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Source: Arctic, Antarctic, and Alpine Research, 35(4) : 447-453

Published By: Institute of Arctic and Alpine Research (INSTAAR), University of Colorado

URL: [https://doi.org/10.1657/1523-0430\(2003\)035\[0447:EODPSD\]2.0.CO;2](https://doi.org/10.1657/1523-0430(2003)035[0447:EODPSD]2.0.CO;2)

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Ecophysiology of Dominant Plant Species during Old-Field Succession in a High Tropical Andean Ecosystem

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Abstract

We compared ecophysiological characteristics of plant species that dominate during different stages of succession in fallow fields of a traditional agroecosystem in the Venezuelan High Andes. For each species we determined during the dry and wet seasons the photosynthetic light response and photosynthesis rate at light saturation (A_{\max}), specific leaf area (SLA), stomatal conductance at light saturation (g_{\max}), midday water potential (ψ), and intrinsic water use efficiency (WUE_i , photosynthesis rate per unit of stomatal conductance). The species studied were the forbs *Rumex acetosella* (early succession dominant) and *Lupinus meridanus* (intermediate stages), the shrubs *Acaena elongata* and *Baccharis prunifolia* (late succession), the giant rosette *Espeletia schultzii*, and the shrub *Hypericum laricifolium* (mature ecosystem dominant). Clear ecophysiological trends were identified: early and intermediate successional species had higher A_{\max} , g_{\max} , and SLA but lower WUE_i . *E. schultzii* maintained a high water potential during the dry season and, together with *B. prunifolia*, was the only species with no significant differences in A_{\max} between seasons. The results indicate that traits generally linked to fast growth (high A_{\max} and SLA) are associated with dominance during early succession, while traits linked with drought resistance (e.g., high WUE_i and thick xeromorphic leaves) are associated with dominance during late succession in this tropical mountain environment.

Introduction

In cold and chronically unproductive environments, such as those found in arctic, temperate alpine, and tropical mountain regions, changes in plant community structure during succession tend to be characterized by shifts in relative abundance more than by species replacement, with most dominant species being present from the early stages (MacMahon, 1981; Svoboda and Henry, 1987; Urbanska, 1997; Sarmiento et al., 2003). This pattern of vegetation regeneration is known as *autosuccession* (Muller, 1952).

Tilman (1993) suggested that in unproductive habitats with autosuccessional dynamics, the difference between being an early or late successional species is likely to be due to differences in potential growth rate. Tilman (1993) and Grime (1979) hypothesized that these differences should be the result of trade-offs between maximum leaf area and photosynthetic capacity (allowing early dominance because of fast growth) and other characteristics that confer competitive advantages under limiting conditions (i.e., low temperatures, or deficits in water or nutrients). Common adaptations of late successional species in unproductive habitats include leaf properties such as xeromorphy (e.g., a thick cuticle that reduces potential transpiration) and a high longevity, which allows the conservation and accumulation of nutrients (Grime, 1979). These characteristics have also been found to be associated with a low leaf area per unit leaf mass (specific leaf area [SLA]) and with low herbivore palatability (Brown and Southwood, 1987; Chapin et al., 1996; Grime et al., 1997; Reich et al., 1997; Diemer, 1998; Schippers et al., 1999). All of these properties, which involve higher allocation to traits such as structural carbohydrates, must result in a trade-off with the allocation of resources to photosynthetic capacity and light capturing area per unit leaf mass.

The few available studies from arctic and alpine regions offer conflicting evidence on the ecophysiological differences between early and late successional species (see Bliss and Peterson, 1992, for a review

of the evidence for the Arctic). The expected trend of a successional decline in growth rates and photosynthetic capacity can be inferred by comparing the results of studies in early successional (Stoner and Miller, 1975; Oberbauer and Oechel, 1989) and late successional species (Chapin and Shaver, 1985) in arctic riparian communities, including forbs and shrubs. However, in arctic mire graminoids, no differences in photosynthetic potential were evident between fast-growing pioneer and slow-growing climax species (Miller et al., 1978; Oberbauer and Oechel, 1989). In a study of photosynthetic responses to light of high-altitude forbs in the Alps (Körner and Diemer, 1987) no clear differences were found between pioneer and climax species either in photosynthetic potential or in SLA.

