

Frida I. Piper · Lohengrin A. Cavieres

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

Received: 27 October 2008 / Accepted: 9 June 2009 / Published online: 16 July 2009
© The Ecological Society of Japan 2009

Abstract The reduction of photosynthetic rates with tree age has been proposed as a major driver of the productivity declination 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

F. I. Piper (✉) · L. A. Cavieres
Departamento de Botánica,
Facultad de Ciencias Naturales y Oceanográficas,
Universidad de Concepción,
Casilla 160C, Concepción, Chile
E-mail: fpiper@udec.cl
Tel.: +56-67-244515
Fax: +56-67-244501

Present address: F. I. Piper
Centro de Investigación en Ecosistemas de la Patagonia (CIEP),
Bilbao 449, Coyhaique, Chile

L. A. Cavieres
Instituto de Ecología y Biodiversidad (IEB),
Casilla 653, Santiago, Chile

conditions experienced by old and young trees. For example, it has been demonstrated that photosynthesis increases with tree age when understory saplings are compared with canopy trees, but these differences disappear if only open-grown saplings are included (Thomas and Winner 2002). Ontogenetic variation in gas exchange also depends on the humidity conditions experienced by different aged-trees. Due to their hydraulic constraints, it is expected that older (i.e., taller) trees close their stomata earlier than younger ones when both age-classes are exposed to a common gradient of soil or air water saturation deficit (Ryan and Yoder 1997), and this has been already found in some temperate coniferous species (Yoder et al. 1994; Hubbard et al. 1999). Nonetheless, stomatal conductance of different aged- and sized-trees of Douglas-fir tend to converge in a similar value as soil or air become drier (McDowell et al. 2005), in spite of a previous study that found that low soil water content imposes stronger hydraulic limitations on older trees when compared to younger ones (Phillips et al. 2002). On the other hand, older trees may offset their hydraulic constraints by accessing deep water sources (Donovan and Ehleringer 1991) or by decreasing the minimal value of leaf water potential needed to maintain it above a critical threshold (Barnard and Ryan 2003), though such compensatory mechanisms are not always enough to avoid the decay in photosynthesis (Yoder et al. 1994; Barnard and Ryan 2003). Non-stomatal limitations of photosynthesis are also expected to be stronger under drier conditions (Chaves et al. 2003), and yet no study has examined ontogenetic variation in non-stomatal limitations under contrasting humidity.

Tropical species might be an adequate model to distinguish the influence of humidity on the physiological variation with tree age. Tropical high-elevation environments are characterized by a lack of seasonal variation in temperature but strong diurnal fluctuations in temperature (Monasterio and Reyes 1980a; Smith and Young 1987). There is a daily variation in humidity closely associated to the variation in temperature. Thus, the effects of humidity variation on photosynthesis of different tree age classes could be adequately inferred from daily cycles in tropical high-elevation plants. In addition, it has been shown that sensitivity of gas exchange to moisture is higher in tropical species than in temperate ones (Park and Furukawa 1999; Cunningham 2004, 2005). Despite the apparent advantages of tropical species in assessing the effect of humidity on the photosynthetic variation with ontogeny, results from these studies have been strongly biased by different light environments on each age class (i.e., closed understory on the smaller tree ages) (Thomas and Winner 2002).

The aim of this study was to assess the ontogenetic variation of photosynthesis of the tropical high-elevation tree species *Alnus jorullensis* Kunth (Betulaceae), examining the influences of environmental humidity under field conditions. We studied daily cycles of gas exchange on leaves of juvenile and mature trees at two

sites with contrasting precipitation in the Venezuelan Andes. The “mesic site” represents the lowest limit of the species distribution along a precipitation gradient, while the “wet site” represents the precipitation level at which this species commonly occurs (Vareschi 1970). In both sites, the two age classes co-occur in open stands without shading effect by canopy trees, implying that the light environment is quite similar between juvenile and mature trees. We hypothesized that photosynthesis should be higher in juvenile trees of *A. jorullensis* than in mature ones, due to lower stomatal and non-stomatal limitations. In addition, these ontogenetic differences in gas exchange should be more evident in the mesic than in the wet site, since hydraulic and biochemical restrictions are likely to be stronger in the drier condition.

Methods

Study species and sites

Alnus jorullensis (Betulaceae) is a monoecious tree that can reach 20–25 m tall and 1.0 m in diameter (Nieto and Rodriguez 2003). This species naturally grows at sites with average annual temperatures of 7–18°C and annual precipitation between 1,000 and 2,500 mm, requiring soils with constant and high humidity content (Vareschi 1970). In the Venezuelan Andes, forests with *A. jorullensis* develop between 2,200 and 3,300 m a.s.l. (Monasterio and Reyes 1980a).

