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MICROCLIMATE AND REGENERATION PATTERNS OF *Polylepis sericea* IN A TREELINE FOREST OF THE VENEZUELAN ANDES

MICROCLIMA Y PATRONES DE REGENERACIÓN DE Polylepis sericea EN UN BOSQUE DEL 'TREELINE' EN LOS ANDES VENEZOLANOS

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ABSTRACT

Tropical high mountains constitute environments where harsh conditions prevail. *Polylepis* forests are found above the continuous forest line throughout the Andes, with *P. sericea* as the only species in Venezuela. Sprouting has been described as an effective establishment strategy in environments where disturbance and/or severe conditions exist. Considering establishment stages as filter phases under stressful environments, we studied different aspects of the regeneration of *P. sericea*: Reproduction type, seeding or sprouting, and their distribution in relation to adult canopies. We also measured different microclimatic conditions under the forest canopies and beyond the forest in order to relate them to *Polylepis*' distribution. The largest number of *P. sericea* individuals occurred in smaller (0-30 cm) size categories. A larger number of plants corresponded to sprouts (56%) during the establishment phase. Seedings occurred more frequently at the edge of the canopies while sprouts were found closer to trunks of adult trees. Establishment of young plants in this particular habitat probably comes down to a compromise between nursing effects by canopies of the adult trees favoring water and temperature conditions and insufficient light limiting photosynthetic processes under the tree canopies. Differences found in reproductive patterns coincide with postulations favoring vegetative regeneration under more extreme conditions.

Key words: Páramo de Mucubají, seedling, sprouting, treeline, Tropical high Andes,

RESUMEN

Las altas montañas tropicales constituyen ambientes donde prevalecen condiciones rigurosas. Los bosques de *Polylepis* se encuentran por encima de la línea continua de bosques a lo largo de la Cordillera de los Andes, con *P. serícea* como la única especie en Venezuela. El rebrote se ha descrito como una estrategia de establecimiento efectiva en ambientes donde el disturbio y/o condiciones extremas ocurren. Considerando a las etapas de establecimiento como las fases filtro en ambientes estresantes, estudiamos diferentes aspectos de la regeneración de *P. serícea*: Tipo de reproducción, por semilla o rebrote, y su distribución en relación a los doseles de los árboles adultos. También medimos distintas características microclimáticas debajo del dosel de los árboles y fuera del bosque con el fin de relacionarlas a la distribución de *Polylepis*. El mayor número de individuos de *P. serícea* ocurrió en la categoría de menor tamaño (0-30 cm). El mayor número de plantas pequeñas durante la fase de establecimiento correspondió a rebrotes (56%). Los individuos provenientes de semillas se encontraron con mayor frecuencia al borde del dosel, mientras que los rebrotes estaban más cerca de los troncos de árboles. El establecimiento de plantas jóvenes en este habitat en particular probablemente corresponde a un compromiso entre un efecto nodriza producido por el dosel de árboles favoreciendo las condiciones de temperatura y humedad, y luz insuficiente que limitaría los procesos fotosintéticos bajo el dosel. Las diferencias encontradas en los patrones reproductivos coinciden con el postulado de que la regeneración vegetativa es favorecida bajo condiciones extremas.

Palabras clave: Altos Andes tropicales, límite arbóreo, Páramo de Mucubají, rebrote, plántula

INTRODUCTION

Polylepis (Rosaceae) forests are found at the treeline in the South American Andes. This genus is represented by 28 different tree species (Schmidt-Lebuhn *et al.* 2006) along the Andes from Venezuela down to Argentina and Chile. The occurrence of this genus, well above the reported worldwide elevation limit for trees, points to the presence of unique functional responses that permit these trees to overcome different environmental limitations imposed by extreme climatic conditions. Azócar *et al*. (2007) described some functional attributes for three different *Polylepis* species which help explain their success along altitudinal and latitudinal gradients. *P. tarapacana* in Bolivia and *P. australis* in Argentina rely on freezing tolerance whereas *P. sericea* avoids freezing through a slight supercooling capacity in the Venezuelan Andes. *P. tarapacana* is the most tolerant species to water stress and mean CO_2 assimilation rates were higher in *P. australis*.

