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Review

Utilizing intraspecific variation in phenotypic plasticity to bolster agricultural and forest productivity under climate change

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ABSTRACT

Climate change threatens the ability of agriculture and forestry to meet growing global demands for food, fibre and wood products. Information gathered from genotype-by-environment interactions (\(G \times E\)), which demonstrate intraspecific variation in phenotypic plasticity (the ability of a genotype to alter its phenotype in response to environmental change), may prove important for bolstering agricultural and forest productivity under climate change. Nonetheless, very few studies have explicitly quantified genotype plasticity–productivity relationships in agriculture or forestry. Here, we conceptualize the importance of intraspecific variation in agricultural and forest species plasticity, and discuss the physiological and genetic factors contributing to intraspecific variation in phenotypic plasticity. Our discussion highlights the need for an integrated understanding of the mechanisms of \(G \times E\), more extensive assessments of genotypic responses to climate change under field conditions, and explicit testing of genotype plasticity–productivity relationships. Ultimately, further investigation of intraspecific variation in phenotypic plasticity in agriculture and forestry may prove important for identifying genotypes capable of increasing or sustaining productivity under more extreme climatic conditions.

Key-words: acclimation; agriculture; forestry; genetic variation; physiology.

INTRODUCTION

Fossil fuel combustion and land use change are contributing to alterations in global climate. Atmospheric [CO\(_2\)] has recently (2002–2011) increased at an average rate of 2.0 μmol mol\(^{-1}\) year\(^{-1}\), which is higher than any measurement period to date over the past 800 000 years (IPCC 2013). Barring substantial reductions in emissions, atmospheric [CO\(_2\)] may exceed 900 μmol mol\(^{-1}\) by the end of the 21st century (Representative Concentration Pathway (RCP) 8.5; IPCC 2013). Rising atmospheric [CO\(_2\)] has contributed to significant atmospheric warming, and global mean surface temperatures could increase 3 to 4 °C by the middle of the century (IPCC 2013). Embedded in this climatic warming trend is an increased frequency of extreme temperature events (Ganguly et al. 2009; Coumou et al. 2013; Stéfanon et al. 2014). Atmospheric warming has also been implicated in more frequent and extreme precipitation and drought events (Groisman et al. 2005; Hansen et al. 2012), and net declines in soil moisture in many, but not all, regions.

Temperature, water availability and atmospheric [CO\(_2\)] are each important regulators of plant growth, function and development. Thus, climate change will likely influence the ability of agricultural systems to meet a growing global population’s (predicted to be 9 billion by 2050) demands for food and fibre. It is expected that food production must increase 70 to 100% by 2050 to meet growing demands (Tilman et al. 2002; Godfray et al. 2010). Troublingly, recent trends suggest that yields are not increasing rapidly enough (Long & Ort 2010 and references therein), and climate change and extreme weather events may already be reducing crop yields in some areas (e.g. Rosenzweig et al. 2001, Lobell & Field 2007). For instance, Australia suffered enormous losses in wheat yield during historic drought in the early 21st century and higher than normal temperatures have contributed to reductions in corn and soybean yields in the United States between 1982 and 1998 (Lobell & Asner 2003). Even with high precipitation, higher temperatures can increase evaporative demand and reduce soil moisture resulting in greater incidence of drought (Wheeler et al. 2000; Challinor et al. 2007; Lobell & Field 2007). A recent analysis of maize and soybean yields in the Midwestern United States showed that although field-scale yields are increasing, they have become increasingly sensitive to drought (Lobell et al. 2014). Alternatively, experimental manipulations have demonstrated that elevated [CO\(_2\)] (eCO\(_2\)) can stimulate C\(_3\) crop yield (Kimball 1983; Ainsworth et al. 2008), yet the magnitude of this increase is uncertain under field conditions where temperature and precipitation can influence the CO\(_2\) fertilization effect (Long et al. 2006).