The study was carried out in the Venezuelan Andes, near the city of Mérida, at two sites with contrasting precipitation intensities; (1) a wet site, La Culata (8°42'N, 71°05'W, 2,500 m a.s.l.), with mean annual precipitation of 1,655 mm and mean annual temperature of 13.6°C (Monasterio and Reyes 1980a); and (2) a mesic site, San José de Acequias (8°30'N, 71°12'W, 2,400 m a.s.l.), with mean annual precipitation of 800 mm and a mean annual temperature of 12°C (Monasterio and Reyes 1980a). Mean air temperature of the study sites is fairly constant throughout the year with a difference of ca. 3°C between the hottest and the coldest month (Ataroff 2003). Precipitation regime in both study sites is bimodal. In San José, peaks of precipitations (> 100 mm of rainfall per month) occur between April and June and between October and November, while from July to September rainfall decreases to ca. 40 mm per month (Monasterio and Reyes 1980b). In contrast, peaks of precipitation in La Culata (> 100 mm of rainfall per month) occur between April and June and between September and November, while precipitations remains above 80 mm per month during July and August (Monasterio and Reyes 1980b). The driest season for both sites occur between December and March, with rainfall amounts of ca. 30 mm per month in San José and ca. 40 mm per month in La Culata (Monasterio and Reyes 1980b). To assess differences in gas exchange between mature and young trees of *Alnus jorullensis*, we conducted our measurements between August and

September, which are the months with high differences in rainfall between the two study sites.

On each site, five trees of two age classes were selected; juvenile trees, defined as individuals of <1.5 m tall and ~10 cm of diameter at breast height (DBH, 1.35 m height), and mature trees, defined as individuals of >15.0 m and ~50 cm DBH. Measurements of gas exchange were carried out on each of these selected trees. In both sites the two age classes co-occur in open stands, without presence of closed canopy.

Gas-exchange measurements

Gas exchange was measured on one one-year-old leaf of each of the selected mature and juvenile trees. Selected leaves were located at a similar solar exposition and height (ca. DBH). Daily cycles of net photosynthesis (A), stomatal conductance (g), leaf temperature (T_l), air temperature (T_a), intercellular CO_2 concentration (C_i), external CO_2 concentration (C_a), and photosynthetically active radiation (PAR) were registered every 2–3 h with an infrared gas analyzer (LCA-2 System, The Analytical Development Co. Ltd, Hoddesdon, England). Respiration rate was recorded when PAR was close to zero while photosynthetic rate was recorded when PAR was positive. Diurnal cycles of gas exchange were recorded in both sites during 9–10–11th August, and during 27–28–29th September. In the wet site, the cycle was performed from 0900 hours of one day to 1300 hours of the following day in August, and from 0900 hours of one day to 0800 hours of the following day in September. In the mesic site, the cycle was performed from 1100 hours of one day to 1000 hours of the following day in August, and from 1100 h of one day to 0930 h of the following day in September.

Daily cycles of vapor-pressure difference between leaf and air (VPD) were calculated in each site, from leaf and air temperatures and relative humidity. Leaf temperatures of mature trees ($n = 3$) were measured every 2–3 h with fine-wire copper-constantan thermocouples attached to the lower leaf surface. Air temperatures were measured with copper-constantan thermocouples placed at 1.5 m above the soil surface. Relative humidity was measured with a ventilated wet-dry bulb psychrometer. VPD was calculated from leaf temperatures of mature trees; as leaf temperatures were similar between age classes (see “Results”), we assumed the same VPD for mature and juvenile trees.

Statistical analyses

Repeated measures ANOVAs were used to test for differences in A and g between sites for each age class and sampling date (month). For these analyses, the hours when measurements were taken represented the repeated measure (i.e., within subject factor) (Sokal and Rohlf

1995). Values of VPD between sites were compared by Student’s t -test.

For each site, gas-exchange measurements recorded during times with PAR levels higher than zero were ordered on the following periods: morning (for measurements taken between 0900 and 1130 hours), midday (for measurements taken between 1200 and 1400 hours), and afternoon (for measurements taken between 1500 and 1830 hours). A fourth period of “early morning” was also included for measurements taken at the mesic site between 0700 and 0730 hours. For each period, mean values of A and g were compared between the two age classes by Student’s t -test. Data were \log_{10} -transformed when they were not normally distributed and/or variances were not homogeneous (Sokal and Rohlf 1995). Negative values of A recorded at times where PAR was zero (i.e., night), were analyzed separately to examine respiration rate. In order to examine the global effects of age-class and site on gas exchange, data of A and g recorded at different hours on each site on both sampling dates (August and September) were pooled for each age-class and then compared by a two-way ANOVA—with *age class* and *site* as fixed factors—. To discard a possible masking effect of light-limitation responses of A in this analysis, only records of A and g taken at > 800 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ of PAR were considered.