In the particular case of the Venezuelan Andes, *Polylepis sericea* Wedd is the only species belonging to this genus, and is mostly associated to rock outcroppings (Arnal 1983). These forests are surrounded by the páramo, a low strata vegetation ecosystem dominated by giant rosettes, shrubs and grasses. Different authors have described more favorable conditions within these forest islands compared to the surrounding open páramo in terms of: buffering of minimum nighttime and maximum daytime temperatures, improved conditions for water and nutrient uptake and lower incoming radiation inputs (Arnal 1983; Azócar and Monasterio 1980; Godstein *et al.* 1994; Azócar *et al*. 2007; Rada *et al*. 2009). Rada *et al*. (1985) report daily osmotic adjustments in *P. sericea* which enhance its supercooling capacity as a response to nighttime freezing temperatures. In addition, this species avoids the unfavorable dry season conditions through seasonal osmotic adjustments and cell wall elasticity changes (Rada *et al*. 1996). CO_2 assimilation rates for *P. sericea* are comparable to those reported for other tropical timberline and alpine plants (Goldstein *et al.* 1994). These authors suggest that high photosynthetic efficiency and frost resistance are the main physiological explanations for *Polylepis´* success at high elevations.

Seeding and sprouting regeneration strategies have been discussed widely for different environments. The success of the latter strategy has been associated to locations where disturbance plays a major role (del Tredici 2001; Vesk and Westoby 2004). Cierjacks and Hensen (2004) describe how grazing leads to an increase of vegetative regeneration in *Quercus ilex* in a Mediterranean ecosystem. Additionally, sprouting has also been described as a successful strategy under very stressful environments. Lloret *et al*. (2004) give evidence of limiting drought effects on seedings compared to sprouts in two Mediterranean trees. Busby *et al*. (2010) find that sprouting is more frequent under drought stress in a study of tree regeneration along a rainfall gradient in a tropical forest ecosystem. Vegetative reproduction has also been described as a general response to extreme climatic conditions of arctic and alpine environments. For instance, Whittaker (1993) observed a larger establishment of sprouts in woody species of a Norwegian glacier foreland. While other authors have described how extreme conditions at high altitude treelines impede the establishment of seedings (Piper *et al.* 2006; Resler 2006). At a more detailed scale, different authors have determined that at treeline, seedlings establish more successfully under the canopy of adult trees compared to the open surroundings (Cuevas 2000; Cierjacks *et al*. 2007).

Considering establishment stages as filter phases that may determine success in a stressful environment, it is important to understand the different aspects that may explain *P. sericea*’s success. Very few studies have dealt with the natural regeneration of *P. sericea*. A high regeneration rate under the canopy of adult trees (Hueck 1960), while a 100% mortality rate of transplanted seedlings to the open páramo (Smith 1977) have been reported. Other studies on *Polylepis* forests along the Andean range have evaluated different aspects of regeneration and establishment. For instance, the effects of fire on the establishment of *P. australis* in the Argentinean Andes (Renison *et al.* 2002) and *P. incana* in Ecuador (Cierjacks *et al.* 2008a) have been studied; Cierjacks *et al*. (2008b) describe the effect of different intensities of cattle grazing on the regeneration patterns of *Polylepis* incana and *P. pauta* in the Ecuatorian Andes. In terms of seeding vs. sprouting strategies, Enrico *et al*. (2004) find a very low incidence in vegetative regeneration of *P. australis* (< 5% in relation to seedings) at 2100 m asl in the Central Argentinean Andes. Additionally, most seeding was found beneath adult individuals. However, Hertel and Wesche (2008) found that seedings were dominant at a lower site forest dominated by *Polylepis lanata* while at the uppermost site *P. pepei* young growth corresponded exclusively to root suckers. Cierjacks *et al*. (2007) also describe an increased vegetative reproduction at higher altitudes in *P. incana* forest stands in Central Ecuador. Rundel *et al.* (2003) describe important vegetative establishment of *P. rugulosa* from fallen branches in an extremely dry high mountain environment of Northern Chile.

