Trait-based studies of páramo vegetation in the northern Andes

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Chapter 5

The role of intraspecific variability in specific leaf area during succession of páramo vegetation in the high Andes

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5.1 - INTRODUCTION

The high Andean grassland vegetation called páramo (Luteyn 1992) represents one of the more species-rich mountain ecosystems in the world (Hughes and Eastwood 2006) and has been categorized as a global biodiversity hotspot (Myers et al. 2000). The páramo vegetation provides crucial environmental services to the Andean people by regulating irrigation and drinking water supply and preventing soil erosion (Buytaert et al. 2005, 2006, Célleri 2009, Hofstede al. 2003). These services are increasingly under threat by encroaching agriculture, overgrazing and global warming (Andrade et al. 2010, Bradley et al. 2006, Tovar et al. 2012, Vuille et al. 2003). For centuries, subsistence agriculture and extensive livestock grazing have been traditional components of the páramo ecosystem (Monasterio and Molinillo 2003). However, because of the intensification and the upward expansion of agriculture and cattle grazing related to climate change (Hofstede et al. 2014), fallow periods are often too short to allow for the adequate recovery of páramo vegetation, and large tracts of páramo vegetation are being converted into pastures composed of introduced grasses. For example, between 1998 and 2007 in the Andes of northern Peru, 25% of the natural Jalca vegetation in the Peruvian Andes was lost to expansion of agriculture, forest plantation and mining (Tovar et al. 2013). As a consequence of this trend, páramo vegetation is increasingly found in a state of succession after being disturbed by burning, plowing, charcoal production, or cattle grazing. Yet, our knowledge of the mechanisms of páramo succession is only based on a handful of quantitative studies.

In the northern Andes páramo succession after disturbance by long-fallow agriculture has been studied locally near Bogotá (Colombia) and Merida (Venezuela) (Abreu et al. 2009, Jaimes and Sarmiento 2002, Llambí et al. 2003, Moreno and Mora-Osejo 1994, Sarmiento et al. 2003). This succession was characterized by an early increase in species richness (within 12 yr 90% of the species richness of natural páramo was recuperated) with the youngest stages typically containing introduced annual and perenial forb species (e.g., *Rumex acetosella*), which disappear at later stages. Furthermore, late-successional phases showed an increased richness of species and growthforms specialized to protect meristems and capture nutrient that are slowly liberated from decomposition (Abreu et al. 2009, Llambí and Sarmiento 1998). Sarmiento et al. (2003) noticed that páramo succession is mostly a matter of changing relative abundances of species present from the start of the succession (Complete initial floristic composition; Egler 1952), instead of the successive appearance and disappearance of species. They explained the low species turnover during páramo succession by assuming that late-successional species possessed a set of life history properties (vital attributes according to Noble and Slatyer 1980, see also Vargas 1996) that would allow them to survive early successional conditions as juveniles (i.e., to pass filters imposed at early successional stages; Jung et al. 2010) and to gain dominance in advancing successional stages. Support for the hypothesis that trait variability between species drives páramo succession was given by Llambí et al. (2003), who studied ecophysiological traits of six plant species characteristic for early-, mid-, and late-successional stages of old-field páramo succession at 3200 m in the páramo near Merida, Venezuela. In line with successional theory (Grime 1979, Huston and Smith 1987, Tilman 1993), they observed that traits linked to fast growth (photosynthesis rate a light saturation and specific leaf area) were associated to species dominance in young fallows, while values for traits linked to drought resistance (intrinsic water use efficiency and leaf thickness) were high among species in older fallows. Thus, inversely correlated traits (Huston and Smith 1987) drive mechanisms of old-field or long-fallow páramo succession: fast growing forb species are dominant in early stages by efficiently exploiting available resources, whereas late-successional species, which are present from the early stages on become dominant in later stages by optimizing efficient water use and nutrient sequestration in perennial plant and soil microbial biomass (Abreu et al. 2009, Hervé 1994, Llambí et al. 2003, Llambí and Sarmiento 1998, Sarmiento and Bottner 2002, Sarmiento et al. 2003).

