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Plant developmental responses to climate change

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ABSTRACT

Climate change is multi-faceted, and includes changing concentrations of greenhouse gases in the atmosphere, rising temperatures, changes in precipitation patterns, and increasing frequency of extreme weather events. Here, we focus on the effects of rising atmospheric CO_2 concentrations, rising temperature, and drought stress and their interaction on plant developmental processes in leaves, roots, and in reproductive structures. While in some cases these responses are conserved across species, such as decreased root elongation, perturbation of root growth angle and reduced seed yield in response to drought, or an increase in root biomass in shallow soil in response to elevated CO_2, most responses are variable within and between species and are dependent on developmental stage. These variable responses include species-specific thresholds that arrest development of reproductive structures, reduce root growth rate and the rate of leaf initiation and expansion in response to elevated temperature. Leaf developmental responses to elevated CO_2 vary by cell type and by species. Variability also exists between C_3 and C_4 species in response to elevated CO_2, especially in terms of growth and seed yield stimulation. At the molecular level, significantly less is understood regarding conservation and variability in molecular mechanisms underlying these traits. Abscisic acid-mediated changes in cell wall expansion likely underlie reductions in growth rate in response to drought, and changes in known regulators of flowering time likely underlie altered reproductive transitions in response to elevated temperature and CO_2. Genes that underlie most other organ or tissue-level responses have largely only been identified in a single species in response to a single stress and their level of conservation is unknown. We conclude that there is a need for further research regarding the molecular mechanisms of plant developmental responses to climate change factors in general, and that this lack of data is particularly prevalent in the case of interactive effects of multiple climate change factors. As future growing conditions will likely expose plants to multiple climate change factors simultaneously, with a sum negative influence on global agriculture, further research in this area is critical.

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1. Introduction

Variation in developmental processes lies at the core of functional differences among plant genotypes and species growing in different environmental conditions. Environmental stresses have varying effects on different organs and tissues within a plant, and as such, molecular, cellular and morphological responses to stress vary among tissues, and throughout the developmental lifetime of a plant. The range in developmental processes across genotypes, and the ability of a plant of a given genotype to dynamically shift these developmental processes in response to the environment is the key to plant success in natural and agricultural settings (reviewed in Nicotra et al. (2010)).

Climate change, entailing shifts in temperature, precipitation, and atmospheric composition among other factors, represents a moving target for plant developmental adaptation. Human activities including fossil fuel burning and deforestation have increased the concentration of greenhouse gases in the atmosphere, resulting in climate warming, and perturbations of hydrologic cycles. Specifically, atmospheric CO_2 is predicted to reach 730–1000 ppm by the end of the century, contributing to expected increases in global average surface temperature of 1.0–3.7 °C during this same time (Meehl et al., 2007; IPCC, 2014). Precipitation patterns are also expected to differ as a result of climate change, with more frequent drought events predicted for regions that are already arid (IPCC, 2014). These climate change factors affect plants at the level of molecular function, developmental processes, morphological traits, and physiology. Here we summarize the knowledge to date on plant responses to these stimuli, with a particular focus on developmental processes, at both the organ, tissue and cell type-specific level as well as the underlying molecular regulatory mechanisms. Finally, we discuss and provide perspective on the most pressing knowledge gaps in our understanding of plant developmental responses to climate change.

Plant developmental responses to the environment can take the form of altered initiation of developmental events, altered timing of developmental events, and altered final form or architecture of individual organs and whole plants. One example of altered initiation of developmental events is repressed initiation of lateral roots in response to water deficit (Babé et al., 2012). Altered timing of developmental events in response to the environment can be observed as an earlier shift from vegetative to reproductive development in response to elevated temperature, for instance, in *Arabidopsis thaliana* (Balasubramanian et al., 2006). These changes can ultimately be observed in the plant's final form or architecture, at the level of individual organs and at the level of the whole plant; for example, the presence of additional leaf nodes and larger leaves in response to elevated CO_2 in soybean (Dermody et al., 2006). These developmental responses demonstrate the plasticity of plant form in an altered environment. The developmental responses to climate change factors described above, including altered lateral root initiation (Babé et al. 2012), altered timing of developmental events (Balasubramanian et al., 2006), and altered number and size of leaves (Dermody et al., 2006) will likely have significant impacts on plant function. Plant functions may be affected by changes in the plant's ability to capture resources (in the case of lateral root number or leaf size/number), and altering allocation of those resources among developing organs (in the case of shifted timing of reproductive development). Such changes in function can have significant impacts on yield in agricultural plants, and fitness in natural populations. An important gap in our knowledge is in the extent of how conserved or species-specific these responses are as well as the underlying molecular regulatory mechanisms. This review will highlight developmental responses to the key climate change factors of rising temperatures, changing precipitation patterns, and rising atmospheric CO_2, their underlying molecular nature, where known and will explore the functional significance of altered development in this context.

2. Effects of elevated CO_2 on plant development and morphology

Since the Industrial Revolution, the CO_2 concentration in the atmosphere has increased from 280 ppm to more than 400 ppm today (Meehl et al., 2007; https://scripps.ucsd.edu/programs/keelingcurve/). CO_2 directly affects plants via impacts on photosynthetic gas exchange and downstream developmental processes (Ainsworth and Long, 2005). CO_2 also has indirect effects on plants, as it is a potent greenhouse gas that contributes to climate warming and associated changes in climate (Meehl et al., 2007). Elevated CO_2 stimulated photosynthetic carbon assimilation rates by an average of 31% across 40 species that have been investigated at twelve Free Air CO_2 Enrichment (FACE) experiments (reviewed in Ainsworth and Long (2005)). In the C_3 species included in the meta-analysis by Ainsworth and Long (2005), aboveground biomass increased by an average of 20% in response to elevated CO_2. Reich et al. (2014) found that elevated CO_2 stimulated aboveground biomass in a grassland by up to 33%, but that the degree of stimulation depended on water and nitrogen availability, with lower biomass stimulation observed in drier, lower nutrient conditions. Root biomass has also been observed to increase significantly in response to elevated CO_2 in many crop species (reviewed in Madhu and Hatfield (2013)). The increase in shoot biomass includes significant increases in seed yield in many species, including soybean, wheat, rice, peanut and bean (reviewed in Hatfield et al., 2011). One particularly well-studied model of whole plant growth and reproductive output responses to elevated CO_2 is soybean (*Glycine max*; Fig. 1; Table 1). Developmental responses of soybean to elevated CO_2 include increased number of leaf nodes and increased leaf size (Dermody et al., 2006), increased root length, altered root depth distribution and nodulation (Gray et al., 2013, 2016), and increased pod number and seed yield (Morgan et al., 2005; Bishop et al., 2014). Yield stimulation makes CO_2 response a trait of agricultural interest and poses the question of how developmental processes interact with CO_2 to alter reproductive output.

