

Opinion

Toward an index of desiccation time to tree mortality under drought

Chris J. Blackman¹, Sebastian Pfautsch¹, Brendan Choat¹, Sylvain Delzon², Sean M. Gleason³ & Remko A. Duursma¹

¹Hawkesbury Institute for the Environment, Western Sydney University, Locked Bag 1797, Penrith, NSW 2751, Australia, ²BIOGECO INRA, Univ. of Bordeaux, 33610 Cestas, France and ³USDA-ARS, Water Management Research, 2150 Center Ave, Build D, Suite 320, Fort Collins, CO 80526, United States

ABSTRACT

Research in plant hydraulics has provided important insights into plant responses to drought and species absolute drought tolerance. However, our ability to predict when plants will die from hydraulic failure under extreme drought is limited by a lack of knowledge with regards to the dynamics of plant desiccation following stomatal closure. Thus, we develop a simple hydraulics model based on branch-level traits that incorporates key aspects of allometry, rates of water loss and resistance to embolism thresholds in order to define species differences in the time it takes plants to desiccate from stomatal closure to lethal levels of drought stress.

Drought-induced tree mortality and forest dieback have become more frequent in response to changing climate in many parts of the world (Allen *et al.* 2010). This issue has generated a highly active field of research internationally, with recent major studies focusing on quantifying the contribution of different mechanisms to drought mortality in trees (McDowell *et al.* 2013; Mitchell *et al.* 2013; Anderegg *et al.* 2015). However, our ability to identify species and/or forest communities most at risk of drought mortality remains limited by a fundamental lack of knowledge with regards to the full range of traits and processes that determine how long it takes before trees die during periods of extreme drought. Here we develop a simple hydraulic model based on branch-level traits for determining the time required for trees and other woody plants to desiccate to lethal water potentials after stomatal closure. We suggest that the time-dependence of hydraulic failure represents an important yet often overlooked piece of the puzzle in understanding response to drought.

Under severe drought, a plant's hydraulic system is increasingly stressed because of increasing tension within the water conducting xylem. This process leads to xylem cavitation and the formation of air emboli, which reduces the capacity of plants to transport water to the leaves (Tyree & Sperry 1989). As drought stress intensifies, increasing levels of xylem cavitation can ultimately lead to catastrophic hydraulic failure (Tyree & Sperry 1988), which has been shown to be a major

mechanism of mortality in many species (Brodribb & Cochard 2009; Anderegg *et al.* 2012; Mitchell *et al.* 2013; Urli *et al.* 2013).

The tension (water potential; –MPa) in the xylem at the point where a plant organ has lost 50% of its capacity to conduct water because of embolism (P_{50}) is commonly used to characterize plant vulnerability to embolism under drought. Because of its central role in plant hydraulic research, the number of species with defined P_{50} values has increased substantially in recent years, especially with the advent of new high-throughput techniques (Cochard *et al.* 2013; Bouche *et al.* 2014). These data indicate that P_{50} differs markedly among woody plants, ranging from near zero in highly vulnerable species to –19 MPa in the most drought resistant species (Maherali *et al.* 2004; Delzon *et al.* 2010; Choat *et al.* 2012; Larter *et al.* 2015). In terms of drought survivorship, emerging data indicate that P_{50} may be lethal for most gymnosperms (Brodribb & Cochard 2009; Brodribb *et al.* 2010), while in angiosperms plant death has been associated with 80–90% loss of conductivity (Resco *et al.* 2009; Barigah *et al.* 2013; Urli *et al.* 2013). Defining these drought mortality thresholds across species will be essential for predictive models of vegetation response to drought (Choat 2013) especially given drought events are predicted to increase in both intensity and frequency with climate change (IPCC 2013). Even so, indices of drought tolerance based on variation in xylem cavitation resistance remain somewhat static for individual species. Moreover, such indices do not characterize species differences in the time it takes plants to reach lethal water potentials during periods of extreme drought.

Drought responses in plants typically proceed in two phases: (1) stomata are open and gradually close in response to soil drying; and (2) stomata are closed but water continues to be lost via stomatal leakiness and cuticular conductance. To date, most studies on plant responses to drought have focused on the first response phase, because of the fundamental need in plants to balance stomatal regulation of dehydration relative to carbon gain (Mackay *et al.* 2015). However, there remains a crucial lack of knowledge of the dynamics of plant desiccation beyond stomatal closure, despite reports from the field of significant lag times between the onset of drought stress and catastrophic hydraulic failure (Anderegg *et al.* 2012; Anderegg *et al.* 2013).

