nature
SUPPLEMENTARY INFORMATION
https://doi.org/10.1038/s41586-018-0240-x
In the format provided by the authors and unedited.

Triggers of tree mortality under drought

Brendan Choat[1]*, Timothy J. Brodribb[2], Craig R. Brodersen[3], Remko A. Duursma[1], Rosana López[1,4] & Belinda E. Medlyn[1]

[1]Hawkesbury Institute for the Environment, Western Sydney University, Richmond, New South Wales, Australia. [2]School of Biological Sciences, University of Tasmania, Hobart, Tasmania, Australia. [3]School of Forestry and Environmental Studies, Yale University, New Haven, CT, USA. [4]PIAF, INRA, Université Clermont Auvergne, Clermont-Ferrand, France. *e-mail: b.choat@westernsydney.edu.au

Table S1: List of plant hydraulic traits (physiological, morphological and anatomical) associated with drought tolerance in trees.

	Trait	Trait Description	Supporting References
Leaves	Stomatal Response	Rate and sensitivity of stomatal closure in response to changes in VPD and leaf water potential	1-9
	Turgor Loss Point & Osmotic Regulation	The water potential at which leaf mesophyll cells lose turgor and leaves wilt, and the adaptive regulation of the osmotic content of leaf mesophyll cells	10-22
	Minimum Stomatal Conductance (g_{min})	Rate of water loss across the leaf cuticle when the stomata are at their minimum aperture	23-25
	Extraxylary Pathways	Changes in resistance of liquid and vapor pathways through the leaf mesophyll and supporting tissue	26-29
	Leaf Shedding	Reduction in leaf area via leaf shedding during drought can slow the rate of desiccation and mitigate water stress to the remaining foliage.	30-32
	Stomatal Anatomy	Shape, size, and distribution of stomata. Influences leaf physiological traits related to water loss.	33,34
Roots	Cortical Lacunae Formation	Disintegration of root cortex cells which decouples the vascular tissue from the epidermis and the surrounding drying soil	35-37
	Fine Root Loss	Shedding of fine roots which decreases the total surface area of the root system in contact with the soil and rebalances the root to shoot ratio	35-39
	Rooting Depth	Growth of deep roots to access more consistent water sources	40-46
Common Traits Among Tissues	Vulnerability to Cavitation (Ψ_{12}, Ψ_{50}, Ψ_{88})	The negative pressure of the xylem sap that induces 12%, 50% or 88% loss of maximum xylem hydraulic conductivity. Associated with point of stomatal closure (Ψ_{12}) and the physiological tipping point for gymnosperms (Ψ_{50}) and angiosperms (Ψ_{88}).	18,24,47-68
	Capacitance	Water storage in tissues surrounding the xylem which can buffer the xylem sap from negative pressures that lead to cavitation events	41,69-73
	Cell Membrane Permeability	Permeability of cell membranes can be altered by the activity of aquaporins, leading to a reduction of hydraulic conductance across transmembrane pathways.	27,74-76
Xylem Anatomical Traits	Xylem conduit size, number and connectivity	The diameter, length and connectivity of xylem conduits (tracheids and vessels) influence maximum hydraulic conductance and vulnerability to cavitation.	61,77,78
	Pit membrane porosity and thickness	Pit membrane anatomy determines the air-seeding thresholds between xylem conduits and influences hydraulic conductance and vulnerability to cavitation.	49,50,60,79,80
	Wood density	Wood density is determined by xylem anatomical traits and is correlated with a number of physiological traits.	55,81,82
	Sectoriality	Spatial separation of vascular tissues that prevents embolism spread between branches	83-88

Literature cited

1 Brodribb, T. J., McAdam, S. A. & Carins Murphy, M. R. Xylem and stomata, coordinated through time and space. *Plant, cell & environment* **40**, 872-880 (2017).

2 Deans, R. M., Brodribb, T. J. & McAdam, S. A. An integrated hydraulic-hormonal model of conifer stomata predicts water stress dynamics. *Plant Physiol*, pp. 00150.02017 (2017).

3 Drake, P. L., Froend, R. H. & Franks, P. J. Smaller, faster stomata: scaling of stomatal size, rate of response, and stomatal conductance. *Journal of Experimental Botany* **64**, 495-505 (2013).

4 Irvine, J., Perks, M., Magnani, F. & Grace, J. The response of Pinus sylvestris to drought: stomatal control of transpiration and hydraulic conductance. *Tree physiology* **18**, 393-402 (1998).

5 Kubiske, M. E. & Abrams, M. D. Photosynthesis, water relations, and leaf morphology of xeric versus mesic Quercus rubra ecotypes in central Pennsylvania in relation to moisture stress. *Canadian Journal of Forest Research* **22**, 1402-1407 (1992).

