

How tree roots respond to drought

Ivano Brunner^{1*}, Claude Herzog^{1,2}, Melissa A. Dawes¹, Matthias Arend³ and Christoph Sperisen¹

¹ Forest Soils and Biogeochemistry, Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland, ² Swiss Federal Institute of Technology Zürich, Zürich, Switzerland, ³ Forest Dynamics, Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland

OPEN ACCESS

Edited by:

Boris Rewald,
University of Natural Resources
and Life Sciences, Austria

Reviewed by:

Bernhard Schuldt,
Georg-August-Universität Göttingen,
Germany
Sergi Munné-Bosch,
University of Barcelona, Spain

*Correspondence:

Ivano Brunner,
Forest Soils and Biogeochemistry,
Swiss Federal Institute for Forest,
Snow and Landscape Research WSL,
Zürcherstrasse 111,
CH-8903 Birmensdorf, Switzerland
ivano.brunner@wsl.ch

Specialty section:

This article was submitted to
Functional Plant Ecology,
a section of the journal
Frontiers in Plant Science

Received: 15 May 2015

Accepted: 06 July 2015

Published: 29 July 2015

Citation:

Brunner I, Herzog C, Dawes MA,
Arend M and Sperisen C (2015) How
tree roots respond to drought.
Front. Plant Sci. 6:547.
doi: 10.3389/fpls.2015.00547

The ongoing climate change is characterized by increased temperatures and altered precipitation patterns. In addition, there has been an increase in both the frequency and intensity of extreme climatic events such as drought. Episodes of drought induce a series of interconnected effects, all of which have the potential to alter the carbon balance of forest ecosystems profoundly at different scales of plant organization and ecosystem functioning. During recent years, considerable progress has been made in the understanding of how aboveground parts of trees respond to drought and how these responses affect carbon assimilation. In contrast, processes of belowground parts are relatively underrepresented in research on climate change. In this review, we describe current knowledge about responses of tree roots to drought. Tree roots are capable of responding to drought through a variety of strategies that enable them to avoid and tolerate stress. Responses include root biomass adjustments, anatomical alterations, and physiological acclimations. The molecular mechanisms underlying these responses are characterized to some extent, and involve stress signaling and the induction of numerous genes, leading to the activation of tolerance pathways. In addition, mycorrhizas seem to play important protective roles. The current knowledge compiled in this review supports the view that tree roots are well equipped to withstand drought situations and maintain morphological and physiological functions as long as possible. Further, the reviewed literature demonstrates the important role of tree roots in the functioning of forest ecosystems and highlights the need for more research in this emerging field.

Keywords: abscisic acid, avoidance, carbon sequestration, hydraulic signals, molecular responses, mycorrhizas, tolerance, tree root traits

Introduction

The ongoing climate change is characterized by increased temperatures and altered precipitation patterns. In addition, the frequency, intensity and duration of extreme climatic events, such as droughts, floods, and storms, has increased in recent decades, and a continuation of this trend is predicted (IPCC, 2007, 2014; Cavin et al., 2013). These changes in environmental conditions are affecting terrestrial ecosystems worldwide and have led to a reduction in the global net primary production (Zhao and Running, 2010). Specifically, negative impacts on forest health associated

with water limitation are major contributors to forest declines at a global level (Allen et al., 2010; Smith, 2011; Choat et al., 2012; Anderegg et al., 2013b).

Drought is a multidimensional environmental constraint that can provoke tree responses from the molecular to the forest stand level (Hamanishi and Campbell, 2011). Negative impacts of drought are observed in many aspects of forest health including seedling recruitment, productivity and mortality of larger/mature trees, susceptibility to pathogen or insect attack, and vulnerability to damage from fire (Zhao and Running, 2010; Reichstein et al., 2013). Consequently, there is considerable demand for an improved understanding of how forest trees respond to drought in order to develop strategies for the preservation of forest tree growth and survival in the face of this particular environmental threat (Hamanishi and Campbell, 2011).

Tree root systems are key components of forest ecosystems: they are responsible for water and nutrient uptake, provide physical stabilization, store nutrients and carbohydrates, and provide C and nutrients to the soil through the process of fine-root turnover (Brunner and Godbold, 2007). In addition, roots may act as sensors for water-deficit conditions and send signals to shoots above ground (Hamanishi and Campbell, 2011). Recent reviews and commentaries about drought in connection with forests or trees demonstrate that most existing research has focused on aboveground tree parts (e.g., McDowell et al., 2008; Hamanishi and Campbell, 2011; Ryan, 2011; Harfouche et al., 2014). In contrast, the responses of tree roots to drought and their role under drought conditions remain unclear and are only marginally mentioned or even neglected entirely in such reviews. Roots are generally less well analyzed than aboveground organs because they are difficult to observe, particularly *in situ*, and methods tend to be laborious, imprecise, and difficult to standardize across experiments.

In total, roots are estimated to make up 20–40% of the biomass of trees (Jackson et al., 1997). Compared to herbaceous plants, root systems of forest trees are complex because they contain roots that differ in morphology and size. Coarse roots (>2 mm in diameter) are responsible for anchoring trees to the soil and serve as organs to transport water from deeper soil horizons. Fine roots (<2 mm in diameter) are important for the uptake of water and nutrients. Fine roots are typically described by several different traits such as biomass, lifespan, specific root length (SRL), C/N ratio, and lignin content. Because fine roots turn over, they provide carbon and nutrients to the soil and, thus, play an important role in carbon sequestration and carbon cycling (Brunner and Godbold, 2007). There is increasing evidence that drought can influence the structure and growth of both coarse and fine tree roots (Kozłowski and Pallardy, 2002). In this review, we summarize and discuss the current understanding of how roots of forest trees respond to dry conditions. We first summarize growth, anatomical, physiological, biochemical, and molecular responses. We then elucidate the role of mycorrhizas in drought resistance, and finally we assess the effects of drought on root traits and the potential consequences for root decomposability, soil organic matter (SOM) formation and SOM persistency.

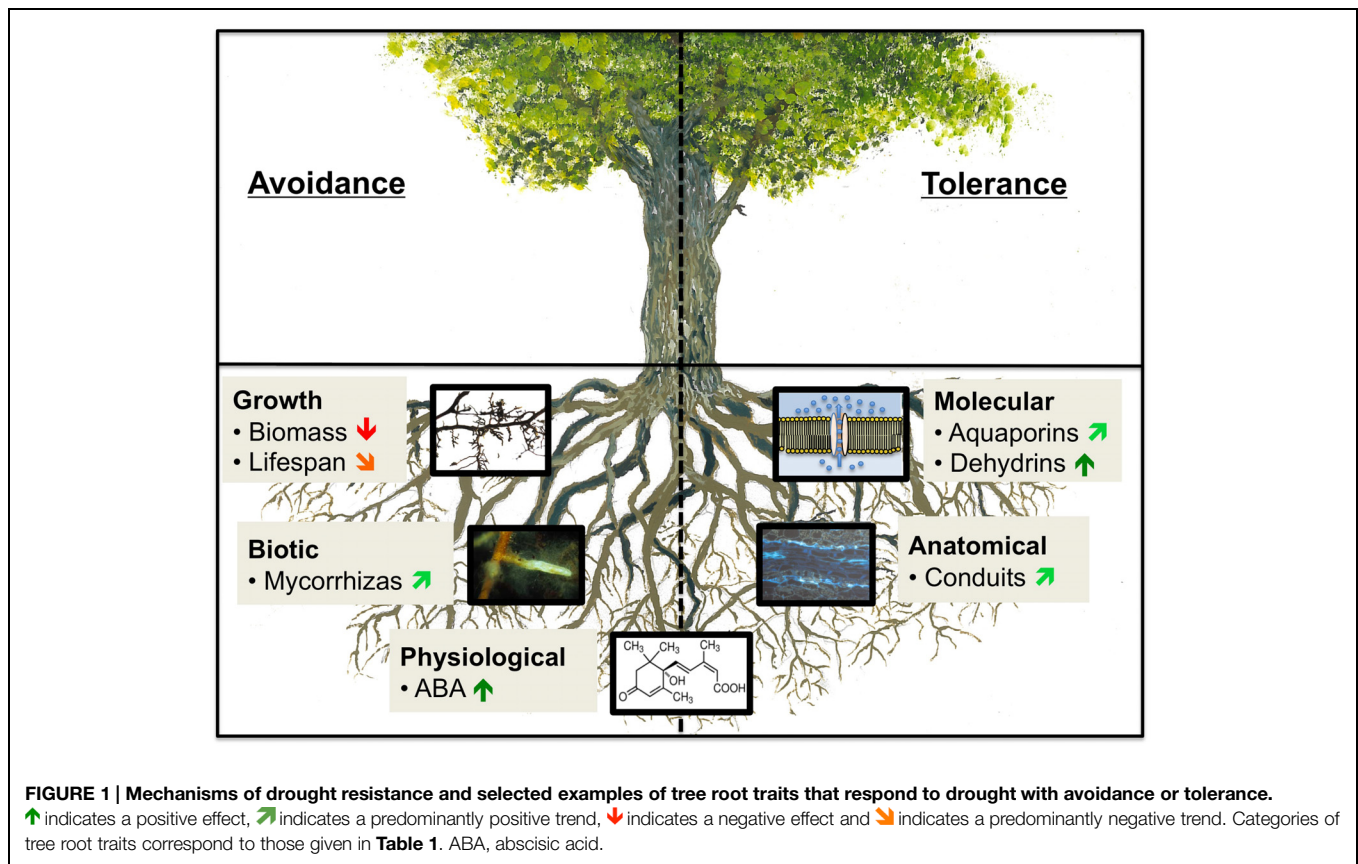
Drought Avoidance and Drought Tolerance

Evidence from physiological, biochemical, and molecular studies suggest that plants have evolved a variety of strategies to cope with drought. These strategies can be divided into those that enable plants to avoid low water potentials and those that enable them to tolerate dehydration (Levitt, 1972; Verslues et al., 2006; **Figure 1**). Strategies to avoid low water potentials rely on mechanisms that maintain the plant's water status, such that the rates of water loss and water uptake remain balanced. Water loss can be limited by stomatal closure and over the longer term by restricting shoot growth, leading to an increased root-to-shoot ratio. Water uptake can be increased through enhanced root fine growth, formation of deep taproots, and accumulation of solutes to lower the water potential in the root tissue. When drought levels become too severe and drought avoidance mechanisms are no longer sufficient, plants respond by activating mechanisms that protect tissues against cellular damage, mainly through the action of protective solutes and proteins (Tuberosa, 2012; Claeys and Inzé, 2013). The physiological integrity of a plant is preserved as long as avoidance and/or tolerance mechanisms are adequate to avoid damage to cellular functions.

Unlike herbaceous plants, woody plants are characterized by extensive secondary growth, which itself can respond to drought conditions. For example, the diameter of the xylem conduits, responsible for the transport of water, and the thickness of their cell walls can be modified, resulting in increased resistance against cavitation in the vascular tissues (Kozłowski and Pallardy, 2002). Consequently, trees seem to have evolved mechanisms to cope with dehydration conditions that are distinct from those of herbaceous plants.

Growth Responses

It is well documented that tree species adapted to dry climatic regimes generally have higher root-to-shoot ratios and deeper root systems than species that are more suited to mesic climatic conditions (Kozłowski and Pallardy, 2002; Hartmann, 2011). A meta-analysis of forest and woodland species from temperate and tropical regions showed a significant increase in the root-to-shoot ratio with a decrease in annual precipitation, from about 0.2 at 3000 mm year⁻¹ to about 0.4 at 500 mm year⁻¹ (Mokany et al., 2006). Similarly, in a survey of 62 tropical tree species, seedlings from dry forests were found to have a higher belowground biomass and deeper roots than seedlings from moist forests (Markesteyn and Poorter, 2009). Therefore, tree species adapted to dry conditions tend to invest more biomass into longer-lasting root organs, thus optimizing water uptake, while simultaneously minimizing water loss from transpiration. These patterns have contributed to the hypotheses that trees respond to water deficit by increasing root-to-shoot ratios and rooting depth (Mainiero and Kazda, 2006; Poorter et al., 2012). Field and laboratory manipulation experiments have indeed shown that many tree species respond to dry conditions with altered allocation to root and shoot growth. In *Populus euphratica*, for example,



gradual water depletion led to a reduction of shoot growth, while root growth was maintained, particularly in the early phase of water depletion, leading to an increased root-to-shoot ratio (Bogeat-Triboulot et al., 2007). Results of a meta-analysis of a large number of experiments, including studies focused on trees, indicate that this growth response is strongly influenced by the severity of the stress (Poorter et al., 2012). Plants exposed to moderate water deficit generally show little change in their growth pattern, with only a small increase in the root biomass relative to the total biomass [root mass fraction (RMF)]. It seems that plants maintain their aboveground growth, and thus their competitiveness for aboveground resources, as long as possible under moderate drought. In contrast, plants exposed to severe drought, i.e., when the biomass is reduced by >50% of that of control plants, respond with a strong increase in RMF, largely due to a decrease in the growth of the stems (Poorter et al., 2012).

Variability in growth responses among studies may also be a consequence of genetic variation at both the species and population level. For example, research carried out on two poplar species revealed significant differences in the root-to-shoot ratio under drought treatment (Yin et al., 2004). Similarly, in a model ecosystem experiment including young oak trees, shoot growth responded more sensitively to drought than root growth, but this growth response differed between populations (Arend et al., 2011; Kuster et al., 2013).

