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Review Paper

Securing African forests for future drier climates: applying ecophysiology in tree improvement

Casparus J Crous^{1*}, Francois S Malan² and Michael J Wingfield¹

¹ Department of Plant and Soil Sciences, Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria, Pretoria, South Africa

² 102, 2nd Avenue, Kleinmond 7195, South Africa

* Corresponding author, email: casper.crous@fabi.up.ac.za

Increasing incidences of drought-induced tree mortality are being recorded worldwide, including Africa. African forests cover a significant proportion of the continent, which implies that African forest sustainability is threatened from a climate-change perspective. This is especially problematic in a developing nation context, because forest ecosystems such as plantation forestry provide important goods and services that sustain human well-being and economic growth. Disentangling the likely triggers of tree mortality (including those linked to drought) in landscapes would not only explain the mechanisms underlying local die-offs, but also better predict future mortality events. Methods applied in the field of ecophysiology are particularly useful to study in situ plant responses to an environment. We consider the status quo of global peer-reviewed publication outputs during the past century that have made use of key ecophysiological research approaches, specifically studies concerning 'tree xylem anatomy', 'tree xylem cavitation', 'tree leaf gas-exchange' and 'tree xylem hydraulic conductivity'. We highlight the growth and applicability of this research field in understanding tree ecology. We also assess the role that the forestry sector has had in promoting such research to ensure future-proof forest products. Most importantly, we consider how Africa with its vast forested landscapes fits within this research spectrum. The last decade saw an increase of up to 60% in the total number of articles published, particularly with a focus on tree xylem cavitation and conductivity. Although forest research contributed greatly to the global tally of ecophysiological studies, and such studies in Africa have also increased by up to 88% in the past decade, there remains a general lack of this research topic in the continent. It is clear an optimisation of applied ecophysiological concepts and techniques will promote an improved understanding of tree mortality patterns. We argue that ecophysiological data will be crucial to future-proof tree improvement strategies in African commodity production landscapes, especially given future drier climates.

Keywords: developing nations, drought tolerance, forest resilience, forest sustainability, plantation forestry, tree hydric strategy, wood anatomical ecology

Introduction

African forests and other woodland ecosystems represent almost 20% (c. 1 billion ha) of the c. 5 billion ha of forest and other wooded land estimated for the globe (FAO 2010). To put these numbers into perspective, the continental average for hectares covered in forest and other wooded land is c. 17% for Africa, with the highest being c. 21% in Europe (Antarctica not included; FAO 2010). The importance of African forests and other wooded land for human well-being in developing countries, across all hierarchies of needs (e.g. aesthetics, cultural, sustenance and security) has been well defined (Shackleton and Shackleton 2004; Sunderlin et al. 2005; Shackleton et al. 2007). Unfortunately, there is good evidence to suggest that global forest sustainability is severely threatened, especially due to drought- or heat-induced mortality (Allen et al. 2010; Choat et al. 2012). Large-scale forest decline could thus be a significant reality for many African countries in the future.

Plantation forestry, especially in South Africa but rapidly growing elsewhere in Africa, is a major part of the production landscape (Wingfield et al. 2015). The stability of this industry is strongly correlated to sustainable socioeconomic conditions, a key premise for developing nations. An important question is whether stakeholders in African forestry have the ability to predict which trees are more likely to be affected under future drier climates. Answering this question is especially relevant to crop production in a developing nation context, where the lack of access to such knowledge would render local land-owners increasingly vulnerable to future environmental change (Lin et al. 2008; Müller et al. 2011).

There are important aspects of comparative plant physiology and anatomy (ecophysiology) that add to our understanding of the adaptation or response of woody tree species to varying water availability in space and time (Carlquist 1977; Grime 1977; Zimmerman 1983; Carlquist 1988). For example, Choat et al. (2007) showed strong intra- and interspecific differences in plant hydraulic properties between nine congeneric species growing across a precipitation gradient. Thus, even closely related species can differ in their ability to mitigate stressful conditions. There is often significant variation in the ability of plant populations and communities to withstand hydraulic failure across landscapes (Pockman and Sperry 2000; Jacobsen et al. 2007a, 2007b, 2008; Crous et al. 2012a, 2012b). The implication of these ecophysiological studies is that we can gain a more mechanistic understanding as to which species, or even functional groups, have a competitive advantage when faced with stressful environmental conditions (Pratt and Black 2006; West et al. 2012; Skelton et al. 2015). Here, a valuable application can be found in the ability to predict tree community assemblage patterns under future environmental change models (Adams et al. 2013a; Gustafson et al. 2015; Skelton et al. 2015), which would then include possible threats by drought-triggered pests and pathogens (Box 1; McDowell et al. 2008; Allen et al. 2010; Anderegg et al. 2015a; Hartmann et al. 2015).

Using methods in ecophysiology, it has been demonstrated how commercially important Eucalyptus hybrid clones in South Africa differed significantly in drought tolerance (Vander Willigen and Pammenter 1998). Being less adapted to water stress would negatively influence plant productivity under harsh climatic conditions (Sperry and Love 2015). Various ecophysiological constraints under shading or sunlight also directly influenced the planting strategy that would best suit important Arabica coffee plantations in tropical Africa (DaMatta 2004a). In fact, for coffee in general, ecophysiological research has shown great potential to improve tree breeding strategies (DaMatta 2004b). Similarly, in Zimbabwe, correlating the xylem structural adaptations of native Pterocarpus angolensis (kiaat) individuals to historical precipitation in the landscape provided valuable insights regarding the likely productivity of this widely planted commodity tree when exposed to variable climatic conditions (Stahle et al. 1999). Knowledge of variance in tree hydraulic structure and function thus allows for more precise and advanced future crop development recommendations (Crous et al. 2013).

In hindsight, many past forest-decline studies could have benefited substantially from using empirical or processbased models of the functional responses of trees to waterstress across environments (Adams et al. 2013a). For example, Pterocarpus angolensis (kiaat) die-back in South Africa was only anticipated to be water-stress related due to the presence of secondary pathogens (Mehl et al. 2010). If so, it would be important to understand the physiological or anatomical mechanisms that have given rise to higher levels of drought susceptibility in these trees. Furthermore, it would be useful to know how this information could be used to advance future tree-planting strategies. There is great value in having a more detailed understanding of all the abiotic and biotic environmental factors responsible for tree die-back, and particularly their interactions in space and time (Adams et al. 2013a; Anderegg et al. 2015a).

Although many western countries have realised the complementarity nature of ecophysiological approaches to

tree-health research (Anderegg et al. 2012; Hartmann et al. 2015), there seems to be a distinct lack of knowledge exploring these concepts in developing countries such as those in Africa. Given that there are increasing risks of large-scale tree decline in African countries due to global climate-change predictions, and following a precautionary principle, there is a need to recapitulate why these research approaches would help to better explain and predict current and future forest die-back. In this review, we consider the status quo of peer-reviewed publication outputs that have made use of key ecophysiological research approaches globally. In this way, we showcase the growth and applicability of this research field to promote a better understanding of plant-water relations in an environment. We highlight the role that the forestry sector has played to advance this research field, thereby future-proofing valuable forest products. Finally, we compare how Africa with its large forested landscapes fits within this research spectrum. We seek to underscore the application of such plant functional research methods to increase our predictive power in modelling future tree-health issues in tree production landscapes in Africa.

Trends in global tree ecophysiology research

The evolution of ecophysiology as a research field

Once established, terrestrial plants are sessile in space and time. Any sudden habitat disturbance, such as an exceptional drought, the introduction of an invasive alien species, or an increase in pest and pathogen pressure, could severely affect local plant survival in an affected landscape. However, some plant species have the ability to either resist or tolerate a variety of environmental stressors (e.g. higher resilience). This ability is a function of both the genetic capacity of a species to adapt to the situation as well as the intensity and/or combination of stress endured by the population (Grime 1977; Cushman and Bohnert 2000; Chaves et al. 2003; Molinier et al. 2006; McDowell et al. 2008; Suzuki et al. 2014). The inability of plants to move to more favourable environments, and the fact that some species are inherently unable to efficiently adapt to local changes in environmental conditions, are well-recognised constraints. This has led to the formulation of key concepts regarding how plant physiological and anatomical trait adaptations enable species to persist across varying environmental conditions (Box 2). The fact that the study of plant functional-trait adaptations to drought has advanced considerably, both conceptually and methodologically, clearly attests to their application and value to tree ecology and thus forest conservation (Carlquist 1977; Grime 1977; Zimmerman 1983; Carlquist 1988; Tyree et al. 1994; Ackerly et al. 2000; Hacke and Sperry 2001; Tyree and Zimmerman 2002; Reich et al. 2003; Ackerly 2004; McDowell et al. 2008; Choat et al. 2012; Anderegg et al. 2015a, 2015b; Gleeson et al. 2015; Sperry and Love 2015; and many other references).

