

Effects of altitude and livestock on the regeneration of two tree line forming *Polylepis* species in Ecuador

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Abstract Regeneration is known to be limited at many temperate tree lines, but very little data is available on the impacts of altitude and anthropogenic disturbance on regeneration patterns along tropical tree lines. The study focused on the reproductive traits of two *Polylepis* species in the Páramo de Papallacta in Ecuador along an altitudinal gradient, and involved different intensities of cattle trampling within subsequent altitudinal ranges. We analyzed flowering, fruit set, seed viability, germination, and seedling establishment as well as stand structure of *Polylepis incana* and *P. pauta*. The numbers of *P. incana* inflorescences and seedlings per m² showed a marginally significant decrease with increasing altitude. Mean tree height was significantly lower at higher altitudes, while stem number increased. The number of *P. pauta* inflorescences also decreased significantly upslope. In both forest types, trampling was found to have a positive impact on seedling abundance, presumably due to the removal of the litter layer. Thus, there was no evidence of negative effects of moderate cattle grazing on both tree line species. However, sapling establishment was minimal inside the forest stands at all altitudes and grazing levels, and we consequently observed a low

proportion of narrow stems within all investigated forests. Our results show that, along with vegetative growth limitations of adult trees, important regeneration traits such as seedling and inflorescence numbers are also influenced by altitude, which might contribute to the formation of the upper tree line. Nevertheless, recruitment in the forest interior was low overall indicating that further factors, such as light conditions, affect regeneration of the studied species.

Keywords Anthropogenic impact · Herbivory · *Polylepis* · Reproduction · Trampling · Tree line

Introduction

The possible causes of tree line formation have been intensively studied, but as yet no fundamental mechanism has been agreed upon. Currently, five principal hypotheses are under discussion (Körner 2003a). Frost and phototoxic stress, mechanical disturbance by wind, snow break etc., insufficient carbon balance, as well as possible limitations of synthetic processes for the formation of plant tissues may affect tree growth at high altitudes. In addition, reproduction may be limited along the tree line (Tranquillini 1979; Hättenschwiler and Smith 1999; Körner 2003a; Camarero and Gutiérrez 2004). Regeneration is not believed to be the main factor in tree line formation as there is no reason why

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arborescent species should have problems with recruitment while other life forms have adapted their regeneration traits to even more extreme conditions (Körner 2003a). However, what we already know about regeneration patterns may provide relevant insights into population dynamics and future stand development.

Former measurements and recently compiled data reveal a close correlation between thermal thresholds and tree line position (5–7°C mean growing season temperature, Körner and Paulsen 2004), suggesting the presence of a common climatic driver, which operates globally regardless of differences in other abiotic or biotic site conditions. In addition, locally differing factors such as human disturbance, fire and grazing (Miehe and Miehe 1994) modulate the tree line position (Körner 1998). Furthermore, rather idiosyncratic causes of tree line formation are described such as differences among species' recruitment strategies (Cuevas 2000; Dullinger et al. 2004), biotic interactions such as herbivory (Cairns and Moen 2004), or multi-factorial effects (Cairns and Waldron 2003). Plant regeneration is generally known to be limited in harsher environments and tree line stands should be no exception to this. In any case, data on recruitment are required in order to devise appropriate management and restoration schemes. Little information is available from tropical tree lines on the whole, and among the various factor complexes, data on regeneration patterns are relatively scarce.

In the northern Andes, the upper tree line is usually formed by highly fragmented *Polylepis* forests that are subject to a variety of anthropogenic disturbances such as wood extraction, burning and grazing, all of which result in severely declining forest cover (Kessler 1995; Purcell and Brelsford 2004). The remaining forest patches usually form abrupt boundaries with the surrounding vegetation (Walter and Medina 1969; Lægaard 1992; Sarmiento 2002), as is equally described for many other tropical high elevation forests in the world (reviewed in Miehe and Miehe 1994; Körner 2003a). The factors influencing the local distribution of *Polylepis* forests have been an important topic in plant ecology for decades (e.g. Ellenberg 1958, 1979, 1996; Walter and Medina 1969; Cabido and Acosta 1985; Hensen 2002; Körner 2003a; Renison et al. 2006), but there is widespread agreement now that forests' current

fragmented distribution largely reflects human influence (Ellenberg 1996; Hensen 2002). Lægaard (1992) and Lauer et al. (2001) both assumed that only the uppermost limit of *Polylepis* stands in central Ecuador is natural and is accordingly determined by edaphic and climatic conditions, because these sites are characterized by a gradual transition towards the adjacent vegetation. In contrast, abrupt forest borders at lower altitudes are attributed to human disturbances, mainly fires (Lægaard 1992; Lauer et al. 2001). Thus, although not a fundamental physiological constraint, anthropo-zoogenic impact should be considered in any study on upper mountain *Polylepis* forests.

Cattle grazing represents the main land use practice in central Ecuador (Sarmiento 2002; Crissman 2003). Although a number of authors have analyzed the impact of grazing on Páramo vegetation (Lægaard 1992; Hofstede 1995a, b, 2001), only a few studies are dedicated to the silvipastoral use of *Polylepis* forests (e.g., Teich et al. 2005). Kessler (1995) reported that rejuvenation of Bolivian *Polylepis* forests is slightly less intense in grazed stands. Grazing by goats and sheep apparently impedes seedling establishment (Hensen 1995, 2002; Kessler 1995). Although cattle do not browse *Polylepis* species in central Ecuador, trampling is expected to have a significant impact (Lægaard 1992). In addition to the impact of domestic herbivores, natural herbivory of *Polylepis* seeds and leaves by caterpillars of Geometridae is known to be a common phenomenon in Ecuadorian Páramos (León Yáñez 2000). Nevertheless, the impact of site conditions and land-use practices on the reproduction of *Polylepis* species has, as yet, been scarcely studied (Smith 1977; Hensen 1995, 2002; Kessler 1995; Renison and Cingolani 1998; Renison et al. 2002a, b).

