Interlinking moss functional traits. A commentary on: ‘Mechanisms behind species-specific water economy responses to water level drawdown in peat mosses’

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Sphagnum mosses have always fascinated researchers as an example of excellent morphological and anatomical adaptations that allow them to cope with, and even engineer, their environment. While most mosses of unshaded habitats have evolved efficient physiological tolerance to dehydration, Sphagnum shoots are optimized for retaining an enormous volume of extracellular capillary water. With climate change that is predicted to and is already bringing frequent droughts, the question of which morphological and anatomical traits best control the water economy in Sphagnum are becoming topical. By focusing on a number of species and structural traits, Bengtsson et al. (2020) address this question in the current issue of Annals of Botany.

Although the morphology and anatomy of the numerous Sphagnum species are generally similar when compared to other mosses, there are characteristic differences that are dependent upon species phylogeny and ecological preferences to water availability. Briefly, differentiation of niches along this ‘hydrology gradient’ can be best illustrated by the model of hummock–hollow dichotomy (simplifying, for this purpose, the hummock–hollow continuum to a simple dichotomy). According to Grime’s plant functional strategies and related plant economics spectra (Grime and Pierce, 2012), sphagnum forming elevated hummocks are stress tolerators characterized by a retentive lifestyle; the hummocks are nutrient-poor water-limited microhabitats formed and maintained by litter of the species growing there. Hummock sphagnum allocate resources to dense branches that serve as water (but also nutrient) retention structures. By contrast, hollow sphagnum are competitors with an acquisitive physiology, as the relatively humid and nutritious microenvironment allows resource allocation to be diverted to shoot growth, i.e. capitula (Mazziotta et al., 2019; Oke and Turetsky, 2020; Fig. 1 of this commentary).

In their study, Bengtsson et al. (2020) studied drought responses in moss patches (turfs) of as many as 13 Sphagnum species representing mainly the hummock–hollow continuum. They measured how water level drawdown affects the water content of the turf and photosynthetic apparatus of moss individuals. They linked these responses to structural functional traits, five morphological traits related to moss turfs and eight anatomical traits related to leaves. Sphagnum leaves are convex, forming large capillary pores. Species with wide leaves had a greater water retention than those with smaller leaves. However, this system functioned only at high water levels because the large capillary spaces drained faster under the induced water deficit. At lower water levels, species forming dense turfs (i.e. possessing smaller capillary spaces typical of hummock sphagnum) resisted loss of water – and hence retained their photosynthetic potential better than typical hollow species.

In summary, Bengtsson et al. (2020) reveal an apparent structural trade-off between the strategies of Sphagnum to maintain water under water-level drawdown (i.e. to minimize the loss of water vs. the need to maximize retention capacity). Although the authors stress the importance of their research for predicting shifts in the composition of Sphagnum communities in response to climate change, they do not draw any further conclusions, perhaps being aware of limitations of their short-term cultivation experiment. For this reason, any structural changes that might develop resulting from acclimation to water-level drawdown are not discussed.

The structural adaptations for retention of capillary water require mechanical strengthening of the moss tissue. This is because maintaining the water in capillary spaces requires maintenance of their shape.

Fig. 1. Contrasting plant functional strategies demonstrated by two closely coexisting sphagnum in a hummock. Dense turf of Sphagnum rubellum (red, tightly packed capitula) build the hummock, providing and maintaining structural support for water retention. Sphagnum angustifolium (yellow capitula) is phylogenetically related to typical hollow species, possessing an acquisitive resource allocation strategy to support its large capitula. Its growth, i.e. competitive potential, is limited by its low water retention, allowing only individual growth, and by desiccation above the matrix of the hummock builder as illustrated. If we follow the individual shoots of S. angustifolium down to the hummock body (and into history) they decay within a couple of centimetres (years); by contrast, hardly any structural changes can be seen in the shoots of S. rubellum, nicely demonstrating the contrasting litter strategies that reflect the two differing plant economies.

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Commentary

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under the negative pressure generated by water deficit—otherwise the desiccating turf would shrink. At the cellular level, this can be illustrated on the empty hyaline cells that dominate in Sphagnum leaves. These cells possess circular pores of a diameter ~100× smaller than that of the convex-leaf capillary space, thus forming small capillary spaces. While the water evaporates from the hyaline cells, they become somewhat flattened but the high modulus of elasticity (rigidity) of the cell wall prevents the cell from shrinking or imploding even under a negative pressure of tens of kilopascals. This cell wall strengthening avoids mechanical cell damage and allows the recovery of its original volume. Furthermore, preventing the structural collapse of this dead shoot matrix during decomposition preserves the structure of capillary pores and hence water retention.

It is here where structural and biochemical traits intersect to impact on decomposability. Hummock species allocating resources to increased water storage have a greater proportion of lignin-like phenols and acid pectins (sphagnan) than hollow species (Bengtsson et al., 2016). These compounds provide plant cell walls with structural rigidity and integrity. Importantly, Bengtsson et al. describe both compounds as significant predictors of low decomposability in Sphagnum (although the mechanistic explanations provided need to be confirmed; Bengtsson et al., 2016). In Sphagnum, consistent with a globally valid pattern (Cornwell et al., 2008), the biochemical traits interconnect the plant economics spectrum with the afterlife litter quality, which controls the rate of decomposition (Fig. 2). Cell wall biochemistry thus confers on hummock sphagna the ability to maintain their own environment within their hummocks, thereby protecting them from competition from more acquisitive species.

The impact of climate change in the form of occasional droughts will, in the short term, result in the loss of liquid water from chlorophyllous cells. This in turn will induce physiological responses, which can activate a desiccation tolerance response within the cell. The degree of desiccation tolerance of Sphagnum mosses is limited by the rate (hardening time), intensity (activity of cellular water) and duration of dehydration. Hollow species are able to develop tolerance faster, and/or to a greater extent, as a result of their lower capacity to contain water when compared with hummock sphagna (Hájek and Vicherová, 2013). On the other hand, the slower dehydration of hummocks provides the capitula with longer acclimation time. In the longer term, morphological, anatomical and perhaps also biochemical acclimation changes may take place; importantly, species’ water level niches are relatively narrow so major, long-term changes in water level will rather result in species replacement.

Hummock sphagna that also tolerate high water levels do, however, have wider water level niches, so a longer-term mesocosm experiment with manipulated water levels could reveal how plastic, and how mechanistically relevant, are the water economy traits across Sphagnum, while avoiding the interfering effects of phylogeny. There are few studies of shoot and leaf structural changes along the water level gradient and biochemical data are even scarcer. Future research employing phenotypic plasticity, which is perhaps the main source of trait responses (Oke et al., 2019), could meaningfully evaluate both structural and biochemical traits, and correlate them with decomposition rates.