In order to understand some functional aspects of the regeneration of *P. sericea*, we characterized for one particular forest: microclimatic conditions within the forest and the surrounding open páramo. We also studied this forest's population structure in size categories, reproduction type (seeding or sprouting) and their distribution in relation to adult canopies. Under the harsh conditions of the high altitude tropical Andes, questions may be raised regarding regeneration patterns and establishment such as: how different are microclimate conditions between *P. sericea*'s forest understory and the surrounding páramo? How are seeding and sprouting spatially distributed in the forest? And which reproductive pattern plays a more relevant role in this forest patch?

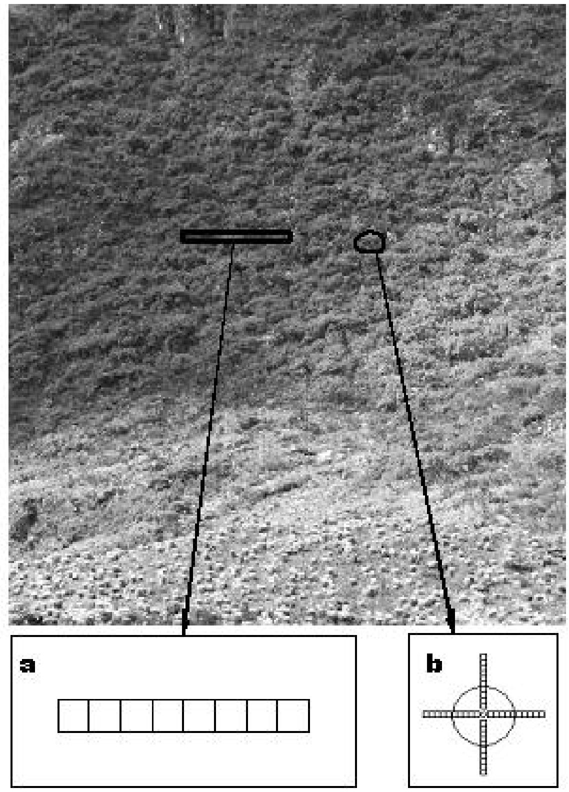

Figure 1. *Polylepis sericea* forest in Páramo de Mucubají. Middle of the figure corresponds to transition between forest (upper) and open shrub-rosette páramo (lower). a. Transects laid out perpendicular to the slope (40 x 5 m, subdivided into 5 x 5 m) for individuals > 10 cm in height. b. 10 m x 1 m wide transects, subdivided every 1 m, along cardinal points were sampled for individuals < 10 cm in height.

MATERIALS AND METHODS

Study species

Arnal (1983), in a very exhaustive study of the distribution and characteristics of all *P. sericea* forests in the Venezuelan Andes, reports that 93% of a total of 256 forests are found on rock outcrops, 70% of these forests located at altitudes between 3500 and 4100 m asl. Mean annual precipitation in these forests varies between 700-1800 mm, while no relationship was found between forest size and amount of precipitation. In the large majority of cases, *Polylepis* forests have very defined boundaries which separate them abruptly from páramo rosette, graminoid and/or shrub associations and do not connect with the high montane cloud forest or any other forest types of the lower páramo. Although there is a great variability with respect to forest sizes, an approximate mean of 9 ha results from all the studied forests. In addition, 65% of all studied forests showed no anthropogenic disturbance; therefore, Arnal (1983) considers it hardly probable that the present forest distribution is due, mainly, to human impact. *Polylepis* forests are practically monospecific in terms of the arborescent stratum. In general, two other strata are described, shrubs and a second one composed of a more herbaceous cover. These other strata are mainly composed of species belonging to the Asteraceae and Poaceae (Arnal 1983).

