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# Leaf traits and herbivory on deciduous and evergreen trees in a tropical dry forest

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## Abstract

Deciduous and evergreen trees coexist in tropical dry forests, but exhibit distinct leaf syndromes for resource-use efficiency and defenses against herbivores. Moreover, these functional groups may have contrasting patterns of temporal variation in leaf traits and herbivory along leaf ontogeny. We tested these predictions by comparing a set of leaf traits related to water stress and defense, and herbivory levels between young and mature leaves from evergreen leaf-exchanger and deciduous species. We evaluated deciduous and evergreen trees within the same habitat type: a tropical dry forest with 90–100% of leaf deciduousness during the dry season. We sampled 10 individuals of three deciduous and three evergreen species. Evergreen plants had greater leaf thickness and concentration of phenolics and tannins. On the other hand, deciduous plants had higher leaf nitrogen content and specific leaf area. Deciduous plants lost twice as much leaf area by herbivory as evergreen plants (6.48% versus 3.20%), and leaf damage was positively related to both phenolic compounds and nitrogen content. Mature leaves from both phenological groups had higher levels of tannins and phenolic compounds, and lower levels of nitrogen and herbivory increment than young leaves. Our results suggest an adaptive convergence on leaf traits primarily related to water stress for different species within each phenological group. Some of these traits also play a role in leaf palatability, although the fitness consequences of the absolute difference in leaf damage (approximately 3%) between evergreen and deciduous species remain unclear.

## Zusammenfassung

Laubwerfende und immergrüne Baumarten koexistieren in tropischen Trockenwäldern, aber sie zeigen unterschiedliche Blattsyndrome hinsichtlich der Effizienz der Ressourcennutzung und der Verteidigung gegen Herbivore. Darüberhinaus können diese funktionellen Gruppen unterschiedliche Muster der zeitlichen Variation bei den Blattmerkmalen und des Herbivorenfraßes im Laufe der Blattentwicklung aufweisen. Wir testeten diese Vorhersagen durch den Vergleich einer Anzahl von Blatteigenschaften mit Bezug zu Wasserstress und Verteidigung und des Herbivorenfraßes bei jungen und voll entwickelten Blättern von immergrünen Blattwechslern und laubwerfenden Arten. Wir untersuchten solche Bäume im selben Habitattyp, einem tropischen Trockenwald mit 90 bis 100% Blattwurf während der Trockenzeit. Wir beprobten jeweils zehn Bäume von drei laubwerfenden und drei immergrünen Arten. Immergrüne besaßen dickere Blätter und höhere Konzentrationen von Phenolen und Tanninen.

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Laubwerfende Bäume wiesen einen höheren Stickstoffgehalt der Blätter und eine höhere spezifische Blattfläche auf. Blattwerfende Bäume verloren doppelt so viel Blattfläche durch Herbivorenfraß wie die Immergrünen (6.48% gegenüber 3.20%), und die Schäden an den Blättern waren positiv mit dem Gehalt an phenolischen Komponenten und Stickstoff verbunden. Reife Blätter von beiden phänologischen Gruppen wiesen höhere Gehalte an Tanninen und phenolischen Verbindungen und geringere Stickstoffgehalte sowie geringeren Herbivorenfraß auf als junge Blätter. Unsere Ergebnisse legen nahe, dass bei unterschiedlichen Arten innerhalb der beiden phänologischen Gruppen eine adaptive Konvergenz bei den mit Wasserstress verbundenen Blattmerkmalen besteht. Einige dieser Merkmale spielen auch eine Rolle in Hinblick auf die Genießbarkeit, obwohl die Auswirkungen auf die Fitness der absoluten Differenz zwischen immergrünen und laubwerfenden Arten bei den Blattschäden (ca. 3%) unklar bleiben.