The aim of the study here presented is to examine how intraspecific trait variability might contribute to páramo succession. Intraspecific trait variability represents the trait plasticity of a species induced by genetic or environmental variabilities (Albert et al. 2011). It can be seen as measure to quantify how a species diversifies its potential niche space through trait variation in response to particular environmental conditions (Albert et al. 2011, Bolnick et al. 2003). As realized niche space is essentially determined by selective mechanisms that act as a filter to species, both mean trait value and intraspecific trait variability contribute to a species' ability to pass filters imposed by the abiotic or biotic environment (Carlucci et al. 2015, Jung et al. 2010, Kichenin et al. 2013). Species experiencing a strong heterogeneity in environmental conditions tend to show a large intraspecific variability in traits through which they respond to these conditions (Sultan and Spencer 2002, Valladares et al. 2014). For example, in alpine grasslands intraspecific variability in several leaf traits was reported to control the short-term species responses to extreme drought events (Jung et al. 2014). In tropical dry secondary forests (Derroire et al. 2018), sapling species showed plasticity regarding specific leaf area (SLA) presumably allowing them to respond quickly to rapid environmental changes, typically occurring during succession. Assuming that páramo succession is primarily driven by inversely correlated traits directed to resource acquisition or conservation (Huston and Smith 1987, Llambí et al. 2003, Sarmiento et al. 2003), species abundance at the extreme ends of páramo succession is in principle determined by one single selective mechanism. As a consequence, at mid-successional stages, species are subjected to both mechanisms to which they should be optimally adapted in order to gain dominance. This would hypothetically imply that, regarding traits through which species respond to maximize their fitness along the acquisition-conservation axis, mid-successional communities are predominantly built up by species that show a larger intraspecific variability than early- or late-successional communities (Figure 5-1).

We studied trait variability of páramo plant species occurring in small plots of different successional age in south and central Colombia. We focused on specific leaf area, which is arguably one of the most frequently studied plant traits (Poorter et al. 2009), although records from high Andean taxa are still rare (Diemer 1998a). SLA is leaf area relative to leaf mass, and indicates how a plant reaches a compromise between longevity and photosynthetic capacity (Westoby et al. 2002). Plants with low SLA values hypothetically follow a strategy to persist in communities by conserving their carbon stocks, as opposed to plants with high SLA values that have optimized their ability to quickly acquiring and releasing carbon (Conti and Díaz 2013). We recorded the abundance of the vascular plant species in a total of 134 plots in early- and late-successional vegetation, recovering from disturbance by agriculture. In all plots, we measured SLA, which allowed us to quantify the degree of intraspecific trait variability, within

