Genetic and Physiological Controls of Growth under Water Deficit[1]

François Tardieu*, Boris Parent, Cecilio F. Caldeira, and Claude Welcker

INRA, Unité Mixte de Recherche 759 Laboratoire d'Ecophysiologie des Plantes sous Stress Environnementaux, F–34060 Montpellier, France

The sensitivity of expansive growth to water deficit has a large genetic variability, which is higher than that of photosynthesis. It is observed in several species, with some genotypes stopping growth in a relatively wet soil, whereas others continue growing until the lower limit of soil-available water. The responses of growth to soil water deficit and evaporative demand share an appreciable part of their genetic control through the colocation of quantitative trait loci as do the responses of the growth of different organs to water deficit. This result may be caused by common mechanisms of action discussed in this paper (particularly, plant hydraulic properties). We propose that expansive growth, putatively linked to hydraulic processes, determines the sink strength under water deficit, whereas photosynthesis determines source strength. These findings have large consequences for plant modeling under water deficit and for the design of breeding programs.

Evolution has selected plants that reduce leaf area and seed number under water deficit, allowing production of at least a few viable seeds, in such a way that their alleles are not lost during dry years. Reducing transpiration rate by decreasing leaf area saves soil water during vegetative stages in favor of reproductive stages and keeps plants at a better water status (Boyer, 1985). It is safer than stomatal closure, which is usually accompanied by an increase in leaf temperature (Guilioni et al., 2008). However, this conservative strategy decreases carbon acquisition by plants, with two drawbacks. First, it reduces seed number and yield, crucial traits for agriculture but also for natural environments because this reduces the number of potential offspring. Second, conservative altruistic plants may be outgrown by fast-growing plants in natural environments and excluded from their niche (Gordon and Rice, 2000).

As a consequence, opposite strategies can lead to drought tolerance, depending on the drought scenario (Tardieu, 2012). The conservative strategy fits most severe and long drought scenarios. A spender strategy involving maintenance of vegetative and reproductive growth allows higher yields under milder drought scenarios at a risk of reproductive failure under severe stresses. Because most species have evolved in a wide range of climatic conditions (Rebourg et al., 2003; Sharbel et al., 2000; Fatichi et al., 2014), the tradeoffs associated with the control of growth result in a wide genetic variability of responses of growth to water deficit. Indeed, a large genetic variability of growth maintenance has been observed in several species: by Tisné et al. (2010) in Arabidopsis (*Arabidopsis thaliana*), Welcker et al. (2011) in maize (*Zea mays*), Parent et al. (2010a) in rice (*Oryza sativa*), and Pereyra-Irujo et al. (2008) in sunflower (*Helianthus annuus*).

We review here the genetic diversity and the potential mechanisms associated with the control of growth under water deficit and their consequences for the modeling of plant growth and for breeding strategies.

INCREASES IN PLANT BIOMASS AND VOLUME DISPLAY DIFFERENT TIME COURSES, RESPOND DIFFERENTLY TO WATER DEFICIT, AND HAVE DIFFERENT GENETIC CONTROLS

Growth in biomass depends on the carbon balance between photosynthesis and respiration. Expansive growth, defined as an increase in organ volume through water entry into growing cells, depends on the interplay of cell wall extensibility, gradients of water potential, and hydraulic conductance on the water pathway to cells (Lockhart, 1965).

Carbon gain and expansive growth have essentially opposite phases. Leaf photosynthesis and whole-plant carbon balance follow changes in light intensity and plant transpiration, with peak values close to midday (Fig. 1; see also Escalona et al., 2003). Conversely, leaf expansion rate corrected for the effect of temperature (Parent et al., 2010b) follows the reciprocal of transpiration rate in maize (Fig. 1), rice (Parent et al., 2010a), and Arabidopsis during the autotrophic phase of leaves (Pantin et al., 2011). The daytime depression of leaf elongation rate is the highest during days with high evaporative demand (high light intensity and

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* Address correspondence to francois.tardieu@supagro.inra.fr.