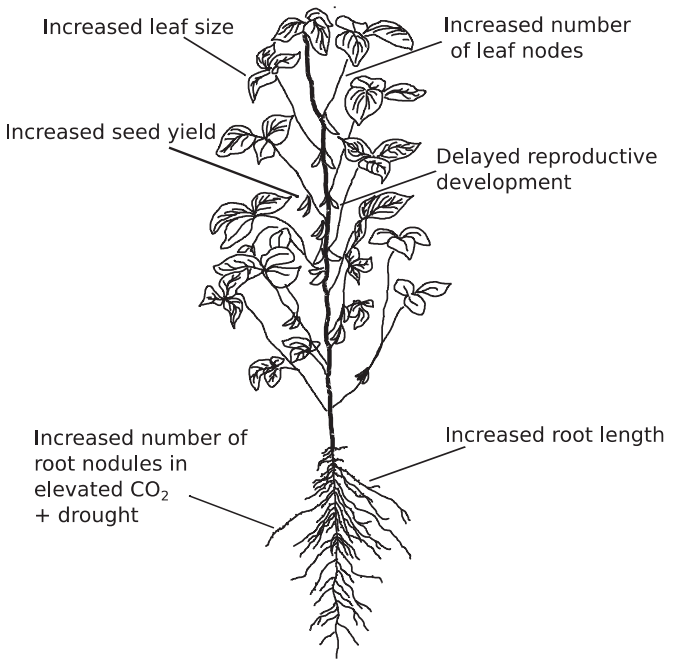

Fig. 1. A diagram illustrating the effects of elevated CO_2 on growth and development of soybean (*Glycine max*). References are as follows: (Dermody et al., 2006; Castro et al., 2009; Gray et al., 2013, 2016; Bishop et al., 2014).
Drawing is adapted from University of Illinois Pocket Guide to Crop Development (http://weeds.cropsci.illinois.edu/extension/Other/POCKETcrop.pdf)

2.1. Leaf developmental responses to elevated CO_2

The stimulation of aboveground biomass by elevated CO_2 is associated with increased average leaf size in soybean and poplar (Dermody et al., 2006; Taylor et al., 2003). Increased leaf size can be the result of increased cell production and/or increased cell expansion, and both of these processes appear to contribute to enhanced leaf size in elevated CO_2 in the species in which these processes have been investigated. Interesting variation exists in these responses across cell types. For example, in the hybrid *Populus* × *euramericana* (*Populus deltoides* × *P. nigra*, clone I-214), Taylor et al. (2003) found that elevated CO_2 increased the size of epidermal cells in developing leaves, but not in mature leaves; whereas spongy and palisade mesophyll cell size increased in response to elevated CO_2 in young and old leaves. Taylor et al. (2003) also found that the rate of production of new epidermal cells was stimulated by elevated CO_2, but that this effect varied along a basipetal gradient. Masle (2000) found that elevated CO_2 had cell type-specific effects on leaf anatomy of wheat, encompassing an additional cell layer and larger intercellular air spaces in the spongy mesophyll, but minimal effects on epidermal anatomy. Enhanced leaf growth in elevated CO_2 has often been hypothesized to be associated with increased cell wall extensibility. Evidence of this effect is apparent in poplar, but is leaf age-dependent (Taylor et al., 2003; Ranasinghe and Taylor, 1996; Ferris et al., 2001). These findings demonstrate that there are spatially-specific, temporally-specific and species-specific cell growth responses to elevated CO_2 in leaves.

Elevated CO_2 has targeted effects on specific cell types or cell type specification within the leaf. In many species, including multiple accessions of Arabidopsis, elevated CO_2 reduces stomatal index (ratio of stomata to epidermal cells) (Woodward and Kelly, 1995). The gene, High CO_2 (*HIC*), a CO_2-responsive negative regulator of stomatal development, has been described to regulate stomatal index in Arabidopsis (Gray et al., 2000). Here, the wild type Arabidopsis accession (C24) did not show a significant change

Table 1
Summary of the effects of climate change factors on the development of soybean (*Glycine max*).

Climate Change Factor	Effect on leaf development	Effect on root development	Effect on flowering	Effect on seed yield	Genotypic variation	References
Elevated CO_2	↑ Leaf size ↑ Number of leaf nodes	↑ Root length ↑ Number of root nodules in elevated CO_2 + drought	Delayed reproductive development	↑ Seed yield	• Seed yield response across 18 genotypes varied from no change to 20% stimulation	Dermody et al., 2006; Castro et al., 2009; Gray et al., 2013; Bishop et al., 2014; Gray et al., 2016
Elevated Temperature	↓ Thermo-stability of leaf cell membranes	↓ Root mass at 34 °C and 40 °C compared to 28 °C ↓ Root nodules at 34 °C and 40 °C compared to 28 °C	↓ Pollen viability when temperature exceeds 30 °C ↓ Pollen tube elongation above 36 °C • Abnormal pollen morphology	↓ Seed yield when average temperature exceeds 23 °C	• Pollen viability response across 44 genotypes varied from tolerant to sensitive	Salem et al., 2007; Hatfield et al., 2011; Munevar and Wollum, 1981
Drought	↓ Final leaf cell number and size	↓ Root nodule number and activity	• Flowering stage is most sensitive to drought stress	↓ Pod set	• Cultivar variation in flowering time may influence drought sensitivity	Williams and De Mallorca 1984; Kaspar et al., 1984
	↓ Rate of leaf emergence	↑ Root length density in intermediate soil depth	↓ Pod number	↓ Seed yield	• Cultivar variation in taproot elongation, soil water depletion	Randall and Sinclair, 1988; Liu et al., 2003; Manavalan et al., 2009; Gray et al., 2016
		↓ Root length density in shallow soil depth	• Shorter period for pod fill	↓ Seed size		

in stomatal index in response to elevated CO_2, but the *hic* mutant showed an increase in stomatal index of 18–28% in response to elevated CO_2, suggesting that *HIC,* a putative 3-keto acyl coenzyme A synthase that plays a role in cell wall wax biosynthesis, is important for negatively regulating stomatal development in response to elevated CO_2 (Gray et al., 2000). Engineer et al. (2014) demonstrated that Arabidopsis double mutants in β-carbonic anhydrase (*ca1 ca4*) showed a reversal of the typical stomatal density reduction in response to elevated CO_2. Further work demonstrated that carbonic anhydrases are involved in an extracellular signaling pathway conferring CO_2 control over stomatal development (Engineer et al., 2014). Ferris et al. (2002) utilized a *P. trichocarpa* × *P. deltoides* mapping population to identify QTL for stomatal response to elevated CO_2. They found that elevated CO_2 reduced stomatal density and stomatal index in *P. deltoides*, but in *P. trichocarpa*, elevated CO_2 did not affect these traits on the adaxial leaf surface. The authors identified QTL for stomatal trait responsiveness to elevated CO_2, but thus far candidate genes have not been identified for these species (Ferris et al., 2002). Potential regulators of stomatal development responses to elevated CO_2 have been recently reviewed by Xu et al. (2016).

In addition to altering the cellular traits of individual leaves, elevated CO_2 alters shoot architecture. Examples of these changes include increases in the total number of vegetative nodes in soybean (Dermody et al., 2006), and promotion of axillary meristems in wheat, which increases the number of tillers, or branches (Nicolas et al., 1993; Christ and Korner, 1995; Slafer and Rawson, 1997). Increased number of tillers has also been described in rice grown in elevated CO_2 (Jitla et al., 1997). Evidence is beginning to build for molecular mechanisms that may contribute to altered shoot architecture in elevated CO_2. Morita et al. (2015) identified a phloem-expressed, CO_2-responsive regulator of starch accumulation (CO_2-Responsive CONSTANS, CONSTANS-like and Time of Chlorophyll a/b Binding Protein1 (CRCT)) in rice. Overexpression of CRCT increased starch content of the leaf sheath, and significantly increased tillering angle, such that branches had a wider lateral spread. Wide tillering angle is a trait that has likely been selected against throughout rice domestication to enable dense planting (Jin et al., 2008), and may pose a challenge for production if this trait is altered by elevated CO_2 in the future.

