

Overview of Phylogenetic Distribution of Salt Tolerance

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Letter to Editor

The distribution of halophytes on phylogenies can tell us much about the macro evolutionary dynamics of salt tolerance. Especially, we will estimate how often salt tolerance has evolved, whether it's more likely to evolve in some lineages than others and if the patterns of diversification of salt-tolerant lineages differ from their non-salt tolerant relatives.

Multiple origins of salt tolerance in grasses

To illustrate this approach, we analysed the patterns of occurrence of salt-tolerant species within the Gramineae (Poaceae). We focused on the Gramineae for several reasons: grasses are an outsized and diverse family with many recorded salt-tolerant species; there have been several phylogenies that have a high degree of coverage, with one complete to genus level, and another 20 to finish to species level; and grasses contain many of the economically important crops species that are the main target of intense breeding efforts to extend salt tolerance, particularly wheat, rice and barley.

We assembled an inventory of reported salt-tolerant grass species and plotted them on a comprehensive phylogeny. We were surprised to seek out that, instead of clustering in groups of related species, salt-tolerant grass species were scattered throughout the phylogeny, such most salt-tolerant species had relatively few identified salt-tolerant relatives. The foremost likely explanation for this pattern is that there are many independent origins of salt tolerance within the Gramineae, each of which is comparatively recent and has given rise to just one or a couple of salt-tolerant species. The 200 identified halophytic grasses have apparently arisen from over 70 different independent origins of salt tolerance. This 'tippy' pattern of the many recent origins of salt tolerance, all at the ideas of the phylogeny instead of deep within the tree defining large clades, is strong to changing the methods or assumptions of the analysis. The tippy pattern was qualitatively an equivalent whether we conducted the analysis on an incomplete species-level tree or an entire genus-level tree. An equivalent pattern was found when considering a subset of halophytes known to possess very high levels of salt tolerance, having the ability to finish their life cycle in conditions like >200 mm NaCl.

Controlling for phylogenetic co-variation

Because they're inherited by many descendants from a standard ancestor, we expect biological traits like photosynthetic pathway and salt tolerance to

tend to be more similar among close relatives. This non-independence of traits confounds attempts to match species to work out whether two traits are causally linked, because relatives will tend to inherit both traits from their ancestors, whether or not the 2 traits are hooked in to one another to determine whether there's a meaningful evolutionary link between traits, beyond their incidental inheritance from a shared ancestor, we will compare multiple independent origins of every trait and ask whether the acquisition of 1 trait during a lineage makes it more likely to also acquire another trait.

For example, lineages with C4 photosynthesis often contain many halophytes, and C4 plants form a better proportion of the vegetation in some saline habitats. This pattern of association has been interpreted as a mirrored image of adaptation to water stress: by increasing water use efficiency, C4 plants reduce the negative impacts of environmental salt on water stress and ion toxicity. During this sense, C4 photosynthesis might be considered an enabling trait for the evolution of salt tolerance. In turn, particular features of leaf anatomy are often considered as enabling traits for the repeated origins of C4 photosynthesis. Like salt tolerance, C4 photosynthesis has evolved repeatedly (more than 60 origins in angiosperms), but more often in some lineages than other. So lineages with particular features of leaf anatomy are more likely to evolve C4 photosynthesis, resulting in a concomitant increased tolerance to water stress and salinity. Conversely, lineages in arid environments, where they're more likely to encounter environmental salinity, are more likely to possess C4 photosynthesis.

In grasses, halophytes are significantly more likely to occur in lineages with C4 photosynthesis, and therefore the pattern of salt tolerance and C4 on the phylogeny suggests correlated evolution of salt tolerance and C4. C3 lineages, against this, have significantly fewer halophytes than would be expected if salt tolerance was random with reference to photosynthetic pathway. This analysis demonstrates that C4 photosynthesis and salt tolerance have a big connection: their co-occurrence in species is neither explained by a random distribution nor explained simply as a matter of shared inheritance of unconnected traits. But this connection doesn't tell us whether C4 increases the prospect of salt tolerance, or salt tolerance increases the prospect of C4 evolving, or whether both traits are connected indirectly. The movement of grass lineages from shady forest environments to open, arid and salt-affected areas may have stimulated the evolution of more water-efficient C4 photosynthesis, or the evolution of C4 may have acted as a potentiating trait that allowed some grass lineages to maneuver into these challenging habitats, or both.

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