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Establishment of *Pinus wallichiana* on a Himalayan Glacier Foreland: Stochastic Distribution or Safe Sites?

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Abstract

The establishment of tree seedlings in primary succession is thought to occur only after an adequate reserve of nutrients has accumulated in the soil. Individuals of Pinaceae are sometimes reported to grow on very recently deglaciated substrates. This study analyzed the colonization of a glacier foreland by *Pinus wallichiana*. Physical, chemical, and biotic aspects of potential and observed seedling microsites were analyzed with regression methods and tests for proportions. Microsites with intermediate to high moisture levels and alkaline nutrient-poor soils were found to be conducive to seedling establishment. The most recently deglaciated parts of the foreland have soils with little nutrients and high pH. There is a linear change in soil variables from low nutrient content and high pH at the most recently deglaciated parts to more nutrient-rich and neutral toward the pre-neoglacial moraines. Surrounding old-growth forests of *Pinus wallichiana* shed an abundance of seeds onto the foreland, are able to germinate and grow, and are predominant among the early pioneers, which makes this species an unusual pioneer of primary succession. Colonization by *P. wallichiana* is not restricted to particular safe sites. Even though individuals look chlorotic and stunted, they grow at near normal rates. Leaf discoloration of seedlings occurs in soils with high pH and low nitrogen content. *P. wallichiana* is also a canopy dominant on some of the oldest terrains and outside the foreland.

Introduction

Data from Mount St. Helens (del Moral, 1993) have shown the stochastic nature of plant dispersal and, consequently, the course of succession. Primary succession is a dispersal-driven process, where neutral models (cf. Hubbell, 2001), or null models, contrast the gradual development; organic soil before tree establishment. Newly exposed substrate lacks a reserve of nitrogen and organic matter. Seedling establishment typically takes place after an adequate nutrient reserve has accumulated in the soil (Marrs and Bradshaw, 1993). However, limited occurrences of late seral species—like members of the family Pinaceae—have been reported on recently deglaciated substrates (Cooper, 1923; Lawrence, 1958, 1979; Reiners et al., 1971; Blundon et al., 1993; Vetaas, 1994; Helm and Allen, 1995; Jumpponen et al., 1999, 2002; Niederfriniger-Schlag and Erschbamer, 2000).

Cooper (1923) stated that individuals of *Picea sitchensis* (Pinaceae) on young moraines were permanently stunted and would not survive to become dominant members of the late seral forests. Lawrence (1979) on the other hand observed seedlings of a late successional species, *Populus trichocarpa* (Salicaceae), on substrates that had been deglaciated as little as 5–10 years. These shrubs survived as semi-prostrate individuals for decades and individuals appeared stunted due to nitrogen deficiency. When nitrogen levels were amended by nitrogen-fixing plants, these pioneers assumed dominance over the seral community (Lawrence, 1958, 1979).

The field work was done on a Little Ice Age glacier foreland (central Himalaya), which is surrounded by mature forest of *Pinus wallichiana* on large parts of the higher-lying neoglacial (pre–A.D. 1250) moraines on both sides of the foreland. Among the pioneer

species, seedlings and saplings of *P. wallichiana* have high cover-abundance. The species increasingly prevails on older phases originating from the maximum extent of Little Ice Age (approx. 1850; cf. Mayewski and Jeschke, 1979) and older neoglacial moraines.

Following the rationale behind the stochastic dispersal model, we aimed to test a hypothesis based on random dispersal from nearby *Pinus wallichiana* A.B. Jacks. (Himalayan blue pine) forests; microsites hosting seedlings are not different from those without, in terms of the sampled environmental variables.

Materials and Methods

STUDY AREA

The field work took place in the upper Manang district of the Annapurna region in western Nepal, at 28°37'N, 84°00'E (Fig. 1). This district lies in the Trans-Himalayas. The surrounding peaks rise 7000–8000 m above sea level (m a.s.l.). The trunk valley is informally called the Manang valley.

The foreland of the Gangapurna North glacier lies in a tributary valley to the trunk valley of Manang. The Gangapurna valley (our denomination) has the glacier at its southern end and opens to the north into the Manang valley (Fig. 2). The Gangapurna glacier foreland extends a little out of the Gangapurna valley and parts of the terminal moraine complex lie north of the Marsyandi river in the Manang valley. The difference in elevation from the terminal moraines to the glacier terminus is approximately 250 m over a distance of 2.5 km. The highest lateral moraines of the foreland on the sides of the valley lie 200–