Leaf transcriptional responses to elevated CO_2 center around altered carbon metabolism. In soybean, Leakey et al. (2009) demonstrated that elevated CO_2 increased transcript abundance of genes related to starch metabolism, sugar metabolism, glycolysis, the tricarboxylic acid cycle, and mitochondrial electron transport. These transcriptional changes were associated with stimulation of photosynthetic carbon assimilation and dark respiration rates (Leakey et al., 2009). Similarly, in Arabidopsis, increased abundance of transcripts in the respiratory pathway co-occurred with increased leaf dark respiration rates (Markelz et al., 2014a), and showed developmental specificity, as the magnitude of transcriptional and respiratory responses to elevated CO_2 increased in mature relative to expanding leaves (Markelz et al., 2014b). Similar transcriptional responses have been described in rice, with elevated CO_2 increasing expression of genes involved in sucrose synthesis, glycolysis, and the TCA cycle (Fukayama et al., 2011). Elevated CO_2 likely alters plant development both by increasing the flux of carbohydrates and related metabolites that are needed for growth and development, and by the action of glucose as a signaling molecule. In Arabidopsis, three glucose-modulated master regulators have been described: hexokinase1 (*HXK1*) glucose sensor, *KIN10/KIN11* kinases, and the target of rapamycin (*TOR*) kinase (Sheen, 2014). These glucose-responsive regulators direct many diverse processes, including regulation of glucose-responsive transcription and plant growth by *HXK1* (Xiao et al., 2000), regulation of the vegetative-to-reproductive phase transition by *KIN10* (Baena-Gonzalez et al., 2007), and regulation of primary and secondary metabolism, transcription, and translation by the *TOR* kinase (reviewed in Sheen (2014)). It remains to be determined if these master regulators are responsible for the altered transcriptional regulation of metabolic genes in rice, soybean and Arabidopsis in elevated CO_2. Thus, conserved transcriptional responses to elevated CO_2 have been described for the leaves of multiple species likely resulting in perturbations in primary carbon metabolism. It is unclear if these transcriptional changes precede the observed changes in leaf anatomy, or are a consequence of the perturbations in leaf anatomy. Furthermore, the role of glucose as a signaling molecule regulating transcriptional and developmental responses to elevated CO_2 seems likely but has yet to be elucidated.

2.2. Root developmental responses to elevated Co_2

Root biomass is significantly increased in response to elevated CO_2 in numerous species. An increase in the root: shoot ratio is also often observed, suggesting increased investment in acquisition of mineral or water resources (Rogers et al., 1997). This increase has been measured in controlled environment experiments as the biomass of total root systems, as estimates of root length from field-based minirhizotron experiments (clear observation tubes which are buried into the soil, enabling imaging of roots with a digital camera), or as estimates of root length per unit volume of soil measured from soil cores.

More detailed studies provide insight into how this increase in biomass can occur by describing changes in root system architecture as well as in changes in cellular anatomy. However, no systematic study has assessed the conservation of all these responses across and within diverse plant species. In soybean, minirhizotron experiments demonstrated that elevated CO_2 increases root length, primarily at shallow and intermediate soil depths, and that elevated CO_2 in combination with reduced precipitation increases the number and density of root nodules, which house *Bradyrhizobia* nitrogen-fixing bacteria (Gray et al., 2013, 2016). Further studies have revealed that the increase in root biomass in agricultural and forest species takes the form of increased root length, enhanced root branching, and increased root diameter (reviewed in Madhu and Hatfield (2013)). In Arabidopsis, elevated CO_2 results in increased primary root length and expansion rate, increased lateral root formation and elongation (Rookshanks et al., 1998). Altered root system architecture in elevated CO_2 may influence the root system's efficiency in water uptake by altering distribution of root length relative to water resources (Gray et al., 2016). Further, altered root depth distribution may impact a plant's ability to gather nutrient resources, which are distributed heterogeneously across soil depth gradients (Lynch, 2015). Altered root system architecture in elevated CO_2 takes the form of increased branching and expansion of lateral roots, contributing to proliferation of roots in shallow layers, rather than growth of the root system into deeper soil in spring wheat, winter wheat, cotton, and sorghum (Reviewed in Pritchard and Rogers (2000)).

At the anatomical level, an increased stele and cortex diameter, increased root diameter in the root maturation zone, and increased total root system volume has been observed in cotton exposed to elevated CO_2 (Rogers et al., 1992). In Arabidopsis, increased cortical cell expansion and cell wall extensibility (Rookshanks et al., 1998) was also reported. Changes in the architecture, cellular anatomy and interactions of root systems with soil microbes may significantly impact root function in a future, high CO_2 environment.

Inter-specific genetic variation in root density responses to elevated CO_2 has been described in *Populus deltoides* and *Populus*

trichocarpa, with *P. trichocarpa* showing a stronger magnitude of root density responses to elevated CO_2 (Rae et al., 2007). 285 members of an F2 population from the *P. deltoides* × *P. trichocarpa* cross were used to identify three QTL associated with root growth rate and primary root density response to elevated CO_2 (Rae et al., 2007). However, these QTL were identified via experiments that used rhizotrons. Rhizotrons likely do not capture the full magnitude of loci controlling the root CO_2 response, as the soil environment surrounding a rhizotron obscures the developmental order of roots and limitations in quantification introduce phenotyping errors. Identification of candidate genes from QTL of plant roots exposed to elevated CO_2 deserves further study. Likewise, changes in gene expression of root tissue in response to elevated CO_2 have been investigated in a very limited number of experiments (e.g. Plett et al., 2015). This results in large gaps in our understanding of the molecular mechanisms and genetic diversity of root responses to this climate change factor.

2.3. Responses of reproductive development and phenology to elevated CO_2

Elevated CO_2 increases seed yield in numerous agricultural species, but the nutritional quality of the grain is generally reduced, due to altered ion profiles, notably reduced iron and zinc content (Loladze, 2014; Myers et al., 2014). Elevated CO_2 also reduces nitrogen and protein content of seeds of non-legume crops (Jablonski et al., 2002; Myers et al., 2014). A meta-analysis of 79 species grown in elevated CO_2 demonstrates consistent effects on reproductive output: elevated CO_2 increased the number of flowers, fruit, and seeds by 16–19% on average, and increased the total seed mass by 25%, but caused a smaller increase (4%) in individual seed mass (Jablonski et al., 2002). This result is corroborated by a study in soybean, in which the increase in seed yield was caused by an increase in pod number or number of seeds per pod, rather than an increase in the mass of individual seeds (Morgan et al., 2005). The molecular mechanism of this increase in seed number that is conserved across all these species is unknown.

Bishop et al. (2014) demonstrated that, across 18 genotypes of soybean, elevated CO_2 stimulated seed yield by an average of 9% across multiple growing seasons, but the partitioning coefficient decreased by 11%. The magnitude of seed yield stimulation of soybean by elevated CO_2 depended on climate, with stimulation of seed yield diminishing to zero in hot, dry conditions (Ruiz-Vera et al., 2013; Bishop et al., 2014; Gray et al., 2016). Jablonski et al. (2002) found that, while crop species and wild species did not differ in their overall biomass response to elevated CO_2, they did differ significantly in their allocation to reproductive output at elevated CO_2. Specifically, crop species showed an average 28% increase in fruit production, while wild species showed only a 4% increase in fruit production, likely reflecting artificial selection for enhanced carbon partitioning to fruit and seed development in crop species (Jablonski et al., 2002). Wild species also showed a greater amount of variability in fruit and seed production responses to elevated CO_2 than domesticated species (Jablonski et al., 2002), potentially reflecting variability in the ecosystems that these species are adapted to, or canalization of traits determining allocation to reproductive tissues in crop plants.

