Abiotic Stress

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Abstract Abiotic stresses such as drought, are the main factors for forest declines globally. There is therefore an increasing interest in understanding the mechanisms underlying tree adaptations and survival to water deprivation. Angiosperm tree species demonstrate an amazing phenotypic plasticity. They sense and respond to adverse changing environmental conditions via a series of physiological, cellular, and molecular processes which are under a tight genetic control. In this book chapter, first we present some key morphological and anatomical features adopted by angiosperm tree species to survive drought. These traits are described at the roots, stem and shoots levels. Then, we provide insights into the dynamics of gene expression and components of regulatory networks associated with drought response, including comparisons among angiosperm tree species. Such comparative genomic approaches have the potential to provide a better understanding of the evolution and diversification process of drought response in angiosperm trees but also to the development of cultivars resilient to drought and other abiotic stresses.

Keywords Angiosperm • Tree • Abiotic stress • Drought Tolerance • Adaptation • Anatomy • Structure-function • Hydraulic conductance Water use efficiency • *Comparative genomics* • QTL • Candidate gene • Gene expression • Stress sensing • Stress signaling

Tree species, because of their long lifespans and their sessile nature, figure among the best biological examples of adaptation and acclimation to changing environmental conditions. Trees have to cope with seasonal changes, and can also be exposed to extreme climatic events involving extended periods of drought, flooding,

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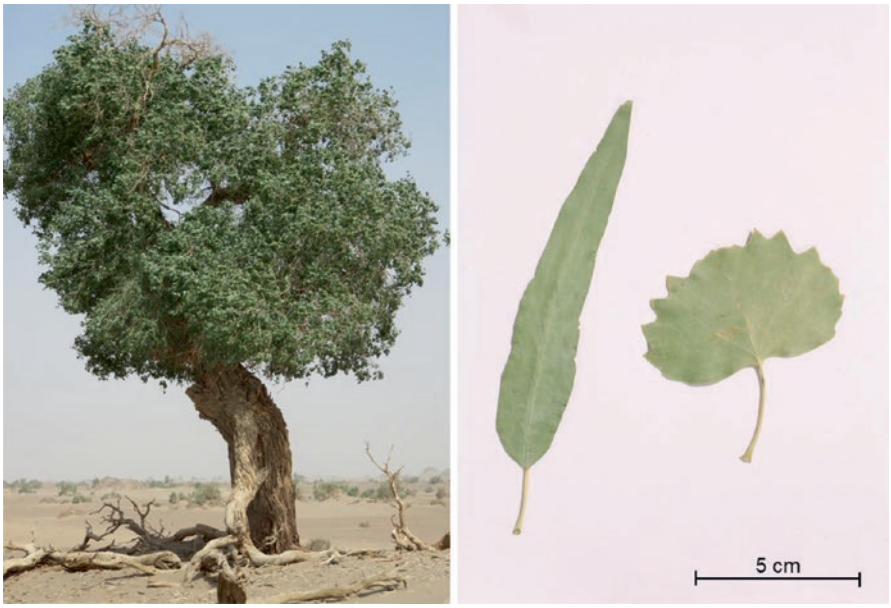


Fig. 1 The desert poplar *Populus euphratica* in China in the Inner Mongolia Autonomous Region, China (*left*) and examples of its heteroblastic dentate broad-ovate and lanceolate leaves associated with contrasting levels of drought tolerance (*right*) (Pictures from Andrew Groover and Suzanne Gerttula)

mechanical stresses, and temperature extremes. Trees can also inhabit marginal ecosystems, such as habitats of the desert poplar *Populus euphratica* characterized by limited water sources that contain high levels of salt (Wang et al. 1996) (Fig. 1). Such abiotic stress strongly influences tree distribution and survival (Sykes et al. 1996; Svenning and Skov 2004; Engelbrech et al. 2007; von Humboldt and Bonpland 2009). Since tree species often cover a broad range of geographic and environmental distribution, adaptation to abiotic stress has been shown to be plastic, with various responses being observed among population and within species (Sparks and Black 1999; Sánchez-Gómez et al. 2011).

To cope with adverse environmental conditions, angiosperm trees have evolved specific avoidance and tolerance mechanisms that allow them to maintain their reproductive fitness and survival. Morphological and physiological changes in response to abiotic stress are well documented at the whole plant level. These changes involve complex molecular processes ranging from stress sensing to the establishment of stress tolerance, which is under genetic and epigenetic control. Due to advances in sequencing technologies, tree responses and tolerance to abiotic stress are understood in increasing detail and have revealed enormous genetic diversity among species.

Here we outline the morphological and anatomical changes in angiosperm trees in response to abiotic stress, along with recent findings describing the genetic and molecular basis of abiotic stress tolerance. A special emphasis is given to drought,

as water limitation is one of the leading contributors to tree declines globally (van Mantgem et al. 2009; Allen et al. 2010; Choat et al. 2012).

Morphological and Anatomical Changes

As discussed below, morphological and anatomical responses to abiotic stress in angiosperm trees are observed in the roots, the stem and the canopy levels, with some changes being unique to angiosperm trees. The presence of a hydraulic system for long distance water transport and the need of maintaining functional tissues and organs for long periods of time are two important characteristics distinguishing woody species within the plant kingdom (Aranda et al. 2012). As compared to conifers, angiosperms are unique in some wood anatomy properties, notably the type of the tracheary elements (Fig. 2). Gymnosperm conducing system is composed of the ancestral tracheids which perform both the conductive and supportive functions. These elongated narrow tube like cell are unicellular, have thick lignified walls presenting bordered pits to facilitate the transfer of liquid between adjacent cells. Such pits present a heterogeneous structure, with an impermeable torus surrounded by a flexible margo. On the contrary, the evolutionary advanced angiosperm conduits are composed of larger vessel elements (and tracheids in some species). They are multicellular and are interconnected by means of plates with pores (perforation plates) through which the water moves up ward. Their wall are thickened in various ways, the pit membrane however, generally lacks the conspicuous specialization of the torus margo membrane and at least superficially has a relatively homogenous texture (Cochard 2006; Delzon et al. 2010). Some of these differences could be at the origin of contrasting levels of abiotic stress resistance observed between the two taxa.

Roots

Roots, as the primary sites of water and nutrient uptake by plants, represent important organs for plant growth and survival, and must respond to environmental cues including water availability and salinity levels. Roots evolved a remarkable capacity of sensing changes in environment conditions perceived from the physicochemical parameters of the soil, and relay that information to the shoot (Hamanishi and Campbell 2011). Roots also respond to external signals by modulating their architecture to find the supply of water and nutrients, which can be limited in abundance and localized (Malamy 2005). In woody plants, this architecture modulation and foraging for belowground resources mainly concerns the fine roots (<2 mm diameter) that are the most active portion of the root system in water uptake, as opposed to the more perennial coarse root system (>3 mm diameter) serving the functions of anchorage, carbohydrate storage, and the transport of nutrients and water (Comas et al. 2013).