Climate change also threatens the ability of forests to meet global demands for wood products (FAO 2006). Although forest plantations only account for 5% of global forest cover,
they supply roughly 35% of global roundwood, with future wood production expected to increase in plantations compared to native forests (FAO 2006, Kirilenko & Sedjo 2007, Nabuurs et al. 2007). Concentrating wood production to smaller areas promotes greater forest protection and mitigation on non-plantation lands (Gladstone & Ledig 1992; Nabuurs et al. 2007), but necessitates sustained productivity over time, which will become more difficult under extreme climatic conditions. Experimental studies have shown that forest trees and plantations may increase productivity under eCO2 (Tissue et al. 1997; Saxe et al. 1998; Tjoelker et al. 1998, 1999; DeLucia et al. 1999), although variability in the growth stimulation is dependent upon variation in soil fertility, temperature and precipitation (Oren et al. 2001; McCarthy et al. 2010). Atmospheric warming is generally expected to increase tree and forest growth in cool climates, but have no effect or reduce growth in warm climates (Tjoelker et al. 1999; Saxe et al. 2001; Way & Oren 2010). In addition, there is mounting evidence that more frequent and intense heatwaves and drought are leading to lower tree growth rates and increased tree mortality in some regions worldwide (Klos et al. 2009; Allen et al. 2010). Although fast-growing mono-specific plantations have high rates of C accumulation (Ryan et al. 2010), lower stand-level genetic diversity may increase their susceptibility to heatwaves and drought stress (Nabuurs et al. 2007).

Utilization of intraspecific (e.g. accession, cultivar, variety, clone, family, provenance) variation in agricultural and forest species responses to climate change may bolster productivity and aid development of greater stress tolerance or resilience (Ainsworth et al. 2008; Nicotra et al. 2010; Leakey et al. 2012; Tausz et al. 2013). Genotypes of a given species often show markedly different physiological, growth and developmental responses to eCO2, temperature variation and soil water availability, exemplified by genotype-by-environment interactions (G × E). Careful examination of genotypes’ plastic responses may reveal individuals that can both increase productivity under optimal conditions, and, in part, sustain production under stressful conditions (Valladares et al. 2007; Nicotra et al. 2010). Despite the potential utility of intraspecific variation in agricultural and forest species responses to climate change, an integrative understanding of the physiological and genetic factors influencing G × E interactions is lacking, and relationships between genotype plasticity and productivity have rarely been tested in the context of agriculture or forestry.

The goal of this paper is to link aspects of plant physiology and genetics that may influence intraspecific variation in agricultural and forest species responses to climate change. In particular, we: (1) conceptualize the importance of intraspecific variation in agricultural and forest species phenotypic plasticity within the context of plant breeding and climate change; (2) highlight some physiological mechanisms underpinning intraspecific variation in agricultural and forest species responses to drought, warming and eCO2; (3) discuss the genetic factors (genetic architecture, gene expression) influencing intraspecific variation in phenotypic plasticity; and (4) discuss future directions in G × E climate change research.

Importance of intraspecific variation in agricultural and forest species plastic responses to climate change

Crop yields and forest productivity are a function of genetic variation (G), environmental variation (E) and G × E interactions (Fig. 1). Where G × E exists, there is evidence of genetic variation in phenotypic plasticity, the ability of a
Phenotypic plasticity in agriculture and forestry

Figure 2. Potential relationships between genotype variation in phenotypic plasticity and genotype mean productivity across a range of environments (adapted from van Kleunen & Fischer 2005; Nicotra et al. 2010). The regression between genotype mean performance across a range of environments and genotype plasticity provides a means of assessing ‘adaptive’ plasticity in the context of agriculture and forestry.
Intraspecific variation in agricultural and forest species responses to drought, warming and elevated CO₂: physiological mechanisms

Drought

Water is the most important determinant of plant growth and function worldwide (Boyer 1982). Therefore, intraspecific variation in agricultural and forest species responses to drought and variable soil moisture has received more attention than any other environmental variable (Bohner et al. 1995). Significant G x E in yield, growth and physiology under variable soil water availability has been documented in many of the world’s most important agricultural crops including maize (Zea mays L.; Maiti et al. 1996; Efeoglu et al. 2009), rice (Gu et al. 2012) and wheat (Monneveux et al. 2006; Rampino et al. 2006). In forest species, significant G x E under variable soil water availability has also been documented, with examples in the genera Eucalyptus (Costa e Silva et al. 2004; Bedon et al. 2012; Dutkowski & Potts 2012), Pinus (Cregg & Zhang 2001) and Populus (Monclus et al. 2006; Cochard et al. 2007).

A clear, but important, distinction between agricultural crops and forest species is that most broad-acre crops are produced as annuals, and their development and yield are highly sensitive to the timing of stress (Fukai & Cooper 1995; Chaves et al. 2003). In crops, water limitation often advances flowering and fruiting, which can limit carbon (C) uptake integrated over time, resulting in lower yields (Fischer & Maurer 1978; Long & Ort 2010). However, if two crop genotypes show the same phenological development under drought, but one maintains higher gas exchange rates due to osmotic adjustment, develops deeper roots with greater access to water or allocates more assimilates to fruiting, it will generally show higher yields (Foulkes et al. 2007). Intraspecific variation in canopy structure and morphology are also critical determinants of plant water use and tolerance to low soil moisture. Drought avoidance genotypes often reduce leaf area by rolling leaves or possess steeper leaf angles to reduce radiation absorption and heat loads (Chaves et al. 2003).