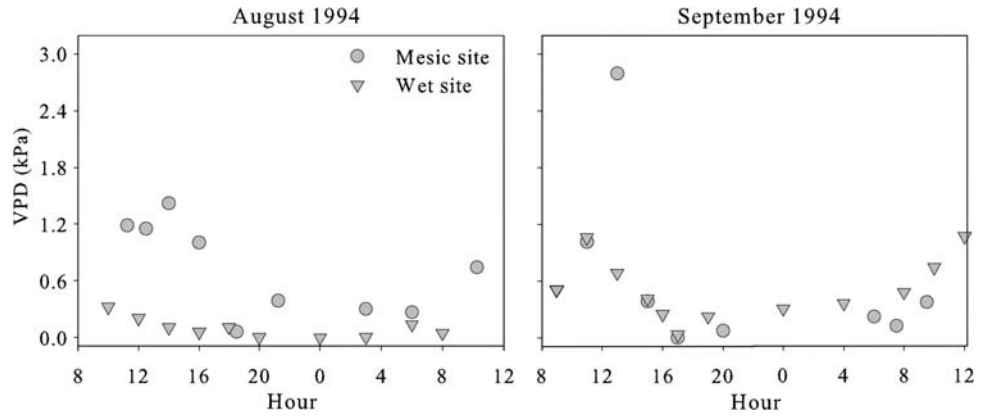
The dependence of A on g and C_i was examined by a linear regression type II fitted for the relationships between A and the other two parameters for each age class in the two sites. Only data taken under a PAR higher than 800 $\mu\text{mol m}^{-2} \text{s}^{-1}$ were included in these analyses, to procure that gas exchange was under light saturating conditions. The statistical package (SMATR (Version 1: Falster DC, Warton DI, Wright IJ; <http://www.bio.mq.edu.au/ecology/SMATR>) was used to examine major axis relationships of A and g in each size class and site, and to test for age-class variation. This package computes standardized major axis (SMA), which is similar to linear regression, although residuals from the regression line are estimated in both the X and Y axes. Linear regression is entirely appropriate for prediction, but is misleading when the purpose is to estimate the line-of-best-fit relating two variables (Falster et al. 2003). In contrast, the SMA analysis is appropriate when the purpose is to estimate the relationship between two variables, usually when the slope of the relationship is of primary interest. For this analysis, g and A were log-transformed in order to normalize distributions, reduce heterogeneity of variance, and improve model fits.

Results

Comparison between sites

Temperature records indicated that the wet site was slightly colder than the mesic one (data not shown) mainly due to the overcast conditions prevailing at the former site. VPD was consistently higher in the mesic

Fig. 1 Daily cycles of vapor pressure deficit at a wet (La Culata) and a mesic site (San José de Acequias) of the Venezuelan Andes during August and September 1994. Values calculated from leaf temperatures on mature trees



than in the wet site only on measurements taken in August (Fig. 1, $t = 3.983$, $P < 0.001$ and $t = 0.326$, $P = 0.748$, for August and September, respectively).

According to daily cycles, A of juvenile trees was higher at the mesic site than at the wet site in both sampling dates (repeated measures ANOVA $F_{1,35} = 120.5$, $P < 0.0001$ and $F_{1,24} = 123.4$, $P < 0.0001$ for August and September, respectively), while in mature trees this occurred only in September ($F_{1,28} = 9.2$, $P = 0.002$). Regarding stomatal conductance, while there were no differences between sites for both mature and juvenile trees during the cycle of September, it was higher and more erratic at the wet site than at the mesic one during the cycle of August in both age-classes (Fig. 2).

Comparison between age classes

Photosynthetic differences between age classes were detected—with the exception of one value—only on the mesic site during the morning and noon periods (times of maximal temperature and PAR; Fig. 2). In this site, photosynthesis in August during the morning was 65% higher in juvenile than in mature trees. In September, photosynthetic rates during the morning and noon were 42 and 36% higher in juvenile trees. The lower values of photosynthesis in large trees at the mesic site occurred concomitantly with higher values of C_i (Fig. 2). In this site, higher stomatal conductance was observed in juvenile trees during the early morning of August and also during the morning, noon, and afternoon in September (Table 1, Fig. 2). At the wet site, only one significant difference between age classes was found; A was slightly higher in mature trees during the morning of August (Fig. 2). In this site, values of A and g were particularly depressed in September likely due to the low PAR associated to cloudy conditions.

Respiration rate differed between age classes only at the wet site in August, when it was 33% higher in juvenile trees ($P = 0.003$). During measurements of the two sampling dates, T_r , T_a , and C_a were almost identical between of age classes.

