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The importance of hydraulic conductivity and wood density to growth performance in eight tree species from a tropical semi-dry climate

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ABSTRACT

Understanding how tropical trees coordinate fast growth with water consumption and carbon investment is of high relevance because climate warming may expose tropical forests to increasing stress. Thus, foresters require more information of native tree species envisaged for reforestation. This study examines the relationship between productivity and possibly growth-determining functional traits of xylem anatomy, hydraulic conductivity, foliar morphology and nutrient status in eight tree species in semi-dry Costa Rica; we further assessed the indicative value of wood density for growth rate and hydraulic efficiency. We tested the hypotheses that (i) wood density is related to both growth rate and hydraulic efficiency contrary to findings from moist tropical forests, and (ii) productivity is closely related to branch xylem properties as well as empirically determined hydraulic conductivity in these drought-adapted species. Growth rate was positively related to tree size, foliar nitrogen content, vessel diameter, specific conductivity and leaf water potential, and negatively to vessel density, wood density and $\delta^{13}C$, indicating that fast-growing tree species with light wood possessed a more efficient hydraulic system but closed their stomata relatively early to prevent xylem dysfunction. We conclude, that in tropical semi-dry climates, productivity is closely associated not only with foliar nitrogen but also with wood anatomical and hydraulic properties. Wood density proved to be a reliable indicator for growth-related, wood anatomical and hydraulic traits in these drought-adapted species.

1. Introduction

There is currently much vital debate on the manner in which tropical trees with different growth rates, light demand and stress tolerances coordinate high carbon gain and fast growth, particularly as climate warming may expose many tropical forests to increasing stress in the future (Cramer et al., 2004; Corlett, 2011; Saatchi et al., 2013). This topic is also relevant to tropical foresters seeking to identify suitable tree species for reforestation projects and in plantation forestry. Large-scale deforestation and rising demand for wood products have encouraged many tropical countries to promote reforestation and increase the extent of plantation forests (Umeh et al., 2001; Van Oosten, 2013). Despite the vast diversity of tree species in tropical forests, only a few native species are currently used either individually in plantations or in species mixtures for reforestation projects (Suárez et al., 2012). The limited success of reforestation programs in the tropics may in part result from a lack of appropriate ecological knowledge on native tree species (Craven et al., 2011). The monitoring of certain plant functional traits can prove useful in predicting woody biomass production and plant responses to climate warming (Martínez-Garza et al., 2013; Soudzilovskaia et al., 2013; Lopez-Iglesias et al., 2014).

As a fundamental process supporting growth, carbon assimilation depends on canopy leaf area and leaf photosynthetic activity. Both processes are partly controlled by water and nutrient availability. When plants are supplied with more water, they typically develop greater leaf areas with thinner and larger, physiologically more active leaves, which is also the case when plants are supplied with additional nitrogen (Wright et al., 2004; Poorter et al., 2009). Thus, growth rate is typically linked to water and nutrient availability. A number of recent studies have been conducted comparing photosynthetic capacity and plant water relationships among large tree species samples (e.g. Brodribb et al., 2002; Feild and Balun, 2008; Choat et al., 2011), but the link between direct measurements of growth rates and xylem hydraulic efficiency has

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rarely been empirically investigated (but see Domec and Gartner, 2003; Zhang and Cao, 2009), while field studies relating branch hydraulic properties to biomass accumulation are virtually absent. Although a growing number of studies have revealed a close relationship between hydraulic efficiency and stem growth for mature tropical trees, they were all based on xylem features of the stem base and related hydraulic traits derived from the Hagen–Poiseuille equation (e.g. Poorter et al., 2010; Fan et al., 2012).

Varying water availability leads to adaptive responses in trees' xylem structures managing the flow path from the roots to the leaves (Machado et al., 2007). When water availability is high, wider vessels with higher hydraulic efficiency and thinner cell walls are usually produced, while xylem embolism resistance is decreased (Maherali et al., 2006; Domec et al., 2010; Choat et al., 2012). However, leaf phenology has been found to modify this relationship (e.g. Choat et al., 2005; Choat et al., 2007; Worbes et al., 2013). By shedding their leaves after the onset of the dry season, tropical drought-deciduous tree species follow an isohydric strategy, whereby they produce very large vessels with high hydraulic efficiencies. In contrast, in seasonally dry climates, wood of evergreen tropical tree species following anisohydric strategies is mostly composed of very narrow vessels, resulting in relatively low hydraulic efficiency along with high resistance to cavitation, i.e. the wood can compensate more negative leaf water potentials (Choat et al., 2005). In general, species with an isohydric strategy possess a strong stomatal control and regulate leaf water potential above a certain threshold that depends on their xylem cavitation resistance, whereas anisohydric species tolerate a declining leaf water potential during drought and close their stomata only at immediate risk of cavitation leading to fluctuating leaf water potential (Tardieu and Simonneau, 1998). Water transport efficiency is accordingly limited by the length of the root-to-canopy flow path due to the increasing risk of xylem cavitation with tree height caused by gravity (Mcdowell et al., 2002; Domec et al., 2008). Taller tropical trees are therefore generally more vulnerable to drought than smaller trees (Van Nieuwstadt and Sheil, 2005; Nepstad et al., 2007; Phillips et al., 2010), and they typically control stomatal opening more sensitively in order to prevent excessive water loss and to maintain a favorable leaf water status under the long flow path conditions (Hartmann, 2011).