Quantifying the global research output of four key ecophysiology research themes

Allen et al. (2010) emphasised the gaps in physiological research that are required to promote an understanding of global forest die-back patterns. Indeed, a greater focus on

Box 1: What kills a tree? The isohydry-anisohydry framework to articulate tree die-back mechanisms

An excellent model to effectively articulate the mechanisms involved in differential plant survival and mortality along a water-stress gradient is the plant isohydry–anisohydry framework as conceptualised by McDowell et al. (2008). Determining whether plants are isohydric (balancing their water potential levels by closing stomata when stressed) or anisohydric (greater fluxes in water potential due to maintaining transpiration under various water conditions) could be used to assess which species will function better under variable drought scenarios. For example, when droughts are short but intense, anisohydric plants will likely experience die-back mainly due to drought-induced embolism. This is because they continue to lower their water potential (plants that operate close to hydraulic thresholds). In turn, when droughts are long-lasting but mild, isohydric plants will likely suffer from carbon starvation because transpiration and, therefore, plant carbohydrate acquisition decreases. A lack of carbon can decrease the quality and quantity of secondary metabolites in trees, which in turn should decrease herbivore resistance (McDowell et al. 2008; Sala et al. 2010). Plants that utilise an isohydric strategy should then take longer to display symptoms of decline. Thus, as a 'rule of thumb', trees that die rapidly in an environment are usually related to catastrophic hydraulic failure, shade-grown trees due to carbon starvation, and slow-dying trees due to a combination of both factors (Sevanto et al. 2014). This model could provide an aid to predict the timing of tree mortality when it is known which drought type to expect.

The isohydry–anisohydry tree-mortality model is further completed by highlighting the role that biotic stressors, i.e. pathogens and pests, play in drought-induced tree die-back. Here it is important to recognise that biotic stressors operate from a different dimension in that they could induce die-back or mortality regardless of the tree's hydric strategy (Box Figure 1). This model is particularly aligned with secondary pests and pathogens, because drought stress is typically a requirement for attack from secondary pests and pathogens (Jactel et al. 2012). Thus, differential biotic damage to trees across space is highly dependent on *in situ* environmental conditions.

There are uncertainties regarding the accuracy of the carbon starvation hypothesis (CSH) as posited in the isohydry–anisohydry model. It is challenging to know exactly which hydric or biotic mechanism is ultimately responsible for killing populations or communities of trees (Hartmann et al. 2015). A proposed flaw of the CSH is that die-back of isohydric plants during prolonged drought events can still be plausible without having exhausted carbon reserves (Sala et al. 2010). The ability of plants to move or reallocate carbon reserves during prolonged drought may therefore still provide the necessary energy to survive (Hartmann et al. 2013). Drought may therefore not directly lead to reduced carbohydrate reserves and thus tree death (Anderegg et al. 2012). One way to explain this phenomenon is that increased atmospheric CO_2 concentration associated with current global environmental change can actually increase the water-use efficiency of plants (Franks et al. 2013). For example, during moderate yet prolonged

droughts, a more efficient carbon-water exchange during times of higher ambient temperature mitigated water stress in Eucalyptus trees (Duan et al. 2013). However, during more intense and lethal droughts where high temperatures prevail, the temperature sensitive kinetics of sugar metabolism (i.e. the inability to efficiently metabolise photosynthate) may well contribute to tree mortality (Adams et al. 2013b). In addition, severe levels of leaf senescence due to prolonged drought can physically disable trees to assimilate the necessary carbon stock in rooting tissue (Landhäusser and Lieffers 2012). The physical loss of transpiring tissue is clearly a cause of concern regarding carbon assimilation, especially leaf-drop in deciduous trees, but also for evergreen trees during the colder season. Sevanto and Dickman (2015) provided an effective solution to moderate the current discrepancies in the CSH as a key mechanism in killing trees. These authors suggested that it is to gain a better understanding of the actual reallocation and transport of stored carbon to those plant tissues or biochemistry pathways that optimise drought resilience. If reallocation or movement of stored carbon to critical hydraulic functioning in trees is decreased in the long run, then the CSH hypothesis is undoubtedly valuable in explaining current and future forest decline.

Ultimately, the multifaceted McDowell et al. (2008) model provides a valuable, perhaps even critical, point of departure to develop research questions regarding tree or forest sustainability in a changing environment. It is clear that this model delivers a more comprehensive and complementary approach to disentangle the often complex mechanisms underpinning tree mortality under variable environmental conditions (Mueller-Dombois 1986; McDowell et al. 2010, 2011; Hartmann et al. 2013; Sevanto et al. 2014; Anderegg et al. 2015a). Given that the time during which a tree is subjected to dangerous hydraulic thresholds could be more important than plant thresholds *per se*, it is possible to be even more precise in applying such tree die-back models (McDowell et al. 2013; see also Choat et al. 2012).



Box Figure 1: The isohydry–anisohydry framework to model tree die-back under various drought conditions. Isohydric plants are more likely to suffer from carbon starvation via limited transpiration, whereas anisohydric plants are more likely to die from hydraulic failure (xylem cavitation) due to continued transpiration under water-stressed conditions. Fundamentally, isohydry means safer water transport in extreme droughts, but eventually lower growth. In turn, anisohydry means more efficient transport of water and nutrients, leading to higher relative growth in the short term, but eventually die-back under extreme and continuing drought events. Biotic attack can exacerbate (amplify) die-back when the plant's defence weakens due to increased water stress. Although drought might initially trigger die-back events, these pests and pathogens can eventually be the 'bullet' that kills the tree. Adapted and redrawn from McDowell et al. (2008)

Box 2: Key hydraulic mechanisms that help to explain and predict tree mortality patterns

Xylem resistance to drought-induced cavitation

An important threat that plant hydraulic systems face is xylem cavitation (Sperry 1995). This is the phenomenon where gas seeds into vessels (angiosperms) or tracheids (conifers) under environmental stress, causing a bubble (an embolism) to form in the conduit and thus leading to a substantial loss in the hydraulic conductance of the plant. This can result in either die-back or a reduction in growth (Sperry and Tyree 1988). The mechanism responsible for water-stress-induced cavitation is explained by the 'air-seeding' hypothesis (reviewed in Hacke and Sperry 2001). According to this hypothesis, air will enter a water-filled conduit when the pressure difference between the xylem water and the air from an empty adjacent vessel (e.g. damaged vessels) exceeds the capillary forces at the air-water interface. Air consequently enters through the inter-conduit pit membrane, and thus porosity of pit membrane structures in the xylem is the underlying cause of cavitation in trees (Choat and Pittermann 2009).

The mechanism determining susceptibility to cavitation between conifers (softwoods) and angiosperms (hardwoods) differs due to different pit membrane architectures. For vessels in particular, air seeding will most likely occur through the largest of these pit pores (Sperry and Tyree 1988; Pockman et al. 1995), because a positive relationship between the pit area per vessel and vulner-ability to cavitation has been measured (Wheeler et al. 2005). Thus, when larger, more porous apertures are less abundant in the vessel elements of hardwoods, the plant may be less prone to cavitation (Christman et al. 2009). In contrast, softwoods have tracheids that have the torus–margo pit membrane structure, where the torus can seal off the inter-conduit pathway when the adjacent (often earlywood) pits becomes aspirated (Pitterman et al. 2005). This limits gas bubbles to a specific tracheid, and because tracheids are not as porous as vessels, this seal-off should theoretically significantly prevent further water supply losses in softwoods (see 'runaway cavitation' below). However, softwoods are not considered to be better equipped to resist xylem cavitation (Sperry 2003), because the torus–margo pit membranes do cavitate when, for example, the margo stretches or ruptures under certain xylem pressure conditions (Sperry and Tyree 1990). In fact, conifers that have thicker tori (less elastic) and deeper pit chambers (more stretching required to seal off) have a significantly higher vulnerability to cavitation (Hacke and Jansen 2009).

Although air-seeding through pit membranes (pit aspiration) is seen as the main cause of xylem cavitation, cavities created by 'cavitation bacteria' in xylem secondary walls, especially when these cavities are near pits, might also induce entry points for gas bubbles into adjacent conduits (Singh and Butcher 1991). Feeding by herbivores can also pierce the sapwood, thereby inducing cavitation into a tracheid or vessel (Zimmerman 1983).

'Runaway cavitation' refers to the amount of cavitation from which the plant will not easily recover and therefore is likely to cause decline or death (Tyree and Sperry 1988). This phenomenon occurs when the plant reaches the P_{50} level (after 50% loss in hydraulic conductivity occurs; e.g. Hacke et al. 2000; Maherali et al. 2006). However, the P_{50} level is only a comparative tool in determining population or community differences in drought-tolerance. Having 50% of vessels filled by gas emboli does not directly infer tree die-back, as there are other safety mechanisms, such as improved leaf-level water regulation, that can still prohibit die-back (Skelton et al. 2015). Nonetheless, from an applied ecological perpective, vulnerability to cavitation measurements makes it possible to compare water potentials (i.e. relative access to soil water) of suites of species against their cavitation percentages associated with runaway cavitation. It is, therefore, possible to establish the ecological range or potential distribution limitations for plants, i.e. the minimum water potential that a species must retain to remain physiologically active (Bhaskar and Ackerly 2006). This is a key factor in predicting species distribution and range for future drier conditions, and was recently highlighted in a study of the highly biodiverse and threatened fynbos biome of South Africa (Skelton et al. 2015).