The present study investigates reproductive traits, site conditions and stand structure of *Polylepis incana* Kunth and *Polylepis pauta* Hieron. in the Ecuadorian Páramo de Papallacta along an altitudinal gradient under different intensities of cattle trampling. In particular, we assessed the following questions: 1. How does altitude affect flowering, fruit set, seed quality, seed predation by Geometrid caterpillars and seedling establishment of both *Polylepis* species? 2. How is stand structure influenced by altitude? 3. What is the impact of trampling on these parameters? Apart from the general theoretical framework on tree

line ecology, detailed knowledge on regeneration parameters under different site and disturbance conditions should facilitate the discrimination of natural and anthropogenic causes of present forest distribution and tree line position, which will be crucial to the development of efficient conservation strategies needed for these endangered plant communities (UNEP-WCMC 2004; Renison et al. 2006).

Methods

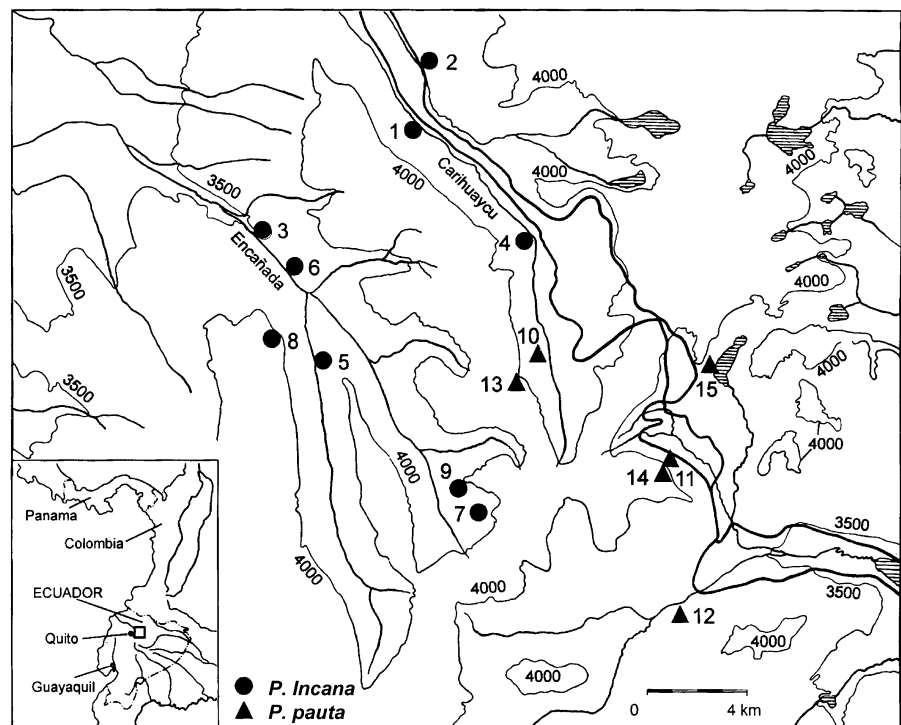
Study area and species

The Páramo de Papallacta (nomenclature follows Lauer et al. 2001) is located in the eastern cordillera of Ecuador between the Cayambe and Antisana volcanoes, about 30 km east of Quito (Fig. 1). The geology of the area is characterized by plio-pleistocene vulcanites that are covered by quaternary pyroclastic and aeolic sediments ('cangagua'; Winckell et al. 1997; Lauer et al. 2001). The study area covers the geocological units of the plateau-like Páramo de Papallacta itself with its young-glacial lakes, bogs and moraines, and the El Tablon/Páramo de Guamaní, which is dominated by glacially formed

valleys that deepened following the erosion of cangagua layers (Lauer et al. 2001). Soils in the area are predominantly Andosols (Winckell et al. 1997; Lauer et al. 2001).

The climate is typical for tropical highlands with limited thermal, but pronounced hygric, seasonality (Sarmiento 1986). Precipitation patterns vary remarkably among exposures and altitudinal levels. The western slopes are drier and receive the highest precipitation between March and May, and from September to November (Lauer et al. 2001). For forest stand 1 (Fig. 1) at 3650 m asl, a mean annual precipitation of 1,500 mm was estimated (Fehse et al. 1999). Precipitation increases with elevation, but is locally modified by circulation patterns and slope inclination (Lauer et al. 2001). In contrast, the eastern slopes receive most precipitation between June and August with an overall amount of 1,433 mm (Papallacta station: 3,150 m asl; Bendix and Rafiqpoor 2001). Although precipitation decreases with altitude, a maximum of about 1,800 mm is reached at 3,800 m asl at the condensation level (Lauer et al. 2001). Mean annual temperatures are also determined by altitude and exposure. For the western slope, Lauer et al. (2001) report 10.5°C at 3,500 m, and 6°C at 4,100 m asl, whereas the eastern slope is

Fig. 1 Study area and location of the forest stands investigated in this study



characterized by a less steep altitudinal gradient with temperatures ranging from 8.5°C to 6°C at the respective altitudes. Climate of all forests was measured exemplarily in order to exclude forest stands with locally particular conditions.

In the Páramo de Papallacta, *Polylepis* forests grow up to an altitude of 4,100 m asl (Fig. 1). On the western slope, stands of *P. incana* prevail while on the eastern slope *P. pauta* forests are predominant. *Polylepis incana* reaches a maximum height of 12 m (Romoleroux 1996). Stands can be found from central Ecuador to southern Peru (Simpson 1979). The pendant inflorescences are short and bear between 3 and 10 flowers. In the Páramo de Papallacta, *P. incana* occupies an altitudinal belt between 3,500 m asl and 4,100 m asl and forms monospecific forests between 3,600 m asl and 3,800 m asl. *Polylepis pauta* also grows up to 12 m in height and is distributed along the eastern slopes of the Andean cordillera from northern Ecuador to southern Peru (Romoleroux 1996; Simpson 1979). In the study area, forests are situated between 3,700 and 4,100 m asl and are always mixed with other tree species such as *Gynoxys* spp., *Solanum stenophyllum* and *Hesperomeles obtusifolia* var. *microphylla*. *Polylepis pauta* is characterized by long, rarely ramified inflorescences with 10–40 flowers (Romoleroux 1996). Both *Polylepis* species continuously produce flowers and fruits (one-seeded nutlets, hereafter referred to as seeds; Simpson 1979).