Study site and microclimatic characteristics

The studied *P. sericea* forest was located in the Páramo de Mucubají (3700 m asl), Sierra de Santo Domingo in Mérida, Venezuela (8º 47` N, 70º 48`W). This particular forest is found on an eastern facing slope imbedded in rock outcrops and surrounded by rosette-shrub and rosette-grass vegetation associations, typical of the open

Table 1. Mean (T_{mean}, ºC), maximum (T_{max}, ºC) and minimum (T_{min}, ºC) air temperatures (5 cm > ground level), air relative humidity (RH, %), minimum relative humidity (RH_{min}, %), photosynthetic photon flux density (PPFD, $\mu molm^{-2}s^{-1}$) and maximum photosynthetic photon flux density ($PPFD_{max}$, $\mu molm^{-2}s^{-1}$) for wet (WS) and dry (DS) seasons under *P. sericea*´s forest understory and in the neighboring open páramo. Mean ± standard error. Different superscript letters correspond to significant differences between wet and dry seasons for forest understory and open páramo separately. Different superscript numbers correspond to significant differences between forest understory and open páramo for each season separately.

	Forest understory		Open páramo	
	WS	DS	WS	DS
T_{mean}	$6.9 \pm 0.2^{a,1}$	$5.3 \pm 0.1^{b,1}$	$7.2 \pm 0.2^{a,1}$	$5.1 \pm 0.2^{b,1}$
T_{max}	$12.3 \pm 0.3^{a,1}$	$14.1 \pm 0.3^{b,1}$	$19.9 \pm 0.6^{a,2}$	$23.1 \pm 0.6^{b,2}$
T_{min}	$2.4 \pm 0.2^{a,1}$	$-0.7 \pm 0.3^{b,1}$	$0.2 \pm 0.2^{a,2}$	$-4.5 \pm 0.4^{b,2}$
RH	$89 \pm 0.1^{a,1}$	$71 \pm 0.2^{b,1}$	$83 \pm 0.2^{a,2}$	$57 \pm 0.3^{b,2}$
RH_{min}	$60 \pm 1^{a,1}$	$47 \pm 3^{b,1}$	$52 \pm 2^{a,2}$	$33 \pm 5^{b,2}$
PPFD	289 ± 13^{1}	-	497 ± 23^{2}	-
$PPFD_{max}$	1078 ± 113^{1}	-	1590 ± 68^{2}	-

páramo. The forest has a relatively open canopy, with some isolated trees in larger open gaps. Mean annual temperature for the Páramo de Mucubaji is 5.4 ºC with little differences between the coldest (December) and warmest (June) month, while daily fluctuations are important. Mean annual precipitation (969 mm) presents a unimodal distribution with a marked dry season between December and February.

Air temperature, relative humidity (RH) and incoming photosynthetic photon flux density (PPFD) were registered every 5 minutes for the wet (October 16 to December 15) and the dry (December 16 to February 5) seasons, with data loggers (HOBO, USA) placed at 5 cm above the ground surface in both forest understory and open páramo. Air temperature and relative humidity sensors were placed inside solar radiation shields (RS1, HOBO, USA).

Spatial distribution of seedings and sprouts

Four transects were placed within the forest, perpendicular to the slope, each 40 m long by 5 m wide. Each transect was subdivided into 5x5 m subplots (25 m^2). Plant height and base diameter were measured in all *P. sericea* individuals above 10 cm in height in four sub-plots of 25 m^2 chosen randomly along each of the four 200 m^2 transects (Figure 1a). To determine density of individuals below 10 cm in height and their distribution in relation to adult trees, four 10 m long x 1 m wide transects, subdivided every 1 m, in all cardinal directions were laid out for each tree individuals selected in such a manner that open patches were around each chosen tree in order to determine if exposition is important in the distribution of smaller plants (Figure 1b). The trees were 4-6 m tall and, in all cases, had extensive canopies averaging 6-8 m in diameter.

For all transects described previously, all small individuals (plants < 10 cm in height) were selected in order to determine their origin. All individuals were partially excavated, leaving part of their roots exposed. The presence of roots or root suckers was easily determined; therefore seedings were differentiated from sprouts without difficulty.

Statistical analysis

A two-way anova was used for the assessment of interactions in microclimate variables between seasons (wet and dry) and between environments (forest understory and open páramo). A t-test was utilized to determine if there were significant differences between occurrence of reproductive strategies, seedings or sprouts.

