Impact of sowing, canopy cover and litter on seedling dynamics of two *Polylepis* species at upper tree lines in central Ecuador

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Abstract: Failure of reproduction is hypothesized as being a main reason for the formation of upper tree lines but there is, as yet, little supportive evidence of such. This study investigates the effects of experimental sowing, canopy cover and litter depth on seedling emergence and survival of *Polylepis incana* and *Polylepis pauta* at the upper distribution limit of the species in the Páramo de Papallacta, central Ecuador. We established 18 study plots located in the interior, at the edge and at the exterior of closed forests at the upper tree line and analysed seedling dynamics for 1 y following experimental sowing with four different litter treatments. For both species, seedling numbers were significantly higher in the forest interior than outside, and higher in the treatments with the litter layer removed. In *P. pauta*, sowing significantly increased seedling number, which was more pronounced within and at the edge of the forest than outside. In contrast, there was no impact of sowing on seedling emergence in *P. incana*. First-year seedling survival and mean growth rate per month were low in both species. Log-linear models did not reveal significant interactions between survival and canopy cover or litter removal. Our data show that seedling recruitment is limited at the upper tree line – presumably due to extreme climatic conditions – which indicates the importance of constraints in sexual regeneration for tree-line formation in central Ecuador.

Key Words: litter, *Polylepis incana*, *Polylepis pauta*, seedling emergence, seedling survival, tree line

INTRODUCTION

The mechanisms of tree-line formation are still subject to an ongoing debate (Holtmeier 2003, Körner 2003, Miehe & Miehe 1994, Tranquillini 1979). Five basic hypotheses are discussed: physiological stress, physical disturbance, insufficient carbon balance, growth limitation and reproductive failure (Körner 2003). According to current knowledge, all tree lines of the world coincide with a thermal threshold in mean growing-season temperature of 5–7 °C, implying a common climatic driver for tree-line formation (Hoch & Körner 2003, 2005; Körner 1998, Körner & Paulsen 2004). On a local scale, other factors such as human disturbance or herbivory may nonetheless modulate the position of tree lines (Cairns & Moen 2004, Körner 1998, Miehe & Miehe 1994).

The reproduction hypothesis is the only mechanism proposed which explicitly addresses differences between life stages of the respective tree species. Differences in dispersal and recruitment behaviour can – among other factors – explain historic tree-line shifts (Dullinger *et al.* 2004). In particular, seedling emergence and survival may be critical for tree recruitment at higher altitudes (Cuevas 2000, Germino & Smith 2002, Holtmeier 2003, Smith *et al.* 2003, Wardle 1985). However, most of the compiled data on the regeneration at tree lines derive from temperate ecosystems (Hättenschwiler & Smith 1999, Tranquillini 1979) and information on tropical tree lines is still scarce (Byers 2000, Cierjacks *et al.* in press, Hoch & Körner 2005).

Tropical tree lines are characterized by a discontinuous, patchy distribution pattern with scattered forest fragments growing amidst high-altitude grasslands (Miehe & Miehe 1994). In South America, the current tree line is commonly formed by species of *Polylepis* (Rosaceae), which grow up to an altitude of 5200 m asl (Hensen 1995, Holtmeier 2003, Kessler 1995). Recent studies in central Ecuador describe only the uppermost distribution limit as natural, which shows a rather continuous transition to the adjacent grassland vegetation, while forest boundaries below this altitude are widely attributed to human disturbance such as fire and grazing (Cierjacks *et al.* in

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press, Ellenberg 1996, Lægaard 1992, Lauer *et al.* 2001, Sarmiento & Frolich 2002). In contrast, a palynological analysis in the area did not provide conclusive evidence that forest cover was greater in the past (Wille *et al.* 2002).

Data on the role of reproduction for tree-line formation at the upper distribution limit of *Polylepis* spp. remains contradictory. Hoch & Körner (2005) found abundant seedling establishment in the uppermost *Polylepis tarapacana* forests of Bolivia, demonstrating that regeneration is not a limiting factor in this species. Intensive natural regeneration was also reported from a Peruvian *Polylepis* tree line (Byers 2000). In contrast, central Ecuadorian *Polylepis* forests show a clear upslope decrease in seedling numbers which implies climatic constraints for germination and seedling establishment (Cierjacks *et al.* in press). In addition, other factors proved to affect seedling dynamics. For instance, seedling number is higher below a closed canopy than at the forest edge or outside, which may indicate climatic as well as dispersal effects. Moreover, seedling abundance diminishes with increasing litter layer depth (Cierjacks *et al.* in press). However, all these studies rely on observations of natural regeneration and the role of germination was not assessed independently from flowering, seed rain and seed viability. Experimental approaches to seedling emergence and survival of *Polylepis* species, on the other hand, have so far been very limited (Smith 1977) and most experiments focused on transplanted saplings (Brandbyge & Holm Nielson 1991, van Voss *et al.* 2001).

