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

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Abstract

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, since 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’, ‘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. While forest research contributed greatly to the global tally of ecophysiological studies, and such studies in Africa have also increased by up to 88% 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. And 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 hectares) of the *c.* 5 billion hectares 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 (aesthetics, cultural, sustenance, security etc.) 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 socio-economic 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, 1988; Grime 1977; Zimmerman 1983). For example, Choat et al. (2007) showed strong intra- and inter-specific

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; Jacobsen et al. 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; Allan 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 process-based models of the functional responses of trees to water-stress 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 what the physiological or anatomical mechanisms have been that gave 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).

While 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-world countries such as those in Africa. Since 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. But 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-recognized 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 attest 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; Anderegg et al. 2015b; Gleeson et al. 2015; Sperry and Love 2015; and many others).

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 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; Anderegg et al. 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 (CJ Crous, *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 ISI Web of Science database (apps.webofknowledge.com) using the words ‘tree xylem anatomy’, ‘tree xylem cavitation’, ‘tree leaf gas-exchange’, ‘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 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* criteria. 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 are in relation to an expected 20% of the global tally. This percentage is derived from the fact that African forests and woodlands cover *c.* one billion hectares of the projected global five billion hectares (FAO 2010). These observed versus expected frequencies were calculated using Chi-square tests in Statistica 12 (Statsoft, Inc.).

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 to 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 (Fig. 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 water-stressed 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 (Fig. 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 (X^2 values ranged between 18.063 and 22.563, $P < 0.001$ in all cases). Ecophysiological research has therefore not been priority in Africa compared to 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 directives 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 since 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 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 since these trees will be planted in areas having vast environmental variation and to which they may or may not be pre-adapted to (*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 shown 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, since 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 since 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 reestablishment 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, since species-specific life-history strategies vary greatly in space and time, the genetic, physiological and biomechanical controls regulating plant hydraulic architecture require greater attention (Read and Stokes 2006; Weitz et al. 2006; Monclus et al. 2006; Jansen and Nardini 2014; Bartholomé et al. 2015; Plomion et al. 2015).

In developing nation countries, where the infrastructure for genetic breeding might more likely be lacking when compared to 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 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 optimized (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 (Fig. 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 (Gonçalves 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:

- Woody plants that grow under conditions of greater water stress show a measureable difference in wood architecture. They also have different physiological needs compared to a 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 large-scale 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-anisohdry 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 to 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 prioritized. 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 optimizing tree improvement strategies. This approach has already contributed positively to optimizing 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 abovementioned endeavours.

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List of Tables:

Table 1: The number of journal and review papers published over the last century, and those published within the last decade, concerning key ecophysiological and wood anatomical parameters globally, in Africa, and from the forestry sector.

<i>Measurement</i>	Since	Global		Africa		Forestry	
		Articles	PLD (%)	Articles	PLD (%)	Articles	PLD (%)
Tree Leaf Gas-exchange	1939	8135	27	74	53	3012	50
Tree Xylem Anatomy	1923	2216	39	48	52	1841	35
Tree Xylem Cavitation	1968	815	58	16	88	549	55
Tree Xylem Hydraulic Conductivity	1973	879	60	22	86	647	60

PLD = Percentage of articles published the last decade

Table 2: Examples of the application of ecophysiological research to tree breeding and plantation forestry given future drier climates.