We argue that traits involved in reducing rates of water loss and their influence on water storage reservoirs and hydraulic

Correspondence: C. J. Blackman. Tel: +61 2 4570 1593; Fax: +61 2 4570 1103; email: c.blackman@westernsydney.edu.au

function after the stomata have closed directly influence how long it takes plants to reach lethal water potentials during severe drought. In evergreen species, stomatal leakiness is an important determinant of minimum canopy conductance following stomatal closure and, thus, also influences rates of plant desiccation during drought (Brodribb *et al.* 2014). The release of water from internal capacitors (Pfautsch & Adams 2013; Pfautsch *et al.* 2015a) and/or xylem conduits following cavitation (Holtta *et al.* 2009) may moderately decrease plant water potential. Furthermore, the dynamics of plant desiccation following stomatal closure will be influenced by static allometric traits, in particular plant leaf area and total water storage capacity (Borchert & Pockman 2005; Gleason *et al.* 2014).

Considering the difficulty in assessing the dynamics of plant desiccation in mature trees, a potentially useful approach for determining species differences in the time it takes plants to desiccate from stomatal closure to lethal water potentials is to assess the dynamics of water loss from excised branches. Indeed, rates of water loss from excised branches have been shown to vary widely across species (Gleason *et al.* 2014; Fig. 1a), although the traits contributing to this variation remain poorly understood. Thus, we have developed a new and simple hydraulic model that allows for variation in key aspects of allometry, rates of water loss and drought tolerance for determining the time it takes trees to desiccate from stomatal closure to lethal levels of water stress (t_{crit} ; s) using excised branches:

$$t_{\text{crit}} = \frac{(\theta_0 - C \cdot \Psi_{\text{crit}}) V_w}{A_L g_0 D} \quad (1)$$

Where θ_0 is the branch relative water content (RWC) at the point where stomata have just closed (g g^{-1}); C is the branch capacitance (RWC MPa^{-1}); Ψ_{crit} is the xylem water potential (MPa) associated with lethal levels of drought stress (equivalent to P_{50} in most conifers and P_{88} in most angiosperms); V_w is the total amount of water available

to the branch (g); A_L is the total leaf area (m^2); g_0 is the canopy conductance after stomatal closure ($\text{g m}^{-2} \text{s}^{-1}$); and D is the vapour pressure deficit of the atmosphere (mol mol^{-1}) (see Supporting Information for model derivation). The combined term ($C \cdot \Psi_{\text{crit}}$) is the RWC at Ψ_{crit} , representing the amount of water left in the branch at lethal water potentials (RWC_{crit} ; g g^{-1}).

Based on our model 1, longer desiccation times (t_{crit}) for a given D can theoretically be achieved by (1) increasing the total volume of water in sapwood relative to leaf area ($V_w:A_L$); (2) reducing minimum canopy conductance (g_0); (3) decreasing stem vulnerability to embolism (more negative Ψ_{crit}) and/or increasing branch capacitance (C); or (4) a combination of these (Fig. 2). Note that some of these variables are often inversely correlated with one another across species (Scholz *et al.* 2011). Importantly, all parameters in the model can be measured directly or indirectly using branch material 'dried-down' in the lab, in conjunction with measurements of air temperature and relative humidity to calculate D (assuming leaf temperature does not differ meaningfully from air temperature). While Ψ_{crit} can be determined from species' vulnerability to embolism curves (generated by branch-dehydration or centrifuge techniques), rates of water loss in separate branch material can be determined accurately and simply using a high capacity laboratory balance (Borchert & Pockman 2005; Gleason *et al.* 2014).