Although the root-to-shoot ratio tends to increase under drought conditions, the biomass of fine roots in particular is

often reduced as a consequence of reduced transpiration and respiration rates. This response has been shown repeatedly using field and laboratory experiments (e.g., Joslin et al., 2000; Konôpka et al., 2007; Rühr et al., 2009; Eldhuset et al., 2013; Herzog et al., 2014; Zang et al., 2014), across precipitation gradients (Leuschner et al., 2004; Meier and Leuschner, 2008a), and in meta-analyses of a number of studies (Cudlin et al., 2007; Yuan and Chen, 2010). Along with reduced fine root biomass, root length and root tip frequency typically decrease as well (e.g., Rühr et al., 2009; Eldhuset et al., 2013; Zang et al., 2014). However, other root traits, such as SRL, root tissue density (RTD), and root area index (RAI), often remain unchanged, as shown for oak (*Quercus* sp.) saplings exposed to drought (Arend et al., 2011) and in a semi-arid pine (*Pinus sylvestris*) forest that was irrigated (Herzog et al., 2014). A recent meta-analysis indicated that SRL seems to be especially resistant to drought, although SRL values varied greatly among the analyzed studies (Ostonen et al., 2007). On the other hand, a greenhouse experiment using 1-year-old seedlings of ten different tree and shrub species revealed that fine roots (diameter < 2 mm) had a reduced biomass under drought conditions, whereas very fine roots had an increased biomass (diameter < 0.5 mm; Olmo et al., 2014). In the same study, very fine roots had an increased SRL and RTD under drought but a smaller mean root diameter and a lower N concentration.

Whether a tree maintains old roots or sheds old roots and produces new ones in response to drought is, according to Eissenstat et al. (2000), determined by the benefit to cost ratio

in terms of water uptake and carbon expenditure. Root shedding and the construction of new roots mean the investment of a considerable amount of energy in the process of root turnover. The benefit, however, is that young roots are able to take up water more efficiently than older ones, and thus, root shedding and regrowth represent a more suitable acclimation of plants to reduced water supply if the plant can afford this strategy. In a throughfall exclusion experiment using sub-canopy roofs, Gaul et al. (2008) concluded that fine root production was stimulated under mild drought (soil water matrix potential of -0.06 MPa), suggesting a compensation for enhanced mortality due to water shortage, whereas fine root mortality occurred without replacement under stronger drought conditions (-0.12 MPa). However, other factors, such as soil conditions and climate, may strongly influence the response of fine root systems to reduced soil water content (Gaul et al., 2008). For example, Persson et al. (1995) observed that fine roots of Norway spruce trees in Sweden shifted into deeper mineral soil horizons in response to experimentally induced drought, whereas Blanck et al. (1995) did not find such redistribution in a similar experiment in Germany with the same species. Finally, in a study with young oak trees, Kuster et al. (2013) found a redistribution of root biomass under drought conditions and a general reduction of the total root biomass.

Having a reduced root biomass under drought conditions does not necessarily imply that root production and root turnover rate are reduced as well. There are various methods and formulae to assess and calculate turnover rates of roots, and therefore results are often controversial (Gaul et al., 2009; Gaudinski et al., 2010; Lukac, 2012; Brunner et al., 2013; Ahrens et al., 2014). In their study of a *Picea abies* forest using rainfall exclusion treatments, Gaul et al. (2008) found a slightly higher turnover rate in the drought treatment compared to the control treatment, whereas Brunner et al. (2009) did not find any significant changes in turnover rate with an irrigation treatment in a *Pinus sylvestris* forest in a semi-arid area. On a global scale, root production and turnover rate were not correlated with mean annual precipitation but with mean annual temperature (Gill and Jackson, 2000; Finér et al., 2011). However, a meta-analysis by Yuan and Chen (2010) indicated a slightly significant correlation of tree root production and turnover rate with mean annual precipitation: lower water availability corresponded to a lower root turnover rate.

Analyses of root lifespan, the reciprocal value of turnover rate, indicate that lifespan tends to become shorter if water availability is hampered (Eissenstat et al., 2013). McCormack and Guo (2014) proposed a conceptual model indicating that root lifespan most likely depends on water availability. Adding water and alleviating drought should increase whole-plant productivity and increase root lifespan (Mainiero and Kazda, 2006; Meier and Leuschner, 2008b). However, additional water applied to an environment that already has adequate moisture may in fact reduce root lifespan (Leppälampi-Kujansuu et al., 2014), as a greater frequency of anoxic conditions increases root stress and pressures from external factors (McCormack and Guo, 2014). As suggested by Prieto et al. (2012), hydraulic redistribution may also play a role in mediating responses of fine roots to

drought. In a study by Bauerle et al. (2008) using the woody shrub *Vitis vinifera*, the lifespan of fine roots growing in dry soil was reduced in the absence of hydraulic redistribution. However, when conditions allowed for a redistribution of water from wetter soil to dryer soil, the lifespan of roots in dry soil was maintained at the same level as roots under conditions without water stress (McCormack and Guo, 2014). In a review of root lifespan, Chen and Brassard (2013) found that fine root lifespan did not change with soil water addition when evaluated using pooled lifespan data but was marginally longer with water addition when evaluated based on the size of the treatment effect.

A compilation of the above-mentioned root traits of trees and the responses to drought is given in **Table 1**.

Anatomical Responses

Water transport in trees is dependent on plant branching architecture, plant size, and plant developmental stage (Mencuccini, 2015). Compared to stems and branches, studies on the anatomical characteristics of the water transport system in roots are very limited. Xylem conduits are assumed to narrow from the roots to the stem and further to the branches and leaf petioles, in order to achieve an optimal structure for the functioning of the vascular elements (e.g., Tyree and Zimmermann, 2002). This assumption was confirmed in recent studies, where the xylem conduit diameters in roots and in aboveground parts of temperate, boreal, and tropical tree species were investigated (e.g., Lintunen and Kallioikoski, 2010; Schuldt et al., 2013). Conduit tapering is commonly believed to control water distribution. By having the lowest conductivities in the minor branches at the end of the flow path, a plant can control the distribution of water regardless of the transport distance. As the most distal organs belowground, fine roots can be sacrificed in response to drought, similar to leaf fall, as observed in various temperate and boreal forests (e.g., Gaul et al., 2008; Chenlemuge et al., 2013; Hertel et al., 2013). Kotowska et al. (2015) postulated a mechanism for fine root die off analogous to that of leaf abscission by defining a 'hydraulic fuse,' a concept evolved from Zimmermann's segmentation hypothesis (Tyree and Zimmermann, 2002). At the root level, this 'hydraulic segmentation' might additionally protect the belowground system from a reverse water flow from the roots back to the dryer soil (Kotowska et al., 2015).

Due to secondary growth, trees have the ability to respond to low water conditions by modifying their vascular tissues (Kozłowski and Pallardy, 2002; Fonti and Jansen, 2012). At the level of individual conduits, there is a tight proportionality between conduit wall reinforcement and cavitation resistance (Hacke et al., 2001). Additionally, the formation of smaller vessels under drought has been observed in stems of various tree species, such as *Quercus* sp. and *Populus* sp. (Arend and Fromm, 2007; Fonti et al., 2013). It was further suggested that smaller vessels may be less susceptible to drought-induced xylem embolism and that they also contribute to the regulation of water flow under water-limiting growth conditions. To date,

TABLE 1 | Effects of drought on tree root traits and potential consequences for root decomposability, soil organic matter (SOM) formation, and SOM persistency.

Root trait categories	Root traits	Effect of drought	Consequences for		
			Root decomposability	SOM formation	SOM persistency
Growth	Biomass	↓	→	↓	→
	Lifespan	↘	→	→	→
	Mortality	↗	→	↗	→
	Production	↘	→	↘	→
	Turnover rate	↘	→	→	→
Architectural	Branching	→	→	→	→
	Length	↘	→	↘	→
	Rooting depth	↗	→	↗	→
	Tip frequency	↘	→	↘	→
Morphological	Diameter	↘	↗	→	→
	Root area index (RAI)	→	→	→	→
	Root tissue density (RTD)	→	→	→	→
	Specific root length (SRL)	→	→	→	→
Anatomical	Conduits	↗	↘	→	↗
Biotic	Mycorrhizas	↗	→	→	↗
Chemical	Carbon (C)	↘	→	→	→
	Nitrogen (N)	↗	→	→	↗
	Phosphorus (P)	↘	↘	→	↘
	C/N ratio	↘	→	→	→
	N/P ratio	↗	↗	→	↗
Biochemical	Cellulose	→	→	→	→
	Lignin/Phenolics	↗	↘	→	↗
	Suberin/Aliphatics	↗	↘	→	↗
Physiological	Abscisic acid (ABA)	↗	→	→	→
	Exudates	↘	↘	→	→
	Proline	↗	→	→	→
	Respiration	↓	→	→	→
	Starch	↘	↘	→	↘
	Sugars/NSC	→	→	→	→
Molecular	Aquaporins	↗	→	→	→
	Chaperons	↗	→	→	→
	Dehydrins	↗	→	→	→

↗ indicates a positive effect, ↘ indicates a predominantly positive trend, ↓ indicates a negative effect, ↘ indicates a predominantly negative trend, → indicates predominantly no effect (categories of root traits and individual root traits are adapted from Brunner et al., 2009; McCormack et al., 2012; Comas et al., 2013; Bardgett et al., 2014). SOM, soil organic matter; NSC, non-structural carbohydrates.

little is known about root anatomical responses to drought. Eldhuset et al. (2013) showed that tracheid diameters and hydraulic conductivity of young drought-stressed *Picea abies* were significantly lower and that tracheids were flatter in trees subjected to severe drought than in control trees, for both long and short roots. Both the reduction in tracheid size and the change to more ellipsoid tracheids might be responsible for the decrease in conductivity in the drought stressed roots (Eldhuset et al., 2013).

The role of Abscisic Acid and Hydraulic Signals in the Drought Response

Evidence from physiological and genetic studies demonstrates that many physiological responses of plants to drought, avoidance as well as tolerance responses, are mediated by the

plant hormone abscisic acid (ABA), although the underlying mechanisms are not fully understood yet (Munns and Cramer, 1996; Claeys and Inzé, 2013).

Abscisic acid is produced in roots as well as in leaves (De Smet and Zhang, 2013), and levels in both plant parts increase upon exposure to drought and are accompanied by major changes in gene expression and physiological responses, such as stomatal closure. ABA has been generally regarded as a hormone with different regulatory properties in growth and development. Under non-stressed conditions, low concentrations of ABA promote root meristem maintenance and root growth (Sharp et al., 2000), whereas under drought conditions enhanced ABA concentrations inhibit growth (Nakashima and Yamaguchi-Shinozaki, 2013). Based on this observation, ABA has been commonly considered a growth limiting stress hormone (Quarrie and Jones, 1977; Trewavas and Jones, 1991). However, the actual role of ABA as a growth-limiting hormone remains obscure, as

contradictory findings suggest an opposite function (Sharp et al., 1994, 2000, 2004; Arend and Fromm, 2013). Genetic evidence that ABA plays a role in growth control comes from a study analyzing a transgenic poplar line that ectopically expresses the mutant *Arabidopsis abil* gene (Arend et al., 2009). Expression of this gene resulted in an ABA-insensitive phenotype with enhanced shoot growth but retarded leaf and root development. This altered growth pattern supports the hypothesis that ABA acts independently from drought as a negative regulator of growth in shoots and as a positive regulator of growth in leaves and roots.

Abscisic acid is transported from roots to leaves, where it acts as a long-distance signal inducing the closure of stomata and triggers the expression of ABA biosynthesis genes and, thus, increases the ABA content in leaves (De Smet and Zhang, 2013). It is likely that both mechanisms are required to induce stomatal closure. However, recent studies question the role of root-born ABA in stomatal closure and instead propose electrical and hydraulic root signals (Christmann et al., 2007, 2013; Schachtman and Goodger, 2008). Electrical signals emanating from water-stressed roots, or from roots after re-irrigation as shown in young avocado plants (*Persea americana*), might be relayed independently from hydraulic signals (Grams et al., 2007; Gil et al., 2008). Root-derived hydraulic signals result in local water potential (Ψ) changes and, concomitantly, in turgor changes that can be compensated with solute adjustments (Christmann et al., 2007). The changes in Ψ are relayed into the inner stele of the roots and increase the tension on the water in the xylem vessels for rapid long-distance signaling. This hydraulic signal is transmitted along the root axis and perceived by parenchyma cells in the shoots, which are sites of ABA biosynthesis (Endo et al., 2008; Christmann et al., 2013). In the shoots, the hydraulic signal promotes the closure of stomata via a biochemical effect on guard cells and via an indirect hydraulic effect, i.e., a decrease in water permeability within leaf vascular tissues (Pantín et al., 2013).

