Tree Physiology

Guillermo Goldstein
Louis S. Santiago *Editors*

Tropical Tree Physiology

Adaptations and Responses in a Changing Environment

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Editors
Guillermo Goldstein
Laboratorio de Ecología Funcional,
Departamento de Ecología Genética y Evolución, Instituto IEGEBA (CONICET-UBA), Facultad de Ciencias Exactas y naturales
Universidad de Buenos Aires
Buenos Aires
Argentina

and

Department of Biology
University of Miami
Coral Gables, FL
USA

Louis S. Santiago
Department of Botany & Plant Sciences
University of California
Riverside, CA
USA

and

Smithsonian Tropical Research Institute
Balboa, Ancon, Panama
Republic of Panama

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Functional Diversity in Tropical High Elevation Giant Rosettes

Fermín Rada

Abstract Strong daily temperature variations, seasonal soil water availability and high air evaporative demands play an essential role in adaptive responses of tropical high elevation mountain plants. Giant rosettes are a perfect example of successful adaptations to these conditions, representing an important life-form of high elevation tropical mountains in the Andes, Hawaii and Africa, a well-known case of convergent evolution. Adaptive radiation resulted in a substantially large number of giant rosette species in the 'paramos', a local name given for tropical alpine Andean vegetation. Plant functional responses: plant water relations, gas exchange characteristics and freezing resistance in giant rosettes are described in order to understand their responses to extreme environmental conditions characteristic of high elevation tropical habitats. Giant rosettes have a large capacitance (water-storage pith) and strong stomatal control to cope with periods of water deficit, resulting in the maintenance of high leaf water potentials on a daily and seasonal basis. Maximum net CO_2 assimilation rates are variable among species (3–10 μmol m^{-2} s^{-1}), all showing photosynthetic decreases from wet to dry seasons. Giant rosettes rely on permanent supercooling of the leaves together with insulating structures protecting stems and apical buds to cope with freezing damage. Even though the general aspect and plant morphology of giant rosettes is similar across all high elevation tropical regions, responses to similar selective pressures resulted in different physiological characteristics in freezing resistance mechanisms, e.g. tolerance versus avoidance, and thermal balance of the rosette. Giant rosette responses under changing global environments are also discussed. The emphasis in the description of physiological and morphological characteristics will be on South American giant rosettes due to the large number of studies and the large number of species occurring in this region.

Keywords Gas exchange · Leaf pubescence · Stem capacitance · Supercooling · Water relations

F. Rada (✉)
Instituto de Ciencias Ambientales y Ecológicas de los Andes Tropicales (ICAE)
Facultad de Ciencias, Universidad de Los Andes, Mérida, Venezuela
e-mail: frada@ula.ve

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Introduction

Tropical high mountains are characterized by strong daily temperature variations. Freezing temperatures frequently occur on any night of the year, while high incoming radiation during the day results in relatively high daytime temperatures at plant and soil surfaces. Hedberg (1964) characterized these environments as "summer" during the day and "winter" at night. Daily temperature variations far exceed seasonal ones (Troll 1968; Sarmiento 1986; Rundel 1994).

The páramos are tropical high Andean ecosystems dominated by tussock grasses, sclerophyllous shrubs and giant rosettes. In general, this vegetation type is found above the natural limit of the continuous forest line of the cloud forest (Monasterio 1979; Smith and Young 1987) from approximately 3000 m up to the permanent snow line at about 4600 m. This ecosystem occurs in higher altitudinal regions of Venezuela, Colombia and Ecuador, with minor extensions towards Panamá and Costa Rica to the north and in Northern Perú to the south between latitudes 11° N and 8° S (Monasterio 1980; Luteyn 1992). The páramo has been considered the most floristically diverse and holds the largest number of endemic species of any mountain ecosystem worldwide (Luteyn 1999).

Intense incoming solar radiation has an impact on the plant and/or soil surface thermal balance, increasing risks of rapid heating after nighttime frosts. Precipitation regimes have a wide range of patterns depending on elevation and slope orientation. In the particular case of the Venezuelan Andes, marked seasonal variations with a dry season between December and March occurs. Annual precipitation ranges between 650 mm for the driest to 1800 mm in the more humid Páramos (Sarmiento 1986). In summary, the combination of different environmental conditions of the high tropical Andes determine thermal and water stresses to which plants are constantly exposed (Fig. 1). Higher daytime incoming radiation and night reirradiation during the dry season result in a greater minimum-maximum temperature range generating significant day and nighttime temperature stresses. Increased cloud cover and fog presence during the wet season dampen day-night temperature extremes reducing thermal stresses; however infrequent clear skies may produce similar dry season temperature effects on some occasions. Wet season night temperatures remain relatively high compared to the dry season. In spite of different seasonal temperature patterns, tropical alpine environments present small oscillations in seasonal mean temperatures. In terms of water characteristics, increased cloud cover, fog and precipitation determine favorable soil water conditions and the low evaporative demand during the wet season drastically contrasts with the dry season. Seasonal water stress may be a key factor in plant adaptations to tropical alpine climates.

Even though the physiognomy of the vegetation of the tropical Andean mountains may vary between regions, dominant plant species belong to one of the following growth forms: acaulescent rosettes, cushion plants, tussock grasses, sclerophyllous shrubs or giant caulescent rosettes (Smith and Young 1987; Azócar and Rada 2006). The giant rosettes may be considered the result of particular