Sampling design

Study plots were established in a partly nested design. In order to cover the entire altitudinal range of each *Polylepis* species, forest stands were grouped into the following altitudinal belts: 3,500–3,700 m, 3,700–3,900 m and 3,900–4,100 m asl for *P. incana*; and 3,700–3,900 m and 3,900–4,100 m asl for *P. pauta*. At each level, three independent forest stands of at least 1 ha in size were selected. Minimum distance among these stands was 1 km. Only unburned stands were included in the study. From the 15 selected forest stands, 14 were privately owned. Stand 15 (Fig. 1) is part of the Ecological Reserve Cayambe-Coca.

Via interviews with the respective landowners, general animal loads were determined at the forest stand level and ranged between 0.13 and 0.17 cattle per ha—with the exception of two stands which were

grazed at higher intensities (Stand 8: 0.44 cattle per ha; stand 12: 1.25 cattle per ha). However, borders of the properties are not fenced, allowing for free roaming of cattle herds in the whole area. As cattle are not evenly distributed in paramo ecosystems due to forage availability (Hofstede 1995b), different levels of disturbance by grazing can be distinguished within single forest stands. Area of cattle paths was considered to indicate repeated and long-term cattle presence. We classified the stand area into three levels of trampling intensity according to the following scheme: no or light trampling (0.0–3.9% of cow paths, but no paths without vegetation), intermediate trampling (4.0–19.9% of cow paths), and heavy trampling (>20.0% of cow paths). Within each trampling level, one plot of 100 m² was randomly selected. All plots were established in closed forest stands at a minimum distance of 5 m to forest edge. This approach resulted in an overall amount of 27 plots for *P. incana*, and 18 for *P. pauta* with three independent replicates for each factor combination. Width and length of all cattle paths within the established plot were measured and the overall path area was calculated.

Data collection and analysis

Data were collected from April to July 2004. In each study plot stem height, diameter at breast height (dbh, or—if not possible—below the first ramification) and canopy diameter of all stems >1.3 m were determined. For multi-stemmed individuals, diameter was calculated from the sum of diameters of all the stems. We took records from every tree where fructification was present. Mean stem number of *Polylepis* and all other tree species per ha, as well as basal area per ha, mean height, mean canopy diameter and percentage of seed bearing *Polylepis* individuals were calculated in accordance with Kramer and Akca (1995). In addition, canopy cover within the plot was estimated visually. Averaged heights and basal areas are strongly influenced by differing numbers of small trees in the studied forests. However, our estimates should still have relevance considering the low overall recruitment in the forest interior at all altitude and grazing levels.

The amounts of seedlings, saplings and asexual ramets <1.3 m were counted in 20 randomly distributed 1-m² subplots within each study plot. Ramets were distinguished from saplings by excavating

possible connections with the mother plant. Generative *Polylepis* individuals >5 cm in height were counted as saplings. In addition, depth of litter layer was recorded and cover of vegetation was estimated in each subplot. Moreover, distances of each seedling from the next herbaceous vascular plant were measured and averaged at the plot level.

Flowers and seeds were counted directly in the canopy layer by climbing to the top of the trees where leaves and flowers are mainly produced. All forest stands were characterized by a closed canopy cover, which implies a similar crown morphology with a 50–100 cm deep layer of foliated and reproductively active branches. For each study plot we counted the inflorescences in five randomly selected 1-m² subplots with the help of a wooden frame. A representative sample of inflorescences (on average 300 in *P. incana* plots and 30 in *P. pauta* plots) was collected and the percentage of racemes with flowers and seeds, as well as the mean numbers of flowers and seeds per raceme was determined. Using these data, the absolute amount of flowers and seeds per m² was calculated. The importance of seed predation by Geometridae on *P. incana* was assessed based on visible feeding signs on collected seeds. The length of all collected seeds was measured and the viability of seeds was tested using a Tetrazolium staining protocol (McKay 1972). Only seeds with an entirely stained embryo were considered viable.

In all forest stands within the same geocological unit (Páramo de Papallacta and El Tablon), soil temperatures at 30 cm depth, atmospheric temperature and atmospheric humidity at 10 cm height were simultaneously measured over 24 h on the same day with data loggers (INFRALOG, Driesen and Kern, Germany). Two data loggers were placed in each stand (untrampled and heavily trampled plot). Additionally, in situ soil moisture at 0–3 cm depth was averaged over five instantaneous measurements per plot using a Theta Probe (HH2 moisture meter, Delta-t Devices Ltd.). *Polylepis incana* stands of El Tablon were analyzed from 10th to 11th of July 2004 and those of Páramo de Papallacta from 12th to 13th of July 2004. Both days were sunny and dry with slight easterly winds. *Polylepis pauta* forests were measured from 14th to 15th of July 2004 during cloudy and rainy weather.

In each plot, soil parameters were analyzed in an air-dried sample of top soil (0–10 cm) mixed together from three subplots. Soil pH was measured in 0.1 mol/l KCl

solution. Contents of exchangeable K⁺, Na⁺, Ca²⁺, and Mg²⁺ were analyzed by applying AAS (VARIO 6, Analytik Jena) after extraction with 0.1 mol/l NH₄Cl. The content of organic matter was determined by loss on ignition, and C/N ratios by gas-chromatography (VARIO CN Analyser, ELEMENTAR).

Statistical analyses were performed using R version 2.3.1 (The R Foundation for Statistical Computing 2006). Altitude and trampled area were the categorical predictor variables and the forests were included as a blocking factor nested within altitude. Stand parameters, litter depth, data on flowering, seed quality and predation as well as the numbers of seedlings, saplings and ramets were response variables. Data were tested for normal distribution (Kolmogorov–Smirnov Test). Data on seedling number had to be ln-transformed to confirm to statistical normality, while analyses of the remaining variables were based on untransformed data relying on the robustness of balanced ANOVA designs (Quinn and Keough 2002). Effects of altitude and grazing level were jointly analyzed using Two-Way ANOVA, followed by Tukey HSD post-hoc tests in cases where differences were significant overall. Due to the partly nested design, the *F*-ratio for the factor altitude was calculated in reference to the MS of the random factor forest nested within altitude, whereas the test of trampling relied on the residual of forest (altitude) × trampling (Quinn and Keough 2002). The datasets of *P. incana* and *P. pauta* were analyzed separately. Linear regressions (Pearson *r*) of the mean forest altitude and mean inflorescence number were performed in order to estimate the altitude at which the number of inflorescences declines to zero. In addition, we determined Pearson correlation coefficients for ln-transformed seedling number and litter depth.