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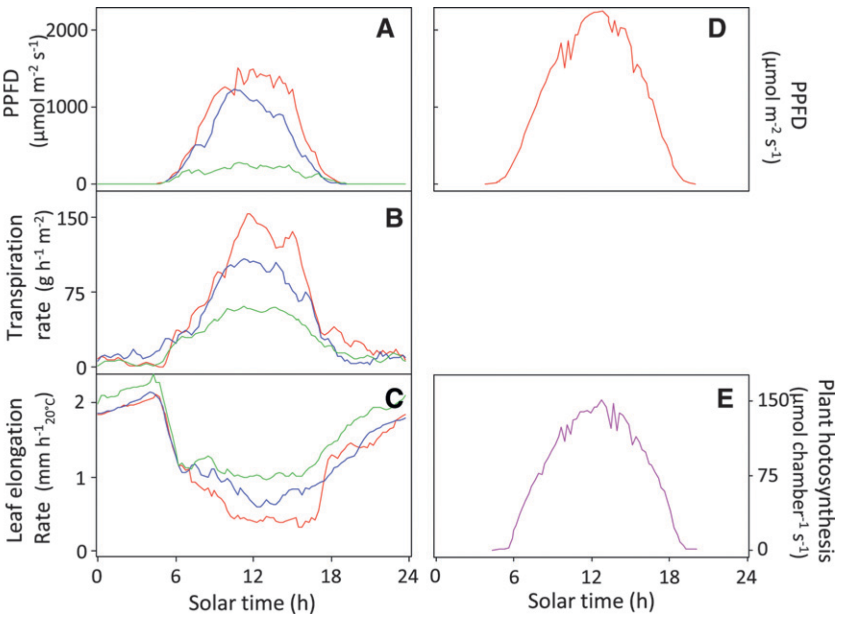

Figure 1. Leaf elongation rate and biomass acquisition have opposite diurnal trends in maize. A to C, Light intensity (photosynthetic photon flux density [PPFD]), transpiration rate, and leaf elongation rate in three typical climatic scenarios. Red, Sunny days with high transpiration; blue, intermediate days; green, cloudy days with low transpiration (Caldeira et al., 2014). D and E, Light intensity and whole-plant photosynthesis in a canopy gas exchange platform (redrawn from Fig. 4 in Kim et al., 2007).

vapor pressure deficit; Fig. 1) and increased by mild water deficit (Parent et al., 2010a, Pantin et al., 2011, Caldeira et al., 2014). However, the negative effect of light intensity on expansive growth only applies when the leaf is mature enough to sustain its own carbon demand through photosynthesis. In Arabidopsis, the expansion rate of very young leaves peaks during the day and is minimal during the night until the leaf is autotrophic (Pantin et al., 2012). This transition between a source-limited and sink-limited period (with positive and negative effects of light, respectively) is also observed in other dicotyledon species (Granier and Tardieu, 1999; Christophe et al., 2008; Walter et al., 2009). The source-limited phase is not observed in monocotyledons, in which leaves are both source and sink during most of their lifespan (Muller et al., 2001, 2011).

Detailed analyses suggest a limited effect of mild water deficit on carbon metabolism. This effect has been best documented in Arabidopsis, in which water deficit increases the concentrations of most sugars in rosettes and does not affect the activities of 30 enzymes belonging to various pathways of carbon metabolism (Hummel et al., 2010). Consistently, transcriptome analyses in Arabidopsis plants subjected to long and moderate water deficit show a surprisingly low change in transcript abundance of genes involved in metabolism (Baerenfaller et al., 2012). The same applies to young ovules of maize, in which sugar concentrations and enzyme activities are essentially unaffected by water deficit (V. Oury, Y. Gibon, F. Tardieu, and O. Turc, unpublished data). In the same way, the young capitulum of sunflower reduces its area and ovule number without noticeable change in carbon status (Dosio et al., 2011). Hence, we propose that plants coordinate the decreases in expansive growth rate and photosynthate flux to growing organs in such a way that the carbon metabolism is not disrupted. This requires an early determinism of seed abortion to avoid carbon stress in remaining ovules. Consistently, it is only under very severe water stresses that sugar deprivation directly causes seed abortion in maize and is relieved by sugar feeding (McLaughlin and Boyer, 2004).

New evidences support different genetic controls for biomass accumulation and expansive growth (Fatichi et al., 2014). In a panel of 350 maize accessions under water deficit, strong negative correlations were observed between ear or silk weight and Suc content at flowering time (Setter et al., 2011). This finding suggests a dilution process, in which the photosynthate amount would be similar in the considered accessions but diluted by a larger water volume in accessions with the highest growth rates. The quantitative trait loci (QTLs) for photosynthesis under water deficit detected by Pelleschi et al. (2006) in a population of recombinant inbred lines (RILs) of maize do not colocalize with QTLs of growth maintenance detected in the same population by Welcker et al. (2011). The same applies to QTLs of photosynthesis and growth maintenance detected in a tropical maize population of RILs by Fracheboud et al. (2002) and Welcker et al. (2011), respectively.