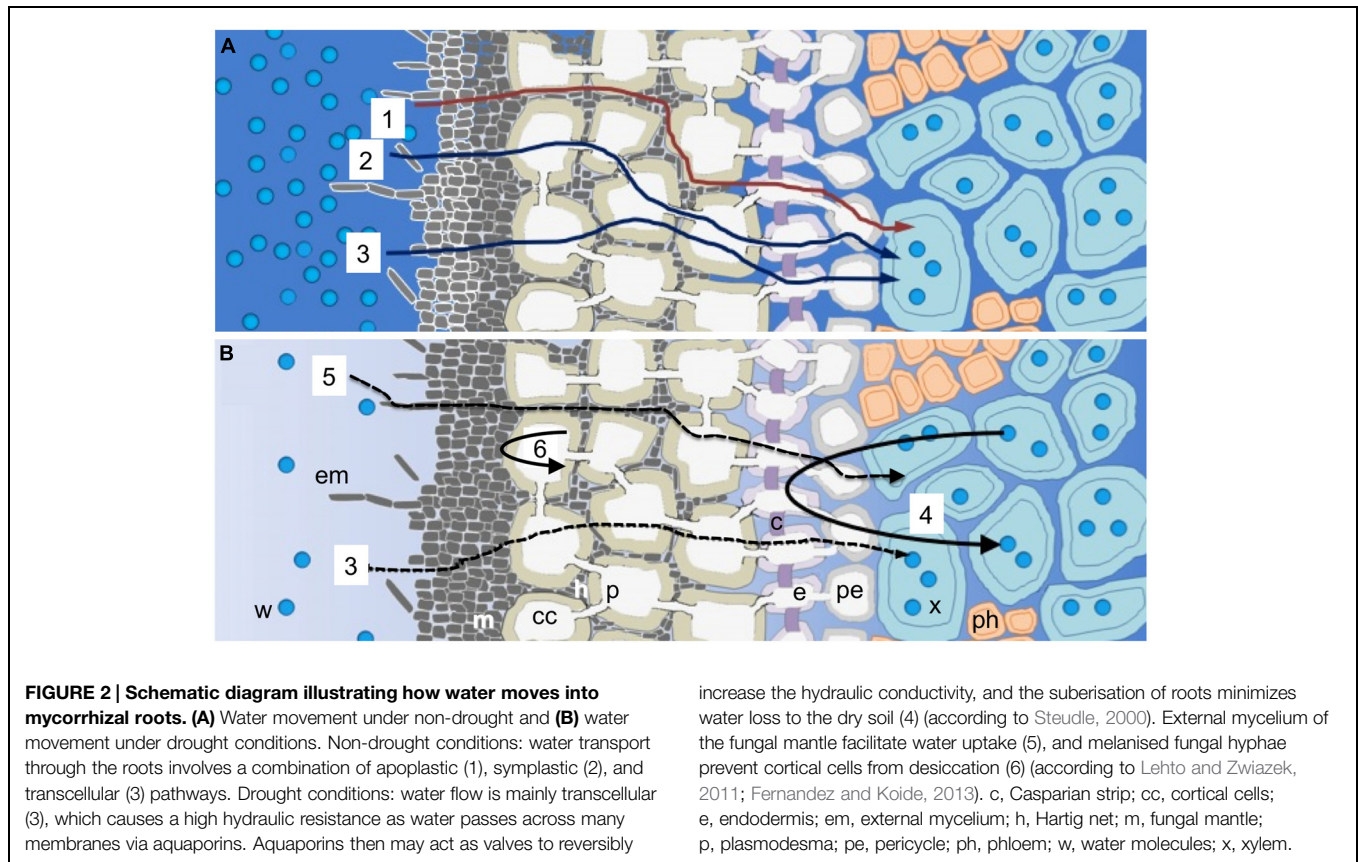
Water always follows a water potential gradient, and thus dehydration in roots can be avoided through a reduction in hydraulic conductivity and osmotic potential. In this context, ABA in roots also mediates an enhancement of the biosynthesis of osmolytes, such as the amino acid proline, and of protective proteins (Davies and Bacon, 2003). However, only a few studies have demonstrated distinctly enhanced proline concentrations in the roots of trees after a drought treatment (Sofó et al., 2004; Cocozza et al., 2010; Naser et al., 2010). In particular, proline plays a dual role as both osmolyte and osmoprotectant ('osmotic adjustment'; Kozłowski and Pallardy, 2002; Claeys and Inzé, 2013). Root water uptake and distribution is controlled by water channel (aquaporin) activity (Almeida-Rodríguez et al., 2011). Under drought conditions, ABA increases aquaporin expression, which translates into increased hydraulic conductance (water uptake at the soil-root interface; Parent et al., 2009).

Water transport through the roots involves a combination of three different pathways: the apoplastic path (around the protoplasts), the symplastic path (through the plasmodesmata), and the transcellular path (across the cell membranes) (Steudle and Peterson, 1998; **Figure 2**). The transcellular water movement

is tightly controlled by the amount and activity of water channels (aquaporins) in the cellular membranes (Chaumont and Tyerman, 2014). There is a rapid exchange of water between parallel radial pathways because, in contrast to solutes such as nutrient ions, water permeates cell membranes readily. The apoplastic barriers consist of the Casparian bands and the suberin lamellae in the exo- and endodermis of roots. By switching the apoplastic path on or off, water uptake is regulated according to demands from the shoots (Steudle, 2000). At high rates of transpiration, the apoplastic pathway is partially used and the hydraulic resistance of roots is low and evenly distributed across the root cylinder, allowing for rapid uptake of water. On the contrary, at low rates of transpiration such as during drought conditions, the apoplastic pathway is used less. Instead, water flow is mainly transcellular, which causes a high hydraulic resistance as water passes across many membranes via aquaporins in its passage across the root cylinder (Steudle, 2000). During conditions of water deficit, the suberisation of roots minimizes water loss to the dry soil. Aquaporins then may act as valves to reversibly increase the hydraulic conductivity and allow for water uptake under drought conditions. It has been shown that aquaporins can be activated by phosphorylation, which, in turn, is affected by factors such as Ψ , turgor, or Ca^{2+} concentration in the apoplast (Steudle, 2000).

Non-Structural Carbohydrates, Carbon and Nitrogen

Important components of the C budget are non-structural carbohydrates (NSC) such as starch and sugars. Thus, the amount of NSC may reflect the drought status of trees, although such compounds are constantly consumed by fine-root production, respiratory metabolism, and osmotic adjustments, eventually leading to a decline in NSC concentrations in later stages of drought (Gaul et al., 2008; McDowell, 2011). A recent study of beech saplings (*Fagus sylvatica*) did not show such a relationship between drought and fine-root starch and NSC concentrations except fructose, although photosynthesis and rhizosphere respiration decreased with increasing drought (Zang et al., 2014). This increased concentration of fructose in the fine roots could be interpreted as a response to soil drought, as this sugar lowers the osmotic potential in the plant as a precursor to enhanced water uptake. Regier et al. (2009) applied drought to two contrasting *Populus nigra* clones and observed two different strategies: the drought-adapted 'Poli' clone had significantly more starch but significantly less sucrose, glucose, and fructose in the roots in the drought treatment, whereas the drought-sensitive '58-861' clone had significantly less starch in the roots in the drought treatment, with the sugars remaining unchanged. It seems that the well-adapted clone from the dry site was not strongly stressed by water shortage, whereas photosynthesis was inhibited by drought in the less-adapted clone from the wet site, causing a reduction of carbohydrate allocation to the roots and inducing degradation of starch to maintain root respiration (Regier et al., 2009). In a study by Galvez et al. (2011) using seedlings of aspen (*Populus tremuloides*), it appeared that they



were adapted to drought, because they were able to switch from growth to root reserves storage. The drought stressed seedlings showed a doubling of sugar and starch content in the roots, and roots of these seedlings contained more starch relative to sugar than those in the controls.

Contrasting results were shown in a drought experiment using two different *Nothofagus* species (*N. dombeyi*, *N. nitida*). Whereas the concentrations in the roots of *N. dombeyi* remained unchanged, *N. nitida* roots showed reduced starch and total soluble sugar (TSS) concentrations under drought conditions (Piper, 2011). An application of a lethal drought treatment to young *Picea abies* trees resulted in a significant decrease in starch and other sugars (Hartmann et al., 2013a), whereas plants that were watered again after a drought period (relative extractable soil water content below 3%) did not experience a significant change in starch and other sugar concentrations in the roots (Hartmann et al., 2013b). Mitchell et al. (2013) found a similar result when applying a lethal drought treatment to two eucalypt (*Eucalyptus globulus*, *E. smithii*) and one pine (*Pinus radiata*) species. Starch concentrations decreased significantly in the roots of all three tree species under drought, whereas the soluble sugar (SS) concentration decreased in the eucalypt roots but increased in the pine roots. All these results show that it is difficult to make general statements about NSC responses to drought.

Carbon (C) and nitrogen (N) concentrations in fine roots have been proposed to be associated with root functioning and are therefore often analyzed simultaneously with other root traits. In

the review of Sardans et al. (2012) about stoichiometric features, the authors reported an altered C/N ratio in roots under drought in only one tree species. *Quercus ilex*, a mediterranean tree species growing in semi-arid areas, showed a drought-induced decrease in C/N ratio but an increase in N/P and C/P ratios, due to reduced C and P concentrations as well as increased N concentrations (Sardans et al., 2008). Similarly, in a more recent study by Herzog et al. (2014), irrigation of a drought suffering pine forest decreased the N concentration in fine roots; however, the C/N ratio and P concentration were not affected.

Suberin and Lignin Formation in Roots Under Drought Conditions

Suberin is a complex and poorly characterized biopolymer of root cell walls comprised of both aliphatic (fatty acid derivative) and aromatic (phenylpropanoid derivative) domains. It is an important component of endo- and exodermal cells, as well as cork cells of the periderm in woody plants (Soler et al., 2007; Ranathunge et al., 2011). The suberisation of roots minimizes water losses to the soil, in particular during conditions with a water deficit (Steudle, 2000). In addition, drought can induce the formation of suberin, as many different abiotic and biotic stresses can induce changes in cell wall composition (Moura et al., 2010). For example, it has been shown that the total concentration of aliphatic monomers in *Quercus ilex* roots from a dry environment

is much higher than that in roots of the same species from a moist environment (Andretta et al., 2013). Further, in roots of the grapevine *Vitis vinifera*, elevated suberin deposition was observed in drought-stressed plants (Vandeleur et al., 2009). Increased root suberin content was found to reduce daytime transpiration rates and increase water-use efficiency during the vegetative period (Baxter et al., 2009).

Lignin is a major component of the vascular plant cell wall, providing the mechanical support that allowed upright plants to adapt to a terrestrial habitat (Cabane et al., 2012). Drought apparently can result in wall tightening and thickening, as observed in the tracheids of drought-stressed Norway spruce roots (Eldhuset et al., 2013). Tightening appears to be caused by a number of mechanisms, including lignification of wall polymers (Moore et al., 2008). An increased amount of lignin improves the mechanical strength of cell walls in a dry environment, and cell wall lignification helps to minimize water loss and cell dehydration (Cabane et al., 2012).

Molecular Responses

Recent transcriptome analyses in roots of *Populus* sp. and *Pinus* sp. underpin several of the metabolic changes identified in physiological and biochemical studies (Wilkins et al., 2009; Cohen et al., 2010; Lorenz et al., 2011; Perdiguero et al., 2012). Comparative analyses of different genotypes led to the identification of several major gene clusters and regulators that are important in the response of roots to drought. Of the interrogated genes, 8% (5331 transcripts) were differentially expressed in poplar and 9% (2445 transcripts) in pine (Cohen et al., 2010; Lorenz et al., 2011). In both species, genes involved in ABA biosynthesis and signaling were differentially expressed. In particular, the 9-*cis*-epoxycarotenoid dioxygenase (*NCED*) gene, catalyzing the first dedicated step in the biosynthesis of ABA, was induced in both species, indicating that root ABA levels increased in response to drought. In pine, numerous transcription factors known to play a role in drought and abiotic stress via ABA-dependent and ABA-independent pathways were differentially expressed. Genes encoding putative DREB1, bZIP, AP2/ERF, MYB, NAC, and WRKY transcription factors were all up-regulated, but none of them was identified as a central node. Nevertheless, one of *WRKY* genes was induced both during drought stress and in the recovery phase and was suggested to play a key role in regulating drought responses. In poplar, several of the *WRKY* genes identified were up-regulated. Consistent with the results of biochemical studies, the transcriptome analyses of both species identified several genes involved in the biosynthesis of osmolytes. In poplar, genes encoding sucrose synthase, galactinol synthase, and raffinose synthase were all up-regulated. Similarly, genes encoding galactinol and raffinose synthases were induced in pine. In addition, several genes of pine with putative functions in the biosynthesis of proline were induced.

A large gene family commonly identified in drought response studies is the late embryogenesis abundant (LEA) protein family, which includes dehydrins. Their precise functions are not known, but they are believed to be involved in a number of protective

processes, including as hydration buffers, antioxidants and both enzyme and membrane stabilizers (Caruso et al., 2002). Dehydrins accumulate in root tissues in response to cellular dehydration caused by osmotic stress, and it is believed that they bind water in their random coil conformation and protect cellular structures from dehydration stress. The transcriptome analyses of both poplars and pines identified several members of this family to be induced. Similarly, several genes encoding chaperones/heat shock proteins (HSPs) and enzymes involved in scavenging reactive oxygen species (ROS) are up-regulated (Gosh and Xu, 2014).

