Letters

Towards an advanced assessment of the hydrological vulnerability of forests to climate change-induced drought

Introduction

Preserving the integrity of the hydraulic system is crucial for survival of trees under dry conditions (Bréda et al., 2006). Maintaining a hydraulic safety margin (HSM) between the water potential (WP) associated with stomatal closure and the WP associated with cavitation can therefore be an important drought resistance trait in many tree species. Based on a broad survey of HSMs across tree species, it was recently concluded that all forest biomes are similarly and strongly threatened by climate change-induced drought (Choat et al., 2012). We submit that while the prevalence of narrow HSMs across tree species and climates is remarkable, additional factors must be considered to assess vulnerability of trees and forests to drought, that is, the degree to which they are susceptible to, and unable to cope with, adverse impacts of drought (IPCC, 2007). In fact, such prevalence of narrow HSM is likely a basis, and a trigger, for the development of a range of strategies to cope with this situation in light of the ever-imminent drought stress. Furthermore, settling for an apparently small HSM alone may slow down research into critical aspects of water-use strategies in trees. For example, the accumulating evidence in recent years for rapid recovery from loss of hydraulic conductivity (Brodersen & McElrone, 2013, and references cited therein) indicates a lesser importance of the HSM and any temporary loss of conductivity than suggested. Here, we briefly review key issues in tree strategies to cope with drought that are critical to consider in addition to HSM, if we are to improve predictions of drought related vulnerability of forests.

Mechanisms of drought-induced tree mortality

Climate predictions indicate drying trends and higher frequency of drought events in many regions worldwide (Alpert et al., 2006; Burke et al., 2006; IPCC, 2007; Zhang et al., 2007), strongly affecting biogeochemical and eco-physiological processes in terrestrial ecosystems (Reichstein et al., 2013). The most alarming consequence of climate change to forests is increased drought- and heat-induced tree die-off in multiple locations across the globe (Adams et al., 2009; Allen et al., 2010; and references cited therein). The following main underlying mortality mechanisms were proposed: (1) carbon starvation in response to stomatal closure

under prolonged drought stress, thus leading to lower photosynthetic activity; (2) increased attacks by biotic agents, such as insect outbreaks, promoted by a reduced ability of plant defense under drought; and (3) cavitation-induced hydraulic failure (McDowell et al., 2008; Adams et al., 2009). The latter occurs where stem water transport is interrupted by air bubbles that form when WP decreases below a species-specific threshold. Some tree-mortality events were attributed to a single mechanism, for example, to carbon starvation in *Pinus edulis* (Adams et al., 2009), to insect outbreak in *Abies concolor* (Ferrell et al., 1994), and to hydraulic failure in conifers of the southern hemisphere (Brodribb & Cochard, 2009). In other situations, a combination of mechanisms might be causing tree die-off in a drier climate (McDowell et al., 2011).

The potential and limits of hydraulic safety margins of trees

Water transport in trees is usually under large negative pressures and, consequently, trees live under the threat of xylem embolism (Tyree & Sperry, 1988; Holbrook et al., 1995; Zwieniecki & Holbrook, 1998) . Embolism breaks the continuity of water columns, thereby reducing hydraulic conductance and water supply to transpiring leaves, with major implications for tree functioning and survival. Twenty-five years ago, the question was posed, whether woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress (Tyree & Sperry, 1988). To answer this question, plant scientists have been defining HSMs in various ways, for example, by the difference in WP between stomatal closure and the point of 50% loss of conductivity (WP_{50}), and by the gap between minimum leaf WP under natural conditions and WP_{50} (Meinzer et al., 2009). Sperry (2004) suggested that narrow HSMs allow for higher xylem functioning, and hence were advantageous in the evolution of higher plants. In woody plants, such low margins are more characteristic of species with high diurnal water storage capacity and low wood density (Meinzer et al., 2009), and are more frequent in pioneer and deciduous tree species than in shade-tolerant and evergreen trees (Markesteijn et al., 2011)