In the alpine context, a decrease in SLA and an increase in xeromorphy are some of the most consistent trends in leaves along altitudinal gradients (Gale, 1973; Woodward, 1983; Körner and Diemer, 1987; Körner et al., 1989). Laboratory and field studies have suggested that the characteristic slow growth rate of alpine species could be associated with their low SLA (Körner and Diemer, 1987; Körner and Pelaez Menendez-Riedl, 1989; Atkin et al., 1996). However, Loveys et al. (2002) have shown that in plants of different life forms and ecosystems, grown at three temperatures, interspecific differences in SLA were not important in determining differences in relative growth rates in the low-temperature treatment (18°C). Hence, for arctic and alpine environments, the available evidence offers an unclear picture of whether differences in growth rates between early and late successional species are associated with differences in their photosynthetic potential and SLA. This relationship is even less clear for high tropical mountain environments in the Andes (locally known as *páramos*), where, to our knowledge, there have been no studies on the comparative ecophysiology of succession.

Tropical high-mountain ecosystems are the only tropical systems subjected to freezing temperatures. They differ from temperate alpine systems in that they show low variability in the yearly cycles of

temperature (but high variability in their daily cycles), so drought becomes the most important seasonal factor (Meinzer et al., 1994). However, they have other characteristics generally found in high mountains such as generally low nutrient availability, low partial pressures of CO₂, and intense ultraviolet radiation (Sarmiento, 1986; Rundel, 1994). This combination of environmental determinants has resulted in the evolution of a unique set of adaptations and the dominance of life forms such as giant caulescent rosettes and sclerophyllous shrubs across the highland tropics (Hedberg and Hedberg, 1979). Their unique environmental conditions and autosuccessional vegetation regeneration (Sarmiento et al., 2003), make tropical high-mountain ecosystems an interesting but largely unexplored environment for evaluating the generality of Grime's (1979) and Tilman's (1993) hypothesis on the ecophysiology of succession in unproductive ecosystems.

Ecophysiological studies in the *páramo* have found an altitudinal increase in xeromorphic characteristics and SLA for the dominant species of the mature ecosystem (Baruch, 1979; Castrillo and Simoes, 1997; Mora-Osejo et al., 1994; Carlquist, 1994; Briceño et al., 2000). In particular, giant rosette species of the *Espeletia* genus have large, thick pubescent leaves and a medullar parenchyma that functions as a water reservoir (Goldstein et al., 1984; Meinzer et al., 1994). These and other attributes of *Espeletia* have been shown to be important in water stress avoidance, the maintenance of a favorable thermal balance, and protection against UV-B radiation (Baruch, 1979; Meinzer and Goldstein, 1984; Monasterio and Sarmiento, 1991; Beck, 1994; Meinzer et al., 1994; Rada et al., 1998; Cross, 2001). However, other growth forms have received comparatively little attention, and their adaptive value is poorly understood (Smith and Young, 1987; Meinzer et al., 1994; Ramsay, 2001).

In this study, we compared some ecophysiological characteristics of the plant species that dominate different successional stages in a traditional fallow system of the Venezuelan high Andes. Based on Tilman's (1993) and Grime's (1979) ideas, we evaluated the following hypothesis: (1) The slow-growing dominant species of late successional and mature *páramo* areas (giant rosettes and sclerophyllous shrubs) should show a lower photosynthesis at light saturation (A_{\max}) and SLA than the species that dominate the early stages (fast-growing forbs); (2) As drought is the most important seasonal factor, dominant late succession species should have a higher water stress resistance than species that dominate during early succession. Hence, they are expected to show less change in A_{\max} , stomatal conductance at light saturation (g_{\max}), and midday leaf water potential between the dry and wet season and to have a higher intrinsic water use efficiency (WUE_i) during the dry season (CO₂ assimilation per unit of stomatal conductance).