Additional genes that were differentially expressed in the response of roots to drought included aquaporins. Aquaporins are a family of channel proteins that are found in cellular membranes and are responsible for water flux and thus play key roles in maintaining the water balance. The protein family can be grouped into five subfamilies, with the plasma membrane intrinsic proteins (PIPs) and the tonoplast intrinsic proteins (TIPs) representing the largest subfamilies (Gupta and Sankararamkrishnan, 2009). In poplar (*Populus trichocarpa*, *Populus balsamifera*, *Populus simonii x balsamifera*), a total of 56 aquaporins have been identified (Gupta and Sankararamkrishnan, 2009; Almeida-Rodriguez et al., 2010). Studies of the expression levels of aquaporins in roots using quantitative RT-PCR showed that an increase in root hydraulic conductance corresponded to increased transcript abundance of 15 aquaporins out of a total of 33 genes. A greater than twofold increase in expression level was found for two *PIPs*, two *TIPs*, and one *NIP*, whereas 2 *PIPs* showed a greater than twofold decrease in expression level (Almeida-Rodriguez et al., 2011). Root water flow and aquaporin expression patterns in hybrid poplars experiencing a sudden drop in humidity were shown to be tightly connected (Laur and Hacke, 2013). The rapid increase in root water flow corresponded to a 75% increase in the cumulative transcript copy numbers of all measured *PIP* genes, mainly due to a twofold increase in the transcript copy numbers of the *PIP1* genes, whereas no significant changes in the expression of *PIP2* genes occurred (Laur and Hacke, 2013). One gene, *PtPIP1;2*, which is consistently highly expressed in response to light (Almeida-Rodriguez et al., 2011), was also up-regulated in response to drought in the roots of *Populus nigra* (Cocozza et al., 2010). However, in the roots of the olive tree (*Olea europaea*), two *PIP* genes (*OePIP1;1*, *OePIP2;1*) were significantly down-regulated after water was withheld (Secchi et al., 2007). These results suggest that a single response of root *PIP* aquaporin expression and *PIP* protein abundance does not occur under drought conditions.

The Role of Mycorrhizas in Drought Resistance

Ectomycorrhizal (ECM) symbioses may improve the water status of trees under drought conditions, through an increased absorbing surface, efficient conduction through mycelial strands, enhanced hydraulic conductivity at the soil-root interface, and

hormonal and nutritional effects modifying stomatal regulation (Breda et al., 2006). According to Lehto and Zwiazek (2011), the clearest direct mechanism for increased water uptake is increased root extension and greater absorbing surface area through external mycelium, mainly by long-distance exploration mycorrhizal types. In a comparison of the root hydraulic conductivity of balsam poplar (*Populus balsamifera*) colonized by the ECM *Hebeloma crustuliniforme* with that of the same tree species colonized by the ectendomycorrhizal *Wilcoxina mikolae*, Siemens and Zwiazek (2008) observed a significant increase in root hydraulic conductivity by the presence of *H. crustuliniforme* but not *W. mikolae*.

Ectomycorrhizal fungi can additionally affect the cell-to-cell pathway through effects on plant aquaporin expression. Experiments on hybrid poplar (*Populus tremula x tremuloides*) seedlings inoculated with *Amanita muscaria* showed that for three of five investigated poplar PIP aquaporin genes, expression did not differ between ECM and non-ECM plants. However, expression of the two other aquaporin genes was more pronounced in roots of ECM plants, indicating that the root-fungus symbiosis may improve the water transport capacity under conditions of reduced water availability (Marjanović et al., 2005). However, ECM formation of the same poplar hybrid is also able to enhance the transcript abundances of aquaporin genes of the fungal symbiont. Transcript abundances of two genes of the ECM fungi *Laccaria bicolor* were enhanced more than twofold in the ECM formation, whereas gene expression of the other members of the aquaporin gene family were only minimally affected or, in one case, reduced by more than twofold (Dietz et al., 2011). In a study with jack pine (*Pinus banksiana*) seedlings inoculated with the ECM fungus *Suillus tomentosus*, a several-fold increase of the root hydraulic conductivity of ECM plants was observed compared to the non-ECM seedlings (Lee et al., 2010). This increase in water transport across the root cortex has been attributed to aquaporin-mediated transport, as measured by the indirect method of inhibiting the aquaporin activity with mercury. In another study using white spruce (*Picea glauca*) seedlings and the ECM fungi *Laccaria bicolor* wildtype (WT) or *L. bicolor* aquaporin over-expressing (OE) strain, OE plants had higher root hydraulic conductivity compared with WT plants and the increases were accompanied by higher expression of *P. glauca* PIP aquaporin expression in roots (Xu et al., 2015). Both WT and OE had increased shoot water potential, transpiration, net photosynthetic rate, root hydraulic conductivity, and root cortical cell hydraulic conductivity in comparison to non-ECM plants. These results lead to the conclusion that the contribution of *L. bicolor* hyphae to root water transport in *P. glauca* involves increased apoplastic water transport in the root intercellular spaces, which may lead to increased hydration at the fungal-root interface and, consequently, impact aquaporin expression and cell-to-cell water transport in ECM roots (Xu et al., 2015). As in the case of the basidiomycete *L. bicolor*, elevated aquaporin gene expression at the plant/fungus interface was also recently observed in hyphae of the ascomycete *Tuber melanosporum* (Hacquard et al., 2013). However, some studies have not shown positive effects of ECM fungi on aquaporin gene expression. A recent study using *Helianthemum almeriense*

and its fungal symbiont *Terfezia clavaryi* was conducted to investigate the expression patterns of five aquaporin genes from the plant and one from its fungal symbiont (Navarro-Ródenas et al., 2013). Results of this experiment indicated that the plant aquaporin genes were not enhanced in the roots by the ECM status and were even significantly reduced in one case. Further, Ψ of leaves of the ECM plants was not affected compared to non-ECM plants (Navarro-Ródenas et al., 2013).

The best-known indirect mechanism for ECM effects on water relations is probably improved nutrient status of the host due to facilitation of nutrient acquisition during drought. Other mechanisms include altered carbohydrate assimilation via stomatal function, possibly mediated by changes in growth regulator balance, increased sink strength in ECM roots, antioxidant metabolism, and changes in osmotic adjustment. None of these possibilities has been sufficiently explored. The ECM structure may also reduce water movement through improved fine root architecture (fungal mantle), cell wall hydrophobicity, or the larger number of membranes that water must cross on the way from the soil to the xylem (Lehto and Zwiazek, 2011). In addition, hydraulic redistribution can support nutrient uptake during prolonged dry periods. Soil water uptake displays a gradual downward shift as the soil dries, and a small fraction of total fine roots/ECM growing deeper in the soil ensures the overnight recovery of the soil-to-tree water potential equilibrium and supports a fraction of tree transpiration during periods of stomatal closure (Breda et al., 2006).

In a recent review, Mohan et al. (2014) concluded that the main effect of ECM associations is to reduce plant stress under drought conditions. They also indicated that the effects of the arbuscular mycorrhizal (AM) symbioses are similar to those reported for the ECM symbioses. Impacts of drought on AM and ECM abundance were mixed, with a slight majority of the studies finding decreased and a slight minority observing increased AM and ECM abundance with diminished soil moisture. Over half of the studies examining drought impacts on AM and ECM activity found no change in the rate of colonization, with the remainder nearly split equally between increased and reduced abundance. In most of the studies, AM and ECM increased plant productivity under drought conditions compared to non-AM/ECM plants. Similarly, while drought directly diminished rates of biogeochemical cycling in most of the studies, in two thirds of these studies biogeochemical rates were higher under drought conditions when plants were inoculated with AM and ECM compared with non-AM/ECM plants. In their meta-analysis on ECM, Cudlin et al. (2007) concluded that drought has a significant negative effect on ECM roots, although this effect was mainly due to the strong negative effect of drought on fine root biomass.

In a study of entire ECM communities, precipitation was found to have a significant effect on the ECM communities of oaks (*Quercus petraea*, *Q. robur*) throughout Europe, although pH and N-deposition were the main drivers (Suz et al., 2014). In contrast, Jarvis et al. (2013) found that precipitation and soil moisture had a strong influence on pine (*Pinus*

sylvestris) ECM in Scotland, and they identified several taxa with variable abundances across the rainfall gradient. The resupinate species *Piloderma sphaerosporum* showed a strong decline in abundance with increasing rainfall, whereas the hypogeous fungus *Elaphomyces muricatus* showed a markedly greater abundance in forests experiencing large amounts of rainfall. Surveys in beech (*Fagus sylvatica*) stands in France demonstrated a larger sensitivity of *Lactarius* sp. to declining soil water potential compared to *Cenococcum geophilum* (Jany et al., 2003). The latter fungus infected free root apices and expanded, while the other ECM declined due to soil water shortage. *C. geophilum* is often mentioned as a particularly drought-tolerant fungus, but this statement has little support from experimental research (Breda et al., 2006). Recent studies suggest that the production of melanin (a class of complex dark polymers), also found in the fungal cell walls of *C. geophilum*, might be a key functional trait in water stress tolerance (Fernandez and Koide, 2013). Melanized cell walls may help prevent water molecules from leaving the cells, thereby increasing the success of the symbioses in resisting desiccation. Herzog et al. (2013) indicated that, although increased temperature and drought negatively affected the relative abundance and enzyme activity of *C. geophilum*, this fungus was able to tolerate severe drought.

Tree Root Decomposability and the Role of Roots for Organic Matter Formation and Persistency

Root responses to drought clearly affect both the amount and traits of living and dead roots in forest ecosystems and, consequently, can have a strong influence on C dynamics and C sequestration in this environment. Living roots grow into soil and explore the soil matrix, and they constantly deposit decaying border cells and mucilage (rhizodeposition), exude enzymes, organic acids, ions and protons, and respire CO₂ to the surrounding soil (Jones et al., 2009). In doing so, roots initiate the weathering of parental rock material and the cycling of nutrients and trace elements (Hinsinger et al., 2009). In addition to contributing to the weathering of rocks and nutrient cycling, living roots have a stimulating effect on the microorganisms that live in the surrounding soil known as the ‘rhizosphere priming’ effect (Kuzyakov, 2002, 2010). Root deposits and exudates fuel microorganisms with easily accessible carbohydrates, which in turn results in the exudation of microbial organic molecules and ions and ultimately leads to the decomposition and transformation of the surrounding organic matter.

Water deficit caused by drought could slow down root growth and reduce the amount of rhizodeposition and exudation. Drought might also alter the quality of roots by enhancing suberin and lignin contents, two key compounds affecting root decomposability, which could influence the transformation of root material into SOM (Von Lütow et al., 2006). Under the ongoing global change, with higher temperatures and altered precipitation patterns, it is likely that shifts in SOM composition may result in overall changes in SOM quality and turnover

(Pisani et al., 2014). In particular, the accumulation of aliphatic root-derived compounds could be relevant because it gives SOM a hydrophobic protection (Dignac and Rumpel, 2013). Lignin, a second important compound, is mainly only degraded by a specific group of microorganisms, white-rot fungi and actinobacteria, which are able to secrete ligninolytic enzymes (Osono, 2007; Baldrian, 2008; Floudas et al., 2012). As a consequence, lignin content, and in particular the lignin/N ratio, is one of the driving forces in the decomposition of fine roots (Silver and Miya, 2001; Heim and Frey, 2004; Klotzbücher et al., 2011; Aulen et al., 2012; Talbot and Treseder, 2012; Talbot et al., 2012; Walela et al., 2014). Drought might affect the secretion and the activity of these extracellular ligninolytic enzymes, as the activity of such enzymes can vary considerably (Snajdr et al., 2011; Baldrian et al., 2013).

Alternatively, drought might shorten the lifespan of roots and accelerate root turnover (McCormack and Guo, 2014). After death, fine roots deliver a considerable amount of dead organic material to the decomposition process, and root-derived SOM plays a major role in C sequestration of forest soils (Rasse et al., 2005). However, under conditions of water deficit, dead roots are not decomposed completely and are instead transformed to a mor or moder type of humus. This can occur because the ‘rhizosphere priming’ effect is hampered (due to low rhizodeposition and exudation rates and due to low microbial activity), because the roots are more difficult to decompose (due to higher lignin and suberin content), or because key microorganisms such as lignin-degrading fungi are missing or inactive (Kuzyakov, 2010). In contrast, under conditions of sufficient water availability, dead roots are completely decomposed and transformed to a mull type of humus. As mentioned above, shifts in SOM composition might have long-term effects on SOM quality and turnover (Pisani et al., 2014).

As an intermittent disturbance of the water cycle, drought interacts with the C cycle differently than other ‘gradual’ changes in climate. During periods of drought, plants use species-specific strategies to respond physiologically and structurally in order to prevent excessive water loss. These responses have clear consequences for C uptake and release by plants. After a drought period, disturbances to soil moisture, organic matter, and nutrient content in the soil, and carbohydrate content in plants lead to longer-term effects on plant C (Van der Molen et al., 2011).