The analysis of gas-exchange measures excluding possible light-limitations on A (where only data recorded at $> 800 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ were included) showed a significant interaction between *age class* and *site*, indicating that trees of different age classes performed differently depending on the site (Table 2, Fig. 3). Juveniles had higher A than mature trees at the mesic site, while values tended to be similar between age classes at the wet site. Stomatal conductance was similar between age classes, and both age classes had greater g at the wet than at the mesic site (Table 2).

Relationships of A with g and C_i

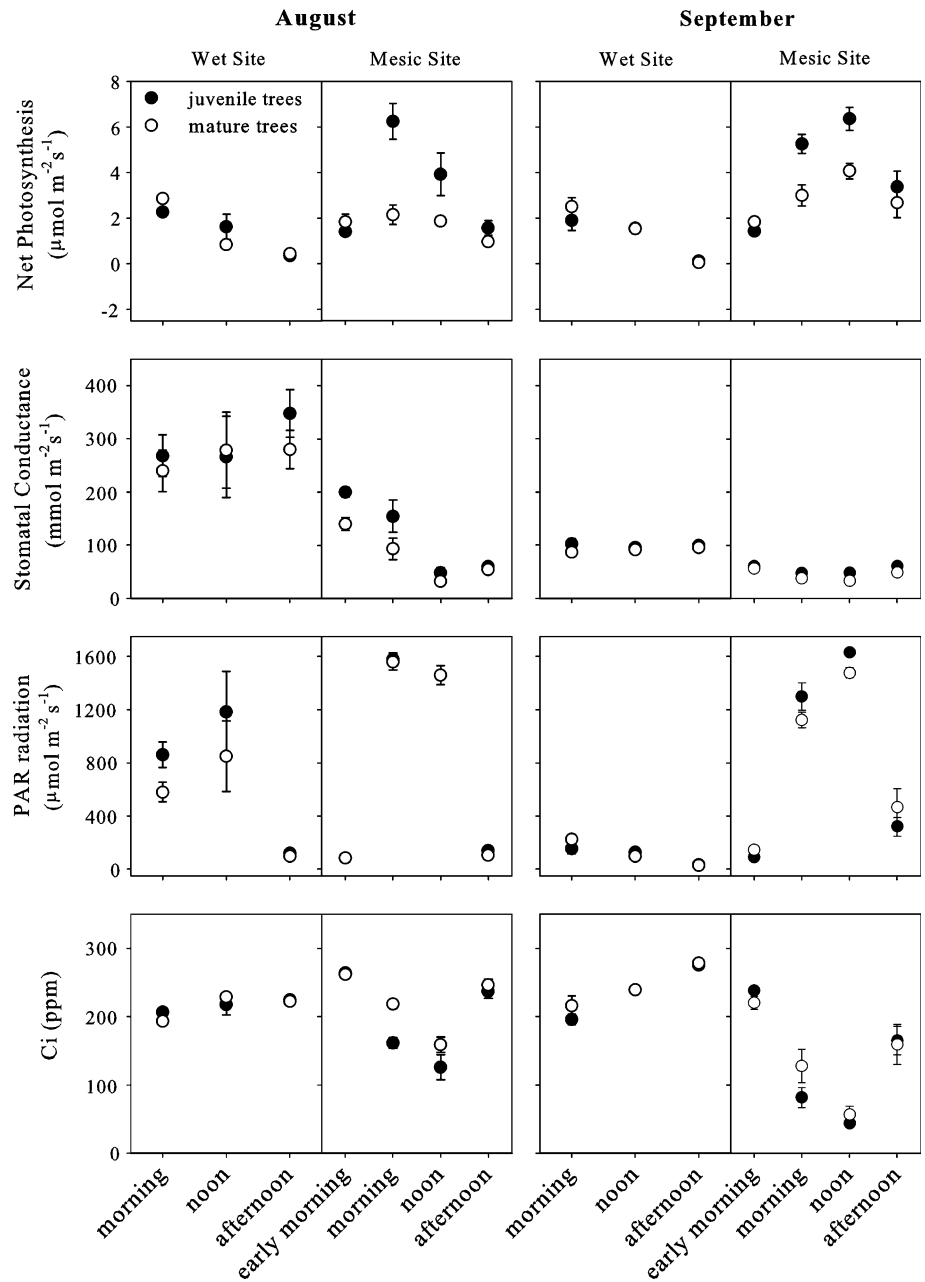
At the wet site, A scaled positively with g in both age classes. Intercepts (i.e., elevations) of the relationship differed between age classes, meaning that for the same value of g , mature trees had higher A . At the mesic site, A scaled positively with g only in juvenile trees (Fig. 4).