Commodity	Study Synthesis	Application
<p><i>Populus deltoides x nigra</i> (Tschaplinski et al. 1998)</p>	<p>For semi-arid areas of Washington state, USA, it was suggested that a <i>Populus deltoides x 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 x deltoides</i> clone would be more suitable. The latter clone has high carbon allocation under more mesic conditions, but as soon 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. This favours greater access to soil water in such conditions and therefore drought-adapted growth (more sustainable growth, better production predictions).</p>	<p>Comparative ecophysiological response to water-stress among forest clones can complement the choice of clones in a variable water-stressed environment.</p>
<p><i>Eucalyptus</i> clones (vander Willigen and Pammenter 1998)</p>	<p>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.</p>	<p>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 event are a fixed variable across time.</p>
<p>Lodgepole Pine (Wang et al. 2003)</p>	<p>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 is considered more vulnerable to drought-induced cavitation.</p>	<p>In breeding programmes, it would be possible to select for subpopulations that have a unique combination of fast growth and high wood density, whilst simultaneously also being</p>

		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 to 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 a 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 since 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, since this would ultimately affect individual growth patterns within that stand. It can also help explain differential growth patterns of trees in a single stand.
<i>Eucalyptus globulus</i>	Under current climate change models,	This is important when

<p>subsp. <i>globulus</i> (Crous et al. 2013)</p>	<p>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.</p>	<p>planning forestry plantations with known temperate species in more tropical areas.</p>
<p><i>Populus</i> hybrid clones (Schreiber et al. 2016)</p>	<p>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 to smaller leaved hybrids, this would significantly affect their productivity in the planted landscape.</p>	<p>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.</p>

List of Figure Captions:

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

Figure 2: The 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 in 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.

List of Figures:

Fig. 1

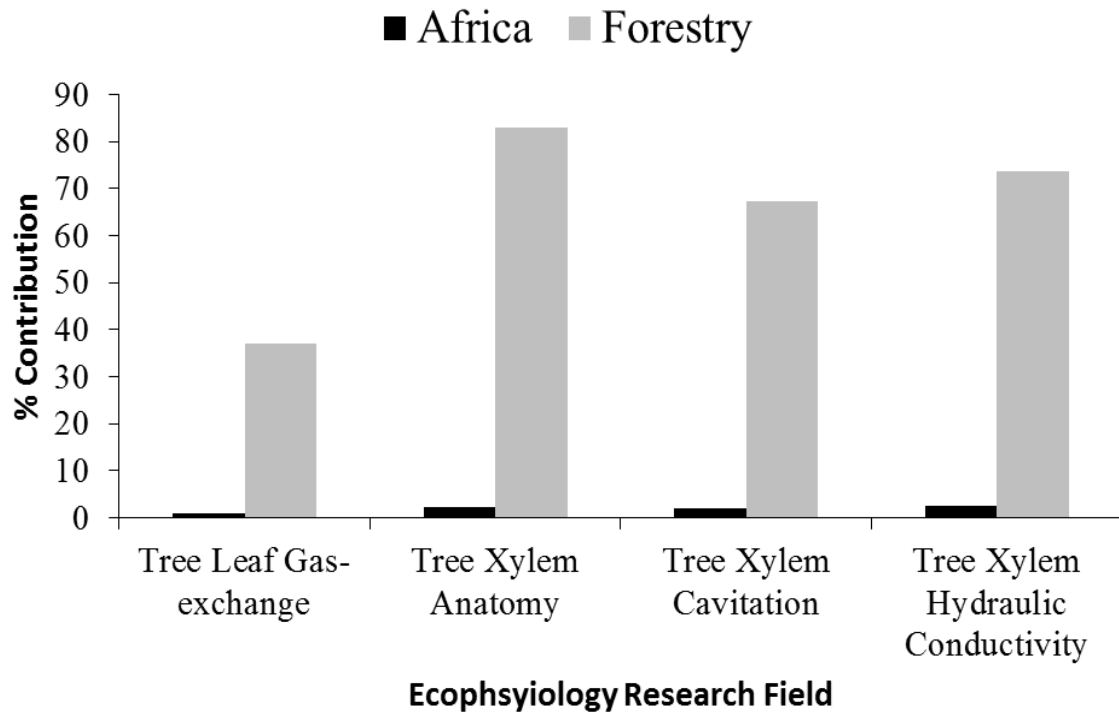
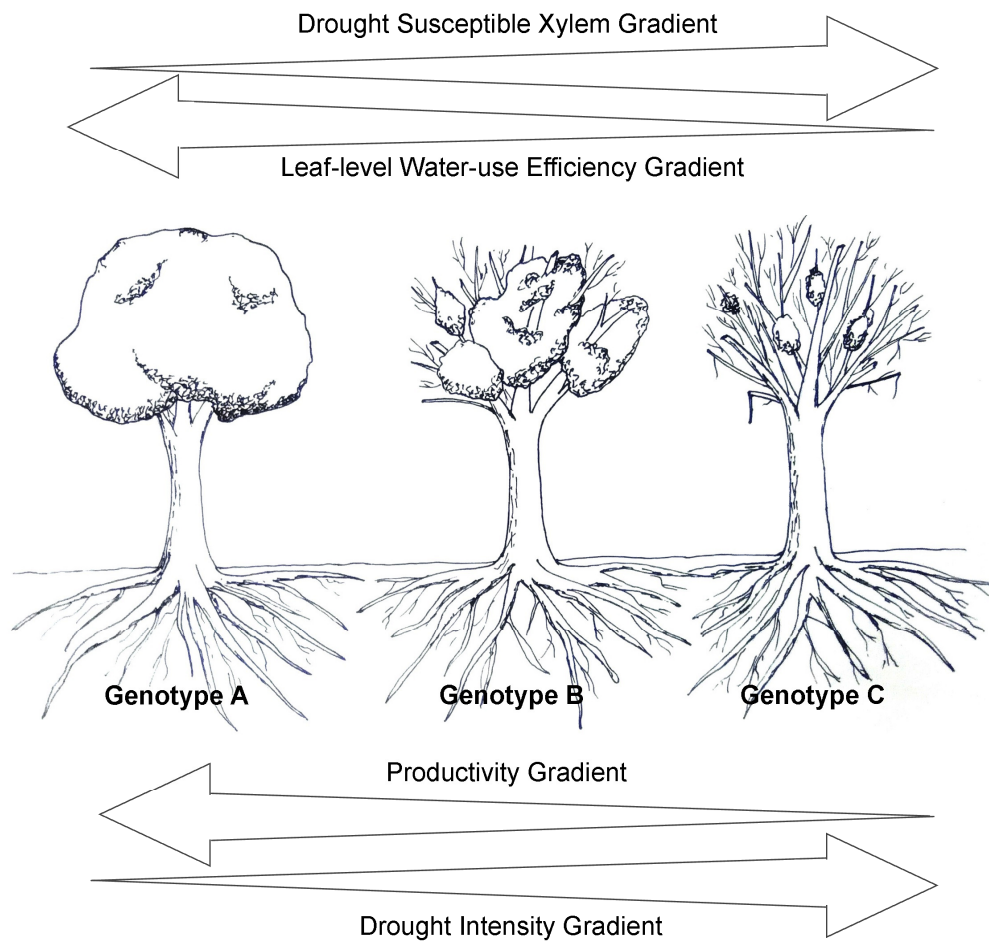
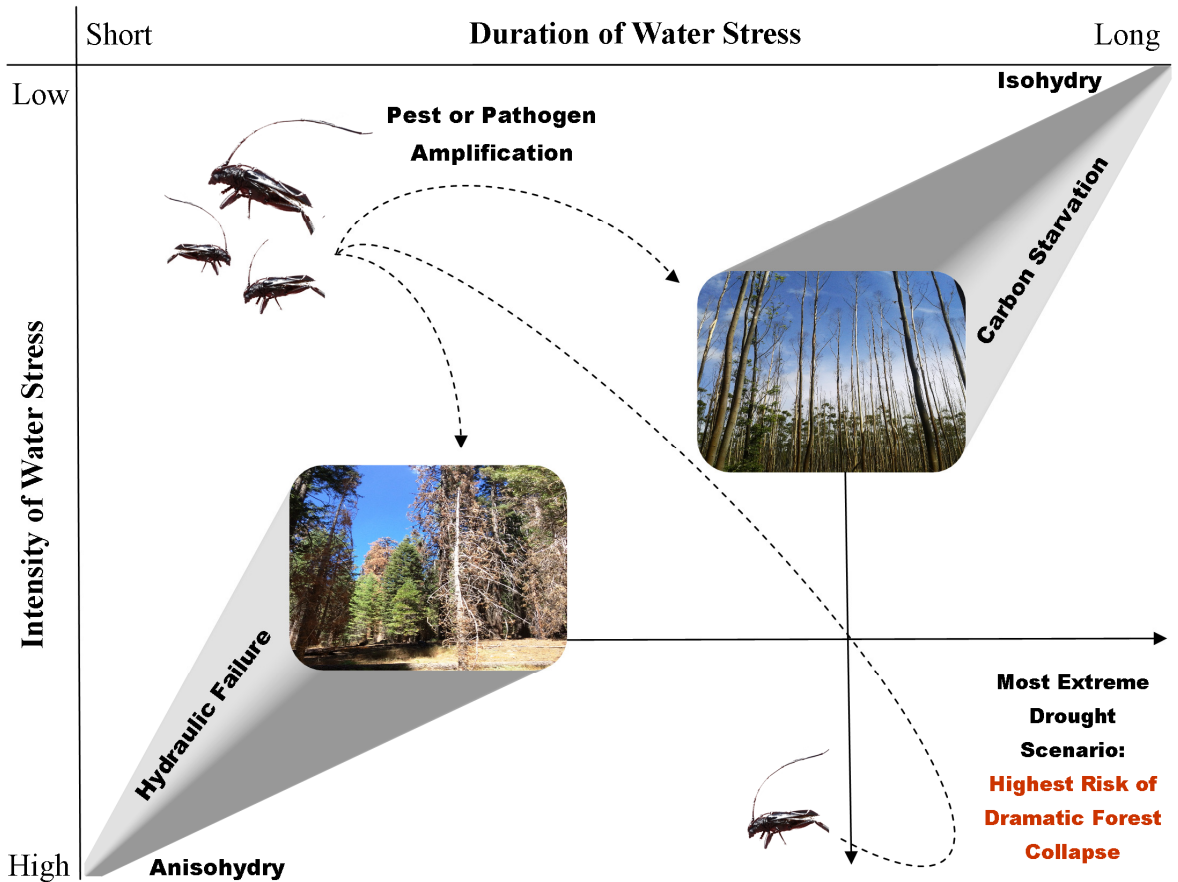