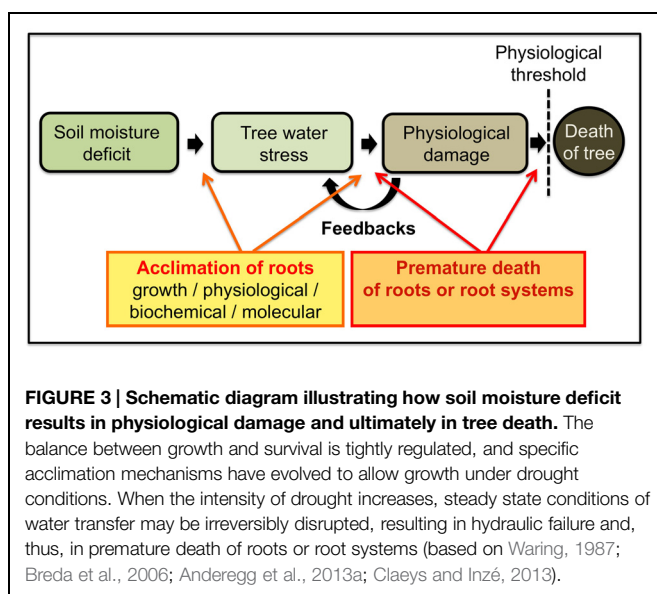
A compilation of root traits and consequences of drought on root decomposability, SOM formation, and SOM persistency is given in **Table 1**.

Feedbacks and Premature Mortality

As the intensity of drought increases, steady state conditions of water transfer in the xylem tissues may be irreversibly disrupted, due to water cohesion breakdown and massive xylem embolism (Anderegg et al., 2013a). The water stress of trees is then apparent as physiological damage that is associated with a number of characteristics, processes, and feedbacks that can impact tree health at various time scales

(Figure 3). One feedback of hydraulic failure is premature mortality of roots or root systems (Waring, 1987; Breda et al., 2006), which leaves a tree more vulnerable to drought the following year. In particular, damage that limits a tree's ability to make use of water or nutrients when they briefly become available again could interact with multi-year drought or other stressors to cause system failure (Anderegg et al., 2013b). Further, if a tree accumulates enough physiological damage, particularly over several years, and if the physiological damage crosses some threshold, tree death may occur (Anderegg et al., 2013b).

Increased mortality of trees during and after drought has been observed in recent years (van Mantgem et al., 2009; Anderegg et al., 2013b). However, the mortality process in trees is poorly understood, as indicated by Meir et al. (2015), and the question of how exactly trees are killed by drought remains unanswered (Hartmann et al., 2013a). Drought affects both tree hydraulics and C balance because trees, as with all vascular plants, respond to decreasing soil water availability with stomatal closure, thereby reducing C assimilation rates. Consequently, long-lived plants such as trees might be forced into a negative C balance, by mobilizing stored C to fulfill metabolic needs, until reserves are eventually depleted (McDowell et al., 2008; Sala et al., 2010). The physiological response of C depletion is closely linked to C reserves, particularly in the root system, which is a large sink for NSC. Roots are entirely dependent on the autotrophic parts of the plant and might require up to half of all the photosynthates produced (Lambers et al., 2008). A drought-stress study of the two poplar species *Populus tremuloides* and *P. balsamifera* indicated that reduced reserve accumulation in the root system during drought decreases the conversion of starch to SSs in roots (Galvez et al., 2013). This response probably contributes to the root death of drought-exposed poplars during the dormant season by compromising the frost tolerance of the root system.



However, recent evidence indicates that, under water deficit, the growth of sink organs such as roots is uncoupled from photosynthesis (Muller et al., 2011). There is usually a robust correlation between C availability and the growth of sink organs, but this relationship becomes weaker or is modified under drought conditions (Muller et al., 2011). Moreover, drought kills trees much faster than C starvation, and pools of stored C, in roots as well as in other organs, are not depleted at the time of death for drought-stressed trees the way they are for C starved, well-watered trees (Hartmann et al., 2013a). Investigating additional mechanisms of tree death due to drought, e.g., pathogen attack could be a priority in future research as well.

Root mortality, as mentioned above, is not necessarily linked to the mortality of the whole organism. In particular, some specific woody perennials have evolved strategies that enable them to overcome extreme stresses including drought and to become essentially immortal, e.g., by vegetative reproduction as in the proteaceous shrub *Lomatia tasmanica* (Munné-Bosch, 2014).

Conclusion

As one of the major disturbances in forest ecosystems, drought forces tree roots to react within a short period to this changed condition with growth, physiological, biochemical, and molecular responses. Reduced fine root biomass is one of the most common growth/morphological responses in trees. Other root traits, such as SRL, RTD, or the C/N ratio, are only slightly affected or remain unchanged. This indicates that tree roots have evolved effective strategies to coordinate the complex metabolic and structural demands required to acclimate and to maintain physiological and morphological functions when faced with drought conditions. However, trees experiencing drought invest large amounts of C in defense and storage systems, such as lignified support tissues, rather than in attaining external resources. This increased allocation to mechanisms for tolerating damage and disturbance can impact the competitive ability of a tree (see also Dietze et al., 2014).

Future research concerning tree roots and drought should focus on establishing accurate and commonly accepted approaches for understanding root functions. Although we are able to measure fine root biomass after destructive sampling, it is still not possible to estimate this parameter without physical damage. Other parameters, such as fine root lifespan and turnover rate, are even more difficult to measure, and the options of indirect quantification via sequential coring, direct measurement using minirhizotrons, and (the most recent method) radiocarbon (^{14}C bomb fallout) techniques all have important restrictions (for reviews see Gaudinski et al., 2010; Lukac, 2012; Ahrens et al., 2014; McCormack and Guo, 2014). More research attention should also be given to the biochemical characterization of tree fine roots. To our knowledge, the lignin and suberin situation in living fine roots of trees after drought has only rarely, if ever,

been studied. Does rebuilding of root structure occur only after a severe drought or mainly after repeatedly occurring droughts? How fast is this process? These root traits could be monitored over time using biomarkers, yet we are not aware of any existing applications of this relatively simple approach. Lignification or suberisation of tree roots has an obvious long-term effect on the decomposability of roots, and hence on the quality of SOM. Overall, a thorough understanding of the terrestrial biosphere and C cycle under the changing climate clearly requires more research on the ‘hidden half’ that exists below ground.

References

- Ahrens, B., Hansson, K., Solly, E. F., and Schruppf, M. (2014). Reconcilable differences: a joint calibration of fine-root turnover times with radiocarbon and minirhizotrons. *New Phytol.* 204, 932–942. doi: 10.1111/nph.12979
- Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., et al. (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For. Ecol. Manage.* 259, 660–684. doi: 10.1016/j.foreco.2009.09.001
- Almeida-Rodriguez, A. M., Cooke, J. E. K., Yeh, F., and Zwiazek, J. J. (2010). Functional characterization of drought-responsive aquaporins in *Populus balsamifera* and *Populus simonii* x *balsamifera* clones with different drought resistance strategies. *Physiol. Plant.* 140, 321–333. doi: 10.1111/j.1399-3054.2010.01405.x
- Almeida-Rodriguez, A. M., Hacke, U. G., and Laur, J. (2011). Influence of evaporative demand on aquaporin expression and root hydraulics of hybrid poplar. *Plant Cell Environ.* 34, 1318–1331. doi: 10.1111/j.1365-3040.2011.02331.x
- Anderegg, L. D. L., Anderegg, W. R. L., and Berry, J. A. (2013a). Not all droughts are created equal: translating meteorological drought into woody plant mortality. *Tree Physiol.* 33, 701–712. doi: 10.1093/treephys/tpt044
- Anderegg, W. R. L., Kane, J. M., and Anderegg, L. D. L. (2013b). Consequences of widespread tree mortality triggered by drought and temperature stress. *Nat. Clim. Change* 3, 30–36. doi: 10.1038/nclimate1635
- Andreotta, A., Dignac, M. F., and Carnicelli, S. (2013). Biological and physico-chemical processes influence cutin and suberin biomarker distribution in two Mediterranean forest soil profiles. *Biogeochemistry* 112, 41–58. doi: 10.1007/s10533-011-9693-9
- Arend, M., and Fromm, J. (2007). Seasonal change in the drought response of wood cell development in poplar. *Tree Physiol.* 27, 985–992. doi: 10.1093/treephys/27.7.985
- Arend, M., and Fromm, J. (2013). Concomitant analysis of cambial abscisic acid and cambial growth activity in poplar. *Trees* 27, 1271–1276. doi: 10.1007/s00468-013-0875-z
- Arend, M., Kuster, T., Günthardt-Goerg, M., and Dobbertin, M. (2011). Provenance-specific growth responses to drought and air warming in three European oak species (*Quercus robur*, *Q. petraea* and *Q. pubescens*). *Tree Physiol.* 31, 287–297. doi: 10.1093/treephys/tpr004
- Arend, M., Schnitzler, J. P., Ehling, B., Hansch, R., Lange, T., Rennenberg, H., et al. (2009). Expression of the *Arabidopsis* mutant *abi1* gene alters abscisic acid sensitivity, stomatal development, and growth morphology in gray poplars. *Plant Physiol.* 151, 2110–2119. doi: 10.1104/pp.109.144956
- Aulen, M., Shipley, B., and Bradley, R. (2012). Prediction of in situ root decomposition rates in an interspecific context from chemical and morphological traits. *Ann. Bot.* 109, 287–297. doi: 10.1093/aob/mcr259
- Baldrian, P. (2008). Wood-inhabiting ligninolytic basidiomycetes in soils: ecology and constraints for applicability in bioremediation. *Fungal Ecol.* 1, 4–12. doi: 10.1016/j.funeco.2008.02.001
- Baldrian, P., Snajdr, J., Merhautova, V., Dobiasova, P., Cajthaml, T., and Valaskova, V. (2013). Responses of the extracellular enzyme activities in hardwood forest to soil temperature and seasonality and the potential effects of climate change. *Soil Biol. Biochem.* 56, 60–68. doi: 10.1016/j.soilbio.2012.01.020

Acknowledgments

We thank Giovanni Zaccaria for input and discussions about this review topic, Hanspi Läser for the tree artwork, and Marco Walser and the whole Pfywald team for their support. We additionally thank two anonymous reviewers for helpful comments and suggestions. Some data are taken from the long-term irrigation experiment Pfywald, which is part of the Swiss Long-term Forest Ecosystem Research programme LWF (www.lwf.ch). This review was partly funded by the Swiss National Science Foundation (SNF), Grant number SNF 31003A_149507.

- Bardgett, R. D., Mommer, L., and De Vries, F. T. (2014). Going underground: root traits as drivers of ecosystem processes. *Trends Ecol. Evol.* 29, 692–699. doi: 10.1016/j.tree.2014.10.006
- Bauerle, T. L., Richards, J. H., Smart, D. R., and Eissenstat, D. M. (2008). Importance of internal hydraulic redistribution for prolonging the lifespan of roots in dry soil. *Plant Cell Environ.* 31, 177–186. doi: 10.1111/j.1365-3040.2007.01749.x
- Baxter, I., Hosmani, P. S., Rus, A., Lahner, B., Borevitz, J. O., Muthukumar, B., et al. (2009). Root suberin forms an extracellular barrier that affects water relations and mineral nutrition in *Arabidopsis*. *PLoS Genet.* 5:e1000492. doi: 10.1371/journal.pgen.1000492
- Blanck, K., Lamersdorf, N., Dohrenbusch, A., and Murach, D. (1995). Response of a Norway spruce forest ecosystem to drought/rewetting experiments at Solling, Germany. *Water Air Soil Pollut.* 85, 1251–1256. doi: 10.1007/bf00477153
- Bogeat-Triboulot, M. B., Brosche, M., Renaut, J., Jouve, L., Le Thiec, D., Fayyaz, P., et al. (2007). Gradual soil water depletion results in reversible changes of gene expression, protein profiles, ecophysiology, and growth performance in *Populus euphratica*, a poplar growing in arid regions. *Plant Physiol.* 143, 876–892. doi: 10.1104/pp.106.088708
- Breda, N., Huc, R., Granier, A., and Dreyer, E. (2006). Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Ann. For. Sci.* 63, 625–644. doi: 10.1051/forest:2006042
- Brunner, I., Bakker, M. R., Björk, R. G., Hirano, Y., Lukac, M., Aranda, X., et al. (2013). Fine-root turnover of European forest trees revisited: an analysis of data from sequential coring and ingrowth cores. *Plant Soil* 362, 357–372. doi: 10.1007/s11104-012-1313-5
- Brunner, I., and Godbold, D. L. (2007). Tree roots in a changing world. *J. For. Res.* 12, 78–82. doi: 10.1007/s10310-006-0261-4
- Brunner, I., Graf Pannatier, E., Frey, B., Rigling, A., Landolt, W., Zimmermann, S., et al. (2009). Morphological and physiological responses of Scots pine fine roots to water supply in a climatic dry region in Switzerland. *Tree Physiol.* 29, 541–550. doi: 10.1093/treephys/tpn046
- Cabane, M., Afif, D., and Hawkins, S. (2012). Lignins and abiotic stresses. *Adv. Bot. Res.* 61, 219–262. doi: 10.1016/B978-0-12-416023-1.00007-0
- Caruso, A., Morabito, D., Delmotte, F., Kahlem, G., and Carpin, S. (2002). Dehydrin induction during drought and osmotic stress in *Populus*. *Plant Physiol. Biochem.* 40, 1033–1042. doi: 10.1016/S0981-9428(02)01468-7
- Cavin, L., Mountford, E. P., Peterken, G. F., and Jump, A. S. (2013). Extreme drought alters competitive dominance within and between tree species in a mixed forest stand. *Funct. Ecol.* 27, 1424–1435. doi: 10.1111/1365-2435.12126
- Chaumont, F., and Tyerman, S. D. (2014). Aquaporins: highly regulated channels controlling plant water relations. *Plant Physiol.* 164, 1600–1618. doi: 10.1104/pp.113.233791
- Chen, H. Y. H., and Brassard, B. W. (2013). Intrinsic and extrinsic controls of fine root life span. *Crit. Rev. Plant Sci.* 32, 151–161. doi: 10.1080/07352689.2012.734742
- Chenlemuge, T., Hertel, D., Dulamsuren, C., Khishigiargal, M., Leuschner, C., and Hauck, M. (2013). Extremely low fine root biomass in *Larix sibirica* forests at the southern drought limit of the boreal forest. *Flora* 208, 488–496. doi: 10.1016/j.flora.2013.08.002

