NEWS & VIEWS

doi:10.1038/nature11756

PLANT ECOLOGY

Forests on the brink

An analysis of the physiological vulnerability of different trees to drought shows that forests around the globe are at equally high risk of succumbing to increases in drought conditions.

BETTINA M. J. ENGELBRECHT

Water is the most limiting factor for ecosystem diversity and productivity worldwide. But the global climate is changing, and both warming and shifts in rainfall patterns are projected, which will leave large areas of the planet with less rain and a higher likelihood of extreme drought events[1,2]. These changes will almost certainly affect forests, which cover more than 30% of the world's land surface. Understanding these effects is imperative: forests play an integral part in carbon and water cycles, they provide timber and other products, and they are home to a vast diversity of plants, animals and microorganisms. But forests occur in a wide range of climatic conditions, so it is a challenge to predict how the vulnerability of trees to changes in water availability compares between different biomes. In a paper published on *Nature*'s website today, Choat *et al.*[3] use a combination of physiological measurements of the vulnerability of trees to drought and of the drought stress they actually experience in their natural habitats to show that forests worldwide are at high risk.

We might expect that trees in forests currently exposed to seasonal or multi-annual droughts, such as in 'Mediterranean-type' systems, are already well adapted and will therefore suffer less from an increase in drought conditions than trees in wet forests. Conversely, but equally reasonably, we could predict that trees in dry areas are already at their physiological limits and would therefore be more vulnerable to increased drought than trees in wet forests. To investigate these questions, Choat and colleagues compared the vulnerability of the tree water-transport system to drought in different species worldwide.

In plants, water is transported through a tubing system, a tissue called xylem that is made up of a multitude of conduits. Loss of water vapour (transpiration) through stomata (pores) in the plants' leaves generates suction that pulls water in the xylem from the soil through the roots and stem to the leaves — much like sucking water through a straw. On its way, the water provides crucial services to the plant: it is the medium for metabolic reactions, it transports nutrients and other substances, and it provides stability. However, the powerful suction that pulls water through the xylem brings with it the risk of pulling air through small holes, called pit pores, in the sides of the conduits. These air bubbles can block the xylem and impair water transport, just like sucking air into a broken straw. This process is called xylem embolism, and the higher the suction in the conduit, the more embolism occurs.

The link between this physiology and drought conditions comes from the fact that suction increases with increasing transpiration and/or decreasing water availability in the soil. Plants can regulate their stomata to delay the increase in suction, but if water is not replenished, more and more conduits will become clogged, leading to hydraulic failure and the eventual death of the plant. However, different plant species have different xylem structures, so the vulnerability of a plant's xylem conduits to embolism, and therefore its ability to tolerate drought, are variable.

The authors compiled data on the xylem vulnerability of 480 tree species from 183 sites worldwide, covering the broad range of climatic conditions in which forests occur. They included both angiosperms (flowering trees, such as oak and maple) and gymnosperms (such as pine and cedar), which vary substantially in their xylem structure. Wherever the data were available, they also included the maximum suction occurring in the trees in their natural habitats. Combining these data enabled Choat *et al.* to explore how the suction that induces hydraulic failure in a given species compares with the suction that it actually experiences. If these values are close together, this represents a small 'safety margin' with respect to hydraulic failure and indicates that the species is at risk; if they are far apart, the species is likely to be able to withstand more intense drought conditions.

The data show that, as expected, trees growing in more arid conditions around the globe are better at withstanding xylem embolism. The exciting finding, however, is that angiosperm trees in all forest biomes have converged on a risky strategy, operating at extremely narrow safety margins. This implies that these trees are already, under current conditions, on the verge of injurious levels of water availability, and that even a minor increase in drought intensity will induce levels of xylem embolism that will impair growth and lead to tree death.

The suggestion that all forests are on the brink of succumbing to drought, and may already be responding to climate change, is supported by observations of increased

B. WERMELINGER, WSL

Figure 1 | Thirsty trees. Reports of drought-induced forest die-off[4], such as that in Switzerland in 1999 shown here, have increased in recent decades, suggesting that climate change is already having an impact on tree health in many locations. Choat and colleagues' study[3] of trees across the globe suggests that they are at high risk from even small increases in drought intensity.

drought-induced forest die-offs and tree mortality in many ecosystems[4] (Fig. 1). For gymnosperms, Choat *et al.* found wider safety margins, suggesting that these trees may have a higher tolerance to increased drought. However, even these trees are threatened by hydraulic failure, as recent regional die-offs of pines show[4]. Taken together, these studies sound a warning bell that we can expect to see forest diebacks become more widespread, more frequent and more severe — and that no forests are immune. The ramifications of this scenario are diverse and, in many respects, dire: forest mortality will be accompanied by changes in species composition, changes in ecosystem function and losses of services and biodiversity[4].

Advancing our knowledge of organismal responses to factors such as drought and temperature is essential to improving predictions of the consequences of climate change[5,6]. Through their meta-analysis of the global distribution of xylem vulnerability, Choat *et al.* have dramatically increased our understanding of the comparative vulnerability of forests. Nevertheless, the mechanisms that actually lead to drought-induced tree mortality still remain elusive; in fact, it is known that some species can survive complete hydraulic failure for extended periods of time[7]. Although many studies have assessed the response of plants to experimentally manipulated precipitation and/or temperature[8], the results of these studies do not lend themselves to comparisons of drought responses across biomes, because of differences in treatments and in the resulting drought intensities. A coordinated network of standardized experiments is needed to further advance understanding of climate-change responses in ecosystems worldwide.

Our ability to forecast the consequences of drought for forests is also limited by the high regional uncertainty in current models for rainfall and drought prediction, for both long-term trends and extreme events[1,2]. A fundamental lesson from Choat and colleagues' study is that even small changes in drought intensity can be expected to lead to mortality in forests all over the world. This only highlights the urgent need for climate models that return more-confident predictions. ■

Bettina M. J. Engelbrecht *is at the Bayreuth Center of Ecology and Environmental Science, Department of Plant Ecology, University of Bayreuth, 95440 Bayreuth, Germany, and at the Smithsonian Tropical Research Institute, Panama.*
e-mail: bettina.engelbrecht@uni-bayreuth.de

1. Parry, M. L. *et al.* (eds) *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (Cambridge Univ. Press, 2007).
2. Field, C. B. *et al.* (eds) *Managing the Risks of Extreme Events and Disasters to Advance Climate Change Adaptation. A Special Report of Working Groups I and II of the Intergovernmental Panel on Climate Change* (Cambridge Univ. Press, 2012).
3. Choat, B. *et al. Nature* http://dx.doi.org/10.1038/nature11688 (2012).
4. Allen, C. D. *et al. Forest Ecol. Mgmt* **259,** 660–684 (2010).
5. Svenning, J.-C. & Condit, R. *Science* **322,** 206–207 (2008).
6. Craine, J. M. *et al. Nature Clim. Change* http://dx.doi.org/10.1038/nclimate1634 (2012).
7. McDowell, N. G. *Plant Physiol.* **155,** 1051–1059 (2011).
8. Wu, Z., Dijkstra, P., Koch, G. W., Penuelas, J. & Hungate, B. A. *Glob. Change Biol.* **17,** 927–942 (2011).