A number of assumptions are made in this simple hydraulic model (Supporting Information). Among these is that the relationship between branch RWC and water potential is linear so that the branch capacitance is relatively constant after stomatal closure. This assumption is broadly supported by experimental data from Gleason *et al.* (2014) (Fig. 1b). We also assume that the sapwood supplies the bulk of the water to canopy transpiration during dry-down. While evidence suggests that this may not be the case in small branches, where leaf water was found to contribute significantly to total water loss, especially at water potentials below -2 MPa (Gleason *et al.* 2014), the

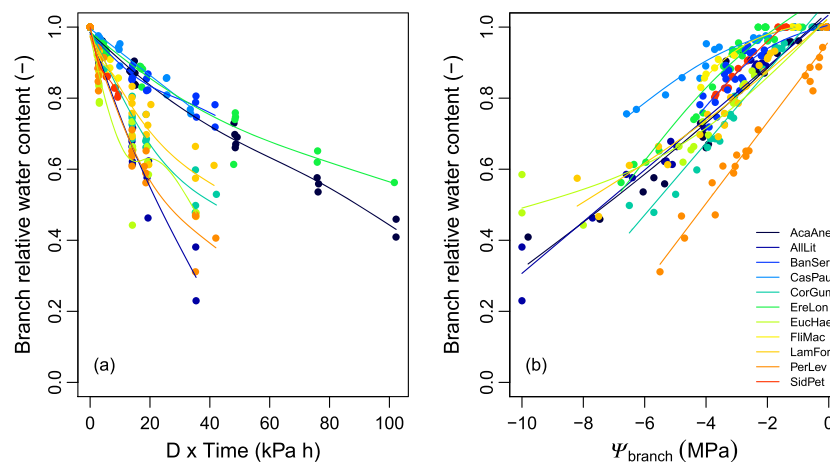


Figure 1. (a) Species differences in the rate of branch desiccation expressed here in terms of the change in branch relative water content (g g^{-1}) over time (h) adjusted by vapour pressure deficit (D); (b) relationships between relative water content and water potential during branch dry-down in different species. Species codes: AcaAne = *Acacia aneura*; AILLit = *Allocasuarina littoralis*; BanSer = *Banksia serrata*; CasPau = *Casuarina pauper*; CorGum = *Corymbia gummifera*; EreLon = *Eremophila longifolia*; EucHae = *Eucalyptus haemastoma*; FilMac = *Flindersia maculosa*; LamFor = *Lambertia formosa*; PerLev = *Persoonia levis*; and SidPet = *Sida petrophila*. Raw data were sourced from Gleason *et al.* (2014).

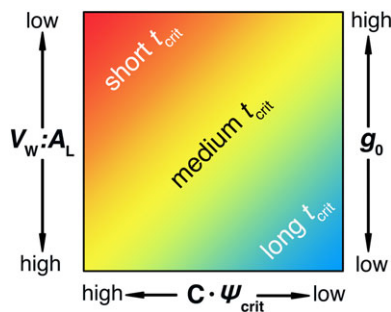


Figure 2. A conceptual model of how the time to reach lethal levels of drought stress (t_{crit}) in branches is influenced by variation in three key terms: the amount of water available in the branch relative to its leaf area ($V_w:A_L$), minimum branch conductance following stomatal closure (g_0), and the combined term ($C \cdot \Psi_{crit}$), which represents the branch relative water content at lethal levels of drought stress (RWC_{crit}). In delaying drought induced mortality following stomatal closure, longer desiccation times could be achieved via some combination of higher $V_w:A_L$, lower g_0 , low vulnerability to embolism (more negative Ψ_{crit}) or high rates of water loss per unit increase in water potential (branch C , which would act to lower RWC_{crit}).

contribution of stored water from the stem (including bark) is substantial (Pfautsch *et al.* 2015b) and should increase with plant size (Phillips *et al.* 2003; Scholz *et al.* 2011). This assumption can be tested experimentally by measuring t_{crit} across a range of branch sizes for a given species. Furthermore, the time to critical levels of drought stress should theoretically increase with increasing plant size, as stem volume increases relative to leaf area (Scholz *et al.* 2011). This suggests that larger trees should be less susceptible to drought mortality, although this tends not to be the case in nature where larger trees are generally more susceptible to drought (Bennett *et al.* 2015).

The model also assumes that g_0 is constant and does not itself depend on D or Ψ (Boyer *et al.* 1997). Again, this expectation can be tested using experimental data. Finally, the model assumes that D is relatively constant throughout the experiment and that the branch is coupled to the ‘atmosphere’ so that transpiration rate is proportional to g_0 and D . In practice, these issues can be addressed by conducting the experiment under relatively controlled laboratory conditions and by suspending branches in the air to limit strong within-canopy boundary layers. In order to better reflect real-world conditions, t_{crit} could ultimately be measured against some reference evaporation, possibly by placing a water-filled petri dish on a balance next to the branch.