Observations of increased drought-induced tree die-off on the one hand, and narrow HSMs in many tree species on the other hand are potentially related. However, the existence of additional factors makes this relationship far more complex than a simple cause and effect. First, tree die-off can occur in spite of a large HSM. For example, *P. edulis* suffered a large-scale mortality episode in the semi-arid woodlands of southwest United States (Breshears et al., 2009), despite an HSM of 2.61 MPa, much higher than the meta-analysis average HSM of 0.47 MPa (Choat et al., 2012). A combination of continuous hydraulic stress, lack of carbon assimilation, and attack by biological agents may be held accountable for this massive tree die-off (McDowell et al., 2011). Second,

xylem cavitation is not always fatal: trees survived extreme droughts even when continuously operating very close to the HSM (e.g. *Quercus alba* during the 1995 heat wave in southeast United States; Baldocchi, 1997) or within the HSM (e.g. *Swartzia racemosa* under rainfall exclusion; Fisher *et al.*, 2006; and *Pinus halepensis* under soil drought; Klein *et al.*, 2011). Third, in other cases WP was kept above the HSM, in spite of extreme drought conditions (e.g. multiple tree species during the 2003 extreme drought in central Europe; Ciais *et al.*, 2005; Leuzinger *et al.*, 2005; Granier *et al.*, 2007; and *Quercus petraea* under soil drought; Kuster *et al.*, 2012). These observations suggest that HSMs cannot be easily used as predictors of forest vulnerability to drought.

Strategies of drought avoidance

Avoiding drought stress is one way to survive under dry conditions. Tree drought-stress avoidance strategies range from the leaf scale to the whole-tree level, and from immediate responses to seasonal changes. In many tree species, when exposed to very low WP, stomata close to protect the xylem from developing embolism (Cruiziat *et al.*, 2002; Brodribb & Holbrook, 2004; Yang *et al.*, 2012). In parallel, photosynthetic rate decreases, though a residual and often sufficient carbon gain is maintained without risking excessively low WP (Larcher *et al.*, 1981; Kuster *et al.*, 2012; Klein *et al.*, 2013; Wolf *et al.*, 2013). Gas exchange can also be maintained by homeostatic adjustments of, for example, the ratio of leaf area to sapwood area (McDowell *et al.*, 2002, 2006; Mencuccini, 2003). Alternatively, carbon supply can be facilitated by carbon mobilization between storage and sinks (Guehl *et al.*, 1993; Canham *et al.*, 1999; Körner, 2003; Sala *et al.*, 2010). To further avoid drought stress, trees may shift growth phenology towards moist periods (Grünzweig *et al.*, 2003; Rotenberg & Yakir, 2010; Klein *et al.*, 2012a), adjust root architecture, mycorrhizal colonization and root distribution in the soil profile (Bréda *et al.*, 2006), and adapt xylem vessel anatomy (Eilmann *et al.*, 2009, 2011). Trees might also adapt leaf-shedding phenology in dry periods according to the sensitivity of leaves to drought (Méndez-Alonzo *et al.*, 2012), which is part of an adjustment strategy of the canopy size to water shortage. At the canopy level, self-shading and hydraulic lift are also important drought avoiding strategies. Such stress avoidance strategies prevent progressively lower WP. In turn, they allow trees that have narrow HSMs to hold off from the 'danger zone' and, in the long term, facilitate their survival under drought irrespective of the HSM.

The prevalence of recovery from embolism

The capacity of xylem refilling to reverse embolism provides another route of survival under drought episodes, which overcomes the narrow HSM. Evidence is accumulating from manipulation experiments and field measurements on the ability of trees to survive low WP and high levels of hydraulic conductivity loss, and xylem embolism (Cochard, 2006; Taneda & Sperry, 2008; Klein *et al.*, 2011). This suggests efficient recovery mechanisms, which are more common and routine than previously assumed (Brodersen & McElrone, 2013). Empiric evidence for the reversibility of

