Commentary

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Nucleic acid requirement of plants from low phosphorus habitats. A Commentary on: Foliar nutrient-allocation patterns in *Banksia attenuata* and *Banksia sessilis* differing in growth rate and adaptation to low-phosphorus habitats

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The availability of phosphorus (P) is one of the leading limitations for global primary productivity, particularly on ancient soils such as those of south-western Australia, where *Banksia* species exhibit high diversification. In this issue of *Annals of Botany*, Han *et al.* (2021) examine use patterns on two species of *Banksia* exhibiting different ecological strategies on the low-P soils of the region. *Banksia attenuata* is a slow-growing species of deep sand that exhibits a conservative P use strategy, including low rates of P acquisition, with a relatively low leaf nitrogen (N) content and an ability to resprout after fire. In contrast, *B. sessilis* is relatively fast growing, with traits suggestive of an r-selection strategy. In addition to its faster growth rate, *B. sessilis* has a higher P acquisition rate (from greater root growth), a higher leaf N content and a greater capacity to reproduce by seeds; it is, however, unable to resprout after fire and instead must rely upon an early and prolific seed production to withstand frequent fire. Because of these different ecological strategies, Han *et al.* (2021) identified these two species as presenting an excellent opportunity to examine the ecological consequences of P allocation strategies in closely related but ecologically divergent species. One of their notable observations was that the faster growing *B. sessilis* invested more P in nucleic acids of leaves than the more conservative *B. attenuata* and, correspondingly, *B. sessilis* had greater leaf N content than *B. attenuata*, implying greater leaf protein costs. They reasoned that greater P-rich rRNA (and ribosomes) supported greater protein synthesis in *B. sessilis* than in *B. attenuata*, and that this in turn enabled faster growth and habitat flexibility. This could be a critical contributor to the different ecological strategies between the two species.

This intriguing finding focuses attention on the important ecological role of nucleic acid investment, which has often been overlooked because the cost of nucleic acids is relatively low in plant tissues. However, because the study focused on P allocation in mature leaves, the underlying mechanism becomes a concern. For example, one might expect a direct relationship between growth rate of immature leaves and nucleic acid P investment if increased nucleic acid content increased the rate of protein synthesis. This could occur for DNA if the copy number increased of highly expressed genes whose transcription rate limits growth rate. Assuming adequate transcription capacity, an increase in mRNA, rRNA and tRNA could support more rapid protein synthesis. However, mature leaves would no longer have such construction requirements, which raises the question: what role might nucleic acid P serve in mature leaves?

DNA is retained in mature plant tissues, with the exception of sieve tube elements which rely on DNA in symplasmically connected companion cells. DNA-P is a relatively small fraction of the total P in mature leaves of plants (Han *et al.*, 2021), but whether plants from low-P habitats have smaller genomes is certainly worth consideration. The rationale here is that there may be variation in the number of non-coding sequences of no known function in the genome and, with slower maximum growth rates, fewer copies of highly expressed genes. Raven (2013) pointed out that carnivorous plants in the genus *Genlisea* (Lentibulariaceae) from low-P habitats have a 1C genome size of only 63 Mbp, among the lowest in flowering plants. However, the largest genome of a carnivorous member of the Lentibulariaceae is 1C = 1620 Mbp (Raven, 2013). More relevant to the results of Han *et al.* (2021) are results for three *Banksia* species (Proteaceae) from dry sclerophyll forest with 1C = 630–1080 Mbp (Jordan *et al.*, 2015), while the smallest flowering plant tree genome (Neale *et al.*, 2017) is 1C = 265 Mbp for *Prunus* from higher P habitats.