Results

Site conditions

Soils of the investigated *P. incana* stands are characterized by a high content of organic matter and slightly acidic pH-values (Table 1). Soil pH decreased with altitude, as did contents of Ca²⁺ and Mg²⁺. *Polylepis pauta* forests grow on more acidic soils with a lower Ca²⁺ and Mg²⁺ content (Table 1).

Table 1 Soil and climate conditions of the investigated *Polylepis* stands (soil conditions: means (SE) of nine plots; microclimate: means (SE) of six parallel measurements)

Altitudinal level (m asl)	<i>Polylepis incana</i>			<i>Polylepis pauta</i>	
	3,500–3,700	3,700–3,900	3,900–4,100	3,700–3,900	3,900–4,100
Mean slope (%)	11 (3)	18 (4)	19 (1)	15 (3)	26 (1)
pH (KCl)	5.5 (0.1)	5.4 (0.1)	4.6 (0.1)	4.1 (0.1)	3.8 (0.1)
Soil humidity (%)	21.4 (1.7)	22.0 (3.2)	52.8 (4.5)	79.2 (4.0)	66.5 (5.6)
Organic matter (%)	25.8 (1.8)	28.6 (3.6)	26.5 (2.2)	23.5 (1.6)	25.2 (3.8)
C/N	16.1 (0.5)	16.3 (0.5)	15.5 (0.3)	14.9 (0.5)	15.1 (0.5)
K ⁺ (mg/100 g)	51.0 (3.8)	59.8 (8.6)	46.1 (8.8)	27.8 (3.2)	31.9 (5.3)
Na ⁺ (mg/100 g)	4.8 (0.9)	3.1 (0.4)	3.6 (0.3)	3.3 (0.2)	3.8 (0.7)
Mg ²⁺ (mg/100 g)	93.8 (6.7)	80.5 (5.0)	54.6 (5.6)	35.7 (4.1)	30.8 (4.1)
Ca ²⁺ (mg/100 g)	238.5 (12.0)	230.4 (11.6)	189.1 (10.7)	113.3 (6.0)	102.9 (8.2)
Mean air temp. (°C)	8.3 (0.4)	8.0 (0.4)	5.1 (0.2)	4.8 (0.3)	3.8 (0.1)
Mean soil temp. (°C)	9.1 (0.2)	8.0 (0.3)	5.5 (0.1)	6.3 (0.4)	4.9 (0.1)
Rel. humidity (%)	78.8 (1.9)	75.7 (2.6)	86.6 (1.4)	91.9 (0.5)	91.8 (0.1)

Soil moisture in *P. incana* stands ranged between 12.9% and 66.7% and increased with altitude. Mean soil temperature decreased at a rate of 0.73 K/100 m, with values falling from 9.7°C to 5.3°C between 3,500 m asl and 4,100 m asl. A similar trend could be observed for atmospheric temperature, which ranged between 9.8°C and 4.5°C. In *P. pauta* forests, both soil moisture and atmospheric humidity were clearly higher than in the *P. incana* stands. Mean soil and atmospheric temperature fluctuated less than in the *P. incana* stands, with values between 7.4°C and 4.3°C, and 5.6°C and 3.2°C, respectively, but the temperature gradient was similar (0.78 K/100 m).

Cattle trampling had significant impact on bulk density in the *P. incana* stands, but not in the *P. pauta* stands (Table 2). The highest and the lowest trampling levels in *P. incana* stands differed significantly (Tukey HSD) and there was an interaction between trampling and altitude. In addition, we found a significant decrease in litter depth at higher trampling intensities (Table 2) with significant differences between low and high trampling intensity for *P. incana* and with significantly lower values at the highest trampling level for *P. pauta* (Tukey HSD).

Stand structure

Overall stem number in the *P. incana* stands differed among altitudinal levels (Table 3) and increased with altitude (Fig. 2a). Mean stem height of *P. incana* was

significantly lower at higher altitudes (Tukey HSD, Fig. 2b, Table 3). Consequently, mean canopy diameter demonstrated a similar trend (Table 3). In contrast, no effect of altitude on stand parameters could be detected in *P. pauta* stands (Table 3). The diameter distribution (dbh) showed a rather low proportion of trees with small diameters (0–10 cm) in all investigated stands with values below 50% (Fig. 3). This indicates low recruitment rates for both species within the stands. Trampling did not affect stand structure in any of the two forest types, but we found a significant interaction between trampling and altitude for the tree height of *P. incana*.

Flowering, fruit set and seed predation

The mean percentage of fruit-setting trees was similar in both forest types (*P. incana* 51.8%, *P. pauta* 55.2%, Table 3) and not related to altitude. In contrast, the number of inflorescences per m² decreased upslope, which was significant in *P. pauta* and marginally significant in *P. incana* (Table 4, Fig. 4). In contrast, seed viability was not affected by altitude. Mean seed length was 3.2 mm for *P. incana* and 3.0 mm for *P. pauta*, and in both viability was low (*P. incana* mean 2.3%, *P. pauta* mean 6.0%; Table 4), mainly because of an absence of, or damage to the embryo. Regression models for inflorescence number estimated a decline to zero at an altitude of 4,115 m for *P. incana* ($r^2 = 0.585$, $P = 0.016$, $N = 9$),

Table 2 Means (SE) of area trampled, depth of litter layer and bulk density as well as the results of Two-Way ANOVA ($N = 3$; $L =$ no trampling or low trampling intensity, $M =$ medium trampling intensity, $H =$ high trampling intensity)