6 Lawson, T. & Blatt, M. R. Stomatal size, speed, and responsiveness impact on photosynthesis and water use efficiency. *Plant Physiol* **164**, 1556-1570 (2014).

7 Saliendra, N. Z., Sperry, J. S. & Comstock, J. P. Influence of leaf water status on stomatal response to humidity, hydraulic conductance, and soil drought in Betula occidentalis. *Planta* **196**, 357-366 (1995).

8 Tardieu, F. & Davies, W. Integration of hydraulic and chemical signalling in the control of stomatal conductance and water status of droughted plants. *Plant, Cell & Environment* **16**, 341-349 (1993).

9 Vilagrosa, A., Bellot, J., Vallejo, V. & Gil-Pelegrín, E. Cavitation, stomatal conductance, and leaf dieback in seedlings of two co-occurring Mediterranean shrubs during an intense drought. *Journal of experimental botany* **54**, 2015-2024 (2003).

10 Baltzer, J., Davies, S. J., Bunyavejchewin, S. & Noor, N. The role of desiccation tolerance in determining tree species distributions along the Malay–Thai Peninsula. *Functional Ecology* **22**, 221-231 (2008).

11 Bartlett, M. K., Scoffoni, C. & Sack, L. The determinants of leaf turgor loss point and prediction of drought tolerance of species and biomes: a global meta-analysis. *Ecol Lett* **15**, 393-405 (2012).

12 Bartlett, M. K. *et al.* Global analysis of plasticity in turgor loss point, a key drought tolerance trait. *Ecol Lett* **17**, 1580-1590 (2014).

13 Chaves, M. M., Flexas, J. & Pinheiro, C. Photosynthesis under drought and salt stress: regulation mechanisms from whole plant to cell. *Annals of botany* **103**, 551-560 (2009).

14 Dichio, B., Xiloyannis, C., Sofo, A. & Montanaro, G. Osmotic regulation in leaves and roots of olive trees during a water deficit and rewatering. *Tree physiology* **26**, 179-185 (2006).

15 Gullo, M. & Salleo, S. Different strategies of drought resistance in three Mediterranean sclerophyllous trees growing in the same environmental conditions. *New Phytol* **108**, 267-276 (1988).

16 Hinckley, T., Duhme, F., Hinckley, A. & Richter, H. Water relations of drought hardy shrubs: osmotic potential and stomatal reactivity. *Plant, Cell & Environment* **3**, 131-140 (1980).