The xylem wood density and drought tolerance link

Xylem density (wood density) is known to be important in plant water transport (Meinzer 2003), because wood tissue responds to gradients in environmental factors, such as soil water availability and temperature (Hacke et al. 2001; Preston et al. 2006; Thomas et al. 2007). Woody species that allocate more wood tissue per unit volume to their stems, and thus have higher wood density, are generally associated with slower growth-rate patterns when compared with trees that have less dense wood (Enquist et al. 1999). Consequently, high wood density decreases hydraulic conductivity of the stems (Wagner et al. 1998; Stratton et al. 2000). This phenomenon is mainly attributed to xylem conduit diameter and the Hagen–Poiseuille Law, which states that conduit lumen conductivity will increase with the fourth power of lumen diameter (Zimmerman 1983; Sperry et al. 2006). Thus, an increase in tracheid or vessel diameter would increase stem hydraulic conductivity as the percentage of lumen area per transverse section of xylem is increased. Maximum hydraulic conductivity (K_{max}) or maximum sapwood specific conductivity (K_{smax} ; xylem-specific flow, i.e. pith excluded) is often measured to depict these differences in water flow (kg s⁻¹ MPa⁻¹ m⁻¹). Not surprisingly, Zimmerman (1983) noted that if such a slight variation in evolutionary development of xylem can be so beneficial to plant hydraulic transport, it is relevant to question why some plants select for this trait while others fail to do so.

When xylem density values are correlated against water stress, it is found that plants that experience the highest level of stress are likely to have denser wood (Ackerly 2004; Jacobsen et al. 2007a). This may be due to a tight evolutionary correlation between drought stress and xylem resistance to embolism (Bhaskar et al. 2007). Water potentials at 50% xylem embolism (P_{50}) have been positively correlated with larger xylem vessel sizes (Kolb and Sperry 1999). This means that, although vessels with larger diameters improve water movement through the xylem, such less dense wood would be more prone to drought-induced xylem cavitation. However, deviations from this pattern do exist because there are various phylogenetic-specific adaptations to a particular region that dictate a preferred wood density strategy (Chave et al. 2006). Nonetheless, higher wood density is an indicator of resistance to cavitation

Box 2 (cont.)

(Hacke et al. 2000, 2001; Pratt et al. 2007) and therefore remains a good predictor of potential drought-induced mortality within tree communities (Westoby and Wright 2006; Chao et al. 2008; Chave et al. 2009).

There is clearly a safety versus efficiency trade-off between optimising hydraulic transport and resisting hydraulic failure due to xylem cavitation, although this trade-off can be quite weak for some plant species and under certain environmental conditions (Gleeson et al. 2015). Crous et al. (2012b) highlighted the important relationship between environmental factors such as mean annual precipitation and wood density, and how plasticity in xylem density could help explain the widespread nature of some invasive alien trees. Indeed, mean annual precipitation can be a useful predictor of drought tolerance (Jacobsen et al. 2007b). Essentially, knowledge of differential xylem anatomical phenotype provides a valuable basic understanding into plant strategies in landscapes that vary in water availability (Read and Stokes 2006; Sperry et al. 2006). Moreover, xylem density measurements are relatively easy and inexpensive to obtain, and a comprehensive wood economics spectrum for a region would feed directly into better models of future vegetation dynamics under changing environmental conditions (Chave et al. 2009).

Xylem wall-to-lumen ratio: resistance to vessel implosion and cavitation

Given that relatively high negative pressures are observed in vessels, some strain or bending pressures do exist between two adjacent conduits (Hacke et al. 2001). Embolised vessels are common in otherwise healthy stems (broken vessels due to scarring from a pest, for example) (Zimmerman 1983). Thus, in the instances where an embolised vessel occurs adjacent to a healthy one and the vessel wall thickness between them is not sufficiently strong, vessel implosion might occur. Although implosion of a vessel has rarely been observed, the effect of bending stress can allow air to enter through the inter-conduit pit membranes (Hacke et al. 2001). Wood density is strongly associated with a higher wall to lumen ratio $(t/b)^2$ of a vessel (Hacke et al. 2001; Hacke and Sperry 2001; Crous et al. 2012b). Vessel $(t/b)^2$ also correlates positively with vessel P_{50} values and has been suggested as a valuable screening experiment for comparing drought tolerance between species (Cochard et al. 2008). In fact, xylem mechanical strength is positively and significantly correlated with greater cavitation resistance (Pratt et al. 2007). This again emphasises the importance of porosity of bordered pit membrane structures in xylem in understanding xylem cavitation and differential drought tolerance strategies in trees (Choat and Pittermann 2009). This knowledge makes it possible to develop valuable hypotheses regarding water-stressed environments, mechanical strength and which plants would better respond to drought conditions (Sperry et al. 2006).

Xylem water potentials: the pressure behind the ascent of sap

Given that plant water potential (pressure) in moist soil is near zero, for water to ascend the xylem to ensure osmoregulation, the pressure at the leaf level must be negative (Zimmerman 1983). Water potentials measurements (Ψ_x) therefore have negative values because they indicate suction (negative pressure). Interestingly, but perhaps not surprising given niche theory, plants vary considerably in the level of suction at the leaf level even in the same environment. This is mainly because pre-dawn Ψ values correspond to the maximum level of soil moisture that plants have access to, and midday Ψ values provide the water potential at the maximum level of water deficit, which is influenced by species-specific hydric strategy. Generally, the lower the water potential (more negative Ψ), the more water-stressed the plant is. These measurements are therefore valuable to study site-specific water stress between plants, e.g. which plants are not operating as efficiently with respect to the soil–plant hydraulic pathway. However, one cannot infer much from water potential on its own, because a plant that operates at low water potentials might have other xylem structural defences against hydraulic failure, such as a low P_{50} value. Thus, water potentials are best used as complementary to other measures of drought stress as mentioned above.

Leaf-level water regulation and drought resistance in trees

Leaves represent the final frontier in the soil-plant-atmosphere continuum, and hold the key to comprehensively understanding plantwater relations in space and time (Sperry 2003). Here, the carbon-for-water or 'supply-loss theory' makes it possible to infer drought adaptation within tree populations or communities (Sperry 2003; Sperry and Love 2015). This theory is especially valuable because it very simply describes the idea that there will always be a trade-off in water loss and carbon or energy supply. Measuring these factors makes it possible to understand the economy of a particular tree species or clonal hybrid. Indeed, the evolutionary response of leaf and stem traits can be quite conservative given a certain level of water stress, and therefore is highly applicable to tree mortality predictions given future climate change (Sperry and Love 2015).

Stem (xylem) drought resistance can also be decoupled from leaf-level drought resistance (Baraloto et al. 2010). This means that two plants can have similar stem hydraulic properties, but it can occur that only one survives under harsh climatic conditions due to it having a more efficient leaf-level water regulation. This concept was recently applied to the highly diverse fynbos region in South Africa, and represents a major advance in how we can functionally predict how native woody species would survive in native environments given future climate change (Skelton et al. 2015). Another example that illustrates the importance of combining both leaf and stem economics in predicting tree mortality comes from the iconic African baobab tree (*Adansonia digitata*). Not only do seedlings avoid droughts through root succulence (rather than stem succulence, which is suggested to be more important regarding adult trees), but also through having a conservative water strategy, i.e. prohibiting leaf-level water loss by more regularly closing stomata when dry conditions prevail (drought-enforced dormancy) (van den Bilcke et al. 2013). Baobab trees have an impressively long lifespan, and this non-risk water-use strategy (being isohydric, Box 1) could explain this. Measures or proxies of leaf gas exchange are thus vital to include in tree drought-stress analyses.

the elements that are responsible for xylem or hydraulic impairment, especially when a tree hydraulic threshold can be derived, remains a priority research field for predicting future forest die-back patterns under scenarios of environmental change (Anderegg et al. 2012, 2015b; Gustafson et al. 2015; Sperry and Love 2015). Seemingly, very few such studies originate from African forest landscapes, which is in contrast to the body of work that already exists for other forest-rich countries (CJC pers. obs.).

To quantify the current publishing trend in plant studies using aspects of tree ecophysiology and xylem anatomy. and also to quantify our anecdotal observation of a lack of such studies from Africa, we searched the Thomson Reuters Web of Science[™] database (apps.webofknowledge.com) using the terms 'tree xylem anatomy', 'tree xylem cavitation', 'tree leaf gas-exchange' and 'tree xylem hydraulic conductivity'. These phrases were chosen because they encompass a wide variety of well-studied ecophysiological research methods (see Box 1). For this reason, many other publications could have been overlooked, but we believe that these research fields should include a relevant component of the literature we sought to compare. Furthermore, because the word 'tree' was used in each search item, there would be a bias towards forests and forestry. However, tree science, as opposed to all woody plants, was the main focus of this review.