RESULTS

Microclimate characterization of forest understory and open páramo

Climatic conditions in *P. sericea*´s forest understory were significantly different in terms of extreme temperatures and relative humidity compared to the neighboring open páramo (Table 1). Temperature oscillations were far more important in the open páramo compared to the forest understory (Figure 2). Mean maximum temperatures were significantly higher in the open páramo compared to the understory for both seasons, with differences of 7 ºC and 9 ºC for wet and dry seasons, respectively. On the other hand, mean minimum temperatures were higher in the understory. It is important to note that although significant differences between these two environments were found in both mean minimum and maximum temperatures between the understory and the páramo, mean temperatures for both wet (approximately 5 ºC) and dry (approximately 7 ºC) periods showed no significant differences. Air evaporative demand was lower in the understory compared to the páramo as observed from the measured RH. Significantly higher RH was always present in the understory for both wet and dry periods, however differences were more pronounced during the latter season. For incoming radiation, the open páramo showed mean values which almost doubled those of the understory.

Tree density and distribution of size categories

A high number of young individuals were found in this forest (Figure 3). The first few categories (0-.3 m) represented the largest number of individuals (a total of 216 plants), with 111 individuals in the first category (0-10 cm) and decreasing drastically for the rest of the size categories. The categories >.3 m were represented by 122 individuals. However, it is important to note that all categories were present. Note that categories from 2.0 to 7.0 m were all grouped into one since their densities were very low, reason why the last bar shows an increased number of individuals.

Regeneration patterns

In relation to seeding or sprout establishment (< 10 cm in size) no differences were found between expositions. Even though there was a large variability between sampled transects, significant differences (P < 0.05) were found between the number of seedings and the number of sprouts per transect/plot (Figure 4). A larger number of plants corresponded to sprouts (56%) compared to seedings (44%). Of the 111 individuals (seedings or sprouts) registered in this study, 93% were found under the canopy of adult trees (distances < 5m,

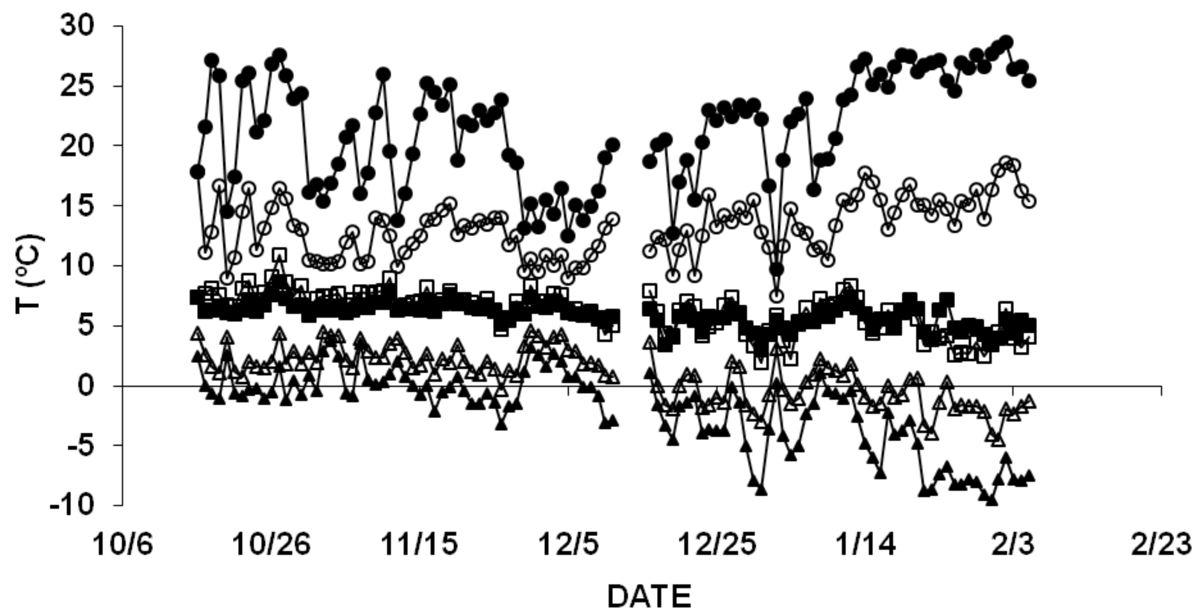

Figure 2. Mean, maximum and minimum registered air temperatures, 5 cm > ground level, for a four month period including wet (October 16 to December 11) and dry (December 16 to February 5) seasons for the *P. sericea* forest understory and the neighboring open surroundings in the Páramo de Mucubají. Forest understory: mean (□), maximum (○) and minimum (Δ), open páramo: mean (■), maximum (●) and minimum (▲).