The study of successional changes in ecophysiological characteristics of the dominant species is an important step in improving our understanding of the mechanisms that determine the dynamics of vegetation regeneration after human disturbance in these systems, which are being subjected to an accelerated process of anthropogenic degradation and transformation (Luteyn, 1992; Drost et al., 1999).

Methods

STUDY AREA AND LONG-FALLOW AGRICULTURE

This study was carried out in the *Páramo de Gavidia*, situated between 3300 and 3800 m a.s.l. in the Venezuelan Andes (8°35'–45' N, 70°52'–58' W). In the *Gavidia* valley, a long-fallow agricultural system has been practised for more than 100 yr. A short potato cultivation period (1 to 3 yr) is followed by a fallow phase of 4 to more than 10 yr (for details, see Sarmiento et al., 1993). Fallow fields are used for extensive cattle grazing. Long-fallow agriculture for potato production

is one of the most common forms of human disturbance in the tropical Andes, currently sustaining more than 3 million peasants in the region (Ferweda, 1987; Sarmiento et al., 1993; Hervé, 1994).

Gavidia is in a valley of glacial origin with well-drained, stony inceptisols (Ustic Humitropept) of a sandy-loam texture, low pH (4.25 to 5.5), and high organic matter levels (up to 20%) but low mineral nutrient contents (Llambí and Sarmiento, 1998).

The natural vegetation of the area is a rosette-shrubland community dominated by *Espeletia schultzei* Wedd. and *Hypericum laricifolium* Juss. (Monasterio, 1980). The precipitation regime is unimodal, with a dry season between December and March and a peak of rainfall between June and July. Mean annual rainfall between 1990 and 1999 was ~1300 mm, with the wet season representing an average of 93% of total precipitation. During the dry season, soil moisture in the first 20 cm of the soil profile frequently drops below the wilting point (–1.5 MPa; Sarmiento, 2000). Mean annual temperature ranges from ~10°C at 3200 to ~6°C at 3800 m a.s.l. Total radiation shows a unimodal pattern, with maximum levels ~600 MJ m⁻² mo⁻¹ during the dry season and minimum levels ~400 MJ m⁻² mo⁻¹ during the rainy season.

PÁRAMO OLD-FIELD SUCCESSION AND SPECIES SELECTION

The available studies on changes in vegetation structure in these fallow systems in the northern humid Andes of Venezuela and Colombia reveal remarkably consistent patterns. The fast-growing forb *Rumex acetosella* L. (introduced as a weed with wheat cultivation in the 18th century) dominates the early stages of succession and progressively decreases in abundance, being replaced as dominant by the slower-growing characteristic life forms of the mature *páramo*: sclerophyllous shrubs and giant rosettes of the *Espeletia* genus (Ferweda, 1987; Montilla, et al., 1992; Moreno and Mora-Osejo, 1994; Sarmiento et al., 2003).

Based on a study in the same valley analyzing the changes in vegetation structure in 123 fields with different fallow lengths and areas of mature *páramo* (Sarmiento et al., 2003), we selected the six most abundant species of the three life forms that dominate the different seral stages (Table 1). *R. acetosella* is a perennial forb and is the dominant species in the initial stages of succession. It shows a clear tendency to decrease in abundance throughout the fallow; *Lupinus meridanus* Moritz. is a nitrogen-fixing forb. It is present throughout the fallow and shows its peak in the intermediate stages; *A. elongata* L., *Baccharis prunifolia* H.B.K. and *H. laricifolium* are sclerophyllous shrubs; *E. schultzei* is a giant caulescent rosette. These last four species are present from the early stages of succession and continuously increase in abundance (Sarmiento et al., 2003).

