to pathogen infection and elevated O_3 have been shown to share components such as ROS production. The oxidative burst caused by elevated O_3 was also shown to affect antagonistic and synergistic interactions between JA, SA, ET, and ABA, all of which are plant growth regulators, as well as important components of the plant defense network against biotrophic and necrotrophic pathogens (Eastburn et al. 2011; Kangasjärvi et al., 1994). Plant exposure to O_3 also increases the activity of several enzymes in the phenylpropanoid, flavonoid and lignin pathways, which play a role in plant defense (Kangasjärvi et al., 1994). Reaction of O_3 with the plant apoplastic space and cell membrane causes increased production of linoleic acid (Mudd, 1998), and in turn biosynthesis of JA, which may attenuate SA-dependent hypersensitive response (HR) and cell death pathways in plants (Rao et al. 2000a,b). Suppression of SA-dependent HR would mean that disease resistance against pathogens would be compromised. Functional SA-signaling pathways are also required for O_3 -induced ET biosynthesis, which is also needed for induction of HR-like cell death (Rao et al., 2002). O_3 -induced ET biosynthesis is also linked to increased biosynthesis of ABA, which regulates both stomatal conductance in plants and sugar signaling (Ahlfors et al., 2004; Leon & Sheen, 2003). This crosstalk can lead to trade-offs in plant growth and defense, which may ultimately affect the plant's ability to respond to biotic stresses.

3.4 Atmospheric elevated $[CO_2]$ and plant biotic stress interactions

As elevated $[CO_2]$ does not directly affect the *in vitro* growth of plant pathogens (Zhang et al., 2015), the observed interactions between disease and elevated $[CO_2]$ are due to the physiological changes that elevated CO_2 exerts on plants and the consequences that this has on pathogen severity and incidence. The plant response to infection with different microorganisms (bacteria, fungi, and viruses) under elevated $[CO_2]$ can be very variable and depending on primary and secondary effects of elevated $[CO_2]$ on plants.

Elevated CO_2 reduces stomatal density and aperture and therefore infectivity of different bacterial and fungal diseases that infect plants through stomata may be reduced (Ainsworth & Rogers, 2007; Eastburn et al., 2011; Li et al., 2015). In a growth chamber study investigating the interactions of *P. syringae* in tomato it was observed that under elevated $[CO_2]$ stomatal aperture was reduced approximately 30%, and the pathogen was not able to reverse stomatal closure to pre-infection levels, which is a strategy used by the pathogen in ambient $[CO_2]$ (Li et al., 2015). It is hypothesized that this defense against disease under elevated $[CO_2]$ is also due to a stimulation of the SA defense pathway that results in the production of nitric oxide that stimulates stomatal closure. The increased SA defense under elevated $[CO_2]$ has been demonstrated to reduce infection and severity of Tomato Mosaic Virus and *P. syringae* in tomatoes (Zhang et al., 2015). However, the JA defense pathway is not stimulated at elevated $[CO_2]$ and a disequilibrium between the SA and JA pathways produces an increase in incidence and severity of diseases that are controlled by the JA defense, such as *B. cinerea* (Zhang et al., 2015). This demonstrates the complexity of hormone signaling responses to the combined abiotic and biotic stress conditions and that more research is needed to understand the effects of elevated $[CO_2]$ on the plant defense system and the interaction with multiple diseases.

Additional work has shown the decrease in disease susceptibility in the field. A 3-year field experiment performed under elevated $[CO_2]$ conditions found the incidence of powdery mildew (*Peronospora manshurica*) was reduced by 60% in soybean. It was hypothesized this was likely due to decreased stomatal conductance in soybean plants grown under elevated $[CO_2]$, lowering the pathogen's ability to enter through the stoma-

ta. Additionally, the decrease in stomatal conductance may have led to lower transpiration and therefore decreased humidity in the canopy, which leads to less favorable conditions for mildew growth (Eastburn et al., 2010, 2011). Conversely, the incidence of brown spot (*Septoria glycines*) and sudden death syndrome (*Fusarium viguliforme*) were not affected by elevated $[\text{CO}_2]$ (Eastburn et al., 2010). This indicates that a reduction in stomatal conductance and transpiration in plants grown under elevated $[\text{CO}_2]$ may not always benefit the host in detriment of the pathogen.