- Choat, B., Jansen, S., Brodribb, T. J., Cochard, H., Delzon, S., Bhaskar, R., et al. (2012). Global convergence in the vulnerability of forests to drought. *Nature* 491, 752–755. doi: 10.1038/nature11688
- Christmann, A., Grill, E., and Huang, J. (2013). Hydraulic signals in long-distance signaling. *Curr. Opin. Plant Biol.* 16, 293–300. doi: 10.1016/j.pbi.2013.02.011
- Christmann, A., Weiler, E. W., Steudle, E., and Grill, E. (2007). A hydraulic signal in root-to-shoot signalling of water shortage. *Plant J.* 52, 167–174. doi: 10.1111/j.1365-3113.2007.03234.x
- Claeys, H., and Inzé, D. (2013). The agony of choice: how plants balance growth and survival under water-limiting conditions. *Plant Physiol.* 162, 1768–1779. doi: 10.1104/pp.113.220921
- Cocozza, C., Cherubini, P., Regier, N., Saurer, M., Frey, B., and Tognetti, R. (2010). Early effects of water deficit on two parental clones of *Populus nigra* grown under different environmental conditions. *Funct. Plant Biol.* 37, 244–254. doi: 10.1071/fp09156
- Cohen, D., Bogeat-Triboulet, M. B., Tisserant, E., Balzergue, S., Martin-Magniette, M. L., Lelandais, G., et al. (2010). Comparative transcriptomics of drought responses in *Populus*: a meta-analysis of genome-wide expression profiling in mature leaves and root apices across two genotypes. *BMC Genomics* 11:630. doi: 10.1186/1471-2164-11-630
- Comas, L. H., Becker, S. R., Cruz, V. M. V., Byrne, P. F., and Dierig, D. A. (2013). Root traits contributing to plant productivity under drought. *Front. Plant Sci.* 4:442. doi: 10.3389/fpls.2013.00442
- Cudlin, P., Kieliszewska-Rokicka, B., Rudawska, M., Grebenc, T., Alberton, O., Lehto, T., et al. (2007). Fine roots and ectomycorrhizas as indicators of environmental change. *Plant Biosyst.* 141, 406–425. doi: 10.1080/11263500701626028
- Davies, W. J., and Bacon, M. A. (2003). Adaptation of roots to drought. *Ecol. Stud.* 168, 173–192. doi: 10.1007/978-3-662-09784-7_7
- De Smet, I., and Zhang, H. (2013). “Abscisic acid in root growth and development,” in *Plant Roots: The Hidden Half*, Vol. 16, eds A. Eshel and T. Beekman (Boca Raton: CRC Press), 1–13.
- Dietz, S., von Bülow, J., Beitze, E., and Nehls, U. (2011). The aquaporin gene family of the ectomycorrhizal fungus *Laccaria bicolor*: lessons for symbiotic functions. *New Phytol.* 190, 927–940. doi: 10.1111/j.1469-8137.2011.03651.x
- Dietze, M. C., Sala, A., Carbone, M. S., Czimczik, C. I., Mantoosh, J. A., Richardson, A. D., et al. (2014). Nonstructural carbon in woody plants. *Annu. Rev. Plant Biol.* 65, 667–687. doi: 10.1146/annurev-arplant-050213-040054
- Dignac, M. F., and Rumpel, C. (2013). Organic matter stabilization and ecosystem functions: proceedings of the fourth conference on the mechanisms of organic matter stabilization and destabilization (SOM-2010, Presqu’île de Giens, France). *Biogeochemistry* 112, 1–6. doi: 10.1007/s10533-012-9768-2
- Eissenstat, D. M., McCormack, M. L., and Du, Q. (2013). “Global change and root lifespan,” in *Plant Roots: The Hidden Half*, Vol. 27, eds A. Eshel and T. Beekman (Boca Raton: CRC Press), 1–13.
- Eissenstat, D. M., Wells, C. E., Yanai, R. D., and Whitbeck, J. L. (2000). Building roots in a changing environment: implication for root longevity. *New Phytol.* 147, 33–42. doi: 10.1046/j.1469-8137.2000.00686.x
- Eldhuset, T. D., Nagy, N. E., Volnarik, D., Borja, I., Gebauer, R., Yakovlev, I. A., et al. (2013). Drought affects tracheid structure, dehydrin expression, and above- and belowground growth in 5-year-old Norway spruce. *Plant Soil* 366, 305–320. doi: 10.1007/s11104-012-1432-z
- Endo, A., Sawada, Y., Takahashi, H., Okamoto, M., Ikegami, K., Koiwai, H., et al. (2008). Drought induction of *Arabidopsis* 9-cis-epoxycarotenoid dioxygenase occurs in vascular parenchyma cells. *Plant Physiol.* 147, 1984–1993. doi: 10.1104/pp.108.116632
- Fernandez, C. W., and Koide, R. T. (2013). The function of melanin in the ectomycorrhizal fungus *Cenococcum geophilum* under water stress. *Fungal Ecol.* 6, 479–486. doi: 10.1016/j.funeco.2013.08.004
- Finér, L., Ohashi, M., Noguchi, K., and Hirano, Y. (2011). Fine root production and turnover in forest ecosystems in relation to stand and environmental characteristics. *For. Ecol. Manag.* 262, 2008–2023. doi: 10.1016/j.foreco.2011.08.042
- Floudas, D., Binder, M., Riley, R., Barry, K., Blanchette, R. A., Henrissat, B., et al. (2012). The Paleozoic origin of enzymatic lignin decomposition reconstructed from 31 fungal genomes. *Science* 336, 1715–1719. doi: 10.1126/science.1221748
- Fonti, P., Heller, O., Cherubini, P., Rigling, A., and Arend, M. (2013). Wood anatomical responses of oak saplings exposed to air warming and soil drought. *Plant Biol.* 15, 210–219. doi: 10.1111/j.1438-8677.2012.00599.x
- Fonti, P., and Jansen, S. (2012). Xylem plasticity in response to climate. *New Phytol.* 195, 734–736. doi: 10.1111/j.1469-8137.2012.04252.x
- Galvez, D. A., Landhäusser, S. M., and Tyree, M. T. (2011). Root carbon reserve dynamics in aspen seedlings: does simulated drought induce reserve limitation? *Tree Physiol.* 31, 250–257. doi: 10.1093/treephys/tp012
- Galvez, D. A., Landhäusser, S. M., and Tyree, M. T. (2013). Low root reserve accumulation during drought may lead to winter mortality in poplar seedlings. *New Phytol.* 198, 139–148. doi: 10.1111/nph.12129
- Gaudinski, J. B., Tom, M. S., Riley, W. J., Dawson, T. E., Joslin, J. D., and Majdi, H. (2010). Measuring and modeling the spectrum of fine-root turnover times in three forests using isotopes, minirhizotrons, and the Radix model. *Global Biogeochem. Cycles* 24:GB3029. doi: 10.1029/2009gb003649
- Gaul, D., Hertel, D., Borken, W., Matzner, E., and Leuschner, C. (2008). Effects of experimental drought on the fine root system of mature Norway spruce. *For. Ecol. Manag.* 256, 1151–1159. doi: 10.1016/j.foreco.2008.06.016
- Gaul, D., Hertel, D., and Leuschner, C. (2009). Estimating fine root longevity in a temperate Norway spruce forest using three independent methods. *Funct. Plant Biol.* 36, 11–19. doi: 10.1071/fp08195
- Gil, P. M., Gurovich, L., Schaffer, B., Alcajaga, J., Rey, S., and Iturriaga, R. (2008). Root to leaf electrical signaling in avocado in response to light and soil water content. *J. Plant Physiol.* 165, 1070–1078. doi: 10.1016/j.jplph.2007.07.014
- Gill, R. A., and Jackson, R. B. (2000). Global patterns of root turnover for terrestrial ecosystems. *New Phytol.* 147, 13–31. doi: 10.1046/j.1469-8137.2000.00681.x
- Gosh, D., and Xu, J. (2014). Abiotic stress responses in plant roots: a proteomics perspective. *Front. Plant Sci.* 5:6. doi: 10.3389/fpls.2014.00006
- Grams, T. E., Koziol, C., Lautner, S., Matyssek, R., and Fromm, J. (2007). Distinct roles of electric and hydraulic signals on the reaction of leaf gas exchange upon re-irrigation in *Zea mays* L. *Plant Cell Environ.* 30, 79–84. doi: 10.1111/j.1365-3040.2006.01607.x
- Gupta, A. B., and Sankaramakrishnan, R. (2009). Genome-wide analysis of major intrinsic proteins in the tree plant *Populus trichocarpa*: characterization of XIP subfamily of aquaporins from evolutionary perspective. *BMC Plant Biol.* 9:134. doi: 10.1186/1471-2229-9-134
- Hacke, U. G., Sperry, J. S., Pockman, W. T., Davis, S. D., and McCulloh, K. (2001). Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia* 126, 457–461. doi: 10.1007/s004420100628
- Hacquard, S., Tisserant, E., Brun, A., Legué, V., Martin, F., and Kohler, A. (2013). Laser microdissection and microarray analysis of *Tuber melanosporum* ectomycorrhizas reveal functional heterogeneity between mantle and Hartig net compartments. *Environ. Microbiol.* 15, 1853–1869. doi: 10.1111/1462-2920.12080
- Hamanishi, E. T., and Campbell, M. M. (2011). Genome-wide responses to drought in forest trees. *Forestry* 84, 273–283. doi: 10.1093/forestry/cpr012
- Harfouche, A., Meilan, R., and Altman, A. (2014). Molecular and physiological responses to abiotic stress in forest trees and their relevance to tree improvement. *Tree Physiol.* 34, 1181–1198. doi: 10.1093/treephys/tpu012
- Hartmann, H. (2011). Will a 385 million year-struggle for light become a struggle for water and for carbon? – how trees may cope with more frequent climate change-type drought events. *Global Change Biol.* 17, 642–655. doi: 10.1111/j.1365-2486.2010.02248.x
- Hartmann, H., Ziegler, W., Kolle, O., and Trumbore, S. (2013a). Thirst beats hunger – declining hydration during drought prevents carbon starvation in Norway spruce saplings. *New Phytol.* 200, 340–349. doi: 10.1111/nph.12331
- Hartmann, H., Ziegler, W., and Trumbore, S. (2013b). Lethal drought leads to reduction in nonstructural carbohydrates in Norway spruce tree roots but not in the canopy. *Funct. Ecol.* 27, 413–427. doi: 10.1111/1365-2435.12046
- Heim, A., and Frey, B. (2004). Early stage litter decomposition rates for Swiss forests. *Biogeochemistry* 70, 301–315. doi: 10.1007/s10533-003-0844-5
- Hertel, D., Strecker, T., Müller-Haubold, H., and Leuschner, C. (2013). Fine root biomass and dynamics in beech forests across a precipitation gradient – is optimal resource partitioning theory applicable to water-limited mature trees? *J. Ecol.* 101, 1183–1200. doi: 10.1111/1365-2745.12124
- Herzog, C., Peter, M., Pritsch, K., Günthardt-Goerg, M. S., and Egli, S. (2013). Drought and air warming affects abundance and exoenzyme