ECOPHYSIOLOGICAL MEASUREMENTS

Measurements were taken during the year 2000 in three adjacent fallow fields of different ages: 3, 6, and 12 yr. Fields of longer fallow times are not available in the area. However, Sarmiento et al. (2003) found that the relative abundance of the different life forms attained values after 12 yr of succession very similar to those found in the mature ecosystem, so the restoration of vegetation physiognomy was relatively fast.

All plots were located at ~3450 m a.s.l. Each species was analyzed in the field where it showed its highest abundance.

Gas Exchange

A portable infrared gas analyzer unit was used in the field (LCA-4 System, The Analytical Development Co. Ltd., Hoddesdon, Herts, England) to determine the net rate of CO₂ uptake per unit leaf area,

TABLE 1

Relative abundance and comparative ranking of some ecological traits of the dominant species analyzed here. LWR = Leaf weight ratio (leaf weight per unit plant weight)

Species	Family	Peak biomass ^a (fallow year)	Relative abundance			Leaf morphology ^c	Palatability ^d (cattle)	LWR ^b	Total leaf N ^{b,e}
			at peak ^a (%)	Life form ^b	Life strategy ^{b,c}				
<i>Rumex acetosella</i>	Polygonaceae	2nd	54.4	Forb	Perennial (dry s. as rosette)	Mesomorphic	Intermediate	Low	High
<i>Lupinus meridanus</i>	Papilionaceae	5th	8.8	Forb	Annual (high dry s. mortality)	Mesomorphic	Not consumed	—	High
<i>Acaena elongata</i>	Rosaceae	8th	7.7	Shrub	Perennial evergreen	—	Intermediate	Interm.	Interm.
<i>Baccharis prunifolia</i>	Compositae	12th	23.5	Shrub	Perennial evergreen	Xeromorphic	Not consumed	High	Interm.
<i>Hypericum loricifolium</i>	Guttiferae	Páramo	9.9	Shrub	Perennial evergreen	—	Not consumed	High	Interm.
<i>Espeletia schultzii</i>	Compositae	Páramo	11.7	Giant rosette	Perennial evergreen	Xeromorphic	Low	Very high	Low

^a Sarmiento et al. (2003).

^b Berbesi (1990).

^c Roth (1973), Mora-Osejo et al. (1994), and Briceno et al. (2000).

^d Molinillo and Monasterio (1997) and Perez (2000).

^e Sarmiento, unpublished results.

stomatal conductance to water vapor (g), and light intensity (measured as the photosynthetically active radiation, PAR). Leaves were artificially shaded during measurement in order to change light intensities to construct photosynthesis–light response curves. The photosynthetic response at different radiation levels was measured on different leaves. Three randomly selected fully expanded healthy leaves per plant were measured (a minimum of 15 plants was used in each case) until we obtained a minimum of 45 measurements per species for the light response curve. Measurements were taken on 10 and 17 March for the dry season and on 26 May and 12 June for the wet season on sunny days between 10:30 and 16:30. The light response curves were described using a standard rectangular hyperbola equation (Ceulemans and Saugier, 1991). We present only the light response curves for the wet season, as these curves are intended to show the response of assimilation to variations in PAR levels with the minimum possible interference from water limitations (as is more likely in the dry season). We also present A_{\max} (per unit leaf weight) as the average net assimilation observed at high PAR (above $1200 \mu\text{mol m}^{-2} \text{s}^{-1}$) for both the dry and the wet season (the number of replicate measurements for calculating average A_{\max} varied between 10 and 32) to evaluate the effect of water limitations on photosynthesis. Maximum stomatal conductance (g_{\max}) was calculated in the same way.

Specific Leaf Area

During the wet season, the area of 10 replicate groups of randomly selected healthy-looking green leaves was determined using a LICOR LI 3100 area meter. These leaves were then oven dried for 72 h at 70°C and weighed. The SLA was calculated as the ratio of area per unit leaf mass.

Leaf Water Potential

Midday xylem water potential (ψ) was determined in the field with a portable pressure chamber. Five randomly selected leaves from 5 adult plants per species were measured. Measurements were carried out between 12:00 and 14:00 on 10 March (dry season) and 26 May (wet season).

