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Original article

Optical and morpho-functional traits of the leaves of tree species growing in a mountain cloud forest

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ABSTRACT

The physiological, anatomical and optical leaf properties relative to photosynthetically active (PAR) and ultraviolet (UV-B) radiation were assessed in *Ticodendron incognitum*, *Drimys granadensis*, *Podocarpus matudae* var. *macrocarpus* and *Vaccinium consanguineum*, growing along an elevation gradient (1520–2550 m asl) in a montane cloud forest in México. PAR and UV-B absorptance, transmittance and reflectance, UV-B absorptance by foliar compounds, chlorophylls, carotenoids, leaf nitrogen, leaf mass per area, leaf blades, cuticles, epidermis and parenchymas thickness were measured. PAR absorptance efficiencies were calculated. Among the evaluated morpho-functional traits, the studied species displayed different patterns of variation with elevation. Leaf traits could be explained in part by changes in elevation or the distribution of PAR and UV-B in the elevation gradient. *Ticodendron* and *Drimys* leaf traits were likely determined by two cloud banks located at 1940 and 2380 m. In *Vaccinium*, eight traits were related to elevation and PAR or UV-B. Contrary to this, in *Podocarpus*, most of the nine leaf traits could be explained by only one of these factors. The morphological traits of the studied species were similar to those of species growing in other oligotrophic ecosystems. Significant differences between sun exposed and shade leaves were limited to particular elevations or to particular traits of each species. *Vaccinium* showed more significant differences between sun and shade leaves than did the other species growing along the gradient. The morpho-functional traits measured in *Podocarpus* and *Vaccinium* showed that, some leaf traits did not change linearly with elevation or PAR. At elevation levels where species co-occur, the species ranking with respect to evaluated traits varied from trait to trait. This indicate that each species copes with light and other environmental factors, that vary with elevation, according to its morpho-functional plasticity and susceptibility to these factors; which may determine the distribution of these species along the gradient.

1. Introduction

Montane cloud forests (MCFs) are known for their cloudy weather conditions (Webster, 1995; Cavelier, 1996). In a dry atmosphere, radiation increases with increased elevation (Jones, 1992), but in MCFs, clouds and fog attenuate the increases associated with elevation in photon flux density (PAR, 16%–53%), and modify light quality. In addition, both of these vary in space and time because of the daily and yearly vertical movements (along the elevational gradient) of the cloud banks and fog (Aylett, 1985). These factors and other variables such as nitrogen availability and temperature could affect the CO_2 assimilation rate of the plants (Körner et al., 1986; Bruijnzeel et al., 1993 Kitayama, 1995; Tanner et al., 1998) and could explain why productivity decreases with increased elevation. Nevertheless, low vapor pressure deficits encourage leaf traits that increase light harvesting without significantly affecting the plant's water balance (Poorter et al., 2000).

Plant adaptation and acclimatization to their growing light conditions (photon flux density and quality) are accurately expressed by leaf traits (Lambers et al., 1998; Sims and Gamon, 2002). Therefore, traits linked to light harvest and/or protection of the photosystems should be indicators of the mean light conditions that plants undergo, as well as the response of the species to environmental factors that change with elevation (Richardson et al., 2001; Richardson and Berlyn, 2002; González et al., 2007). MCFs' species are adapted to shade and sunny conditions, which change in space and time in

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response to the dynamic movements of clouds and fog (Cavelier and Goldstein, 1989; Bruijnzeel and Proctor, 1995), and thus, morpho-functional leaf traits might reflect this changing light condition more than the light changes related to elevation do. However, similarly to sun exposed and shade leaves of tropical rain forest species (Poorter et al., 1995), sun exposed and shade leaves of pioneer and primary species of Venezuelan MCF trees growing at 1750 m asl (Poorter et al., 2000) showed significant but reduced differences between them. In these species, photosynthetically active radiation (PAR, 400–700 nm) absorptance is also similar to that found in the shade leaves of species growing in tropical rain forests and in seasonal forests, which also optimize light absorptance by having horizontal leaves with a low specific leaf weight (Bongers and Popma, 1988) and a high chlorophyll mass-based content (Lambers et al., 1998). Consequently, in MCFs where such environmental factors change with elevation, we may expect a reduced, but significant, variation in the morpho-functional leaf traits associated with variations in PAR or other factors such as moisture and temperature that change with elevation and determine nutrient availability.

In general, UV-B increases by 14–18% for each 1000 m of increased elevation (Caldwell et al., 1989; Jones, 1992), but in MCFs, this change may be reduced by the attenuating effects of clouds and fog on UV-B radiation (Dahlback, 1996; Køiskar et al., 2003). Even though levels of UV-B radiation are low, UV-B radiation (280–320 nm) has been reported to determine the leaf traits of MCF species (Bruijnzeel et al., 1993; Flenley, 1995; Rozema et al., 1997). These increases in UV-B are mainly reflected in the leaf traits (Sullivan et al., 1992; Ziska et al., 1992) of plants growing at the highest elevations (Flenley, 1995). Tropical species at high elevations have high concentrations of UV-B absorbing phenolic compounds in the leaves (Robberecht et al., 1980; Barnes et al., 1987; Bruijnzeel et al., 1993; Ziska, 1996). These compounds increase with elevation, as observed in the montane forests of Jamaica (Rozema et al., 1997). Other functional responses related to the increase in UV-B radiation that have been recorded in plants growing in other ecosystems and in the leaves of trees in montane regions are a reduction in plant growth, a decrease in leaf area, and anatomical changes (Tanner and Kapos, 1982; Caldwell et al., 1989; Antonelli et al., 1997). However, nutrient conditions and temperature may also explain either the decreased leaf size or the presence of sclerophyll leaves in plants growing above 2000 m asl.