At the biochemical level, genetic variation in starch breakdown, sugar remobilization and metabolite accumulation can influence plant water use, C gain, biomass allocation and drought tolerance. For instance, when cell turgor decreases, genotypes capable of rapid sugar remobilization may osmotically adjust, resulting in continued stomatal conductance (gₛ) and C available for continued growth (Gebre et al. 1998; Tschaplinski et al. 2006; Bogeat-Triboulot et al. 2007). This increased C availability may be particularly important for increasing root growth, leading to greater access to water and further C fixation and growth (Serraj & Sinclair 2002; Hummel et al. 2010). In this way, genetic variation in plastic responses at the leaf level might result in correlated structural or morphological changes leading to increased water availability. Alternatively, genotypes that restrict whole-plant water use under high vapour pressure deficit (VPD) conditions and high water availability can maintain higher yields under drought (Schoppach & Sadok 2012; Schoppach et al. 2014).

Although stomatal closure limits A under drought, biochemical down-regulation of A can also occur due to decreased ATP synthesis and reduced RuBP supply (Lawlor & Cornic 2002; Meyer et al. 2014). Genotypes that maintain or increase leaf photosynthetic enzyme concentrations under drought can sustain higher C fixation under stomatal closure resulting in higher water-use efficiency (WUE) and growth (Flexas & Medrano 2002; Bonhomme et al. 2009; Edwards et al. 2012).

Water stress can also trigger heat stress due to stomatal closure and lack of transpirational cooling. Heat stress can result in the production of reactive oxygen species (ROS), which can damage the photosynthetic apparatus (Lawlor & Tezara 2009). Genotypes that are more effective at producing and utilizing antioxidant defence compounds (e.g. raffinose, fructans) may be more effective at scavenging ROS and fending off long-term damage to the photosynthetic machinery (Bogeat-Triboulot et al. 2007; Bedon et al. 2012; Keunen et al. 2013). Similarly, genotypic variation in thermal dissipation mechanisms via xanthophyll cycle activity may provide resilience to temperature and other stresses (Demmig-Adams & Adams 2006; Jung & Niyogi 2009).

In forest tree species, examination of intraspecific variation in drought responses has often focused on comparing anatomical and hydraulic characteristics of genotypes from different environments or genetic backgrounds. In particular, genotypes from xeric sites often show a suite of leaf-level traits associated with lower growth and greater water conservation: smaller, thicker leaves with higher WUE. As such, these genotypes typically show lower productivity but greater drought tolerance than mesic genotypes (Abrams 1994; Cregg & Zhang 2001; Gratani et al. 2003; Corcuera et al. 2011).

Resistance to cavitation is a major determinant of tree growth and survival under drought (Choat et al. 2012). Cavitiation occurs when air bubbles form in the xylem, restricting hydraulic conductivity and the supply of water to leaves. Genotypes that resist cavitation may maintain leaf turgor and function under drought conditions. Some studies have demonstrated intraspecific variation in the stem xylem water potential at which 50% loss of conductivity (P₅₀) occurs, as an indicator of cavitation resistance [Populus, Salix spp. (Cochard et al. 2007), Pinus taeda (Aspinwall et al. 2011)], while others have not [Pinus pinaster (Corcuera et al. 2011; Lamy et al. 2011)]. Interestingly, a study by Wortemann et al. (2011) also found that Fagus sylvatica L. populations showed substantial genetic variation in plasticity of P₅₀. In some but not all studies, genotypes with greater cavitation resistance possess denser wood or thicker cell walls [e.g. hybrid Populus (Fichot et al. 2010)].

Cavitation resistance may be an important factor determining intraspecific variation in tree responses to drought, but some studies have demonstrated negative genetic correlations between cavitation resistance and tree growth (Monclus et al. 2006; Cochard et al. 2007), questioning the utility of breeding for high cavitation resistance. Nonetheless, Fichot et al. (2010, 2011) observed that Populus genotypes with greater cavitation resistance and low hydraulic
conductance had higher relative growth rates, indicating that genetically determined growth–cavitation resistance trade-offs are not universal.

