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Gas exchange of juvenile and mature trees of *Alnus jorullensis* (Betulaceae) at sites with contrasting humidity in the Venezuelan Andes

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Abstract The reduction of photosynthetic rates with tree age has been proposed as a major driver of the productivity decline along ontogeny. It is not clear, however, how environmental humidity affects stomatal conductance and biochemical potential of photosynthesis in trees belonging to different age-classes. We assessed daily cycles of gas exchange on leaves of juvenile and mature individuals of the tropical high-elevation tree *Alnus jorullensis* Kunth (Betulaceae), at two sites with contrasting precipitation in the Venezuelan Andes. Photosynthesis and stomatal conductance were higher in juvenile trees during the morning and at noon in the mesic site, and were in general similar between age-classes in the wet site. Under light-saturating conditions, the net photosynthetic rate was similar between the age-classes at the wet site and higher for juvenile trees at the mesic site, whereas stomatal conductance did not differ between age-classes and was higher at the wet site. Daily cycles of gas exchange and a type II regression model between photosynthesis and intercellular CO₂ concentration indicated that the better performance of juvenile trees at the mesic site was due to lower non-stomatal limitations. These results support the proposal that non-stomatal limitations—rather than stomatal ones—are

involved in the decay of photosynthesis in mature trees, and suggest that such limitations may be evident only under drier conditions.

Keywords *Alnus* · High altitude · Ontogeny · Photosynthesis · Venezuelan Andes

Introduction

The quest for a universal explanation for the decline of forest productivity during ontogeny has revealed noticeable physiological variation among different aged-trees (Becker et al. 2000; Bond 2000; Thomas and Winner 2002; Mencuccini et al. 2005; Pennisi 2005; Ryan et al. 2006). In many species it has been found that stomatal conductance and photosynthesis decrease with tree age (Yoder et al. 1994; Hubbard et al. 1999; McDowell et al. 2005; Nabeshima and Hiura 2008). The age-dependent photosynthetic decrease has been attributed to the stronger difficulties for water flux that occur with increases in tree height and architectural complexity along with age, which promote lower stomatal conductance for CO₂ diffusion into intercellular spaces (Ryan and Yoder 1997; Bond 2000). Photosynthesis of older trees, however, has been observed to decrease even at relatively high intercellular CO₂ concentrations (Day et al. 2001; Niinemets 2002; but see Delzon et al. 2005), indicating that the biochemical potential for photosynthesis (i.e., non-stomatal limitations) may be constrained with age. Other studies suggest that photosynthetic decay on older trees may be part of a genetically controlled maturation process (Becker et al. 2000; Bond 2000; Day et al. 2001).

The photosynthetic decay along ontogeny is not a universal observation; there is evidence showing that photosynthesis actually increases with age (Cavender-Bares and Bazzaz 2000; Rijkers et al. 2000; Thomas and Winner 2002; Kenzo et al. 2006). From these studies it became evident that ontogenetic variation in the photosynthetic rate is influenced by the environmental

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