***Keywords:*** Evolutionary convergence; Phenological groups; Leaf herbivory; Deciduous forest; Leaf-trait syndromes

## Introduction

Adaptive convergence in defensive leaf traits among different phenological groups has been a well-documented subject in ecological studies in the last decades (Chaturvedi, Raghubanshi, & Singh 2011; Eamus 1999; Mooney & Gulmon 1982). In general, these studies addressed the trade-off in resource allocation between photosynthesis and growth and the investment in defense against herbivores and pathogens (Mooney & Gulmon 1982; Pringle et al. 2011). Several leaf traits can be used to infer adaptation in a selective context, and thus, plant defenses can be approached as multiple attributes (e.g., defense syndromes) that interact synergistically to maximize plant fitness (see Agrawal & Fishbein 2006).

In tropical seasonal terrestrial ecosystems, water stress is a fundamental problem and different adaptive strategies enable both deciduous and evergreen species to colonize such habitats (Eamus & Prior 2001; Franco et al. 2005). Evergreen (drought-tolerant) plants retain their leaves for longer periods and need to be adapted to water conservation during the severe dry season. On the other hand, deciduous (drought-avoiding) plants drop their leaves during the dry season to reduce water loss, and optimize their growth and photosynthesis rates during the rainy season (Eamus & Prior 2001; Tomlinson et al. 2013). The morpho-physiological traits related to such contrasting phenological strategies usually also lead plant species in each group to differ significantly in their resource-use efficiency (e.g., $CO_2$ and nitrogen) (Eamus & Prior 2001; Sobrado 1991). Deciduous species invest less in the production of non-photosynthetic leaf tissues and maintain higher water use efficiency to sustain higher photosynthetic rates per unit of water loss in relation to evergreen species (Eamus 1999; Franco et al. 2005; Sobrado 1991). Thus, it is likely that deciduous and evergreen species in seasonal environments will possess distinct leaf traits related to water use and conservation (Franco et al. 2005; Pringle et al. 2011; Tomlinson et al. 2013).

In terrestrial environments, herbivory is predominantly controlled by bottom-up forces (Coley & Barone 1996; Stiling & Moon 2005), mainly through leaf traits that may converge according to habitat conditions (Powers & Tiffin 2010) and plant functional group (Dirzo & Boege 2008; Pringle et al. 2011). Thus, evergreen and deciduous plants may exhibit different sets of leaf traits primarily related to water stress that also influence herbivory attack. Usually, drought tolerance by evergreen species involves producing leaves with high levels of structural carbon-based compounds (Eamus 1999; Mooney & Gulmon 1982; but see Pringle et al. 2011). On the other hand, drought-avoiding by deciduous species involves producing leaves with lower C/N ratio (Franco et al. 2005; Sobrado 1991). Also, the constant availability of leaves on evergreen plants increases their apparency and risk of being encountered by herbivores. There is evidence that this increased herbivory pressure favored higher investment in structural defenses (e.g., fibers, lignin and high carbon:nitrogen ratio) on evergreen plants in seasonal forests (Dirzo & Boege 2008; Janzen & Waterman 1984), which would be less edible for herbivores compared to deciduous plants (Dirzo & Boege 2008; Pringle et al. 2011).

In tropical dry forests (TDFs), the consumption of plant biomass is performed primarily by insects, which synchronize their life cycles with the production of new leaf tissues by both evergreen and deciduous plants (Pezzini et al. 2014; Villalobos, González-Carcacía, Rodríguez, & Nassar 2013) at the beginning of the rainy season (Dirzo & Domínguez 1995). Regardless of the phenological strategy, foliage nutritional quality usually changes during leaf maturation and senescence, with increasing levels of fiber, phenolics and tannins (Boege 2005; Janzen & Waterman 1984; Silva & Neves 2014) and reduced nitrogen content (Silva, Espírito-Santo, & Melo 2012), resulting in lower consumption of mature leaves. Such variations should be more drastic on long-lived leaves of evergreen species, which persist from the rainy to the dry season and experience the severe and extended water deficits during the dry season and may be forced to even more conservative water use (see Eamus & Prior 2001; Tomlinson et al. 2013). The short-lived leaves of deciduous species only occur during the rainy season and undergo less pronounced seasonal changes along this 4–6 months period.