Altitudinal level (m asl)	3,500–3,700	3,700–3,900	3,900–4,100	<i>P</i>		
				Altitude	Trampl.	Interact.
<i>Polylepis incana</i>						
Area of cow paths (m ²)						
<i>L</i>	1.8 (1.0)	1.2 (0.6)	1.3 (0.5)			
<i>M</i>	9.6 (1.4)	8.0 (2.4)	8.9 (3.0)			
<i>H</i>	27.5 (3.7)	22.9 (1.9)	28.9 (1.1)			
Depth of litter layer (cm)						
<i>L</i>	3.0 (0.6)	3.3 (0.4)	4.5 (0.7)	0.376	<0.001	0.047
<i>M</i>	2.6 (0.5)	3.3 (0.4)	2.7 (0.8)			
<i>H</i>	1.3 (0.2)	1.6 (0.5)	2.9 (0.7)			
Bulk density (g/cm ³)						
<i>L</i>	0.3 (0.1)	0.4 (0.0)	0.3 (0.0)	0.281	0.004	0.033
<i>M</i>	0.5 (0.1)	0.4 (0.0)	0.4 (0.0)			
<i>H</i>	0.5 (0.1)	0.4 (0.0)	0.4 (0.0)			
<i>Polylepis pauta</i>						
Area of cow paths (m ²)						
<i>L</i>	–	0.0 (0.0)	0.4 (0.4)			
<i>M</i>	–	8.6 (1.7)	13.3 (1.8)			
<i>H</i>	–	23.5 (0.4)	23.0 (0.7)			
Depth of litter layer (cm)						
<i>L</i>	–	3.4 (0.6)	2.9 (0.1)	0.855	0.005	0.291
<i>M</i>	–	2.7 (0.2)	2.3 (0.1)			
<i>H</i>	–	1.1 (0.4)	1.8 (0.5)			
Bulk density (g/cm ³)						
<i>L</i>	–	0.3 (0.1)	0.3 (0.0)	0.905	0.199	0.373
<i>M</i>	–	0.3 (0.0)	0.4 (0.1)			
<i>H</i>	–	0.4 (0.1)	0.4 (0.1)			

and 4,220 m asl for *P. pauta* ($r^2 = 0.513$, $P = 0.109$, $N = 6$). Flowering and fruit-set were not influenced by trampling, but inflorescence number of *P. incana* showed a significant interaction between trampling and altitude.

Seed predation by Geometridae in *P. incana* forests ranged between 5.9% and 34.4%. There was no effect of altitude, but a significant impact of trampling on seed predation (Table 4).

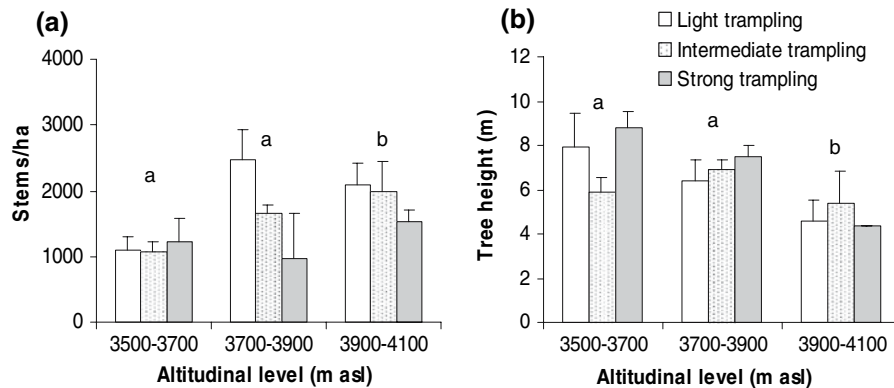
Seedlings and seedling establishment

Seedlings were found in all investigated forest stands. Their average number was 1.5 seedlings/m² in *P. incana* forests and 11.1 seedlings/m² in *P. pauta* stands

(Table 5). Ramets on the other hand were rare in both forest types. The number of *P. incana* seedlings per m² differed significantly between the investigated trampling regimes (Fig. 5a) and marginally significant between the altitude levels without interaction (Table 5). Post-hoc tests clearly distinguished the highest trampling level and the highest altitude level. Density of *P. pauta* seedlings also increased with increased trampling, but no impact of altitude was detected (Fig. 5b, Table 5). The highest and the lowest trampling intensities were significantly different according to post-hoc tests. This was related to a significant correlation of litter depth and seedling number in both species ($r^2 = 0.696$, $N = 27$, $P < 0.001$ for *P. incana*; $r^2 = 0.409$, $N = 18$, $P = 0.004$ for *P. pauta*). In contrast,

Table 3 Stand structure of the investigated *Polylepis* species and ANOVA results (means (SE) of nine plots)

Altitudinal level (m asl)	3,500–3,700	3,700–3,900	3,900–4,100	P		
				Altitude	Trampl.	Interact.
<i>Polylepis incana</i>						
Mean stem number (all species N/ha)	1,133 (128)	1,700 (286)	1,878 (185)	0.048	0.101	0.245
Basal area (m ² /ha)	7,233 (743)	10,429 (518)	7,339 (788)	0.027	0.178	0.235
Mean diameter (cm)	27.3 (3.1)	26.0 (3.3)	25.9 (2.1)	0.957	0.157	0.015
Mean height (m)	7.5 (0.6)	6.9 (0.4)	5.3 (0.6)	0.041	0.229	0.041
Mean canopy diameter (m)	4.7 (0.5)	3.8 (0.4)	3.7 (0.4)	0.085	0.282	0.191
Mean rate of fruit setting <i>Polylepis</i> trees (%)	59.9 (7.2)	62.1 (6.3)	40.9 (5.6)	0.169	0.922	0.312
<i>Polylepis pauta</i>						
Mean stem number (all species N/ha)	–	1,544 (255)	1,578 (182)	0.936	0.869	0.650
Basal area (m ² /ha)	–	5,080 (461)	7,592 (1,334)	0.101	0.812	0.709
Mean diameter (cm)	–	27.6 (3.8)	29.0 (3.7)	0.800	0.591	0.539
Mean height (m)	–	6.6 (0.6)	6.3 (0.5)	0.601	0.362	0.569
Mean canopy diameter (m)	–	4.3 (0.5)	4.6 (0.5)	0.304	0.775	0.812
Mean rate of fruit setting <i>Polylepis</i> trees (%)	–	69.4 (8.6)	56.2 (5.9)	0.282	0.919	0.784

**Fig. 2** Mean stem number per ha (a) and mean tree height (b) of *P. incana* stands at different altitudinal and grazing levels

degree of vegetation cover and mean seedling distance from the next vascular plant did not demonstrate any relation to the number of seedlings.