conductivity loss and embolism on a diurnal timescale has become available for over a decade (Tyree *et al.*, 1999). Recently, sub-diurnal cycles of embolism and refilling were also shown and visualized in the laboratory for grapevine (Brodersen *et al.*, 2010; Zufferey *et al.*, 2011), bamboo (Yang *et al.*, 2012), and poplar (Secchi & Zwieniecki, 2011). Routine embolism repair was shown in the field for a desert woody shrub (Schenk & Espino, 2011). Hydraulic conductance can be also recovered by growth of new xylem vessels (Cochard *et al.*, 2001; Ameglio *et al.*, 2002; Eilmann *et al.*, 2010). These mechanisms enable activity and survival at or beyond the HSM, inferring it a less important role. Nevertheless there are constrains to recovery from embolism: First, xylem refilling is limited by the threshold of water extraction by roots. Second, accumulating deterioration of the plant hydraulic system was reported as a consequence of repeated cavitation and its repair (Hacke *et al.*, 2001; Anderegg *et al.*, 2013). Third, in some tree species, the evidence for refilling must be verified with the most current methodology (Wheeler *et al.*, 2013). Fourth, in various tree species, no recovery has been demonstrated (Brodersen & McElrone, 2013). In fact, such inter-specific variation is yet another indication that similarity in forest vulnerability to drought cannot be expected.

The probability of soil and atmospheric drought

A realistic assessment of forest-tree vulnerability to drought must also consider the site-specific conditions that interact with its water-use strategy to determine the tree's fate. Environmental drivers of leaf WP are the WP of soil and atmosphere, which are primarily influenced by precipitation, evapotranspiration, and vapor pressure deficit (VPD). These parameters not only vary with time, but also largely differ among biomes. Annual trends of daily VPD were measured in eight flux-tower sites representing various biomes across the Americas (data adopted from the BIGFOOT dataset; Turner *et al.*, 2012). Notably, VPD > 4 kPa was recorded in only two biomes (desert grassland and tall grass prairie), whereas at the boreal, temperate, and tropical forest sites, VPD was never above 2 kPa. To some extent, the effect of high VPD on tree function should vary among biomes, as tree species in those biomes that are less prone to atmospheric drought are less adapted to high VPD. Yet WP is regulated by stomatal closure, and when VPD increases stomatal conductance tends to converge across species (Oren *et al.*, 1999). In this way, the effect of high VPD should be rather similar among trees in dry and humid biomes. Tree vulnerability to drought is hence mostly determined by the probability that VPD reaches (or remains below) a critical threshold. While VPD maxima may change from one year to the next or in the course of climate change, it is assumed that not all forest biomes are similarly threatened by atmospheric drought.

In the soil, water availability is often studied locally without reference to a standard scale, and hence 'soil drought' can have different meanings in different studies (Vicca *et al.*, 2012). This is because water availability for transpiration depends on the local soil and plant hydraulic properties, that is, soil water retention curves and the WP threshold for root uptake (Sinclair,

2005). Soil water retention changes with soil type, which is mostly independent of the forest biome type, and should therefore introduce additional variation among biomes to their susceptibility to soil drought. Knowledge of soil water retention and the WP threshold for root uptake for a specific soil structure and tree species allows for the calculation of the actual amount of transpirable soil water content (tSWC). It has recently been demonstrated that changes in tSWC predicted to a high degree episodes of tree mortality in a semi-arid pine forest (Klein *et al.*, 2012b). Quantification of tSWC (and its decay) offers a general framework for the extent of soil drought, and thereby allows comparisons among different forest ecosystems in terms of their hydraulic vulnerability.

Limitations on forest water-use

An ecosystem approach might be necessary to evaluate the limitations on forest water-use (i.e. hydrological limitations) and to improve our understanding of forest–climate interactions. Forest drought vulnerability was assessed for the Amazon rainforest and the Alaska boreal forest (Phillips *et al.*, 2009; Welp *et al.*, 2007, respectively), but those studies focused mainly on carbon pools and fluxes rather than on hydrological vulnerability. A recent analysis of the water balance in various biomes showed that water-use in most forests worldwide is smaller than expected from potential evapotranspiration, and hence was below the demand and supply limits, that is, well within the hydrological range (Williams *et al.*, 2012). This implies first that water-use in forests is adapted to the current variation in climate. Second, a system-based approach needs to be applied for determining safety margins at the forest scale and, in turn, identifying forests that may be most vulnerable to climate change.