In the present work, we hypothesized that, irrespective of the cloudy and foggy environment, morpho-functional leaf traits will reflect the increases in PAR associated with elevational gradients. Specifically, photosynthetic pigments (chlorophylls and carotenoids per unit area) and the leaf mass per area will increase. The leaf content of UV-B screening compounds, the cuticle and the epidermis thickness will increase in response to UV-B. PAR and UV-B absorptance will increase with the elevation gradient, but the PAR absorptance efficiencies, defined as PAR absorptance per unit chlorophyll, carotenoid, biomass or leaf thickness, will decrease. To test these hypotheses in an elevational gradient ranging from 1520 to 2550 m asl, we selected three of the most abundant MCF species located in Santa Cruz Tepetotutla, Oaxaca, México with a wide distribution across different elevations (*Vaccinium consanguineum*, *Podocarpus matudae* var. *macrocarpus* and *Drimys granadensis*) and one species with a narrow distribution (*Ticodendron incognitum*).

2. Materials and methods

2.1. Study zone

This study was conducted in the area surrounding Santa Cruz Tepetotutla, a village in the North of the state of Oaxaca, México (17°38′–17°40′ N, 96°32′–96°33′ W). This region has an abrupt topography with slopes between 10° and 50°. The soils are shallow, derived from metamorphic rocks, and have a high content of organic matter. The soils of the upper portion of the toposequence are Podzols, whereas those of the lower portion of the toposequence are Cambisols (Álvarez et al., 2008). Soils are acidic and lack significant amounts of bases and available nitrogen. Total carbon content decreases as the elevation increases (Álvarez et al., 2008).

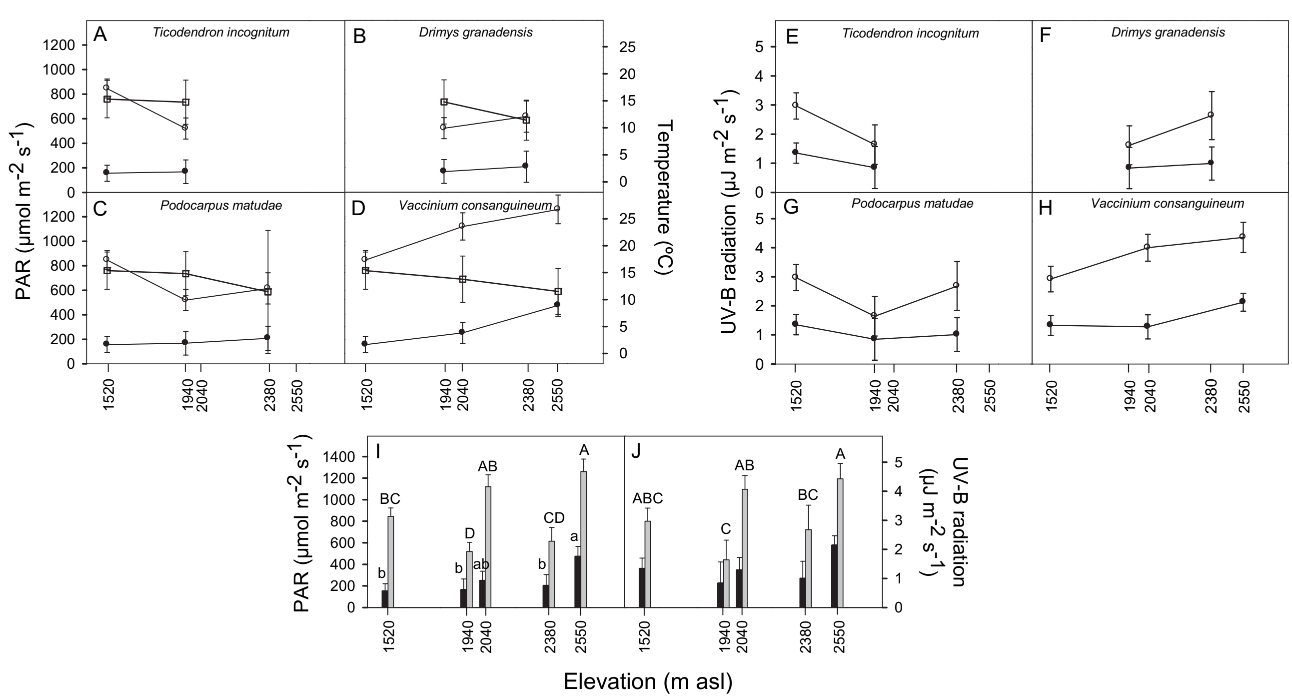

Fig. 1. Mean values (±SE) of environmental data for the elevations where each species was collected. A-D) photosynthetically active radiation (PAR, circles) and temperature (squares). E-H) UV-B radiation. I-J) elevational distribution of PAR and UV-B. Sunny (open circles or gray bars) and cloudy days (closed circles or black bars). Letters indicate significant differences inside seasons, small letters for the rainy season and capital letters for the dry season.