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Commentary

Why do trees adjust water relations and hydraulic architecture in response to nutrient availability?

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Studies on tree water relations, hydraulic architecture and effects of nutrients on growth have been carried out for many years, but not often concurrently. Only recently have the functional relations of these groups of plant traits been investigated with a more integrative approach (e.g. Harvey and van den Driessche 1997, Clearwater and Meinzer 2001, Ewers et al. 2000, 2001, Bucci et al. 2006, Hacke et al. 2010, Faustino et al. 2013). We attempt to answer the question of why the water relations and hydraulic architecture of trees are functionally related to their nutrient availability. We will focus on the results of studies where nutrient limitations have been removed or alleviated by the addition of the two most important macronutrients: nitrogen (N) and phosphorus (P). Plants can grow in soils where nutrient availability is high or in soils where either nitrogen, phosphorus or both chronically limit their growth and development. The response of tree species to the removal of nutrient limitation depends on which nutrient has been limiting. The typical method for assessing nutrient constraints is to fertilize the plants with each nutrient (e.g. N or P), which is expected to limit the growth and/or other plant processes. However, this approach has some drawbacks because it may overlook other factors or resources which are less available and essential for plant growth but which may control the distribution of a species in a given environment. From this point of view, adding N, P or N + P may not result in any significant response if some other resource is the bottleneck for plant growth. We assume that nutrients are the main limiting resources and that factors such as light, water availability, salinity and temperature do not interfere with the response to removal of nutrient limitations.

Nitrogen and phosphorus concentrations in plant biomass are determined by the balance of N and P uptake, carbon assimilation, and the losses of carbon (C), N and P through turnover, leaching, exudation and herbivory (Chapin and Shaver 1989, Aerts and Chapin 2000, Eckstein and Karlsson 2001, Gusewell 2004). Physiological research in temperate and boreal regions has tended to highlight the role of N in plant growth (e.g. Roy and Garnier 1994). Mechanisms determining plant responses to P deficiency have been investigated mainly in agricultural research and tropical forests and savannas (e.g. Bucci et al. 2006). In this issue of *Tree Physiology*, Faustino et al. (2013) has studied trees of *Pinus taeda* L. fertilized with N, P or N + P. They found an increase in growth with P and N + P additions, while with N additions they observed a negative effect on tree growth. Nitrogen fertilization resulted in a substantial decrease in the efficiency of water transport to the leaves, leading to more negative water potential, lower stomatal conductance and a probable reduction of carbon assimilation. Although P fertilization also had an impact on hydraulic architecture, the magnitude of the impact did not result in a decline in leaf water potential or stomatal conductance (Faustino et al. 2013). Opposite or different intensity responses of plant growth and water relation to N or P addition are common in fertilization experiments (e.g. Vitousek and Farrington 1997, Lovelock et al. 2004, Bucci et al. 2006); however, the negative effect of N fertilization on growth is fairly uncommon. This example suggests that there is not a single, predictable response of plants to fertilization with a single nutrient. We focus, in this Commentary, on the positive effect of the removal of all or most nutrient limitations, by N + P fertilization, on plant

growth and its consequences for water relations and hydraulic traits. The most plausible explanation of these relationships is to assume that the chain of causal links is (i) an increase in growth and then (ii) the concomitant adjustments of carbon allocation patterns, wood anatomy, water relations and hydraulic architecture.

Figure 1 depicts the relationship between growth, water relations and hydraulic traits of trees as a function of increasing nutrient availability, produced by continuous N and P fertilizations. To avoid the complexity of the specific responses to fertilization by N or P alone, Figure 1 depicts the response to fertilization with both nutrients. Even though these functional relationships are theoretical, all of them have been corroborated by empirical studies, as outlined in detail below. Not all the references that provide empirical support for these theoretical relationships remove nutrient limitation by N + P fertilization. Some studies included here are the result of a single nutrient addition but only if they found an enhancement of growth rate. Growth rates increase with the removal of nutrient limitation (Figure 1A), a relationship that has been long established in the literature (e.g. Phillips et al. 1999, Ewers et al. 2001, Giardina et al. 2003, Amponsah et al. 2004, Lovelock et al. 2004, Bucci et al. 2006). The decrease in wood density (Figure 1B) is not the direct consequence of the fertilization but a secondary consequence of growth rate. Enquist et al. (1999) derived an allometric model to predict growth rates of tropical trees using wood density as an independent variable and found that there was a trade-off between growth rate and allocation of biomass to tissue density, with species that allocate less biomass to their stems per unit volume (light woods) increasing in basal diameter faster than species that allocate comparatively more biomass to stems (dense woods). The model highlights the central role of allometric scaling and wood density in determining life history traits and the growth rate of trees. Changes in wood density imply variation in anatomical