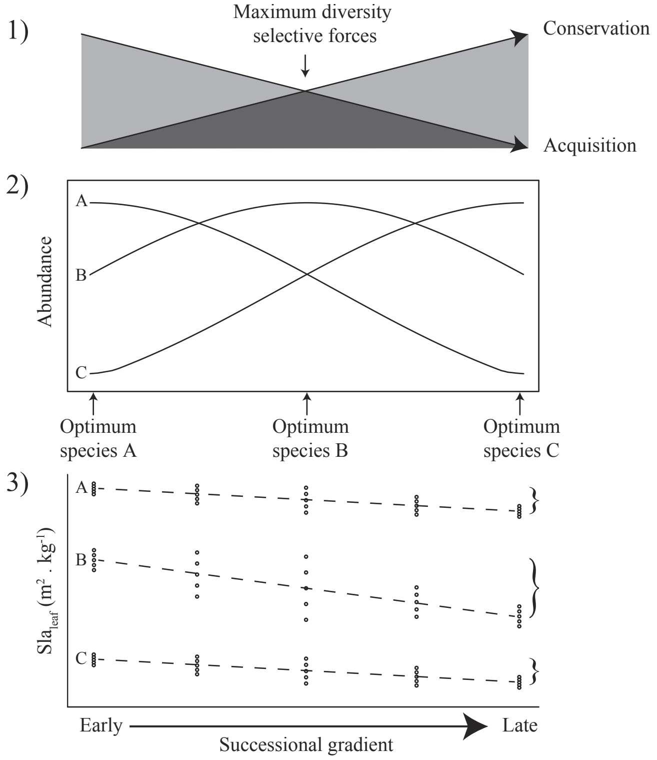

Figure 5-1: Simplified expected patterns of the SLA variability along a successional gradient in páramo vegetation. The uppermost graph (1) visualizes how filtering mechanisms force species to adopt acquisitive or conservative strategies in order to gain dominance. Graph 2 shows the Gaussian abundance curves of three species with optima at early-, mid- and late-successional stages. Notice that all species occur along the successional gradient ('autosuccession'; Muller, 1952). Graph 3 shows expected SLA values (open, small dots) sampled along the gradient in five plots, with the dashed lines connecting the mean SLA values at each plot. Notice that the plot means of all species decrease with advancing succession, that the within-plot SLA variability of all species is highest in the mid-successional plot, and that species B (that has a mid-successional optimum) shows the highest within-plot and between-plot intraspecific variability (the latter illustrated by the curly brackets).

and between plots across the successional gradient. We expected that community weighed means (Grime 1998) of the species' mean SLA values would show a downward trend along the successional gradient as dominance in the course of succession would be obtained by species that increasingly follow a conservative strategy, showing lower mean SLA values (Llambí et al. 2003, Sarmiento et al. 2003). Furthermore, as we assumed that species that were most abundant in mid-successional communities would be best adapted to follow both conservative and acquisitive strategies, we expected that the mid-successional community weighted means of the species' intraspecific SLA variability would be larger than those observed at early- or late successional stages. Our principal research question was: how do the mean and intraspecific variability of the SLA values of páramo plant communities change with succession?

5.2 - METHODS

Study sites

In 2013 and 2014, we established a total of 134 square 1-m^2 plots in páramo vegetation at elevations between 3300 m and 3800 m above sea level (asl), situated at four sites: Cumbal (0°56' N and 77°50' W), Ovejas-Tauso (1°09' N and 77°20' W), Paja Blanca (0°59' N and 77°37' W), and Verjon (4°57' N and 74°0' W) (Figure 5-2). Biogeographically, the páramos of Cumbal, Ovejas-Tauso and Paja Blanca belong to the Cordillera Central and Macizo Colombiano, whereas the páramo of Verjon belongs to the Cordillera Oriental (Londoño et al. 2014). In all areas, the mean annual precipitation is between 900 mm and 2000 mm and the soils are generally developed in volcanic ashes, showing a high organic matter content and a strong acidity (Morales et al. 2007, Solarte-Cruz et al. 2007, Ussa-Garzón 2010). Commonly found vascular plant species belong to *Ageratina*, *Azorella*, *Blechnum*, *Calamagrostis*, *Carex*, *Disterigma*, *Espeletia*, *Festuca*, *Jamesonia*, *Miconia*, *Oreobolus* and *Paspalum*.

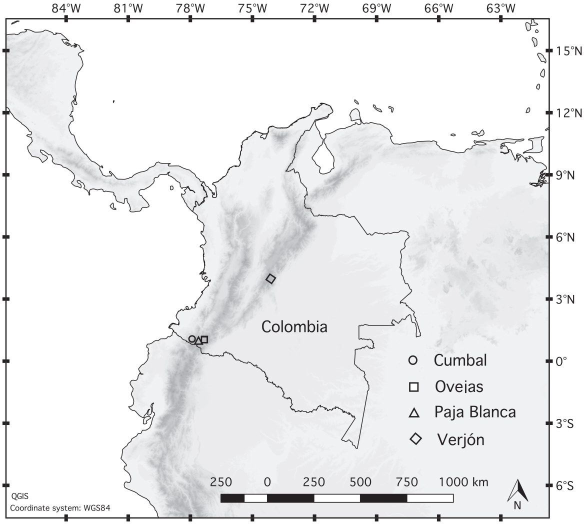

Figure 5-2: Location of the fieldwork sites.

