

## Photosynthetic parameters of diverse woody species in Panama are correlated with foliar nitrogen and phosphorus content

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Phosphorus (P) availability exerts a strong control on the productivity of lowland tropical forests. However, the observed variation in productivity across P gradients is poorly represented in terrestrial biosphere and Earth system models because the models lack routines to estimate P availability and its influence on productivity. While detailed biogeochemical models of P availability are currently being developed, the physiological effect of phosphorus limitation is often represented as a stoichiometric downscaling of GPP, if it is included at all. To inform the development of a physiological model of P limitation, we developed empirical relationships between foliar P content and photosynthetic parameters for tropical trees in Panama. We measured the A-Ci relationship in upper canopy leaves of about 90 woody species at two locations differing in soil fertility and floristic composition. Measurements with LiCor 6400 systems were made from canopy cranes in a seasonally dry forest, Parque Natural Metropolitano near Panama City, and a moist forest, Parque Nacional San Lorenzo near Colon. After determination of leaf area and dry mass, leaves were analyzed for nitrogen (N) and P content at the Smithsonian Tropical Research Institute.

Foliar C:N:P ratios varied widely across species, with N:P ratios ranging from 7 to 42, suggesting that some trees may have been N-limited, some P-limited, and many co-limited by N and P. Vcmax, Jmax, and TPU were correlated with both leaf P and N contents across all species; all relationships were stronger when nutrient contents were expressed on a leaf area basis. From a multivariate perspective the best expression of photosynthetic traits predicted Jmax from both N and P, with Vcmax predicted in relation to Jmax. Nutrient contents and photosynthetic parameters were significantly less at the more nutrient-poor San Lorenzo site, but trees from both sites could be described by the same relationships. Although all of the species measured in this study are classified as the same plant functional type (broadleaf tropical evergreen) in most models, they were taxonomically and functionally diverse. Models may be more accurate if this PFT could be defined more narrowly with nutrient and photosynthetic parameters specific to a well-defined subgroup. However, variation in photosynthetic parameters among species was unrelated to phylogenetic position. Wood density, which may be a surrogate measure of growth rate or successional status, was a significant predictor of Jmax, strengthening the relationship with N and P for a subset of plants for which wood density data were available. Trait covariance may be a useful approach for improving physiological expressions of photosynthesis in nutrient enabled models.