The number of saplings was low overall, and there was no evidence of effects of trampling or altitude.

Discussion

Impact of altitude

Our data shows that along with vegetative growth limitations, generative regeneration of both *Polylepis* species is influenced by altitude. Numbers of

($N = 3$; error bars: SE; small letters indicate significantly different groups in post-hoc test of factor altitude)

inflorescences decreased with altitude, and seedling number showed a similar trend with altitude in *P. incana*. Based on the regression of the inflorescence numbers, zero reproduction is expected at about 4,100 m for *P. incana* and at about 4,200 m for *P. pauta*, which coincides surprisingly well with the observed upper tree line for these species in the area. Low recruitment is known to be a common phenomenon at tree lines (Tranquillini 1979; Bader et al. in press). At highly seasonal tree line ecotones, a later and shorter flowering period at higher altitudes may be the main reason for reduced regeneration, as is described by Vera (1995) for woody plant species in

Fig. 3 Diameter (dbh) distribution of *P. incana* and *P. pauts* (means of all plots)

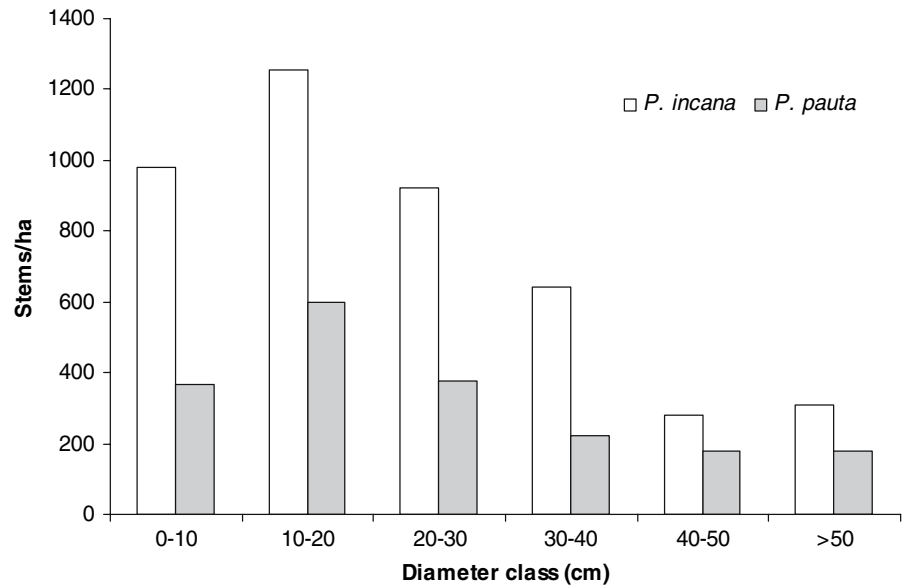


Table 4 Parameters of generative reproduction and ANOVA results (means (SE) of nine plots)

Altitudinal level (m asl)	3,500–3,700	3,700–3,900	3,900–4,100	P			
					Altitude	Trampl.	Interact.
<i>Polylepis incana</i>							
Racemes per m ²	374 (84)	195 (34)	98 (15)	0.055	0.292	0.003	
Flowers per m ²	173 (39)	68 (27)	44 (17)	0.141	0.206	0.028	
Seeds per m ²	160 (62)	56 (19)	50 (15)	0.260	0.609	0.298	
Seeds per raceme	2.3 (0.2)	2.0 (0.2)	2.3 (0.2)	0.527	0.058	0.055	
Mean seed length (mm)	3.2 (0.1)	3.3 (0.1)	3.0 (0.1)	0.543	0.778	0.296	
Mean rate of viability (%)	2.0 (0.6)	3.8 (0.9)	2.0 (0.9)	0.306	0.831	0.152	
Mean rate of seed predation by Geometridae (%)	7.9 (2.0)	10.3 (1.7)	19.6 (4.3)	0.251	0.043	0.983	
<i>Polylepis pauts</i>							
Racemes per m ²	–	12.9 (4.4)	9.3 (1.6)	0.034	0.808	0.407	
Flowers per m ²	–	35.8 (5.6)	30.6 (3.0)	0.958	0.560	0.357	
Seeds per m ²	–	3.3 (0.1)	3.5 (0.3)	0.238	0.759	0.598	
Seeds per raceme	–	0.1 (0.1)	0.0 (0.0)	0.290	0.720	0.551	
Mean seed length (mm)	–	0.0 (0.0)	0.1 (0.0)	0.154	0.859	0.279	
Mean rate of viability (%)	–	12.9 (4.4)	9.3 (1.6)	0.441	0.165	0.760	

Spain. Along tropical latitudes with weakly or without pronounced seasonality, but with more or less ongoing seed production, a direct impact of temperature—as opposed to season length—on inflorescence production might be more probable. The crown morphology of the sampled trees is not expected to have influenced the results as we exclusively analyzed plots with similar canopy cover

and a rather two dimensional reproductive layer. We found a significant interaction of the trampling and altitude effects with inflorescence number in the *P. incana* stands, which is a consequence of the very pronounced impact of altitude at the intermediate trampling level. However, there was no evidence of any direct effects of trampling on stand structure, calling for further research on this phenomenon.