- profiles of *Cenococcum geophilum* associated with *Quercus robur*, *Q. petraea* and *Q. pubescens*. *Plant Biol.* 15(Suppl. 1), 230–237. doi: 10.1111/j.1438-8677.2012.00614.x
- Herzog, C., Steffen, J., Graf Pannatier, E., Hajdas, I., and Brunner, I. (2014). Nine years of irrigation cause vegetation and fine root shifts in a water-limited pine forest. *PLoS ONE* 9:e96321. doi: 10.1371/journal.pone.0096321
- Hinsinger, P., Bengough, A., Vetterlein, D., and Young, I. (2009). Rhizosphere: biophysics, biogeochemistry and ecological relevance. *Plant Soil* 321, 117–152. doi: 10.1007/s11104-008-9885-9
- IPCC. (2007). “Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change,” in *Climate change 2007: The Physical Science Basis*, eds S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, et al. (Cambridge: Cambridge University Press).
- IPCC. (2014). “Contribution of working group II to the fifth assessment report of the intergovernmental panel on climate change (Part A: Global and sectoral aspects. Summary for policymakers),” in *Climate Change 2014: Impacts, Adaptation, and Vulnerability*, eds C. B. Field, V. R. Barros, D. J. Dokken, K. J. Mach, M. D. Mastrandrea, T. E. Bilir, et al. (Cambridge: Cambridge University Press).
- Jackson, R. B., Mooney, H. A., and Schulze, E. D. (1997). A global budget for fine root biomass, surface area, and nutrient contents. *Proc. Natl. Acad. Sci. U.S.A.* 94, 7362–7366. doi: 10.1073/pnas.94.14.7362
- Jany, J. L., Martin, F., and Garbaye, J. (2003). Respiration activity of ectomycorrhizas from *Cenococcum geophilum* and *Lactarius* sp. in relation to soil water potential in five beech forests. *Plant Soil* 255, 487–494. doi: 10.1023/A:1026092714340
- Jarvis, S., Woodward, S., Alexander, I. J., and Taylor, A. F. S. (2013). Regional scale gradients of climate and nitrogen deposition drive variation in ectomycorrhizal fungal communities associated with native Scots pine. *Global Change Biol.* 19, 1688–1696. doi: 10.1111/gcb.12178
- Jones, D., Nguyen, C., and Finlay, R. (2009). Carbon flow in the rhizosphere: carbon trading at the soil – root interface. *Plant Soil* 321, 5–33. doi: 10.1007/s11104-009-9925-0
- Joslin, J. D., Wolfe, M. H., and Hanson, P. J. (2000). Effects of altered water regimes on forest root systems. *New Phytol.* 147, 117–129. doi: 10.1046/j.1469-8137.2000.00692.x
- Klotzbücher, T., Kaiser, K., Guggenberger, G., Gatzek, C., and Kalbitz, K. (2011). A new conceptual model for the fate of lignin in decomposing plant litter. *Ecology* 92, 1052–1062. doi: 10.1111/j.1365-2389.2006.00797.x
- Konópka, K., Noguchi, K., Sakata, T., Takahashi, M., and Konópková, Z. (2007). Effects of simulated drought stress on the fine roots of Japanese cedar (*Cryptomeria japonica*) in a plantation forest on the Kanto Plain, eastern Japan. *J. For. Res.* 12, 143–151. doi: 10.1007/s10310-006-0257-0
- Kotowska, M. M., Hertel, D., Rajab, Y. A., Barus, H., and Schuldt, B. (2015). Patterns in hydraulic architecture from roots to branches in six tropical tree species from cacao agroforestry and their relation to wood density and stem growth. *Front. Plant Sci.* 6:191. doi: 10.3389/fpls.2015.00191
- Kozłowski, T. T., and Pallardy, S. G. (2002). Acclimation and adaptive responses of woody plants to environmental stresses. *Bot. Rev.* 68, 270–334. doi: 10.1663/0006-8101(2002)068[0270:AAAROW]2.0.CO;2
- Kuster, T. M., Arend, M., Günthardt-Goerg, M., and Schulin, R. (2013). Root growth of different oak provenances in two soils under drought stress and air warming conditions. *Plant Soil* 369, 61–71. doi: 10.1007/s11104-012-1541-8
- Kuzakov, Y. (2002). Factors affecting rhizosphere priming effects. *J. Plant Nutr. Soil Sci.* 165, 382–396. doi: 10.1002/1522-2624(200208)165:4<382::AID-JPLN382>3.0.CO;2-#
- Kuzakov, Y. (2010). Priming effects: interactions between living and dead organic matter. *Soil Biol. Biochem.* 42, 1363–1371. doi: 10.1016/j.soilbio.2010.04.003
- Lambers, H., Chapin, F. S. III, and Pons, T. L. (2008). *Plant Physiological Ecology*. New York, NY: Springer. doi: 10.1007/978-0-387-78341-3
- Laur, J., and Hacke, U. G. (2013). Transpirational demand affects aquaporin expression in poplar roots. *J. Exp. Bot.* 64, 2283–2293. doi: 10.1093/jxb/ert096
- Lee, S. H., Calvo Polanco, M., Chung, G. C., and Zwiazek, J. J. (2010). Cell water flow properties in root cortex of ectomycorrhizal (*Pinus banksiana*) seedlings. *Plant Cell Environ.* 33, 769–780. doi: 10.1111/j.1365-3040.2009.02103.x
- Lehto, T., and Zwiazek, J. J. (2011). Ectomycorrhizas and water relations of trees: a review. *Mycorrhiza* 21, 71–90. doi: 10.1007/s00572-010-0348-9
- Leppälampi-Kujansuu, J., Salemaa, M., Kleja, D. B., Linder, S., and Helmisaari, H. S. (2014). Fine root turnover and litter production of Norway spruce in a long-term temperature and nutrient manipulation experiment. *Plant Soil* 374, 73–88. doi: 10.1007/s11104-013-1853-3
- Leuschner, C., Hertel, D., Schmid, I., Koch, O., Muhs, A., and Holscher, D. (2004). Stand fine root biomass and fine root morphology in old-growth beech forests as a function of precipitation and soil fertility. *Plant Soil* 258, 43–56. doi: 10.1023/B:PLSO.0000016508.20173.80
- Levitt, J. (1972). *Responses of Plants to Environmental Stresses*. New York, NY: Academic Press.
- Lintunen, A., and Kallioikoski, T. (2010). The effect of tree architecture on conduit diameter and frequency from small distal roots to branch tips in *Betula pendula*, *Picea abies* and *Pinus sylvestris*. *Tree Physiol.* 30, 1433–1447. doi: 10.1093/treephys/tpq085
- Lorenz, W. W., Alba, R., Yu, Y. S., Bordeaux, J. M., Simões, M., and Dean, J. F. D. (2011). Microarray analysis and scale-free gene networks identify candidate regulators in drought-stressed roots of loblolly pine (*P. taeda* L.). *BMC Genomics* 12:264. doi: 10.1186/1471-2164-12-264
- Lukac, M. (2012). “Fine root turnover,” in *Measuring Roots*, ed. S. Mancuso (Berlin: Springer), 363–373. doi: 10.1007/978-3-642-22067-8_18
- Mainiero, R., and Kazda, M. (2006). Depth-related fine root dynamics of *Fagus sylvatica* during exceptional drought. *For. Ecol. Manag.* 237, 135–142. doi: 10.1016/j.foreco.2006.09.034
- Marjanović, Z., Nehls, U., and Hampp, R. (2005). Mycorrhiza formation enhances adaptive response of hybrid poplar to drought. *Ann. N.Y. Acad. Sci.* 1048, 496–499. doi: 10.1196/annals.1342.080
- Markestijn, L., and Poorter, L. (2009). Seedling root morphology and biomass allocation of 62 tropical tree species in relation to drought- and shade-tolerance. *J. Ecol.* 97, 311–325. doi: 10.1111/j.1365-2745.2008.01466.x
- McCormack, M. L., Adams, T. S., Smithwick, E. A. H., and Eissenstat, D. M. (2012). Predicting fine root lifespan from plant functional traits in temperate trees. *New Phytol.* 195, 823–831. doi: 10.1111/j.1469-8137.2012.04198.x
- McCormack, M. L., and Guo, D. (2014). Impacts of environmental factors on fine root lifespan. *Front. Plant Sci.* 5:205. doi: 10.3389/fpls.2014.00205
- McDowell, N. G. (2011). Mechanisms linking drought, hydraulics, carbon metabolism, and vegetation mortality. *Plant Physiol.* 155, 1051–1059. doi: 10.1104/pp.110.170704
- McDowell, N. G., Pockman, W. T., Allen, C. D., Breshears, D. D., Cobb, N., Kolb, T., et al. (2008). Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb? *New Phytol.* 178, 719–739. doi: 10.1111/j.1469-8137.2008.02436.x
- Meier, I. C., and Leuschner, C. (2008a). Belowground drought response of European beech: fine root biomass and carbon partitioning in 14 mature stands across a precipitation gradient. *Global Change Biol.* 14, 2081–2095. doi: 10.1111/j.1365-2486.2008.01634.x
- Meier, I. C., and Leuschner, C. (2008b). Genotypic variation and phenotypic plasticity in the drought response of fine roots of European beech. *Tree Physiol.* 28, 297–309. doi: 10.1093/treephys/28.2.297
- Meir, P., Mencuccini, M., and Dewar, R. C. (2015). Drought-related tree mortality: addressing the gaps in understanding and prediction. *New Phytol.* 207, 28–33. doi: 10.1111/nph.13382
- Mencuccini, M. (2015). Dwarf trees, super-sized shrubs and scaling: why is plant stature so important? *Plant Cell Environ.* 38, 1–3. doi: 10.1111/pce.12442
- Mitchell, P. J., O’Grady, A. P., Tissue, D. T., White, D. A., Ottenschlaeger, M. L., and Pinkard, E. A. (2013). Drought response strategies define the relative contributions of hydraulic dysfunction and carbohydrate depletion during tree mortality. *New Phytol.* 197, 862–872. doi: 10.1111/nph.12064
- Mohan, J. E., Cowden, C. C., Baas, P., Dawadi, A., Frankson, P. T., Helmick, K., et al. (2014). Mycorrhizal fungi mediation of terrestrial ecosystem responses to global change: mini-review. *Fungal Ecol.* 10, 3–19. doi: 10.1016/j.funeco.2014.01.005
- Mokany, K., Raison, R. J., and Prokushkin, A. S. (2006). Critical analysis of root:shoot ratios in terrestrial biomes. *Global Change Biol.* 12, 84–96. doi: 10.1111/j.1365-2486.2005.001043.x
- Moore, J. P., Vitré-Gibouin, M., Farrant, J. M., and Driouich, A. (2008). Adaptations of higher plant cell walls to water loss: drought vs desiccation. *Physiol. Plant.* 134, 237–245. doi: 10.1111/j.1399-3054.2008.01134.x