Progress has been made in understanding the physiological basis of intraspecific variation in agricultural and forest species yield or productivity responses to drought. Yet, no studies have explicitly tested for associations between genotype physiological plasticity and performance across different water availabilities. Even so, we used data from Ullah et al. (2008), who found significant $G \times E$ for leaf gas exchange and yield among 32 cotton genotypes growing under well-watered and water-limited field conditions, to test for associations between genotype physiological plasticity and yield. A significant negative association was found between genotype photosynthetic plasticity and genotype mean yield across treatments, with high plasticity genotypes showing stomatal closure, low $A$ and low yield under water limitation (Fig. 3). The cause of genotypic differences in gas exchange in response to water limitation (e.g. osmotic adjustment) was not examined, and relationships between genotype leaf gas exchange and yield are likely obscured by other factors (e.g. plant size, leaf area). Nonetheless, this is an example of a test for genotype plasticity–productivity associations, and facilitates further hypothesis testing regarding the mechanisms of genotypic variation in productivity in response to water availability. Examining linkages between plastic changes occurring at the molecular, biochemical, leaf- and whole-plant level will be crucial for integrating the mechanisms of intraspecific variation in yield and productivity under water stress.

Warming and heat stress

Atmospheric warming can prompt strong responses in agricultural and forest species. In annual crop species, higher temperatures can accelerate vegetative and reproductive development, decreasing the period of photosynthetic activity and reducing yields (Battisti & Naylor 2009; Long & Ort 2010). Thus, intraspecific variation in phenological plasticity may be an important determinant of intraspecific variation in crop yield under warming (Sadras et al. 2009). In trees, warming can have a variable effect on tree growth and development depending upon the taxon’s origin (Saxe et al. 2001; Way & Oren 2010). In cool-origin species and genotypes, warming often advances phenological development, extends the growing season (Vitasse et al. 2010), and increases productivity. In some warm-origin taxa, warming can have a negative effect on growth (Way & Oren 2010).

One widely reported physiological response of plants to warming is thermal acclimation, which is a reversible metabolic adjustment in response to temperature, which serves to optimize C gain and reduce C loss (i.e. respiration; $R$). Typically, acclimation begins with a range of molecular, biochemical and cellular responses that in more effective physiological function (Atkin & Tjoelker 2003). The size and activity of C sinks as well as plasticity in catalytic turnover rate of Rubisco (ribulose 1·5-bisphosphate carboxylase/oxygenase) may contribute to the thermal acclimation of $A$ (Koch 1996; Stitt et al. 2007; Cavanagh & Kubien 2013). The short-term (min, h) temperature dependency of $R$ is governed by enzyme activity at low temperatures and C availability at high temperature (Tjoelker et al. 2008). Short-term responses to temperature change can also be intensified by longer term developmental changes resulting from growth under new temperature conditions (Atkin & Tjoelker 2003).

In agricultural species, intraspecific variation in thermal acclimation of $A$ could be the result of differences in maximum rates of carboxylation by Rubisco ($V_{\text{max}}$), possibly linked to differential protein synthesis associated with photosystem II (PSII; Gesch et al. 2003). However, intraspecific differences in the temperature response of $A$ might also depend upon RuBP regeneration, which is highly sensitive to temperature (Long & Ort 2010).

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Numerous studies in trees have examined intraspecific variation in thermal acclimation of $A$ and $R$ in trees. For example, in loblolly pine (Teskey & Will 1999) and sugar maple (Acer saccharum; Gunderson et al. 2000), strong acclimation of $A$ and $R$ was observed, yet populations did not vary in thermal acclimation. However, in red maple (Acer rubrum), Weston et al. (2007) and Weston & Bauerle (2007) found that cool- and warm-origin populations showed similar thermal acclimation of $A$, but the warm-origin population maintained higher $A$ and increased $V_{\text{max}}$ under warm-weather conditions. In jack pine (Pinus banksiana), Tjoelker et al. (2009) found that compared with cool-origin populations, warm-origin populations showed a wider seasonal range in basal $R$ rates and in the temperature sensitivity of $R$. Tjoelker et al. (2008) also demonstrated that similar levels of thermal acclimation of $R$ among Pinus banksiana populations were mainly driven by shifts in foliar N and soluble sugars, highlighting the biochemical responses, which underlie thermal acclimation.

Acute, short-term heat stress can trigger different physiological responses than observed with warming, and constitutive genotypic differences in leaf physiology and biochemistry may underlie genotypic variation in heat stress responses. In agricultural species, heat stress can induce kernel abortion, suppress grain maturation and reduce crop yield even under eCO$_2$ (Moya et al. 1998). Intraspecific differences in kernel abortion resistance during heat stress may be associated with differences in ethylene production (Stone & Nicolas 1994; Hays et al. 2007). At the leaf level, genetic variation in $g$, can directly affect crop thermo-tolerance and yield, with high $g$, genotypes exhibiting lower leaf temperatures due to transpirational cooling and higher yields (Radin et al. 1994). However, in the absence of adequate transpirational cooling, extreme heat events can induce the production of harmful ROS species (Dash & Mohanty 2002; Larkindale & Knight 2002). Genotypes capable of substantial ROS detoxification under extreme heat events may avoid reductions in photosynthetic capacity (Iba 2002; Mittler 2002).