Intrinsic Water Use Efficiency

The WUE_i was calculated as the ratio of A_{\max} per unit of g_{\max} . This is a more appropriate expression to compare water use efficiency

in CO_2 assimilation between different species than the commonly used quotient of assimilation per unit of transpiration, as it excludes the effect of external factors on transpiration (Osmond et al., 1982).

STATISTICAL ANALYSIS

The SPSS v. 10.0 was used for all statistical analysis. For the comparison of means between species and seasons for A_{\max} , g_{\max} , ψ , and SLA, a nonparametric Kruskal-Wallis test was used because the one-way ANOVA assumptions of homoscedasticity (Levene's test) and normality (Kolmogorov-Smirnov test) were not satisfied. Multiple treatment comparisons were done using Dunnett's C test, which does not assume homoscedasticity.

Results

CARBON ASSIMILATION AND SPECIFIC LEAF AREA

The light response curves showed high light saturation points well above $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ for all species (Fig. 1). *B. prunifolia* and *E. schultzii* showed a lower quantum yield (lower initial slopes) than the rest of the species (statistically significant differences in the estimation of the parameters by least square regression, $\alpha = 0.05$). The high R^2 values obtained on the fit to a rectangular hyperbola (from 0.87 to 0.98) indicate that possible differences in stomatal conductance in the measuring interval did not play a significant role in our analysis of the response of assimilation to light.

A_{\max} rates were higher in the wet season for all species except *B. prunifolia* and *E. schultzii*, which did not show significant differences in photosynthesis between seasons (Fig. 2). In the dry season *L. meridanus* and *R. acetosella* presented significantly higher A_{\max} compared to the rest of the species. In the wet season *R. acetosella* showed the highest average rate, followed closely by *L. meridanus* and then by *A. elongata*, while the late species showed the lowest rates (Fig. 2).

R. acetosella showed the highest SLA, followed by *L. meridanus*. Then, *A. elongata*–*B. prunifolia* and *H. loricifolium*–*E. schultzii* formed two groups with successively lower values (Fig. 3).

WATER RELATIONS

ψ was higher in the wet season for all species except *E. schultzii*, which showed no significant differences between seasons. In the dry

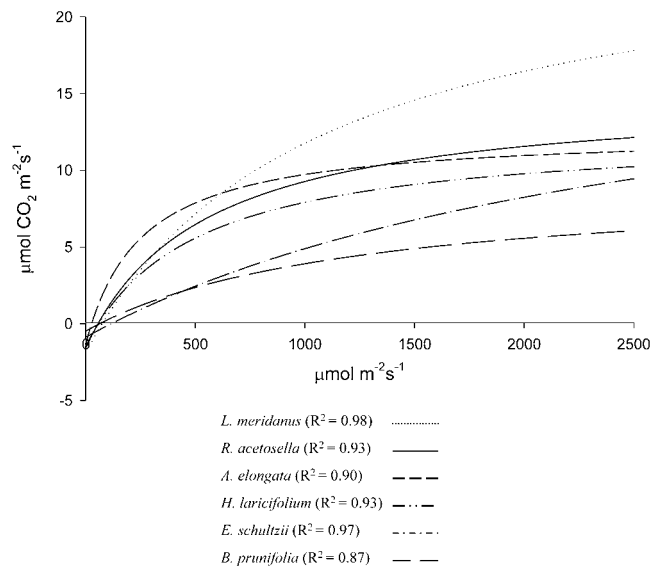


FIGURE 1. Net CO_2 exchange for the wet season ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) as a function of the photosynthetically active radiation (irradiance: $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) as predicted by a rectangular hyperbola model fitted through least squares regression (see R^2 values). The species in the legend appear in the same order as their corresponding light response curve.