Conclusions and perspectives for a vulnerability assessment

Mechanisms of drought avoidance, xylem refilling at low WP, and fundamental differences among biomes in the probability of drought events suggest that similarity in HSMs in trees of various origins does not imply similarity in forest vulnerability to drought. An advanced assessment of the hydrological vulnerability at the forest scale also needs to apply a system-based approach and integrate the often opposing water-use strategies of different tree species, for example, into the framework of dynamic vegetation models (Van der Molen *et al.*, 2011; Reichstein *et al.*, 2013). More large-scale field manipulation experiments, studies along regional or global water-availability gradients, and monitoring of impacts of extreme events are required. Considering the complex nature of such multi-scale analysis, a realistic vulnerability assessment can yield a highly heterogeneous forest map, with various levels of drought vulnerability depending on local site conditions, tree species, and their interaction.

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References

Adams HD, Guardiola-Claramonte M, Barron-Gafford GA, Villegas JC, Breshears DD, Zou CB, Troch PA, Huxman TE. 2009. Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought. *Proceedings of the National Academy of Sciences, USA* **106**: 7063–7066.

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 overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management* **259**: 660–684.

Alpert P, Baldi M, Ilani R, Krichak S, Price C, Rodo X, Saaroni H, Ziv B, Kishcha P, Barkan J *et al.* 2006. Relations between climate variability in the Mediterranean region and the tropics: ENSO, South Asian and African monsoons, hurricanes and Saharan dust. *Developments in Earth and Environmental Sciences* **4**: 149–177.

Ameglio T, Bodet C, Lacointe A, Cochard H. 2002. Winter embolism, mechanisms of xylem hydraulic conductivity recovery and springtime growth patterns in walnut and peach trees. *Tree Physiology* **22**: 1211–1220.

Anderegg WRL, Plavcova L, Anderegg LDL, Hacke UG, Berry JA, Field CB. 2013. Drought's legacy: multiyear hydraulic deterioration underlies widespread aspen forest die-off and portends increased future risk. *Global Change Biology* **19**: 1188–1196.

Baldocchi D. 1997. Measuring and modeling carbon dioxide and water vapor exchange over a temperate broad-leaved forest during the 1995 summer drought. *Plant, Cell & Environment* **20**: 1108–1122.

Bréda N, Huc R, Granier A, Dreyer E. 2006. Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Annals of Forest Science* **63**: 625–644.

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 Environment* **7**: 185–189.

Brodersen CR, McElrone AJ. 2013. Maintenance of xylem network transport capacity: a review of embolism repair in vascular plants. *Frontiers in Plant Science* **4**: 1–11.

Brodersen CR, McElrone AJ, Choat B, Matthews MA, Shackel KA. 2010. The dynamics of embolism repair in xylem: *in vivo* visualizations using high-resolution computed tomography. *Plant Physiology* **154**: 1088–1095.

Brodribb TJ, Cochard H. 2009. Hydraulic failure defines the recovery and point of death in water-stressed conifers. *Plant Physiology* **149**: 575–584.

Brodribb TJ, Holbrook NM. 2004. Stomatal protection against hydraulic failure: a comparison of coexisting ferns and angiosperms. *New Phytologist* **162**: 663–670.

Burke EJ, Brown SJ, Christidis N. 2006. Modeling the recent evolution of global drought and projections for the twenty-first century with the Hadley centre climate model. *Journal of Hydrometeorology* **7**: 1113–1125.

Canham CD, Kobe RK, Latty EF, Chazdon RL. 1999. Interspecific and intraspecific variation in tree seedling survival: effects of allocation to roots versus carbohydrate reserves. *Oecologia* **121**: 1–11.

Choat B, Jansen S, Brodribb TJ, Cochard H, Delzon S, Bhaskar R, Bucci SJ, Feild TS, Gleason SM, Hacke UG *et al.* 2012. Global convergence in the vulnerability of forests to drought. *Nature* **491**: 752–755.

Ciais P, Reichstein M, Vivoy N, Granier A, Ogee J, Allard V, Aubinet M, Buchmann N, Bernhofer C, Carrara A *et al.* 2005. Europe-wide reduction

in primary productivity caused by the heat and drought in 2003. *Nature* **437**: 529–533.