Hence, expansive growth and biomass gain are almost entirely uncoupled over days. The coupling between them occurs over longer timescales through feedbacks but is far from tight in case of water deficit (Muller et al., 2011; Tardieu et al., 2011). Our view is summarized in Figure 2, in which expansive growth (vegetative and reproductive) and photosynthesis are considered to have largely independent environmental and genetic controls.

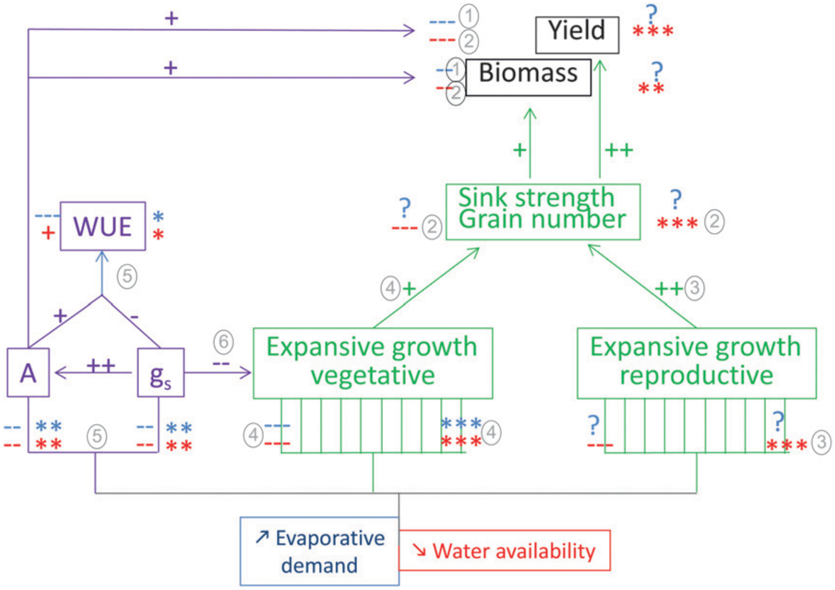

Figure 2. Effect of decreased water availability and increased evaporative demand on expansive growth of vegetative and reproductive organs, gas exchanges, and integrated variables. [asterisk], Genetic variability of the response of the considered trait to decreased water deficit (red) or increased evaporative demand (blue); [question mark], unknown effect or genetic variability; green or purple signs, size and direction of the effect of one trait on another trait; red or blue signs, size and direction of the effect of soil water deficit or evaporative demand on the considered trait. Variables with a common color are considered to have a genetic control that is largely common. Numbers refer to generalist references on the topic: 1, Lobell et al., 2011; 2, Lobell et al., 2013; 3, Boyer, 1996; 4, Tardieu et al., 2011; 5, Blum, 2009 and Condon et al., 2004; and 6, Caldeira et al., 2014.

A LARGE GENETIC VARIABILITY OF SENSITIVITIES OF EXPANSIVE GROWTH TO WATER DEFICIT OR HIGH EVAPORATIVE DEMAND

In three mapping populations of maize, the most sensitive RILs stopped leaf elongation in a relatively wet soil (soil water potential of −0.5 MPa), whereas the less sensitive RILs grew in a soil as dry as −1.3 MPa (Welcker et al., 2011). A large range has also been observed between rice lines with different origins (Parent et al., 2010a). Genetic variations of sensitivity have been observed in dicotyledons, although the genetic analysis is made more complex in this case, because leaf expansion rate largely varies during the day (Poiré et al., 2010) and between days (Granier and Tardieu, 1998; Granier et al., 2002; Walter et al., 2009). The fraction of soil water reserve that causes a decrease in expansion rate of sunflower leaves ranges from 0.15 (dry soil) for the least sensitive hybrids to 1.0 (close to retention capacity) for the most sensitive ones (Casadebaig et al., 2008). The rosette area of Arabidopsis plants subjected to a moderate water deficit is reduced by 20–60%, with high heritability, depending on accessions or RILs (Aguirrezabal et al., 2006; Tisné et al., 2010; Vile et al., 2012). Reductions in final leaf area are partly caused by a genetic variability in the sensitivity to water deficit of leaf expansion rate in Arabidopsis (Aguirrezabal et al., 2006) and sunflower (Pereyra-Irujo et al., 2008). However, this variability does not always translate into changes in final leaf area because of large and genetic-dependent differences in the duration of expansion in monocotyledons.