Castro et al. (2009) observed that elevated CO_2 delayed reproductive development of soybean overall. The length of the growing season of elevated CO_2-grown soybean was extended through addition of new leaf nodes, rather than extending the life of individual leaves (Dermody et al., 2006). Additionally, full bloom and beginning seed stages were extended in elevated CO_2-grown soybean, associated with an increased number of stem nodes and an extended period for addition of new leaves (Castro et al., 2009). Springer and Ward (2007) found that, depending on the genotype, elevated CO_2 could delay, accelerate, or not affect flowering time in Arabidopsis. Ward and coauthors (2012) identified MOTHER OF FT AND TFL1 (MFT) as a likely player in CO_2-regulation of flowering time. These authors developed a mapping population by crossing a genotype selected for high fitness at elevated CO_2 (Selection Genotype; SG), which showed delayed flowering in elevated CO_2, to the Cape Verde Islands ecotype, which did not show a flowering time response to elevated CO_2. A QTL was then identified which explained almost one third of the variation in flowering time response to elevated CO_2, leading to identification of MFT as a gene candidate, as the knock-out mutant for this gene showed earlier, rather than delayed, flowering in elevated CO_2 (Ward et al., 2012). Springer et al. (2008) demonstrated that an Arabidopsis genotype exhibiting delayed flowering in elevated CO_2 showed sustained expression of FLOWERING LOCUS C (FLC) in elevated CO_2; whereas a genotype that did not exhibit delayed flowering in response to elevated CO_2 showed no significant differences in FLC expression in elevated CO_2 compared to ambient CO_2. This research demonstrates that this known repressor of flowering plays a role in CO_2-regulation of this process, and contributes to genotypic diversity in this response. Delays in timing of reproductive developmental events may prolong the period for carbon capture and nutrient acquisition, contributing to increased seed yield of plants grown in elevated CO_2; however, this extended growth period could also increase the risk of reproductive failure from terminal drought (Springer and Ward, 2007).

Delayed senescence in response to elevated CO_2 has been described in tree species. In poplar (*P. tremuloides* and *P.* × *euramericana)*, elevated CO_2 delayed autumnal senescence in two separate field sites (Taylor et al., 2008). A delay in senescence of *P. euramericana* trees was associated with increased leaf anthocyanin content and increased expression of transcripts involved in the anthocyanin biosynthesis pathway (Tallis et al., 2010). Anthocyanins can play protective roles with regards to UV damage, pathogen stress, and scavenging of reactive oxygen species, and may thereby enhance leaf longevity (Gould, 2004).

3. Effects of elevated temperature on plant development and morphology

Rising concentrations of CO_2 and other greenhouse gases have contributed to an increase of 0.85 °C in global average surface temperature from 1880 to 2012 (Hartmann et al., 2013). Global mean surface temperature is projected to rise by 1.0–3.7 °C by the end of the century (IPCC, 2014). In addition to a consistent increase in background global mean temperatures, plants will also experience heat stress via increased frequency, intensity, and duration of heat waves (IPCC, 2014). Unlike atmospheric CO_2, which is well mixed and thus quite uniform across the globe, future predictions for global surface temperature vary significantly across geographical regions, and as such will be experienced differently by plants growing in different regions. For example, the surface temperature in the Arctic is projected to rise faster than the global average (IPCC, 2014). The range of today's global surface temperature paired with variability in how different latitudes will experience temperature increases mean that global warming will result in different degrees of temperature stress for plants growing in different regions. For example, elevated temperatures are expected to cause 2.4% yield losses of soybean (*Glycine max)* growing in the Southern U.S., but a 1.7% increase in yield in the Midwestern U.S. (Hatfield et al., 2011). Similarly, Lobell and Asner (2003) demonstrated that temperature had different effects on yield of maize and soybean in the Midwestern U.S. compared to the Northern Great Plains. In regions where yield showed a negative relationship with temperature, a 17% decrease in yield was

estimated for every 1 °C increase in growing season temperature for both maize and soybean (Lobell and Asner, 2003).

Species-specific factors relating to changes in plant development and physiology will also influence yield in response to temperature (reviewed in Hatfield et al. (2011)). One clear example of how elevated temperature changes plant physiology is the variability in rates of photosynthetic carbon assimilation. Ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubsico) catalyzes the fixation of CO_2 from the atmosphere into organic compounds in the plant. While Rubisco itself is heat-stable up to 50 °C (Crafts-Brandner and Salvucci, 2000), limitations to photosynthesis at more moderate temperature increases can be explained by reduced function of Rubisco activase, an enzyme that removes inhibitory molecules from the catalytic site of Rubisco; or by reduced regeneration of ribulose-1,5-bisphosphate (RuBP; the 5 carbon sugar that serves as a substrate for the carboxylation reaction of Rubisco) (Sage et al., 2008). The temperature optimum for photosynthesis varies between species (Sage et al., 2008), with species adapted to hot, desert climates having a higher temperature optimum and safe operating range compared to species adapted to more moderate or cold-adapted climates (reviewed in Sage and Kubien (2007)). Photosynthetic functional type also influences response to temperature, as C_3 plants exhibit a lower thermal optimum for photosynthesis compared to C_4 plants (Sage and Kubien, 2007). This range provides a functional lens through which to view plant yield responses to warming—the photosynthetic response to rising temperature, and thus plant growth and yield will depend upon the species-specific temperature optimum.

3.1. Leaf developmental responses to elevated temperature

Leaf development is strongly regulated by temperature. In Arabidopsis, the rate of leaf initiation, leaf expansion, and the duration of expansion increases linearly with temperature in the range of 6–26 °C (Granier et al., 2002). Similarly, the pace of addition of new leaves throughout a crop plant's vegetative development increases as temperature increases, until a species-specific optimum temperature (ranging from 26 °C for wheat to 37 °C for cotton) and corresponding rate of leaf initiation is exceeded (Hatfield et al., 2011). Leaf morphology, as well as rate of emergence is sensitive to temperature. Leaf and stem developmental and morphological responses to temperature stress are similar to those observed in the shade avoidance response, including auxin-dependent hypocotyl and petiole elongation (Gray et al., 1998; Franklin, 2009; van Zanten et al., 2009). The molecular mechanisms by which elevated temperature regulates leaf morphology and the rate of leaf initiation and expansion are largely unknown.

3.2. Root developmental responses to elevated temperature

As soil temperature is closely related to, and dependent on, air temperature (Zheng et al., 1993), the projected 1.0–3.7 °C increase in global average surface temperature this century will result in increased soil temperatures (IPCC, 2014). Root development may be affected directly by elevated soil temperatures, or may be affected indirectly via changes in the physiology, development and resource acquisition of the shoot in response to warmer air temperatures, or by a combination of both factors. In a broad sense, allocation to roots may be increased in response to elevated temperature, and rising temperatures may also have significant impacts on critical root functions, including respiration (Atkin et al., 2000) and nutrient uptake (Awal et al., 2003).

Elevated temperature stimulates root growth rate up to a species-specific temperature optimum, and significantly alters several root architecture parameters. The following species-specific examples have typically been studied in only one genotype; however, given genotypic variation in molecular and morphological responses to temperature stress in other tissues (*e.g.* Bita et al., 2011; Kumagai and Sameshima, 2014), it is likely that there is significant intra-species variation in root traits, in addition to the inter-species variation that is described here. In maize (*Zea mays*), increasing the temperature of hydroponic media from 13 °C to 22 °C caused significant increases in total root length, but root length plateaued at 22–25 °C (Nagel et al., 2009). Similarly, oilseed rape (*Brassica napus)* tap root length and lateral root number increased as root growth media temperature increased from 10 to 20 °C (Nagel et al., 2009). In cotton, taproot length and lateral root number increased from 10 °C to 35 °C, but decreased at temperatures greater than 35 °C. In sunflower, the optimal temperatures (before inhibition of growth) for tap root length and lateral root number is 25–30 °C (McMichael and Quisenberry, 1993).