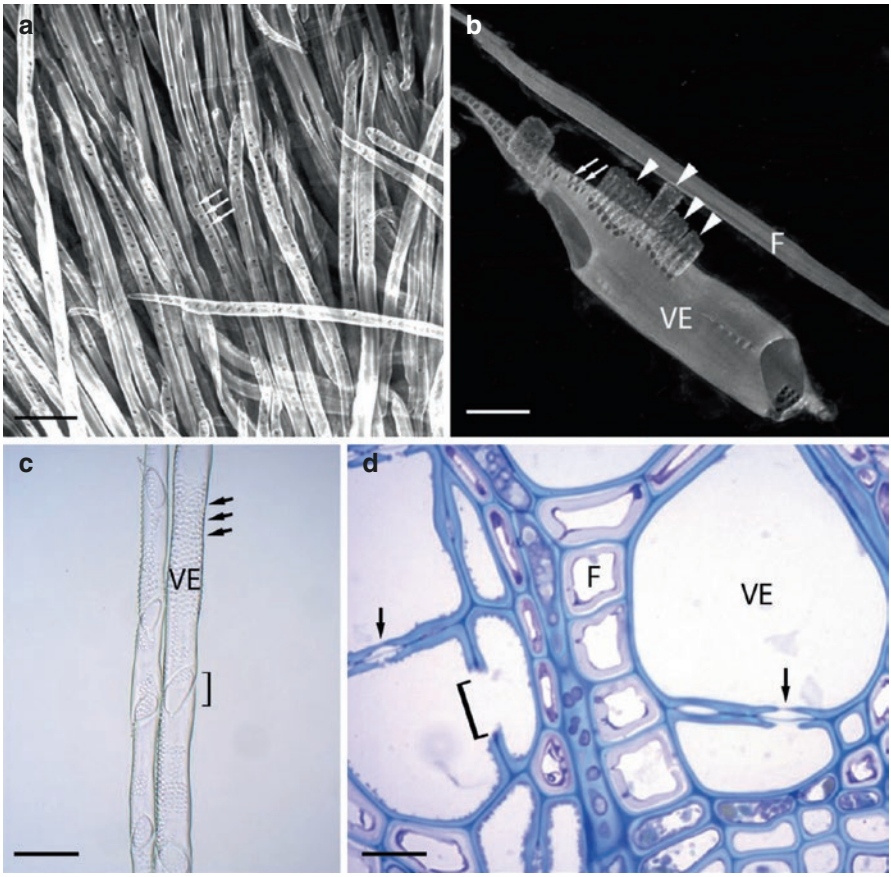


Fig. 2 Microscopic observations showing the anatomy of tracheary elements in gymnosperm and angiosperm tree species. (**a**, **b**) show confocal reflectance images of macerated wood cells, of respectively, *Podocarpus* spp and *Populus deltoides* × *P. nigra*, after staining with calcofluor. In (**c**) macerated vessel elements of *Populus tremula* × *alba* were observed under bright field microscope without any staining (image from Tixier 2013). The gymnosperm tracheids are narrow, elongated, unicellular and serve the double role of support and water transport. They have thick lignified walls presenting bordered pits (*arrows*) to facilitate the transfer of liquid between adjacent cells. The angiosperm vessel elements (*VE*) serve only the function of solute transport, while the fibers (*F*) provide support to the woody stem. VE are larger, multicellular and are interconnected by means of perforation plates (*squared bracket*) through which the water moves up ward. Their wall also present pits allowing liquid transfer radially between vessel elements, or in connection to ray parenchyma cells (*arrow heads*). (**d**) shows a cross section of *Populus tremula* × *alba* stem after toluidine blue staining (image from Tixier 2013). The homogeneous pit membrane of angiosperm can be observed. Hence they lack the conspicuous specialization of the torus margo membrane in gymnosperm tracheids. (not shown in this figure). Scale = 50 µm in (a, b), 100 µm in (c) and 10 µm in (d)

There is a great diversity of root architecture, in terms of root length, thickness, depth, partitioning and distribution that varies among forest trees, shrubs and horticultural trees species (Stone and Kalisz 1991). Such architecture can contribute to drought tolerance. For example, as a stress avoidance strategy, the deep and wide-

spreading roots systems of some drought-tolerant oak species seem to be important for optimizing the water intake in water-limited habitats, as opposed to the shallow root system of drought sensitive species such as dogwood and sugar maple (Hinckley et al. 1981). Other root traits associated with maintaining productivity of both herbaceous and woody plants under drought include smaller fine root diameters with greater specific root length. These features are conducive to higher hydraulic conductance by increasing the surface area in contact with soil water as well as the volume of soil that can be explored for water. In addition, this increases root hydraulic conductivity by decreasing the apoplastic barrier of water entering the xylem (Comas et al. 2013).

Water flows from the roots to the shoot in a continuum that is governed by a combination of the driving forces and the hydraulic properties of the pathway. During drought periods, water tension in the root xylem can reach critical values (Ψ_{crit}), leading to the interruption of the water column. Such embolized, air-filled xylem conduits become non functional (Domec et al. 2004). In many woody plants, hydraulic failure is more likely to take place in roots than in shoots. In fact, previous investigations have demonstrated that xylem in roots is not only more vulnerable to embolism than in stems, but also operates closer to the Ψ_{crit} than stems (Alder et al. 1996; Hacke and Sauter 1996; Martínez-Vilalta et al. 2002; Domec et al. 2004; Froux et al. 2005; Comas et al. 2013), so small reductions in Ψ_{soil} can significantly enhance root embolism rates. Further, fine (<2 mm diameter) and medium (2–3 mm diameter) roots are more vulnerable to embolism than coarse roots (>3 mm diameter) (Sperry and Ikeda 1997). Upon rewetting of the roots, root xylem functions can be restored by refilling the embolized conduits (Jaquish and Ewerts 2001; Domec et al. 2004), or by the growth of new roots (Domec et al. 2004). In the case of a persistent drought or for severely cavitated roots, embolisms may be irreversible (Seiler and Johnson 1988; Hacke et al. 2000) and a substantial reduction of the fine root biomass may be observed (Meier and Leuschner 2008; Zang et al. 2014). Because the roots and rhizosphere are likely to contain the most vulnerable components of the soil-to-leaf hydraulic pathway (Jackson et al. 2000), avoidance of hydraulic failure in drying soil may play a major role in the success of species growing under a wide range of precipitation regimes. It has been suggested that partial loss of root hydraulic conductivity through embolism could result in the generation of a hydraulic signal transmitted to the shoots that reduces stomatal conductance (g_s) (Colchard et al. 1996). This would in term reduce transpiration, and maintain shoot water potential at a nearly constant minimum value above Ψ_{crit}. This behavior, referred as an isohydric behavior, is opposed to anisohydric behavior where water potential decreases following the evaporative demand experienced during the day. (Cochard et al. 1996; Domec et al. 2004; Sade et al. 2012). A number of tree species exhibits at least partial isohydric behavior during gradual soil drying cycles (Gollan et al. 1985; Klein 2014), but the extent to which stomatal regulation of leaf water status is determined by shoot versus root and rhizosphere water status and hydraulic properties is largely unexplored (Domec et al. 2004).

In addition to some key architectural root traits, tree species adapted to dry climatic regimes also tend to have a reduced above ground biomass, resulting in a higher root-to-shoot ratio (Kozlowski and Pallardy 2002; Markesteijn and Poorter

2009). Such increase of the root-to-shoot ratio seems to largely depend on the level of drought stress, as well as on the tree species and even the population (Bongarten and Teskey 1987; Pallardy and Rhoads 1993; Yin et al. 2004; Aspelmeier and Leuschner 2006; Poorter et al. 2012; Kuster et al. 2013; Brunner et al. 2015).

