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Climatic influences on leaf phenology, xylogenesis and radial stem changes at hourly to monthly scales in two tropical dry forests

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ABSTRACT

Assessing the effects of climate on leaf phenology and xylem development will improve our understanding of how wood formation and carbon uptake occur in tropical tree species. Wood formation depends on how tree stems enlarge, shrink or swell at multiple temporal scales. To address these issues we analyzed climate data, leaf phenology, xylogenesis and radial increment at hourly to monthly scales of ten tree species in two tropical dry forests with different drought seasonality and severity (the wet Tuluá site is located in Colombia and the dry INPA site is situated in Bolivia). Leaf flushing and radial growth occurred during the wet season at both sites, reflecting the influence of high precipitation, a positive water balance and low vapor pressure deficit on the development of new leaves and xylem cells. In Tuluá, the xylem growing season was associated with low air temperatures, while in INPA it was related to high air temperatures. At both sites, the high air temperatures registered throughout the day negatively affected radial-increment rates at hourly scales, probably by rising vapor pressure deficit and enhancing evapotranspiration rates. Tree species could face adverse dry conditions by growing in periods of the day when temperatures decrease and water loss due to evapotranspiration is reduced, particularly at dry INPA site. Stem shrinkage and swelling were observed at hourly to daily scales in all tree species, but most INPA species also registered strong reversible shrinkage at monthly scales. The strength of the positive association between leaf flushing and radial-increment rates was species-specific and it related to sapwood density. Thus, *Cedrela fissilis*, a pioneer deciduous species with low sapwood density showed the strongest associations between leaf flushing and radial-increment rates, whereas *Acosmium cardenasii*, a shade-tolerant deciduous species showed the reverse characteristic. The time-dependent growth responses of tree species to water availability should be explicitly considered to properly forecast their responses to climate warming and to evaluate their relevance as carbon sinks under warmer and drier conditions.

1. Introduction

The temporal variability of tree growth occurs at different temporal scales and thus can be utilized as an indicator of environmental impacts on tropical forests (Bräuning et al., 2008). However, most of the long-term assessments of growth responses to climate in tropical forests are based on annual tree rings (Rozendaal and Zuidema, 2011; Worbes, 2002). Integrated approaches comparing leaf phenology and radial growth assessed at multiple time scales should allow better understanding how coupled climate and leaf phenology and radial growth are in tropical trees (Camarero et al., 2013; Yáñez-Espinosa et al., 2006).

Tropical dry forests (hereafter TDF) constitute a valuable system to disentangle climate–phenology–growth relationships because (i) they host many coexisting tree species showing different tolerances to water deficit, and (ii) these species experience seasonally contrasting soil moisture availability but respond to water deficit with contrasting phenologies (Bullock et al., 1995; Eamus, 1999).

Abbreviations: DOY, day of the year; Md, manual band dendrometer; Ma, automatic band dendrometer; Mc, microcore; P, precipitation; PET, potential evapotranspiration; P-PET, water balance; T, temperature; TDF, tropical dry forest; VPD, vapor pressure deficit.

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Several mechanisms of drought tolerance have been identified in TDF tree species as different leaf fall behaviors (Borchert, 1999, 1994; Eamus and Prior, 2001) and contrasting seasonal patterns of stem hydraulic conductivity (Brodribb et al., 2002). Changes in stem and bark water storage are also prominent among TDF tree species and depend on wood anatomical features (Poorter et al., 2014; Rosell et al., 2014), which are possibly related to xylem phenology (xylogenesis).

In tropical forests, only few studies have explicitly dealt with the links between leaf phenology and radial growth at intra-annual scales (Coster, 1927; Lisi et al., 2008; Schöngart et al., 2002; Worbes et al., 2013). Particularly, the leaf phenology is tightly coupled to changing water availability and stem water content in TDFs (Borchert, 1994). Therefore, seasonal water deficit should modulate leaf development and senescence in TDF tree species and this influence should translate into different radial-growth rates and xylogenesis. A better knowledge of these relationships would allow understanding long-term growth responses of TDFs to climate warming and drought (Rozendaal and Zuidema, 2011; Worbes, 2002, 1995).

Xylogenesis in tropical trees is determined by seasonal cambial dormancy induced by several environmental stressors including a dry season, flooding or fluctuations in salinity in the case of mangroves (Borchert, 1999; Chowdhury et al., 2008; Schöngart et al., 2002). Usually, the transition from the dormant season to the growing season represents a critical period for understanding the dynamics of stem wood formation in tropical tree species. In the case of TDFs, the duration of the transition from the dry to the rainy season affects xylem growth rates, whilst the onset of xylem growth is related to leaf emergence (Mendivelso et al., 2014).

Here we quantify intra-annual tree growth (xylogenesis) and leaf phenology as related to climate at two TDFs. We analyze if growth and leaf phenology relate to tree species traits (e.g., leaf habit, wood porosity, sapwood density) and drought severity. Our objectives were: (i) to evaluate climate effects on monthly leaf phenology and xylogenesis, (ii) to determine the relationship between four climatic variables (precipitation, temperature, water balance and vapor pressure deficit) and radial-increment dynamics from hourly to monthly scales, and (iii) to assess if leaf phenology, radial increment and tree species traits are linked.

