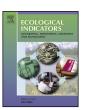
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Tree responses to moisture fluctuations in a neotropical dry forest as potential climate change indicators



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ABSTRACT

Trees in tropical dry forests (TDFs) have manifold drought coping strategies including succulence of different plant organs, wood anatomical traits and leaf phenology. As water availability to plants is the limiting factor for physiological activity, changes in precipitation patterns are assumed to have strong influences on tree phenology, growth and water turnover. Our objectives were to assess patterns in leaf phenology, radial stem circumference changes and sap flux responses to fluctuating moisture regimes of selected species. Based on these findings we evaluated the potential suitability as indicator species for climate change effects. The study was implemented at different elevational positions in a submontane dry forest of southern Ecuador. Annual rainfall is 600 mm with an eight months dry period; moisture availability slightly increases with altitude because of moist air coming from the Pacific. At three altitudes, we studied the tree species Ceiba trichistandra (leaf deciduous, stem succulent), Eriotheca ruizii (leaf deciduous, root succulent) and Erythrina velutina (leaf deciduous). Reversible stem swelling and shrinking was observed for all three species during the whole study period and at all positions at the altitudinal gradient. However, it was most pronounced and sensitive in the stem succulent C. trichistandra and at the lowest (driest) position. C. trichistandra flushed leaves at dry season intermittent rain events, and from dry to wet season leaf out was earlier, and in this period sap flux was high while stem circumference decreased. Length of the leaved periods of all species increased with altitude. Thus, clear differences among species, topographic positions, radial growth and tree water use patterns are revealed; especially C. trichistandra responded very sensitive to fluctuating moisture regimes with leaf phenology, sap flux and stem diameter variations, and can be regarded as a sensitive indicator for assessing climatic variations. © 2016 Elsevier Ltd. All rights reserved.

1. Introduction

Tropical drylands and seasonally dry forests host around 20% of the number of major centers of plant biodiversity and endemism (Maestre et al., 2012; Estrada-Medina et al., 2013). Tropical dry forests (TDFs) are composed of trees exhibiting different drought coping mechanisms, with a majority of deciduous tree species and a small number of evergreens (Bullock et al., 1995). A distinct seasonality in rainfall with the occurrence of a prominent dry season of at least six months duration and monthly mean precipitation below

matic factors vary considerably between regions and tree species across the tropics (Wagner et al., 2014, 2016). Besides regional climate, local site conditions related to topography (e.g. slope angle, exposition, altitude) have an influence on moisture availability for trees. In tropical South America, the Tumbesian dry forests cover a vast territory of approx. 87,000 km² of the equatorial Pacific region of Ecuador and Peru; however, they have thus far received little scientific attention (Espinosa et al., 2011). Previous research in TDFs mainly focused on tree growth dynamics (e.g. Volland-Voigt

et al., 2009, 2011) or succession dynamics and conservation aspects

(Dupuy et al., 2012; Pineda-Garcia et al., 2013; Buzzard et al., 2015).

100 mm is the decisive factor controlling phenological phases, seasonal tree growth rhythms and water consumption of trees (Sayer

and Newbery, 2003; Mayle, 2004; Krepkowski et al., 2011; Spannl

et al., 2016). However, trees' responses to the seasonality of cli-

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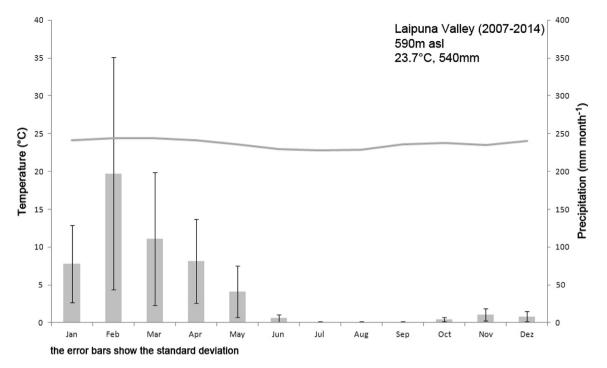


Fig. 1. Climate diagram of the study area.