Stem

In angiosperm trees, the evapotranspiration at the stomatal chambers of the leaves creates the negative pressure that supports water transport from the roots via the plant's conduit network of tracheary elements (Tyree and Zimmermann 2002). During drought events or freeze-thaw cycles in winter months, negative pressure increases in xylem vessels, leading to possible cavitation events (Lens et al. 2013). Resistance to cavitation seems to be an important factor in both angiosperm and gymnosperm evolution, since hydraulic failure has been found to drive tree mortality (McDowell et al. 2008). Hence, associations were found between increasing cavitation resistance and increasing aridity (Maherali et al. 2004; Choat et al. 2012). Different vulnerability to stem xylem embolism have been observed among tree species, and some phylogenic trends have been observed which might explain species distribution and survival (Sperry et al. 1994; Maherali et al. 2004; Choat et al. 2012; Meinzer and McCulloh 2013). For instance, angiosperm trees seem capable of surviving high levels of xylem embolism, with a threshold of 88 % loss of stem hydraulic conductivity for some angiosperm trees before leading to any irreversible drought damage, as compared to 55 % for conifers (Urli et al. 2013). But in the other hand, angiosperms were also found to be more prone to embolisms since they operate at a lower safety margin (defined as the difference between naturally occurring xylem pressures and pressures that would cause hydraulic dysfunction) than gymnosperms (Maherali et al. 2004; Choat et al. 2012). Additionally, species that show denser wood usually show higher cavitation resistance (Sperry et al. 2006).

Various attempts have been made to identify relevant wood anatomical parameters explaining the differences in cavitation vulnerability observed among tree species. The importance of the diameter of the conduits has been discussed, (Sperry and Tyree 1988; Sperry and Saliendra 1994; Hargrave et al. 1994; Lo Gullo et al. 1995; Hacke and Sauter 1996), with wider conduits generally being more vulnerable to xylem embolism as compared to narrower conduits. In that regard, the reduction of the size of the vessel elements observed in poplar, eucalyptus as well as in various oak species appears to be an adaptive response to drought stress (Villar-Salvador et al. 1997; Garcia-Gonzalez and Eckstein 2003; Corcuera et al. 2004; Eilmann et al. 2006; Arend and Fromm 2007). However, other studies suggest that vulnerability to cavitation would mainly be explained by the quantity as well as the quality of the interconduit pits present in the lignified cell walls of the tracheids and vessel elements (Zimmermann 1983; Choat et al. 2004; Cochard 2006; Jansen et al. 2011). Pits facilitate water exchange between neighboring cells but are also important sites for preventing air-seeding and spreading of embolism between

neighboring conduits (Lens et al. 2013). In term of quantity, the probability of a vessel to cavitate increases with the pit area (the rare pit area theory) (Christman et al. 2009; Lens et al. 2011), as well as the pit aperture diameter (Choat et al. 2003; Sano 2005; Jansen et al. 2009). Hence, the bigger the conduit, the larger its surface and the more pits are located in its wall, the greater probability of a defective, wide, or less efficient pit that could be an air-seeding starting point (Badel et al. 2015). In support of the rare pit hypothesis, there is a significant relationship between pit area per vessel and increasing vulnerability across species (Christman et al. 2012). In terms of quality, thicker and less porous pit membranes are associated with greater resistance to cavitation by air-seeding because more pressure is required to pull air across them (Lens et al. 2011). In this regard, the higher resistance to cavitation observed in gymnosperm might be due to the heterogeneous structure of the pit membranes of the ancestral gymnosperm tracheids, constituted by an impermeable torus surrounded by a flexible porous margo allowing for low-resistance water transfer between tracheary elements (Cochard 2006; Delzon et al. 2010). When a pit connects a functional tracheid with an embolized one, the margo stretches in response to the pressure difference, so that the torus seals the opening of the pit and prevents propagation of embolism. In the majority of angiosperm tree species, water flows through the homogenate membrane pit of the vessel elements, and air sealing of the pits depends entirely on the stretching of this membrane (Hacke et al. 2004). Mechanical modelling of pit membranes behavior in angiosperm tree species has provided better understanding of their resistance to cavitation (Sperry and Hacke 2004; Tixier et al. 2014).

If embolism occurs, studies have revealed that trees can potentially recover water conductivity by refilling the embolized xylem conduits or by developing new functional xylem tissue during the secondary growth (Zwieniecki and Holbrook 2009). Refilling of the embolized vessels is made possible by generation of a positive pressure on the xylem by the roots or by the stem itself (Tyree and Sperry 1989), by creating osmotic forces through the accumulation of soluble sugars in the vessels (Ewers et al. 2001; Secchi and Zwieniecki 2010). These sugars could notably be released from the starch stored in xylem parenchyma, and would create a low water potential leading to water movement from the parenchyma cells into the xylem vessels (Ewers et al. 2001; Ameglio et al. 2001; Nardini et al. 2011). This would occur mainly during winter and spring, when in absence of evaporative forces, xylem tensions are smaller than the positive osmotic pressure developed by the accumulation of solute (Ameglio et al. 2001; Ewers et al. 2001). The presence of a range of osmotic pressures within a tree allowing for refilling during the growing season is still debated (Brodersen et al. 2013; Cochard and Delzon 2013; Cochard et al. 2015; Choat et al. 2016; Bouche et al. 2016).

Xylem embolism resulting from freezing of water in the stem has been measured seasonally in angiosperm tree species of the Northern hemisphere (Sperry and Saliendra 1994; Zhu et al. 2000; Ameglio et al. 1995, 2001; Ewers et al. 2001; Sakr et al. 2003), including the sugar maple (*Acer saccharum*) (Sperry et al. 1988). Some phylogenic trends for tree capacity to refill embolized xylem have been noted, with a lower capacity in conifers as compared to angiosperms (Johnson et al. 2012). One

hypothesis is that such differences could reflect the lower amount of xylem parenchyma in conifers in comparison with angiosperm trees, as well as differences in non-structural carbohydrate concentrations in their stems which may be required for embolism repair (Johnson et al. 2012). However, there is some controversy over the possibility that the observation of xylem refilling in some of these studies was actually an artifact of the destructive sampling technique used (Cochard et al. 2000; Sperry 2013; Wheeler et al. 2013). Using non-destructive, high-resolution computed tomography, Choat et al. (2016) saw no evidence of refilling of coast redwood (*Sequoia sempervirens*) xylem after imposition of a severe drought stress. To address the gap in our understanding of embolism repair in woody plants, there is an urgent need of applying such direct methods in angiosperm tree species.

More generally, abiotic stress at the stem level has been shown to considerably impact tree growth with a significant reduction of stem diameter under drought (Spieß et al. 2012). In fact, the process of radial growth has been shown to be highly sensitive to water deprivation, with the demonstration of reduced tree rings size (Orwig and Abrams 1997; Kozlowski and Pallardy 1997; Breda et al. 2006). This impacts tree productivity for industry in term of wood quality and yield, but also increases tree susceptibility to insects, diseases as well as mechanical damages (Lundstrom et al. 2008).