The present study analysed the impact of experimental sowing and site conditions on seedling emergence and survival of *Polylepis incana* Kunth and *Polylepis pauta* Hieron. at their upper distribution limit in the Páramo de Papallacta, central Ecuador. The aim was to assess whether limited seedling establishment due to extreme climatic conditions might be an important factor for tree-line formation. In particular, the study addressed the following questions: (1) How is seedling emergence of two *Polylepis* species at the tropical tree line influenced by experimental sowing, canopy cover and litter depth? (2) Is there any impact of canopy cover or litter layer on seedling survival?

To our knowledge, this is the first time sowing experiments have been accomplished at upper tropical tree lines. A better understanding of the regeneration processes will also contribute to the design of more efficient restoration strategies for high-Andean forest communities.

METHODS

Study site and species

The Páramo de Papallacta (in the sense of Lauer *et al.* 2001) is a glacial landscape located about 30 km east from the Ecuadorian capital Quito between the Cayambe and the Antisana volcanoes. Plio-pleistocene vulcanites covered by pyroclastic and aeolic sediments show the long volcanic history of the study site. The geomorphology is characterized by a plateau covered by young-glacial moraines, lakes and bogs in the central and north-eastern parts and deep U-shaped valleys in the west (Lauer *et al.* 2001). The main soil types of the area are Andosols, which developed on sequentially deposited volcanic ash and have a high allophane content and a slightly acidic soil reaction (Lauer *et al.* 2001).

The climate is a typical tropical highland climate with limited annual variation, but which is locally variable depending on altitude, slope and circulation patterns (Lauer *et al.* 2001). Western slopes receive less precipitation than eastern slopes and rainfall seasons vary (March–May and September–October in the western parts, and June–August in the eastern parts, Lauer *et al.* 2001). At the nearest climatic station in Papallacta (3140 m asl), mean annual precipitation is 1433 mm with a mean annual temperature of 8.3 °C (Bendix & Rafiqpoor, 2001). Soil temperature decreases on average by 0.7–0.8 K per 100 m on both slopes (Cierjacks unpubl. data).

In the Páramo de Papallacta, *Polylepis* forests grow at altitudes of up to 4100 m asl and the remaining stands are among the largest in the country. On the eastern slopes and in the central part of the region, *P. pauta* is the most abundant species. It grows up to 12 m in height and is characterized by long pendant inflorescences with 10–40 flowers and up to eight pairs of leaflets per leaf (Romoleroux 1996). The remaining forests are commonly mixed with other tree species such as *Gynoxis acostae* Cuatrec. and *Solanum stenophyllum* Dun. Below 3700 m asl, *P. pauta* forests are replaced by Andean cloud forests. In the western part of the study area, *P. incana* forests prevail occupying the altitudinal belt between 3500 and 4100 m asl. Stands between 3700 and 3900 m asl are monospecific, while those at upper or lower elevations are mixed with *Gynoxis* spp. *Polylepis incana* can be distinguished from *P. pauta* by its three leaflets per leaf and clearly shorter inflorescences. Maximum growth height is also 12 m (Romoleroux 1996). Both species produce flowers and seeds continuously throughout the year without pronounced seasonality (Simpson 1979), and are capable of vegetative layering by rooted horizontal branches. Seeds are one-seeded nutlets with limited dispersal capacity and a length of about 3 mm.

All stands in the area are subjected to grazing by cattle, horses and white-tailed deer (*Odocoileus virginianus*). The current grazing regime is accompanied by the burning of the bunch grass, which is done in order to promote resprouting of palatable leaves and for cultural reasons (Kessler 2002, pers. obs.). Fire often spreads towards the remaining forest stands and particularly affects the boundary zones of the forests.

For each species, one forest stand at the upper distribution limit was selected. The positions of the stands are S 00°20.185′W 78°16.358′ for *P. incana*, and S 00°20.522′W 78°13.568′ for *P. pauta*. Both stands are characterized by a closed canopy layer and a continuous transition towards the adjacent paramo vegetation at their upper boundary. The size of the stands is 17 ha (*P. incana*) and 30 ha (*P. pauta*). No burning or wood extraction occurred during the period of data collection.

Study design

The impact of sowing, canopy cover and litter depth was analysed in a hierarchical design. At the upper boundary of each stand, we established three blocks of permanent plots located in different parts of the forest separated by more than 300 m. Only sites without visible signs of burning or cutting were selected. In each block, three plots of 15 × 15 m were arranged along a transect perpendicular to the upper forest edge: one plot outside the forest at more than 8 m from the forest edge, the second one including the edge zone, and the third one within the forest at more than 8 m from the forest edge. Altitude, exposure and slope were comparable in all plots (4017–4112 m asl; exposure: NE–NNE; slope: 15–40°). Each of the nine plots was fenced-off between July and August 2004 in collaboration with the owners of the area in order to exclude domestic and wild ungulates.