Fig. 2



Box 1

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



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, while 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 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).

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 since 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 (Figure 1). This model is particularly aligned with *secondary* pests and pathogens, since 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 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 CO₂ 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 metabolize photosynthate) may well contribute to tree mortality (Adams et al. 2013b). Also, 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. They 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 optimize 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 does provide 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; McDowell et al. 2011; Hartmann et al. 2013; Sevanto et al. 2014; Anderegg et al. 2015a). Since 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 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 vulnerability 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 tracheid’s 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 limit gas bubbles to a specific tracheid, and since 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), since 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 perspective, 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), since 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 having higher wood density, are generally associated with slower growth rate patterns when compared to 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 ($K_{s\max}$; xylem-specific flow, i.e., pith excluded) is often measured to depict these differences in water flow ($\text{kg}\cdot\text{s}^{-1}\text{MPa}^{-1}\text{m}^{-1}$). 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 was 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 (Hacke et al. 2000; Hacke et al. 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

Since relatively high negative pressures are observed in vessels, some strain or bending pressures do exist between two adjacent conduits (Hacke et al. 2001). Embolized 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 embolized 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

Since 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 predawn Ψ -values correspond to the maximum level of soil moisture that plants have access to, and midday Ψ -values provides 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, since 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 plant-water 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 are 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. 2015). 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 did 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.