One common response of plants to heat stress is the production of heat shock proteins (Hsp; Heckathorn et al. 1998), which primarily serve to protect proteins, membranes and other cellular components, in addition to maintenance of PSII and electron transport during stress (Feder & Hofmann 1999). In some cases, genotypes from more stressful habitats or grown under warmer temperatures, have higher Hsp concentrations (Barua et al. 2008), possibly indicating genetic variation in thermotolerance (Barua et al. 2003). In wheat and maize, for example, genotypic variation in thermotolerance was strongly associated with variation in the synthesis of different Hsp’s (Blumenthal et al. 1990; Ristic et al. 1996). Clearly, some of the physiological mechanisms underlying intraspecific variation in agricultural and forest species responses to warming and heat stress are understood. Yet, examining how plastic variation at the biochemical level is associated with leaf-level responses, and ultimately yield, will be crucial for developing an integrated understanding of intraspecific variation in plant responses to warming and heat stress.

**Elevated CO$_2$**

Assessment of C$_3$ crop responses to eCO$_2$ suggest that yields might increase roughly 13% under eCO$_2$ (Long et al. 2006), although importantly, eCO$_2$ generally has a negative effect on grain protein levels (Erbs et al. 2010; Fernando et al. 2012). In general, eCO$_2$ does not stimulate C$_4$ crop (e.g. maize) yields, except under water-limited conditions. However, given that drought severity is predicted to increase, examining intraspecific variation in C$_4$ crop responses to eCO$_2$ and drought may reveal germ plasm capable of sustaining production in dry environments.

A number of studies have demonstrated that C$_3$ crop yield responses to eCO$_2$ are largely genotype dependent (see Tausz et al. 2013). For example, rice (Oryza sativa L.) cultivars have shown a wide range of responses to eCO$_2$, ranging from a 31% relative yield reduction to a 241% relative yield enhancement (Ziska et al. 1996; Moya et al. 1998; Shimon et al. 2009). Rice genotypes, which show greater growth enhancement under eCO$_2$ prior to heading may be most productive under increasing atmospheric CO$_2$ (Shimon et al. 2009). Soybean (Glycine max L.) cultivars have also shown substantial variation in yield responses under eCO$_2$: a 20 to 80% relative yield increase depending upon genotype (Ziska et al. 1998, 2001). In some cases, genotypic variation in yield under eCO$_2$ is not associated with genotypic variation in $A$, but rather differences in biomass allocation. In soybean, Ziska et al. (2001) showed that yield variation under eCO$_2$ was genetically correlated with increased seed production on axillary branches, not variation in $A$. Wheat (Triticum durum) cultivars have shown similar variation in yield responsiveness to eCO$_2$ (Ziska et al. 2004; Thilakarathne et al. 2013). In general, studies in C$_3$ crops suggest that intraspecific differences in yield under eCO$_2$ are primarily related to changes in C allocation and not to physiological traits related to carbon assimilation. These studies have documented tremendous diversity in eCO$_2$ responsiveness within some of the world’s most important food crops, suggesting that selection for eCO$_2$ responsiveness may ensure sustained productivity in a higher CO$_2$ world (Ainsworth et al. 2008; Leahey et al. 2012; Ziska et al. 2012; Tausz et al. 2013).

Although studies are limited, observed genotypic variation in forest tree responsiveness to eCO$_2$ is substantial. In the Populus genus, for example, genotypes have shown relative changes in total dry mass or stemwood volume production ranging from –16 to 58% (Ceulemans et al. 1996; Dickson et al. 1998; Isebrands et al. 2001). A study by Mohan et al. (2004) also demonstrated that the effects of family, population and provenance in Acer rubrum all interacted with growth under eCO$_2$, highlighting the complexity and importance of intraspecific variation in responsiveness to eCO$_2$. Nonetheless, there are also cases of limited intraspecific variation in forest species responsiveness to eCO$_2$ (Cantin et al. 1996).

Even when eCO$_2$ increases tree growth, the implications should be carefully considered. Higher growth under eCO$_2$ is usually associated with increased canopy leaf area,
particularly in younger trees. Larger tree canopies require more water, which can make forests more susceptible to drought-induced dieback (Warren et al. 2011). Moreover, several studies have shown that eCO2 effects on plant and ecosystem productivity are largely dependent upon interactions with temperature, and nutrient or water availability, and are species dependent (Tschaplinski et al. 1995; Norby et al. 2000; McCarthy et al. 2010). These studies highlight the complexity of plant responses to multiple climate change factors and suggest that intraspecific variation in responsiveness to climate change will ultimately depend upon genotype sensitivity to the interactive effects of drought, warming and eCO2.