The genetic control of the sensitivities of leaf growth is largely common to the effects of evaporative demand and soil water deficit. In a meta-analysis of QTLs in three mapping populations and four introgression libraries, 75% of QTLs were common when leaf elongation rate was measured in plants subjected to either a range of evaporative demands in well-watered conditions or a range of soil water potentials under low evaporative demand (night periods; Welcker et al., 2011). A genetic correlation was also observed in rice between sensitivities to soil water deficit and evaporative demand (Parent et al., 2010a).

The genetic control of expansive growth is also partly shared between several organs of a plant. Tight genetic correlations have been observed between rosette area and total root length in an Arabidopsis population of RILs (Bouteillé et al., 2012). Among eight genomic regions harboring QTLs of rosette area, seven of them also involve QTLs of primary root length or total root length. In the same way, among nine consensus QTLs of leaf elongation rate of maize, five of them colocate with QTLs of the growths of other leaves, shoots, roots, or young reproductive organs with consistent allelic effects (Dignat et al., 2013). Colocation of QTLs also applies to the sensitivity of growth of several organs to water deficit, with common QTLs for the sensitivities of leaf and silk growth to water deficit (Welcker et al., 2007).

For Figure 2 overall, the above paragraphs suggest (1) a large genetic variability for the sensitivity of the growth of several organs to water deficit, (2) a partly common genetic control of growth and sensitivity between organs, and (3) a largely common genetic control for the responses of leaf growth to soil water deficit and evaporative demand.

A LARGE RANGE OF POTENTIAL MECHANISMS ARE INVOLVED IN THE REDUCTION IN LEAF GROWTH WITH SOIL WATER DEFICIT OR HIGH EVAPORATIVE DEMAND

Cell turgor pressure causes an irreversible stretch of the cell wall when it exceeds a threshold (Bunce, 1977;

Bouchabké et al., 2006; Ehlert et al., 2009; Zhang et al., 2011). Cell wall relaxation would cause a decrease in turgor and growth without a concomitant water transfer from the xylem to growing cells (Matyssek et al., 1991). Hydraulic processes are therefore essential. Chemical compounds that reversibly affect hydraulic conductance through aquaporin activity have large effects on both turgor and leaf elongation rate, with similar effects of acid load, anoxia, and H_2O_2 treatments (Ehlert et al., 2009). The plasma membrane intrinsic protein aquaporins probably play a crucial role in view of their distributions in growing leaves (Hachez et al., 2008). Indeed, genetic manipulation of hydraulic conductance results in changes in leaf expansion rate in Arabidopsis (Martre et al., 2002) and maize (Parent et al., 2009), especially during soil rehydration.

Cell wall plasticity is controlled by several wall enzymes (Cosgrove, 2005; Park and Cosgrove, 2012) associated with changes in expansive growth (Cho and Cosgrove, 2000; Wu and Cosgrove, 2000; Muller et al., 2007). It decreases with water deficit (Nonami and Boyer, 1990a, 1990b), consistent with the abundance of expansin transcripts and proteins in leaves (Muller et al., 2007; Harb et al., 2010) or roots (Wu and Cosgrove, 2000). Cell wall peroxidase activity and caffeate *O*-methyltransferase abundances increase in the elongating region of monocotyledonous leaves under water deficit, thereby stiffening cell walls (Bacon et al., 1997; Vincent et al., 2005; Zhu et al., 2007). These changes in cell wall properties are, in part, mediated by abscisic acid (ABA), possibly combined with ethylene (Sobeih et al., 2004), apoplastic pH (Thompson et al., 1997; Wilkinson and Davies, 2008), or reactive oxygen species (Sharp, 2002; Liszkay et al., 2003).

We have argued elsewhere (Granier and Tardieu, 2009; Tardieu et al., 2011) that the changes in cell division rate with water deficit may follow those changes in expansion rate, without a crucial contribution.

A CENTRAL ROLE FOR HYDRAULIC PROCESSES IN THE CONTROL OF EXPANSIVE GROWTH?