Shoots and Leaves

Angiosperm trees manifest a great diversity of leaf shapes and structures that ranges from developmental sequences within a shoot in response to microenvironment, to variation among, and within species at the population level (Nicotra et al. 2011). Since leaves play a critical role by providing the necessary sugars needed for growth and survival through photosynthesis, it has been proposed that variation in the leaf shape would reflect the effects of natural selection. Leaf size, thickness, margin and venation characteristics have been found to follow a predictable pattern based on climate and growth habitat. For instance, leaves of desert or Mediterranean angiosperm species are more finely dissected than leaves of temperate-zone angiosperm trees (Hinckley et al. 1981), whereas mesic, evergreen tropical forests contain almost exclusively species with entire-margined leaves (Bailey and Sinnott 1916; Gentry 1969). Smaller, thick leaves are also commonly associated with more xeric sources of temperate-zone angiosperm trees (Ying and Bagley 1976; Kozlowski and Pallardy 1997; Abrams 1994), as well as harsh environmental conditions such as cold, hot, dry, saline environments or many of these factors in combination (Ying and Bagley 1976; Dancik and Barnes 1975; Pallardy 1981; Kozlowski and Pallardy 1997; Abrams 1994). In addition, leaves may also exhibit a remarkable phenotypic plasticity in response to abiotic stress (Kessler and Sinha 2004; Barkoulas et al. 2007). The leaf shape and structure are defined mainly in a brief period of primary morphogenesis based on the possible role of reaction–diffusion systems and can be altered by allometric expansion (Frank and Britton 2000; Dengler and Kang 2001). For instance,

in response to drought, modulation of total leaf area is important to regulate water use, and can be associated with the decline in cell and leaf size or leaf senescence, and hence tree productivity (Battaglia et al. 1998; Le Dantec et al. 2000). Drastic changes in leaf shape in response to environmental changes have been also observed in some tree species. In the *Eucalyptus* Wilsons Promontory seedlings, the rapid shift from the broad, thin, horizontally oriented, dorsiventral and hypostomatal juvenile leaves to the narrow, thick, vertically oriented, isobilateral and amphistomatal adult leaves may confer an adaptive advantage within its native habitat, which is exposed to strong winds and salt spray (Potts and Jordan 1994; James and Bell 2001). Heteroblasty is also observed in the desert poplar *P. euphratica* (Fig. 1), and seems to be correlated with drought and desertification, with changes in leaf shape from lanceolate to dentate broad-ovate, the latter being associated with increased drought tolerance (Li and Zheng 2005; Zheng et al. 2007).

Stomata, the pores found on leaf surfaces, play a key role in regulating water movement and retention in response to environmental conditions. As a short-term response enabling plants to contend with fluctuating water supply, the closure of stomatal aperture leads to a decrease in water loss from the plant, but also limits CO_2 entry into the intercellular airspace, thus potentially limiting photosynthesis (Cowan and Farqhar 1977; Chaves et al. 2003). Stomatal movements, and drought avoidance strategies to increase water use efficiency (WUE, defined as the amount of C assimilated, e.g. in term of biomass or μmol CO_2, per unit water loss) and maintain production were found to differ greatly among trees. For instance drought tolerant poplar clones were shown to exhibit lower gas exchange rates under well-watered conditions and a more gradual decline in photosynthesis and stomatal conductance as drought proceeds, while drought sensitive clones tend to achieve higher basal gas exchange when well-watered but then close their stomata more rapidly when subjected to drought, and hence show greatly reduced productivity (Silim et al. 2009; Theroux-Rancourt et al. 2015). In addition, stomatal closure is shown to prevent the development of substantial xylem embolism in aboveground woody tissue, if xylem reaches a critical tension during periods of high transpiration (Jones and Sutherland 1991). In this context, there is growing evidence of functional coordination between vulnerability to xylem cavitation and the regulation of stomatal conductance to maintain water potential above the range that would lead to cavitation (Maherali et al. 2006; Sparks and Black 1999). This mechanism has been demonstrated for several species of woody plants (Sperry et al. 1993; Nardini and Salleo 2000; Vilagrosa et al. 2003). However, relationships between stomatal conductance and xylem cavitation seem to be highly species-specific and were found to not hold true among certain species such as poplar hybrids, suggesting that other drought-resistant strategies may also play a key role in such genotypes exposed to drought stress (Fichot et al. 2010; 2011; Arango-Velez et al. 2011).

Finally, stomatal responses were found to be highly interactive to water availability in the soil, leaf, and atmosphere, but the response to these environmental and internal variables were shown to depend on the species (Running 1976; Sandford and Jarvis 1986; Bond and Kavanagh 1999). For instance, in the western United States, stomatal conductance of gymnosperms tends to be more sensitive to vapor

pressure deficit (VPD) than for angiosperms (Marshall and Waring 1984; Bond and Kavanagh 1999). The origin of such differences might be found in the leaf hydraulic design. The extent to which the time-varying flux of water through the leaf might affect the performance of the photosynthetic cells depends both on the hydraulic linkage between xylem and epidermis, and on the degree to which the mesophyll is hydraulically uncoupled from the transpiration stream. The former has implications for stomatal control of xylem tensions, while the latter bears on the effects of transient imbalances in supply and demand on the water status of the mesophyll (Zwieniecki et al. 2007). In that regard, the hydraulic isolation of the epidermis to the xylem in conifers could involve more negative water potential in the epidermis than in the xylem, e.g. following changes in VPD, and thus correspond to stomatal closure before the xylem has experience significant water potential drop (Zwieniecki et al. 2007). Inversely, the high hydraulic connectivity often observed between the xylem and the epidermis in angiosperms could allow for efficient water supply from the xylem and for fast stomatal control following variations in xylem water potential. Such fast stomatal closure does not necessarily impact photosynthesis, since the mesophyll of the majority of angiosperms is hydraulically uncoupled from the xylem. This allows those cells to buffer the propagation of transient changes in transpiration and minimize the degree to which short-term variation in transpiration affects the mesophyll (Zwieniecki et al. 2007). For instance, this lack of synchronicity between stomatal closure and the decline of photosynthetic traits such as mesophyll conductance (g_m), permit some poplar genotypes to maintain higher WUE during the early stages of drought stress (e.g. Flexas et al. 2002; Braatne et al. 1992; Theroux-Rancourt et al. 2014, 2015). Such genotypes even recover better from short term deficit in water supply by being able to restore high rates of carbon assimilation faster after a return to well-watered conditions (Theroux-Rancourt et al. 2015). Nonetheless, the longer the duration of the drought, the longer it takes for leaves to recover their pre-drought transpiration and leaf hydraulic conductivity rates. This often takes over a month and substantially limits leaf-level processes (Blackman et al. 2009). Other tree species, such as *Eucalyptus*, exhibit a high connectivity with the mesophyll, thus making the leaf highly responsive to the environment and, although not buffering the mesophyll cells, could allow for an increase in both photosynthesis and mesophyll conductance as stomatal conductance increases (e.g. Cano et al. 2014).

Finally, as mature leaves sense environmental conditions, plants can also develop longer lasting stomatal-based responses to persistent water deficit by adjusting stomatal density in developing leaves (Lake et al. 2001; Miyazawa et al. 2006; Casson and Hetherington 2010; Hamanishi et al. 2012). Lower stomatal density restricts the number of sites for water loss and decreases evapotranspiration. Modification of stomatal density in response to drought varies between tree species and is contingent on the severity of water deficit. For example, reduced stomatal densities after drought treatment have been observed in oak species (*Quercus series*, *Q. virgiana* and *Q. oleoides*; Cavender-Barres et al. 2007) as wells as in *Populus balsamifera* (Hamanishi et al. 2012) and *Betula pendula* (Pääkkönen et al. 1998), but no alteration in stomatal densities was found in *Prunus avium* (Centritto et al. 1999), *Q. petraea* and *Pinus pinaster* (Guehl et al. 1994).