- Moura, J. C. M. S., Bonine, C. A. V., De Oliveira Fernandes Viana, J., Dornelas, M. C., and Mazzafera, P. (2010). Abiotic and biotic stresses and changes in the lignin content and composition in plants. *J. Integr. Plant Biol.* 52, 360–376. doi: 10.1111/j.1744-7909.2010.00892.x
- Muller, B., Pantin, F., Génard, M., Turc, O., Freixes, S., Piques, M., et al. (2011). Water deficits uncouple growth from photosynthesis, increase C content, and modify the relationships between C and growth in sink organs. *J. Exp. Bot.* 62, 1715–1729. doi: 10.1093/jxb/erq438
- Munné-Bosch, S. (2014). Perennial roots to immortality. *Plant Physiol.* 166, 720–725. doi: 10.1104/pp.114.236000
- Munns, R., and Cramer, G. R. (1996). Is coordination of leaf and root growth mediated by abscisic acid? *Opin. Plant Soil* 185, 33–49. doi: 10.1007/BF02257563
- Nakashima, K., and Yamaguchi-Shinozaki, K. (2013). ABA signaling in stress-response and seed development. *Plant Cell Rep.* 32, 959–970. doi: 10.1007/s00299-013-1418-1
- Naser, L., Kourosha, V., Bahmana, K., and Reza, A. (2010). Soluble sugars and proline accumulation play a role as effective indices for drought tolerance screening in Persian walnut (*Juglans regia* L.) during germination. *Fruits* 65, 97–112. doi: 10.1051/fruits/20010005
- Navarro-Ródenas, A., Bárzana, G., Nicolás, E., Carra, A., Schubert, A., and Morte, A. (2013). Expression analysis of aquaporins from desert truffle mycorrhizal symbiosis reveals a fine-tuned regulation under drought. *Mol. Plant Microbe Interact.* 26, 1068–1078. doi: 10.1094/MPMI-07-12-0178-R
- Olmo, M., Lopez-Iglesias, B., and Villar, R. (2014). Drought changes the structure and elemental composition of very fine roots in seedlings of ten woody tree species. Implications for a drier climate. *Plant Soil* 384, 113–129. doi: 10.1007/s11104-014-2178-6
- Osono, T. (2007). Ecology of ligninolytic fungi associated with leaf litter decomposition. *Ecol. Res.* 22, 955–974. doi: 10.1007/s11284-007-0390-z
- Ostonen, I., Püttsepp, U., Biel, C., Alberton, O., Bakker, M. R., Löhmus, K., et al. (2007). Specific root length as indicator of environmental change. *Plant Biosyst.* 141, 426–442. doi: 10.1080/11263500701626069
- Pantin, F., Monnet, F., Jannaud, D., Costa, J., Renaud, J., Muller, B., et al. (2013). The dual effect of abscisic acid on stomata. *New Phytol.* 197, 65–72. doi: 10.1111/nph.12013
- Parent, B., Hachez, C., Redondo, E., Simonneau, T., Chaumont, F., and Tardieu, F. (2009). Drought and abscisic acid effects on aquaporin content translate into changes in hydraulic conductivity and leaf growth rate: a trans-scale approach. *Plant Physiol.* 149, 2000–2012. doi: 10.1104/pp.108.130682
- Perdiguero, P., Collada, C., del Carmen Barbero, M., Casado, G. G., Cervera, M. T., and Soto, A. (2012). Identification of water stress genes in *Pinus pinaster* Ait. by controlled progressive stress and suppression-subtractive hybridization. *Plant Physiol. Biochem.* 50, 44–53. doi: 10.1016/j.plaphy.2011.09.022
- Persson, H., von Fircks, Y., Majdi, H., and Nilsson, L. O. (1995). Root distribution in a Norway spruce (*Picea abies* (L.) Karst.) stand subjected to drought and ammonium-sulphate application. *Plant Soil* 168–169, 161–165. doi: 10.1007/BF00029324
- Piper, F. I. (2011). Drought induces opposite changes in the concentration of non-structural carbohydrates of two evergreen *Nothofagus* species of differential drought resistance. *Ann. For. Sci.* 68, 415–424. doi: 10.1007/s13595-011-0030-1
- Pisani, O., Hills, K. H., Courtier-Murias, D., Haddix, M. L., Paul, E. A., Conant, R. T., et al. (2014). Accumulation of aliphatic compounds in soil with increasing mean annual temperature. *Org. Geochem.* 76, 118–127. doi: 10.1016/j.orggeochem.2014.07.009
- Poorter, H., Niklas, K. J., Reich, P. B., Oleksyn, J., Poot, P., and Mommer, L. (2012). Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. *New Phytol.* 193, 30–50. doi: 10.1111/j.1469-8137.2011.03952.x
- Prieto, I., Armas, C., and Pugnaire, F. I. (2012). Water release through plant roots: new insights into its consequences at the plant and ecosystem level. *New Phytol.* 193, 830–841. doi: 10.1111/j.1469-8137.2011.04039.x
- Quarrie, S. A., and Jones, H. G. (1977). Effects of abscisic acid and water stress on development and morphology of wheat source. *J. Exp. Bot.* 28, 192–203. doi: 10.1093/jxb/28.1.192
- Ranathunge, K., Schreiber, L., and Franke, R. (2011). Suberin research in the genomics era - new interest for an old polymer. *Plant Sci.* 180, 399–413. doi: 10.1016/j.plantsci.2010.11.003
- Rasse, D. P., Rumpel, C., and Dignac, M.-F. (2005). Is soil carbon mostly root carbon? Mechanisms for a specific stabilisation. *Plant Soil* 269, 341–356. doi: 10.1007/s11104-004-0907-y
- Regier, N., Streb, S., Cocozza, C., Schaub, M., Cherubini, P., Zeeman, S. C., et al. (2009). Drought tolerance of two black poplar (*Populus nigra* L.) clones: contribution of carbohydrates and oxidative stress defence. *Plant Cell Environ.* 32, 1724–1736. doi: 10.1111/j.1365-3040.2009.02030.x
- Reichstein, M., Bahn, M., Ciais, P., Frank, D., Mahecha, M. D., Seneviratne, S. I., et al. (2013). Climate extremes and the carbon cycle. *Nature* 500, 287–295. doi: 10.1038/nature12350
- Rühr, N. K., Offermann, C. A., Gessler, A., Winkler, J. B., Ferrio, J. P., Buchmann, N., et al. (2009). Drought effects on allocation of recent carbon: from beech leaves to soil CO₂ efflux. *New Phytol.* 184, 950–961. doi: 10.1111/j.1469-8137.2009.03044.x
- Ryan, M. G. (2011). Tree responses to drought. *Tree Physiol.* 31, 237–239. doi: 10.1093/treephys/tpq022
- Sala, A., Piper, F., and Hoch, G. (2010). Physiological mechanisms of drought-induced tree mortality are far from being resolved. *New Phytol.* 186, 274–281. doi: 10.1111/j.1469-8137.2009.03167.x
- Sardans, J., Peñuelas, J., and Ogaya, R. (2008). Drought-induced changes in C and N stoichiometry in a *Quercus ilex* Mediterranean forest. *For. Sci.* 54, 513–522.
- Sardans, J., Rivas-Ubach, A., and Peñuelas, J. (2012). The C:N:P stoichiometry of organisms and ecosystems in a changing world: a review and perspectives. *Perspect. Plant Ecol.* 14, 33–47. doi: 10.1016/j.ppees.2011.08.002
- Schachtman, D. P., and Goodger, J. Q. D. (2008). Chemical root to shoot signaling under drought. *Trends Plant Sci.* 13, 281–287. doi: 10.1016/j.tplants.2008.04.003
- Schuldt, B., Leuschner, C., Brock, N., and Horna, V. (2013). Changes in wood density, wood anatomy and hydraulic properties of the xylem along the root-to-shoot flow path in tropical rain forest trees. *Tree Physiol.* 33, 161–174. doi: 10.1093/treephys/tps122
- Secchi, F., Lovisolo, C., Uehlein, N., Kaldenhoff, R., and Schubert, S. (2007). Isolation and functional characterization of three aquaporins from olive (*Olea europaea* L.). *Planta* 225, 381–392. doi: 10.1007/s00425-006-0365-2
- Sharp, R. E., LeNoble, M. E., Else, M. A., Thorne, E. T., and Gherardi, F. (2000). Endogenous ABA maintains shoot growth in tomato independently of effects on plant water balance: evidence for an interaction with ethylene. *J. Exp. Bot.* 51, 1575–1584. doi: 10.1093/jexbot/51.350.1575
- Sharp, R. E., Poroyko, V., Hejlek, L. G., Spollen, W. G., Springer, G. K., Bohnert, H. J., et al. (2004). Root growth maintenance during water deficits: physiology to functional genomics. *J. Exp. Bot.* 55, 2343–2351. doi: 10.1093/jxb/erh276
- Sharp, R. E., Wu, Y., Voetberg, G. S., Saab, I. N., and LeNoble, M. E. (1994). Confirmation that abscisic acid accumulation is required for maize primary root elongation at low water potentials. *J. Exp. Bot.* 45, 1743–1751. doi: 10.1093/jxb/45.Special_Issue.1743
- Siemens, A. J., and Zwiazek, J. J. (2008). Root hydraulic properties and growth of balsam poplar (*Populus balsamifera*) mycorrhizal with *Hebeloma crustuliniforme* and *Wilcoxina mikolae* var. *mikolae*. *Mycorrhiza* 18, 393–401. doi: 10.1007/s00572-008-0193-2
- Silver, W. L., and Miya, R. K. (2001). Global patterns in root decomposition: comparisons of climate and litter quality effects. *Oecologia* 129, 407–419. doi: 10.1007/s004420100740
- Smith, M. D. (2011). The ecological role of climate extremes: current understanding and future prospects. *J. Ecol.* 99, 651–655. doi: 10.1111/j.1365-2745.2011.01833.x
- Snajdr, J., Cajthaml, T., Valaskova, V., Merhautova, V., Petrankova, M., Spetz, P., et al. (2011). Transformation of *Quercus petraea* litter: successive changes in litter chemistry are reflected in differential enzyme activity and changes in the microbial community composition. *FEMS Microbiol. Ecol.* 75, 291–303. doi: 10.1111/j.1574-6941.2010.00999.x
- Sofa, A., Dichio, B., Xiloyannis, C., and Masia, A. (2004). Lipoxigenase activity and proline accumulation in leaves and roots of olive tree in response to drought stress. *Physiol. Plant.* 121, 58–65. doi: 10.1111/j.0031-9317.2004.00294.x
- Soler, M., Serra, O., Molinas, M., Huguet, G., Fluch, S., and Figueras, M. (2007). A genomic approach to suberin biosynthesis and cork differentiation. *Plant Physiol.* 144, 419–431. doi: 10.1104/pp.106.094227
- Stedde, E. (2000). Water uptake by roots: effects of water deficit. *J. Exp. Bot.* 51, 1531–1542. doi: 10.1093/jexbot/51.350.1531

- Stedle, E., and Peterson, C. A. (1998). How does water get through roots? *J. Exp. Bot.* 49, 775–788. doi: 10.1093/jxb/49.322.775
- Suz, L. M., Barsoum, N., Benham, S., Dietrich, H. P., Fetzner, K. D., Fischer, R., et al. (2014). Environmental drivers of ectomycorrhizal communities in Europe's temperate oak forests. *Mol. Ecol.* 23, 5628–5644. doi: 10.1111/mec.12947
- Talbot, J. M., and Treseder, K. K. (2012). Interactions among lignin, cellulose, and nitrogen drive litter chemistry-decay relationships. *Ecology* 93, 345–354. doi: 10.1890/11-0843.1
- Talbot, J. M., Yelle, D. J., Nowick, J., and Treseder, K. K. (2012). Litter decay rates are determined by lignin chemistry. *Biogeochemistry* 108, 279–295. doi: 10.1007/s10533-011-9599-6
- Trewavas, A. J., and Jones, H. G. (1991). "An assessment of the role of ABA in plant development," in *Abscisic Acid: Physiology and Biochemistry*, eds W. J. Davies and H. G. Jones (Oxford: BIOS Scientific Publishers), 169–188.
- Tuberosa, R. (2012). Phenotyping for drought tolerance of crops in the genomics era. *Front. Physiol.* 3:347. doi: 10.3389/fphys.2012.00347
- Tyree, M. T., and Zimmermann, M. H. (2002). *Xylem Structure and The Ascent of Sap*. Berlin: Springer. doi: 10.1007/978-3-662-04931-0
- Van der Molen, M. K., Dolman, A. J., Ciaia, P., Eglin, T., Gobron, N., Law, B. E., et al. (2011). Drought and ecosystem carbon cycling. *Agr. Forest Meteorol.* 151, 765–773. doi: 10.1016/j.agrformet.2011.01.018
- van Mantgem, P. J., Stephenson, N. L., Byrne, J. C., Daniels, L. D., Franklin, J. F., Fulé, P. Z., et al. (2009). Widespread increase of tree mortality rates in the western United States. *Science* 323, 521–524. doi: 10.1126/science.1165000
- Vandeleur, R. K., Mayo, G., Shelden, M. C., Gillham, M., Kaiser, B. N., and Tyerman, S. D. (2009). The role of plasma membrane intrinsic protein aquaporins in water transport through roots: diurnal and drought stress responses reveal different strategies between isohydric and anisohydric cultivars of grapevine. *Plant Physiol.* 149, 445–460. doi: 10.1104/pp.108.128645
- Verslues, P. E., Agarwal, M., Katiyar-Agarwal, S., Zhu, J., and Zhu, J.-K. (2006). Methods and concepts in quantifying resistance to drought, salt and freezing, abiotic stresses that affect plant water status. *Plant J.* 45, 523–539. doi: 10.1111/j.1365-313X.2005.02593.x
- Von Lütow, M., Kögel-Knabner, I., Ekschmitt, K., Matzner, E., Guggenberger, G., Marschner, B., et al. (2006). Stabilization of organic matter in temperate soils: mechanisms and their relevance under different soil conditions – a review. *Eur. J. Soil Sci.* 57, 426–445. doi: 10.1111/j.1365-2389.2006.00809.x
- Walela, C., Daniel, H., Wilson, B., Lockwood, P., Cowie, A., and Harden, S. (2014). The initial lignin:nitrogen ratio of litter from above and below ground sources strongly and negatively influenced decay rates of slowly decomposing litter carbon pools. *Soil Biol. Biochem.* 77, 268–275. doi: 10.1016/j.soilbio.2014.06.013
- Waring, R. H. (1987). Characteristics of trees predisposed to die. *Bioscience* 37, 569–574. doi: 10.1016/S0166-1116(08)70878-1
- Wilkins, O., Waldron, L., Nahal, H., Provart, N. J., and Campbell, M. M. (2009). Genotype and time of day shape the *Populus* drought response. *Plant J.* 60, 703–715. doi: 10.1111/j.1365-313X.2009.03993.x
- Xu, H., Kempainen, M., El Kayal, W., Lee, S. H., Pardo, A. G., Cooke, J. E. K., et al. (2015). Overexpression of *Laccaria bicolor* aquaporin JQ585595 alters root water transport properties in ectomycorrhizal white spruce (*Picea glauca*) seedlings. *New Phytol.* 205, 757–770. doi: 10.1111/nph.13098
- Yin, C. Y., Duan, B. L., Wang, X., and Li, C. Y. (2004). Morphological and physiological responses of two contrasting poplar species to drought stress and exogenous abscisic acid application. *Plant Sci.* 167, 1091–1097. doi: 10.1016/j.plantsci.2004.06.005
- Yuan, Z. Y., and Chen, H. Y. H. (2010). Fine root biomass, production, turnover rates, and nutrient contents in boreal forest ecosystems in relation to species, climate, fertility, and stand age: literature review and meta-analyses. *Crit. Rev. Plant Sci.* 29, 204–221. doi: 10.1080/07352689.2010.483579
- Zang, U., Goisser, M., Häberle, K. H., Matyssek, R., Matzner, E., and Borken, W. (2014). Effects of drought stress on photosynthesis, rhizosphere respiration, and fine-root characteristics of beech saplings: a rhizotron field study. *J. Plant Nutr. Soil Sci.* 177, 168–177. doi: 10.1002/jpln.201300196
- Zhao, M., and Running, S. W. (2010). Drought-induced reduction in global terrestrial net primary production from 2000 through 2009. *Science* 329, 940–943. doi: 10.1126/science.1192666

Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Copyright © 2015 Brunner, Herzog, Dawes, Arend and Sperisen. This is an open-access article distributed under the terms of the Creative Commons Attribution License (CC BY). The use, distribution or reproduction in other forums is permitted, provided the original author(s) or licensor are credited and that the original publication in this journal is cited, in accordance with accepted academic practice. No use, distribution or reproduction is permitted which does not comply with these terms.