Work done on rice blast fungus (*Pyricularia oryzae*) found leaf lesions increased by 65% in plants grown in elevated $[\text{CO}_2]$, which was attributed to disruption in the leaf cuticle and cell wall (Cruz-Mirieleles et al., 2021). Silicate accumulation in rice leaves increases cuticle strength and therefore resistance to rice blast (Kim et al., 2002; Rodrigues et al., 2004). Additionally, when plants are grown at elevated levels of CO_2 , plant transpiration is reduced due to lower stomatal conductance (Leakey et al., 2009) reducing the bulk of nutrients that reach the canopy (McGrath & Lobell, 2013). This decreases the amount of silicate in rice leaves debilitating the cuticles and cell walls which facilitates the infection of rice blast fungus (Kobayasi et al., 2006).

When considering the infection of pathogens that are carried by insect vectors, the physiological effects of elevated CO_2 on plant growth may also impact the fitness of the insect vector. For example, aphids (*Ropalosiphum padi*) are insect vectors for barley yellow dwarf virus (BYDV), which can decrease yield and quality up to 70% in infected wheat plants (Smith & Sward, 1982). As elevated CO_2 increases the carbohydrate content and reduces the amino acid content of leaves and phloem sap (Ainsworth & Long, 2005; Trebicki et al., 2016), the growth and reproduction of aphids may be reduced as they need a higher proportion of N than C for proper development (Trebicki et al., 2016). In non-infected plants grown under elevated CO_2 , this has been demonstrated, as growth and reproduction of aphids is slower in comparison with plants grown under ambient $[\text{CO}_2]$. However, when the plants are infected with BYDV, the quantity of amino acids in the phloem sap and the aphid's gut was higher than non-infected plants. This would suggest that BYDV may cause metabolic changes in wheat that favor the growth and reproduction of the aphid under elevated CO_2 (Trebicki et al., 2016). This has been further demonstrated in field experiments where wheat plants grown in elevated $[\text{CO}_2]$ in Australia have shown higher incidence of BYDV in a 4-year experiment (Trebicki et al., 2017).

It has been hypothesized that the higher virus incidence observed under elevated $[\text{CO}_2]$ could also be caused by a secondary effect of elevated CO_2 over the plants and insects that facilitate virus transmission (Ainsworth & Long, 2020). As elevated CO_2 decreases stomatal conductance and transpiration (Leakey et al., 2009), canopy temperature can increase by 1-2 °C at midday in comparison with the ambient CO_2 plots (Bernacchi et al., 2007) which can increase aphid performance and therefore the spread viruses (O'Neill et al., 2011; Trebicki et al., 2017; Ainsworth & Long, 2020).

In this review we have shown with different examples that the disease effect on crops under elevated $[\text{CO}_2]$ depends on how elevated CO_2 both directly and indirectly affects the plant and is also dependent on the type of pathogens and the mechanisms of infection and defense. Although the research on how the interaction between disease and elevated $[\text{CO}_2]$ affects plants has increased in the last 20 years, more information is necessary to evaluate how a CO_2 -enriched atmosphere will affect the plant-pathogen interactions. To do so, more research needs to be done to understand the interaction between different abiotic stresses such as drought and high temperature and plant pathogens under elevated $[\text{CO}_2]$.

TRADE-OFFS AND FEEDBACKS IN PLANT RESPONSES TO ABIOTIC AND BIOTIC STRESSES

Responding to multiple stresses is costly because plants need to balance efficient resource allocation between defense and growth, which may compromise plant productivity and ultimately yield. Increased resistance to pathogens can be accompanied by a decrease in plant fitness that decreases tolerance to both abiotic stress and ambient growth conditions (Huang et al., 2010; Todesco et al., 2010; Kissoudis et al., 2014). Plants have developed mechanisms that allow them to sense biotic/abiotic stresses and respond to them, minimizing

damage while conserving valuable resources for growth and reproduction. Identifying genes that are involved in balancing a plant's response to multiple stresses while restoring its fitness in growth is a challenging task for breeding programs focused on developing stress-tolerant plant varieties (Ashraf & Aisha, 2009; Fukuoka et al., 2015; Cohen & Leach, 2020).