Within each plot, we established 10 subplots of 2 × 2 m, which were marked with PVC tubes. The area of each subplot was divided into four 1-m^2 sections, in which the litter layer was manipulated according to the following scheme: Treatment (a) litter layer and vegetation removed; (b) litter layer and vegetation removed, with *Polylepis* litter from the surrounding forest added to a depth of 2–3 cm; (c) original litter and vegetation layer; and (d) original vegetation and litter layer, with 2–3 cm of litter added.

In March and April 2005, 50 seeds per treatment were superficially sown into five of the ten subplots. *Polylepis incana* seeds were collected from about 25 trees located in stands with abundant seed production at altitudes of 3600–3700 m asl. Seeds of *P. pauta* were collected from some 20 trees at altitudes between 3800 and 4000 m asl. The yield of each species was carefully mixed before sowing in order to avoid any genetic bias. Seed collection was carried out less than 4 wk before sowing. Germination of the mixed samples was determined in a greenhouse at 2900 m asl between April and October 2005. For each species, 50 seeds were placed in each of 10 plastic pots (diameter 10 cm) filled with forest soil from the study area. Germination was monitored every 14 d for 154 d.

Data collection and analysis

Soil temperature at 10 cm depth was measured along with atmospheric temperature and humidity at 20 cm above soil surface within the *P. pauta* stand from March 2005 to February 2006 with a data logger (INFRALOG, Driesen & Kern, Germany; data logger deployed in all other plots including those of *P. incana* unfortunately failed to measure). In addition, depth of litter layer was measured at three points per treatment in each subplot on all sampling dates and mean litter depth during sampling was calculated.

Stand structure was determined measuring dbh (or, where not possible, diameter below the first ramification), height and canopy diameter of all *Polylepis* trees >1.3 m in height that were present within each plot. In order to distinguish sexual recruitment from basal ramification, the diameter of multi-stemmed individuals was derived from the sum of diameters of all stems. Based on these data, we calculated stem number, basal area, mean dbh, mean height and mean canopy diameter in accordance with Kramer & Akca (1995). Canopy cover was estimated visually. Furthermore, we counted all saplings and ramets between 0.05 and 1.3 m in height. Both could easily be distinguished by excavation of any possible connection with the mother tree.

Seedling emergence and survival were recorded approximately every 6–10 wk from April 2005 to March 2006. Each emergent seedling was marked with a numbered wooden stick and its size was measured at each sampling date. Seedlings already present before sowing were marked and not considered for further analysis. Seedling mortality and mean life expectancy were determined using a life-table approach. For this we first calculated the stationary population by adding the total number of seedlings that emerged during the observation period to the number of seedlings that had survived until the end of the observation time, and then divided this number by two (Gibson 2002). Observation time comprised 335 d in the *P. incana* forest and 323 d in the *P. pauta* stand. Mean life expectancy was subsequently calculated as the stationary population multiplied by the observation time divided by the total number of seedlings emerged.

Statistical analysis was calculated using R, version 2.2.1 (2005). *Polylepis incana* and *P. pauta* were analysed separately. We applied two basic approaches for analysis: for seedling emergence the number of all seedlings that emerged during the sampling year was summed for each factor combination. Due to the hierarchical design, a multifactor ANOVA with litter treatment nested within sowing, sowing nested within canopy cover, and canopy cover nested within sampling block was run. Different error terms for each nesting level allowed for the inclusion of pseudo-replicated data at plot level into the calculation

(Quinn & Keough 2002). In the case of significant ANOVA results, this was followed by a Tukey HSD post hoc test if the factor had more than two levels (position, litter depth). For stand parameters, which were analysed at plot level, simplified ANOVAs with canopy cover nested within sampling blocks were calculated. We analysed untransformed data, relying on the robustness of tests in balanced ANOVA designs (Quinn & Keough 2002).

For the analysis of seedling survival we assessed the life time of each seedling recorded as follows: only seedlings that emerged by the penultimate sampling (middle of January 2006) were included into the analysis. Seedlings that died before the last sampling were considered dead, while those seedlings that survived were recorded as alive. In order to detect interactions of seedling survival with canopy cover and litter treatment, a three-way contingency table was prepared with the counts of dead and alive seedlings being cross-classified with each canopy cover and litter treatment level. According to this table, log-linear models with and without the respective factor interactions were fitted. In order to reduce cells with zero counts, we combined litter treatments (a) with (b), and (c) with (d) for analysis. The models were selected according to G^2 and the Akaike Information Criterion (AIC) (Quinn & Keough 2002).