At Cumbal and Verjon, we sampled both early- and late-successional páramo vegetation. At Ovejas and Pajablanca we only sampled late-successional vegetation. Late-successional vegetation lacked signs of human impact and had been untouched by crop cultivation or cattle grazing for at least 10 years, as we inferred from farmers living nearby. In contrast, early-successional vegetation was visibly recovering from strong agricultural disturbances (plowing, burning or cutting) that had completely removed the aboveground biomass for the purpose of crop cultivation (usually potatoes). The Verjon area is part of the páramo of Cruz Verde, from which Jaimes and Sarmiento (2002) reported the species composition in 18 plots in six successional stages. We compared the species observed in these stages with the species composition we recorded in the Verjon plots (presence-absence of fully identified species on the basis of the Sørenson similarity coefficient; Legendre and Legendre 1998). Our early- and late-successional Verjon plots mostly resembled the younger (< 8 yr) and older successional stages (> 8 yr) at Cruz Verde, respectively (Table 5-1), which was in accordance with our estimate of successional ages based on our local sources.

Table 5-1: Sørenson similarity between vascular plant species composition of early- and late-successional plots at Verjon and successional stages at Cruz Verde reported by Jaimes and Sarmiento (2002) (m: months, y: years).

	Successional stages at Cruz Verde					
	< 10 m	10 m - 3 y	3 - 6 y	6 - 8 y	8 - 12 y	Páramo
Early-successional	0.23	0.33	0.31	0.29	0.26	0.28
Late-successional	0.15	0.25	0.21	0.26	0.34	0.38

Plot and soil data

All plots were situated at locations that were randomly selected under the condition that inaccessible terrain (steep slopes, ravines, peat bogs) was avoided. Plot locations were at least 100 m apart from each other (as the crow flies). Elevation and coordinates were recorded using a global positioning system device. At each plot, one soil sample was taken at a depth between 10 to 15 cm. Soil samples were analyzed at the soil laboratory of the Universidad de Nariño and comprised: pH (H_2O) in a volumetric 1:2 soil:water solution; percentage of organic C, according to the Walkley–Black method; exchangeable aluminium by extraction in 1 N KCl; available P by extraction with 0.1 N HCl and 0.13 N NH_4F, according to BrayII; and bulk density (IGAC 1990). Most soil samples were acid (mean soil pH of 4.4 (SD = 0.4)), and showed a high content of organic matter (mean soil C of 17 (SD = 16.8) %) coupled with a low bulk density (mean of 0.6 (SD = 0.1) g . cm^3) (Table 5-2).

Table 5-2: Summary of soil and elevation data. Shown are mean ± one SD for N plots.

	N	pH	P mg.kg^{-1}	Al cmol+.kg^{-1}	C %	Density g.cm^{-3}	Elevation m
Early-successional							
Cumbal	14	4.6±0.4	12.7±6.9	3.7±2.0	13.0±5.2	0.59±0.11	3509±92
Verjon	18	4.3±0.4	26.3±32.3	6.8±3.1	16.0±4.9	0.66±0.09	3371±47
Late-successional							
Cumbal	26	4.5±0.3	13.3±7.7	4.1±2.0	13.5±4.9	0.60±0.09	3612±69
Ovejas-Tauso	28	4.6±0.5	10.1±5.9	3.3±2.3	22.4±5.4	0.52±0.08	3636±35
Pajablanca	26	4.2±0.4	22.4±18.5	4.6±1.9	18.1±6.8	0.60±0.09	3550±42
Verjon	22	4.1±0.2	13.2±13.2	7.7±2.7	17.6±6.3	0.65±0.09	3436±35

Plant species sampling and trait measurements

In each plot we counted the number of individuals from each vascular plant species. Clonally growing plants were defined as a plant clump of continuous cover that was spatially separated from neighbouring clumps of the same species. Unidentified plant species were collected for taxonomical identification at the herbarium of the Universidad de Nariño. Nomenclature followed Tropicos (2017). In all plots, following standardized procedures (Cornelissen et al. 2003), we randomly selected five plants with fully developed leaves from each vascular plant species. From these plants we collected five full-grown leaves for SLA measurements. If only five or less plants could be selected, these were all included in the leaf sampling. All leaf samples were stored in plastic bags, and scanned afterwards. Folded leaves (e.g., *Rhynchospora* sp., *Carex* sp.) were cut and fully expanded on the scanner using transparent sticky tape. Leaf areas of scanned images were determined using ImageJ software (Abramoff et al. 2004). After scanning, leaves were dried during for 48 hr at 70° and weighed with a precision of 0.1 mg. Furthermore, from all plants subjected to leaf sampling, we measured the height as the length from the soil surface to the apical leaf, using a tape (± 0.1 cm). These measurements were used to estimate the plant ontogeny, defined as the plant height divided by the maximum plant height recorded of a particular species in all plots. Young plants (i.e., relatively small plants if plant height is taken as indicator for ontogeny) that are reported to show relatively high SLA values (Derroire et al. 2018, Lusk and Warton 2007), likely occur in young-successional stages.

