

## SPOTLIGHT

### NUTRIENT TURNOVER RATES IN ANCIENT TERRESTRIAL ECOSYSTEMS

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The use of nutrients by plants is linked to a variety of processes that scale from individual leaves to ecosystems. Theory and observations support a scaling in plants between nutrient use and growth rate (Reich et al., 2006; Enquist et al., 2007), and nutrient turnover rates have measurable downstream effects on litter decomposition rates (Kobe et al., 2005; Kazakou et al., 2006; Parton et al., 2007) and ecosystem productivity (Garnier et al., 2004). These are in turn linked to population dynamics (Shipley et al., 2006) and regional biogeochemical cycling (Chapin, 2003). All of these correlated properties and processes offer real opportunities to paleobiologists for placing firmer constraints on the operation of ancient terrestrial ecosystems, but until recently there have been few methods for quantifying paleonutrient cycling rates.

Beginning in the 1970s, plant ecologists recognized the correlation of a core set of fundamental leaf traits: plants with high mass-based rates of photosynthesis tend to have high mass-based rates of respiration, high mass-based concentrations of nitrogen and phosphorus, low leaf mass per unit area, and short leaf lifespans (Fig. 1; Small, 1972; Reich et al., 1997; Westoby et al., 2002; Díaz et al., 2004; Wright et al., 2004; Whitfield, 2006). This trait axis represents a continuum of coordinated tradeoffs, whereby species investing in leaves with a high leaf mass per area have low photosynthetic rates but leaves are long-lived, such that their lower revenue of fixed carbon per unit time is compensated by a longer-lasting revenue stream (Reich et al., 1997; Westoby et al., 2002; Wright et al., 2004). This continuum is sometimes called the leaf economics spectrum (Wright et al., 2004) and is one component of a broader ecological continuum that runs from rapid resource acquisition (so called fast-return species) to resource retention (slow-return species; Grime, 1977, 2001; Grubb, 1998). This broader continuum is sometimes called the r-K continuum or C-S-R triangle (Grime, 1977). Importantly, the interrelationships among leaf economic traits are not strongly impacted by phylogeny (Ackerly and Reich, 1999; Wright et al., 2007) or climate. The analysis of a global data set composed of >2500 species from 175 sites found that <20% of the variation in the leaf-economic trait axis could be explained by climate (Wright et al., 2004, 2005).

Because of the coordinated nature of leaf economic traits, knowledge of one trait provides insight into the other traits, as well as interconnected processes in the ecosystem. These linkages provide a critical benefit to paleobiologists, who are often faced with a patchy and difficult-to-interpret fossil record. There are two ways to reconstruct fossil leaf economics. The first is to rely on traits that commonly covary with the central leaf economic traits; examples of secondary traits (Westoby et al., 2002) that are pertinent to paleobiologists include insect herbivory and seed size (Fig. 1). The intensity of insect herbivory is typically highest in fast-return species, because leaves with a high concentration of nitrogen and phosphorus provide more nutrition to insects and are physically easier to eat because they have a low leaf mass per area. Fast-return species also tend to invest less in chemical toxins and other deterrents to herbivory (e.g., Coley, 1983, 1988; Coley et al., 1985; Westoby et al., 2002). Insect herbivory can be measured directly and reliably on most leaf fossils (Beck and Labandeira, 1998; Labandeira, 1998; Wilf and Labandeira, 1999;

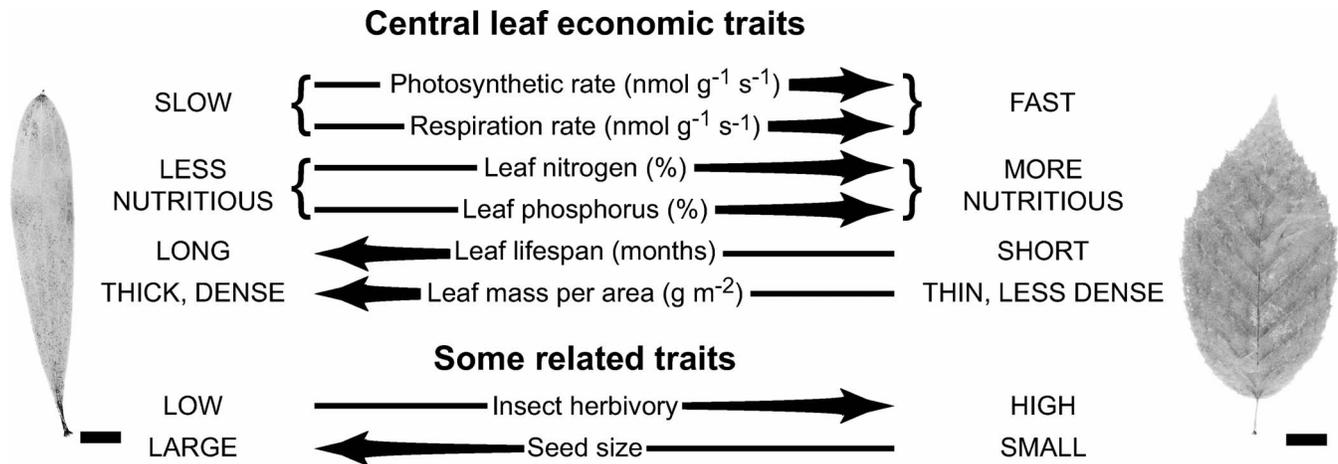
Wilf et al., 2000, 2001, 2005, 2006; Labandeira et al., 2002; Currano et al., 2008). Correspondingly, small, wind-dispersed seeds are common in disturbed, open habitats (Baker, 1972; Salisbury, 1974; Foster and Janson, 1985; Westoby et al., 1992) where fast-return species typically dominate (Grime, 1977, 2001; Garnier et al., 2004); seeds are moderately abundant in the fossil record and their size can usually be measured reliably (e.g., Tiffney, 1984).