The transition zone of the primary root of Arabidopsis defines the transition from the proximal meristem to the zone of elongation and differentiation/maturation. In the proximal meristem, high concentrations of auxin promote degradation of the Aux/IAA auxin signaling repressor, short hypocotyl 2 (SHY2) enabling cell division (Perilli et al., 2012). In contrast, high concentrations of cytokinin in the transition zone and zone of elongation/differentiation up-regulate SHY2, repressing auxin-responsive gene expression and promoting cell elongation over cell division (Perilli et al., 2012). Hanzawa et al. (2013) demonstrated that elevated temperature (29 °C compared to 23 °C) stimulated primary root elongation rate via increased cell division rates. In addition to increasing the rate of root elongation, elevated temperature also increased root auxin content in Arabidopsis, and increased the rate of the root reorientation response to a gravity stimulus (Hanzawa et al., 2013). Further, Hanzawa et al. (2013) found that elevated temperature reduced vacuolar content of the auxin efflux carrier PIN2, suggesting improved efficiency of PIN2 localization in the plasma membrane and enhanced shootward auxin transport. The authors used this finding to explain the seemingly contradictory result of increased root auxin content and increased root elongation in elevated temperature: they reasoned that the plants had an enhanced ability to transport auxin out of the cell and thereby maintain intracellular auxin homeostasis even in the presence of increased total root auxin content.

In addition to effects on primary root length, the overall shape and architecture of a root system can be altered by growth temperature. Elevated temperature can impact root elongation in a spatially explicit manner. For example, increased primary root branching angle in higher temperature conditions could lead to a root system with a more shallow and broad root distribution relative to plants grown in lower temperatures. Nagel et al. (2009) found that, in plants exposed to gradients in root zone temperature, root growth along a depth gradient was modified dynamically leading to increased root density in the depth of growth media with the most favorable growth temperatures. An increased number and length of lateral root branches has been reported for increasing temperatures up to 30 °C in sunflower and up to 35 °C in cotton (McMichael and Quisenberry, 1993). Lateral root branching increased in response to temperature increases (up to the optimal temperature), and was more sensitive than tap root growth. Lateral root angle also responded significantly to temperature, with branching angle being significantly greater in plants growing at 20 °C compared to those growing at 10 °C (Nagel et al., 2009).

Projections for rising soil temperature associated with climate change are more complex than the corresponding changes in air temperature, because soil temperature is influenced by a wide range of factors including soil texture and moisture properties, degree of insulation by snowpack or vegetation, latitude, and

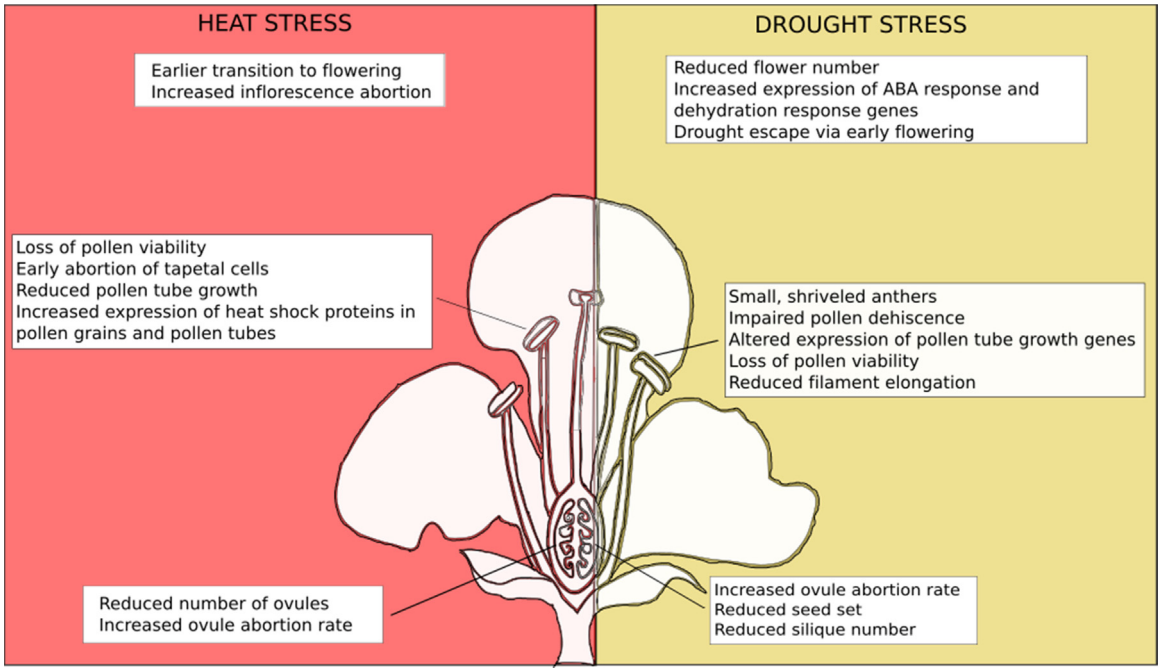

Fig. 2. A diagram illustrating the effects of elevated temperature stress (left) and drought stress (right) on reproductive development of *Arabidopsis thaliana.* References are as follows: (Blázquez et al., 2003; Warner and Erwin, 2005; Balasubramanian et al., 2006; Oshino et al., 2007; Sakata and Higashitani, 2008; Whittle et al., 2009; Yang et al., 2009; Zinn et al., 2010; Parish et al., 2012; Su et al., 2013; van Zanten et al., 2013; Ma et al., 2014).

season (Jungvist et al., 2014). Specific model predictions for increases in soil temperature in the second half of this century include up to 4 °C increase in boreal forest soil in Northern Sweden (Jungvist et al., 2014), and up to 5 °C increase in black spruce forest soil in eastern Canada (Houle et al., 2012). These increases in soil temperature will likely result in regionally-specific root developmental responses to rising temperatures.

3.3. *Reproductive development responses to elevated temperature*

Plant developmental responses to elevated temperature vary significantly by tissue and developmental stage. For example, in rice, peak vegetative biomass is observed at 33 °C, while grain formation and yield are adversely affected by temperatures above 25 °C (Matsushima et al., 1964; Baker et al., 1995). These thresholds vary significantly by species as well; in sorghum the optimum temperature range for vegetative growth is 26–34 °C, while the optimum range for reproductive growth is 25–28 °C (Maiti, 1996). In Arabidopsis, abortion of the entire inflorescence was observed starting at heat stress treatments of 36 °C (Warner and Erwin, 2005). Thus, the final impact of temperature stress on yield or reproductive fitness depends on the developmental stage at which high temperature stress occurs.

Elevated temperature may impact reproductive development by altering the timing of reproductive events, or by causing heat damage to reproductive structures (Fig. 2). Reproductive developmental events tend to occur earlier when plants are grown at elevated temperature. For example, an earlier transition to flowering has been well documented in Arabidopsis grown at elevated temperature (Blázquez et al., 2003; Balasubramanian et al., 2006; van Zanten et al., 2013). Numerous crop species are reported to progress more rapidly through vegetative and reproductive development as temperature rises, up to a species-specific optimum, after which growth and development slows and eventually stops (Hatfield et al., 2011). Acceleration of flowering in elevated temperature conditions may reduce the plant's ability to accumulate the resources required for successful gamete production (Zinn et al., 2010). Interestingly, Burghardt et al. (2016) recently demonstrated that fluctuating warm temperatures caused flowering to occur even earlier than constant warm temperatures in several Arabidopsis accessions, suggesting that temperature range plays a role in regulating flowering time, in addition to average temperature. Rising temperatures may also affect the timing and success of reproductive development by altering winter chilling conditions. Fruit and nut trees, for example, have winter chilling thresholds that are required for synchronous flowering and successful fruit set. Luedeling et al. (2009) used various greenhouse gas emission scenarios to model winter chill in important production regions in California, and found that the area of land that will meet the safe winter chill requirements for many trees is projected to decrease by 90–100% by the end of the century. Such a change in conditions in the current area of production has important agricultural and economic implications, and further research is needed to elucidate the molecular mechanisms of the response of reproductive development to rising temperature in these species.