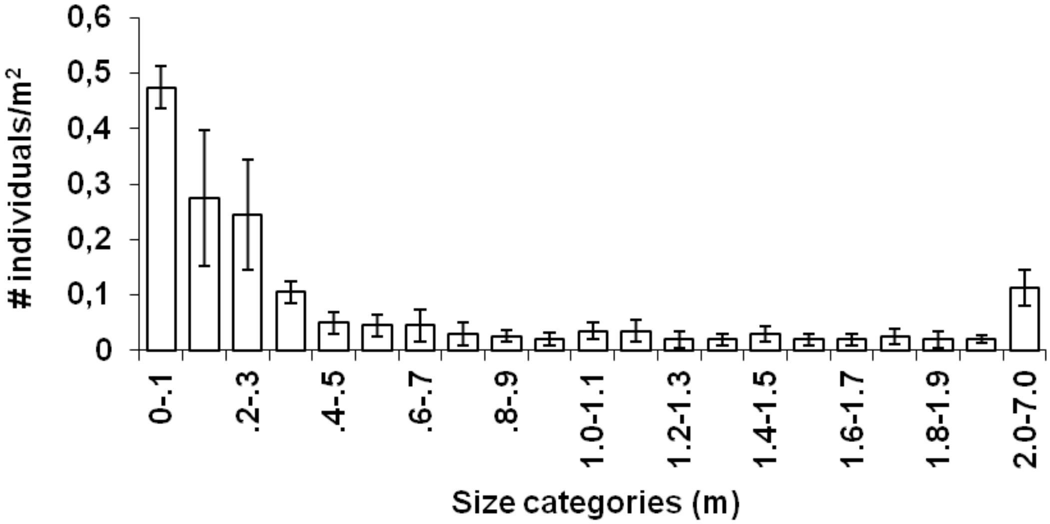

Figure 3. Number of individuals (seedings and sprouts) per square meter according to size classes (height, m) for the forest in Páramo de Mucubaji. In total 336 individuals were recorded. Bars represent one standard error from the mean. Note that the increase in number of individuals in the last size class is due to the addition of all classes above 2 m in height.

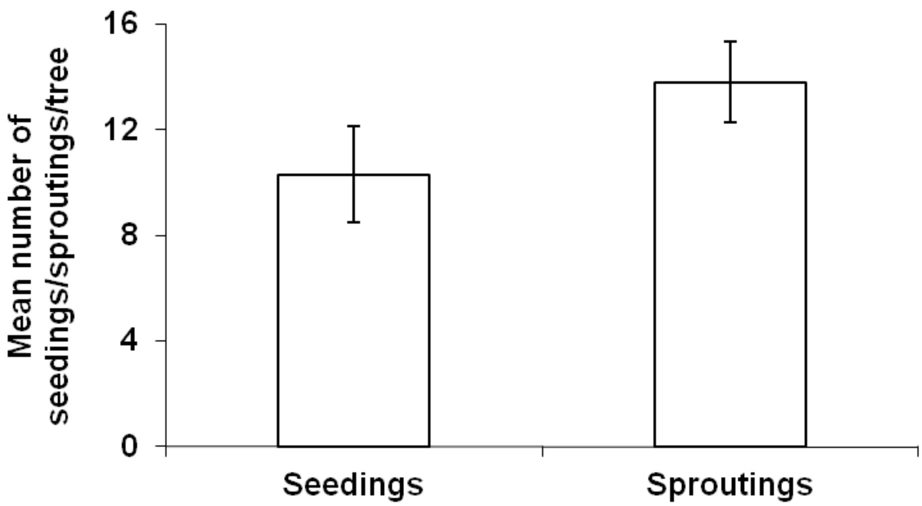

Figure 4. Mean number of seedings and sprouts found around the different trees (n=10) studied in this forest. Seedings corresponded to 44% and sprouts to 56% of all saplings < 10 cm in height.