A different approach is that of Guignard *et al.* (2016), who investigated the flora of herbaceous plants in the Park Grass experiment set up in 1856 at the Rothamsted Experimental Station in south-east England. Specifically, these authors used replicate plots that had been under the same regime for >100 years and had a pH >4.5; the four regimes were no fertilizer, mineral P, mineral N and mineral P + mineral N. The genome 1C size of all species was measured, and weighted by the fraction of total biomass contributed by that species. The biomass-weighted 1C values for the control, P and N treatments were not significantly different, while the 1C value of the P + N treatment was significantly higher. These data give no support for smaller genome sizes in the control than the P treatment. However, the P availability in the non-fertilized plot in the Park Grass experiment is greater than that in the very P-deficient habitats of the *Banksia* species examined by Han *et al.* (2021). Overall, there is no convincing evidence of genome size limitation by restricted P availability.

RNA-P is a larger fraction of total P than is DNA-P in mature leaves of plants (Han *et al.*, 2021). rRNA (and tRNA and mRNA) in mature leaves is needed for protein synthesis to replace non-functional proteins; this protein turnover can be quantified by methods discussed by Nelson and Millar (2015). With the assumption that the rate of peptide elongation per unit rRNA in mature leaves is the same as that in growing leaves, there is an excess of rRNA in mature leaves. However, this assumption has not been tested by studies of *in vitro* translation rates.

A further requirement for the protein synthesis apparatus (RNA plus associated protein) is in replacing functional proteins that were damaged post-translationally. Examples are the proteins damaged by reactive oxygen species (ROS), by absorption of UV and, for proteins involved in photochemical reactions of photosynthesis, photosynthetically active

radiation (PAR). In the case of the D1 (psbA) protein in the reaction centre of PSII damaged by PAR and UV, the rate at which damage occurs is roughly proportional to the rate of photon absorption by the light-harvesting apparatus of PSII. Synthesis of new D1 only occurs in the light in the cyanobacteria and the flowering plants that have been tested, but it also occurs in the scotophase of the light–dark cycle in diatoms (Li *et al.*, 2016). Li *et al.* (2016) point out that the diatoms they examined can be subject to frequent (several times per photophase) fluctuations in incident photon flux density in their natural habitat. The capacity to repair PSII in the dark would, all other things being equal, decrease the requirement for rRNA since its use in D1 synthesis can occur over the full light–dark cycle rather than just in the photophase (see Raven, 2013).

More broadly, the resource, especially P, cost of synthesis of replacements for damaged proteins must be compared with the resource cost of the mechanisms that limit the extent of protein damage. For ROS that are too reactive to be removed enzymically, these are scavengers such as ascorbate and phenolics for hydroxyl radicals, and quenchers such as carotenoids for singlet oxygen. The more stable ROS superoxide and hydrogen peroxide are removed by superoxide dismutase, and peroxidase and catalase, respectively. In the case of UV radiation, damage can be limited by the production of UV-absorbing compounds, e.g. phenolics, or UV-reflecting structures between the UV source and the proteins (and nucleic acids) that could be damaged (Vignolini *et al.*, 2013). For high excitation energy in PSII, damage limitation by energy dissipation involves non-photochemical quenching and, to a lesser extent, state transitions diverting excitation energy to PSI. All of these damage avoidance mechanisms involve protein synthesis, and hence RNA, though the magnitude of this requirement is difficult to estimate. Furthermore, the damage avoidance mechanisms are generally produced during growth of the leaves, so RNA is involved in leaf development rather than in mature leaves.

However, there is the little discussed likelihood of absorbed UV damage to the phenolic compounds that scavenge hydroxyl radicals and UV-absorbing compounds. These chemically changed protective molecules may cease to offer protection from hydroxyl radicals, singlet oxygen and UV radiation, and they may be replaced in mature leaves. An obvious example are hydroxyl radical scavengers that are necessarily chemically changed by the action of scavenging (Treml and Šmejkal, 2018). It is possible that such replacement would require additional protein synthesis and hence RNA function, although it is not possible to estimate these requirements.

Thus, for the moment it is not possible to determine the extent to which the RNA content of mature leaves can be explained in terms of the requirement for protein turnover. Despite these unknowns, the results of Han *et al*. (2021) raise some intriguing possibilities regarding the role of P in mature leaves and how this investment relates to fitness in a range of P-deficient habitats. Understanding the underlying mechanism should provide new avenues to explain the dynamics of plant diversity in terms of ecological strategy.

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