The commonality of QTLs presented above challenges the view that sensitivities to soil water deficit and evaporative demand depend on different mechanisms. Sensitivity to evaporative demand is widely believed to depend on hydraulic signals and effectors, whereas sensitivity to soil water deficit is often considered to depend on cell wall properties, themselves under the control of chemical signals. We are not aware of published genetic analyses of plant hydraulic properties or cell wall mechanical properties, which would allow one to compare QTLs of these mechanisms with QTLs of the sensitivity of expansion rate to water deficit. No QTL of sensitivity of expansive growth to water deficit has been cloned yet (Collins et al., 2008), and therefore, the ways of action of polymorphisms are not precisely known. The hydraulic mechanism that has been best analyzed genetically is osmotic adjustment (Blum et al., 1999; Zhang et al., 1999). However, the common practice is to measure it in mature tissues, which may not reflect the genetic variability of osmotic adjustment in growing tissues.

Another method for identifying causal chains is a careful characterization of time constants of changes in leaf expansion rate compared with time constants of potential mechanisms. Leaf elongation rate of monocotyledons changes in less than 30 min, rapidly stabilizes, and returns to its original value when light is switched on in a growth chamber (Munns et al., 2000) or, in the early morning in natural conditions (Caldeira et al., 2014). This is also the case when evaporative demand increases via a change in air vapor pressure deficit with constant light (Sadok et al., 2007) when salt or manitol is added to a nutrient solution (Munns et al., 2000), when droughted plants are rehydrated (Hsiao et al., 1970), or when plants are subjected to a sudden anoxia (Ehlert et al., 2009). Such short time constants are compatible with only a few mechanisms, particularly hydraulic processes that occur over seconds to minutes (Ye and Steudle, 2006; Tang and Boyer, 2008; Parent et al., 2009), osmotic adjustment, which can be equally rapid (Frensch and Hsiao, 1994), or posttranslational protein modifications, such as phosphorylation/dephosphorylations (Novak et al., 2010; Bonhomme et al., 2012). Cell wall stiffening in growing leaves is observed over minutes in response to a rapid decrease in root water potential with an osmoticum (Chazen and Neumann, 1994), potentially involving posttranslational protein modifications probably with a hydraulic signaling between roots and leaves. Short time constants are also compatible with the transfer of a plant hormone, such as ABA, over short distances from the apoplast to the symplast (Hartung et al., 2002) but probably not with de novo synthesis of hormones, changes in cell wall composition, or changes in the cell cycle duration (Granier and Tardieu, 1998; Granier et al., 2000). The time course of osmotic adjustment in growing cells is controversial. Several experiments show that leaf growth is inhibited by water deficit or salt stress despite a maintained turgor in growing tissues as a result of osmotic adjustment (Tang and Boyer, 2002). However, the opposite behavior has also been observed (Shackel et al., 1987; Hsiao and Xu, 2000; Bouchabké et al., 2006).

Recent evidence leads us to argue in favor of the dominance of hydraulic mechanisms for changes in expansion rate. In maize, the morning decline of leaf elongation rate has a time constant that (1) varies with allelic values at QTLs of sensitivity to evaporative demand (Sadok et al., 2007) and (2) differs in transgenic lines that present contrasting root hydraulic conductivities and stomatal controls after an underproduction or overproduction of ABA (Caldeira et al., 2014).

The overall coordination between expansive growth and biomass accumulation over long timescales can be interpreted if one considers that expansive growth determines the future sink strength as presented in Figure 2. Organs would expand through hydraulic- or cell wall-related mechanisms and then, rapidly need carbon and energy for structural growth (Dale, 1988; Pantin et al., 2011). Expansion would, therefore, determine the sink strength for assimilates, thereby increasing the final organ weight (Minchin et al., 1993; Marcelis, 1996; Fatichi et al., 2014).