Genetic Control of Abiotic Stress Tolerance of Angiosperm Trees

Tree response to abiotic stress is a complex biological process. The ability of trees to adapt and survive harsh environments is a consequence of a variety of biochemical and physiological processes at the whole plant level. Many of which are the result of stress signal perception leading to alterations in the transcriptome that result in an adaptive response (Kozlowski and Pallardy 2002; Lei et al. 2006). Numerous studies on woody plants show intra- and interspecific genetic variation in characteristics associated with drought resistance, such as vulnerability of xylem to cavitation (Kavanagh et al. 1999; Maherali et al. 2006), hydraulic conductance (Alder et al. 1996), WUE (Lauteri et al. 2004) and stomata size and density (Bruschi et al. 2003). Drought tolerance involves many genes and biochemical-molecular mechanisms, but also depends on large genome×environment interactions (Tardieu and Tuberosa 2010). In fact, in the case of forest tree species, such as *Castanea sativa*, *Populus przewalski*, and *Quercus suber*, differential responses to drought have been reported at the population level for different geographical origins (Lauteri et al. 1997; Lei et al. 2006; Ramirez-Valiente et al. 2009; Aranda et al. 2012). This suggests the maintenance of a large adaptive intra-specific genetic variability to acclimate to stressful environments. In recent years, in addition to our knowledge of phenotypic variations, much progress has been made in elucidating the molecular and genetic determinants of tree responses to abiotic stress. Such research particularly benefits from the completion of a draft sequence of various tree species such as *Populus trichocarpa* (Tuskan et al. 2006), *Malus×domestica* (Velasco et al. 2010), *Prunus persica* (Verde et al. 2013), *Picea glauca* (Birol et al. 2013), *Picea abies* (Nystedt et al. 2013), *Eucalyptus grandis* (Myburg et al. 2014), as well as the release of the loblolly pine *Pinus taeda* genome (Neale et al. 2014). This opens promising avenues for comparative genomics in woody plants to fully understand the evolutionary basis of gene function and molecular network underlying tree responses to abiotic stress.

Below we present and compare the main findings made across tree species in the understanding of the genetic basis of tolerance to drought. In particular, we discuss the degree of similarity or differences in drought response between species and how such information could be used to gain insight into tree adaptation to drought.

Quantitative Trait Loci Involved in Drought Stress Response

Using genomic and transcriptomic data, Street et al. (2006) identified 30 QTLs associated with drought tolerance in an F2 pedigree of *Populus trichocarpa×P. deltoides*. Some of these QTLs co-localized with genes that were found to be up or down-regulated in response to drought. These might represent candidate genes for the tree response to water depletion (e.g. *GIGANTEA* dehydration-stress protein, glutathione-peroxidase 1, universal stress protein). Interestingly, in many cases, candidate genes supported previous functional descriptions in other species. In F1 and F2 hybrid populations of *Salix* and *Eucalyptus*, from eight to 66 minor drought

QTLs were identified (Rönnberg-Wästljung et al. 2005; Teixera et al. 2011). Such studies highlight that many genes of modest effect control tree adaptation to drought, with each QTL explaining a low to moderate proportion of total phenotypic variance (from 5 to 30 %).

When similar experimental procedures and phenotypic parameters are used to evaluate drought response, the availability of orthologous markers among unrelated mapping families or species (Casasoli et al. 2006; Aranda et al. 2012) allows comparative QTL mapping. Such analyses have been conducted for QTLs controlling carbon isotope discrimination, an important measure of drought tolerance, in two closely related genus within the family Fagaceae. In comparison of the European white oak (*Quercus robur*) and the European chestnut (*Castanea sativa*), which are widely distributed across Europe, oak displayed seven QTLs controlling carbon isotope discrimination, which were then compared to the positions of eight QTLs identified in chestnut using orthologous microsatellite markers. Overall, the genetic architecture of this adaptive trait was similar between oak and chestnut in term of QTL number and contribution to the phenotypic variance, no QTL for carbon isotope discrimination was conserved between both species (Casasoli et al. 2006). This could reflect the complex and contrasting evolution strategies of tree responses to drought, even in two closely related genus. Additionally, there can be significant overlap or correlations between different traits associated with WUE or drought. For instance, a major QTL governing water-use efficiency in *Quercus robur* was found to co-localize with a major QTL governing stomatal density (Brendel et al. 2008; Gailing et al. 2008). Many QTLs for drought-specific traits also co-localized in a *Populus trichocarpa* × *P. deltoides* F2 population (Street et al. 2006). Such co-localization may occur by chance, due to clustering of genes, or may be a consequence of pleiotropic effects. The latter may indicate overlapping or similar molecular basis of both phenotypic traits.