Fig. 4 Mean number of inflorescences at different levels of altitude and trampling for a single census in 2004. **(a)** *P. incana*, **(b)** *P. pauta* ($N = 3$; error bars: SE; small letters indicate significantly different groups in post-hoc test of factor altitude)

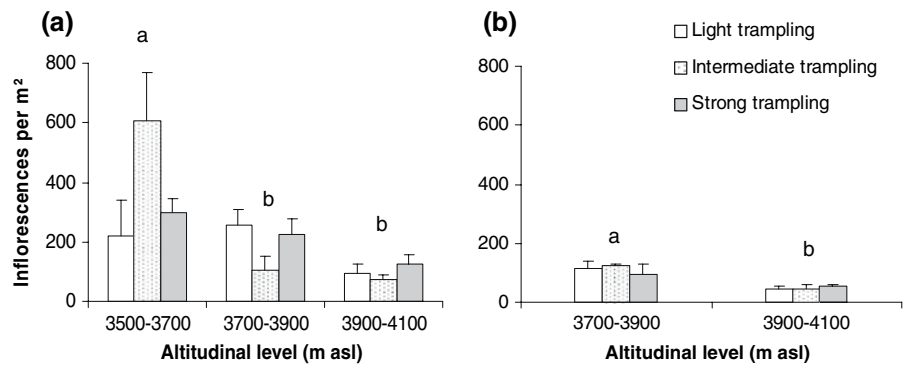
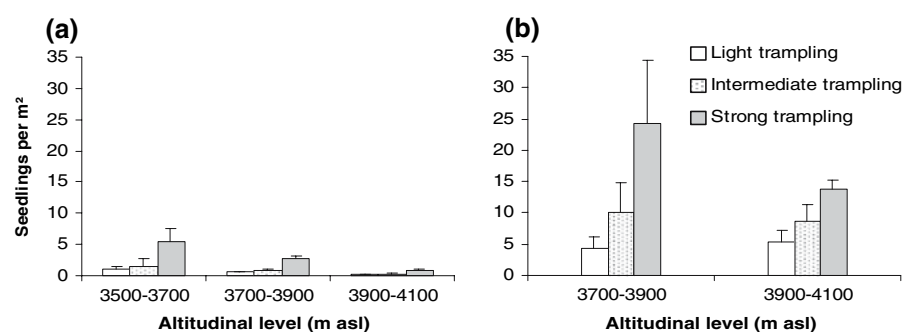


Table 5 Numbers of seedlings, saplings and ramets and related parameters for both *Polylepis* species (mean (SE) of nine plots)

Altitudinal level (m asl)	3,500–3,700	3,700–3,900	3,900–4,100	P		
				Altitude	Trampl.	Interact.
<i>Polylepis incana</i>						
Seedlings per m ²	2.6 (1.0)	1.3 (0.4)	0.4 (0.1)	0.060	<0.001	0.923
Mean vegetation cover (%)	39.5 (7.5)	28.3 (7.7)	31.4 (4.3)	0.782	0.268	0.614
Mean distance of seedling to next vascular plant (cm)	6.3 (1.1)	10.1 (2.1)	9.1 (2.0)	0.570	0.669	0.448
Saplings per m ²	0.1 (0.0)	0.0 (0.0)	0.0 (0.0)	0.180	0.597	0.223
Ramets per m ²	0.2 (0.2)	0.1 (0.0)	0.1 (0.0)	0.786	0.521	0.374
<i>Polylepis pauta</i>						
Seedlings per m ²	–	112 (13)	49 (6)	0.938	<0.001	0.276
Mean vegetation cover (%)	–	86 (36)	90 (25)	0.652	0.888	0.238
Mean distance of seedling to next vascular plant (cm)	–	293 (61)	152 (47)	0.646	0.887	0.702
Saplings per m ²	–	5.7 (0.7)	7.2 (0.8)	0.561	0.523	0.265
Ramets per m ²	–	3.0 (0.1)	2.9 (0.1)	0.148	0.148	0.148

Fig. 5 Mean number of seedlings at different levels of altitude and trampling. **(a)** *P. incana*, **(b)** *P. pauta*; $N = 3$; error bars: SE



In contrast, seed quality was not affected by altitude. Seed lengths hardly changed along the altitudinal gradient and seed viability was consistently low. This was supported by the fact that seed predation by Geometridae did not differ among the altitudinal levels in the *P. incana* stands. Sensitivity

to herbivory is closely related to the capacity of the plant species to produce specific and non-specific secondary compounds that deter or are toxic to herbivores (Mills 1986). Thus, a lack of altitudinal gradients in Geometridae herbivory does not provide evidence of major changes in the composition of

secondary compounds either, and may also indicate a more or less similar seed quality along the altitudinal gradient. However, we found a significant influence of trampling on herbivory. This might be ascribed to possible impacts on the life cycle of the insect species involved, but again, this argument remains tentative.

Altitude is directly linked to a variety of ecological factors with significant impact on plant growth and tree line formation (e.g. temperature, humidity, soil), which were not considered separately in this field study. However, our results reinforce the idea of there being a general thermal constraint on tree lines worldwide (Walter and Medina 1969; Tranquillini 1979; Miede and Miede 1994; Körner 2003a). We confirmed the altitudinal decrease of soil and air temperatures described by Lauer et al. (2001) and Bendix and Rafiqpoor (2001) for *Polylepis* forests in the study area. The eastern slopes with *P. pauta* are characterized by lower temperatures and higher humidity. Mean soil temperature at the uppermost forest stands ranges from 5.6°C to 4.3°C according to our own (Table 1), and previous (Bendix and Rafiqpoor 2001), measurements. This supports the findings of Körner and Paulsen (2004) that critical temperatures for tree growth in the tropics are 1–2 K lower than at higher latitudes with thresholds of 5–7°C.

In accordance with Körner (2003a), we expect soil temperature to be highly correlated to the underlying physiological mechanism of tree line formation. Körner (1998) favors a general effect of low temperatures on growth. The underlying factors may include limited photosynthetic activity—though unlikely with respect to available data (Hoch and Körner 2003; Körner 2003b)—or limited growth capabilities. In the study area, there was an increase in the number of stems in *Polylepis* forests at higher altitudes, accompanied by a decline in stand height and canopy diameter, which provides evidence of reduced growth, as is described for several tree line ecotones by Tranquillini (1979) and Körner (2003a). These growth limitations also may affect reproductive parameters like flowering and fruit set leading to a low overall seed production and a consequent decline in seedling number at higher altitudes. Hence, regeneration followed similar altitudinal gradients as did vegetative growth of adult trees. With our data, we cannot assess whether low regeneration contributes to the maintenance of the current upper tree line

as population dynamics cannot be estimated on a single census basis. In addition, it remains unknown as to how many successful recruitment events are needed for a stable state tree population. Seedling populations reflected the decline of inflorescence number only in the case of *P. incana*; whereas in *P. pauta*—with more than 10 times the seedling number—consequences of flower and seed production on population dynamics are far less likely. Still, the overall recruitment was low at all altitude levels, which indicates that further factors influence regeneration success. In conclusion, long-term research is required to better understand the impact of altitude on the population dynamics of the study species.