We emphasize that our model of branch desiccation times to mortality is based on hydraulic traits and processes, although we acknowledge that non-hydraulic traits and processes (e.g. carbohydrate dynamics) have been shown to contribute to prolonging plant function as drought stress increases (O’Brien *et al.* 2014). Our model is not intended to be used to determine the contribution of different mechanisms to mortality in different species. Rather, it represents a novel quantitative approach for understanding species differences in the time from stomatal closure it takes before plants desiccate to water potentials associated with catastrophic hydraulic failure.

We acknowledge that rooting depth plays a major role in mitigating drought stress in trees *in situ*, with deeper roots

prolonging hydraulic and gas exchange function during severe drought (Nardini *et al.* 2016). Furthermore, roots provide additional water storage capacity, which could be incorporated into our model of t_{crit} by either measuring rates of water loss in young intact plants after their roots have been carefully separated from the soil, or by estimating root water volume using allometric relationships. Importantly, information on plant rooting properties could be used in conjunction with branch-level measurements of t_{crit} to examine potential trade-offs inherent in different water-use strategies, especially among co-occurring species (Nardini *et al.* 2003; Lindh *et al.* 2014). In applying our model of t_{crit} for measuring desiccation times in trees *in situ*, it will also be important to consider whether roots become hydraulically isolated from drying soils, and thus, prevents transfer of water from the roots to the soil (North & Nobel 1997).

In addition, factors related to the cumulative impacts of past drought (Mitchell *et al.* 2016) and the ability of plants to refill embolised vessel elements (Brodersen & McElrone 2013) may contribute to the risk of plant exposure to drought-induced mortality in the field, although the occurrence of embolism refilling in nature remains controversial (Delzon & Cochard 2014). In regard to our model, high levels of native embolism in branch segments should act to shorten the time to Ψ_{crit} because gas-filled xylem conduits act to reduce the amount of available water in the branch (Tyree & Yang 1990). We also acknowledge that some species from seasonally dry habitats shed leaves in response to severe drought, in order to reduce evaporative surface area and slow rates of dehydration. In these species, rates of water loss would need to be adjusted during branch dry-down to incorporate changes in both leaf area (A_L) and minimum canopy conductance (g_0), while xylem water potential could be measured using a stem psychrometer.

In conclusion, defining t_{crit} provides a novel approach for integrating traits that influence how long different species across different plant sizes can withstand increasing levels of drought stress that precedes complete hydraulic failure and plant death. Studying these traits should lead to a more complete picture of trade-offs and linkages that define differences in water use strategies across species, environments and whole biomes (Reich 2014). Knowledge of the dynamics of plant desiccation from stomatal closure to plant death could be combined with hydraulic models of plant responses to drought during stomatal closure (e.g. Mackay *et al.* 2015; Sperry & Love 2015) to provide comprehensive whole plant models that account for all the parameters implicated in plant dehydration *in situ* during extreme drought. This information would be particularly useful for dynamic global vegetation models that currently do not account for the dynamics of plant water loss in different species across all phases of drought stress (McDowell 2011; Anderegg *et al.* 2015).

REFERENCES

- Allen C.D., Macalady A.K., Chenchouni H., Bachelet D., McDowell N., Venetier M., ... Cobb N. (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.