During reproductive stages of growth, the largest developmental impacts of temperature on crop production occur through the extreme sensitivity of the male gametophyte to this stress (Zinn et al., 2010). The male gametophyte is more sensitive to high temperature stress than the pistil or the female gametophyte (Hedhly, 2011). For example, as rice flowers near mid-day, a maximum mid-day temperature above 33 °C reduces viability of pollen, and viability decreases to zero at mid-day temperatures of 40 °C (Kim et al., 1996). Pollen viability can be further reduced by early abortion of tapetal cells and programmed cell death in pollen mother cells in response to elevated temperature (Oshino et al., 2007; Sakata and Higashitani, 2008; Parish et al., 2012). Significant genetic diversity has been described among Arabidopsis accessions in response to heat stress, and pollen tube growth has been identified as a key factor differentiating more sensitive from more resistant ecotypes (Zinn et al., 2010). If, despite all of these barriers to male gametogenesis at high temperatures, successful fertilization does occur, grain number and quality is likely to be reduced by temperature stress (Bita and Gerats, 2013). Sensitivity of female floral organs can also contribute to loss of reproductive success in

response to heat stress. In Arabidopsis, heat stress reduces the number of ovules and increases ovule abortion rate (Whittle et al., 2009). In peach trees, there is a shorter window of time during which the stigmas can support pollen germination at 30 °C compared to 20 °C (Hedhly et al., 2005).

Extreme heat stress can affect plant reproductive development, through consistent exposure or transient exposure. Ruiz-Vera et al. (2013) found that constant exposure to elevated temperature (3.5 °C above ambient) tended to reduce seed yield of soybean, but the effect depended upon interactions with CO_2 treatment and field season. Siebers et al. (2015) demonstrated that heat waves (6 °C above ambient) as short as three days caused rapid induction of, and recovery from, photosynthesis reductions and oxidative stress in soybean. The impacts of heat waves on seed yield depended upon the developmental stage at which the heat wave occurred, as heatwaves during early pod development reduced seed yield by 10–17%, but heat waves during later pod development did not significantly affect seed yield. The effects of heatwaves on yield could be attributed to a reduced number of pods, rather than reduced individual seed weight, or a reduced number of seeds per pod, suggesting that increased pod abortion rates in response to heat stress occurred, but only when pods were at beginning pod or full pod stage during the heat stress (Siebers et al., 2015). These data demonstrate the importance of considering increased occurrence of extreme events as an element of climate change, as stresses such as elevated temperature cause distinct effects when experienced at different times or with differing severity. It is apparent from this research that both consistent exposure to elevated temperature (Ruiz-Vera et al., 2013) and brief exposure to extreme temperature (Siebers et al., 2015) significantly influence plant reproductive development and yield.

Underlying the morphological and developmental responses to elevated temperature described above are molecular and cellular responses that occur over many tissue types, as well as some cell type-specific responses. Cellular responses to temperature stress include altered organization of organelles, cytoskeleton, and membrane structure (Weis and Berry, 1988). To maintain membrane stability and normal cellular functions in response to heat stress, plants induce synthesis of heat shock proteins (HSPs), molecular chaperones that prevent protein misfolding or aggregation (Vierling, 1991); as well as other co-chaperones, hormones, and other protective molecules (Bray et al., 2000). Expression of HSPs is induced by heat-stress transcription factors (HSFs) that bind to heat shock elements in the promoters of HSPs (von Koskull-Doring et al., 2007). There are many steps of regulation allowing dynamic control of this heat stress response, as the HSFs themselves can be post-transcriptionally modified (Liu et al., 2008). In addition to the constitutive role that HSPs play in heat stress response across cell types, these proteins can acquire specialized functions that regulate developmental responses of particular organs to environmental stress. For example, expression of Arabidopsis *TMS1 (Thermosensitive Male Sterile 1)*, an Hsp40 homolog, is increased in response to heat shock in pollen grains, pollen tubes, and vegetative tissues, but appears to play a particularly significant role in pollen tube thermotolerance, as mutants had impaired pollen tube growth in high temperatures (Yang et al., 2009).

Heat stress responsive gene expression is regulated at multiple levels. The interaction of the nucleosome containing H2A.Z with DNA is altered by temperature stress, suggesting a role for chromatin remodeling in gene expression responses to heat stress (Bita and Gerats, 2013). In further support of the role of altered chromatin accessibility in response to temperature, Sullivan et al. (2014) used DNase I hypersensitive sites and genomic footprinting to identify changes in transcription factor (TF) occupancy in *Arabidopsis* seedlings exposed to heat shock. These authors identified heat-activated and heat-repressed DNase hypersensitivity sites, with many of the heat-activated sites being located within known heat response genes, including HSPs and HSFs. Interestingly, they also found that motifs that were significantly enriched in the heat-activated DHSs included MADS box motifs. MADS box genes regulate critical and wide-ranging developmental processes, including floral organ identity and flowering time (Rounsley et al., 1995; Pelaz et al., 2000), as well as root apical meristem properties including meristem size and organization (Tapia-López et al., 2008). Recent evidence demonstrates that FLOWERING LOCUS M (FLM), a MADS box gene that regulates flowering time (Scortecci et al., 2001), is alternatively spliced in a temperature-dependent manner, and that the FLM-δ isoform likely affects flowering time by de-repressing FT and SOC1 in warm temperatures (Lutz et al., 2015). Thus, multiple mechanisms of transcriptional regulation likely play a role in the developmental phenotypes in floral and other organs in response to heat stress. Much of the molecular work described here has been conducted in Arabidopsis. It is likely that similar pathways operate in crop species, contributing to the detrimental impacts that elevated temperature has on gametophyte and fruit/pod development. Future research to elucidate the molecular mechanisms of heat stress response in crop reproductive tissue would facilitate breeding climate-resistant crops.

4. Plant developmental and morphological responses to drought stress

Plants growing in many regions of the world will experience increasing water stress as a result of climate change. Already, the area affected by drought has increased substantially since the middle 20th Century (Dai, 2011), and the frequency of droughts is predicted to increase in regions that are already dry by the end of the 21st Century (IPCC, 2014). Droughts can consist of varying degrees of intensity and duration of water stress, resulting in a wide range of impacts on plant growth and development, but drought can generally be defined as a period of abnormally dry weather long enough to cause serious hydrologic imbalances (IPCC, 2014). Water availability has long been known as one of the most important abiotic factors governing crop yield (Boyer, 1982), owing to the central role it plays in plant growth and development processes. Drought stress already causes large losses in plant production and agricultural yield, with the magnitude of the effects depending upon the developmental stage at which plants experience drought stress (Skirycz et al., 2010; Verelst et al., 2010) and soil-related parameters such as soil texture (Daryanto et al., 2015). Additionally, inter-specific and intra-specific variation in developmental and physiological responses to drought stress means that there will be a wide range of sensitivities to climate change-associated droughts across different ecosystems, both natural and agricultural.

Specific developmental responses to drought vary among plant organs and tissues. In a broad sense, drought stress causes plants to invest resources in root tissue at the expense of shoot tissue. This can be measured coarsely as an increased ratio of root: shoot biomass (Poorter and Nagel, 2000), and at the molecular level, shifts in allocation of resources from shoots to roots in response to drought stress can also be observed in metabolite profiles of each tissue. For example, Gargallo-Garriga et al., 2014 reported that drought increased the root content of sugars, amino acids, and nucleosides, while decreasing the content of these metabolites in the shoot tissue in two grass species (*Holcus lanatus* and *Alopecurus pratensis*). These opposite patterns in metabolite content between the two tissue types reflect the growth patterns in each tissue in response to drought stress: root elongation is often maintained in drought, while shoot growth ceases (Sharp and

Davies, 1989). According to the functional equilibrium theory, plants will shift allocation among tissues to optimize the acquisition of the most limiting resource (Brouwer, 1983). In times of water deficit, investment in root tissue over leaf tissue also has the benefit of reducing the area for water loss via transpiration. Adaptations like these may enable a plant to continue through its developmental program and reach reproductive maturity, even in the face of water deficit.