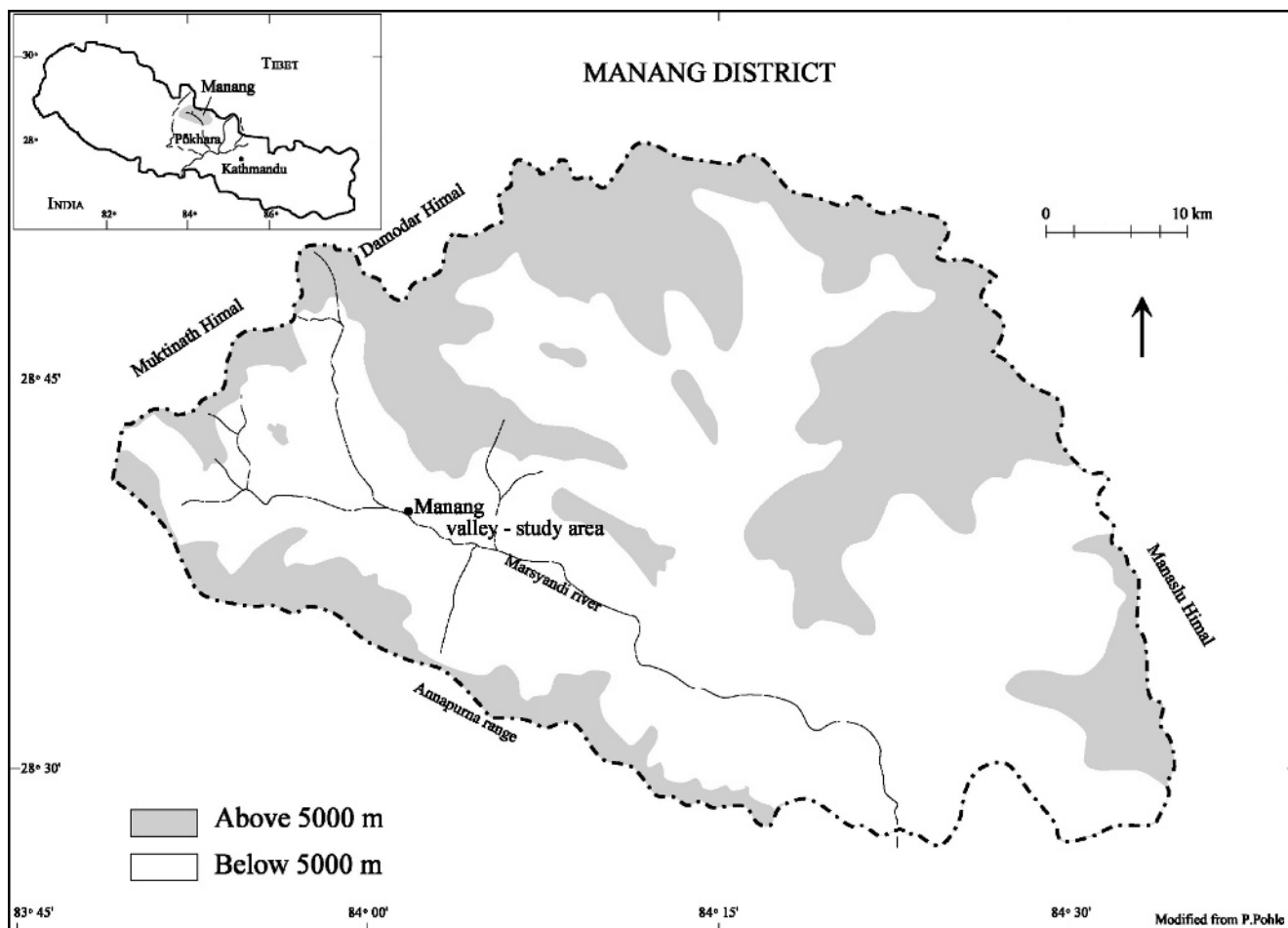


FIGURE 1. Map of Nepal and the Manang district. The Gangapurna glacier foreland is south of the Manang village. Modified from Bhattarai et al. (2004).

300 m above the valley floor. The parent material of the area contains quartzites with layers of hematite, slates, and limestone with clays and marl (Hagen, 1969).

Climatic data were inferred from the nearest climate station, at Jomsom, which is 30 km to the west and has a similar climate. The annual precipitation is approximately 400 mm (Anonymous, 1999). Most downpour falls during the monsoon season from June to September. There is a pronounced dry period in April and May. The occurrence of salt flats on the foreland indicates that annual evaporation may exceed precipitation. Interpolated mean January temperatures range from 0 to -2°C in the altitudinal belt from 3500 to 3800 m a.s.l., respectively. The mean maximum/minimum temperatures range from -2 to 8°C in winter and 14 to 23°C in summer in these altitudes (Anonymous, 1999; Bhattarai et al., 2004). Snow is common during winter.

The plant species of the area derive from the Sino-Japanese and Central Asian phytogeographic regions. The north-facing mountain side of the Manang valley is covered with montane conifer forests. *Pinus wallichiana* is the predominant species, and its old growth forests infringe most of the Gangapurna valley along the lateral moraines. Above 4000 m a.s.l., dominance is shared with *Abies spectabilis* and *Betula utilis* up to the tree line at approximately 4300 m a.s.l. The floor of the trunk valley consists mainly of cultivated land with scattered *Juniperus* spp., *Berberis* spp., and some Rosaceae. The terminal moraines are bordered by this vegetation. *Pinus wallichiana* is conspicuously absent from the vicinity of the village.

There is alpine scrub above the tree line up to approximately 5000 m a.s.l., which consists of species such as *Caragana* spp., *Ephedra gerardiana*, *Juniperus communis*, *J. squamata*, *Rosa sericea*, *R. webbiana*, *Ribes glaciale*, and *Spiraea arcuata*.

Since the Manangi people's livelihood comes from agriculture, pastoralism, and tourism, anthropogenic impacts on the vegetation are grazing, trampling, litter collection, and wood-cutting. Grazers are domestic goats, cattle, and yak.

FIELD SAMPLING

Data were collected (24 April to 28 May 2001) from plots in three different types of terrain on the foreland, where the terrain was level enough to be accessible and where the vegetation was sufficiently unperturbed by sliding debris to have a vegetation development: (1) the terminal moraine complex, (2) the benches of the eastern lateral moraine, and (3) the scree between these benches (Fig. 2). Transect lines were allocated parallel to the glacier margin at the time of material deposition, hence each transect is within a temporal phase of deglaciation. The transects were measured and plots of 5×10 m were placed systematically along the line. Two transects with four plots each were located on the youngest part of the terminal moraine complex which is south of the river (transects T1 and T2). Five transects (T3 to T7) with three plots each were located on the older part north of the river. A section of the lateral moraines include five benches 5–20 m wide