The second and more direct way to reconstruct fossil leaf economics is to quantify one of the core leaf economic traits. Unfortunately, none of these traits can be measured directly from fossils (see Fig. 1), and so we must rely on proxies. Extensive leaf mats are commonly interpreted as derived from species with a deciduous leaf habit (leaf lifespan <12 months; Spicer and Parrish, 1986). Comparison to nearest living relatives is sometimes also used to infer leaf lifespan (Chaloner and Creber, 1990). A fundamental drawback to these approaches is that they are qualitative and can discern, at best, deciduous versus evergreen leaf habits; this limits their ability to infer other traits that are linked to the leaf economics spectrum.

Currently, there are two quantitative methods for reconstructing leaf economic traits. The first uses morphological properties of growth rings in fossil wood to reconstruct leaf lifespan (Falcon-Lang, 2000a, 2000b). This technique has been important for deducing leaf lifespan in ancient



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**FIGURE 1**—Coordinated traits related to the leaf economics spectrum. The leaf on the slow-return end of the spectrum (left side) is modern *Hakea dactyloides* (Proteaceae), collected near Sydney, New South Wales, Australia. The leaf on the fast-return end of the spectrum (right side) is *Ostrya virginiana* (Betulaceae), collected in Duke Forest, North Carolina, USA. Note that the petiole for *H. dactyloides* is thicker than for *O. virginiana*, despite its smaller leaf size. Following the scaling relationship of Royer et al. (2007), this implies a higher leaf mass per area for *H. dactyloides*, which is consistent with measured values (*H. dactyloides* leaf = 257 g m<sup>-2</sup>; *O. virginiana* leaf = 24.1 g m<sup>-2</sup>). Scale bar units = 1 cm.

polar forests (Falcon-Lang and Cantrill, 2001; Brentnall et al., 2005), but the technique is prone to error (Falcon-Lang, 2005; Taylor and Ryberg, 2007) and is, by definition, limited to wood with growth rings. Also, current calibrations are restricted to gymnosperm species. More recently, Royer et al. (2007) introduced a method for reconstructing leaf mass per area from fossils. The method is based on the biomechanical scaling between petiole width and leaf mass; heavy leaves require thicker petioles for reasons of support, and vice-versa for light leaves. The two measurements that are required for this proxy are petiole width and leaf area, and these are commonly measurable in leaf fossils. The initial calibration set, from 65 extant sites worldwide, was restricted to woody dicot species, but a small calibration based on broad-leaved gymnosperms showed a similar scaling.

Royer et al. (2007) applied this method to two well-known fossil floras: Republic (Washington, USA; 49 Ma) and Bonanza (Utah, USA; 47 Ma). Republic is dominated by species with low leaf mass per area, whereas Bonanza shows a broader range. Critically, in both floras leaf mass per area and insect herbivory are negatively correlated, which is consistent with the fundamental tradeoffs associated with the leaf economics spectrum (Fig. 1). One implication of these data is that paleonutrient cycling rates were higher at Republic than at Bonanza, at least among woody dicot species (Royer et al., 2007).

Currano et al. (2008) measured insect herbivory and reconstructed leaf mass per area for five fossil floras spanning the Paleocene–Eocene Thermal Maximum (PETM). During the PETM, globally averaged temperatures warmed ~5 °C within ~10<sup>5</sup> years and atmospheric CO<sub>2</sub> levels probably increased three-to-four fold (Zachos et al., 2003). The PETM is thus one of the better fossil analogs for predicting the impacts of future climate change. Levels of insect herbivory on these fossil leaves positively track temperature, reaching their peak during the PETM; these patterns are consistent with present-day observations of insect herbivory being highest in the tropics (e.g., Coley and Aide, 1991). The insect herbivory patterns noted in Currano et al. (2008) are also consistent with the expected effects of CO<sub>2</sub>; i.e., high CO<sub>2</sub> leads to a drop in the C:N ratio of leaves (Luo et al., 2006; Stiling and Cornelissen, 2007), which forces insects to consume a larger volume of leaf tissue (Lincoln and Fajer, 1993; Stiling and Cornelissen, 2007). Importantly, Currano et al. (2008) found no significant differences among sites in leaf mass per area. This result implies that at least some of the interrelationships within the leaf economic spectrum were partially decoupled during the PETM. This decoupling likely led to a reduction during the PETM in the amount of

carbon fixed per unit leaf area integrated over the leaf lifespan (carbon-use efficiency), because the investment of carbon per unit volume of leaf tissue (i.e., leaf mass per area) during the PETM did not change, but the intensity of herbivory increased, resulting in a net loss of potential carbon fixation. This pattern is consistent with the acquisition of carbon being inexpensive in a high-CO<sub>2</sub> world.

Analysis of the paleoeconomics of leaves is still in its infancy, but it may hold a key for understanding fundamental plant and ecosystem processes in the past. Fruitful areas of future investigation include further calibration of proxies in the present day and application to critical intervals of Earth's vegetated history.

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