17 Lenz, T. I., Wright, I. J. & Westoby, M. Interrelations among pressure–volume curve traits across species and water availability gradients. *Physiologia Plantarum* **127**, 423-433 (2006).
18 Martínez-Vilalta, J., Prat, E., Oliveras, I. & Piñol, J. Xylem hydraulic properties of roots and stems of nine Mediterranean woody species. *Oecologia* **133**, 19-29 (2002).
19 Morgan, J. M. Osmoregulation and water stress in higher plants. *Annual review of plant physiology* **35**, 299-319 (1984).
20 Patakas, A., Nikolaou, N., Zioziou, E., Radoglou, K. & Noitsakis, B. The role of organic solute and ion accumulation in osmotic adjustment in drought-stressed grapevines. *Plant science* **163**, 361-367 (2002).
21 Pita, P. & Pardos, J. A. Growth, leaf morphology, water use and tissue water relations of Eucalyptus globulus clones in response to water deficit. *Tree Physiology* **21**, 599-607 (2001).
22 Tyree, M. & Hammel, H. The measurement of the turgor pressure and the water relations of plants by the pressure-bomb technique. *Journal of Experimental Botany* **23**, 267-282 (1972).
23 Barnard, D. & Bauerle, W. The implications of minimum stomatal conductance on modeling water flux in forest canopies. *Journal of Geophysical Research: Biogeosciences* **118**, 1322-1333 (2013).
24 Delzon, S., Douthe, C., Sala, A. & Cochard, H. Mechanism of water-stress induced cavitation in conifers: bordered pit structure and function support the hypothesis of seal capillary-seeding. *Plant, Cell & Environment* **33**, 2101-2111 (2010).
25 Jordan, G. J. & Brodribb, T. J. Incontinence in aging leaves: deteriorating water relations with leaf age in Agastachys odorata (Proteaceae), a shrub with very long-lived leaves. *Functional Plant Biology* **34**, 918-924 (2007).
26 Barbour, M., Farquhar, G. & Buckley, T. Leaf water stable isotopes and water transport outside the xylem. *Plant, cell & environment* **40**, 914-920 (2017).
27 Scoffoni, C. *et al.* Outside-xylem vulnerability, not xylem embolism, controls leaf hydraulic decline during dehydration. *Plant Physiol*, pp. 01643.02016 (2017).
28 Scoffoni, C. *et al.* Leaf vein xylem conduit diameter influences susceptibility to embolism and hydraulic decline. *New Phytol* **213**, 1076-1092 (2017).
29 Trifiló, P., Raimondo, F., Savi, T., Lo Gullo, M. A. & Nardini, A. The contribution of vascular and extra-vascular water pathways to drought-induced decline of leaf hydraulic conductance. *Journal of experimental botany* **67**, 5029-5039 (2016).
30 Vilagrosa, A., Bellot, J., Vallejo, V. R. & Gil-Pelegrín, E. Cavitation, stomatal conductance, and leaf dieback in seedlings of two co-occurring Mediterranean shrubs during an intense drought. *Journal of Experimental Botany* **54**, 2015-2024, doi:10.1093/jxb/erg221 (2003).
31 Williams, L. J., Bunyavejchewin, S. & Baker, P. J. Deciduousness in a seasonal tropical forest in western Thailand: interannual and intraspecific variation in timing, duration and environmental cues. *Oecologia* **155**, 571-582, doi:10.1007/s00442-007-0938-1 (2008).
32 Williams, R. J., Myers, B. A., Muller, W. J., Duff, G. A. & Eamus, D. Leaf phenology of woody species in a North Australian tropical savanna. *Ecology* **78**, 2542-2558 (1997).
33 Sack, L., Cowan, P. D., Jaikumar, N. & Holbrook, N. M. The 'hydrology' of leaves: co-ordination of structure and function in temperate woody species. *Plant Cell Environ* **26**, 1343-1356, doi:DOI 10.1046/j.0016-8025.2003.01058.x (2003).
34 Brodribb, T. J., Jordan, G. J. & Carpenter, R. J. Unified changes in cell size permit coordinated leaf evolution. *New Phytol* **199**, 559-570, doi:10.1111/nph.12300 (2013).

35 Cuneo, I. F., Knipfer, T., Brodersen, C. R. & McElrone, A. J. Mechanical failure of fine root cortical cells initiates plant hydraulic decline during drought. *Plant Physiol* **172**, 1669-1678 (2016).
36 North, G. B. & Nobel, P. S. Changes in hydraulic conductivity and anatomy caused by drying and rewetting roots of Agave deserti (Agavaceae). *Am J Bot*, 906-915 (1991).
37 Zhu, J., Brown, K. M. & Lynch, J. P. Root cortical aerenchyma improves the drought tolerance of maize (Zea mays L.). *Plant, cell & environment* **33**, 740-749 (2010).
38 Jackson, R. B., Mooney, H. & Schulze, E.-D. A global budget for fine root biomass, surface area, and nutrient contents. *Proceedings of the National Academy of Sciences* **94**, 7362-7366 (1997).
39 López, B., Sabaté, S. & Gracia, C. Fine roots dynamics in a Mediterranean forest: effects of drought and stem density. *Tree physiology* **18**, 601-606 (1998).
40 Bleby, T. M., Mcelrone, A. J. & Jackson, R. B. Water uptake and hydraulic redistribution across large woody root systems to 20 m depth. *Plant, Cell & Environment* **33**, 2132-2148 (2010).
41 Bréda, N., Huc, R., Granier, A. & Dreyer, E. 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 (2006).
42 Canadell, J. *et al.* Maximum rooting depth of vegetation types at the global scale. *Oecologia* **108**, 583-595 (1996).
43 McElrone, A. J., Pockman, W. T., Martínez-Vilalta, J. & Jackson, R. B. Variation in xylem structure and function in stems and roots of trees to 20 m depth. *New Phytol* **163**, 507-517 (2004).
44 Padilla, F. & Pugnaire, F. Rooting depth and soil moisture control Mediterranean woody seedling survival during drought. *Functional Ecology* **21**, 489-495 (2007).
45 Pinheiro, H. A., DaMATTA, F. M., Chaves, A. R., Loureiro, M. E. & Ducatti, C. Drought tolerance is associated with rooting depth and stomatal control of water use in clones of Coffea canephora. *Annals of botany* **96**, 101-108 (2005).
46 Schulze, E.-D. *et al.* Rooting depth, water availability, and vegetation cover along an aridity gradient in Patagonia. *Oecologia* **108**, 503-511 (1996).
47 Blackman, C. J., Brodribb, T. J. & Jordan, G. J. Leaf hydraulic vulnerability is related to conduit dimensions and drought resistance across a diverse range of woody angiosperms. *New Phytol* **188**, 1113-1123 (2010).
48 Brodribb, T. J., Bowman, D. J., Nichols, S., Delzon, S. & Burlett, R. Xylem function and growth rate interact to determine recovery rates after exposure to extreme water deficit. *New Phytol* **188**, 533-542 (2010).
49 Choat, B., Ball, M., Luly, J. & Holtum, J. Pit membrane porosity and water stress-induced cavitation in four co-existing dry rainforest tree species. *Plant Physiol* **131**, 41-48 (2003).
50 Choat, B., Jansen, S., Zwieniecki, M. A., Smets, E. & Holbrook, N. M. Changes in pit membrane porosity due to deflection and stretching: the role of vestured pits. *Journal of experimental botany* **55**, 1569-1575 (2004).
51 Dalla-Salda, G., Martinez-Meier, A., Cochard, H. & Rozenberg, P. Genetic variation of xylem hydraulic properties shows that wood density is involved in adaptation to drought in Douglas-fir (Pseudotsuga menziesii (Mirb.)). *Annals of forest science* **68**, 747-757 (2011).
52 Fonti, P. *et al.* Studying global change through investigation of the plastic responses of xylem anatomy in tree rings. *New Phytol* **185**, 42-53 (2010).
53 Hacke, U. G. & Sperry, J. S. Functional and ecological xylem anatomy. *Perspectives in plant ecology, evolution and systematics* **4**, 97-115 (2001).