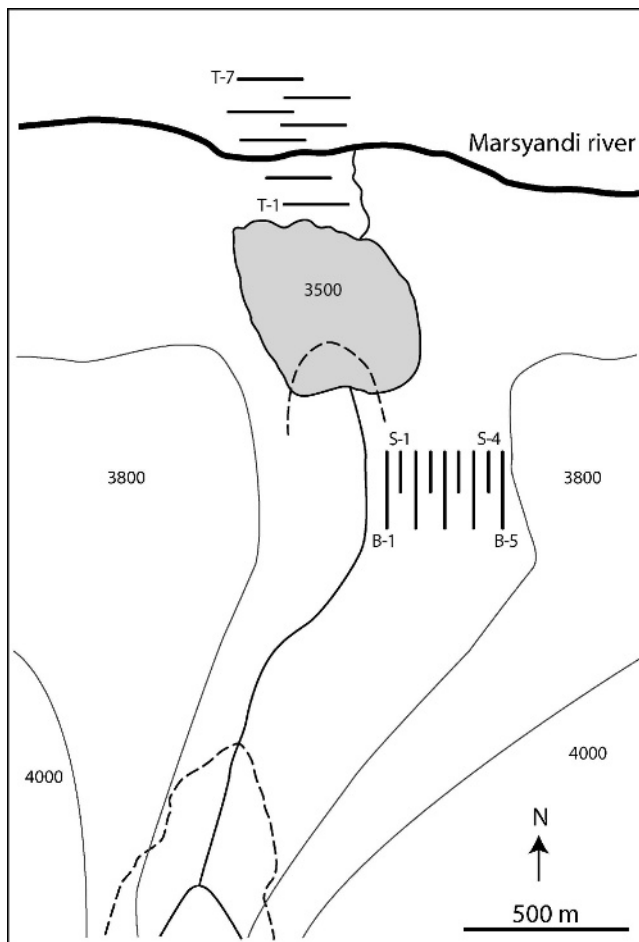


FIGURE 2. Map over the Gangapurna valley and the location of transects. The Marsyandi River runs toward the East, down the Manang valley. The glacial lake lies directly south of the terminal moraine complex with transects T-1 to T-7. The broken line indicates the approximate position of the glacier terminus in 1952 (from a photo in Hagen, 1969). Bench-transects B-1 to B-5 and scree-transects S-1 to S-4 are on the least steep section of the eastern lateral moraine. The broken line near the valley bottom indicates the approximate position of the terminus in 1980 (from a photo by Röthlisberger, 1986). The unbroken line is the glacier terminus in 2003. Numbers are altitudes above sea level in meters. Old-growth forests with *P. wallichiana* cover most of the area between 3800 and 4000 m a.s.l. (Map was made by Beate Helle Ingvarsten).

and up to 170 m long that are relatively intact from landslides. Transects were drawn through the benches (B-1 to B-5 from lowest [youngest] to highest) and five plots located at even distances on each line. The steep screes (ca. 32–37° slope) between the benches were sampled along four transects, S-1 to S-4 (lowest to highest), and these have three plots each.

The following variables were sampled in the plots: (1) altitude (altimeter), (2) aspect and slope (clinometer compass), (3) the curvature of the ground (classified as convex, flat, shallow concave, or deep concave), and (4) subjective assessments of percentage stone cover and vegetation cover, as well as an estimation of cover-abundance of common taxa. A relative radiation index (RRI), which is a relative measure of the substrate's annual exposure to radiation (Oke, 1987; Vetaas, 1992), was estimated as a function of latitude, aspect, and slope.

The sampling followed a stratified random sampling procedure where two types of 1 × 1 m quadrats were sampled in each

plot: subplots and microsities. Seven subplots were randomly allocated in each plot, representing a random sample of potential, but vacant, microsities (a site on the spatial scale of a seedling, *sensu* Titus and del Moral, 1998). Each *P. wallichiana* seedling (<40 cm) in a plot marked the center of an (actual) microsite.

There are conspicuously few *P. wallichiana* north of the river. On the sampled terrain there were only two individual trees on the terminal moraine complex (on transect T-6) north of the river. The old growth forests on top of the lateral moraines most likely shed an abundance of seeds on to this terrain, as well as on to all other part of the foreland. The fall speed of *P. wallichiana* seeds is 1.12 m/s (Lanner, 1998). Therefore, it follows that moderate wind can easily move seeds from the old growth forests to the terminal moraine complex that lies less than 1 km away and 200–300 m lower in elevation.

Data were not sampled from the microsities and the subplots on transect T-5, nor the scree-transects, because vegetation development was poor or negligible, and there was high uniformity of environmental factors. Altogether there were 177 microsities and 315 subplots. The variables sampled in quadrats (microsities and subplots) were the same as in the plots. Forty-one seedlings found in subplots were collected. A disc was sampled at each of the rootnecks of 35 seedlings that were over one year old to provide data on diameter, age, and growth rate.

All individuals of *Pinus wallichiana* are divided into four groups: (1) seedlings <40 cm, (2) saplings <137 cm, (3) juveniles >137 cm without cones, and (4) adults with cones. Height categories are relatively small because many *P. wallichiana* had a stunted growth.

Stress levels or vigor might be revealed by leaf color. The foliage of each *P. wallichiana* was put into six subjective color categories: (0) brown or with marked leaf loss, (1) yellow, (2) more yellow than green, (3) equally yellow and green, (4) more green than yellow, and (5) green.

Due to the remoteness of the study area, five days' walk from the nearest road, only a limited number of soil samples was collected: one sample from a randomly chosen subplot of each plot. All samples were sifted through a 2 mm mesh and analyzed later for moisture content and loss on ignition (LOI). The pH, nitrogen, and phosphorus were determined accordingly: pH in water suspension (1:2), total nitrogen (N) by the Kjeldahl digestion procedure, and phosphorus (P) by isolation in acetate-lactate and estimated by spectrophotometer. All methods are described in Black (1965). Field identifications were carried out in accordance with Stainton and Polunin (1997) and Stainton (1997). Nomenclature follows Hara et al. (1978, 1982) and Hara and Williams (1979).