Photosynthesis correlated negatively with C_i in both age-classes and sites, indicating that the lowest values of A under light saturating conditions were not associated with limiting CO_2 intercellular concentrations (Fig. 4). In the wet site, intercepts of relationships were similar between age classes. In the mesic site, however, A was higher in juvenile trees when both age-classes were compared at common values of C_i , indicating higher biochemical potential to photosynthesis on that age class.

Discussion

Our study reveals ontogenetic variation in the gas exchange of *Alnus jorullensis* associated to the precipitation regimes of the study sites. Juvenile trees of *Alnus jorullensis* showed higher photosynthesis than mature trees, this difference being only evident at the mesic site (Figs. 2, 3). This pattern was observed even when VPD was very similar between sites (i.e., September, Figs. 1, 2), suggesting that different soil water content associated to the precipitation regimes of each site might promote

Fig. 2 Daily cycles of gas exchange in mature and juvenile trees of *Alnus jorullensis* at a wet (La Culata, 8°42'N, 71°05'W, 2500 m a.s.l.) and a mesic site (San José de Acequias, 8°30'N, 71°12'W, 2400 m a.s.l.) of the Venezuelan Andes during 9–10–11th August 1994 and 27–28–29th September 1994. Data are the average of five replicates. Error bars indicate standard error



the ontogenetic variation in gas exchange. Low PAR in the afternoon and early morning constrained photosynthesis of both mature and juvenile trees. Although in the daily cycles the lower photosynthesis of mature trees at the mesic site occurred—in general—concomitantly with lower stomatal conductance, the absence of a relationship between A and g and the lower intercept in the $A-C_i$ regression suggest that a lower biochemical potential—rather than stomatal limitations—limited the photosynthesis of mature trees in that site (Fig. 4). In addition, the higher C_i of mature trees along with their lower A , especially in those hours when PAR and g were similar between ages, supports the occurrence of non-stomatal limitations to photosynthesis (Fig. 2). The

comparison from pooled data recorded at $> 800 \mu\text{mol m}^{-2} \text{s}^{-1}$, clearly indicates as well that stomatal conductance of mature trees at the mesic site was not the cause of the lower photosynthesis that they showed comparing to juvenile trees (Fig. 3). Although we discard stomatal limitations on the photosynthesis of mature trees, we cannot make extensive this result for all sizes of mature trees. Low stomatal conductance in older trees is associated to physical impediments imposed by a taller tree (Ryan and Yoder 1997), but the relationship between photosynthesis and size may be not linear (Niinemets 2002). In this regard, the tallest trees we sampled were around 35% shorter than the maximum height of the species (Nieto and Rodriguez 2003).

Non-stomatal limitations—such as a decreased maximum photosynthetic capacity—have been demonstrated to contribute in the photosynthesis reduction occurred with the increase of age and size of temperate species such as *Picea rubens* (Day et al. 2001), *Picea abies* and *Pinus sylvestris* (Niinemets 2002). In tropical tree species, however, non-stomatal limitations to

photosynthesis have been found to be actually higher in younger age classes (Rijkers et al. 2000; Kenzo et al. 2006), though such results were influenced by the pervasive closed understory conditions where younger age classes grow (Thomas and Winner 2002). Our results were obtained in open forests where there is no shading effects by canopy trees, suggesting that previous discrepancies in the patterns of photosynthesis along ontogeny between tropical and temperate species may be partly reconciled if differences in the light environment are considered.

At the wet site, photosynthesis during daily cycles was largely depressed in both age classes (Fig. 2). Although PAR was quite lower than in the mesic site, we discard that PAR levels during measurements cycles are related with the depressed photosynthesis at the wet site; photosynthetic rates of August were similar to those of September even when PAR levels were extremely lower at the latter month (Fig. 2). We also discard water deficit as a cause of the low photosynthesis at the wet site, because none of the age classes increased their photosynthesis in response to increased C_i (Fig. 4). Moreover, climatic analyses for La Culata indicate that humidity at this site is not limiting, even at the driest period of the year (Monasterio and Reyes 1980b), which is supported by our records of VPD (Fig. 1). Other factors associated with the high and constant humidity might have limited photosynthesis in the wet site. For example, excessive humidity and occasional water-logging on the root system may promote stomatal closure constraining photosynthesis (Ortuño et al. 2006). The positive relationship between photosynthesis and stomatal conductance at the wet site (Fig. 4) indicates that low values of photosynthesis occurred along with low stomatal conductance, supporting water-logging as a possible cause of the depressed photosynthesis of *A. jorullensis* at the wet site. In addition, the slightly lower temperature at the wet site might have depressed the rates of photosynthesis. Constraints imposed by water-logging or temperature probably hid the higher photosynthetic performance of juvenile trees evidenced at the mesic site.