This overview of the extent and apparent physiological basis of intraspecific variability in agricultural and forest species responses to drought, warming, extreme heat and eCO2 highlights some of what we know about the mechanisms of G × E. Although these studies demonstrate G × E in physiological traits, which influence genotype performance, they often lack tests of ‘adaptive’ plasticity, for example, regressing genotype trait plasticity against genotype mean yield or productivity across environments (see Nicotra et al. 2010). This is partially due to the fact that most studies include only a handful of genotypes. This represents a critical gap in our ability to assess the importance of intraspecific variation in plasticity within agricultural and forest species. In the following section, we examine some of the genetic and genomic factors influencing G × E.

Genetics and genomics of intraspecific variation in responsiveness to drought, warming and elevated CO2

Genetic architecture

The genetic architecture of traits and trait responses is recognized as a key regulator of intraspecific variation in plant responses to environmental change (see Des Marais et al. 2013a). Patterns of G × E are sometimes attributed to architectural aspects such as pleiotropy, differential sensitivity and non-additive effects. Pleiotropy occurs when a single gene affects two apparently unrelated phenotypic traits. Differential sensitivity occurs when a gene’s effect varies depending upon the environment, and non-additive effects can occur when allelic effects at many loci confer different degrees of plasticity.

Pleiotropic effects are often inferred where strong genetic correlations exist between traits. Evidence for a pleiotropic linkage between flowering time and WUE has been shown in Arabidopsis; for example, early flowering genotypes showed low WUE and late flowering genotypes showed high WUE (McKay et al. 2003). Here, selection for one trait would constrain the direction of change in another trait and the pattern of G × E. Antagonistic pleiotropy can also occur when a particular allele may increase a trait value in one environment, but reduce it in another. Lovell et al. (2013) demonstrated a case of ‘adaptive pleiotropy’ where expression of a particular gene (FRIGIDA) can result in different strategies for coping with drought; for example, escape (early flowering, low WUE) or avoidance (late flowering, high WUE). While the causes of genetic correlations among traits remain poorly understood, it is apparent that intraspecific variation in agricultural and forest species responses to climate change may be strongly determined by the direction and magnitude of genetic correlations among traits.

Quantitative trait loci (QTL) studies, which examine sections of the genome associated with a particular trait or response, and examination of cross-environment genetic correlations have been useful tools for inferring the underlying genetic architecture of G × E. In Arabidopsis, for example, WUE and flowering time were affected by five different QTL each (Juenger et al. 2005), although regions of the genome contained QTL for both traits suggesting a potential pleiotropic effect. In a simulation of QTL effects on maize growth, water use and yield, a QTL that accelerated leaf elongation under well-watered conditions also increased leaf area and yield, but reduced yield under stress (Chenu et al. 2009). Pleiotropic effects on silk elongation and grain set magnified the QTL effect on yield. Studies in trees, particularly Populus, have also provided important insight into the genetic architecture of responsiveness to eCO2. For example, Ferris et al. (2002) found that QTL for adaxial stomatal density under ambient and eCO2 were located on the same linkage group, suggesting similar patterns of genetic control across treatments. Likewise, Rae et al. (2006) found many QTL for leaf traits, which mapped to common positions in ambient and eCO2 in Populus, and Rae et al. (2007) identified QTL linked to aboveground and belowground growth responses to eCO2. The identification of these QTL may allow breeders to target regions of the Populus genome, which may confer differences in genotype productivity under eCO2.

Although many QTL studies have provided evidence for pleiotropic effects, more than 50% have identified QTL that lack a significant effect in another environment (Des Marais et al. 2013a), suggesting that differentially sensitive QTL are a common architectural feature of G × E. Interestingly, QTL associated with differential sensitivity tend to confer lower plasticity than QTL associated with antagonistic pleiotropy (Des Marais et al. 2013a).

The strength and direction (i.e. positive, negative) of cross-environment genetic correlations can also provide insight into genetic architecture of traits and how traits may respond to abiotic stress (Juenger 2013). In Brassica rapa, for instance, genotypes with low WUE under well-watered conditions had high WUE under drought (Edwards et al. 2012), indicating possible antagonistic gene action. These findings call attention to the role of genetic architecture in influencing patterns of G × E and emphasize the importance of integrating knowledge of trait genetic architecture into physiological studies of agricultural and forest species responses to climate change.