Gradient analysis

We selected partial canonical correspondence analysis (*pCCA*) to model the successional gradient as follows:

$$pCCA.result = CCA(Spec \sim Succession.stage + condition(Env))$$

in which *CCA* was the default cca function as implemented in the vegan package (Oksanen et al. 2018), Spec the site-to-species matrix filled with the square root transformed plant counts of the species (identified (morpho)species and unidentified taxa), *Succession.stage* the binary vector representing early- or late successional stages, and Env a plot-to-variable matrix, composed of the following conditioning variables: soil pH, ln-transformed soil P, soil density, elevation, and location. Soil Al, soil C, and longitude were excluded as explanatory variables because they correlated strongly with soil pH (Spearman rs = -0.69), soil density (rs = -0.50), and latitude (rs = 0.92), respectively. We took the plot scores of the first axis of the pCCA analysis as representing the successional gradient. By using the conditioning variables, we reduced the chance that any pattern in mean and intraspecific SLA variability as function of this successional gradient would be confounded by effects of elevation (Diemer 1998a), soils or location, on SLA values. The first pCCA axis was highly significant ($p < 0.001$, permutation test under reduced model), even though it explained only 2.6% of the total inertia (the variance explained by the conditioning variables was 10.0%). On the whole, early- and late-successional plots were clearly separated along the first pCCA axis (Figure 5-3). If a late-successional plot contained species that also occurred in early-successional plots, the position of this plot shifted towards the central part of the successional gradient, and vice-versa.

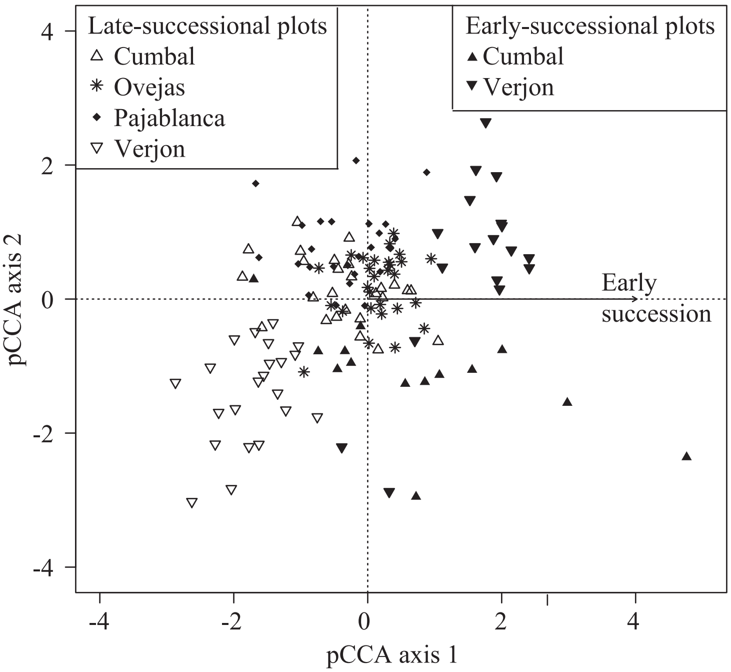

Figure 5-3: Ordination diagram showing the plot scores of the pCCA ordination.

Mean and intraspecific variability of SLA

We calculated the mean and the intraspecific variability of SLA across all leaves of a species, within a plot or between plots, disregarding the plants to which the leaves belonged. For each species the SLA values of the leaves (SLA_{leaf}) were log-normally distributed. Therefore, we calculated the average of the SLA_{leaf} values of each species in arithmetic units (Thomopoulos 2017) as follows:

$$Mean_i = exp(\mu_i) * sqrt(\sigma_i^2)$$

with μ_i and σ_i^2 as the maximum likelihood estimators of the mean and variance of the ln-transformed SLA_{leaf} values of species i across all plots.