Gene Expression

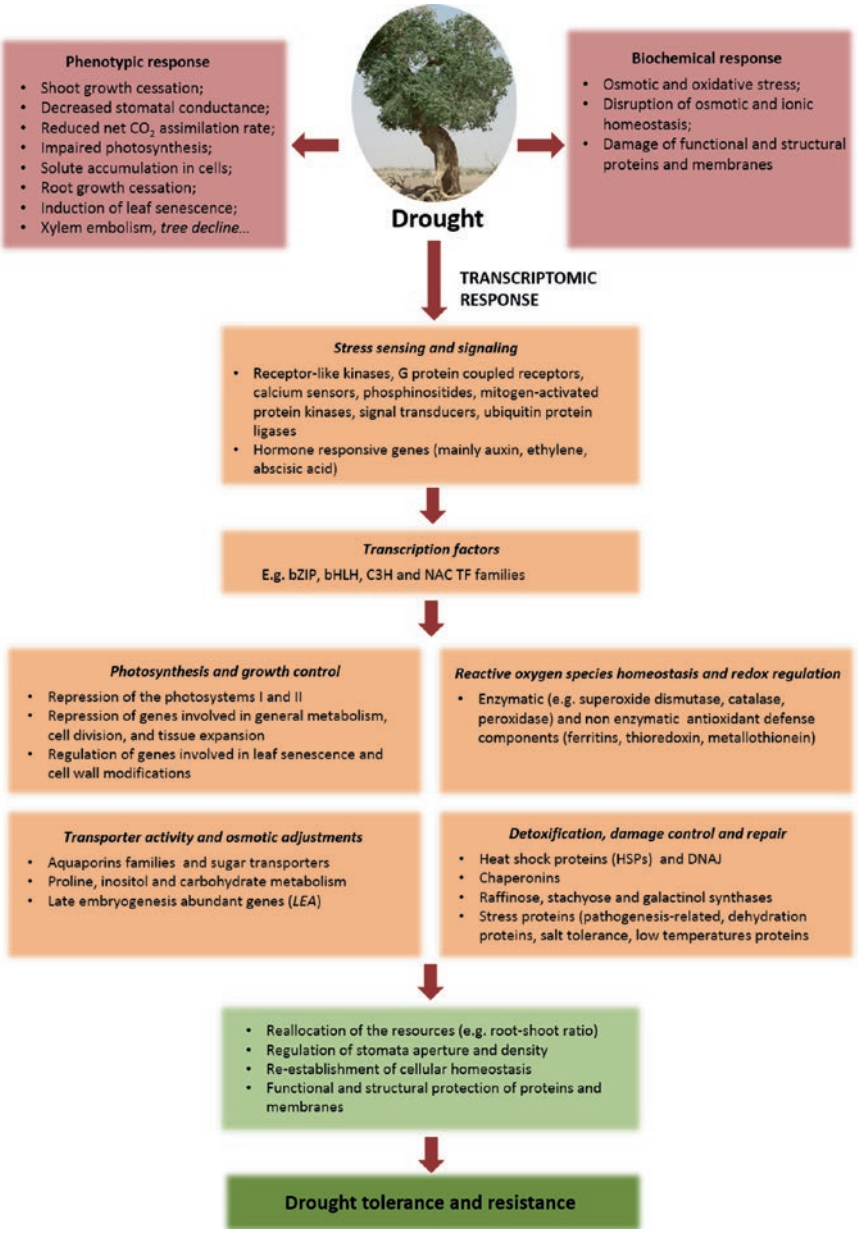
In the past years, numerous gene expression studies investigating water deprivation have been undertaken in various angiosperm tree species, with *Populus* being the most studied. Species included *Populus euphratica* (Brosché et al. 2005; Bogeat-Triboulot et al. 2007; Qiu et al. 2011; Yan et al. 2012; Tang et al. 2013), *P.* × *canadensis* (Caruso et al. 2008), *P. balsamifera* (Hamanishi et al. 2010), *P. simonii* (Chen et al. 2013), *P. trichocarpa* (Tang et al. 2015), *P. alba* (Berta et al. 2010), *P. yunnanensis* (Peng et al. 2012), *Quercus robur* (Spieβ et al. 2012), *Eucalyptus camaldulensis* (Thumma et al. 2012), *Malus* × *domestica* cultivars (Wisniewski et al. 2008), as well as various interspecific hybrids and genotypes: *Populus deltoides* × *P. nigra* (Wilkins et al. 2009; Cohen et al. 2010), *P. trichocarpa* × *P. deltoides* (Street et al. 2006), *P. nigra* × P. *maximowiczii* (Wilkins et al. 2009), *Salix viminalis* × (*S. viminalis* × *S. schwerinii*) (Pucholt et al. 2015).

Together, these studies revealed the regulation of hundreds or even thousands of differentially expressed genes involved in drought stress. These genes serve as

potential markers for tree breeding programs to develop genotypes resistant to the effects of drought. Such studies also provide a starting basis for comparative genomics initiatives, which have emerged as a powerful tool for deciphering the molecular basis of drought responses and reveal physiologically relevant processes (Wilkins et al. 2009; Cohen et al. 2010; Hamanishi et al. 2010). For example, comparative genomic studies conducted on poplar and willow have revealed some common, but also unique transcriptional pathways between and within tree species in response to drought (Cohen et al. 2010; Hamanishi et al. 2010; Pucholt et al. 2015; Tang et al. 2015). For example, Tang et al. (2015) highlighted differential expression of H^+-ATPase, rubisco activase, laccases and expansin genes in *Populus trichocarpa* but not in the desert poplar *P. euphratica*. In addition, when comparing pine and poplar drought transcriptomic responses to *Arabidiopsis thaliana*, strong species-dependent features were revealed, with none of the 27 genes reliably responsive to water stress in *Arabidiopsis* being regulated under drought in poplar nor pine (Bray 2004; Polle et al. 2006). This might reveal that angiosperm trees, regardless of species or hybrids, are likely to have different mechanisms in response to drought stress and they are highly variable among species and genotypes.

However, a major difficulty for comparing the outcomes of different tree transcriptomic studies is that the elicited responses not only differ among genotypes, but also differ depending on the organ and developmental stage of the plant sampled, as well as on the severity and duration of the stress applied (Cohen et al. 2010; Spieß et al. 2012; Pucholt et al. 2015). For example, when a severe stress might induce rapid responses such as stomatal closure, a gradual water depletion regime gives the plant the time to better react and adapt to the stress by implementing additional mechanisms of stress protection (e.g. adjustment of the leaf osmotic potential, which is a relatively slow process) (Arndt et al. 2001; Tesche 1992; Bruce et al. 2007; Blum 2009; Spieß et al. 2012). As a result, varying water depletion regimes seems to induce the transcriptional activation of different gene networks. For example, in oak, loblolly pine, and poplar, regulation of distinct sets of genes were observed across the time, and among the water deficit regimes applied (Watkinson et al. 2003; Spieß et al. 2012; Yan et al. 2012). In general, the higher the water deficit intensity was, the more wide-ranging the regulatory changes and the cellular responses observed (Bogeat-Triboulot et al. 2007; Hamanishi et al. 2010; Yan et al. 2012). To add to this complexity, transcriptional response to drought stress in trees, such as poplar, has been also found to vary depending on the time of the day (Wilkins et al. 2009; Hamanishi et al. 2010), on gender, as well as on the clone growth history. Vegetatively-propagated poplars from the same clone that were previously exposed to different environmental conditions developed differences in transcript abundance patterns and DNA methylation levels in response to the same drought treatment, indicating potential roles for epigenetic regulation of drought responses (Raj et al. 2011; Peng et al. 2012). These studies highlight the high complexity of gene expression studies in response to abiotic stress.

Among the various transcriptional studies investigating angiosperm trees response to drought, some general biological pathways can be identified. A description of such pathways along with putative genes involved is presented in Fig. 3. In the various studies, most genes displaying altered expression during water deficit


Phenotypic response
Shoot growth cessation;
Decreased stomatal conductance;
Reduced net CO_2 assimilation rate;
Impaired photosynthesis;
Solute accumulation in cells;
Root growth cessation;
Induction of leaf senescence;
Xylem embolism, tree decline...
Drought
Biochemical response
Osmotic and oxidative stress;
Disruption of osmotic and ionic homeostasis;
Damage of functional and structural proteins and membranes
TRANSCRIPTOMIC RESPONSE
Stress sensing and signaling
Receptor-like kinases, G protein coupled receptors, calcium sensors, phosphinositides, mitogen-activated protein kinases, signal transducers, ubiquitin protein ligases
Hormone responsive genes (mainly auxin, ethylene, abscisic acid)
Transcription factors
E.g. bZIP, bHLH, C3H and NAC TF families
Photosynthesis and growth control
Repression of the photosystems I and II
Repression of genes involved in general metabolism, cell division, and tissue expansion
Regulation of genes involved in leaf senescence and cell wall modifications
Reactive oxygen species homeostasis and redox regulation
Enzymatic (e.g. superoxide dismutase, catalase, peroxidase) and non enzymatic antioxidant defense components (ferritins, thioredoxin, metallothionein)
Transporter activity and osmotic adjustments
Aquaporins families and sugar transporters
Proline, inositol and carbohydrate metabolism
Late embryogenesis abundant genes (LEA)
Detoxification, damage control and repair
Heat shock proteins (HSPs) and DNAJ
Chaperonins
Raffinose, stachyose and galactinol synthases
Stress proteins (pathogenesis-related, dehydration proteins, salt tolerance, low temperatures proteins
Reallocation of the resources (e.g. root-shoot ratio)
Regulation of stomata aperture and density
Re-establishment of cellular homeostasis
Functional and structural protection of proteins and membranes
Drought tolerance and resistance

returned to the control levels after the plants were re-irrigated and allowed to recover, indicating that these are transient responses to drought (Bogeat-Triboulot et al. 2007). Besides these functionally annotated genes, many genes of unknown functions have been found to be differentially regulated in these studies and represent an additional source of candidate genes for drought tolerance (Wilkins et al. 2009; Thumma et al. 2012; Spieß et al. 2012; Yan et al. 2012).