54 Hacke, U. G., Sperry, J. S. & Pittermann, J. Analysis of circular bordered pit function II. Gymnosperm tracheids with torus-margo pit membranes. *Am J Bot* **91**, 386-400 (2004).
55 Hacke, U. G., Sperry, J. S., Pockman, W. T., Davis, S. D. & McCulloh, K. A. Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia* **126**, 457-461 (2001).
56 Hoffmann, W. A., Marchin, R. M., Abit, P. & Lau, O. L. Hydraulic failure and tree dieback are associated with high wood density in a temperate forest under extreme drought. *Global Change Biology* **17**, 2731-2742 (2011).
57 Jansen, S., Baas, P., Gasson, P., Lens, F. & Smets, E. Variation in xylem structure from tropics to tundra: evidence from vestured pits. *Proceedings of the National Academy of Sciences of the United States of America* **101**, 8833-8837 (2004).
58 Jansen, S., Baas, P., Gasson, P. & Smets, E. Vestured pits: do they promote safer water transport? *International Journal of Plant Sciences* **164**, 405-413 (2003).
59 Maherali, H., Pockman, W. T. & Jackson, R. B. Adaptive variation in the vulnerability of woody plants to xylem cavitation. *Ecology* **85**, 2184-2199 (2004).
60 Pittermann, J., Sperry, J. S., Hacke, U. G., Wheeler, J. K. & Sikkema, E. H. Torus-margo pits help conifers compete with angiosperms. *Science* **310**, 1924-1924 (2005).
61 Sperry, J. S., Hacke, U. G. & Pittermann, J. Size and function in conifer tracheids and angiosperm vessels. *Am J Bot* **93**, 1490-1500 (2006).
62 Wheeler, J. K., Sperry, J. S., Hacke, U. G. & Hoang, N. Inter-vessel pitting and cavitation in woody Rosaceae and other vesselled plants: a basis for a safety versus efficiency trade-off in xylem transport. *Plant, Cell & Environment* **28**, 800-812 (2005).
63 Willson, C. J. & Jackson, R. B. Xylem cavitation caused by drought and freezing stress in four co-occurring Juniperus species. *Physiologia Plantarum* **127**, 374-382 (2006).
64 Choat, B. *et al.* Global convergence in the vulnerability of forests to drought. *Nature* **491**, 752-755 (2012).
65 Choat, B. & Way, D. Predicting thresholds of drought-induced mortality in woody plant species. *Tree Physiol* **33**, 669-671 (2013).
66 Pockman, W. T. & Sperry, J. S. Vulnerability to xylem cavitation and the distribution of Sonoran desert vegetation. *Am J Bot* **87**, 1287-1299 (2000).
67 Tyree, M. T. & Sperry, J. S. Vulnerability of xylem to cavitation and embolism. *Annu Rev Plant Biol* **40**, 19-36 (1989).
68 Urli, M. *et al.* Xylem embolism threshold for catastrophic hydraulic failure in angiosperm trees. *Tree physiology* **33**, 672-683 (2013).
69 Borchert, R. & Pockman, W. T. Water storage capacitance and xylem tension in isolated branches of temperate and tropical trees. *Tree Physiol* **25**, 457-466 (2005).
70 Goldstein, G. *et al.* Stem water storage and diurnal patterns of water use in tropical forest canopy trees. *Plant, Cell & Environment* **21**, 397-406 (1998).
71 McCulloh, K. A., Johnson, D. M., Meinzer, F. C. & Woodruff, D. R. The dynamic pipeline: hydraulic capacitance and xylem hydraulic safety in four tall conifer species. *Plant, Cell & Environment* **37**, 1171-1183 (2014).
72 Meinzer, F. C., Johnson, D. M., Lachenbruch, B., McCulloh, K. A. & Woodruff, D. R. Xylem hydraulic safety margins in woody plants: coordination of stomatal control of xylem tension with hydraulic capacitance. *Functional Ecology* **23**, 922-930 (2009).
73 Meinzer, F. C. & McCulloh, K. A. Xylem recovery from drought-induced embolism: where is the hydraulic point of no return? *Tree physiology* **33**, 331-334 (2013).