To get an impression of minimum time since deglaciation of different phases, increment cores were drilled from the largest adults of *Pinus wallichiana* in each plot with a Swedish Mora increment borer.

NUMERICAL METHODS

Generalized Linear Models (GLMs; McCullagh and Nelder, 1989) were employed to analyze relationships between soil variables and seedling density. Seedling density was calculated from counting the number of seedlings in each of the 60 plots; therefore, a Poisson probability distribution was expected (Quinn and Keough, 2002).

Generalized Additive Models (GAMs; Hastie and Tibshirani, 1990) were used to model the functional dependence of leaf color on soil variables. GAMs were chosen because the parametric class

of the response variable (or the residuals) is difficult to assume when the dependent variable is categorical.

All models were subjected to the *F*-test because it is more robust when testing log-linear regressions where the probability distribution of the response is over-dispersed (Hastie and Pregibon, 1993). Singular independent variables in Poisson regression models were assessed by the D^2 -value (= [null deviance – deviance]/null deviance), which is analogous to R^2 (Yee and Mitchell, 1991).

Stepwise selection routines were used to find the most parsimonious multiple regression models predicting seedling density and leaf color as functions of soil variables. All possible predictor terms were tested to the second order of power in GLM, and four degrees of freedom of the smoothing spline in GAM. Akaike Information Criteria (AIC-statistics) were calculated for each resulting model. AIC-statistics provide a means for selecting the best combination of predictors for a multiple regression model because it identifies and excludes variables that are redundant due to high correlation with other variables or to negligible contribution to the explanatory power of the model (Quinn and Keough, 2002).

A Chi-square-based test of proportions was used to find associations between *P. wallichiana* seedlings and microsite characteristics like microtopography and facilitation. The test was employed to find if the proportion of a characteristic in the random sample of subplots ($n = 315$) was different from the proportion of the same characteristic in the microsites ($n = 177$) hosting seedlings. No association gives approximately equal proportions. There may be positive and negative associations, indicating net negative or net positive influence on seedling establishment. The tests performed were two-sided because the presence of any characteristic may facilitate as well as inhibit seedlings (cf. Jumpponen et al., 1998, 1999).

Soil variables except pH were transformed with the Napierian logarithm ($\ln = \log^e$). All analyses were done using R (R Development Core Team, 2003).

Results

The tree ring data suggest a relative age sequence for the following transects, from the youngest to the oldest: B-1 < B-2 < T-1 < T-2 < B-3 < B-4 < B-5 (see Fig. 2). Increment samples from the largest trees indicate that the two highest benches, B-4 and B-5, were deglaciated before the Little Ice Age. Although the largest trees had rotten cores with rings that were not possible to count, they still displayed up to 200 annual increments. Geologists who have worked in the area also see this part of the terrain as much less recently deglaciated than the lower parts of the foreland (Hagen, 1969, Röthlisberger, 1986, Nagaoka, 1990). The age sequence for the remaining transects on the terminal moraine may be inferred from their spatial distribution: T-3 < T-4 < T-5 < T-6 < T-7 (see Fig. 2). Likewise, the sequence including the scree transects on the lateral moraines should be: B-1 < S-1 < B-2 < S-2 < B-3 < S-3 < B-4 < S-4 < B-5.

Soil variables, vegetation cover, and the basal area of *P. wallichiana* were linear functions of inferred relative age of transects B-1 to B-5 and T-1 and T-2 [$\Pr(F) < 0.05$, $n = 7$]. All soil variables increased toward older terrain except pH-level, which decreased. Soil variables displayed the same linear trends toward the older terminal transects, which could not be included in the inferred relative age sequence, either because tree-ring data was not present or because it was corrupted by rotten cores.