Stress Sensing, Signaling and Transcription Control

Drought, cold and salt stress are different abiotic stresses yet share a cluster of signaling pathways linked to water stress. After sensing of water deficit at the cellular level (e.g. through changes in turgor pressure trough the roots), one of the first plant response is the activation of signal cascades triggering alterations in gene expression. This in turn leads to changes at the cellular, physiological and developmental level. In angiosperm trees, known drought response signaling genes encode for proteins including receptor-like kinases, G protein coupled receptors, calcium sensors, phosphinositides, mitogen-activated protein kinases, signal transducers (XLG2), ubiquitin protein ligases and calmodulin (Wisniewski et al. 2008; Berta et al. 2010; Spieβ et al. 2012; Tang et al. 2013). In various studies, a large number of genes encoding for transcription factors (TF) have also been found to be differentially expressed. Up to 25.1 % of genes encoding for TF genome-wide were regulated in the desert poplar *Populus euphratica* in response to water deprivation, indicating massive remodeling of gene expression (Tang et al. 2013). In this particular study, MYB and MYB-related TF family were the most abundant, followed by those matching to the bZIP, bHLH, C3H and NAC TF families. Plant hormones also seem to play central roles in the ability of plants to adapt to changing environments, and hence, response to abiotic stress, by mediating growth, development,

Fig. 3 Overall model of tree response to drought. At the whole plant scale, under a gradual soil water depletion, impact on the phenotype usually begins with shoot growth cessation, followed by decreased stomatal conductance, leading in turn to a reduced net CO_2 assimilation rate, impaired photosynthesis, solute accumulation in cells, root growth cessation and finally, when water availability is very low, induction of leaf senescence and plant decline (Passioura 1996). At the biochemical level, drought causes cellular damages and secondary stresses, such as osmotic and oxidative stress. In angiosperm trees tolerant to drought, such abiotic stress will activate a cascade of transcriptomic responses. First, stress perception at the cellular level (e.g. through changes in turgor pressure by the roots or through sensing of the secondary osmotic and oxidative stress) triggers downstream signaling cascades (hormone dependent or independent) and activation of transcriptomic factors. Such transcriptomic factors will in turn regulate genes acting in various biological processes such as photosynthesis and plant growth, reactive oxygen species (ROS) homeostasis and redox regulation, osmotic adjustments, detoxification, damage control and repair. Activation of such stress-responsive mechanisms participates in optimizing tree water use efficiency, re-establishing cellular homeostasis, and protecting and repairing damaged proteins and membranes

nutrient allocation and source/sink ratio (Peleg and Blumwald 2011). Differentially expressed genes associated with various hormones were identified in trees in response to drought (Street et al. 2006; Caruso et al. 2008; Berta et al. 2010; Cohen et al. 2010; Hamanishi et al. 2010; Qiu et al. 2011; Peng et al. 2012; Yan et al. 2012; Chen et al. 2013; Tang et al. 2013). Although auxin (IAA), ethylene (ET) and abscisic acid (ABA) figure among the most studied across different taxa, studies have also revealed the importance of brassinosteroid (BR), gibberellic acid (GA), jasmonate (JA), salicylic acid (SA), and cytokinin (CK). Recent evidence in plant physiology indicated that plant hormones are involved in multiple processes. For instance, among other important functions of ABA in seed maturation and germination, as well as in the regulation of gene expression, one of its most prominent roles is the adaptation to abiotic stress via the regulation of stomatal movements (Leung and Giraudat 1998; Wilkinson and Davies 2002). In addition, cross-talk between the different plant hormones often results in synergetic or antagonic interactions that play crucial roles for the adaptation of plants to abiotic stress (Peleg and Blumwald 2011).

Reactive Oxygen Species and Antioxidant Defense Machinery

Besides these signaling molecules, a broad repertoire of protective genes was found to be regulated in response to abiotic stress. Abiotic stress often leads to the production reactive oxygen species (ROS), which can be important in plant signaling but, if produced in excess, can also damage proteins, lipids, carbohydrates and DNA, and ultimately results in an oxidative stress (Gill and Tuteja 2010). In trees, enzymatic (superoxide dismutase, catalase, peroxidase, ascorbate peroxidase, glutathione-S-transferase, oxidoreductase, aldehyde dehydrogenase) as well non-enzymatic antioxidant defense components (ferritins, thioredoxin, glutaredoxin, metallothionein) were found to be regulated in response to drought (Brosché et al. 2005; Street et al. 2006; Bogeat Triboulot et al. 2007; Cohen et al. 2010; Qiu et al. 2011; Peng et al. 2012; Spieβ et al. 2012; Yan et al. 2012; Chen et al. 2013; Tang et al. 2015). Such molecules might work in concert to maintain cellular redox homeostasis and protect plant cells from oxidative damage by scavenging of ROS.

Photosynthesis and Growth Control

Photosynthesis and cell growth are among the primary processes to be affected by drought. Hence, in addition to genes regulating the stomata aperture (e.g. *OPEN STOMATA* 1; genes related to the regulation of ABA; Chen et al. 2013) as well as stomata density and distribution (e.g. *STOMATOGEN*, *ERECTA*, *FAMA*; Hamanishi et al. 2012), down-regulation of many genes associated to photosynthesis was demonstrated in trees under drought stress. Such genes are mainly components of the electron-transport chains, the photosystems I and II (Wisniewski et al. 2008; Cohen et al. 2010; Peng et al. 2012; Yan et al. 2012; Spieβ et al. 2012; Thumma et al. 2012; Chen et al. 2013).

Alteration of photosynthetic metabolism can arise either from the direct decreased of CO_2 availability due to diffusion limitations through the stomata and the mesophyll, or can arise as a secondary effect of the oxidative stress (Chaves et al. 2009). In this latter case, one hypothesis would be that, in order to maintain ROS homeostasis under drought stress, trees would suppress photosynthetic capability by broadly reducing electron transport in photosystem I and photosystem II (Tang et al. 2015).