Cochard H. 2006. Cavitation in trees. *Comptes Rendus Physique* **7**: 1018–1026.

Cochard H, Lemoine D, Ameglio T, Granier A. 2001. Mechanisms of xylem recovery from winter embolism in *Fagus sylvatica*. *Tree Physiology* **21**: 27–33.

Cruiziat P, Cochard H, Ameglio T. 2002. Hydraulic architecture of trees: main concepts and results. *Annals of Forest Science* **59**: 723–752.

Eilmann B, Buchmann N, Siegwolf R, Saurer M, Cherubini P, Rigling A. 2010. Fast response of Scots pine to improved water availability reflected in tree-ring width and $\delta^{13}C$. *Plant, Cell & Environment* **33**: 1351–1360.

Eilmann B, Zweifel R, Buchmann N, Fonti P, Rigling A. 2009. Drought-induced adaptation of the xylem in *Pinus sylvestris* and *Quercus pubescens*. *Tree Physiology* **29**: 1011–1020.

Eilmann B, Zweifel R, Buchmann N, Graf Pannatier E, Rigling A. 2011. Drought alters timing, quantity, and quality of wood formation in Scots pine. *Journal of Experimental Botany* **62**: 2763–2771.

Ferrell GT, Otrosina WJ, Demars CJJ. 1994. Predicting susceptibility of white fir during a drought-associated outbreak of the fir engraver, *Scofyrus ventralis*, in California. *Canadian Journal of Forest Research* **24**: 302–305.

Fisher RA, Williams M, Lobo do Vale R, da Costa ACL, Meir P. 2006. Evidence from Amazonian forests is consistent with isohydric control of leaf water potential. *Plant, Cell & Environment* **29**: 151–165.

Granier A, Reichstein M, Bréda N, Janssens IA, Falge E, Ciais P, Grünwald T, Aubinet M, Berbigier P, Bernhofer C et al. 2007. Evidence for soil water control on carbon and water dynamics in European forests during the extremely dry year: 2003. *Agricultural and Forest Meteorology* **143**: 123–145.

Grünzweig JM, Lin T, Rotenberg E, Schwartz A, Yakir D. 2003. Carbon sequestration in arid-land forest. *Global Change Biology* **9**: 791–799.

Guehl JM, Clement A, Kaushal P, Aussenac G. 1993. Planting stress, water status and non-structural carbohydrate concentrations in Corsican pine seedlings. *Tree Physiology* **12**: 172–183.

Hacke UG, Stiller V, Sperry JS, Pittermann J, McCulloh KA. 2001. Cavitation fatigue. Embolism and cycles can weaken cavitation resistance of xylem. *Plant Physiology* **125**: 779–786.

Holbrook NM, Burns MJ, Field CB. 1995. Negative xylem pressures in plants: a test of the balancing pressure technique. *Science* **270**: 1193–1194.

IPCC. 2007. *Fourth assessment report of the Intergovernmental Panel on Climate Change*. Cambridge, UK & New York, NY, USA: Cambridge University Press.

Klein T, Cohen S, Yakir D. 2011. Hydraulic adjustments underlying drought resistance of *Pinus halepensis*. *Tree Physiology* **31**: 637–648.

Klein T, Di Matteo G, Rotenberg E, Cohen S, Yakir D. 2012a. Differential ecophysiological response of a major Mediterranean pine species across a climatic gradient. *Tree Physiology* **33**: 26–36.

Klein T, Rotenberg E, Cohen-Hilaleh E, Raz-Yaseef N, Tatarinov F, Ogée J, Cohen S, Yakir D. 2012b. Quantifying transpirable soil water and its relations to tree water use dynamics in a water-limited pine forest. *Ecohydrology*. doi:10.1002/eco.1360.

Klein T, Shpringer I, Fikler B, Elbaz G, Cohen S, Yakir D. 2013. Relationship between stomatal regulation, water-use, and water-use efficiency of two coexisting key Mediterranean tree species. *Forest Ecology and Management* **302**: 34–42.