We used the variance and the coefficient of variation (Albert et al. 2010b) in arithmetic units to quantify intraspecific SLA variability. For each plot p and species i the within-plot variance $VARw_{ip}$ and coefficient of variation CVw_{ip} were calculated as follows:

$$VARw_{ip} = exp(2 * \mu_{ip}^2 + \sigma_{ip}^2) * (exp(\sigma_{ip}^2) - 1)$$

$$CVw_{ip} = sqrt(exp(\sigma_{ip}^2) - 1)$$

in which μ_{ip}^2 and σ_{ip}^2 were the maximum likelihood estimator of the variance of the ln-transformed SLA_{leaf} values of species i in plot p, respectively. $VARw_{ip}$ and CVw_{ip} were were undefined for two species (*Melpomene moniliformis* and Orchidaceae sp. 6), because of insufficient data. For each species also across-plot averages of $VARw_{ip}$ and CVw_{ip} calculated as:

$$VARw_i = \Sigma_1^k VARw_{ip}/k$$

$$CVw_i = \Sigma_1^k CVw_{ip}/k$$

in which k was the number of plots in which SLA$_{leaf}$ values of species i were recorded.

The between-plot intraspecific SLA variability quantified how the plot-specific means of the SLA$_{leaf}$ values of each species varied across plots (see also Fig. 5-1). First, for each species i in plot p a plot-specific average of the SLA$_{leaf}$ values was obtained in arithmetic units, as follows:

$$Mean_{ip} = exp(\mu_{ip}) * (sqrt(\sigma_{ip}^2))$$

Because these plot-specific averages were log-normally distributed we calculated for each species i the between-plot variance ($VARb_i$) and coefficient of variation (CVb_i) in arithmetic units, as follows:

$$VARb_i = exp(2 * \mu_i + \sigma_i^2) * (exp(\sigma_i^2) - 1)$$

$$CVb_i = sqrt(exp(\sigma_i^2) - 1)$$

in which μ_i and σ_i^2 were the maximum likelihood estimators of the mean and variance of the ln-transformed Mean$_{ip}$ values, respectively. $VARb_i$ and CVb_i were undefined for 40 species from which SLA$_{leaf}$ values were recorded in only one plot.

Community weighted means

Using the observed number of plants relative to the total number of plants of each species i in plot p ($Prop_{ip}$), we calculated for each plot a community weighted mean (CWM; Díaz et al. 2007), as follows:

$$CWM = \Sigma_1^S Prop_{ip} t_{ip}$$

in wich S was the species richness in plot p. To calculate the CWM for the mean SLA$_{leaf}$ value in a plot ($CWMmean_p$), t_{ip} represented the $Mean_{ip}$ values of species i in plot p. Likewise, t_{ip} represented the $VARw_{ip}$, CVw_{ip}, $VARb_i$, or CVb_i values of species i in plot p to obtain the CWM values fo the four measures of intraspecific variability (i.e., $CWMvarw_p$, $CWMcvw_p$, $CWMvarb_p$, and $CWMcvb_p$, respectively).

We tested if each of these community weighted means differed between early- and late-successional plots by means of a Kruskal-Wallis test. To test for non-linearity against the successional gradient, we regressed them against the plot scores of the first pCCA axis, as follows:

$$Model = lm(ln(CWM) \sim Gradient_p + I(Gradient_p^2) + sqrt(Ontogeny_p))$$

in which $Gradient_p$ and $I(Gradient_p^2)$ were the scores and the squared scores of the first pCCA axis in plot p. Residual analyses of all regression models are in Appendix 5-1. All analyses were done R (R Core Team, 2017).

5.3 - RESULTS

Summary information of species and environment

In the 134 1-m^2 plots we recorded 15866 vascular plants belonging to 165 identified species (including morphospecies) and 27 unidentified taxa (Appendix 5-2). On average, a plot contained 118 (SD = 67.2) plants, and 11.9 (SD = 3.5) species. Early-successional plots contained significantly less species (10.5 (SD = 3.5) than late-successional plots (12.3 (SD = 3.5) (Kruskal-Wallis test, Chi^2 = 4.9, p = 0.027). Only 21 species were found limited to early-successional plots. Far more species (77) were restricted to late-successional plots or were recorded in both early- and late-successional plots (67).