- Anderegg L.D.L., Anderegg W.R.L., Abatzoglou J., Hausladen A.M. & Berry J.A. (2013) Drought characteristics' role in widespread aspen forest mortality across Colorado, USA. *Global Change Biology* **19**, 1526–1537.
- Anderegg W.R.L., Berry J.A., Smith D.D., Sperry J.S., Anderegg L.D.L. & Field C.B. (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 United States of America* **109**, 233–237.
- Anderegg W.R.L., Flint A., Huang C.-y., Flint L., Berry J.A., Davis F.W., ... Field C.B. (2015) Tree mortality predicted from drought-induced vascular damage. *Nature Geoscience* **8**, 367–371.
- Barigah T.S., Charrier O., Douris M., Bonhomme M., Herbette S., Ameglio T., ... Cochard H. (2013) Water stress-induced xylem hydraulic failure is a causal factor of tree mortality in beech and poplar. *Annals of Botany* **112**, 1431–1437.
- Bennett A.C., McDowell N.G., Allen C.D. & Anderson-Teixeira K.J. (2015) Larger trees suffer most during drought in forests worldwide. *Nature Plants* **1**, 15139.
- Borchert R. & Pockman W.T. (2005) Water storage capacitance and xylem tension in isolated branches of temperate and tropical trees. *Tree Physiology* **25**, 457–466.
- Bouche P.S., Larter M., Domec J.-C., Burrett R., Gasson P., Jansen S. & Delzon S. (2014) A broad survey of hydraulic and mechanical safety in the xylem of conifers. *Journal of Experimental Botany* **65**, 4419–4431.
- Boyer J.S., Wong S.C. & Farquhar G.D. (1997) CO₂ and water vapor exchange across leaf cuticle (epidermis) at various water potentials. *Plant Physiology* **114**, 185–191.
- Brodersen C.R. & McElrone A.J. (2013) Maintenance of xylem network transport capacity: a review of embolism repair in vascular plants. *Frontiers in plant science* **4**, 108–108.
- Brodribb T.J., Bowman D.M.J.S., Nichols S., Delzon S. & Burrett R. (2010) Xylem function and growth rate interact to determine recovery rates after exposure to extreme water deficit. *New Phytologist* **188**, 533–542.
- Brodribb T.J. & Cochard H. (2009) Hydraulic failure defines the recovery and point of death in water-stressed conifers. *Plant Physiology* **149**, 575–584.
- Brodribb T.J., McAdam S.A.M., Jordan G.J. & Martins S.C.V. (2014) Conifer species adapt to low-rainfall climates by following one of two divergent pathways. *Proceedings of the National Academy of Sciences of the United States of America* **111**, 14489–14493.
- Choat B. (2013) Predicting thresholds of drought-induced mortality in woody plant species. *Tree Physiology* **33**, 669–671.
- Choat B., Jansen S., Brodribb T.J., Cochard H., Delzon S., Bhaskar R., ... Zanne A.E. (2012) Global convergence in the vulnerability of forests to drought. *Nature* **491**, 752–755.
- Cochard H., Badel E., Herbette S., Delzon S., Choat B. & Jansen S. (2013) Methods for measuring plant vulnerability to cavitation: a critical review. *Journal of Experimental Botany* **64**, 4779–4791.
- Delzon S. & Cochard H. (2014) Recent advances in tree hydraulics highlight the ecological significance of the hydraulic safety margin. *New Phytologist* **203**, 355–358.
- Delzon S., Douthe C., Sala A. & Cochard H. (2010) Mechanism of water-stress induced cavitation in conifers: bordered pit structure and function support the hypothesis of seal capillary-seeding. *Plant, Cell and Environment* **33**, 2101–2111.
- Gleason S.M., Blackman C.J., Cook A.M., Laws C.A. & Westoby M. (2014) Whole-plant capacitance, embolism resistance and slow transpiration rates all contribute to longer desiccation times in woody angiosperms from arid and wet habitats. *Tree Physiology* **34**, 275–284.
- Holtta T., Cochard H., Nikinmaa E. & Mencuccini M. (2009) Capacitive effect of cavitation in xylem conduits: results from a dynamic model. *Plant, Cell and Environment* **32**, 10–21.
- IPCC (2013) *The Physical Science Basis*. Cambridge University Press, Cambridge.
- Larter M., Brodribb T.J., Pfautsch S., Burrett R., Cochard H. & Delzon S. (2015) Extreme Aridity Pushes Trees to Their Physical Limits. *Plant Physiology* **168**, 804–807.
- Lindh M., Zhang L., Falster D., Franklin O. & Braennstroem A. (2014) Plant diversity and drought: The role of deep roots. *Ecological Modelling* **290**, 85–93.
- Mackay D.S., Roberts D.E., Ewers B.E., Sperry J.S., McDowell N.G. & Pockman W.T. (2015) Interdependence of chronic hydraulic dysfunction and canopy processes can improve integrated models of tree response to drought. *Water Resources Research* **51**, 6156–6176.