Körner C. 2003. Carbon limitation in trees. *Journal of Ecology* **91**: 4–17.

Kuster TM, Arend M, Bleuler P, Guenthardt-Goerg MS, Schlin R. 2012. Water regime and growth of young oak stands subjected to air-warming and drought on two different forest soils in a model ecosystem experiment. *Plant biology* **15**: 138–147.

Larcher W, De Moraes JAPV, Bauer H. 1981. Adaptive responses of leaf water potential, CO_2 gas exchange and water use efficiency of *Olea europaea* during drying and re-watering. In: Margaris NS, Mooney HA, eds. *Components of productivity of Mediterranean-climate regions basic and applied aspects tasks for vegetation science, vol.4* . The Hague, the Netherlands: Dr W. Junk publishers, 77–84.

Leuzinger S, Zotz G, Asshoff R, Körner C. 2005. Responses of deciduous forest trees to severe drought in Central Europe. *Tree Physiology* **25**: 641–650.

Markesteijn L, Poorter L, Bongers F, Paz H, Sack L. 2011. Hydraulics and life history of tropical dry forest tree species: coordination of species' drought and shade tolerance. *New Phytologist* **191**: 480–495.

McDowell NG, Adams HD, Bailey JD, Hess M, Kolb TE. 2006. Homeostatic maintenance of ponderosa pine gas exchange in response to stand density changes. *Ecological Applications* **16**: 1164–1182.

McDowell NG, Beerling DJ, Breshears DD, Fisher RA, Stitt M. 2011. The interdependence of mechanisms underlying climate-driven vegetation mortality. *Trends in Ecology and Evolution* **26**: 523–532.

McDowell NG, Phillips N, Lunch C, Bond BJ, Ryan MG. 2002. An investigation of hydraulic limitation and compensation in large, old Douglas-fir trees. *Tree Physiology* **22**: 673–774.

McDowell NG, Pockman WT, Allen CD, Breshears DD, Cobb N, Kolb TE, Plaut J, Sperry J, West A, Williams DG et al. 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytologist* **178**: 719–739.

Meinzer FC, Johnson DM, Lachenbruch B, McCulloh KA, Woodruff DR. 2009. Xylem hydraulic safety margins in woody plants: coordination of stomatal control of xylem tension with hydraulic capacitance. *Functional Ecology* **23**: 922–930.

Mencuccini M. 2003. The ecological significance of long-distance water transport: short-term regulation, long-term acclimation and hydraulic costs of stature across plant life form. *Plant, Cell & Environment* **26**: 163–182.

Méndez-Alonzo R, Paz H, Cruz Zuluaga R, Rosell JA, Olson ME. 2012. Coordinated evolution of leaf and stem economics in tropical dry forest trees. *Ecology* **93**: 2397–2406.

Oren R, Sperry JS, Katul GG, Pataki DE, Ewers BE, Phillips N, Schaefer KVR. 1999. Survey and synthesis of intra- and interspecific variation in stomatal sensitivity to vapour pressure deficit. *Plant, Cell & Environment* **22**: 1515–1526.

Phillips OL, Aragao LEOC, Lewis SL, Fisher JB, Lloyd J, Lopez-Gonzalez G, Malhi Y, Monteagudo A, Peacock J, Quesada CA et al. 2009. Drought sensitivity of the Amazon rainforest. *Science* **323**: 1344–1347.

Reichstein M, Bahn M, Ciais P, Frank D, Mahecha MD, Seneviratne SI, Zscheischler J, Beer C, Buchmann N, Frank D et al. 2013. Climate extremes and the carbon cycle. *Nature* **500**: 287–295.

Rotenberg E, Yakir D. 2010. Contribution of semi-arid forests to the climate system. *Science* **327**: 451–454.

Sala A, Piper F, Hoch G. 2010. Physiological mechanisms of drought-induced tree mortality are far from being resolved. *New Phytologist* **186**: 274–281.

Schenk HJ, Espino S. 2011. *Nighttime sap flow removes air from plant hydraulic systems. 8th International workshop on sap flow*. Voltera, Italy.