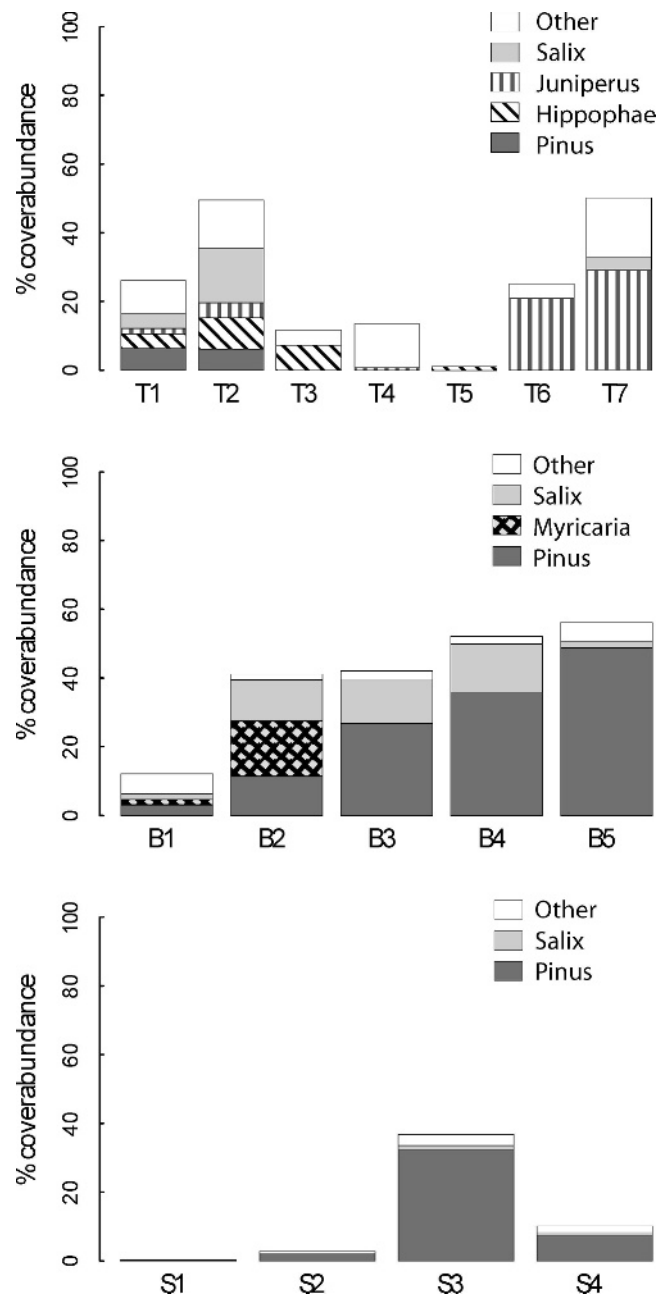


FIGURE 3. Cover-abundance of major taxa as fraction of mean percent vegetation cover on transects on different types of terrain. (a) Transects on terminal moraine complex, (b) transects on benches, and (c) transects on screens. Taxa listed as “Other” are *Aster indamellus*, *Berberis* spp., *Cotoneaster* spp., *Ephedra Gerardiana*, *Lonicera myrtillus*, *Potentilla fruticosa*, *Ribes glaciale*, *Rosa* ssp., and *Spiraea arcuata*.

Vegetation cover and the basal area of *P. wallichiana* were low on the older terminal transects north of the river.

The two predominant taxa on the youngest terrains were *Pinus wallichiana* and *Salix* spp. (Figs. 3a, 3b, and 3c). There were 438 *P. wallichiana* in the sampled terrain; 264 of these were seedlings, 67 saplings, 61 juveniles, and 46 adults. The oldest benches had the highest occurrence of adult trees. Nonetheless, there were three adult trees on T-1, six on T-2, one on each of T-6 and B-2, and nine on B-3.

There were seedlings on every transect that had a *P. wallichiana* population, which is to say on every transect south of the river. The density of seedlings were lower on the terminal

TABLE 1

Plot mean soil and topographical variables modeled individually as predictors of *P. wallichiana* seedling density with GLMs. Sample size $n = 60$.

Models	Res. <i>df</i>	Res. dev.	<i>F</i> -value	Dev. expl.	Pr(<i>F</i>)
ln (moisture)	58	657.6	78.39	10.6%	<0.0001
ln (LOI)	57	660.5	37.76	10.3%	<0.0001
pH	58	722.8	13.19	1.8%	<0.001
ln (nitrogen)	57	612.0	61.99	16.8%	<0.0001
ln (phosphorus)	57	570.1	82.93	22.5%	<0.0001
Vegetation cover (%)	57	686.3	24.84	6.8%	<0.0001
Stone cover (%)	56	72.5	2.82	1.2%	<0.05
Slope	58	661.5	74.45	10.1%	<0.0001
RRI	58	634.3	101.73	13.8%	<0.0001

Note: Res. *df*: residual degrees of freedom. Res. dev.: residual deviance. Dev. expl.: regression coefficient (D^2) * 100. Pr(*F*): probability of the *F*-distribution that H_0 is correct. The regression *df*, or polynomial, is sample size $n - 1 -$ residual *df*.

moraines (T-1 [2.5 per plot], T-2 [0.5 per plot]) than on the bench transects (between 7.4 and 15.2 per plot) and the scree transects (between 2 and 32 per plot). The sampled environmental variables did not vary significantly between the terminal moraines and the benches (two-way ANOVA). The within-site variance was high both at the terrain type level (terminal or benches) and at the transect level. Recently deglaciated terrain was alkaline with a low content of nitrogen, phosphorus, organic soil material, and with a low ability to hold moisture. Soil variables displayed linear trends toward the older terrain, where pH decreased and all other factors increased. The distribution of microsite characteristics were comparable all over the terrain, but vegetation cover increased with time elapsed since deglaciation.

Phosphorus and nitrogen are the best predictors of plot seedling density, but all soil variables yield significant models (Table 1). When data from screes were omitted, the explanatory power of some variables changed. This may be caused by the high occurrence of seedlings in some of the scree plots and the topographical homogeneity of all the screes—slope and aspect,

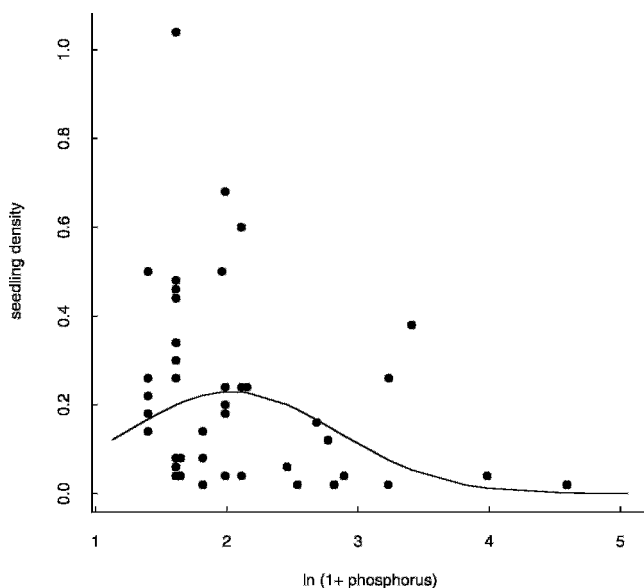


FIGURE 4. Seedling density in plots modeled for functional dependence of phosphorus. Higher seedling densities are predicted at low phosphorus content in the substrate; $n = 60$.