To depict possible differences in the number of studies for 'tree xylem anatomy', 'tree xylem cavitation', 'tree leaf gas-exchange' and 'tree xylem hydraulic conductivity', we compared the number of peer-reviewed journal articles and reviews published during the last century (1914-2014; end date August 2014) for (1) globally, (2) Africa, searching within the global tally using the key word 'Africa', and (3) the portion of the literature specifically linked to forest science by selecting 'Forestry' under the Research Area criterion. We also tallied the number of articles published in the last decade within each of the three categories. Finally, we compared the number of research articles from Africa with those publications that are listed as forest research globally. However, as ancillary to this latter comparison, we calculated whether the percentage of articles published from African countries is in relation to an expected 20% of the global tally. This percentage is derived from the fact that African forests and woodlands cover c. 1 billion ha of the projected global 5 billion ha (FAO 2010). These observed versus expected frequencies were calculated using chi-square tests in Statistica 12 (StatSoft, Inc., Tulsa, OK, USA).

Global scientific output and the role of forestry science

Globally, there has been increased activity on the topics of 'tree xylem cavitation' and 'xylem hydraulic conductivity' when compared with historically older research fields such as 'tree xylem anatomy' or 'leaf gas-exchange' (Table 1). This highlights the fact that these measures, which are known to effectively compare drought tolerance and other important hydraulic characteristics of woody plants, are increasingly being applied worldwide. These topics are also increasingly being applied to forestry. In fact, forestry science has contributed substantially to the global tally of publications that made use of these ecophysiological methods (Figure 1).

As expected, the number of articles from African wooded landscapes was low for each of the categories considered (Table 1). However, a similar trend showing an increase in 'tree xylem cavitation' and 'xylem hydraulic conductivity' could be seen in studies from Africa during the last decade (88% and 86% increase, respectively; Table 1). This clearly has much to do with the fact that the latter methods are newer concepts that have required greater technological advances to measure (Ackerly et al. 2004). Nonetheless, from this survey, we could conclude that across all three groups, the role of ecophysiological aspects of water transport in the xylem is increasingly being appreciated. This is a positive trend considering the increased need for such data to map global tree die-back risks under waterstressed conditions (Allen et al 2010; Anderegg et al. 2015a; Gustafson et al. 2015; Hartmann et al. 2015).

Given that our analysis was limited to specific topics, it was clear that research on African forests that focus on a mechanistic understanding of ecological tree structure and function has received significantly less attention than forest science in general (Figure 1). The sampled number of articles from African forests was evidently far from a 20% distribution as would be expected given relative forest and woodland area (χ^2 values ranged between 18.063 and 22.563, *P* < 0.001 in all cases). Ecophysiological research has therefore not been a priority in Africa compared with its progression globally. Clearly, to compare developing nations with more technologically advanced nations should also be factored into these analyses. Nonetheless, an increased understanding of the ecophysiological and wood anatomical knowledge of healthy forests should be promoted.

Future directions for sustainable forestry in Africa

Applying ecophysiology to improve drought resilience in forestry plantations

In line with what was demonstrated earlier, there are many examples of how the global forestry sector has used methods in ecophysiology to screen for vulnerability to drought-induced hydraulic failure (Table 2). An example from South Africa was where large-scale die-back of commercially important *Eucalyptus* hybrid clone plantations was attributed to some genotypes being less drought tolerant than others in the landscape (Table 1; vander Willigen and Pammenter 1998). Apart from the huge financial losses incurred by such a large-scale tree die-back, the worrying aspect is that important species of a widely planted genus in many parts of Africa may have significant differences in drought tolerance.

Differential drought resilience in commercially important tree species has often been observed, especially in *Populus* hybrid clones (Table 2). For poplar genotypes there exists a neat and practical way of pre-screening tree drought tolerance where leaf size is considered (Table 2; Schreiber et al. 2016). A leaf size index is appropriate because there is a positive correlation between higher leaf area and higher hydraulic transport capacity (Santiago et al. 2004). Thus, certain tree genotypes with relatively more 'thirsty' leaves could have an increased risk of hydraulic failure during drought events (Schreiber et al. 2016). Indeed, to incorporate levels of photosynthesis in **Table 1:** Number of journal and review papers published during the last century (1914–2014), and those published within the last decade, concerning key ecophysiological and wood anatomical parameters globally, in Africa, and from the forestry sector. PLD = percentage of articles published during the last decade

Maggurament	Cinco	Global		Africa		Forestry	
Measurement	Since	Articles	PLD (%)	Articles	PLD (%)	Articles	PLD (%)
Tree leaf gas exchange	1939	8 135	27	74	53	3 012	50
Tree xylem anatomy	1923	2 216	39	48	52	1 841	35
Tree xylem cavitation	1968	815	58	16	88	549	55
Tree xylem hydraulic conductivity	1973	879	60	22	86	647	60



Figure 1: Percentage contribution of selected ecophysiological and anatomical peer-reviewed articles and reviews from forestry research in general, and from Africa in particular. Percentages were calculated from the global tally

plantation tree selection can be particularly useful to predict their growth suitability across varying climatic conditions (Crous et al. 2013; Table 2). Even when the forest canopy cannot be readily accessed for such conventional empirical measurements, remote sensing of transpiration strategies between various plantation trees may also provide an indication of tree stress, as was shown for *Eucalyptus* plantations in South Africa (Dye et al. 2004). Collectively, there are many interesting and highly practical approaches that can be used to facilitate an ecophysiological approach to tree improvement strategies.

Considering the fact that many plantation forestry sectors make use of non-native trees, it is important to question whether trees being bred and selected are also drought tolerant. This question is especially relevant because these trees will be planted in areas having vast environmental variation and to which they may or may not be pre-adapted (*sensu* Näsholm et al. 2014). By knowing that a particular plantation crop is more or less drought susceptible, tree breeders can improve drought resistance, as was suggested for multiple genotypes within the widely planted *Populus* (Monclus et al. 2006) and *Eucalyptus* (Bartholomé et al. 2015). For both these widely planted genera, it was suggested that modifying the genes responsible for higher water-use efficiency (i.e. to genetically improve the leaf traits that can optimise tree adaptation

to drier conditions) would be possible, without sacrificing productivity. Indeed, Battie-Laclau et al. (2016) recently showed that there was no relationship between leaf-level water-use efficiency and stand-level water-use efficiency (wood growth per water use) for a commercially important *Eucalyptus grandis* clone in Brazil.

For crops in arid and semi-arid areas specifically, it could also be possible to genetically inhibit drought-induced leaf senescence, thereby optimising drought tolerance via artificially inducing higher water-use efficiency at the leaf level (Rivero et al. 2007). This might sound counter-intuitive, because leaf shedding is a positive response of especially arid and semi-arid plant individuals to water stress in the landscape (a less dense canopy means a decreased water budget per tree individual; Fischer and Turner 1978). It is suggested that this inhibition can actually 'rewire' a plant to rapidly adapt to in situ water-limited conditions because leaf shedding is no longer an option for that plant (Rivero et al. 2007). Maintaining more plant organs that are conservative water regulators may ultimately also maintain levels of carbon assimilation during moderate but prolonged droughts, and thus sustain growth and productivity in drylands (see carbon starvation hypothesis in Box 1).

On the other hand, for tropical or temperate crops where large quantities of water would be more readily available after droughts, another promising breeding strategy would be to select for rapid leaf shedding under drought, and rapid leaf re-establishment at the end of the drought. This is because wood growth in an area is more likely a function of leaf area (site occupancy) and higher photosynthesis when water is available (White et al. 2014). As such, these crops should have better protection from mortality during drought and a better potential for maintenance of rapid growth when water becomes available again. On the whole, the genetics of plant hydraulics is arising as an exciting and topical opportunity for breeding drought-resilient yet productive trees. Indeed, because species-specific life-history strategies vary greatly in space and time, the genetic, physiological and biomechanical controls regulating plant hydraulic architecture require greater attention (Monclus et al. 2006; Read and Stokes 2006; Weitz et al. 2006; Jansen and Nardini 2014; Bartholomé et al. 2015; Plomion et al. 2016).

In developing countries, where the infrastructure for genetic breeding might more likely be lacking when compared with developed countries, forest managers may focus on reducing stand density of planted compartments. Reducing the planted biomass per unit land area can increase water availability in the landscape (Bosch and Hewlett 1982). Remaining tree individuals in thinned stands Table 2: Examples of the application of ecophysiological research to tree breeding and plantation forestry given future drier climates