Detailed knowledge on relations between climatic conditions and tree water-use is scarce (Mendivelso et al., 2016), the same holds true for drought coping mechanisms of co-existing tree species with distinct physiological and phenological traits and resulting tree growth patterns. Such information however is needed to derive better knowledge on the provisioning of ecosystem services, possible climate change-related threats for dry forest ecosystems, and to choose best options for sustainable land use management (Knoke et al., 2014).

Trees growing in drought-stressed environments developed different strategies to cope with seasonal water shortage, like e.g. drought avoiders and drought tolerant species (Gebrekirstos et al., 2006). Tree physiological and wood anatomical traits and phenological behavior determine the degree of water stress experienced by different tree species. Several studies conducted in dry forests examined leaf traits like stomatal conductance, turgor, and water potential (Brodribb and Holbrook, 2003; Brodribb et al., 2003; Bucci et al., 2005; Fu et al., 2012), indicating that plant water use is usually controlled by a combination of plant physiological and architectural traits. Wood saturated water content, which is inversely related to wood density, buffers the impact of seasonal drought, and enables flowering and flushing during the dry season (Borchert, 1994; Stratton et al., 2000). Seasonal changes in stem diameter can thus be used as an in-direct measure of changes in tree water status (Borchert, 1994). Interactions between transpiration, stem water storage and environmental factors result in species-specific patterns of phenology and tree water use (Singh and Kushwaha, 2016), and have a high ecological significance in drought stressed environments. We studied tree responses to seasonal changes and inter-seasonal fluctuating moisture conditions in a dry tropical forest in southern Ecuador. Our objectives were to assess response patterns in leaf phenology, stem diameter variations, tree growth dynamics, and sap flux to fluctuating moisture conditions for different tree species and at different sites. The main aim of our study was to identify tree species that are sensitive indicators for climatic variations throughout the seasons, and which could be used to monitor climate change effects in TDFs.

2. Material and methods

2.1. Study area and tree species

The study was conducted in the Laipuna Forest Reserve in southern Ecuador, which belongs to the Tumbesian dry forest ecoregion. The region is characterized by hilly terrain and altitudes of 600–1450 m asl. Annual precipitation strongly varies interannually and ranges between 350 and 800 mm. Moisture availability increases with elevation due to an increase in precipitation and a decrease of temperature and related atmospheric vapor pressure deficit (VPD). Annual precipitation distribution shows a distinctive dry season from June to December, but even during the rainy season which lasts from January to May, shorter drought periods are common (Pucha Cofrep et al., 2015). Moisture bringing air masses during the wet season originate mainly from the Pacific Ocean, and precipitation events mostly occur during night times (Spannl et al., 2016). Annual mean temperature is 23.7 °C and shows little variability throughout the year.

To study tree responses to climatic and site conditions along an elevation gradient, three study plots were established at altitudes of 670, 860 and 1100 m asl. We selected three tree species (Eriotheca ruizii (K. Schum.) A. Robyns (Malvaceae), Ceiba trichistandra (A. Gray) Bakh. (Malvaceae), Erythrina velutina Willd. (Fabaceae)) that are characteristic for the South Ecuadorian dry forest and belong to the most abundant species. Importance Value Indices (IVI = relative abundance + relative dominance + relative frequency) according to Curtis and McIntosh (1951) were 48.3 for E. ruizii, 37.4 for C. trichistandra, and 24.3 for E. velutina in this forest (Homeier, unpublished). All three species are canopy trees with a large ecological amplitude, only the abundance of *C. trichistandra* decreases towards higher elevation. C. trichistandra and E. ruizii are endemic to the region, whereas E. velutina shows a wider distribution and is commonly used in reforestation projects, e.g. Brazil (Souza et al., 2016). All three species are deciduous but differ in their drought coping strategies, which makes them excellent study objects as indicator species, i.e. E. ruizii is a root succulent, C. trichistandra is a stem succulent, and E. velutina shows a corked bark. C. trichis-

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