CONSEQUENCES FOR PHENOTYPING AND BREEDING IN DROUGHT-PRONE ENVIRONMENTS

The coordination between controls of the growth of several organs could explain unexpected genetic correlations between traits observed in a phenotyping platform and the field (Tuberosa et al., 2002; Chapuis et al., 2012). In the former study, the sensitivity of maize grain number to water deficit was determined individually in maize hybrids in a network of field experiments as the slope of the relationship between grain number and the mean soil water potential around flowering time. Surprisingly, a high genetic correlation was observed between the sensitivity to water deficit of grain number and the sensitivity of leaf elongation rate in a phenotyping platform. This correlation may be partly caused by a common genetic control for the sensitivities of leaf and silk growths to water deficit (Welcker et al., 2007). Silk growth largely determines the anthesis-silking interval (Fuad-Hassan et al., 2008), itself clearly linked to grain number (Bolaños and Edmeades, 1996). We cannot exclude an effect of pollen or ovule fertility, which is largely affected by water deficit, high temperature, and evaporative demand in maize and wheat (Saini and Aspinall, 1982; Saini et al., 1984; Fonseca and Wesgate, 2005), although the genetic link with the sensitivity of leaf elongation rate to water deficit would be less straightforward in this case than the link with silk growth. In any case, this result has large implications for phenotyping at early stages in a platform.

Breeding strategies for drought tolerance and the architecture of crop models can be influenced by the coordination proposed here. Both of them consider traits individually for identifying most promising ideotypes (Reynolds et al., 2012) or simulating growth in a range of genotypes and environmental conditions (Hammer et al., 2010). If growth and sensitivity of several organs are coordinated through a partly common genetic control, this considerably reduces the degrees of freedom for an ideotype and causes correlations between model parameters involved in the vegetative and reproductive phases. This coordination has been indirectly observed in a modeling exercise of the effect of QTLs on leaf growth sensitivity (Chenu et al., 2008; Chenu et al., 2009). Indeed, the dimension of the parameter space was considerably smaller in observed data than in a random distribution because of a genetic correlation between parameters.

CROP MODELS FOR IDENTIFYING WHICH ALLELES FOR GROWTH SENSITIVITY ARE SUITED TO WHICH ENVIRONMENTS?

Crop models allow one to test the value of a given trait in a large range of scenarios representing the diversity of climates in a continent (Chenu et al., 2013) for tens of years of current and future climates (Harrison et al., 2014). This potentially allows one to test the value of alleles over climatic series (Chapman et al., 2002; Hammer et al., 2006; Messina et al., 2011). This exercise has been done for simulating the effect on yield of QTLs affecting the sensitivity of maize leaf growth to water deficit and evaporative demand (Chenu et al., 2009), with the output that a given QTL of leaf sensitivity has different impacts on yield in mild drought scenarios and terminal drought scenarios. This potentially allows one to identify the agronomic value of a combination of QTLs over a long series of climatic data in a mesh of sites covering the considered geographic area (Tardieu and Tuberosa, 2010; Harrison et al., 2014). This approach is still in its infancy but has a large potential for model-assisted breeding.

CONCLUSION

The view presented in this paper (Fig. 2) assumes largely independent controls of photosynthesis and expansive growth and partly common controls for the expansive growth of different organs under water deficit (this review) or high temperature (Parent and Tardieu, 2012). The genetic variability of these controls is probably larger than that of photosynthesis and largely common for the responses to soil water deficit and evaporative demand. Expansive growth of several organs would determine the sink strength and largely, seed number. Sink strength and photosynthesis would interact at this stage by determining plant biomass and yield, but also via a feedback of sink strength on photosynthesis. Noteworthy, (1) in Figure 2, yield has a greater genetic variability than biomass under water deficit, consistent with the large effect of seed number on yield. (2) Both water deficit and evaporative demand cause yield loss (Boyer, 1996; Lobell et al., 2013) in addition to other environmental cues, such as high temperature. Mechanisms of action of evaporative demand on grain number and the genetic variability of the resulting sensitivity are largely unknown to our knowledge. They are difficult to analyze because of the confusion of effects between light intensity per se (positive effect on biomass accumulation and yield) and evaporative demand per se (presumably negative effect but highly correlated with light intensity). (3) Stomatal conductance has a dual effect on growth: positive on photosynthesis rate and negative on leaf expansion rate because of decreased leaf water potential (Caldeira et al., 2014).

The view in Figure 2 is based on the literature review presented in this paper, but many points remain to be clarified (in particular, the extent of the genetic variability of the response of expansive growth traits in several species and the mechanisms of action that cause this variability). Another question is how to reconcile the short-term mechanisms of control that are presented here with potential longer term controls. The latter may be emergent properties derived from short-term controls (our favorite hypothesis) or may involve independent long-term mechanisms. We believe that these views and questions, and their applications in plant modeling may have a large impact on strategies of breeding for drought tolerance.

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