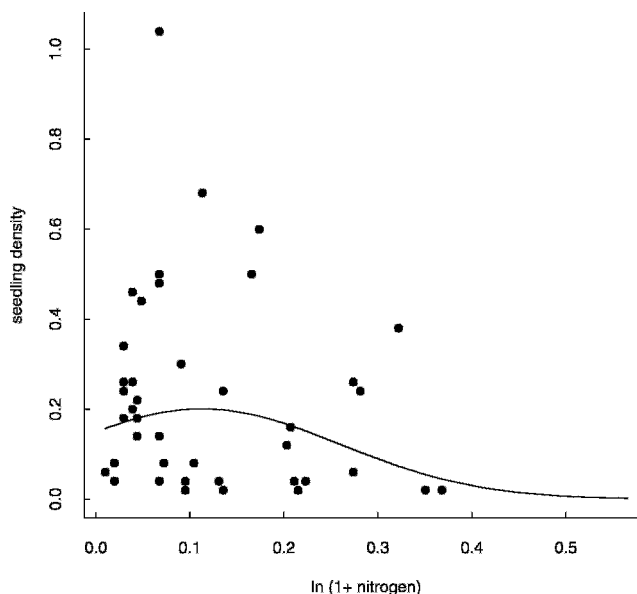


FIGURE 5. Seedling density in plots modeled for functional dependence of nitrogen. Higher seedling densities are predicted at low nitrogen content in the substrate; $n = 60$.

and consequently RRI, are very similar on all the screes. In these analyses moisture is the best predictor of seedling density along with phosphorus and nitrogen (Figs. 4, 5, and 6).

Phosphorus accounted for more than 20% of the deviance in seedling density models, whereas moisture, nitrogen, LOI, and RRI explained between 10% and 20%. The best multiple regression model for seedling density suggested by the stepwise selection procedure was a function of moisture and nitrogen. It had an explained deviance of 36.3%, and the Pr(*F*) were less than 0.0001 for both terms. Seedling occurrence was predicted to peak at intermediate to high moisture values and low soil nitrogen content.

Pinus wallichiana seedlings are negatively associated with convex microsites, protruding stones, and nitrogen fixing plants.

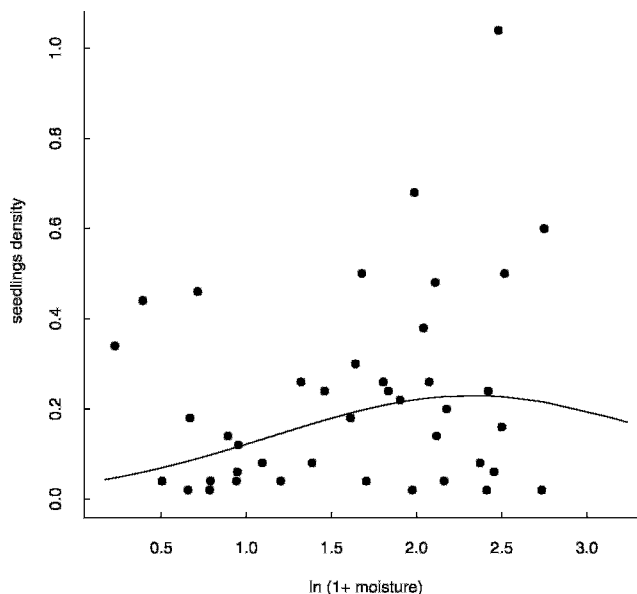


FIGURE 6. Seedling density in plots modeled for functional dependence of moisture. Higher seedling densities are predicted at intermediate moisture content in the substrate; $n = 60$.

TABLE 2

Expected proportion of seedling presence in subplots with various types of potentially facilitating features tested against observed proportion of microsites with seedling presence. Chi-square test for proportions. Sample sizes: subplots $n = 315$, microsites $n = 264$.

Potential facilitation	Expected proportion	Observed proportion	<i>p</i> -value
Convex	0.086	0.042	<0.05
Flat	0.657	0.638	n.s.
Shallow concave	0.200	0.264	0.083
Deep concave	0.057	0.057	n.s.
Stone	0.460	0.268	<0.001
Shrub	0.289	0.223	0.085
Canopy	0.413	0.528	<0.01
N-fixer	0.095	0.0	<0.001

Note: *p*-value: probability that H_0 is correct. Significant *p*-values have bold typefaces. n. s.: not significant.

The only significant positive association is with canopy. There may be associations (not significant) with shallow concave (positive) and shrub-nucleation (negative). Deep concave and flat terrain had observed seedling presence in concordance with what was expected in relation to the random distribution of microtopographical characteristics in the plots, and gave not significant results in the tests. The tests for proportions are listed in Table 2.

Two seedlings had leaf color type 0, which means they were probably dead. Thirteen seedlings had leaf color type 1, 58 had 2, 43 had 3, 89 had 4, and 59 had leaf color type 5.

Most individual trees with more yellow than green color in the foliage were seedlings. Hence, only data from seedlings were employed in the analyses of leaf color. All the soil variables were significant predictors (Table 3). Stepwise selection found pH and nitrogen to be the best explanatory variables in a multiple GAM. This model explained 49.4% of the deviance with a $\text{Pr}(F) < 0.001$. *Pinus wallichiana* seedlings are more likely to have yellow foliage at high pH-values and low levels of nitrogen. At the intermediate and lower range of the pH-gradient in nitrogen poor soil, seedlings sometimes have green leaves.

The growth rate of seedlings that had equally green and yellow foliage or more green foliage did not have significantly higher growth rates than seedlings that had more yellow than green foliage (1.12 mm/ring and 1.05 mm/ring, respectively). None of the variables sampled in plots were significant predictors of growth rates of seedlings ($p > 0.2$), although the sample size was limited ($n = 35$).