RESULTS

Climate and stand characteristics

Mean temperatures within the *P. pauta* stand were 5.4 °C at 20 cm above the soil surface and 5.9 °C at 10 cm soil depth. Mean atmospheric humidity was 93.0% with a minimum of 24.6% on a warm day. Atmospheric temperature means ranged between 4.7 and 5.9 °C (Figure 1) and showed a low annual variation with slightly lower temperatures during the main rainfall season between June and September. The lowest temperature minima, however, were measured between October and November 2005 with values as low as −2.3 °C.
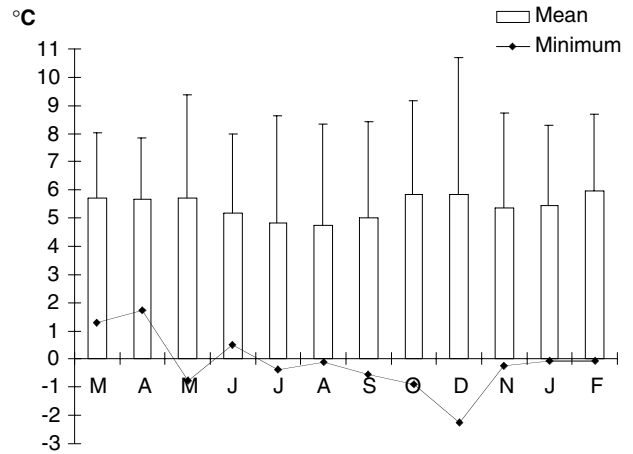

Figure 1. Mean and minimum atmospheric temperatures (20 cm above the soil surface) in the forest interior of the *Polylepis pauta* stand between March 2005 and February 2006 (Error bars: 1 SD).

Stand characteristics of the study plots are summarized in Table 1. In the *P. incana* stand, litter layer was significantly thicker within the forest than at the edge or outside (F = 11.3, df = 2, P = 0.022, N = 9), whereas differences in the *P. pauta* forest were not significant (F = 5.07, df = 2, P = 0.080, N = 9). In both species, estimated canopy cover was significantly different at all transect positions (*P. incana*: F = 149, df = 2, P < 0.001; *P. pauta*: F = 122, df = 2, P < 0.001, N = 9).

In the diameter distribution of both species, the proportion of stems with a dbh < 10 cm was below 50%, which indicates a poor tree recruitment in the study sites (Figure 2). However, the proportion of small stems in the *P. pauta* forest was clearly higher than in the *P. incana* stand. This pattern coincided with the overall low sapling number in *P. incana* in comparison to the *P. pauta* stand, where saplings were significantly more abundant at the forest edge than inside or outside the forest (F = 9.12, df = 2, P = 0.032, N = 9). For *P. incana*, we could not detect significant differences between the transect positions due to the low overall sapling counts (F = 1.00, df = 2, P = 0.444, N = 9). In

Table 1. Stand characteristics at the forest interior, the edge and the forest exterior (mean of three study plots, letters refer to significantly different group means according to the Tukey HSD post hoc tests for factor position).

| Position	Number of *Polylepis* stems per plot	Basal area ($m^2 ha^{-1}$)	Mean dbh (cm)	Mean height (m)	Mean canopy diameter (m)	Estimated canopy cover (%)	Litter depth (cm)	Ramet number per plot	Sapling number per plot
Polylepis incana									
Outside	0.0[a]	0.0[a]	–	–	–	1.0[a]	0.4[a]	1.0[a]	0.0[a]
Edge	13.3[ab]	22.7[b]	20.7	5.4	2.9	46.7[b]	0.7[a]	22.7[b]	1.0[a]
Inside	19.3[b]	32.1[b]	21.5	5.2	2.9	75.0[c]	1.6[b]	6.0[ab]	0.3[a]
Polylepis pauta									
Outside	0.3[a]	0.1[a]	8.7	2.0	2.0	0.3[a]	0.7[a]	0.0[a]	0.0[a]
Edge	10.7[b]	18.1[b]	19.3	5.6	3.9	46.7[b]	1.3[a]	20.0[a]	13.7[b]
Inside	12.0[b]	21.9[b]	19.0	5.4	3.3	65.0[c]	2.0[a]	10.0[a]	1.3[a]
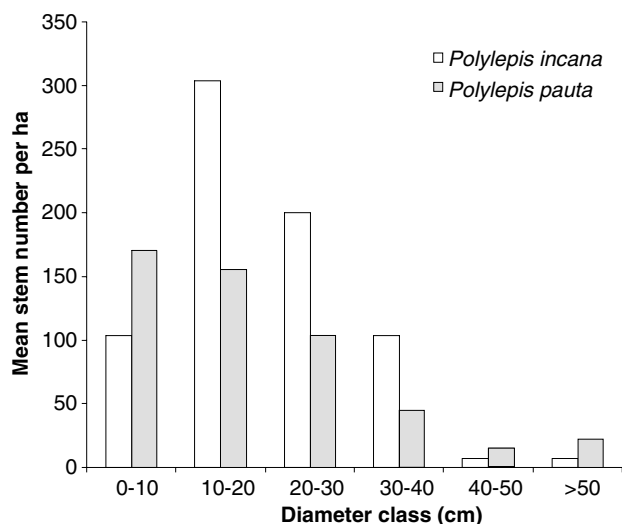
Figure 2. Diameter distributions of *Polylepis incana* and *P. pauta* (means of all plots within the forest and at forest edge; N = 6).

