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Permalink
https://escholarship.org/uc/item/6bq209jb

Journal
Annals of Botany, 130(3)

ISSN
0305-7364

Author
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Publication Date
2022-09-19

DOI
10.1093/aob/mcac040

Peer reviewed

Commentary

Annals of Botany **130(3):** ix–xi, 2022
Available online at www.academic.oup.com/aob
https://doi.org/10.1093/aob/mcac040

Cycads defy expectations for the coordination between drought and mechanical resistance. A commentary on: 'Correlations between leaf economics, mechanical resistance and drought tolerance across 41 cycad species'

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Keywords: Cycads, mechanical resistance, drought tolerance

The leaf economics spectrum is one of the few organizing principles in plant ecology. Across thousands of species from biomes worldwide, correlations among leaf structural, chemical and physiological traits constrain trait variation to a single axis (Wright *et al.*, 2004). Along this axis, leaf syndromes range from 'fast', with traits that facilitate resource acquisition and growth (e.g. a high nitrogen content and maximum photosynthetic rate), to 'slow', with traits that conserve resources and support leaf persistence (e.g. high structural investment and mechanical strength) (Onoda *et al.*, 2011; Reich, 2014). The physiological trade-offs that generate the leaf economics spectrum have been hypothesized to mechanistically link these traits to other stress resistance syndromes, which would integrate an even wider range of ecological and evolutionary strategies into a single, universal spectrum (Hallik *et al.*, 2009; Reich, 2014; Nadal *et al.*, 2018; Zhu *et al.*, 2018). However, other findings have challenged this view (Bartlett *et al.*, 2012; Maréchaux *et al.*, 2020), and raised questions about how and why coordination between leaf traits varies across the plant kingdom (Mason and Donovan, 2015; Fletcher *et al.*, 2018). In this issue of *Annals of Botany*, Meng *et al.* (2022) test whether the same relationships between the leaf economics spectrum and drought tolerance apply to phylogenetically diverse angiosperms and a clade of closely related gymnosperms, cycads. They show that cycads exhibit new and, initially, counterintuitive relationships between drought and mechanical resistance that are the opposite from angiosperms, allowing these taxa to use different strategies to diversify across similar climatic gradients.

Drought tolerance has been hypothesized to be a part of a 'slow', persistent strategy (Reich, 2014). Meng *et al.* measured drought tolerance as the leaf turgor loss point (π_{tlp}), or the water potential at which the cells lose turgor pressure and cell walls collapse (Cheung *et al.*, 1975). Turgor loss disrupts water transport and gas exchange and causes the leaves to wilt (Brodribb *et al.*, 2003; Scoffoni *et al.*, 2017). A more negative π_{tlp} indicates greater drought tolerance since turgor loss occurs at a more negative water potential. π_{tlp} is determined by the cell solute concentration, but, across species, a more negative π_{tlp} is generally correlated with greater cell wall stiffness (i.e. a higher modulus of elasticity, ε) (Bartlett *et al.*, 2012). Stiffer walls help maintain cell hydration by providing structural resistance to the changes in cell volume required for water loss (Cheung *et al.*, 1975; Bartlett *et al.*, 2012). This relationship to ε has been hypothesized to link π_{tlp} to the leaf economics spectrum (Salleo and Nardini, 2000; Nadal *et al.*, 2018), since stiffer cell walls are expected to be thicker, and modelling analyses suggest wall thickness is a major driver of the economics spectrum traits (John *et al.*, 2017; Onoda *et al.*, 2017). Increasing wall thickness would increase the leaf dry mass per area (LMA), which increases the mechanical strength of the leaves and, thus, leaf lifespan (Wright *et al.*, 2004; Onoda *et al.*, 2011). However, increasing wall thickness would also reduce the leaf nitrogen content, and potentially impede mesophyll conductance, both of which would reduce the maximum photosynthetic rate (Onoda *et al.*, 2017; Nadal *et al.*, 2018). Together, these relationships would generate the trade-offs between resource acquisition and persistence traits that define the leaf economics spectrum and link this spectrum to π_{tlp}. Mechanical resistance would thus be a fundamental adaptation to dry environments (Salleo and Nardini, 2000; Reich, 2014).

However, support for this hypothesis has been mixed. ε was found to correlate with leaf density (Niinemets, 2001) and cell wall thickness (Peguero-Pina *et al.*, 2017), but not specific leaf area (LMA^{-1}) (Salleo and Nardini, 2000). A more negative π_{tlp} and 'slow' economics traits were both correlated (Zhu *et al.*, 2018) and unrelated (Bartlett *et al.*, 2012) across phylogenetically diverse angiosperms from a wide range of ecosystems. π_{tlp} and economics spectrum traits were also unrelated across co-occurring species from tropical ecosystems (Rosas *et al.*, 2019; Maréchaux *et al.*, 2020) and across a clade of closely related Mediterranean species (Fletcher *et al.*, 2018). Overall, the consensus has been that π_{tlp} can be functionally decoupled from the economics spectrum traits, potentially because different tissues govern leaf hydraulics and photosynthesis (Li *et al.*, 2015), while the correlations observed across species from different ecosystems reflect selection for both resource conservation and drought tolerance by drier environments (Salleo and Nardini, 2000; Nardini, 2022).