4.1. Leaf developmental responses to drought stress

Cell division and cell expansion are the two main processes defining the developmental program of a leaf, and both of these processes are significantly affected by drought stress across diverse species and accessions (Aguirrezabal et al., 2006; Baerenfaller et al., 2012; Clauw et al., 2015). Generally, leaf expansion is reduced in response to drought stress in several species although this is dependent on leaf developmental stage. In Arabidopsis, total rosette area, individual leaf size, and epidermal pavement cell area and number are all reduced by mild drought stress (Clauw et al., 2015). The strength of the effect of drought stress on final leaf size depends upon the developmental stage of the leaf when drought is imposed. For example, in *Ricinus communis*, reductions in leaf expansion rates caused by drought stress could be rescued by rehydration if leaves were longer than 12 cm when drought treatment started, but re-watering could not rescue the final size of leaves that were smaller when drought stress was imposed (Schurr et al., 2000). This suggests that normal cell division processes in early development are critical to the leaf reaching its final size, and if cell division is arrested at this stage, the final leaf size cannot recover. Genes that form a conserved transcriptional response to mild drought stress across six diverse Arabidopsis accessions included abscisic acid (ABA) signaling genes, proline metabolism-associated genes, and genes annotated as functioning in cell wall adjustments (Clauw et al., 2015). The transcriptional response is determined by leaf developmental stage, as genes that were up-regulated in response to mild drought in young leaves, but not in older leaves included genes related to synthesis, loosening, or remodeling of cell wall components. These genes, including pectin lyases and expansins, presumably function to enable growth to continue at a low rate in young leaves, even in conditions of low turgor pressure (Clauw et al., 2015).

4.2. Root developmental responses to drought stress

In contrast to shoot growth, root growth is often maintained, or may even be stimulated in response to drought stress. Smaller reductions in root growth rate relative to shoot growth rate have been described in maize, soybean, cotton and squash (Spollen et al., 1993). Observations of enhanced root growth and shifts to a deeper root depth distribution in response to drought through manipulation of the root's response to gravity has been reported in numerous species, pointing to plasticity in root stress response that is dynamic across soil depths and the developmental timeline of both the root and the whole plant.

In field-grown soybean, drought stress stimulated root growth rates; and the magnitude of this effect depended upon the plant's developmental stage and the soil depth, with the strongest stimulation in root growth rate occurring in late vegetative and early reproductive developmental stages, and in soil depths deeper than 0.6 m (Hoogenboom et al., 1987). Rellán-Álvarez et al., (2015) used non-destructive imaging of soil-grown Arabidopsis roots to demonstrate that water deficit expanded the size of the root system and reoriented lateral root tips downward. They also found that mutants in the auxin receptor *TIR1 (TRANSPORT INHIBITOR RESPONSE 1)* did not change their root angle in response to water deficit, suggesting a critical role for auxin in redirecting root growth angles downward in response to drought stress (Rellán-Álvarez et al., 2015). Uga et al. (2013) cloned *DEEPER ROOTING 1* (DRO1), a gene that regulates rooting depth of rice via a steeper root growth angle of nodal roots. They found that this allele did not alter biomass of roots or shoots, and did not affect grain yield in well-watered conditions, but significantly increased grain yield in moderate or severe drought conditions (Uga et al., 2013). DRO1 exerts its influence on root angle via altering the root's response to gravity—in response to a gravity challenge, auxin causes polar expression patterns of DRO1 across the root, with an increase at the outer edge of the elongation zone, presumably stimulating cell elongation on the upper side of the root (Uga et al., 2013). These results demonstrate distinct genetic regulation of one specific root morphological trait, and these results show that seed yield can be directly affected by root traits in stress conditions.

Sharp and colleagues used kinematics to describe dynamics of root elongation responses to drought in maize roots at a range of distances from the root apex. They found that elongation peaked at a lower rate, and at a shorter distance from the root apex in water stressed plants compared to well-watered plants, resulting in a shorter elongation zone (Sharp et al., 1988). In maize, growth responses of leaf and shoot tissue to water stress depend upon abscisic acid (ABA) signaling, which may prevent excess ethylene production (Saab et al., 1990; Spollen et al., 2000). Turgor provides the driving force for cell expansion, and the rate of expansion is determined by the yielding properties of the cell wall (Spollen et al., 1993). Cell turgor is reduced by drought stress in the absence of osmotic adjustment, and the sensitivity of cell expansion to water deficit varies along the elongation zone of roots (Sharp et al., 1988; Spollen and Sharp, 1991). The fact that expansion can be maintained in roots experiencing drought stress despite low root water potential suggests changes to cell wall properties to make them more yielding, such as changes through the action of cell wall remodeling enzymes such as xyloglucan *endo*transglycosylase (XET), which cuts and rejoins xyloglucan polymers, and which is activated by ABA accumulation (Wu et al., 1994). ABA also plays important roles in regulating cell type-specific developmental responses to drought stress. For example, the outermost cortex layer of the roots of many species differentiates into exodermis with the deposition of suberin, and this developmental transition may be hastened by drought stress (Enstone et al., 2002). Barberon et al. (2016) demonstrated that treatment with exogenous ABA (a classical drought-responsive and drought-mitigating hormone) was sufficient to induce suberization in root cortex cells and to lead to premature/ectopic deposition of suberin in young root tissue.

Root system architecture and depth distribution may be altered by elongation of primary roots, and by changes in the rate of lateral root initiation. Lateral roots initiate from pericycle tissue in a tightly controlled series of cell divisions (Péret et al., 2009). The number or density of lateral roots initiating along a primary root has long been known to be responsive to environmental stimuli, including osmotic stress (Deak and Malamy, 2005). Lateral root development is halted by exogenous application of the drought stress-signaling hormone ABA in Arabidopsis roots (De Smet et al., 2003; Seo et al., 2009). Reduced lateral root initiation in response to drought stress has also been demonstrated in crop species. In barley and maize, water stress represses lateral root initiation (Babé et al. 2012). Recent evidence describing the phenomenon of hydropatterning demonstrates that lateral root initiation can also be differentially regulated across the radial axis of a root in response to spatial heterogeneity in water availability. This occurs via regulation of the location of lateral root founder cells, with the side of the root nearer to the water initiating more lateral roots (Bao et al., 2014). Changes in root cellular anatomy, including formation of aerenchyma and reduced area or number of cortical

cells have been associated with improved performance of maize plants exposed to drought stress, consistent with the "steep, cheap, and deep" ideotype of optimal root growth in water scarcity (Lynch, 2015).

4.3. Reproductive developmental responses to drought stress

Time to flowering can be an important determinant of a plant's reproductive success in a dry environment. Two strategies have been described regarding flowering time adaptations for coping with drought stress: drought escape, or early flowering and completion of reproductive development before the onset of late-season droughts (Sherrard and Maherali, 2006; Heschel and Riginos, 2005); and drought avoidance, or increased water use efficiency to avoid dehydration in ecosystems that experience early-season droughts (Heschel et al., 2002). The Arabidopsis gene FRIGIDA (FRI) encodes a transcription factor that positively regulates flowering locus C (FLC), delaying flowering (Searle et al., 2006). In addition to the well-known roles of FRI and FLC in regulating flowering time responses to vernalization (Searle et al., 2006), Lovell et al. (2013) demonstrated that variation in allelic state of FRI plays a role in regulating flowering time response to drought stress in *Arabidopsis thaliana*. Specifically, functional alleles of FRI were associated with a dehydration avoidance strategy, and non-functional alleles of FRI conferred a drought escape strategy, encompassing low water use efficiency and early flowering (Lovell et al., 2013). The relative fitness consequences of these strategies depend on the severity and timing of the drought stress (Schmalenbach et al., 2014).