Figure 5). There was also a clear differentiation in the position of seedings and sprouts with respect to the canopies. Sprouts were found closer to the tree trunk, most found between 1 and 3 m from the trunk in a more shaded position, whereas seedings were established at a greater distance from the trunk, most found at a distance between 3 and 5m, towards the edge of the canopy (Figure 5).

DISCUSSION

Microclimatic conditions in the Polylepis forest and the surrounding páramo

Climatic conditions within the forest understory

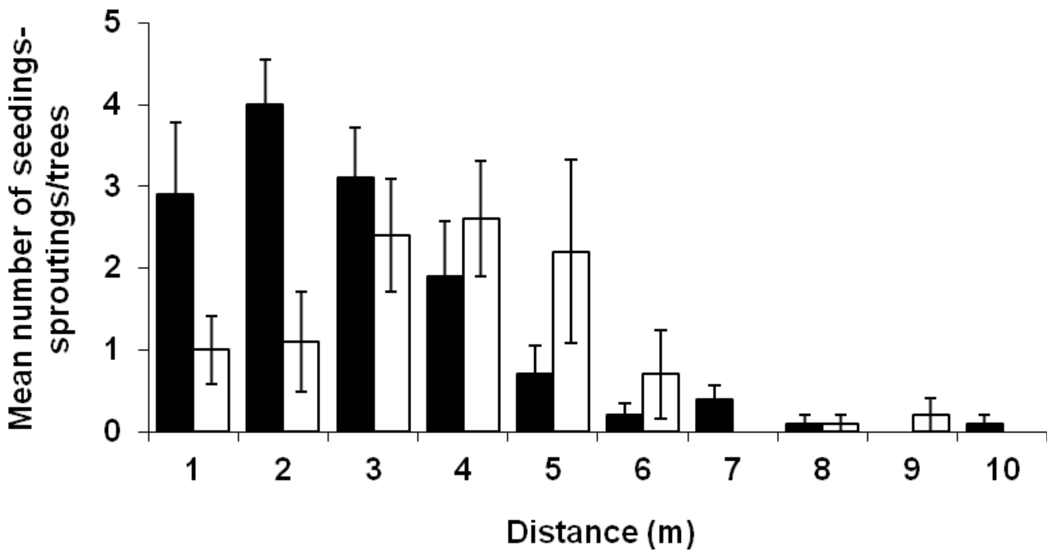

Figure 5. Mean number of juveniles (seedings (□) and sprouts (■), <10 cm in height) in relation to the distance from the trunks of adult *Polylepis* trees (n=10). Bars represent one standard error from the mean.

are more favorable compared to the open surrounding páramo. Our results support those of other authors who describe these particular *Polylepis* forest environments as thermal refugees where temperature oscillations are buffered (Smith 1977; Azócar and Monasterio 1980). Bader *et al.* (2007a) report smaller temperature oscillations in six tropical and subtropical forests in the Andean treeline when compared to the neighboring open vegetation. The greatest daily oscillation within the forest and the open páramo occurred in the middle of the dry season ranging between -4.5 ºC and 18.6 ºC for the former and -9.5 and 28.6 for the latter. Rada *et al*. (2009) report injury temperatures of approximately -7 ºC for *P. sericea* saplings in this same forest, suggesting that low temperature resistance mechanisms are not sufficient to colonize more open harsher environments.

Nevertheless, different authors suggest other added possible limitations related to unfavorable water conditions and/or incident radiation. Goldstein *et al*. (1994) state that conditions in these forests, not only are thermally buffered, but water losses from the soil are also reduced and air humidity increased, resulting in more favorable conditions, especially during the dry season. Rundel *et al.* (2003) describe how *Polylepis rugulosa* establishes under the extremely low rainfall and high evaporative demand conditions of the Northern Chilean pre-altiplano at 3550 m asl., but more importantly, they suggest that this species population structure is determined by highly episodic seedling establishment during favorable wet years. There are several studies which emphasize the importance of high radiation inputs in limiting tree establishment at tropical (Enrico *et al.* 2004; Bader *et al.* 2007b) and temperate (Germino *et al.* 2002; Maher *et al.* 2005) high altitudes. These issues will be reconsidered in the next section integrating them with regeneration patterns.