Commodity	Study synthesis	Application		
Populus deltoides × P. nigra (Tschaplinski et al. 1998)	For semi-arid areas of Washington State, USA, it was suggested that a <i>Populus deltoides</i> \times <i>P. nigra</i> clone was the more appropriate clone to plant when there was insufficient water (e.g. little to no irrigation). In contrast, where water was not a limitation, a <i>Populus trichocarpa</i> \times <i>P. deltoides</i> clone would be more suitable. The latter clone has high carbon allocation under more mesic conditions, but as soon as drought ensues it starts to shed leaves, which indicates that it would lose its growth advantages in that scenario. The former clone would thus be a better choice, as it allocates more carbon to rootstocks under drought conditions and therefore drought-adapted growth (more sustainable growth, better production predictions).	Comparative ecophysiological response to water stress among forest clones can complement the choice of clones in a variable water-stressed environment.		
<i>Eucalyptus</i> clones (vander Willigen and Pammenter 1998)	For four <i>Eucalyptus</i> clones planted in KwaZulu-Natal, South Africa, differences in xylem and leaf-specific hydraulic conductivity was more closely related to <i>in situ</i> water availability than to genetic make-up, i.e. there was phenotypic plasticity in one clone when scaled from xeric to mesic sites. The clones also differed in vulnerability to drought-induced cavitation.	These data could help model areas where certain clones would be vulnerable to die-back given future climatic predictions, or on the premise that infrequent but severe events are a fixed variable across time.		
Lodgepole pine (Wang et al. 2003)	Properties, such as tree height and wood density, are strongly indicative of a certain drought-tolerance strategy within lodgepole pine. Tall, fast-growing trees with lower wood density are considered more vulnerable to drought-induced cavitation.	In breeding programmes, it would be possible to select for subpopulations that have a unique combination of fast growth and high wood density, whilst simultane- ously also being drought tolerant.		
<i>Eucalyptus</i> and <i>Corymbia</i> spp. (Rice et al. 2004)	In their native range in Australia, ironbark populations (<i>Eucalyptus</i> spp.) were shown to be much more prone to stem die-back and mortality compared with bloodwood populations (<i>Corymbia</i> spp.). A possible explanation for the lower levels of stem mortality in the bloodwood adults and juveniles is a drought avoidance strategy, i.e. having deeper rooting. Moreover, even though the ironwoods have a higher cavitation resistance, a shallower root system would mean that under infrequent but severe droughts, an individual would operate under very low water potentials (lesser relative access to soil water), and stem die-back would be more prevalent.	<i>Eucalyptus</i> and <i>Corymbia</i> are popular commercial genera planted outside their native ranges, and this information is thus valuable to screen species for a particular environment.		
<i>Salix</i> spp. (Wikberg and Ögren 2004)	Drought-sensitive interbreeding willows (<i>Salix</i> spp.) that are intensively propagated for biomass production showed differences in drought adaptation. They also show that possible trade-offs, such as gaining higher wood density, which improves cavitation resistance but leads to lower growth height, could be achieved.	These findings provided insight into opportunities to genetically manipulate cultivars to be more drought resistant.		
<i>Populus</i> hybrid clone (Raj et al. 2011)	A <i>Populus</i> hybrid clone, sourced from multiple nurseries, may have greater phenotypic plasticity than expected, especially because foresters could assume that it has a similar genotype and therefore should respond similarly within a planted block.	The nursery effect, i.e. sourcing plant material from a variety of geographical areas (although a single clone), must be taken into account when planting stands, because this would ultimately affect individual growth patterns within that stand. It can also help explain differential growth patterns of trees in a single stand.		
Eucalyptus <i>globulus</i> subsp. <i>globulus</i> (Crous et al. 2013)	Under current climate-change models, ecophysiological traits, such as photosynthesis, were useful to predict the suitable areas where <i>Eucalyptus globulus</i> subsp. <i>globulus</i> could be planted outside of its native range, i.e. where plantations of this species would likely have low productivity under climate change.	This is important when planning forestry plantations with known temperate species in more tropical areas.		
<i>Populus</i> hybrid clones (Schreiber et al. 2016)	There was a significant relationship between leaf size and vulnerability to drought-induced cavitation in five commercially important <i>Populus</i> hybrid clones. Hybrid poplars with larger leaves had wider vessel lumens and thus increased hydraulic capacity. They were also less drought tolerant. During drought, selecting for hydraulic efficiency (higher water use) and being less drought tolerant significantly increases die-back likelihood. In turn, compared with smaller-leaved hybrids, this would significantly affect their productivity in the planted landscape.	When selecting across a variety of genotypes to plant given future drier climates, screening for clone leaf phenotypic diversity could be an easy and highly practical tool to predict survival likelihood.		

could therefore have more water available, and thus an increased likelihood of staying productive during extended drought events. In turn, highly stocked compartments might suffer die-back and would thus be less productive (Bréda et al. 1995). Indeed, when coupled with an effective nutrition strategy, compartment thinning could significantly mitigate drought-induced productivity loss (White et al. 2009).

The tools to explain current tree die-back and to predict future tree decline are widely available and continuously being optimised (Sperry and Love 2015). Indeed, integrating ecophysiology with forest landscape models to better predict future distribution models under climatic uncertainty is of substantial current interest (Gustafson et al. 2015), specifically at the farm scale (Hartmann et al. 2015). The main message is that in examining the variation in hydraulic structure and function between commodities in a given landscape, we obtain a better idea of how they respond to *in situ* environmental conditions and what the likely consequences on productivity may be.

Given the predicted climate changes, these data would be especially valuable as screening tools for future clone deployment in plantation forestry in Africa (Figure 2). There are also genetic and landscape-level management options to mitigate drought risk in African forests. Indeed, a multidisciplinary approach to manage Eucalyptus plantations in Brazil was recently highlighted (Goncalves et al. 2013). We therefore propose that for every tree commodity that is currently in production in Africa, or those trees or genotypes still planned for future planting, a suite of stem and leaf hydraulic traits accompany health screening protocols. Many of these measures, for example wood density and leaf size indices, are easy to execute and inexpensive. This would ensure commodity production landscapes that are drought resilient given the vagaries of climate-change predictions. The scientific confidence to apply these research methods to help explain and to predict tree mortality in drought-stricken African landscapes can be derived from two consistent tree ecological phenomena:



Figure 2: Use of plant hydraulics to predict the drought susceptibility and productivity within genotypes of commercially important tree hybrids during screening trials (e.g. in provenance gardens or monitoring plots). This conceptual model follows the 'supply-loss theory' as described by Sperry and Love (2015). Maintaining more plant organs that are conservative or safer water regulators in time may ultimately maintain some growth and productivity in those landscapes. Using this productivity gradient approach, it can be argued that a somewhat smaller crop would be preferable to no crop at all

- Woody plants that grow under conditions of greater water stress show a measureable difference in wood architecture. They also have different physiological needs compared with conspecific trees growing under more favourable conditions. This can easily be measured, and important species-specific thresholds and gradients can be obtained.
- Where anatomical and physiological adaptations are divergent within and between tree species, it should be possible to model which tree species, or populations of trees, would be better adapted to a site during predicted environmental variability. This is because it is hard to 'cheat' the physics of plant hydraulics *in situ*.

Drought-resilience and pest screening in forestry plantations: a further application of ecophysiology

Mueller-Dombois (1986) alluded to the fact that when largescale tree die-back events occur, biotic causes are usually assumed. Indeed, primary pests, here including insects and microbial pathogens, are a major cause of damage in commodity production landscapes in Africa and elsewhere (Wingfield et al. 2015). However, drought stress in trees is also a major lure for secondary pests (Mueller-Dombois 1986; Desprez-Loustau et al. 2006; Beattie 2011; Jactel et al. 2012; Dietze and Matthes 2014). Given the predicted future global climate change, it becomes clear that the interactions between tree drought tolerance and pest and pathogen attack would also be more uncertain (Anderegg et al. 2015a). The ideal is to be able to know the drought resilience or hydraulic strategy of planted crops, and then to relate this information back to drought-triggered pest predictions (the isohdry-anisohydry framework, Box 1). It is therefore no surprise that plant anatomical and ecophysiological traits within the tree-herbivore realm remain an important subject of study worldwide (Dukes et al. 2009).

In southern Africa, the presence and management of forest pests is exceptionally well documented (Wingfield et al. 2008, 2013, 2015). However, very little is known about the interaction between pest presence and the levels of water stress experienced by plantation crops. For example, there is a strong pattern showing that at the highest level of infection by a pest, percentage loss in xylem conductivity is the most rapid contributor to stand-level mortality when compared with other pathogen and insect pathways, e.g. phloem, roots or stems (Dietze and Matthes 2014). This information could help to streamline the search for the mechanisms behind die-back in plantations. It would also allow for a more rapid response to curb future similar issues. Ecophysiology is thus highly complementary to untangling biotic-induced mortality patterns (Anderegg et al. 2015a), and would ultimately help assess the impact of climate change on forests and food security (Gregory et al. 2009).

Conclusions

We have reviewed the value of using tree ecophysiological measures to better understand tree dispersion patterns in space and time. Clearly, the functional response of woody species to predicted drier climates is an important topic at present. It was therefore no surprise to find that the ecophysiology field is evolving at a faster rate than in the past, and is especially prevalent in forestry research. We believe this growth to be a relic of its worldwide application and value to explain tree mortality patterns. However, there is a general lack of this research type within the African forestry sector. A clue to this pattern is likely that many African countries are considered developing, and this research type is to be fully prioritised. That said, it was encouraging to find that there has also been a considerable increase in ecophysiological studies in Africa during the last decade. Ecophysiological work should be strongly encouraged in African forestry studies, and one means to achieve this goal will be to highlight and better communicate its value in optimising tree improvement strategies. This approach has already contributed positively to optimising forestry practice elsewhere (Hanson and Weltzin 2000; Breshears et al. 2009). This knowledge would reduce the vulnerability of developing nations to the negative impact of predicted increases in drought-induced tree die-back, thereby promoting sustainable socio-economic growth ideals (Lin et al. 2008; Müller et al. 2011).