Gene expression

Gene expression studies have provided critical insight into the function of specific genes and regulatory networks during drought and heat stress (Shinozaki & Yamaguchi-Shinozaki
M. J. Aspinwall et al.

1997; Saibo et al. 2009; Cutler et al. 2010; Fujita et al. 2011). Additionally, there has been increasing recognition of the importance of carbohydrate-mediated gene expression during stress (Stitt et al. 2007), with carbon sink size and activity regulating photosynthetic activity via gene expression and sugar-mediated regulation of photosynthetic enzymes (Koch 1996; McCormick et al. 2008). Genes associated with metabolic functions are often up-regulated under C depletion, and the sensitivity of carbohydrate-responsive gene expression might aid acclimation responses.

Beyond basic knowledge of gene expression responses, a number of studies have demonstrated genotype-specific patterns of gene expression under different soil moisture and temperature conditions, providing insight into the molecular mechanisms of intraspecific variation in growth and performance (Wilkins et al. 2009; Des Marais et al. 2014). For example, in a comparison of two Arabidopsis ecotypes under progressive soil drying, minimal physiological changes were observed, but hundreds of transcripts showed differential expression between ecotypes (Juenger et al. 2010). Such results could indicate that physiological homeostasis may be underlain by high molecular plasticity. Similarly, Populus clones have shown contrasting patterns of gene expression responses with a drought-sensitive clone showing larger transcriptional responses in roots indicative of low C availability linked to low C fixation at the leaf level (Cohen et al. 2010). A comparison of the molecular responses of two Eucalyptus genotypes under drought also found marked differences in gene expression, which corresponded with clone differences in productivity (Villar et al. 2011). A few studies have also examined transcript profiles of genotypes growing under ambient and eCO2. One particularly interesting study by Cseke et al. (2009) found that a CO2-responsive Populus clone showed transcript patterns associated with increased C partitioning to stress defence and growth, while a CO2-unresponsive clone partitioned more C towards chemical defence and cell wall thickening.

Gene expression responses alone cannot explain patterns of $G \times E$ in growth and physiology, but examining gene expression patterns and physiological responses may provide a powerful way forward for understanding intraspecific variation in responsiveness to environmental change (van Kleunen & Fischer 2005; Des Marais et al. 2013b). It is particularly evident that intraspecific variation in molecular responses may have downstream impacts on carbon source – sink dynamics, which impact genotype function and productivity under stressful conditions and eCO2. Ultimately, understanding differential patterns of gene expression between individuals, and how these patterns are associated with the physiological traits, which influence yield and productivity will be crucial to harnessing the potential utility of $G \times E$.

Lastly, epigenetic effects, which change gene activity during development without altering DNA sequences may play important roles in regulating phenotypic responses to environmental factors and patterns of $G \times E$. Epigenetic effects arise from signals from receptors and signalling cascades and have been linked to DNA methylation (Bender 2004). Epigenetic effects are reversible, yet heritable in encoding antecedent environmental conditions that have carry-over effects on phenotypic responses of progeny. They can therefore constrain a genotype’s plastic response to future stress events or increased resource availability (Chinnusamy & Zhu 2009). For example, genotypic differences in Populus clone transcript abundance under drought have reflected similar patterns of DNA methylation, where individual ramets of clones with the most divergent transcriptomes and clone history showed the largest differences in DNA methylation (Raj et al. 2011). Clearly, epigenetic studies demonstrate huge potential in assessing the influence of environment on intraspecific variation in plastic responses to environmental change.

**FUTURE DIRECTIONS**

Our assessment of previous studies illustrates that there is substantial intraspecific variation in phenotypic plasticity in response to drought, warming, heat stress and eCO2 within many agricultural and forest species. Our understanding of the physiological mechanisms and genetic factors, which influence intraspecific variation in responsiveness to these climate change factors, has also advanced tremendously. However, in our view, the following areas require further attention.

Firstly, more explicit examinations of genotype (clone, cultivar, family) plasticity–productivity relationships should be conducted in agriculture and forestry. Many of the studies we examined report differential growth and physiological responses to particular climate change factors, but to our knowledge, none have reported the degree to which genotype trait plasticity (physiology, morphology, phenology) is associated with genotype performance across environments. Where genotypic variation in agricultural and forest species responses to drought, temperature or eCO2 are substantial, and genotype plasticity has a beneficial effect on productivity, improving or sustaining productivity under climate change might require targeting not only individual traits under genetic control, but also genotypic variation in plasticity to environmental change (Sadras & Lawson 2011).