season *B. prunifolia* showed the lowest average, whereas *E. schultzi* maintained the highest, with the rest of the species having intermediate values. *E. schultzi* also exhibited the highest potential in the wet season, followed by *R. acetosella* and then the rest of the species (Table 2). Average g_{max} was considerably higher in the wet season than in the dry season for all species. In both seasons g_{max} was much higher in *L. meridanus* than in the rest. *R. acetosella* showed intermediate values, while the late species had lower averages (Table 2). The percent

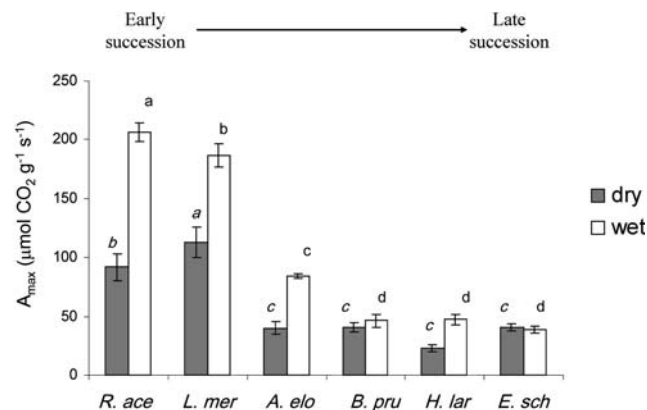


FIGURE 2. Net CO_2 assimilation at light saturation (A_{max}) on a leaf mass basis for the different species shown in the order of peak dominance in succession from left to right: *R. acetosella* (*R. ace*), *L. meridanus* (*L. mer*), *A. elongata* (*A. elo*), *B. prunifolia* (*B. pru*), *H. laricifolium* (*H. lar*), and *E. schultzi* (*E. sch*). Differences between the two seasons are significant for all species (Kruskal-Wallis, $P < 0.001$) except for *B. prunifolia* ($K-W, H_{(1,N=53)}=2.43, P=0.121$) and *E. schultzi* ($K-W, H_{(1,N=52)}=0.63, P=0.426$). Differences in A_{max} between species are significant for both seasons: dry ($K-W, H_{(5,N=145)}=103.96, P < 0.001$) and wet ($K-W, H_{(5,N=99)}=74.93, P < 0.001$). The letters correspond to comparisons between species in the same season. Values with the same letter are not significantly different (Dunnnett's multiple comparison test). Error bars: standard error.

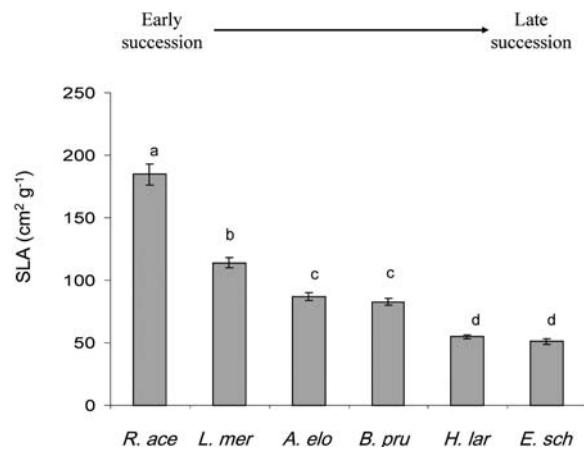


FIGURE 3. Specific leaf area (SLA) of the different species (wet season) shown in the order of peak dominance in succession from left to right (Kruskal-Wallis, $H_{(5,N=60)}=55.20, P < 0.001$): *R. acetosella* (*R. ace*), *L. meridanus* (*L. mer*), *A. elongata* (*A. elo*), *B. prunifolia* (*B. pru*), *H. laricifolium* (*H. lar*), and *E. schultzi* (*E. sch*). Values with the same letter are not significantly different (Dunnnett's multiple comparison test). Error bars: standard error.

reduction in stomatal conductance was lowest in *E. schultzi* (41.2%) and highest in *R. acetosella* (79.3%).