TABLE 3

Plot variables modeled individually as predictors of *P. wallichiana* seedling leaf color. GAMs with a quasi-likelihood and 4 degrees of freedom for the cubic spline smoothers are used. Sample size $n = 264$.

Models	GCV-score	Chi square	Dev. expl.	<i>t</i> -ratio	<i>p</i> -value
ln (moisture)	1.401	47.011	16.3%	48.02	<0.0001
ln (LOI)	0.833	254.75	50.4%	62.34	<0.0001
pH	0.799	279.48	52.5%	63.68	<0.0001
ln (nitrogen)	0.862	238.05	48.6%	61.25	<0.0001
ln (phosphorus)	1.102	124.65	33.2%	53.97	<0.0001
slope	1.531	8.82	3.3%	45.3	<0.01
RRI	1.569	2.25	0.8%	44.75	<0.0001

Note: Dev. expl.: regression coefficient (D^2) * 100. n. s.: not significant. The regression *df*, or polynomial, is sample size $n - 1$ - residual *df*.

Discussion

Pinus wallichiana and *Salix* spp. have the highest cover-abundance of the six taxa present in the terrain that has been most recently deglaciated (Figs. 3a, 3b, 3c). Other studies show that trees are capable of seedling establishment on newly exposed terrain in primary succession provided seeds can reach the site (Blundon et al., 1993; Chapin et al., 1994; Niederfringer-Schlag and Erschbamer, 2000). In contrast to other studies, however, the tree *P. wallichiana* persists and predominates throughout the succession on the benches of the Gangapurna North glacier foreland. Successions where the pioneer community is similar to a late successional community are mentioned by Matthews and Whittaker (1987), but thought to occur only in species-poor alpine habitats above the tree line.

The limited occurrence of *P. wallichiana* on the terminal moraines is probably linked to anthropogenic influence, because the ranges of soil variables and the distribution of microsite characteristics are comparable between the benches and the terminal moraines. Domestic animals are kept close to the village during winter (local people, personal commun.), where they forage on all available greenery. Goats were observed browsing on *P. wallichiana* foliage early in the season.

There are populations of *P. wallichiana* on the screes as well, but frequent landslides hinder the succession. The highest vegetation cover was not on the oldest scree (S-4), but on the least steep scree (S-3), probably because there are fewer perturbations in less steep terrain.

Seedling density in the plots had a significant relationship with slope, RRI, and the presence of adult *P. wallichiana*. Schickhoff (1996) noted that in the Kaghan valley, North Pakistan, this species has its main abundance on relatively dry south-facing slopes. This is in contrast to the Manang valley, where there is a conspicuous paucity of this species on the south-facing side, whereas the north-facing side is clad with it. This is probably attributable to more pronounced aridity in Manang.

Pinus wallichiana seedlings are associated with high pH, intermediate to high moisture levels, and low phosphorus and nitrogen values in the plots. This may seem contrary to Schickhoff's (1996) observation that *P. wallichiana* is affiliated with mildly acidic sites, but according to Scholes and Nowicki (1998), *Pinus* spp. are known to colonize moderately alkalic soils in arid environments. Furthermore, because they acidify soils on which they grow, they contribute to the subsequent acidification of these sites. Crocker and Major (1955) found the pH to be virtually unchanged since deglaciation on unvegetated patches of substrate, but more acidic under *Alnus* sp. (Betulaceae) and *Picea sitchensis* in the same phases.

Microsites with moderate depressions of the ground (shallow concave) have near significant higher proportions of seedlings than other microsites, indicating that a moderate depression may ameliorate microsites. Many early pioneers often colonize microsites with depressions (Wood and del Moral, 1988; del Moral and Wood, 1993; Jumpponen et al., 1999; Niederfringer-Schlag and Erschbamer, 2000). Jumpponen et al. (1999) suggested that moderate depressions hold more substrate moisture as well as slow down the wind speed—and consequently receive more seeds and reduce wind desiccation of germinants. The results of this study are not contrary to this, but successful establishment of *P. wallichiana* seedlings is not restricted to depressions.

Microsites with convex ground surfaces have a significantly lower proportion of seedlings than other microsites, suggesting that this type of ground has negative effects on seedling establishment.

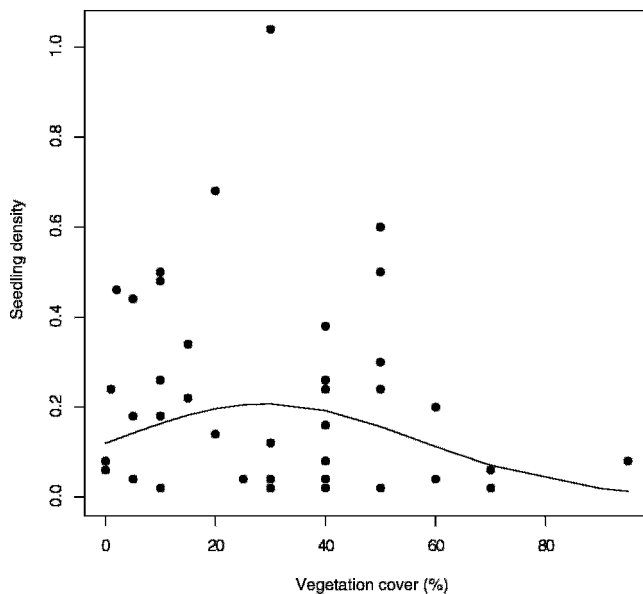


FIGURE 7. Seedling density in plots modeled for functional dependence of percent vegetation cover. Higher seedling densities are predicted at intermediate to low vegetation cover; $n = 60$.