In conclusion, this study reveals ontogenetic variation in photosynthetic rates of *Alnus jorullensis*. We found higher photosynthesis in juvenile trees than in mature ones, though this difference was only evident at the mesic environment. Thus, the ontogenetic variation

Table 1 Effect of age-class on photosynthetic rate and stomatal conductance of *Alnus jorullensis* at a wet and a mesic site of the Venezuelan Andes, during two sampling dates

		Time of the day	Photosynthesis <i>P</i> -value	Stomatal conductance <i>P</i> -value
August				
Wet site	Morning		0.039	0.623
	Noon		0.150	0.899
	Afternoon		0.258	0.252
Mesic site	Early morning		0.282	0.005
	Morning		< 0.001	0.122
	Noon		0.270	0.230
	Afternoon		0.109	0.344
September				
Wet site	Morning		0.095	0.431
	Noon		0.950	0.638
	Afternoon		0.750	0.667
Mesic site	Early morning		0.126	0.251
	Morning		0.004	0.004
	Noon		0.010	0.005
	Afternoon		0.438	0.037

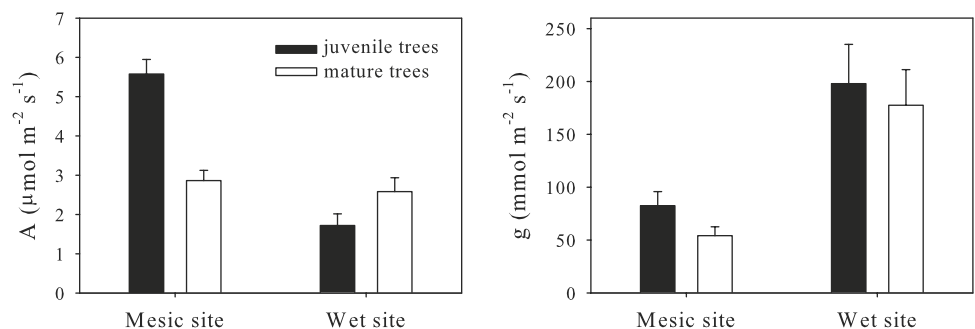
Values shown in the table correspond to *P*-values. Values lower than 0.05 indicate a significant effect

Table 2 ANOVA examining effects of age class and site on photosynthesis and stomatal conductance of *Alnus jorullensis* at the Venezuelan Andes

Response variable	Effect	<i>df</i>	<i>F</i> -ratio	<i>P</i> -value
Photosynthesis	Age class	1	5.96	0.020
	Site	1	29.89	< 0.001
	Age class * site	94	22.29	< 0.001
Stomatal conductance	Age class	1	2.35	0.130
	Site	1	55.22	< 0.001
	Age class * site	94	1.20	0.28

Only data recorded at PAR levels $> 800 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ were analyzed

Fig. 3 Mean photosynthetic rate (*A*) and stomatal conductance (*g*) for juvenile and mature trees of *Alnus jorullensis* at a wet and a mesic site of the Venezuelan Andes. Data are the average of all values recorded at $> 800 \mu\text{mol m}^{-2} \text{s}^{-1}$ of PAR. Error bars indicate standard error