Reproductive development is the stage that is most sensitive to drought stress (reviewed in Saini and Westgate (1999); Fig. 2). Development of male floral organs and gametophytes are particularly vulnerable to the effects of drought. In cereal crops, water deficit during inflorescence development may slow the rate of development of inflorescence, or lead to partial or complete inhibition of flowering (Saini and Westgate, 1999). Similarly, overall reproductive development responses to drought in Arabidopsis include early arrest of floral development (Su et al., 2013). Drought stress during reproductive development leads to anthers that are reduced in size, shriveled and unable to dehisce in wheat and rice (Saini and Aspinall, 1981; Sheoran and Saini, 1996). In Arabidopsis, drought stress reduced filament elongation and led to abnormal anther phenotypes (Su et al., 2013). Arabidopsis mutants in *MYB DOMAIN PROTEIN 21* (*myb21*) showed a stronger reduction in male filament elongation in response to drought than did wild type, suggesting an important role for this transcription factor in maintaining normal floral development during stress (Su et al., 2013). During gametophyte development, loss of pollen viability is the predominant response to water deficit across crop species and model species, leading to reduced seed set or grain yield in cereal crops (Saini and Westgate, 1999; Su et al., 2013).

Reproductive development of female floral structures and gametophytes are less affected by drought stress compared to development of male reproductive structures. Su et al. (2013) suggested that protection of female reproductive development over male reproductive development is an effective strategy to maintain fecundity in a stressful environment, as pollen are numerous and small compared to ovules. In Arabidopsis, Su et al. (2013) found that drought stress imposed from the start of flowering to seed maturation increased ovule abortion rates. Ma et al. (2014) exposed Arabidopsis to moderate and severe drought stress, and found that, while plants were able to maintain near-normal flowering in moderate drought stress, severe drought stress reduced branch number, flower number, silique number and seed count. Unique transcriptional signatures were associated with severe drought stress compared to moderate drought stress of inflorescence tissue. Genes involved in ABA and water deprivation response and pollen tube growth were among those upregulated in moderate drought; a greater number of genes were differentially expressed only in severe drought stress, including nuclear factor Y's, which are known to play roles in drought resistance and regulation of flowering (Ma et al., 2014). Kakumanu et al. (2012) found that fertilized maize ovary tissue showed stronger transcriptional responses to drought compared to leaf tissue, with more than three times as many differentially expressed genes in the ovary tissue compared to the leaf meristem tissue. Specific processes that were over-represented in drought stress up-regulated genes in the ovary but not in the leaf meristem included ABA-related processes and sucrose metabolism related genes, suggesting a role of hormone signaling and sugar signaling in maize kernel responses to drought stress (Kakumanu et al., 2012). These data demonstrate the tissue specificity of the response to drought stress: reproductive processes show greater sensitivity to drought than do vegetative processes, and male reproductive development is more drought sensitive than female reproductive development.

5. Interactive effects of climate change factors on development

In the future, plants will not experience climate change factors individually, but will be exposed to multiple elements of environmental change simultaneously. However, most studies of plant developmental responses to climate change expose plants to only one climate change factor at a time. While exposure of plants to a single climate change factor is more experimentally tractable, it also limits our ability to make inferences about plant responses to realistic climate change scenarios. The studies that have been conducted on interactive climate change factors have often demonstrated interactions that differ strongly from the effects of climate change factors applied independently. For example, research on soybean has demonstrated that the predicted stimulation of seed yield by elevated CO_2 diminishes as drought stress increases (Bishop et al., 2014; Gray et al.,2016). Factors contributing to the loss of yield stimulation in drought coupled with elevated CO_2 include increased canopy size and canopy temperature in elevated CO_2 (Gray et al., 2016). Additionally, elevated CO_2 increased root length density of soybean in both drought and control precipitation, but elevated CO_2 significantly increased the number of root nodules and altered seed nitrogen content only when combined with reduced precipitation (Gray et al., 2013). Researchers have also found that the stimulation of leaf area by elevated CO_2 is reduced when plants are exposed to drought in combination with elevated CO_2 in multiple species, including American sycamore (*Platanus occidentalis*), sweetgum (*Liquidambar styraciflua*) and sugar maple (*Acer saccharum Marsh.)* (Tschaplinski et al., 1995). These studies suggest that drought conditions, which will likely co-occur with elevated CO_2 in the future, will modify previously observed plant growth and development responses to elevated CO_2 only. Furthermore, the molecular mechanisms of plant response to these combined treatments are unknown.

Similar to the studies on elevated CO_2 and drought, elevated temperature reduces the benefits of elevated CO_2 to growth and seed yield in soybean during a warm field season, albeit with inter-annual variation (Ruiz-Vera et al., 2013). Benlloch-Gonzalez et al. (2014) also demonstrated that elevated CO_2 stimulated root and shoot growth of wheat, but this stimulation was reduced when plants were grown in combined elevated temperature and elevated CO_2. Ruiz-Vera et al. (2015) found that in the C_4 crop maize, elevated CO_2 did not significantly affect shoot biomass or

seed yield, but elevated temperature reduced seed yield in both ambient and elevated CO_2. Reduced seed yield in elevated temperature was the result of fewer kernels per cob, suggesting a lack of successful fertilization or increased ovule abortion rates in response to elevated temperature, independent of CO_2 treatment (Ruiz-Vera et al., 2015). Fukayama et al. (2011) found that, in flag leaves of rice grown in elevated CO_2, genes associated with sucrose synthesis, glycolysis and the TCA cycle were increased in expression, and that larger numbers of differentially expressed genes were observed when elevated CO_2 was combined with elevated temperature. This research suggests altered magnitude of transcriptional response to elevated CO_2 when it is combined with temperature stress; however, our understanding of this process would benefit from a systems approach to characterize biological processes that are over-represented in the differentially expressed genes. Overall, these results demonstrate that the effects of a particular element of climate change on plant developmental processes often depend upon the presence of other climate change factors. As many studies on the interactive effects of climate change factors have focused on big-picture elements of plant response such as biomass and seed yield, further research should focus on molecular and cellular elements of these responses to improve our mechanistic understanding of these interactions.

6. Conclusion

Climate change will alter plant development in ways that will have significant impacts on the function of crop plants and plants in natural ecosystems. Future growing conditions will bring increased temperature, increased frequency of extreme events including heatwaves and drought events, and changes in the composition of the atmosphere (IPCC, 2014). Plant developmental plasticity in response to climate change will be critical in maintaining ecosystem function and agricultural productivity in the future. Currently, our ability to understand and predict plant developmental responses to climate change is limited by the number of experiments that are conducted in physiologically relevant stress conditions. For example, our understanding of the molecular mechanisms of plant response to extreme drought stress is stronger than our understanding of the mechanisms at play in mild drought stresses (Clauw et al., 2015). A more holistic understanding of plant responses to the elements of climate change requires integration of data from multiple levels of biological research, including molecular studies of developmental processes at a finer spatial resolution. Molecular studies should be carried out at the tissue and cell type-specific levels in multiple species in controlled environments and in realistic field environments, where effects of molecular and developmental changes on whole plant morphology and yield can be assessed. Finally, climate change factors will not impact plants in isolation: increased greenhouse gas concentrations in the future will coincide with rising temperatures, changing precipitation patterns, and increasing frequency of extreme climatic events (IPCC, 2014). Improving our mechanistic understanding of plant developmental responses to multiple, interacting factors of climate change will be critical for anticipating impacts on agricultural and natural systems.

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