4.1 Photosynthesis as a hub for crosstalk and feedback responses

Pathogen infection has been shown to decrease photosynthesis and water use efficiency, as well as affect stomatal patterning, all of which decrease plant productivity and tolerance to abiotic stress (Bilgin et al. 2010; Grimmer et al., 2012; Kissoudis et al., 2014). Downregulation of photosynthesis-related genes is a core response of plants to abiotic stress, as well as during damage due to biotic agents, including arthropods, fungi, bacterial or viral pathogens (Bilgin et al., 2010; Cohen & Leach, 2020). Overexpression of a master-regulator gene of photosynthesis, HYR (HIGHER RICE YIELD), enhanced drought tolerance in rice (Ambavaram et al., 2014). Mutants of protein phosphatases, localized to the chloroplast and involved in photosynthetic pathways, showed reduced lesion development and pathogen multiplication, indicating regulatory genes involved in both photosynthesis and plant immune suppression could be key targets to understand plant growth and defense trade-offs (Akimoto-Tomiyama et al., 2018). Such downregulation of photosynthesis when exposed to stress along with upregulation of genes involved in defense marks the transition from growth/reproduction to defense, as has been explained in the growth-differentiation hypothesis (Herms & Mattson, 1992). Meta-analytic studies involving transcriptome surveys from several different plant species and biotic stress factors indicated slow turnover of various photosynthesis-related proteins and supported the hypothesis that plants invest resources in immediate defense needs but without long-term losses in photosynthetic capability and productivity (Bilgin et al., 2010; Akimoto-Tomiyama et al., 2018). In addition to photosynthesis being a hub of crosstalk, downregulation of these genes is likely a protective mechanism against photooxidative damage during abiotic stress (Dalal & Tripathy, 2018).

4.2 Complex biotic and abiotic stress interactions and feedbacks

In addition to trade-offs between growth and defense, increasing tolerance to one stress may be at the expense of tolerance to another stress (Rizhsky et al., 2004; Mittler, 2006; Atkinson & Urwin, 2012). For example, heat stress causes stomata to open, but having open stomata could lead to more water loss, which would be detrimental under drought conditions. Such interaction of stress factors is said to occur when the presence of the initial stress leads to an acclimation response which alters the plant's normal response when subjected to a second stress. Recent reviews looking at the interactive effects of two or more stresses have found outcomes of these combined stresses can be positive, negative, or neutral depending on timing, nature, and severity of each stress (Mittler & Blumwald, 2010; Suzuki et al., 2014; Rivero et al., 2022). Additionally, the presence of abiotic stress has been found to enhance host susceptibility towards some pathogens, or reduce susceptibility to some pathogens, thus, the effect of multiple stresses is not simply additive. Thus, challenging growth conditions associated with climate change necessitates breeding programs need to evaluate durability of resistant cultivars in presence of abiotic stresses.

Abiotic stress can also have a positive impact on the outcome of pathogen stress. In barley, increasing salt-induced osmotic stress directly correlates with resistance to powdery mildew (*Blumeria graminis* f. sp. *hordei* race A6) (Wiese et al. 2004), and drought stress can enhance resistance to *B. cinerea* in tomatoes (Achu et al. 2006). Additionally, pathogens interfere with water relations during pathogenesis by inducing stomatal closure to reduce water loss from infected tissue, which can have a positive effect on plant tolerance against abiotic stress conditions (Goel et al. 2008; Beattie, 2011). Drought-stressed tomato leaves accumulate high levels of defense compounds that reduce the herbivore *Spodoptera exigua*'s ability to feed (English-Loeb et al. 1997). Additionally, infection with plant viruses can provide protection against drought stress (Xu et al. 2008), as seen with tobacco (*Nicotiana*), beet (*Beta vulgaris*), and rice. This was shown to be due to virus-induced accumulation of osmoprotectants and antioxidants anthocyanins. Future work is needed to identify key targets for breeding which address the complex nature of the plant growth environment with responses to both abiotic and biotic stress.