Figure 3. Germination of *Polylepis incana* and *P. pauta* during the sampling period from April 2005 to March 2006 (means of all plots per species, N = 9; error bars: 1 SD).

contrast, vegetative layering was abundant in both species. Ramet numbers were higher at the forest boundary. The difference was significant in the *P. incana* forest (F = 12.7, df = 2, P = 0.019, N = 9), but not in the *P. pauta* stand (F = 4.27, df = 2, P = 0.101, N = 9).

Seedling emergence

In the greenhouse, mean germination was 5.6% for *P. incana* and 2.4% for *P. pauta* (for both species, N = 10 pots of 50 seeds). In the study plots, overall germination was clearly lower. Taking all sown subplots together, totals of 144 (*P. incana*) and 139 (*P. pauta*) seedlings
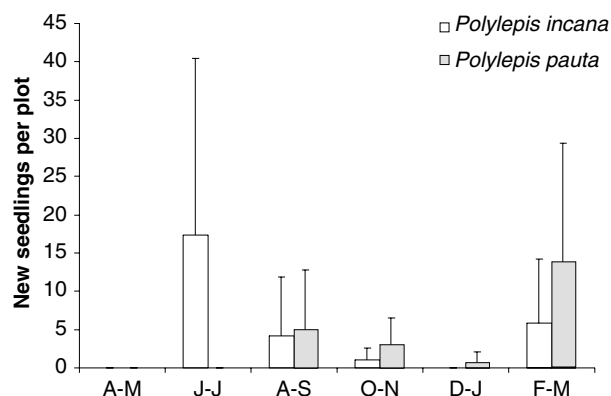
emerged in the course of the year, despite the 9000 additional seeds sown for each species. In the subplots without additional sowing, the total seedling number was 111 in *P. incana* and 55 in *P. pauta.* Thus, sowing increased germination by only 0.4% (*P. incana)* and 0.9% (*P. pauta*).

Seedling emergence varied widely in the course of the sampling period (Figure 3). The highest germination levels were observed between June and September, and February and March. Between October and January germination was limited, which coincided with the period of the lowest minimum temperatures (Figure 1). Almost no seedlings emerged outside the forests. In the *P. pauta* forest, germination was significantly higher inside and at the edge of the forest than outside, and experimental sowing led to a significantly higher seedling number (Table 2; Figure 4b). The positive impact of sowing clearly

Table 2. Multifactor ANOVAs for the seedling numbers of *Polylepis incana* and *P. pauta.*

	df	*Polylepis incana*			*Polylepis pauta*		
		SS	F-ratio	P	SS	F-ratio	P
Error block							
Residuals	2	56.6			16.5		
Error block × Position							
Position	2	193	7.84	0.041	52.5	9.30	0.031
Residuals	4	49.3			11.3		
Error block × Position × Sowing							
Sowing	1	3.03	0.47	0.518	19.6	49.0	< 0.001
Sowing × Position	2	38.1	2.97	0.127	12.2	15.2	0.004
Residuals	6	38.5			2.40		
Error block × Position × Sowing × Litter							
Litter	3	100	6.61	0.001	16.7	4.28	0.011
Litter × Position	6	101	3.33	0.010	13.5	1.73	0.143
Litter × Sowing	3	32.7	2.15	0.110	4.82	1.23	0.311
Litter × Position × Sowing	6	50.4	1.66	0.159	21.9	2.80	0.024
Residuals	36	182			46.9		
Error within							
Residuals	288	958			497		