The presence of a potentially protective stone at a microsite significantly lowers the probability of seedling establishment. This may be because seedlings do not need it in terms of protection and because the stone surface reduces available space for germination in quadrats. Using a slightly different approach, where the distance to nearest the rock is measured, other workers have found that stones on glacier forelands provide important safe sites for several early colonizers, also members of Pinaceae (Stöcklin and Bäumler, 1996; Jumpponen et al., 1999; Niederfriniger-Schlag and Erschbamer, 2000). Jumpponen et al. (1999) and Niederfriniger-Schlag and Erschbamer (2000) conveyed that rocks may protect from irradiation as well as increase moisture levels. At our study area, the sun is near zenith during midday—compared to higher latitudes, rocks may not provide notable protection from irradiation.

Pinus wallichiana seedlings are negatively associated with presence of shrubs, although not significantly (Table 2), and seedling density is modeled to peak at 20–40% vegetation cover (Table 1, Fig. 7). Franco and Nobel (1988) found that competing plants may inhibit seedlings by shading out photosynthetically active radiation. Other authors have found that seedlings may benefit from nucleation because nurse plants ameliorate soil conditions and surface temperatures (Jacquez and Patten, 1996). Jumpponen et al. (1998) found evidence for simultaneous canopy inhibition and soil facilitation of establishment of *Pinus contorta* seedlings under *Salix* spp. shrubs. Niederfriniger-Schlag and Erschbamer (2000) found that seed germination is facilitated under the canopy of nurse-shrubs, but subsequent seedling establishment is inhibited. del Moral et al. (1985) argued that species in a climatically severe environment of low productivity will not be sensitive to competition for resources and there will be no signs of inhibition, whereas in highly productive communities there will be competitive interactions like inhibition. The first assumption is supported by Houle (1997), who found no signs of interspecific interactions in the first stage of a succession in subarctic coastal dunes.

Microsites under a canopy have a significantly higher proportion of seedlings than expected. Interpreting this is not straightforward, because canopy cover on the sampled terrain consists mostly of *P. wallichiana*. This means that the seed rain at

these microsites is higher than at other sites. It is also contrary to the definition of facilitation, i.e. two different species improving conditions for each other (Connell and Slatyer, 1977; Begon et al., 1990; Chapin et al., 1994). Because there is a positive association between seedlings and canopy, there may be a positive effect on seedlings growing in the litter under conspecific adults. This effect may be caused by a higher probability of ectomycorrhiza inoculation or less dense thickets of competing shrubs.

Nitrogen-fixing plants often play an important role in primary succession (Sprent, 1993), but *P. wallichiana* seedlings display a negative association with these according to the results of this study, although the test for proportions may be subject to stochastic variance due to the sparse occurrence of nitrogen-fixing plants on the glacier foreland. Seedling densities are modeled to peak at the low end of the nitrogen gradient (fig. 5), suggesting that nitrogen facilitation is not required by the target species.

Although *P. wallichiana* seedling density peaks at the high end of the pH gradient and at the low end of the nitrogen gradient, seedlings tend to display signs of leaf discoloration at such sites. Lawrence (1958, 1979) observed yellowish foliage on several species of trees which are normally late successional (e.g. Pinaceae), but which had established as seedlings on recently deglaciated moraines. Tree seedlings close to nitrogen sources, e.g. animal bones or feces, had blue-green foliage. When ammonium nitrate was applied to seedlings of *Populus trichocarpa* (Salicaceae), their leaves turned green (Lawrence, 1958, 1979). Based on this it was concluded that yellow leaves are a symptom of nitrogen deficiency. This is supported by our results, which point out nitrogen as a good predictor of seedling leaf coloration. Soil pH is also a good predictor of leaf color. Calcifuge plants growing on chalky soil often suffer from phosphorus or iron deficiencies. The symptom of the latter in conifers is yellow leaves. The leaves may turn yellow because nitrogen mobilization decreases at high alkalinity (Larcher, 1995). Nitrogen may also be less available to *P. wallichiana* in alkaline substrates because nitrogen will predominantly be in the form of nitrates, which are assimilated less efficiently by its ectomycorrhizal symbiont (Scholes and Nowicki, 1998). Malagoli et al. (2000) found the net uptake of ammonium (low pH) to be six times higher than nitrates (high pH) in *Pinus sylvestris*.

Jumpponen et al. (2002) found established *Abies lasiocarpa* (Pinaceae) on barren terrain deglaciated for 20–23 years. No traces of symbiont sporocarps were found on these seedlings. Chapin et al. (1994) and Jumpponen et al. (2002) suggested that the alkalinity of recently deglaciated substrate may be too high for growth and/or inoculation of ectomycorrhizae.

There are linear relationships between relative time since deglaciation and environmental variables (cf. above; Mong, 2003). Therefore, it is difficult to discern which characteristics are most important to safe sites on different types of terrain. The microsite requirements may be different on terrains of different ages, both in terms of how much a safe site is needed and which characteristics are required by the seedlings. The optimal soil values for seedling establishment seem to be those that typically prevail on the youngest substrates. This seems like an avoidance of terrains with an advanced soil formation, but is probably a trade-off effect—that seedlings prefer low nutrient levels, lack of organic matter in the substrate, and high pH, rather than facing the increased competition on terrains with more vegetation. Although seedlings of *P. wallichiana* prefer some moisture, and possibly also absence of competition, it is important to note that seedlings did occur in microsites that were not safe as characterized by the criteria above. In contrast, Wood and Morris (1990) and del Moral and Wood (1993) showed that virtually all colonization on the pumice plains

of Mount St. Helens took place in safe sites, hence establishment was limited by the paucity of safe sites rather than by seed dispersal. Reports from glacier forelands portray a more moderate role of microsites, where safe sites influence the distribution of colonizers, but are not, as with the results of this study, a strong limiting factor (Blundon et al., 1993; Jumpponen et al., 1999; Niederfringer-Schlag and Erschbamer, 2000).

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