ECOSYSTEM SCIENCE

Plump trees win under drought

The long-held assumption that the storage of starch and related compounds helps plants cope with drought stress is now supported by much needed experimental evidence.

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Plants, particularly trees, require lots of water, and drought induced by climate change can cause forest die-back[1]. Using models to determine which forests are more vulnerable is challenging[2]. Under drought, water availability and transport are insufficient to replace water lost through stomata (tiny pores in leaves) and the tension in the vascular water transport system (xylem) of plants increases. This may cause hydraulic failure and death[3]. To minimize this risk, plants close stomata to prevent water loss. However, stomatal closure also prevents CO_2 diffusion into the leaf, halting photosynthesis. If carbon supply from photosynthesis becomes limiting, plants rely on non-structural carbon (NSC) compounds such as carbohydrates to provide substrates for the maintenance of living cells. Although convincing, this argument has escaped proper testing. Now, as they report in *Nature Climate Change*, Michael O'Brien and colleagues[4] provide experimental evidence that NSC storage mitigates the effects of drought by ameliorating water relations — a finding important for plant physiologists, restoration ecologists and modellers.

Plants are exposed to the desiccating effect of the air, which increases tension in the xylem. In addition, their living cells, including those that transport assimilates, need to be under turgor pressure (generated by water pressing against their cell walls) to remain functional. However, plants do not have energy-consuming organs that acquire and circulate water throughout their bodies. Rather, water moves passively along gradients of energy (from high to low total water potential, Ψ). Therefore, turgid, living cells can only absorb water under tension from the xylem (low Ψ) if their respective Ψ is even lower. They do so by accumulating solutes.

Assuming no gravitational effect, the water potential of a cell is the sum of pressure potential (Ψ_p) and osmotic potential (Ψ_π), and varies from 0 (maximum) to negative values. Ψ_p can be positive (for example, in living cells), or negative (for example, in xylem conduits). Ψ_π is proportional to the concentration of solutes and is always negative (solutes decrease the free energy of water). Solute accumulation in living cells, therefore, lowers their Ψ_π and offsets the positive Ψ_p. Indeed, adjustment of Ψ_π is critical for water relations[5]. Solute accumulation may also help refill 'emptied' xylem conduits under drought[6].

Plant cells use inorganic and organic solutes to retain or acquire water. The work by O'Brien *et al.*[4] is consistent with the role of NSC as a source of organic solutes: both within and among species, seedlings with higher NSC before drought maintained higher water potential after drought relative to those with lower NSC. Their clever experimental approach minimized differences in plant morphology between relatively NSC-enriched and NSC-depleted seedlings. Neither soil moisture nor stomatal conductance varied significantly between the two groups of plants, indicating that the higher water potential in NSC-enriched seedlings was not due to greater stomatal regulation of water loss, but from a greater ability to retain water. The specific mechanisms by which this osmotic effect enhances survival, however, are not fully understood. For instance, additional data are needed to rule out limitations on the transport of carbohydrates.

In contrast with inorganic solutes, organic carbon-based solutes do not require compensation to maintain electrical neutrality, they are synthesized and interconverted by the plant (rather than acquired from the soil), and, importantly, large amounts can be stored in osmotically inactive compounds (for example, starch or fructans). This could buffer against the diurnal, seasonal and interannual fluctuations of water availability that plants experience. Stored NSC may be critical for plants to retain water and offset the ever-present risk of excessive water loss, serving as a source of osmotically active sugars — or of carbon skeletons for the synthesis of other organic compounds — that can be constantly exchanged.

Current thinking about NSC storage in trees has been shaped by the common assumptions that NSC accumulates passively when carbon assimilation exceeds demand, and serves primarily as a carbon reservoir for future consumption for growth and energy[7]. Most ecosystem models of forest

ANNABELLE VALTAT

In addition to increasing forest mortality, drought can affect flowering frequency. Pictured here is the drought-induced flowering of Dipterocarpaceae trees around the Danum Valley River in Sabah, Malaysia.

growth are based on these assumptions. Similarly, relatively high NSC pools in trees have been interpreted as an overabundance of carbon. This has generated a heated debate about the extent to which mature trees are carbon-limited, with important implications for modelling[8].

Transplanted seedlings with more NSC perform better[9]. The study by O'Brien *et al.*[4] is consistent with this, and supports a change in the way we think about NSC storage[10]. NSC storage may not be a passive 'overflow', but a requirement to protect plants from dehydration. If so, carbon assimilation and demand for growth and storage should be tightly coordinated, and slow growth could be, in part, an evolutionary selected strategy to allow storage. Because trees are large and long-lived, those that 'play it safe' and allow greater storage have a greater chance to cope with future stress and survive. In the long term, surviving trees may accumulate NSC, but this may reflect, in part, a consequence of the safest evolutionary strategy.