(a) *Polylepis incana*
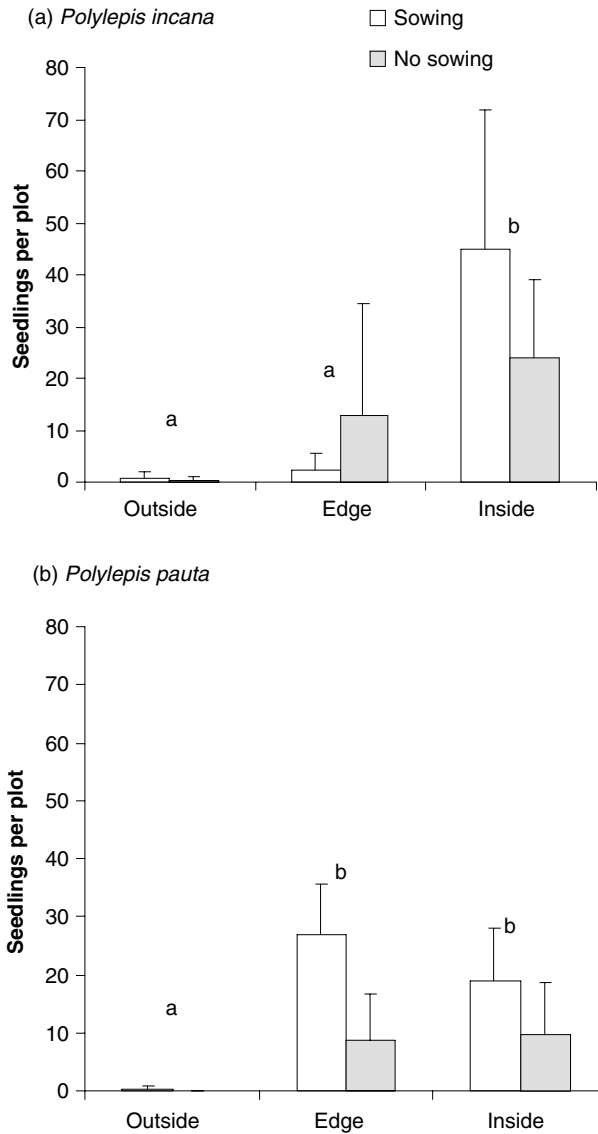

(b) *Polylepis pauta*

Figure 4. Mean seedling numbers per plot of *Polylepis incana* (a) and *P. pauta* (b) pooled for the factors sowing and transect positions (means of three plots, small letters refer to significant differences of pooled data in Tukey HSD post hoc tests according to the factor canopy cover, error bars: 1 SD).

Figure 5. Germination of *Polylepis incana* and *P. pauta* in different litter treatments. (a) Litter layer and vegetation removed; (b) litter layer and vegetation removed with added litter; (c) original litter layer; (d) original litter layer with added litter. Data pooled for all plots, letters refer to significant and marginally significant differences in Tukey HSD post hoc tests, lower-case letters: *P. incana*, upper-case letters: *P. pauta*; error bars: 1 SD.

Table 3. Seedling counts distinguishing between individuals which survived until the last sampling, and individuals that died before, cross-classified to transect positions and litter treatments. Seedlings that emerged at the last sampling (*Polylepis incana*: 57 seedlings; *P. pauta*: 127 seedlings) were not considered.

| | | Survival at last sampling | | | |
| | | *Polylepis incana* | | *Polylepis pauta* | |
Position	Litter treatment	Alive	Dead	Alive	Dead
Outside	a	0	0	0	0
	b	1	1	0	0
	c	0	0	0	0
	d	0	0	0	0
Edge	a	5	23	19	9
	b	3	5	7	14
	c	0	0	0	0
	d	0	2	1	3
Inside	a	14	58	0	1
	b	11	60	1	5
	c	0	5	0	0
	d	0	10	2	5

increased towards the forest interior, which is supported by the significant interaction of transect position with sowing. In *P. incana*, germination was significantly higher inside the forest than at the edge or outside, but the increase in seedling numbers through sowing inside and outside the forest was not significant (Table 2, Figure 4a).

The removal of the original litter and vegetation layer had a significantly positive impact on germination in both species, whereas litter addition did not affect seedling emergence (Table 2, Figure 5). Interactions with transect position in *P. incana*, as well as with transect position
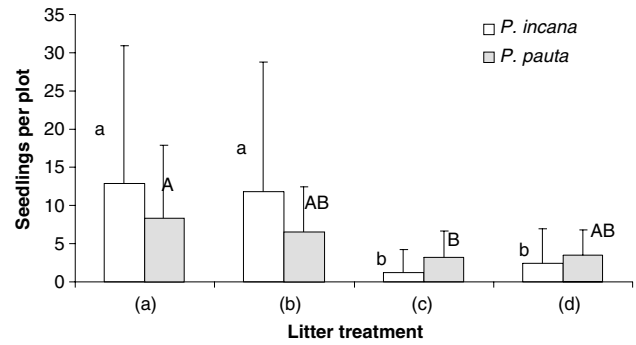
and sowing in *P. pauta*, indicate that the effect of vegetation/litter layer removal is moderated by these factors.

Seedling survival

The majority of the marked seedlings died before the last sampling (Table 3). Seedling mortality was 0.83 in *P. incana* and 0.55 in *P. pauta*. Mean seedling life expectancy was 196 and 216 d, and mean growth rates of all seedlings emerged during the experiment were $0.14 \, \text{cm} \, \text{mo}^{-1}$ and $0.16 \, \text{cm} \, \text{mo}^{-1}$ for *P. incana* and *P. pauta* respectively. Hierarchical comparisons of log-linear models did not reveal clear interactions of seedling survival with canopy cover or litter treatment (Table 4). In *P. incana*, the reduced model (model 1) without interaction could not be rejected in favour of the saturated model, which indicates complete independence

Table 4. Deviance statistics and AIC of the fitted log-linear models for seedling counts in different combinations of the factors canopy cover (C), litter treatment (L) and survival (S) in comparison to the saturated model.