- Maherali H., Pockman W.T. & Jackson R.B. (2004) Adaptive variation in the vulnerability of woody plants to xylem cavitation. *Ecology* **85**, 2184–2199.
- McDowell N.G. (2011) Mechanisms linking drought, hydraulics, carbon metabolism, and vegetation mortality. *Plant Physiology* **155**, 1051–1059.
- McDowell N.G., Fisher R.A., Xu C., Domec J.C., Holtta T., Mackay D.S., ... Pockman W.T. (2013) Evaluating theories of drought-induced vegetation mortality using a multimodel-experiment framework. *New Phytologist* **200**, 304–321.
- Mitchell P., O'Grady A.P., Pinkard E.A., Brodribb T.J., Arndt S.K., Blackman C.J., ... Tissue D.T. (2016) An eco-climatic framework for evaluating the resilience of vegetation to water deficit. *Global Change Biology* **22**, 1677–1689.
- Mitchell P.J., O'Grady A.P., Tissue D.T., White D.A., Ottenschlaeger M.L. & Pinkard E.A. (2013) Drought response strategies define the relative contributions of hydraulic dysfunction and carbohydrate depletion during tree mortality. *New Phytologist* **197**, 862–872.
- Nardini A., Casolo V., Dal B.A., Savi T., Stenni B., Bertoincin P., ... McDowell N.G. (2016) Rooting depth, water relations and non-structural carbohydrate dynamics in three woody angiosperms differentially affected by an extreme summer drought. *Plant, Cell and Environment* **39**, 618–627.
- Nardini A., Salleo S., Trifilo P. & Lo Gullo M.A. (2003) Water relations and hydraulic characteristics of three woody species co-occurring in the same habitat. *Annals of Forest Science* **60**, 297–305.
- North G.B. & Nobel P.S. (1997) Root-soil contact for the desert succulent Agave deserti in wet and drying soil. *New Phytologist* **135**, 21–29.
- O'Brien M.J., Leuzinger S., Philipson C.D., Tay J. & Hector A. (2014) Drought survival of tropical tree seedlings enhanced by non-structural carbohydrate levels. *Nature Climate Change* **4**, 710–714.
- Pfautsch S. & Adams M.A. (2013) Water flux of Eucalyptus regnans: defying summer drought and a record heatwave in 2009. *Oecologia* **172**, 317–326.
- Pfautsch S., Holtta T. & Mencuccini M. (2015a) Hydraulic functioning of tree stems-fusing ray anatomy, radial transfer and capacitance. *Tree Physiology* **35**, 706–722.
- Pfautsch S., Renard J., Tjoelker M.G. & Salih A. (2015b) Phloem as capacitor: radial transfer of water into xylem of tree stems occurs via symplastic transport in ray parenchyma. *Plant Physiology* **167**, 963–971.
- Phillips N.G., Ryan M.G., Bond B.J., McDowell N.G., Hinckley T.M. & Cermak J. (2003) Reliance on stored water increases with tree size in three species in the Pacific Northwest. *Tree Physiology* **23**, 237–245.
- Reich P.B. (2014) The world-wide 'fast-slow' plant economics spectrum: a traits manifesto. *Journal of Ecology* **102**, 275–301.
- Resco V., Ewers B.E., Sun W., Huxman T.E., Weltzin J.F. & Williams D.G. (2009) Drought-induced hydraulic limitations constrain leaf gas exchange recovery after precipitation pulses in the C-3 woody legume, *Prosopis velutina*. *New Phytologist* **181**, 672–682.
- Scholz F.G., Phillips N., Bucci S.J., Meinzer F.C. & Goldstein G. (2011) Hydraulic capacitance: biophysics and functional significance of internal water sources in relation to tree size. In *Size- and Age-related Changes in Tree Structure and Function* (eds F.C. Meinzer, B. Lachenbruch & T.E. Dawson), pp. 341–361. Springer, Dordrecht.
- Sperry J.S. & Love D.M. (2015) What plant hydraulics can tell us about responses to climate-change droughts. *New Phytologist* **207**, 14–27.
- Tyree M.T. & Sperry J.S. (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 M.T. & Sperry J.S. (1989) Vulnerability of xylem to cavitation and embolism. *Annual Review of Plant Physiology and Plant Molecular Biology* **40**, 19–38.
- Tyree M.T. & Yang S.D. (1990) Water-storage capacity of Thuja, Tsuga and Acer stems measured by dehydration isotherms. *Planta* **182**, 420–426.
- Urli M., Porte A.J., Cochard H., Guengant Y., Burrett R. & Delzon S. (2013) Xylem embolism threshold for catastrophic hydraulic failure in angiosperm trees. *Tree Physiology* **33**, 672–683.

Received 3 January 2016; accepted for publication 7 April 2016

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Supporting Information: A simple model for desiccation dynamics