The osmotic role of NSC storage in seedlings[4] highlights the need for a better understanding of the role and regulation of NSC storage in mature trees, and suggests that current attempts to incorporate NSC storage in ecosystem models[11] are certainly worthwhile. ❐

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References

1. Williams, A. P. *et al. Nature Clim. Change* **3,** 292–297 (2012).
2. McDowell, N. G. *et al. Trends Ecol. Evol.* **26,** 523–532 (2011).
3. Choat, B. *et al. Nature* **491,** 752–755 (2012).
4. O'Brien, M. J., Leuzinger, S., Philipson, C. D., Tay, J. & Hector, A. *Nature Clim. Change* **4,** 710–714 (2014).
5. Bartlett, M. K., Scoffoni, C. & Sack, L. *Ecol. Lett.* **15,** 393–405 (2012).
6. Nardini, A., Lo Gullo, M. A. & Salleo, S. *Plant Sci.* **180,** 604–611 (2011).
7. Kozlowski, T. T. *Bot. Rev.* **58,** 107–222 (1992).
8. Sala, A., Woodruff, D. R. & Meinzer, F. C. *Tree Physiol.* **2,** 764–775 (2012).
9. Landhaüser, S. M. *et al. For. Ecol. Management* **275,** 43–51 (2012).
10. Dietze, M. C. *et al. Ann. Rev. Plant Biol.* **65,** 667–687 (2014).
11. Tague, C. L., McDowell N. G. & Allen, C. D. *PLoS ONE* **8,** e80286 (2013).

BIODIVERSITY

Penguins in peril

Climate-driven demographic changes could cause drastic decline in the global emperor penguin population, driving some colonies to extinction.

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Few species depend on sea ice to the extent that emperor penguins do. Recent climate change, especially warming in the Antarctic, has substantially reduced seasonal sea ice concentration and duration, and these patterns are predicted to continue[1,2]. What might this mean for emperor penguins? In a study published in *Nature Climate Change*, Stéphanie Jenouvrier and colleagues[3] show that the global emperor penguin population will decline drastically, and many colonies will face substantial risk of extinction by 2100.

Standing over 1.2 m tall and weighing up to 45 kg, emperor penguins are the largest of all extant penguin species. The stars of film and documentary alike, they are visually appealing and biologically fascinating; they are adapted to the extreme Antarctic environment and are the only species of penguin with the habit of breeding in the middle of winter. Many important aspects of their life cycle depend on sea ice[1,2,4]. Penguins depend on fixed sea ice (fast ice) for successful reproduction and gather at traditional breeding sites (colonies) during March–April when sea ice is thickening. They need just the right amount of sea ice at just the right time. Too little sea ice will constrain the availability of breeding sites, reduce prey availability and can also make penguins vulnerable to predation. Too much sea ice means longer foraging trips for parents, lower feeding rates for chicks, and consequently, lower adult survival and reproductive success. Higher air or sea surface temperatures and early breakup of sea ice will reduce survival, and multiple years of poor sea ice will cause population declines and eventually local extinction[2,5].

Using long-term demographic information from the Terre Adélie penguin population, sea ice concentration data, and sophisticated, multi-pronged modelling techniques, Jenouvrier *et al.*[3] investigate what the future might hold for these obligate sea ice breeders. First, they linked seasonal sea ice concentration anomalies (SICa; deviations from long-term seasonal averages) to survival and reproduction of penguins by modelling these parameters as functions of SICa for four biologically relevant seasons in the penguin life cycle. Based on these estimates, they developed a two-sex, seasonal, climate-driven population model. Next they employed an ensemble of ten IPCC climate models to forecast sea ice concentration, which allowed the determination of SICa. Finally, they fed the projected SICa data to the demographic model, which was subsequently used for population projections and viability analyses. Their results indicate that the Terre Adélie population of emperor penguins will decline from around 6,000 to only 400 breeding pairs by 2100, and that the population will face a high risk of quasi-extinction (a reduction to less than 10% of its current size). These conclusions are not new[4,7]. But the present study is innovative and exciting because of the steps Jenouvrier *et al.*[3] took to expand the Terre Adélie population study to make a species-level threat assessment.

There are 45 currently known colonies of emperor penguins. The authors argue that most of these colonies have never been visited by humans, and it is highly improbable that they will ever be the focus of long-term demographic studies. How does one go about making species-level inferences when detailed data are only available for one out of 45 colonies? Emperor penguins depend on sea ice for breeding, brood rearing and feeding. We also know that climate change will undoubtedly affect the sea ice environment in and around