Secondly, despite important logistical and methodological challenges, more effort should go towards systematically assessing intraspecific variation in agricultural and forestry species responses to multiple climate change factors (e.g. eCO2, warming) under field conditions (Leakey et al. 2012). Numerous studies have investigated intraspecific variation in growth and function in response to one climate change factor under controlled environmental conditions (e.g. growth chambers, glasshouses and open top chambers), but studies conducted under field conditions with several genotypes and multiple climate change factors are rare (Moya et al. 1998). The lack of studies under field conditions creates uncertainty regarding the potential for genetic variation to buffer the combined effects of climate change. Independent of whether the mechanisms of intraspecific variation in growth and function in response to interacting climate change factors are known, screening large numbers of genotypes in the field and assessing the magnitude of $G \times E$ will be a key step forward.
in identifying genotypes, which can persist under stressful conditions and maximize productivity under optimal conditions. Identifying such genotypes may be especially beneficial for forestry, where genotype productivity–stress tolerance trade-offs are common.

Likewise, data collected from established agricultural and forestry field trials replicated across environmental gradients should be more fully utilized (e.g. Rehfeldt et al. 1999). By understanding variation in key local environmental conditions and genotype responses to those conditions, we may better understand thresholds for genotypes performance under climate change. In fact, re-examination of long-term data collected from established forestry provenance trials could partially address the lack of $G \times E$ studies under field conditions. Analysis of long-term agricultural yield data might also provide insight into intraspecific variation in agricultural species yield responses to recent climate change. Nonetheless, newer, more extensive field trials should be established along key environmental gradients where climate change is likely to exert the strongest selective pressures. Provenance and field trials are a classical approach to assessing the degree of $G \times E$, and they deserve continued focus.

Thirdly, the growth and stress tolerance of ancestral or less domesticated genetic material in response to the main and interactive effects of drought, warming and eCO2 should be examined. For instance, there has been some speculation that plant breeding has inadvertently selected for genotypes which are more responsive to rising CO2, yet older genetic material has shown greater positive responses to eCO2 than newer genetic material (e.g. Ziska et al. 2004). In support of this finding, undomesticated natural species generally demonstrate greater plasticity to environmental change than agricultural species (1.8-fold difference; Des Marais et al. 2013a), most likely reflecting the lack of a legacy of targeted artificial selection. Thus, surveying intraspecific variation in phenotypic plasticity to environmental change in ancestral or less domesticated genetic material conserved in gene banks or as landraces could prove useful for adapting agriculture and forestry to climate change (Bellon et al. 2011). Equally, concerted efforts to preserve agricultural and forest species genetic diversity should be made, as genotypes previously selected against may show desirable responses to novel climatic conditions (Mercer & Perales 2010).

Fourthly, there remains an urgent need to develop high-throughput tools for screening phenotypic traits in many individual genotypes growing across a range of conditions (Furbank & Tester 2011; White et al. 2012). This is not a new recommendation (see Ainsworth et al. 2008), but one that requires continued focus if we are to utilize variation in genetically controlled traits and genetic variation in phenotypic plasticity.

Lastly, plants are highly integrated organisms with traits often co-varying across hierarchical levels. Phenotypic changes occurring at any ‘level’ must coherently respond to changes occurring at another level, or risk reductions in plant growth, reproduction or survival under stress. For this reason, multivariate analyses which account for genetic covariation in trait values across scales may provide greater insight into the mechanisms and constraints on intraspecific variation in phenotypic plasticity. It may be particularly insightful to integrate responses occurring at the transcriptome, metabolome and physiological level (Walsh & Blows 2009). Carefully examining linear and non-linear relationships between gene expression and physiological traits may also provide insight into stress thresholds for individual genotypes (Meyer et al. 2014).

**CONCLUSION**

We have conceptualized the significance of intraspecific variation in phenotypic plasticity (i.e. $G \times E$) within agricultural and forest species within the context of plant breeding and climate change, and have identified some of the important physiological and genetic factors influencing $G \times E$. Although the ecological literature has recognized phenotypic plasticity as a means of buffering the effects of climate change, studies in agriculture and forestry have generally regarded $G \times E$ as a limitation to selecting stable genotypes, thereby overlooking the potential utility of intraspecific variation in phenotypic plasticity. We stress the need for a more integrated understanding of intraspecific variation in agricultural and forest species responses to climate change. Most importantly, we argue for more explicit testing of genotype plasticity–productivity relationships, and for assessing genotypes based on not only their mean trait values, but also their plasticity. This may be crucial for identifying genotypes of agricultural of forest species capable of increasing or maintaining productivity under more variable climatic conditions.

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