TARGETS FOR FUTURE RESEARCH EFFORTS

Several studies have been done at the whole genome level to analyze gene expression under single and combined abiotic and biotic stresses (Vos et al., 2015; Coolen et al., 2016; Davila et al., 2017; also see Fujita et al., 2006; Atkinson & Urwin, 2012, and Suzuki et al., 2014; Rivero et al., 2022 for review). From this work and subsequent meta-analytic studies, key signaling pathways and genes sit at the intersection of biotic and abiotic stress responses. Below we outline those key targets, understanding that plant response to multiple stresses often produces gene expression and signaling patterns unique to those of a singular stress (Zarattini et al 2021).

5.1 Transcription factors

Previous reviews had identified several transcription factor families as hubs for plant responses to multiple stresses (Fujita et al., 2006; Atkinson & Urwin, 2012; Rivero et al., 2022). MYC2 is a central player in plant responses to biotic and abiotic stress (Anderson et al., 2004), and plays a role in JA-induced defense genes and is a key regulator by which ABA controls signaling related to biotic stress (Atkinson & Urwin, 2012). MYB transcription factors are also a key group, as they have been shown to be induced by drought, UV-B radiation, cold stress as well as biotic stress (Atkinson & Urwin, 2012). Additionally, NAC and AP2/ERF transcription factors have broad spectrum responses to biotic and abiotic stress in multiple species (Atkinson & Urwin, 2012). More targets for future research include WRKY, bZIP, TCP, and calmodulin-binding transcription factor activator (CAMTA) transcription factors (Atkinson & Urwin, 2012; Kissoudis et al., 2014 Rivero et al., 2022). Several members of these transcription factor families (ERF, MYB, bHLH, NAC, and WRKY) have been suggested to act as switches controlling transcriptional reprogramming during plant development as well as in tolerance to biotic and abiotic stresses. These transcription factors are ideal candidates for engineering stress-tolerant plants (Erpen et al. 2017, Baillo et al. 2019)

Furthermore, understanding post-translational regulation of transcription factors is important, as this impacts expression of downstream genes that can be key regulators of plant stress response. These downstream genes include proline-rich proteins. For example, when proline-rich proteins from pigeonpea (*Cajanus cajan* L.) were constitutively expressed in Arabidopsis they provided enhanced tolerance to multiple abiotic stresses such as osmotic, salt, and heat stress. Meta-analyses of transcriptome datasets have revealed additional core abiotic stress responsive genes (Dossa et al., 2019, Saidi et al., 2022), include genes belonging to a member of the late embryogenesis abundant family (LEA) (Huang et al. 2016, Chen et al. 2019), and alcohol dehydrogenase (ADH) family members (Shi et al. 2017). Additionally, the resistance gene, *Xa7*, conferring bacterial blight resistance in rice functions better at high temperatures, indicating elevated temperature can have a positive impact on plant defense responses to pathogens (Cohen et al., 2017). These genes could be key targets for future research efforts.

5.2 Hormone signaling

Significant work has been done to investigate plant hormone signaling crosstalk between biotic and abiotic stresses (for review see Shigenaga et al., 2017; Ku et al., 2018). This work has found ABA is a key regulator of abiotic stress and biotic stress responses. ABA is considered “the” abiotic stress hormone (Shigenaga et al., 2017), and through its antagonistic relationships with SA and JA/ET signaling pathways, it allows for crosstalk at multiple levels in biotic stress responses for both necrotrophic and biotrophic pathogens (Atkinson & Urwin, 2012; Kissoudis et al., 2014). Future research efforts should focus on ABA signaling pathways, along with their interaction with SA, JA/ET, to increase plant resilience to climate change. Other growth hormones have been implicated in biotic and abiotic stress responses, including gibberellin, cytokinin, auxin, and brassinosteroids (Kissoudis et al., 2014). Additionally, it has been recently demonstrated through genetic analysis that modification of epistatic interactions between the hormone jasmonate and the photoreceptor phyB uncoupled the plant growth and defense trade-off in Arabidopsis (Campos et al., 2016). This indicates that future breeding efforts involving hormone signaling may overcome growth-defense tradeoffs associated with combined biotic-abiotic stress responses.