Zimmerman (1983) dedicated his book, *Xylem Structure* and the Ascent of Sap, to Godfrey Lowell Cabot, who established the Maria Moors Cabot Foundation for Botanical Research at Harvard University in 1937. In his dedication, he mentioned how Cabot described the foundation:

The primary purpose is, by artificial selection and other methods, to increase the capacity of the Earth to produce fuel by the growth of trees and other plants. Secondly, to increase and cheapen other products of the vegetable kingdom valuable to man. Third, to disseminate information helpful and stimulating to others who may wish to enter this field of effort.

We thus argue that a greater understanding, collaboration, and subsequent research output regarding the ecophysiological underpinnings of forest health in developing countries will serve all three above-mentioned endeavours.

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References

- Ackerly DD. 2004. Functional strategies of chaparral shrubs in relation to seasonal water deficit and disturbance. *Ecological Monographs* 74: 25–44.
- Ackerly DD, Dudley SA, Sultan SE, Schmitt J, Coleman JS, Linder CR, Sandquist DR, Geber MA, Evans AS, Dawson TE Lechowicz MJ. 2000. The evolution of plant ecophysiological traits: recent advances and future directions. *Biosciences* 50: 979–995.
- Adams HD, Germino MJ, Breshears DD, Barron-Gafford GA, Guardiola-Claramonte M, Zou CB, Huxman TE. 2013b. Nonstructural leaf carbohydrate dynamics of *Pinus edulis* during drought-induced tree mortality reveal role for carbon metabolism in mortality mechanism. *New Phytologist* 197: 1142–1151.

Adams HD, Williams AP, Xu C, Rauscher SA, Jiang X, McDowell

NG. 2013a. Empirical and process-based approaches to climateinduced forest mortality models. *Frontiers in Plant Science* 4: Art.#438, 5 pp.

- Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, Vennetier M, Kitzberger T, Rigling A, Breshears DD, Hogg EH et al. 2010. A global review of drought and heat-induced tree mortality reveals emerging climate changing risks for forests. *Forest Ecology and Management* 259: 660–684.
- Anderegg WRL, Berry JA, Smith DD, Sperry JS, Anderegg LDL, Field CB. 2012. The roles of hydraulic and carbon stress in a widespread climate-induced forest die-off. *Proceedings of the National Academy of Sciences of the USA* 109: 223–237.
- Anderegg WRL, Flint A, Huang C, Flint L, Berry JA, Davis FW, Sperry JS, Field CB. 2015b. Tree mortality predicted from droughtinduced vascular damage. *Nature Geoscience* 8: 367–371.
- Anderegg WRL, Hicke JA, Fisher RA, Allen CD, Aukema J, Bentz B, Hood S, Lichstein JW, Macalady AK, McDowell N et al. 2015a. Tree mortality from drought, insects, and their interactions in a changing climate. *New Phytologist* 208: 674–683.
- Baraloto C, Paine CET, Poorter L, Beauchene J, Bonal D, Domenach A-M, Hérault B, Patiño S, Roggy JC, Chave J. 2010. Decoupled leaf and stem economics in rain forest trees. *Ecology Letters* 13: 1338–1347.
- Bartholomé J, Mabiala A, Savelli B, Bert D, Brendel O, Plomion C, Gion J-M. 2015. Genetic architecture of carbon isotope composition and growth in *Eucalyptus* across multiple environments. *New Phytologist* 206: 1437–1449.
- Battie-Laclau P, Delgado-Rojas JS, Christina M, Nouvellon Y, Bouillet J-P, de Cassia Piccolo M, Moreira MZ, de Moraes Gonçalves JL, Roupsard O, Laclau J-P. 2016. Potassium fertilization increases water-use efficiency for stem biomass production without affecting intrinsic water-use efficiency in *Eucalyptus grandis* plantations. *Forest Ecology and Management* 364: 77–89.
- Beattie GA. 2011. Water relations in the interaction of foliar bacterial pathogens with plants. *Annual Review of Phytopathology* 49: 533–555.
- Bhaskar R, Ackerly DD. 2006. Ecological relevance of minimum seasonal water potentials. *Physiologia Plantarum* 127: 353–359.
- Bhaskar R, Valiente-Banuet A, Ackerly DD. 2007. Evolution of hydraulic traits in closely related species pairs from mediterranean and nonmediterranean environments of North America. *New Phytologist* 176: 718–726.
- Bosch JM, Hewlett JD. 1982. A review of catchment experiments to determine the effect of vegetation changes on water yield and evapotranspiration. *Journal of Hydrology* 55: 3–23.
- Bréda N, Granier A, Aussenac G. 1995. Effects of thinning on soil and tree water relations, transpiration and growth in an oak forest (*Quercus petraea* (Matt.) Liebl.). *Tree Physiology* 15: 295–306.
- Breshears DD, Myers OB, Meyer CW, Barnes FJ, Zou CB, Allen CD, McDowell NG, Pockman WT. 2009. Tree die-off in response to global change-type drought: mortality insights from a decade of plant water potential measurements. *Frontiers in Ecology and the Environment* 7: 185–189.
- Carlquist S. 1977. Ecological factors in wood evolution: a floristic approach. *American Journal of Botany* 64: 887–896.
- Carlquist S. 1988. Comparative wood anatomy: systematic, ecological, and evolutionary aspects of dicotyledon wood. Berlin: Springer-Verlag.
- Chao K-J, Phillips OL, Gloor E, Monteagudo A, Torres-Lezama, Martínez RV. 2008. Growth and wood density predict tree mortality in Amazon forests. *Journal of Ecology* 96: 281–892.
- Chave J, Coomes D, Jansen S, Lewis SL, Swenson NG, Zanne AE. 2009. Towards a worldwide wood economics spectrum. *Ecology Letters* 12: 351–366.
- Chave J, Muller-Landau HC, Baker TR, Easdale TA, ter Steege H, Webb CO. 2006. Regional and phylogenetic variation of

wood density across 2456 neotropical tree species. *Ecological Applications* 16: 2356–2367.

- Chaves MM, Maroco JP, Pereira JS. 2003. Understanding plant responses to drought from genes to the whole plant. *Functional Plant Biology* 30: 239–264.
- Choat B, Jansen S, Brodribb TJ, Cochard H, Delzon S, Bhaskar R, Bucci SJ et al. 2012. Global convergence in the vulnerability of forests to drought. *Nature* 491: 752–755.
- Choat B, Pitterman J. 2009. New insights into bordered pit structure and cavitation resistance in angiosperms and conifers. *New Phytologist* 182: 557–560.
- Choat B, Sack L, Holbrook NM. 2007. Diversity of hydraulic traits in nine Cordia species growing in tropical forests with contrasting precipitation. New Phytologist 175: 686–698.
- Christman MA, Sperry JS, Adler FR. 2009. Testing the 'rare pit' hypothesis for xylem cavitation resistance in three species of *Acer. New Phytologist* 182: 664–674.
- Cochard H, Barigah ST, Kleinhentz M, Eshel A. 2008. Is xylem cavitation resistance a relevant criterion for screening drought resistance among *Prunus* species? *Journal of Plant Physiology* 165: 976–982.
- Crous CJ, Jacobs SM, Esler KJ. 2012a. Drought-tolerance of an invasive alien tree, *Acacia mearnsii* and two native competitors in fynbos riparian ecotones. *Biological Invasions* 14: 619–631.
- Crous CJ, Jacobs SM, Esler KJ. 2012b. Wood anatomical traits as a measure of plant responses to water availability: invasive *Acacia mearnsii* De Wild. compared with native tree species in fynbos riparian ecotones, South Africa. *Trees* 26: 1527–1536.
- Crous KY, Quentin AG, Lin Y-S, Medlyn BE, Williams DG, Barton CVM, Ellsworth DS. 2013. Photosynthesis of temperate *Eucalyptus globulus* trees outside their native range has limited adjustment to elevated CO₂ and climate warming. *Global Change Biology* 19: 3790–3807.
- Cushman JC, Bohnert HJ. 2000. Genomic approaches to plant stress tolerance. *Current Opinion in Plant Biology* 3: 117–124.
- DaMatta FM. 2004a. Ecophysiological constraints on the production of shaded and unshaded coffee: a review. *Field Crops Research* 86: 99–114.
- DaMatta FM. 2004b. Exploring drought tolerance in coffee: a physiological approach with some insights for plant breeding. *Brazilian Journal of Plant Pathology* 16: 1–6.
- Desprez-Loustau M-L, Marçais B, Nageleisen L-M, Piou D, Vannini A. 2006. Interactive effects of drought and pathogens in forest trees. *Annals of Forest Science* 63: 597–612.
- Dietze MC, Matthes JH. 2014. A general ecophysiological framework for modelling the impact of pests and pathogens on forest ecosystems. *Ecology Letters* 17: 1418–1426.
- Duan H, Amthor JS, Duursma RA, O'Grady AP, Choat B, Tissue DT. 2013. Carbon dynamics of eucalypt seedlings exposed to progressive drought in elevated CO₂ and elevated temperature. *Tree Physiology* 33: 779–792.
- Dukes JS, Pontius J, Orwig D, Garnas JR, Rodgers VL, Brazee N, Cooke B, Theoharides KA, Stange EE, Harrington R et al. 2009. Responses of insect pests, pathogens, and invasive plant species to climate change in the forests of north-eastern North America: what can we predict? *Canadian Journal of Forest Research* 39: 231–248.
- Dye PJ, Jacobs S, Drew D. 2004. Verification of 3-PG growth and water-use predictions in twelve *Eucalyptus* plantation stands in Zululand, South Africa. *Forest Ecology and Management* 193: 197–218.
- Enquist BJ, West GB, Charnov EL, Brown JH .1999. Allometric scaling of production and life-history variation in vascular plants. *Nature* 401: 907–911.
- FAO (Food and Agriculture Organization of the United Nations). 2010. *Global forest resources assessment 2010*. Rome: FAO.
- Fischer RA, Turner NC. 1978. Plant productivity in the arid and

semiarid zones. Annual Review of Plant Physiology 29: 277-317.