Analyses of CWM values

As expected, the early-successional plots showed higher CWM values of the species' mean SLA$_{leaf}$ values than late-successional plots (Kruskal-Wallis test, p <0.0001). In the regression analysis, only the linear term of the plot scores representing the successional gradient was significant (Table 5-3; Figure 5-4). Also the CWM values of each of the four measures of intraspecific variability of SLA$_{leaf}$ values were higher in early-successional plots than in late-successional plots (Kruskal-Wallis tests, p < 0.007 for all measures). In regression against the modeled plot scores, they showed a downward, monotonic trend, similar to that of the CWM of the species' mean SLA$_{leaf}$ values (Figure 5-4; Table 5-3).

Table 5-3: Results of regression analyses of community weighted means of mean, within-plot intraspecific variability and between-plot intraspecific variability of SLA$_{leaf}$ values (compare Fig. 5-4). Shown are the F values of the partial regression coefficients. * 0.01 <= P < 0.05; ** 0.001 <= P < 0.01; *** P < 0.001.

Response	Gradient$_p$	I(Gradient$_p^2$)	sqrt(Ontogeny$_p$)
Ln(CWMmean$_p$)	53.6***	0.3	0.01
Ln(CWMvarw$_p$)	18.7***	2.5	2.1
Ln(CWMcvw$_p$)	16.1***	0.6	0.9
Ln(CWMvarb$_p$)	20.9***	0.2	2.4
Ln(CWMcvb$_p$)	14.8**	2	0.0004

5.4 - DISCUSSION

Community weighted means of species' mean SLAleaf values were higher in early-successional than in late-successional plots. In accordance with succession theory (Huston and Smith 1987, Grime 1979, Tilman 1993), and in line with other studies in páramo (Llambí et al. 2003, Sarmiento et al. 2003) and temperate herbaceous communities (Garnier et al. 2004), we explain these results by assuming that the most dominant species in early páramo succession are selected for their capacity to quickly acquire external resources enabling fast growth, while

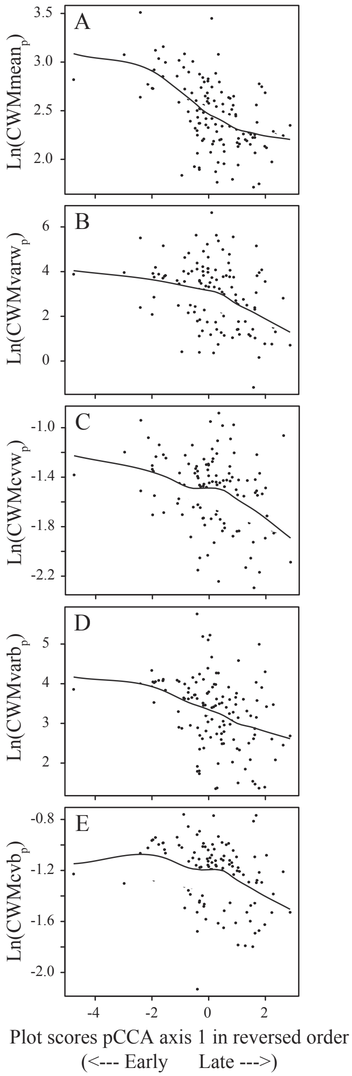

Figure 5-4: Patterns of community weighted means of mean (A), within-plot intraspecific variability (B, C) and between-plot intraspecific variability (D, E) of SLA$_{leaf}$ values along the successional gradient represented by the plot scores of the pCCA axis 1 in reversed order.

species in late-successional stages of páramo vegetation attain dominance through a more efficient nutrient uptake, resource conservation and an improved resistance to drought. Our results thus suggested that the mean SLA values of species represent a factor of differential species performance (Pickett et al. 1987) that affects community assembly in succession.