5.3 MAPK cascades and heat shock factors (HSFs)

MAPK cascades are a key step in transduction of environmental cues to internal signaling pathways (Rodriguez et al., 2010). MAPK signaling cascades are involved in biotic stress and abiotic stress responses in a range of plant species, including *Arabidopsis*, rice, tomato and cotton, and link other pathways related to ROS and hormone signaling (Fujita et al., 2006; Atkinson & Urwin, 2012; Kissoudis et al., 2014; Rivero et al., 2022). This integration of signals from multiple stresses and plant hormones indicates MAPK cascades are particularly important in regulating biotic-abiotic stress crosstalk. Heat shock proteins (HSPs) are molecular chaperones that protect and stabilize proteins during stressful conditions (Bartels & Sunkar, 2005). HSPs are controlled by HSFs, which are induced under biotic and abiotic stresses, including heat, high light, and drought, across multiple species (Atkinson & Urwin, 2012). HSFs also protect plants from oxidative stress and serve as sensors for ROS to activate stress-responsive genes downstream (Atkinson & Urwin, 2012). For example, recent work has shown increased expression of specific HSF (*HSFA1b*) in oilseed rape led to increased resistance to stress and maintenance of yield (Mullineaux et al., 2011). Taken together, both MAPKs and HSFs are key potential regulators for conferring resiliency to biotic and abiotic stress conditions under future climate change.

5.4 ROS signaling

ROS scavenging and signaling play a key role in plant responses to both biotic and abiotic stress conditions (Pastori & Foyer, 2002; Fujita et al., 2006; Ton et al., 2009; Atkinson & Urwin, 2012; Kissoudis et al., 2014; Morales et al., 2016). During abiotic stress conditions, such as osmotic stress and high light, elevated levels of ROS must be detoxified by the plant to prevent damage to cell membranes and degradation of proteins, including important protein complexes related to photosynthesis (Staehelin & van der Staay, 1996; Wu et al., 2013; van Eerden et al., 2015; Kobayashi, 2016). Detoxification occurs through the action of antioxidants, including superoxide dismutase (SOD), enzymes and metabolites from the ascorbate-glutathione cycle, and catalase (CAT) (see de Carvalho et al., 2013 for review). During biotic stress conditions, plants generate ROS to limit pathogen spread by initiating the hypersensitive response and cell death (Atkinson & Urwin, 2012). In both cases, ROS serve as a signal of stress conditions and elicit downstream ROS-responsive genes. This includes transcription factors, ABA biosynthetic genes, and antioxidant metabolism genes (Atkinson & Urwin, 2012). Additionally, many biotic and abiotic stresses activate ROS production through NADPH oxidase (RBOH) proteins. RBOH proteins are regulated through several post-translational mechanisms by both biotic (aphid, bacterial, fungal infection) and abiotic stresses (salinity, heat, high light), making them a central hub for integrating multiple stress conditions (Rivero et al., 2022). Therefore, master regulators of ROS signaling mechanisms would be key targets for future research.