WUE_i in the dry season showed a very clear trend of increasing from the early successional forbs to the late successional shrubs, with the highest value in *E. schultzi* (Table 2).

Discussion

The high light saturation point for all studied species has been recognized as characteristic of alpine plants (Körner and Diemer, 1987). Our values for A_{max} are within the ranges reported by Körner (1999) from an extensive review of the literature for alpine forbs, shrubs, and rosettes, which also showed their mean photosynthetic capacity to decrease in the same order that we found. This suggests that to some extent the lack of consistent successional trends for A_{max} (and also for SLA) in the arctic and alpine literature between pioneer fast-growers and climax slow-growers could be attributable to whether or not the species compared belong to the same life form (see "Introduction"). It is also important to consider that other components apart from SLA and A_{max} , such as whole plant biomass allocation patterns, can influence differences in relative growth rates. Data from Berbesi (1990) in the Venezuelan páramo suggest that the proportion of plant mass allocated to leaves (leaf mass ratio) increases from early to late successional species (Table 1). Hence, the lower assimilation rates per unit leaf mass in the late successional species seems to be partially compensated by a higher plant biomass allocation to photosynthetic tissues.

The successional decrease of A_{max} found in this study is probably associated with the higher nitrogen concentration per unit leaf mass in the dominant early successional species reported by Berbesi (1990) in the Gavidia Valley (see Table 1). Several authors have found the same positive relation between A_{max} and leaf N concentration (Reich et al., 1997).

The clear decrease in SLA from early to late successional species appears to be associated with an increase in xeromorphy in late successional species (Roth, 1973; Mora-Osejo et al., 1994; see Table 1). For example, in *B. prunifolia*, xeromorphic characters include thickened epidermal cell walls covered by cuticle, and water storage in epidermal cells. Some of the suggested roles of xeromorphic traits in páramo shrub leaves are the avoidance of excessive transpiration and

TABLE 2

Means (plus standard errors) for water potential (ψ) and maximum stomatal conductance (g_{\max}) for the dry and wet seasons. The percent reduction in average stomatal conductance between seasons and the intrinsic water use efficiency (WUE_i) for the dry season are also presented. Species appear in the order of peak dominance in succession from top to bottom. Superscript letters (Dunnnett's multiple comparison test): values with the same letter in each column are not significantly different

Species	Water potential (MPa) dry	Water potential (MPa) wet	g_{\max} (mol m ⁻² s ⁻¹) dry	g_{\max} (mol m ⁻² s ⁻¹) wet	Reduction in g_{\max} (%)	WUE_i (A_{\max}/g_{\max}) dry
<i>R. acetosella</i>	-1.45 (0.08) ^a	-0.64 (0.04) ^a	0.12 (0.01) ^a	0.37 (0.07) ^a	79.3	41.4
<i>L. meridanus</i>	-1.58 (0.04) ^a	-0.95 (0.02) ^b	0.27 (0.04) ^b	0.96 (0.14) ^b	71.8	36.4
<i>A. elongata</i>	-1.46 (0.03) ^a	-1.10 (0.02) ^b	0.05 (0.01) ^c	0.11 (0.01) ^c	56.2	90.8
<i>B. prunifolia</i>	-2.32 (0.13) ^b	-1.07 (0.02) ^b	0.05 (0.01) ^c	0.10 (0.01) ^c	46.5	94.0
<i>H. laricoides</i>	-1.61 (0.07) ^a	-1.08 (0.04) ^b	0.03 (0.01) ^c	0.13 (0.01) ^c	76.2	136.3
<i>E. schultzii</i>	-0.58 (0.04) ^c	-0.35 (0.07) ^c	0.04 (0.01) ^c	0.07 (0.01) ^c	41.2	192.4

protection against high UV-B levels (Hedberg, 1964; Smith and Young, 1987; Mora-Osejo et al., 1994). On the other hand, Molinillo and Monasterio (1997) and Perez (2000) found in a study in the Venezuelan páramo that *R. acetosella* and *A. elongata* were relatively more palatable for cattle than *E. schultzii*, while *H. laricifolium*, *L. meridanus*, and *B. prunifolia* were not consumed at all (Table 1). This finding offers some support to the idea that xeromorphy and low SLA could be associated with the resistance of páramo species to grazing by cattle in the fallow fields. The low palatability of *L. meridanus* is likely to be related more to the presence of chemical defense mechanisms than to leaf xeromorphy.