Model		*Polylepis incana*				*Polylepis pauta*			
		G^2	df	P	AIC	G^2	df	P	AIC
1	$C + L + S$	9.28	7	0.233	67.7	17.8	7	0.013	65.7
2	$C + L \times S$	2.55	6	0.862	66.2	16.2	6	0.013	68.2
3	$L + C \times S$	7.56	5	0.182	76.5	13.7	5	0.018	70.0
4	$S + C \times L$	8.15	5	0.982	77.1	5.79	5	0.327	62.0
5	$C \times L + L \times S$	1.42	4	0.841	75.7	4.09	4	0.394	64.6
6	$C \times S + L \times S$	0.83	4	0.934	75.1	12.0	4	0.017	72.5
7	$C \times L + C \times S$	6.43	3	0.092	86.0	1.64	3	0.650	66.3
8	$C \times L + C \times S + L \times S$	0.00	2	0.999	84.8	1.45	2	0.484	70.3
9	Saturated model	0	0			0	0		

of survival, canopy cover and litter treatment. According to the AIC however, model 2 – with interaction between litter treatment and survival – showed a slightly better fit than model 1, which is supported by the significant test of conditional independence for the factors survival and litter (comparison of model 7 vs. model 8, $G^2 = 6.43$, df $= 1$, P $= 0.011$). Thus, there is weak evidence that seedling survival is influenced by litter depth. In the *P. pauta* sample, the reduced model could be rejected in favour of the saturated model. However, the AIC chose the model with the canopy cover and litter interaction (model 4), whereas all models with survival interactions (models 2, 3 and 6) were rejected. Tests of conditional independence for the interactions survival × litter treatment (model 7 vs. model 8, $G^2 = 0.19$, df $= 1$, P $= 0.662$) and survival × canopy cover (model 5 vs. model 8, $G^2 = 2.64$, df $= 2$, P $= 0.267$) were not significant, which shows that seedling survival is not influenced by canopy cover or litter layer.

DISCUSSION

Seedling emergence

Our data provide evidence that transect position – corresponding to canopy cover – has significant impact on seedling emergence of *P. incana* and *P. pauta* at their upper distribution limit in central Ecuador. In both species, seedling numbers were significantly higher within the forest stand than outside where, despite experimental sowing, almost no seedlings emerged during the study period. This pattern was not substantially altered by sowing, although its impact was different in both species. In the *P. incana* stand, sowing did not lead to significantly higher seedling numbers, presumably due to high natural seed rain at the forest edge (Figure 4), but the increase of seedling number within the forest was clearly higher than outside. In the *P. pauta* stand, seedling emergence increased significantly after sowing, but the significant interaction with transect position indicates that the sowing effect is moderated by microclimatic conditions.

The results of our sowing experiments have to be attributed to climatic constraints on germination rather than to seed availability. In both species, overall seedling emergence was much lower at tree line in comparison to germination determined with the same seed stock in a greenhouse experiment at lower altitudes and to data on seed viability in the area (Brandbyge & Holm Nielson 1991, Cierjacks unpubl. data). Below a closed canopy layer, mean temperatures are lower, but extreme temperature minima are less frequent than outside forests. Our assumption that germination processes are impeded by climatic conditions is supported by the fact that seedling emergence clearly decreased during the months with the lowest temperature minima. Previous studies in the area revealed a clear upslope decrease in seedling numbers (Cierjacks *et al.* in press), which similarly shows the negative effect of climate on germination.

Climatic changes along forest edges have been measured in a variety of forest ecosystems (Abe *et al.* 2002, Chen *et al.* 1995, Gehlhausen *et al.* 2000, Kremsater & Bunnell 1999), and there are some data available for *Polylepis* tree-line ecotones (Bendix & Rafiqpoor 2001, Goldstein *et al.* 1994, Cierjacks *et al.* in press). Vulnerability of seedlings to the extreme climatic conditions was also described for other tree-line species (Cuevas 2000, Holtmeier 2003, Wardle 1985, Wardle & Coleman 1992). In *P. sericea*, Smith (1977) found a higher seedling survival in microsites sheltered by rocks. Even individual trees or groups of trees might facilitate tree establishment through alteration of microclimate (Germino & Smith 2002, Miller & Halpern 1998). Thus, the sensitive seedling stage may be advantaged in the more balanced forest interior (Bach *et al.* 2005, Benítez-Malvido 1998, Hättenschwiler & Smith 1999, Pereira de Souza & Válio 2001), although one has to keep in mind that the response to edge effects is always species-specific (Chen *et al.* 1992, Meiners *et al.* 2002, Sanford *et al.* 2003) and also depends on the light requirements of the species (Arcos *et al.* 2006, Luken & Goessling 1995).