5.5 Other signaling mechanisms

Another key area for future research is small RNAs, which can play important regulatory roles in plant responses to stress. Work done in *Arabidopsis* has indicated microRNAs (miRNA) are involved in response to phosphate stress, while miRNAs are responsive to cold stress in *Brachypodium distachyon* (Fujii et al., 2005; Chiou et al., 2006; Zhang et al., 2009). Gene expression analysis in soybean indicates miRNAs play a role in mediating drought and fungal stress (soybean rust fungus) through modulation of regulation of ROS (Kulcheski et al., 2011). Small interfering RNAs (siRNAs), including nat-siRNAs, have also been shown to regulate both abiotic and biotic stress responses in *Arabidopsis* and rice (Atkinson & Urwin, 2012). Additionally, small RNAs play a role in plant developmental processes, including flowering time and fertility (Atkinson & Urwin, 2012), indicating their key role at the intersection of plant defense and productivity. This indicates small RNAs would be a viable future area of research to understand plant responses to combined stresses. Additional pathways of interest for future work include genes involved in calcium signaling, mitochondrial functions, vesicle trafficking, apoptosis, as well as pathway regulation of the hyper-sensitivity response, epigenetic regulation, and the role of *cis*-regulatory elements (CREs) (Fujita et al., 2006; Atkinson & Urwin, 2012; Kissoudis et al., 2014; Nejat & Mantri, 2017; Shigenaga et al., 2017; Romero-Puertas et al., 2021; Singh et al., 2021; Zarratini et al., 2021).

ADDRESSING GAPS IN OUR KNOWLEDGE

In addition to the future research targets outlined above, additional experimental approaches and techniques could be used to enhance our understanding of crosstalk and trade-offs of plant biotic and abiotic stress responses imposed by climate change.

I. Experiments in both controlled environments and in the field that address realistic depictions of future climate. This includes evaluating regional versus global impacts of specific abiotic and biotic stress interactions. By assessing climate scenarios that have resolution at the regional scale, we can more accurately predict the impacts of future growing conditions on crops of interest (Leisner, 2020), as well as gain a better understanding of the mechanisms involved in crop responses to stress combinations at the physiological, molecular, and genetic level (Rivero et al., 2022). Additionally, knowledge gaps related to different plant pathosystems should be addressed, to expand our understanding to specific plant-pathogen interactions under future climate scenarios. *II. Modeling and predictive tools for decision making.* Precision agriculture is a large field that is focused on using advanced robotics, image analysis, and mapping technologies to improve a farmer's ability to make decisions regarding soil and water supplies in real-time (Cisternas et al., 2020). This can help make decision support tools available for stakeholders to manage plant responses to climate change. We need to increase efforts to utilize the same concepts of precision agriculture to the management of pathogen infection. This includes predicting climate change effects on pathogen emergence using artificial intelligence and giving decision-makers automated analyses of risk to make educated decisions during the growing season (Garrett et al., 2022). *III. Interdisciplinary research to tackle complex problems.* We need to take a systems biology approach to gain a complete picture of how plants interact with their changing environment. This includes addressing issues of physiological responses of plants to their environment, how these are linked to changes at the genetic level, and how these changes at the whole plant level might translate into ecological impacts in natural or agroecosystems. Additionally, links between belowground factors (soil composition, rhizosphere interactions) and the plant microbiome (Hacquard et al., 2022) will be key to increasing plant health, defense, and productivity under future climate conditions.

CONCLUSIONS

Plants must adapt and respond to an ever-changing environment. Human influence has led to increased CO₂ in our atmosphere, warming of our land, and changes in precipitation patterns. These changes to our global ecosystem will also lead to changes in the prevalence and virulence of plant pathogens, and plant herbivores. To ensure sustainable future food production, we must understand the crosstalk and trade-offs resulting from combined abiotic and biotic stress impacts on plant growth and defense. Outcomes from experiments where plants are exposed to multiple stresses are often unique from the individual stress alone, especially at the level of gene expression. There is, however, significant crosstalk among these stresses, with key hubs of integration of signals across stresses involving transcription factors, hormones (ABA, SA, JA), ROS, small RNAs, and MAPK cascades. These are key targets for future research efforts. More combinatorial stress work is needed in the future to understand growth and defense trade-offs and crosstalk among plant biotic and abiotic stress responses. This work should incorporate realistic depictions of future climate, leverage interdisciplinary teams of researchers, and employ advanced tools in precision agriculture and predictive tools for decision making (**Fig. 1**).

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

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FIGURE LEGENDS

Figure 1. Targets for future research and approaches to assess crosstalk and trade-offs of combined abiotic and biotic stress in plants. Abiotic and biotic stresses covered in this review are illustrated, along with gene targets and areas of future work needed to advance our capability for sustainable future food production under future climate change conditions.

Figure 1.