Early-successional communities were predominantly built up by species that showed a higher SLA plasticity (i.e., a lower degree of specialization for high SLA values) than expected. On the other hand, late-successional communities seemed built up by species that showed a low SLA plasticity (i.e., that specialized in showing low SLA). None of the community weighted means of the intraspecific SLA variability measures showed a peak at mid-successional stages. These results call for rejecting our hypothesis that intraspecific SLA variability would show a unimodal response along the successional gradient. In vegetation science, it is generally believed that environmental variability decreases with advancing succession, and that early-successional species show a broader (generalistic) physiological response to the environment than late-successional species (Bazzaz 1979). Assuming this to be true for páramo vegetation and páramo species, early-successional species might obtain dominance by compensating low SLA levels with appropriate levels of other traits (for example, linked to dispersal, colonization, or reproduction). In addition, the observed successional trends in intraspecific SLA variability might relate to environmentally specific costs of SLA plasticity (Coleman et al. 1994, Sultan 1995, Sultan and Spencer 2002). Vascular plants in páramo vegetation cope with the harsh páramo environment, which is characterized by low temperatures with a frequent chance on frost, strong wind, high intensity UV-B radiation, and a continuous aseasonal productivity on a yearly basis, with 12 hr growth period each day (Körner 1999, Smith 1972). Diemer (1998b) argued that páramo species are selected for showing long leaf life spans as that would permit sufficient carbon gain even if the species' physiological capacity would be limited by a low temperature and a low nutrient availability under conditions of a constant 12 hr photoperiod. In this light, and especially for slow-growing late-successional species, a large intraspecific SLA variability might represent an important cost by putting at risk the required carbon return ratio. In late-successional stages characterized by low rates of resource acquisition and habitat disturbance, a species may not be able to counteract the effects of a short leaf span (associated with a high SLA) by enhanced leaf initiation or leaf growth, or by increasing levels of recruitment and settlement of plants as a whole. Hence, by showing a high SLA plasticity late-successional species run a large risk to be filtered out. On the other hand, in early-successional stages where dominance is primarily reached through competitive growth, a species may still persist even its growth is limited by its leaves being tough and long-living (showing low SLA) (Sarmiento et al. 2003). In early-successional páramo vegetation, slow growth does not constrain species in reaching viable carbon return ratios, for which reason SLA plasticity does not represent a cost and species do not specialize regarding SLA (Sultan and Spencer 2002). Overall, the successional trends in the community weighted means of species means and intraspecific variability of SLA values were largely similar (Table 5-3, Fig. 5-4) but were interpreted differently. The species mean SLA values mostly influence the chance that a species is present and becomes dominant somewhere along the successional gradient in páramo vegetation. The SLA intraspecific variability, on the other hand, affects the chance that a species is present in late-successional páramo vegetation. Considering that the coefficient of variation by definition represents variability independent from the mean, the strong similarity in the successional trends shown by variance or coefficient of variation (Fig. 5-4) underlined this independence of the effects of mean and intraspecific SLA variability on successional change in páramo vegetation.

To appreciate our results, we warn that our plot scores, which we took to represent the successional gradient, were modeled interpolations derived from samples in only two successional stages of páramo vegetation. We applied pCCA analyses, because the interpretation as optima of the species scores along the canonical axis (Ter Braak 1986) came closest to our initial model (Fig. 5-1). In correspondence analyses plots that contain many plants contribute more to the ordination output than plots with few plants (Legendre and Gallagher 2001). To mitigate this effect we applied the square root transformed plant counts of the species (see methods). Plot scores obtained with the alternative method of a partial redundancy analysis with Hellinger transformed species abundances, were highly correlated with the pCCA scores (Pearson correlation coefficient of 0.93 for the first axes). A better way to obtain reliable estimates of the successional position of plots would be obtained by sampling more successional stages. Most preferably, however, successional information should be derived from vegetation change in permanent plots (e.g., those from the Gloria network; Cuesta et al. 2012), reducing the need to infer process from pattern. Finally, in view of the expanding areas of páramo vegetation disturbed by agriculture and intensive grazing (Hofstede et al. 2014), we expect that late-successional plant communities are facing progressively severe problems because of the increasing habitat destruction. Our study suggested that it is even more imminent to conserve and protect these communities, because they are mostly built up by species that show low levels of intraspecific SLA variability, which reduces their adaptive potential to maintain viable populations in changing páramo environments.

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