The removal of vegetation and litter layer had a positive influence on seedling emergence in both species. A thick litter layer is known to impair successful germination, due to the higher distance between seed and soil, and to the reduced solar radiation if seeds are covered by litter (Facelli & Picket 1991, Peterson & Facelli 1992). A reduction of litter and vegetation cover is also caused by ungulate trampling (Olson-Rutz *et al.* 1996, Yates *et al.* 2000). In the Páramo de Papallacta, seedling number was higher at trampled *Polylepis* sites than at sites without trampling (Cierjacks *et al.* in press). Experimental litter addition however, did not lead to a significant decrease in *Polylepis* seedling number – presumably due to the subsequent reduction of litter density and depth by wind, which was frequent at the forest exterior. Greenhouse experiments with *P. australis* showed no significant differences between germination with and without litter addition (Renison & Cingolani 1998), which might indicate different properties of naturally and artificially deposited litter. However, as we removed the vegetation together with litter layer, and experimentally applied litter did not affect seedling number, we are not able to distinguish between the effect of litter and possible interspecific competition effects as proposed by Smith (1977).

Seedling survival

In contrast to data on other species (Crow 1992, Kellman 2004), we found no evidence that survival of *Polylepis* seedlings was influenced by canopy cover, and there was only a weak interaction between survival and litter layer in *P. incana*. This is in line with records of seedling and sapling survival of *P. australis*, which was also hardly influenced by microclimatic conditions (Renison *et al.* 2002, 2005). As already described for forest gaps, seedling emergence and survival do not necessarily show a similar response to changes in microclimatic conditions (Abe *et al.* 2002, Bullock 2000), and edge effects might influence distinct life stages of a single species in a different manner (Bach *et al.* 2005).

We observed high seedling mortality in the course of the study in both forest stands. Mean life expectancy of the freshly germinated seedlings was only about 200 d. Mean growth rates were less than 2 mm mo^{-1}, and were thus in accordance with the low values reported for branch growth of adult *Polylepis* individuals at upper tree lines in Venezuela and Bolivia (Cárdenas 2000, Colmenares 2002, Hoch & Körner 2005). The diameter distributions of both species – with less than 50% of stems < 10 cm – show that natural recruitment by means of sexual regeneration is poor and might not be sufficient to allow for further upslope migration of the species, even if human disturbances were excluded. In contrast, diameter

distribution of *P. tarapacana* at a tree line in Bolivia had much more abundant recruitment with more than 50% of all stems being in a height class of below 1 m (Hoch & Körner 2005). Stem number and mean height inside the forest clearly showed lower values than reported by Fehse *et al.* (1999) for a mature *P. incana* stand with similar mean diameter at 3600 m asl in the Páramo de Papallacta, which indicates a less balanced age structure and a lower growth rate at the upper tree line. In *P. pauta*, seedling survival was slightly higher than in *P. incana*, which coincides with higher sapling numbers and a higher ratio of narrow stems. The more vigorous recruitment in *P. pauta* might explain differences in the altitudinal limits of the species, which in Ecuador are at 4200 m asl for *P. pauta*, and at about 4100 m asl for *P. incana* (Romoleroux 1996).

In summary, our results show that the seedling dynamics of *P. incana* and *P. pauta* are influenced by the extreme climatic conditions at the upper tree line. Seedling emergence is almost entirely restricted to the shelter of remaining forest stands, and seedling survival is low despite the exclusion of large herbivores. The limited seedling abundance coincides with low sapling numbers and poor tree recruitment. The contribution of asexual ramets to tree recruitment at the upper distribution limit in Ecuador is difficult to assess because of the clumped distribution of ramets, which results in a high intraspecific competition and ramet mortality (pers. obs.). Layering might be as relevant for stand survival as in other tree lines of the world (Holtmeier 2003). However, a further upslope shift of the current tree line by means of sexual regeneration seems unlikely. Regeneration failure caused by climate therefore might not be ruled out as an important mechanism in the formation of tropical tree lines.

The seedling dynamics of *Polylepis* in the Páramo de Papallacta should also be taken into account for possible reforestation approaches. At the upper distribution limit of these species, plantation schemes will be very difficult and time-consuming due to high mortality and low growth rates. That is the reason why conservation of the uppermost forest stands, as opposed to reforestation, should have a high priority. Due to their microclimate, forest remnants have a crucial function for successful restoration of these forest communities. If shelter from extreme climatic conditions by remaining forest stands is not available, plants have to be protected by rocks and plastic tubes (Renison *et al.* 2002). Moreover, litter should be removed in order to facilitate germination processes. Although consequences of ungulate trampling on litter layer proved to have a positive impact on germination, exclusion of animals is recommended for new plantations (Fjeldså & Kessler 1996).

Further research on regeneration at tropical tree lines is still needed. We recommend additional sowing

and plantation experiments in the study area which also consider recruitment patterns at lower altitudes. Preliminary data from sowing experiments at forest-gap transitions far below the upper tree line do not indicate any climatic limitations to seedling recruitment, which supports our findings (Cierjacks unpubl. data). Future studies should also track growth and survival of saplings and ramets, because the short duration of the present study and the overall low growth rates did not allow for reliable data on these aspects.

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