Wood density is another wood trait often used for characterizing tree functionality due to its relevance to architecture, mechanical support, water storage, efficiency and safety of hydraulic transport, carbon gain and growth rate (King et al., 2006; Chave et al., 2009; Zanne and Falster, 2010). Functional classifications of tropical trees are likewise often based on wood density, because light wood can be related to low construction costs, thereby favoring high growth rates, while dense wood can provide increased biomechanical and hydraulic safety, but at the cost of slow growth (Poorter et al., 2010). Although the expected negative relationship between wood density and growth rate has been found in a number of studies on tropical trees (e.g. King et al., 2006; Poorter et al., 2008; Maharjan et al., 2011; Hietz et al., 2013), the association is often weak (Nascimento et al., 2005; Chave et al., 2009) or even lacking (Russo et al., 2010; Fan et al., 2012). Indeed, it appears that high growth rates among tropical trees depend more on hydraulic properties of the flow path than on wood density, which can be explained by the positive influences that favorable leaf water status and higher transpiration rates have on photosynthesis (Brodribb et al., 2002). Recent work on tropical trees has proven that species with wider vessels and resultant higher hydraulic conductivity in the root-to-leaf flow path generally grow faster than species with smaller vessels (Poorter et al., 2010; Maharjan et al., 2011; Fan et al., 2012). However, studies from tropical moist forests failed to detect any relationship between wood anatomical and derived hydraulic traits and wood density (Poorter et al., 2010; Schuldt et al., 2013). This contradicts the common assumption that hydraulic efficiency and wood density are negatively related to each other (Bucci et al., 2004; Mcculloh et al., 2011; Mcculloh et al., 2012) and indicates that the trade-off between growth rate, carbon investment in the woody tissue measured as wood density as well as hydraulic efficiency are not necessarily inter-related for any given environment. The relationship between wood density and hydraulic efficiency is complicated by the fact that wood density is not only influenced by vessel dimensions and vessel density but by properties of the fibers and surrounding parenchyma cells as well (Fan et al., 2012). Correspondingly, vessel size and pit pore properties have been shown to not necessarily be closely associated with wood density (Russo et al., 2010; Zanne and Falster, 2010). As such, the causal links between wood density, hydraulic properties and productivity are not well understood in tropical trees.

The situation is aggravated by the fact that nearly all reforestations in the tropics are established as monocultures (Kelty, 2006), and the selection of native tree species for reforestation is a continuing challenge (Calvo-Alvarado et al., 2007). This highlights the importance to identify easily accessible plant functional traits as a diagnostic tool to predict growth rates of tree species envisaged for reforestation. This study examines the co-variation of diameter and height growth rates in eight neotropical tree species with largely different juvenile growth rates from semi-dry Costa Rica along with a range of potentially growth-determining functional traits including wood characteristics, hydraulic conductivity, leaf water status, and leaf morphology and nutrient status. The main study aim was to examine the relative importance of wood density versus hydraulic traits for the productivity of drought-adapted tropical tree species. We tested the hypotheses that (i) wood density is related to both growth rate and hydraulic efficiency contrary to findings from moist tropical forests, and (ii) growth rate is closely related to both branch xylem properties and to empirically measured hydraulic conductivity in these drought-adapted species. Our focus was on young trees because their growth performance largely determines the success of tropical reforestation initiatives.

2. Material and methods

2.1. Study site, tree species and microclimatic conditions

The study was conducted in Hatillo in the north-eastern section of Costa Rica's Nicoya Peninsula (Santa Cruz, province Guanacaste, 10°17′17″N, 85°42′46″W) at 44 m a.s.l. in a grassland area covering 2100 m^2. Eight tree species frequently used in the Latin American timber industry were chosen to reforest former cattle pasture land within a fenced plot in July 2006. The species were selected according to the following criteria: (i) commercial value, (ii) affiliation with the indigenous flora, and (iii) representation across a broad range of growth rates from fast- to slow-growing. The seedlings were purchased from a local nursery (Universidad Estatal a Distancia, Centro Universitario de Santa Cruz, CR) and planted in a rectangular grid with 4.5 m spacing between plants (irregular mixing, c. 100 trees in total). The climate of the region is characterized by a dry season lasting from mid-December to April when little or no precipitation falls. Mean annual precipitation in Santa Cruz close to our study site was 1882 mm (26-yr average, Instituto Meteorologico Nacional, San José, Costa Rica), while the mean monthly temperature between 1977 and 2010 was 27.5 °C. Field measurements in the mixed plantation were initiated in the middle of January 2012, about four weeks after the onset of the dry season, and lasted for four weeks. Onsite microclimatic conditions were recorded with three temperature and air humidity sensors (HOBO®