74 Maurel, C., Verdoucq, L., Luu, D. T. & Santoni, V. Plant aquaporins: Membrane channels with multiple integrated functions. *Annu Rev Plant Biol* **59**, 595-624, doi:10.1146/annurev.arplant.59.032607.092734 (2008).

75 McElrone, A. J. *et al.* Aquaporin-mediated changes in hydraulic conductivity of deep tree roots accessed via caves. *Plant Cell Environ* **30**, 1411-1421, doi:10.1111/j.1365-3040.2007.01714.x (2007).

76 Vandeleur, R. K. *et al.* The Role of Plasma Membrane Intrinsic Protein Aquaporins in Water Transport through Roots: Diurnal and Drought Stress Responses Reveal Different Strategies between Isohydric and Anisohydric Cultivars of Grapevine. *Plant Physiol* **149**, 445-460, doi:10.1104/pp.108.128645 (2009).

77 Loepfe, L., Martinez-Vilalta, J., Pinol, J. & Mencuccini, M. The relevance of xylem network structure for plant hydraulic efficiency and safety. *J Theor Biol* **247**, 788-803, doi:10.1016/j.jtbi.2007.03.036 (2007).

78 Martinez-Vilalta, J. *et al.* Spatial Distribution and Packing of Xylem Conduits. *Am J Bot* **99**, 1189-1196, doi:10.3732/ajb.1100384 (2012).

79 Li, S. *et al.* Intervessel Pit Membrane Thickness as a Key Determinant of Embolism Resistance in Angiosperm Xylem. *Iawa J* **37**, 152-171, doi:10.1163/22941932-20160128 (2016).

80 Pittermann, J. *et al.* The Relationships between Xylem Safety and Hydraulic Efficiency in the Cupressaceae: The Evolution of Pit Membrane Form and Function. *Plant Physiol* **153**, 1919-1931, doi:10.1104/pp.110.158824 (2010).

81 Chave, J. *et al.* Towards a worldwide wood economics spectrum. *Ecol Lett* **12**, 351-366, doi:10.1111/j.1461-0248.2009.01285.x (2009).

82 Li, X. M. *et al.* Tree hydraulic traits are coordinated and strongly linked to climate-of-origin across a rainfall gradient. *Plant Cell Environ* **41**, 646-660, doi:10.1111/pce.13129 (2018).

83 Ellmore, G. S., Zanne, A. E. & Orians, C. M. Comparative sectoriality in temperate hardwoods: hydraulics and xylem anatomy. *botanical Journal of the Linnean Society* **150**, 61-71 (2006).

84 Orians, C. M., Babst, B. & Zanne, A. E. Vascular constraints and long-distance transport in dicots. *Vascular transport in plants*, 355-371 (2005).

85 Orians, C. M., Smith, S. D. & Sack, L. How are leaves plumbed inside a branch? Differences in leaf-to-leaf hydraulic sectoriality among six temperate tree species. *Journal of Experimental Botany* **56**, 2267-2273 (2005).

86 Schenk, H. J. Clonal splitting in desert shrubs. *Plant Ecology* **141**, 41-52 (1999).

87 Schenk, H. J. *et al.* Hydraulic integration and shrub growth form linked across continental aridity gradients. *Proceedings of the National Academy of Sciences* **105**, 11248-11253 (2008).

88 Zanne, A. E., Sweeney, K., Sharma, M. & Orians, C. M. Patterns and consequences of differential vascular sectoriality in 18 temperate tree and shrub species. *Functional Ecology* **20**, 200-206 (2006).