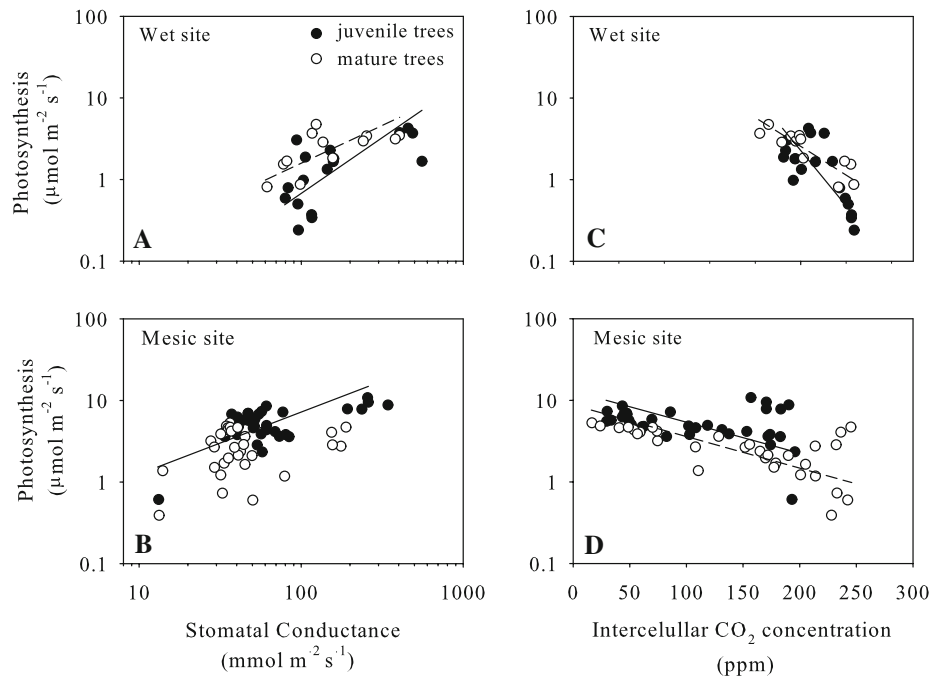


Fig. 4 Photosynthesis versus stomatal conductance (a, b) and intercellular CO₂ concentration (c, d) in juvenile and mature trees of *Alnus jorullensis* at a wet (La Culata) and a mesic site (San José de Acequias) in the Venezuelan Andes. **a** juvenile trees (solid line) $\log y = -2.905 + 1.367 \cdot \log x$, $R^2 = 0.416$, $P = 0.0038$; mature trees (broken line) $\log y = -1.651 + 0.925 \cdot \log x$, $R^2 = 0.417$, $P = 0.023$. Standardized major axes of age classes do not differ significantly in slope ($P = 0.247$) nor along the common slope ($P = 0.324$), but they do in elevation ($P = 0.011$). **b** juvenile trees, $\log y = -0.672 + 0.764 \cdot \log x$, $R^2 = 0.382$, $P = 0.0001$; mature trees, there is no significant relationship between photosynthesis

and stomatal conductance ($P = 0.093$). **c** Juvenile trees, $\log y = 3.751 - 0.017 \cdot x$, $R^2 = 0.547$, $P = 0.0005$; mature trees, $\log y = 2.169 - 0.009 \cdot x$, $R^2 = 0.759$, $P = 0.0002$. Standardized major axes of age classes differ significantly in slope ($P = 0.007$), but not along the common slope ($P < 0.109$) neither in elevation ($P < 0.104$). **d** Juvenile trees, $\log y = 1.11 - 0.0038 \cdot x$, $R^2 = 0.13$, $P = 0.036$; mature trees, $\log y = 0.942 - 0.0039 \cdot x$, $R^2 = 0.424$, $P = 0.001$. Standardized major axes of age classes do not differ significantly in slope ($P = 0.92$), but they do along the common slope ($P < 0.0001$) either the elevation ($P = 0.005$)

in photosynthetic rates likely depend on the humidity condition of the environment, being the soil water content—rather than VPD—the driving factor. Higher photosynthesis in juvenile trees appears to be associated with higher biochemical potential for photosynthesis rather than to stomatal conductance, which is in line with other studies on temperate species (Day et al. 2001; Niinemets 2002).

Acknowledgments We thank Fermín Rada, Marino Cabrera, Gerardo Pérez, Elysaúl Rangel, and David Martínez for their assistance in the field. We appreciated the worthy contribution of the editor and three anonymous reviewers who helped us to significantly improve the manuscript from its early version. This research was supported by the Red Latinoamericana de Botánica (RLB), fellowship P5-1993. Frida I. Piper has a postdoctoral fellowship, Fondecyt 3080057. BBVA Prize for Conservation of Biodiversity in Latin America 2004 is also acknowledged. This paper is part of the research activities of the Institute of Ecology and Biodiversity (IEB) funded by P05-002 F ICM.

References

- Ataroff M (2003) Selvas y bosques de montaña. In: Aguilera M, Azócar A, González-Jiménez E (eds) Biodiversidad en Venezuela. CONICIT-Fundación Polar, Caracas, pp 762–810
- Barnard HR, Ryan MG (2003) A test of the hydraulic limitation hypothesis in fast-growing *Eucalyptus saligna*. *Plant Cell Environ* 26:1235–1245
- Becker P, Meinzer FC, Wullschlegel SD (2000) Hydraulic limitation of tree height: a critique. *Funct Ecol* 14:4–11
- Bond B (2000) Age-related changes in photosynthesis of woody plants. *Trends Plant Sci* 5:349–353
- Cavender-Bares J, Bazzaz FA (2000) Changes in drought response strategies with ontogeny in *Quercus rubra*: implications for scaling from seedlings to mature trees. *Oecologia* 124:8–18
- Chaves MM, Maroco JP, Pereira JS (2003) Understanding plant responses to drought: from genes to the whole plant. *Funct Plant Biol* 30:239–264
- Cunningham S (2004) Stomatal sensitivity to vapour pressure deficit of temperate and tropical evergreen rainforest trees of Australia. *Trees* 18:399–407
- Cunningham SC (2005) Photosynthetic responses to vapour pressure deficit in temperate and tropical evergreen rainforest trees of Australia. *Oecologia* 142:521–528
- Day ME, Greenwood MS, White AS (2001) Age-related changes in foliar morphology and physiology in red spruce and their influence on declining photosynthetic rates and productivity with tree age. *Tree Physiol* 21:1195–1204
- Delzon S, Bosc A, Cantet L, Loustau D (2005) Variation of the photosynthetic capacity across a chronosequence of maritime pine correlates with needle phosphorus concentration. *Ann For Sci* 62:537–543
- Donovan LA, Ehleringer JR (1991) Ecophysiological differences among juvenile and reproductive plants of several woody species. *Oecologia* 86:594–597