traits of the wood such as vessel size and density, which directly correlate with the hydraulic properties of water transport systems (e.g. Hacke et al. 2001). A more porous xylem tissue in fertilized plants (e.g. Ewers et al. 1999) will exhibit a more efficient water transport system, that is, a higher hydraulic efficiency. In Figure 1C, higher specific hydraulic conductivity is correlated with increases in nutrient availability (Amponsah et al. 2004, Lovelock et al. 2004, 2006, Bucci et al. 2006). Faster growth rate not only implies faster diameter growth but also a larger gas exchange surface area (e.g. Aber et al. 1989, Phillips et al. 2001, Bucci et al. 2006). Higher carbon fixation capacity per individual has a cost in terms of evaporative water loss that is facilitated by higher hydraulic conductivity, which helps supply water to the transpiring leaves. However, these hydraulic adjustments may not compensate for the large increase in leaf surface area (Ewers et al. 1999; Bucci et al. 2006). In more technical terms, xylem-specific hydraulic conductivity (a measure of intrinsic properties of the stem xylem tissue) substantially increases; however, leaf-specific hydraulic conductivity (a measure of the efficiency of stem water supply per unit leaf surface area) is not sufficiently enhanced to compensate for increases in leaf area. Although stomatal control increases (stomatal conductance decreases) with increasing nutrient availability (e.g. Bucci et al. 2006, Samuelson et al. 2008) (Figure 1D) to avoid larger water losses, this adjustment may be insufficient to prevent an increase in water deficit (water potential becoming more negative) (Figure 1E).

Even though it may appear counterintuitive, because wood density decreases with increasing nutrient availability as a consequence of faster growth rate (Figure 1B), resistance to cavitation is enhanced (Figure 1F, e.g. Harvey and van den Driessche 1997, Ewers et al. 2000, Bucci et al. 2006). Other xylem anatomical characteristics (e.g. pit membranes traits) rather than conduit diameter may be responsible for the

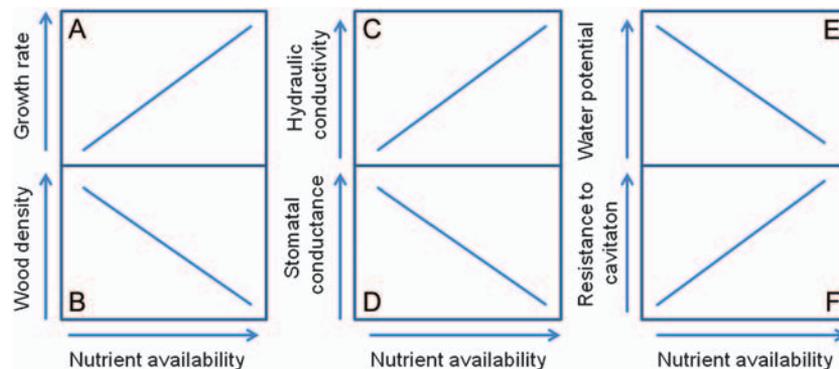


Figure 1. Theoretical relationships between growth rate, water relations and hydraulic traits as a function of variation in nutrient availability produced by N and P fertilizations. The shape of the trait response to decreasing nutrient limitation removal is described in each case as a linear relationship to indicate the trend of the response, either an increase or decrease in the magnitude of the variable with increasing nutrients. The arrow in each axis shows the increases in the level of resources or the direction of the variable change. The Y-axis could have an arithmetic or exponential scale, depending on the shape of the relationship.

avoidance of hydraulic failure (Tyree and Zimmermann 2002, Hacke et al. 2004, Cochard et al. 2009, Jansen et al. 2009). Increases in resistance to cavitation with the removal of nutrient limitation do not imply that fertilized plants are at lower risk of embolism formation. Fertilized plants usually have more negative water potentials; consequently, they may operate closer to the point of catastrophic dysfunction; that is, these plants may have a smaller hydraulic safety margin (Tyree and Sperry 1988).

The functional link between growth rate, wood density and hydraulic architecture has been examined further from a theoretical point of view and using modeling approaches (e.g. Enquist et al. 1999); however, additional empirical studies are needed to clarify the causal links with nutrient availability. Other properties of tree hydraulic architecture should be included in future integrative studies linking nutrient availability with water relations and growth, such as the role of the internal stem water storage and the impact of water uptake and biomass allocation to roots in buffering the effect of nutrient limitation removal on water deficits.

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Conflict of interest

None declared.

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