Meng and co-workers provide an interesting new perspective on these relationships by showing that drought and mechanical resistance can be negatively correlated, and that strong selection for economics spectrum traits can generate seemingly counterintuitive associations between a higher π_{tlp} and drier environments. The authors measured leaf structure, nutrient content, gas exchange, mechanical strength, construction costs and π_{tlp} for 41 cycad species in a common garden. Previous studies have characterized relationships between the leaf economics spectrum traits in cycads (e.g. Zhang *et al.*, 2015; Marler and Lindström, 2018), and this study extends these findings to mechanics, construction costs and drought tolerance. The authors compared trait correlations across the cycads and woody angiosperm species from similar ecosystems, and tested trait relationships with climate in the cycads' native geographical ranges, to evaluate which traits drove the diversification of the Zamiaceae species from the more primitive Cycadaceae. Across the cycads, greater drought tolerance was significantly associated with thinner leaves, less mechanical toughness and lower construction costs, while these correlations were significant in the opposite direction for the angiosperms. Further, the Zamiaceae diversified into drier environments by increasing leaf

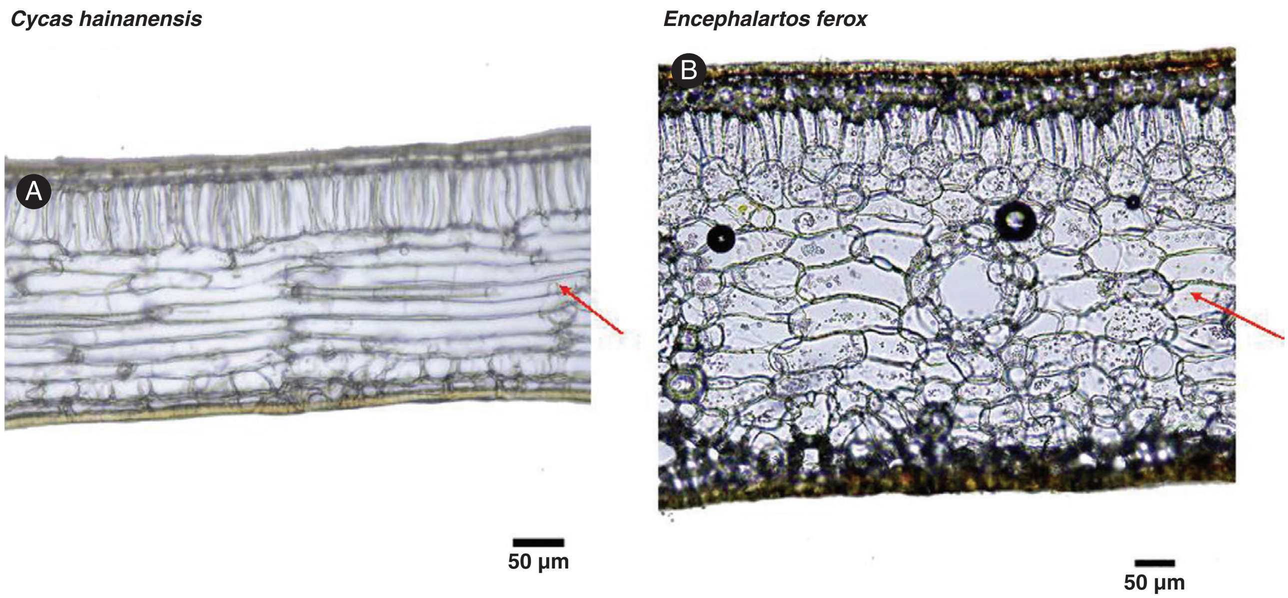

Fig. 1. Representative leaf cross-sections for a Cycadaceae species, *Cycas hainanensis* (A), and a Zamiaceae species, *Encephalartos ferox* (B). Red arrows indicate accessory transfusion tissue. The thicker leaves in the Zamiaceae contain more accessory transfusion tissue, which is important to water transport and storage. Note the differences in scale between A and B. Images provided by the authors of Meng *et al.* (2022).

thickness, and, unexpectedly, π_{tlp}, since these traits were positively correlated. Few studies have compared the role of different leaf traits in species diversification, but these results are contrary to findings for Mediterranean woody shrubs, where the subgenus *Cerastes* diversified from *Ceanothus* into drier environments by evolving more negative π_{tlp}, independently of the economics spectrum traits (Fletcher *et al.*, 2018).

Meng *et al.* suggest that these seemingly counterintuitive results reflect selection for greater succulence in the Zamiaceae. They found that thicker leaves contained a larger cross-section of accessory transfusion tissue (Fig. 1). Transfusion tissue is a universal structure in gymnosperms, while accessory transfusion tissue, which extends between the palisade and spongy mesophyll, is unique to cycads and some *Podocarpus* species (Hu and Yao, 1981). Transfusion tissue is involved in water transport and storage, suggesting thicker cycad leaves contain more dilute, readily water-releasing cells, which would increase π_{tlp}. Consistent with this hypothesis, succulence also increased π_{tlp} in angiosperms (Leverett *et al.*, 2021). Interestingly, in *Taxus*, water stress induced a reversible collapse in the transfusion tissues that acted as a 'circuit-breaker' to stop transpiration before the xylem embolized, analogous to the role of declines in extraxylary conductance in angiosperm leaves (Zhang *et al.*, 2016; Scoffoni *et al.*, 2017). Thus, more vulnerable transfusion tissues could potentially help the Zamiaceae avoid embolism in drier environments.

Altogether, Meng and co-workers show that cycads have fundamentally different patterns in trait coordination and adaptations to dry environments than co-occurring angiosperms, indicating the relationship between drought and mechanical resistance is more complex than a single, universal spectrum across plants. Their findings also highlight the need for more studies within closely related clades to understand the evolutionary drivers of trait coordination.

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