Secchi F, Zwieniecki MA. 2011. Sensing embolism in xylem vessels: the role of sucrose as a trigger for refilling. *Plant, Cell & Environment* **34**: 514–524.

Sinclair TR. 2005. Theoretical analysis of soil and plants traits influencing daily plant water flux on drying soils. *Agronomy Journal* **97**: 1148–1152.

Sperry JS. 2004. Coordinating stomatal and xylem functioning – an evolutionary perspective. *New Phytologist* **162**: 568–570.

Taneda H, Sperry JS. 2008. A case-study of water transport in co-occurring ring- versus diffuse-porous trees: contrasts in water status, conducting capacity, cavitation and vessel. *Tree Physiology* **28**: 1641–1651.

Turner DP, Gregory MJ, Ritts WD. 2012. *BIGFOOT Meteorological Data for North and South American Sites, 1991–2004. Data set.* [WWW document] URL http://daac.ornl.gov/ from Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, USA. doi: 10.3334/ORNLDAAC/1065 [accessed 23 December 2012].

Tyree MT, Salleo S, Nardini A, Lo Gullo MA, Mosca R. 1999. Refilling of embolized vessels in young stems of Laurel. Do we need a new paradigm? *Plant Physiology* **120**: 11–21.

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.

Van der Molen MK, Dolman AJ, Ciais P, Eglin T, Gobron N, Law BE, Meir P, Peters W, Phillips OL, Reichstein M et al. 2011. Drought and ecosystem carbon cycling. *Agricultural and Forest Meteorology* **151**: 765–773.

Vicca S, Gilgen AK, Camino Serrano M, Dreesen FE, Dukes JS, Estiarte M, Gray SB, Guidolotti G, Hoeppner SS, Leakey ADB et al. 2012. Urgent need for a common metric to make precipitation manipulation experiments comparable. *New Phytologist* **195**: 518–522.

Welp LR, Randerson JT, Liu HP. 2007. The sensitivity of carbon fluxes to spring warming and summer drought depends on plant functional type in boreal forest ecosystems. *Agricultural and Forest Meteorology* **147**: 172–185.

Wheeler JK, Huggett BA, Tofte AN, Rockwell FE, Holbrook NM. 2013. Cutting xylem under tension or supersaturated with gas can generate PLC and the appearance of rapid recovery from embolism. *Plant, Cell & Environment.* doi: 10. 1111/pce.12139.

Williams CA, Reichstein M, Buchmann N, Baldocchi D, Beer C, Schwalm C, Wohlfahrt G, Hasler N, Bernhofer C, Foken T *et al.* **2012.** Climate and vegetation controls on the surface water balance: synthesis of evapotranspiration measured across a global network of flux towers. *Water Resources Research* **48**: W06523.

Wolf S, Eugster W, Ammann C, Häni M, Zielis S, Hiller R, Stieger J, Imer D, Merbold L, Buchmann N. 2013. Contrasting response of grassland versus forest carbon and water fluxes to spring drought in Switzerland. *Environmental Research Letters* **8**: 035007.

Yang S-J, Zhang Y-J, Sun M, Goldstein G, Cao K-F. 2012. Recovery of diurnal depression of leaf hydraulic conductance in a subtropical woody bamboo species: embolism refilling by nocturnal root pressure. *Tree Physiology* **32**: 414–422.

Zhang X, Zwiers FW, Hegerl GC, Lambert HL, Gillett NP, Solomon S, Stott PA, Nozawa T. 2007. Detection of human influence on twentieth-century precipitation trends. *Nature* **448**: 461–465.

Zufferey V, Cochard H, Ameglio T, Spring J-L, Viret O. 2011. Diurnal cycles of embolism formation and repair in petioles of grapevine (*Vitis vinifera* cv. Chasselas). *Journal of Experimental Botany* **62**: 3885–3894.

Zwieniecki MA, Holbrook NM. 1998. Diurnal variation in xylem hydraulic conductivity in white ash (*Fraxinus Americana* L.), red maple (*Acer robrum* L.) and red spruce (*Picea rubens* Sarg.). *Plant, Cell & Environment* **21**: 1173–1180.

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