Impact of trampling

Cattle activity estimated in terms of trampling density neither had pronounced effects on seed production or viability nor on *Polylepis* stand structure parameters, unlike other grazing systems (Cierjacks and Hensen 2004; Renison et al. 2004). The interaction between trampling and the effect of altitude on tree height might be attributed to the weak decrease in tree height at the intermediate trampling intensity. Trampling by cattle on the other hand was associated with a significant increase in seedling numbers in the stands of both *Polylepis* species. Smith (1977) assumed that seedling survival of *P. sericea* is highly influenced by interspecific competition, but our results coincide with those on *P. australis* of Renison et al. (2005), who also failed to find any correlation between seedling survival and vegetation cover. Furthermore, no influences of stand structure or canopy cover on seedling abundance could be observed. Instead, depth of litter layer was strongly negatively correlated to trampling, a pattern described before for other plant communities (e.g. Olson-Rutz et al. 1996; Yates et al. 2000). A deep litter layer is known to inhibit seedling establishment (Keever 1973; Rotundo and Aguiar 2005), and especially where seeds remain on the upper stratum (Fowler 1986; Hamrick and Lee 1987; Li and Ma 2003). This is particularly probable in the study area where continuous leaf shedding sustains a thick litter layer throughout the year. Trampling results in litter layer reduction and thus creates safe-sites for the establishment of *Polylepis*

seedlings. The significant interaction of altitude with trampling in *P. incana* points to a less pronounced litter reduction by trampling in the highest forest stands. Direct mortality of seedlings caused by cow hooves on the other hand is apparently not important for seedling survival due to the low to intermediate animal loads in the study area (<0.2 animals per ha). A similar result was obtained by Oosterheld and Sala (1990) for herbaceous species in Argentina.

Another explanation for the increased seedling number in the trampled plots could be that both factors co-vary with a third one, such as soil fertility, which improves both fodder value of the herbaceous stratum and availability of regeneration niches for seedling establishment. However, we found no evidence that soil parameters were positively correlated to trampling intensity. On the contrary, trampling significantly increased bulk density in *P. incana*, which was less pronounced in the uppermost forest stands as indicated by the interaction between altitude and trampling. Thus in terms of soil conditions, trampling should have detrimental rather than positive effects on tree recruitment (Renison et al. 2002 a).

In contrast to seedlings, numbers of saplings were very limited in the studied *Polylepis* stands. As there was no correlation to trampling intensity or altitude, this finding indicates low seedling establishment in the forest interior. Moreover, diameter distribution suggests poor sapling recruitment as stems of diameter class 0–10 cm represented only less than 50% of the overall stem number at all altitudinal levels. Studies of Enrico et al. (2004) on woodlands of *P. australis* in Argentina, describe comparable diameter distribution patterns. Such population structures within forest stands are typical for shade-intolerant species that do not successfully regenerate below a closed canopy (e.g. Lambrecht 1989; Everard et al. 1995; West et al. 2000). A similar decline of seedling survival with increasing canopy cover was described for light-demanding *Quercus* species (Crown 1992), and Palmer et al. (2004) recorded low growth rates under dense canopies for *Quercus* saplings. Shade affects regeneration of *Polylepis* species. Enrico et al. (2004) found a higher recruitment rate of *P. australis* in open scrubland than in closed forest. In addition, *P. incana* and *P.*

pauta proved to regenerate more vigorously at the forest edge (Cierjacks et al. 2007, Cierjacks et al. in press) which explains their limited recruitment within closed forest stands.

Grazing intensity in the major part of the study area is rather low with livestock numbers being <0.2 animals per ha. According to Hofstede (1995b, 2001), a cattle density of up to 0.1 animals per ha is sustainable for Páramo ecosystems, while a load of 0.5 animals per ha is expected to lead to overgrazing. Although high values of individual forest stands (8 and 12) imply more severe grazing impact, free roaming of cattle in the whole study area apparently prevents overgrazing because, even in these stands, zones with low trampling intensities could be distinguished. In accordance, effects on the stand structure of *P. incana* or *P. pauta* were nonexistent. One possible reason could be the overall low sapling density, despite increased seedling numbers, under the canopies in trampled plots. In their study in New Zealand, Bellingham and Allan (2003) emphasized that high seedling numbers found in long-term deer exclosures do not necessarily lead to a higher stem number in forest stands. A second reason lies in the fact that cattle do not browse the studied *Polylepis* species (Lægaard 1992).

In summary, low to moderately intense grazing of cattle in *P. incana* and *P. pauta* forests proved to be a sustainable land-use practice, at least with respect to the tree component. As *Polylepis* species in the Páramo de Papallacta are not browsed, the severe consequences for tree rejuvenation and population structure described for Bolivian *Polylepis* species by Hensen (1995, 2002) and Kessler (1995) are not apparent. On the contrary, trampling of cattle may even facilitate recruitment in gaps, providing a more extensive seedling bank on the forest ground. Grazing alone is thus not responsible for the abrupt forest boundaries commonly found at lower altitudes. However, grazing is often accompanied by further disturbances such as burning and selective cutting. The rise of the upper limit of agriculture along with increased burning activity often leads to conflicts between local communities and conservationists (Mena Vásquez 1995). The combined impact of grazing and cutting or burning might finally prevent sufficient vegetation regeneration, which was shown by Hofstede (1995b) for grass Páramo, and by Kok et al. (1995) for Ecuadorian mountain forests.

Therefore, a careful management of the remaining forest stands as well as suitable reforestation measures will be crucial for the long-term conservation of these endangered forest communities.

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