- Franks PJ, Adams MA, Amthor JS, Barbour MM, Berry JA, Ellsworth DS, Farquhar GD, Ghannoum O, Lloyd J, McDowell N et al. 2013. Sensitivity of plants to changing atmospheric CO₂ concentration: from the geological past to the next century. *New Phytologist* 197: 1077–1094.
- Gleeson SM, Westoby M, Jansen S, Choat B, Hacke UW, Pratt RB, Bashkar R, Brodribb TJ, Bucci SJ, Cao K-F et al. 2015. Weak tradeoff between xylem safety and xylem-specific hydraulic efficiency across the world's woody plant species. *New Phytologist* 209: 123–136.
- Gonçalves JLD, Alvares CA, Higa AR, Silva LD, Alfenas AC, Stahl J, Ferraz SFD, Lima WDP, Brancalion PHS, Hubner A et al. 2013. Integrating genetic and silvicultural strategies to minimize abiotic and biotic constraints in Brazilian eucalypt plantations. *Forest Ecology and Management* 301: 6–27.
- Gregory PJ, Johnson SN, Newton AC, Ingram JSI. 2009. Integrating pests and pathogens into the climate change/food security debate. *Journal of Experimental Botany* 60: 2827–2838.
- Grime JP. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* 111: 1169–1194.
- Gustafson EJ, de Bruijn AMG, Pangle RE, Limousin J-M, McDowell NG, Pockman WT, Sturtevant BR, Muss JD, Kubiske ME. 2015. Integrating ecophysiology and forest landscape models to improve projections of drought effects under climate change. *Global Change Biology* 21: 843–856.
- Hacke UG, Jansen S. 2009. Embolism resistance of three boreal conifer species varies with pit structure. *New Phytologist* 182: 675–686.
- Hacke UG, Sperry JS. 2001. Functional and ecological xylem anatomy. *Perspectives in Plant Ecology, Evolution and Systematics* 4: 97–115.
- Hacke UG, Sperry JS, Pittermann J. 2000. Drought experience and cavitation resistance in six shrubs from the Great Basin, Utah. *Basic Applied Ecology* 1: 31–41.
- Hacke UG, Sperry JS, Pockman WT, Davis SD, McCulloh KA. 2001. Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia* 126: 457–461.
- Hanson PJ, Weltzin JF. 2000. Climate change, forests and drought disturbance from climate change: response of United States forests. *Science of the Total Environment* 262: 205–220.
- Hartmann H, Adams HD, Anderegg WRL, Jansen S, Zeppel MJB. 2015. Research frontiers in drought-induced tree mortality: crossing scales and disciplines. *New Phytologist* 205: 965–969.
- Hartmann H, Ziegler W, Kolle O, Trumbore S. 2013. Thirst beats hunger – declining hydration during drought prevents carbon starvation in Norway spruce seedlings. *New Phytologist* 200: 340–349.
- Jacobsen AL, Agenbag L, Esler KJ, Pratt RB, Ewers FW, Davis SD. 2007a. Xylem density, biomechanics and anatomical traits correlate with water stress in 17 evergreen shrub species of the Mediterranean-type climate region of South Africa. *Journal of Ecology* 95: 171–183.
- Jacobsen AL, Pratt RB, Davis SD, Ewers FW. 2008. Comparative community physiology: nonconvergence in water relations among three semi-arid shrub communities. *New Phytologist* 180: 100–113.
- Jacobsen AL, Pratt RB, Ewers FW, Davis SD. 2007b. Cavitation resistance among 26 chaparral species of southern California. *Ecological Monographs* 77: 99–115.
- Jactel H, Petit J, Desprez-Loustau M-L, Delzon S, Piou D, Battisti A, Koricheva J. 2012. Drought effects on damage by forest insects and pathogens: a meta-analysis. *Global Change Biology* 18: 267–276.
- Jansen S, Nardini A. 2014. From systematic to ecological wood

anatomy and finally plant hydraulics: are we making progress in understanding xylem evolution. *New Phytologist* 203: 12–15.

- Kolb KJ, Sperry JS. 1999. Differences in drought adaptation between subspecies of sagebrush (*Artemisia tridentata*). *Ecology* 80: 2373–2384.
- Landhäusser SM, Lieffers VJ. 2012. Defoliation increases risk of carbon starvation in root systems of mature aspen. *Trees* 26: 653–661.
- Lin BB, Perfecto I, Vandermeer J. 2008. Synergies between agricultural intensification and climate change could create surprising vulnerabilities for crops. *BioScience* 58: 847–854.
- Maherali H, Moura CF, Caldeira MC, Willson CJ, Jackson RB. 2006. Functional coordination between leaf gas exchange and vulnerability to xylem cavitation in temperate forest trees. *Plant, Cell and Environment* 29: 571–583.
- McDowell NG, Allen CD, Marshall L. 2010. Growth, carbon-isotope discrimination, and drought-associated mortality across a *Pinus ponderosa* elevational gradient. *Global Change Biology* 16: 399–415.
- McDowell NG, Beerling DJ, Breshears DD, Fisher RA, Raffa KF, Stitt M. 2011. The interdependence of mechanisms underlying climate-driven vegetation mortality. *Trends in Ecology and Evolution* 26: 523–532.
- McDowell NG, Fisher RA, Chonggang X, Domec JC, Holtta T, Mackay DS, Sperry JS, Boutz A, Dickman L, Gehres N et al. 2013. Evaluating theories of drought-induced vegetation mortality using a multimodel-experiment framework. *New Phytologist* 200: 304–321.
- McDowell NG, Pockman WT, Allen CD, Breshears DD, Cobb N, Kolb T, Plaut J, Sperry JS, West A, Williams DG, Yepez EA. 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytologist* 178: 719–739.
- Mehl JWM, Geldenhuys CJ, Roux J, Wingfield MJ. 2010. Die-back of kiaat (*Pterocarpus angolensis*) in southern Africa: a cause for concern? *Southern Forests* 72: 121–132.
- Meinzer FC. 2003. Functional convergence in plant responses to the environment. *Oecologia* 134: 1–11.
- Molinier J, Ries G, Zipfel C, Hohn B. 2006. Transgeneration memory of stress in plants. *Nature* 442: 1046–1049.
- Monclus R, Dreyer E, Villar M, Delmotte FM, Delay D, Petit J-M, Barbaroux C, Le Thiec D, Bréchet C, Brignolas F. 2006. Impact of drought on productivity and water-use efficiency in 29 genotypes of *Populus deltoides × Populus nigra*. *New Phytologist* 169: 765–777.
- Mueller-Dombois D. 1986. Perspectives for an etiology of stand-level dieback. *Annual Review of Ecology and Systematics* 17: 221–243.
- Müller C, Cramer W, Hare WL, Lotze-Campen H. 2011. Climate change risks for African agriculture. *Proceedings of the National Academy of Sciences of the USA* 108: 4343–4315.
- Näsholm T, Palmroth S, Ganeteg U, Moshelion M, Hurry V, Franklin O. 2014. Genetics of superior growth traits in trees are being mapped but will the faster-growing risk-takers make it in the wild? *Tree Physiology* 34: 1141–1148.
- Pitterman J, Sperry JS, Hacke UG, Wheeler JK, Sikkema EH. 2005. Torus-margo pits help conifers compete with angiosperms. *Science* 310: 1924.
- Plomion C, Bastien C, Bogeat-Triboulot MB, Bouffier L, Déjardin A, Duplessis S, Fady B, Heuertz M, Le Gac AL, Le Provost G et al. 2016. Forest tree genomics: 10 achievements from the past 10 years and future prospects. *Annals of Forest Science* 73: 77–103.
- Pockman WT, Sperry JS. 2000. Vulnerability to xylem cavitation and the distribution of Sonoran Desert vegetation. *American Journal of Botany* 87: 1287–1299.

Pockman WT, Sperry JS, O'Leary JW. 1995. Sustained and

significant negative water pressure in xylem. *Nature* 378: 715–716.