Together with the repression of tree growth observed in the various studies, transcriptome analysis revealed a strong down regulation of genes related to general metabolism, cell division, and tissue expansion (Cohen et al. 2010; Bogeat-Triboulot et al. 2007; Wisniewski et al. 2008; Thumma et al. 2012; Tang et al. 2015). Interestingly, premature leaf drop during drought was associated with the regulation of genes involved in senescence, such as *CLPR1*, *SENESCENCE-ASSOCIATED GENE 21*, as well as proteins including PUTATIVE SENESCENCE-ASSOCIATED PROTEIN, WRKY transcription factors as well as cysteine proteases (Brosché et al. 2005; Cohen et al. 2010; Spieβ et al. 2012; Tang et al. 2013; Chen et al. 2013). In addition, the observation in poplar of a pronounced induction of Asn Synthetase prior to leaf senescence might suggests a strong remobilization of nitrogen (Bogeat-Triboulot et al. 2007). Cell wall and cuticle properties have been also shown to change after drought treatment (Zwiazek 1991; Potters et al. 2007; Moore et al. 2008). Hence, various cell-wall related genes (e.g. pectin esterases, o-methyltransferases, expansins, cellulose synthases, laccases, cell wall-associated kinases, endoxyloglucan) and genes involved in epicuticular wax biosynthesis (e.g. *CER1*) have been found to be regulated in response to water deprivation (Street et al. 2006; Caruso et al. 2008; Berta et al. 2010; Cohen et al. 2010; Hamanishi et al. 2010; Spieβ et al. 2012; Thumma et al. 2012; Chen et al. 2013; Tang et al. 2015).

Transporter Activity and Osmotic Adjustments

Among other transporters, genes encoding for aquaporins (NIP, SIP, TIP and PIP) and sugar transporters (e.g., STP1; ATINT1; glucose-6-phosphate transport, GPT2) were the most represented (Wilkins et al. 2009; Brosché et al. 2005; Bogeat-Triboulot et al. 2007; Berta et al. 2010; Cohen et al. 2010; Qiu et al. 2011; Yan et al. 2012; Chen et al. 2013). Collectively, these products transport water and sugars through the plasma membranes and the tonoplast and can help cells adjust to changes in osmotic pressure. For instance, members of the PIP1 family of aquaporins have been shown to be important for recovery from xylem embolism, in poplar (Secchi and Zwieniecki 2010; Laur and Hacke 2013) and in spruce (Laur and Hacke 2014). Variation of transcript abundance of various aquaporins family members was also found in poplar species having contrasting drought response strategies at the whole plant level (Almeida-Rodriguez et al. 2010). Such variability may reflect the importance of aquaporins with respect to water transport and drought tolerance in trees (Hamanishi and Campbell 2011).

Osmotic adjustment was also evidenced by genes related to proline (e.g. delta-1-pyrroline-5-carboxylate synthase, *P5CS*; *P5C* dehydrogenase, *P5CDH*; ornithine aminotransferase, *OAT*), inositol (e.g. myo-inositol oxygenase; inositol-triphosphate

5- phosphatase 2 – like), carbohydrate metabolism (such as beta-amylase, endochitinase, malate dehydrogenase, sucrose synthase, starch synthase) as well as late embryogenesis abundant genes (*LEA* 4, 5- D, 14-A) that showed significantly up or down-regulation (Brosché et al. 2005; Street et al. 2006; Peng et al. 2012; Yan et al. 2012; Spieβ et al. 2012; Tang et al. 2013, 2015; Chen et al. 2013; Pucholt et al. 2015).

Detoxification, Damage Control and Repair

In the desert poplar *Populus euphratica*, a great diversity of heat shock proteins (HSPs) (including transcripts for DNAJ heat shock family proteins, members of small HSPs, HSP70, HSP90, HSP100), heat shock transcription factors (e.g. HSFA2, HSF4, HSFC1) and chaperonins were induced by all the different drought levels (Caruso et al. 2008; Wisniewski et al. 2008; Cohen et al. 2010; Peng et al. 2012; Thumma et al. 2012; Chen et al. 2013; Yan et al. 2012; Tang et al. 2013; Pucholt et al. 2015). Such molecules are involved in protein repair and protection against denaturation, which are normally synthesized in response to abiotic stress such as drought and high temperatures. That many more genes for heat-shock proteins and regulatory factors that were found in *P. euphratica* compared to other species (Spieβ et al. 2012) might suggest that this species has evolved a robust mechanism for preventing proteins from being denatured in harsh environments combining both water depletion and high temperatures. In accordance with ROS production and detoxification processes, up-regulation of raffinose, stachyose and galactinol synthases were detected in poplar leaves under drought. An increase in such compound could improve osmoprotection and ROS scavenging (Cohen et al. 2010; Hamanishi et al. 2010). Finally, various stress proteins were shown to be differentially regulated under drought stress: PR proteins (e.g. chitinase, osmotin, PR protein 1, peroxidase, thaumatin-like proteins), dehydration proteins (early-responsive to dehydration stress protein ERD4, ERD6, ERD7 and ERD15; dehydrin LEA; dehydration responsive factor RD19, RD21, RD22, RD26; drought-induced DI19, DI21; xerico), salt tolerance proteins (salt tolerance zinc finger proteins) as well as low temperatures induced genes (e.g. cold-regulated *LTCOR12*; rare-cold-inducible *RCI2A*, *RCI2B*; frostbite 1) (Bogeat-Triboulot et al. 2007; Caruso et al. 2008; Wisniewski et al. 2008; Cohen et al. 2010; Hamanishi et al. 2010; Thumma et al. 2012; Spieß et al. 2012; Yan et al. 2012; Chen et al. 2013; Pucholt et al. 2015).

Conclusion

Climate change, conducing notably to extreme drought events, affects forest tree survival worldwide. This emphasizes the need to better understand the mechanisms of tree adaptation to abiotic stress. Angiosperm tree species show a remarkable plasticity that shapes tree evolution and distribution. They respond to adverse changing environmental conditions via a series of physiological, cellular, and molecular processes culminating in stress tolerance. Such processes were shown to

be under a tight genetic control and a great variability of gene expression was found across species, but also within the same tree species.

Future studies making use of comparative genomic approaches have the potential to provide new insights into the evolution and diversification of drought response strategies in various angiosperm tree species and taxa. One critical aspect for future studies is to develop standardized experimental conditions for imposing drought treatments, and standardized methods for measuring drought response traits and sampling tissues for genomic analysis. Such efforts would greatly enhance the ability to make comparisons among species, and begin to systematically describe and quantify drought response mechanisms within and across species. These future studies have the potential to make significant contributions not only to the basic biology of drought response in angiosperm trees, but also to the development of cultivars resilient to drought and other abiotic stresses.

Glossary

Isohydric water-balance behavior involves the maintenance of a constant leaf water potential at midday, even under drought conditions. In contrast, plants exhibiting anisohydric behavior can markedly decrease water potentials following the evaporative demand experienced during the day. This permits lower leaf water potentials in the presence of drought stress.

Mesophyll conductance (g_m) estimates the restriction to the influx of carbon dioxide from the leaf internal airspace to the site of carboxylation. Together with stomatal conductance, it constitutes a crucial component of the diffusive limitation of photosynthesis.

Ψ_{crit} critical xylem water potential, beyond which hydraulic failure is likely to occur, expressed in megapascals (MPa)

Ψ_{soil} soil water potential (MPa)

Stomatal conductance usually measured in mmol m^{-2} s^{-1}, is the measure of the rate of water vapor exiting through the stomata of a leaf, from which one can estimate the rate of carbon dioxide (CO_2) entering.

Vapour Pressure Deficit (VPD) is the difference between the amount of moisture in the air and saturated vapour pressure, i.e. how much moisture the air can hold when it is saturated, at a certain temperature.

Water use Efficiency (WUE) represents the tradeoff between C assimilation and water loss, expressed as the ratio of C assimilated, e.g. in term of biomass or photosynthetic rate, to the rate of transpiration.

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