We would expect that in drought-adapted species, photosynthesis would decline less in the dry season (Lambers et al., 1998). This behavior is shown in our study by *E. schultzii* and *B. prunifolia*, with nonsignificant differences in assimilation between both seasons. The maintenance of a stable A_{\max} between seasons and of a high ψ by *E. schultzii* has been reported by other authors (e.g., Goldstein et al., 1984; Rada et al., 1998). While drought-avoidance mechanisms such as the presence of a water storage pith in the stem are of primary importance in *E. schultzii* (Goldstein et al., 1984), in tropical alpine shrubs lacking sufficient water storage capacity, drought-tolerance mechanisms should be expected (Meinzer et al., 1994). Our results showing more reduction in g_{\max} between the two seasons and of lower midday water potential in the dry season in the shrubs than in *E. schultzii* support this idea.

The clear successional increase in WUE_i suggests that late successional species' much lower stomatal conductance could allow them to drastically reduce water loss while reducing assimilation proportionally less than the early successional species (Körner, 1999).

In general, our results show a very clear trend for a successional decline for the dominant species in traits associated with fast growth (SLA and A_{\max}), while traits associated with drought resistance appear to accompany dominance during late succession. These results support Grime's (1979) and Tilman's (1993) ideas (see also Smith and Huston, 1989) on the expected ecophysiological differences between early and late successional species in unproductive environments with autosuccessional dynamics. The differences found in this study between early and late successional species could be the results of two kinds of trade-offs: (1) between the decrease of water losses through stomatal control and the increase of photosynthesis rates and (2) between having a high leaf area per unit leaf mass (and hence photosynthetic leaf area) and allocating a high proportion of leaf mass to xeromorphic characteristics such as a thick cuticle.

The high WUE_i and thick xeromorphic leaves of late successional species are likely to be related to the ability of shrubs and giant rosettes to retain their leaves during the dry season (allowing them to be more effective in nutrient accumulation and to maintain a positive carbon balance throughout the year). In contrast, the annual *L. meridanus* suffers high mortalities during the dry season and individuals of the

perennial *R. acetosella* either die or survive as smaller rosettes (Berbesi, 1990; Briceño et al., 2000; Llambi, unpublished data).

In the functionally diverse environment of the high tropical Andes, different life forms dominate during the different stages of succession, although most dominant species are present from the early stages. Fast-growing forbs such as *R. acetosella* are probably able to dominate during early succession by rapidly exploiting the available resources. A more efficient use of water and a slow but progressive nutrient sequestration in perennial standing phytomass in the characteristic mature páramo life forms could be an important factor in explaining their ability to displace as dominants the early successional species. For a more complete understanding of the processes influencing changes in community structure in páramo old-field succession, we need to evaluate the extent to which these and other ecophysiological differences exist in the large number of other subdominant and rare species, specially within the same life form.

Acknowledgments

We wish to thank O. Atkin, A. Fitter, C. Körner, R. Law, A. Hodge, D. Acevedo, and two anonymous referees for insightful comments on the manuscript. We also wish to thank the technical staff of the ICAE, especially N. Marquez and A. Nieto, for their help during the fieldwork. This work was done within the framework of the TROPANDES Project (European Union INCO-DC Contract No. IC18-CT98-0263). The British Council Chevening Award and the Fundayacucho Foundation provided financial support for L. D. Llambí. Very special thanks to the people of the Páramo de Gavidia in the Venezuelan Andes for their hospitality and for allowing us to work on their farms.

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Ms submitted October 2002