Population structure and regeneration patterns

Our results reveal a high proportion of juveniles in this forest, showing a large number of individuals smaller than 30 cm in height and progressively decreasing as size increases but nevertheless individuals always present in all categories. These results suggest a dynamically stable growing population. This partially coincides with Hueck (1960) who finds a large number of juveniles and adult *Polylepis sericea* trees, but a low number of individuals in the intermediate categories. In contrast, Rundel *et al.* (2003) find a marked absence of young plants, none below 50 cm in height, in a *Polylepis rugulosa* population in the Chilean northern Andes. The large number of individuals (< 10 cm category) underneath the canopies found in our study suggests that there are more favorable microclimatic conditions, for example, buffered extreme low and high temperatures, greater soil moisture and nutrient content (Goldstein *et al*. 1994). However, on the contrary, low incoming radiation reaching the ground beneath the canopy may determine limiting conditions for photosynthetic processes and, consequently, growth.

It is interesting to note that the great majority of seedings are found at the edge of the canopies where light conditions are favorable, while sprouts are found well beneath the canopy. The latter ones may depend less on light conditions as they are still connected to adults which may supply sprouts with assimilates for their development. However, an alternative explanation may be the fact that sprouts may occur where roots concentrate more near the stem. In any case, practically no seedlings, seedings or sprouts, were found in gaps away from the canopies. Enrico *et al.* (2004), in a shrubland of the Cordoba Mountains in Argentina, find that most seedlings of *P. australis* were established beneath adult individuals which may be exerting a nursing effect. Cierjacks *et al.* (2007) report that forest edges of *P. incana* and *P. pauta* stands in Central Ecuador are zones of high natural recruitment.

The effect of soil moisture differs between seedings and sprouts. Different authors report resprouting as an advantageous tree regeneration strategy under water stress (Dietze and Clark 2008, Busby *et al*. 2010). García-Núñez *et al.* (2010) find that *Casearia sylvestris* sprouts maintain a more favorable water status compared to *Palicourea rigida* seedings under water stress conditions of a tropical seasonal savanna. Lloret *et al*. (2004) find that *Quercus ilex* sprouts were less affected by lower soil moisture compared to *Phillyrea latifolia* seedlings, supporting the hypothesis that the former receive resources from their parent plant. Sprouts in this *P. sericea* forest were significantly higher when compared to seedings. However, our results show that sexual reproduction is important in these refuge habitats. It is also clear that colonization by either seedings or sprouts is limited in open páramo habitats. As stated by Stöcklin and Bäumler (1996), the functional significance of establishment from seeds and clonal growth should not be regarded as an antithesis but as compensatory. Success in seeding establishment will increase genotype fitness, while clonal growth reduces the risk of extinction under extreme unfavorable ambient conditions. Establishment of young plants in these particular habitats comes down to a compromise between nursing effects by canopies of the adult trees favoring water and temperature conditions, among other conditions not studied here, and insufficient light limiting photosynthetic processes. From our results and the cited literature one may conclude that there is a distinct more favorable site at the edge of the canopy, with a very low chance of survival in the direction of the open gaps, and a limited chance of survival towards the most inner portion under the tree canopies near the stem. In our particular study case, differences in reproductive patterns coincide with predicted assumptions that vegetative regeneration will be favored under the inner canopy where markedly low radiation inputs occur. Even though freezing temperatures have an impact on seedling establishment in colder open páramo environments (Rada *et al.* 2009), this study suggests that high radiation inputs may be essential in *Polylepis*' establishment and survival in open areas as suggested by Enrico *et al.* (2004) and Bader *et al*. (2007b). Control experiments separating low nighttime temperature from high radiation effects will reveal their relative importance.

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