2. Material and methods

2.1. Study sites

Two TDFs subjected to different drought severity were chosen for this study. The wettest site is situated in the "Juan María Céspedes" botanical garden which is located 7 km away from Tuluá (hereafter Tuluá) in an inter-Andean valley in south-western Colombia (4°02′ N, 76°10′ W, 1050–1430 m a.s.l.). It is a 154 ha secondary forest situated over hilly terrain with acid soils (pH = 6.3) containing abundant organic matter (3.1%) in the upper soil layer (depth of 15 cm), where soils are of sandy and sandy-loam textures. This TDF has been undisturbed for the past 44 years. Most of the tree species are semi-deciduous and evergreen. Fabaceae is the dominant family, and the most abundant tree species are *Guazuma ulmifolia* Lam, *Cupania americana* L. and *Guarea guidonia* (L.) Sleumer. The studied forest has 31 tree species ha^{-1} and basal area of 12.4 m^2 ha^{-1} (Adarve et al., 2013).

The driest site is a lowland and deciduous TDF located 32 km away from Concepción in eastern Bolivia (16°07′ S, 61°43′ W, 380 m a.s.l.). It is a private property of INPA PARKET Ltda (hereafter INPA). This site belongs to the Chiquitano forest formation, which is considered one of the largest and most diverse TDF occupying about 16.4 millions of ha in the transition between the Amazonian lowland evergreen rain forest in the north and the Chaco dry scrubland southwards (Killeen et al., 1998). INPA is situated on the Precambrian Brazilian shield and the soils are acid (pH = 5.8), present low organic matter contents (1.4%) in the upper soil layer, and have a sandy-loam texture. The study area is flat to gently sloping. Most of the tree species are deciduous. The studied forest has 34 tree species ha^{-1} and basal area of 19.7 m^2 ha^{-1} (Villegas et al., 2009).

According to climatic data from Tuluá-Farfán (4°06′ N, 76°14′ W, 955 m a.s.l) and Concepción (16°15′ S, 62°06′ W, 410 m a.s.l) meteorological stations, the mean annual precipitation in Tuluá (1317 mm) and INPA (1226 mm) did not significantly differ for the 1984–2011 period (t = −1.49, P = 0.14; see Fig. A1). In contrast, INPA shows a mean temperature (24.0 °C) significantly higher (t = 7.25, P < 0.001) than Tuluá (22.6 °C; see Fig. A1). Therefore, the seasonal distribution of rainfall, drought severity and the relationship between monthly precipitation and temperature differ between sites. Tuluá shows low rainfall records (<60 mm) and negative water balance from June to August, whilst in INPA the driest period normally goes from June to September but the potential evapotranspiration exceeds precipitation from April to October (Fig. A1). The relationship between monthly precipitation and temperature is significantly positive in INPA, but it is negative in Tuluá (Fig. A1). Precipitation in Tuluá was more than twice that recorded in INPA during the study period (July 2010–September 2011) with 42% and 21% of rainy days in the former and latter sites, respectively (Fig. 1).

2.2. Tree species

In total 10 tree species were selected in this study, four species were sampled in Tuluá and six species were sampled in INPA. They belong to six different families and display contrasting crown positions, leaf habit, wood porosity and sapwood density (Table 1). The tree species from Tuluá are widespread tropical taxa [*Cordia alliodora* (Ruiz & Pav.) Oken, *Cupania americana* L., *Pithecellobium dulce* (Roxb.) Benth. and *Zanthoxylum rhoifolium* Lam.]. Two of the six species studied in INPA [*Amburana cearensis* (Allemão) A.C. Sm. and *Cedrela fissilis* Vell.] belong to the red list of threatened tree species (see http://www.iucnredlist.org), whilst one species (*Acosmium cardenasii* H.S. Irwin & Arroyo) is restricted to the Bolivian Chiquitano TDF. The remaining three species are found in other TDFs [*Aspidosperma cylindrocarpon* Müll. Arg., *Aspidosperma tomentosum* Mart., *Centrolobium microchaete* (Mart. ex Benth.) H.C. Lima].

2.3. Links between leaf phenology, radial increment and sapwood density

To reduce the effects of tree size on growth, all trees selected for recording leaf phenology, stem radius variation and xylem formation had similar diameter at 1.3 m (Table 1). Leaf phenology data were registered monthly for 10 individuals per species using binoculars and by calculating the percentage of trees presenting the crown covered by swelling buds, mature leaves or without leaves. We quantified the changes in stem perimeter of the same individuals using manual band dendrometers (DB20, EMS Brno, Czech Republic). In addition, automatic band dendrometers (DRL26, EMS Brno, Czech Republic) were installed in one individual per species to record perimeter changes and air temperatures near the stem at hourly scales. In *Amburana* and *Aspidosperma t.* only 2–3 individuals were monitored using manual band dendrometers. All dendrometers were installed at breast height (1.3 m). A total of 84 individuals were considered in these analyses (Table 1).

Before installing the dendrometers the outer layer of dead bark was carefully removed and then we measured the tree perimeter and diameter at 1.3 m. Manual band dendrometers were read