- Pratt RB, Black RA. 2006. Do invasive trees have a hydraulic advantage over native trees? *Biological Invasions* 8: 1331–1341.
- Pratt RB, Jacobsen AL, Ewers FW, Davis SD. 2007. Relationships among xylem transport, biomechanics and storage in stems and roots of nine Rhamnaceae species of the California chaparral. *New Phytologist* 174: 787–798.
- Preston KA, Cornwell WK, DeNoyer JL. 2006. Wood density and vessel traits as distinct correlates of ecological strategy in 51 California coast range angiosperms. *New Phytologist* 170: 807–818.
- Raj S, Bräutigam K, Hamanishi ET, Wilkins O, Thomas BR, Schroeder W, Mansfield SD, Plant AL, Campbell MM. 2011. Clone history shapes *Populus* drought responses. *Proceedings of the National Academy of Sciences of the USA* 108: 12521–12526.
- Read J, Stokes A. 2006. Plant biomechanics in an ecological context. *American Journal of Botany* 93: 1546–1565.
- Reich PB, Wright IJ, Cavender-Bares J, Craine JM, Oleksyn J, Westoby M, Walters MB. 2003. The evolution of plant functional variation: traits, spectra, and strategies. *International Journal of Plant Sciences* 164: 143–164.
- Rice KJ, Matzner SL, Byer W, Brown JR. 2004. Patterns of tree dieback in Queensland, Australia: the importance of drought stress and the role of resistance to cavitation. *Oecologia* 139: 190–198.
- Rivero RM, Kojima M, Gepstein A, Sakakibara H, Mittler R, Gepstein S, Blumwald E. 2007. Delayed leaf senescence induces extreme drought tolerance in a flowering plant. *Proceedings of the National Academy of Sciences of the USA* 104: 19631–19636.
- Sala A, Piper F, Hoch G. 2010. Physiological mechanisms of drought-induced tree mortality are far from being resolved. *New Phytologist* 186: 274–281.
- Santiago LS, Goldstein G, Meinzer FC, Fisher JB, Machado K, Woodruff D, Jones T. 2004. Leaf photosynthetic traits scale with hydraulic conductivity and wood density in Panamanian forest canopy trees. *Oecologia* 140: 543–550.
- Schreiber SG, Hacke UG, Chamberland S, Lowe CW, Kamelchuk D, Bräutigan K, Campbell MM, Thomas BR. 2016. Leaf size serves as a proxy for xylem vulnerability to cavitation in plantation trees. *Plant, Cell and Environment* 39: 272–281.
- Sevanto S, Dickman LT. 2015. Where does the carbon go? Plant carbon allocation under climate change. *Tree Physiology* 35: 581–584.
- Sevanto S, McDowell NG, Dickman LT, Pangle R, Pockman WT. 2014. How do trees die? A test of the hydraulic failure and carbon starvation hypotheses. *Plant, Cell and Environment* 37: 153–161.
- Shackleton CM, Shackleton SE. 2004. The importance of non-timber forest products in rural livelihood security and as safety nets: evidence from South Africa. *South African Journal of Science* 100: 658–664.
- Shackleton CM, Shackleton SE, Buiten E, Bird N. 2007. The importance of dry woodlands and forests in rural livelihoods and poverty alleviation in South Africa. *Forest Policy and Economics* 9: 558–577.
- Singh AP, Butcher JA. 1991. Bacterial degradation of wood cell walls: a review of degradation patterns. *Journal of the Institute of Wood Science* 12: 143–157.
- Skelton RP, West AG, Dawson TE. 2015. Predicting plant vulnerability to drought in biodiverse regions using functional traits. *Proceedings of the National Academy of Sciences of the* USA 112: 5744–5749.
- Sperry JS. 1995. Limitations on stem water transport and their consequences. In: Gartner BL (ed.), *Plant stems: physiology and functional morphology*. San Diego: Academic Press. pp 105–120.

- Sperry JS. 2003. Evolution of water transport and xylem structure. International Journal of Plant Sciences 164: 115–127.
- Sperry JS, Hacke UG, Pittermann J. 2006. Size and function in conifer tracheids and angiosperm vessels. *American Journal of Botany* 93: 1490–1500.
- Sperry JS, Love DM. 2015. What plant hydraulics can tell us about responses to climate-change droughts. *New Phytologist* 207: 14–27.
- Sperry JS, Tyree MT. 1988. Mechanism of water stress-induced xylem embolism. *Plant Physiology* 88: 581–587.
- Sperry JS, Tyree MT. 1990. Water-stress-induced xylem embolism in three species of conifers. *Plant, Cell and Environment* 13: 427–439.
- Stahle DW, Mushove PT, Cleaveland MK, Roig F, Haynes GA. 1999. Management implications of annual growth rings in *Pterocarpus angolensis* from Zimbabwe. *Forest Ecology and Management* 124: 217–229.
- Stratton L, Goldstein G, Meinzer FC. 2000. Stem water storage capacity and efficiency of water transport: their functional significance in a Hawaiian dry forest. *Plant, Cell and Environment* 23: 99–106.
- Sunderlin WD, Angelsen A, Belcher B, Burgers P, Nasi R, Santoso L, Wunder S. 2005. Livelihoods, forests, and conservation in developing countries: an overview. *World Development* 33: 1383–1402.
- Suzuki N, Rivero RM, Shulav V, Blumwald E, Mittler R. 2014. Abiotic and biotic stress combinations. *New Phytologist* 203: 32–43.
- Thomas DS, Montagu, KD, Conroy JP. 2007. Temperature effects on wood anatomy, wood density, photosynthesis and biomass partitioning of *Eucalyptus grandis* seedlings. *Tree Physiology* 27: 251–260.
- Tschaplinski TJ, Tuskan GA, Gebre GM, Todd DE. 1998. Drought resistance of two hybrid *Populus* clones grown in a large-scale plantation. *Tree Physiology* 18: 653–658.
- Tyree MT, Davis SD, Cochard H. 1994. Biophysical perspectives of xylem evolution: is there a tradeoff of hydraulic efficiency for vulnerability to dysfuction. *IAWA Journal* 15: 335–360.
- Tyree MT, Sperry JS. 1988. Do woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress?: answers from a model. *Plant Physiology* 88: 574–580.
- Tyree MT, Zimmerman MH. 2002. *Xylem structure and the ascent of sap* (2nd edn). Berlin: Springer.
- van den Bilcke N, de Smedt S, Simbo DJ, Samson R. 2013. Sap flow and water use in African baobab (Adansonia digitata L.) seedlings in response to drought stress. South African Journal of Botany 88: 438–446.
- vander Willigen C, Pammenter NW. 1998. Relationship between growth and xylem hydraulic characteristics of clones of *Eucalyptus* spp. at contrasting sites. *Tree Physiology* 18: 595–600.
- Wagner KR, Ewers FW, Davis SD. 1998. Trade-offs between hydraulic efficiency and mechanical strength in stems of four co-occurring species of chaparral shrubs. *Oecologia* 117: 53–62.
- Wang T, Aitken SN, Kavanagh KL. 2003. Selection for improved growth and wood quality in lodgepole pine: effects on phenology, hydraulic architecture and growth of seedlings. *Trees* 17: 269–277.
- Weitz JS, Ogle K, Horn HS. 2006. Ontogenetically stable hydraulic design in woody plants. *Functional Ecology* 20: 191–199.
- West AG, Dawson TE, February EC, Midgley GF, Bond WJ, Aston TL. 2012. Diverse functional responses to drought in a Mediterranean-type shrubland in South Africa. *New Phytologist* 195: 396–407.
- Westoby M, Wright IJ. 2006. Land-plant ecology on the basis of functional traits. *Trends in Ecology and Evolution* 21: 261–268.
- Wheeler JK, Sperry JS, Hacke UG, Hoang N. 2005. Inter-vessel pitting and cavitation in woody Rosaceae and other vesselled

plants: a basis for a safety versus efficiency trade-off in xylem transport. *Plant, Cell and Environment* 28: 800–812.

- White DA, Crombie DS, Kinal J, Battaglia M, McGrath JF, Mendham DS, Walker SN. 2009. Managing productivity and drought risk in *Eucalyptus globulus* plantations in south-western Australia. *Forest Ecology and Management* 259: 33–44.
- White DA, McGrath JF, Ryan MG, Battaglia M, Mendham DS, Kinal J, Downes GM, Crombie DS, Hunt ME. 2014. Managing for water-use efficient wood production in *Eucalyptus globulus* plantations. *Forest Ecology and Management* 331: 272–280.
- Wikberg J, Ögren E. 2004. Interrelationships between water use and growth traits in the biomass-producing willows. *Trees* 18: 70–76.
- Wingfield MJ, Slippers B, Hurley, BP, Coutinho, TA, Wingfield BD, Roux J. 2008. Eucalypt pest and diseases: growing threats to plantation productivity. *Southern Forests* 70: 139–144.
- Wingfield MJ, Roux J, Slippers B, Hurley BP, Garnas J, Myburg AA, Wingfield BD. 2013. Established and new technologies reduce increasing pest and pathogen treats to eucalypt plantations. *Forest Ecology and Management* 301: 35–42.
- Wingfield MJ, EG Brockerhoff, Wingfield BD, Slippers B. 2015. Planted forest health: the need for a global strategy. *Science* 349: 832–836.
- Zimmerman MH. 1983. *Xylem structure and the ascent of sap.* Berlin: Springer-Verlag.