- Falster DS, Warton DI, Wright IJ (2003) Standardised major axis tests and routines. <http://www.bio.mq.edu.au/ecology/SMATR>. In, 1.0 edn. Department of Biological Sciences, Macquarie University, Sydney, NSW 2109, Australia
- Hubbard RM, Bond BJ, Ryan MG (1999) Evidence that hydraulic conductance limits photosynthesis in old *Pinus ponderosa* trees. *Tree Physiol* 19:165–172
- Kenzo T, Ichie T, Watanabe Y, Yoneda R, Ninomiya I, Koike T (2006) Changes in photosynthesis and leaf characteristics with tree height in five dipterocarp species in a tropical rain forest. *Tree Physiol* 26:865–873
- McDowell N, Licata J, Bond B (2005) Environmental sensitivity of gas exchange in different-sized trees. *Oecologia* 145:9–20
- Mencuccini M et al (2005) Size-mediated ageing reduces vigour in trees. *Ecol Lett* 8:1183–1190
- Monasterio M, Reyes S (1980a) Diversidad ambiental y variación de la vegetación en los páramos de los Andes Venezolanos. In: Monasterio M (ed) Estudios ecológicos en los páramos andinos. Ediciones de la Universidad de los Andes, Mérida, Venezuela, pp 47–92
- Monasterio M, Reyes S (1980b) Las formaciones vegetales de los páramos de Venezuela. In: Monasterio M (ed) Estudios ecológicos de los páramos andinos. Ediciones de la Universidad de los Andes, Mérida, Venezuela, pp 93–158
- Nabeshima E, Hiura T (2008) Size-dependency in hydraulic and photosynthetic properties of three *Acer* species having different maximum sizes. *Ecol Res* 23:281–288
- Nieto VM, Rodríguez J (2003) Species descriptions. In: Vozzo JA (ed) Tropical tree seed manual. United States Department of Agriculture Forest Service, Washington, DC, pp 292–293
- Niinemets Ü (2002) Stomatal conductance alone does not explain the decline in foliar photosynthetic rates with increasing tree age and size in *Picea abies* and *Pinus sylvestris*. *Tree Physiol* 22:515–535
- Ortuño M, García-Orellana Y, Conejero W, Ruiz-Sánchez M, Alarcón J, Torrecillas A (2006) Stem and leaf water potentials, gas exchange, sap flow, and trunk diameter fluctuations for detecting water stress in lemon trees. *Trees Struct Funct* 20:1–8
- Park SY, Furukawa A (1999) Photosynthetic and stomatal responses of two tropical and two temperate trees to atmospheric humidity. *Photosynthetica* 36:181–186
- Pennisi E (2005) Tree growth: the sky is not the limit. *Science* 310:1896–1897
- Phillips N, Bond BJ, McDowell NG, Ryan MG (2002) Canopy and hydraulic conductance in young, mature and old Douglas-fir trees. *Tree Physiol* 22:205–211
- Rijkers T, Pons TL, Bongers F (2000) The effect of tree height and light availability on photosynthetic leaf traits of four neotropical species differing in shade tolerance. *Funct Ecol* 14:77–86
- Ryan MG, Yoder BJ (1997) Hydraulic limits to tree height and tree growth. *BioScience* 47:235–242
- Ryan MG, Phillips N, Bond BJ (2006) The hydraulic limitation hypothesis revisited. *Plant Cell Environ* 29:367–381
- Smith AP, Young TP (1987) Tropical Alpine plant ecology. *Ann Rev Ecol Syst* 18:137–158
- Sokal RR, Rohlf FJ (1995) Biometry: the principles and practice of statistics in biological research, 3rd edn. W. H. Freeman and Company, New York
- Thomas SC, Winner WE (2002) Photosynthetic differences between saplings and adult trees: an integration of field results by meta-analysis. *Tree Physiol* 22:117–127
- Vareschi V (1970) Flora de los páramos de Venezuela. Ediciones del Rectorado, Mérida, Venezuela
- Yoder BJ, Ryan MG, Waring RH, Schoettle AW, Kaufmann MR (1994) Evidence of reduced photosynthetic rates in old trees. *For Sci* 40:513–527