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Distribution and community structure of treeline birch (*Betula utilis* D. Don) forest in a trans-Himalayan dry valley was studied in Manang (central Nepal) with the major focus on regeneration. Along 5 vertical transects, a total

of 41 square quadrats (10 m x 10 m) were sampled to determine the importance value index (IVI) of tree species, distribution pattern of seedlings and saplings, and soil attributes. Regeneration was assessed by a density-diameter curve. Moisture plays an important role in spatial (horizontal) distribution of *Betula utilis*. Pure *Betula* forest forming the treeline was mature, with high basal area (2.3%), but mixed *Betula* forest at lower elevations was young. This might have developed after large-scale clear cutting of *Abies spectabilis*. If not severely disturbed, mixed *Betula* forest may be replaced by *Abies spectabilis*. In general, *Betula utilis* was regenerating, as evident from a reverse J-shaped density-diameter curve for both forests. However, the distribution of seedlings and saplings was spatially heterogeneous and appeared to depend on canopy cover. The stands with highest seedling and sapling densities of *Betula utilis* had no trees. *Betula* seedlings were absent where the tree density and basal area (BA) exceeded 20 stems/100 m² and 1.0% respectively. It was apparent that *Betula* seedlings could not establish under their own closed canopy even if they produced viable seeds. Partial canopy opening may induce seedling establishment and hence continuous regeneration of *Betula utilis* at mature stands. The treeline formed by *Betula utilis* was abrupt—the anthropo-zoogenic type—without the krummholz zone.

Keywords: *Abies spectabilis*; anthropo-zoogenic treeline; density-diameter curve; soil moisture; Manang; Nepal.

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Introduction

Betula utilis D. Don (*bhojpatra* birch) forms treeline vegetation all along the Nepal Himalayas, and extensive stands of this species can be found on northern shady slopes and ravines (TISC 2002). It is the only broadleaved angiosperm tree species in the Himalayas which dominates an extensive area at subalpine altitudes (Zobel and Singh 1997). *Betula* spp. show a high

freezing tolerance (Sakai and Larcher 1987) which enables them to form a treeline in the Himalayas (Zobel and Singh 1997; TISC 2002) as well as in the Scandinavian region (Cairns and Moen 2004).

Lack of sufficient regeneration is a major problem of mountain forests (Kräuchi et al 2000). Most studies on subalpine forests have reported poor seedling recruitment in understories of undisturbed old-growth forests (Coates 2002; Mori and Takeda 2004). Regeneration of *Betula utilis* forest and spatial patterns of seedling distribution in the Central Himalayas have not been studied, though the regeneration of *Betula* spp. has been studied extensively elsewhere in the world (Marquis 1965; Houle 1998; Catovsky and Bazzaz 2000). Here we report on the community structure and regeneration status of the *Betula utilis* forest—a major habitat of *Moschus chrysogaster* (a protected mammal in Nepal) in the Manang valley of the trans-Annapurna mountain range, central Nepal. The *Betula utilis* forest forms treeline vegetation between 3500 and 4200 m on northern slopes of the inner Himalayas (Stainton 1972). The present study was undertaken with the following specific objectives: 1) to document distribution and community structure of *Betula utilis* forest; 2) to study spatial patterns of seedling distribution and regeneration behavior of *Betula utilis*; and 3) to understand treeline structure.

Materials and methods

Study site

The study area (28° 37'–38' N, 84° 01'–05' E; altitude: 3500–4200 m) lies in the upper part of Manang district, central Nepal. The upper Manang (Nyishang) has a glacially formed U-shaped valley (3000–3400 m) traversed by the Marsyangdi River and surrounded by high mountains (> 6000 m). The peaks are formed of paragneiss and schists encroached by quartzites with layers of haematite, slates, and limestone with clays and marl (Hagen 1969). The valley lies in a rain shadow area of the trans-Annapurna region with a mean annual precipitation of 444 mm (at 3420 m) and mean annual temperature of 6.2° C (Miehe et al 2001). It is covered by snow during winter for about 5 months (November to March). Snowmelt water is the main source of soil moisture for forest growth. Forest vegetation is mostly confined to the moist north-facing slope of Annapurna, and the valley floor. However, isolated trees and small stands of *Juniperus indica* at lower elevations and *Betula utilis* at higher elevations are found on the sunny slope. On the north-facing slope the lower belt (3000–3500 m) has blue pine (*Pinus wallichiana*) and juniper (*Juniperus indica*) forests, while the upper belt (3500–4200 m) has fir (*Abies spectabilis*) and birch (*Betula utilis*) forests up to the treeline (4200 m). However *Betula utilis* has

TABLE 1 Spearman's correlations (*r*) among different attributes of plant communities and soil. The coefficients were determined among all attributes but the Table shows only significant values for relevant parameters.

Characteristics	Attributes	Correlation coefficient
Elevation	Tree density: <i>Pinus wallichiana</i>	-0.96 ^a
	Sapling density: <i>Abies spectabilis</i>	-0.89 ^a
	Total tree BA	0.82 ^b
	Tree BA: <i>Betula utilis</i>	0.86 ^b
	Soil moisture	0.81 ^a
	Soil pH	-0.93 ^a
	Soil organic matter	0.86 ^b
	Soil N	0.86 ^b
Tree density for <i>Betula utilis</i>	Soil N	0.86 ^b
Tree density for <i>Abies spectabilis</i>	Sapling density: <i>Abies spectabilis</i>	0.81 ^b
Seedling density for <i>Betula utilis</i>	Basal area: <i>Betula utilis</i>	-0.82 ^b
Total basal area	Soil moisture	0.34 ^b
Basal area for <i>Betula utilis</i>	Soil pH	-0.89 ^a
	Soil organic matter	0.79 ^b
	Soil N	0.79 ^b

^a) significant at $p < 0.01$; ^b) significant at $p < 0.05$

descended to the valley floor (3000 m) along moist water courses. It is also found as isolated stands on the southwest-facing slope of the valley where soil moisture is relatively high. Moist alpine scrub above the treeline on the north-facing slope was dominated by *Rhododendron anthopogon*, *Juniperus indica*, *Caragana* spp., etc. On the dry southern slope alpine scrub has dwarf and prostrate junipers (*Juniperus indica*, *J. recurva*, *J. squamata*), *Rhododendron lepidotum*, *Rosa* spp., *Berberis* spp., *Ephedra Gerardiana*, etc.

The *Betula utilis* forest sampled in the study included part of the Humde and Braka Village Development Committee area. The sampling represented mixed (3500–3900 m) and pure (3900–4200 m) forests, as well as disturbed and undisturbed forests. The mixed *Betula utilis* forest has *Abies spectabilis* and *Pinus wallichiana* as associated species, where stumps of large trees of these 2 later species were frequent. Pure *Betula* forest, with closed canopy, has a few isolated specimens of *Abies spectabilis*. The forest is relatively undisturbed except for severe fires that occurred at some sites more than 40 years ago, according to local elders. These fire-damaged sites had large fallen tree trunks, but living trees were either very sparse or absent. Subalpine *Betula utilis* forests and alpine meadows were the main grazing lands for livestock and wild animals (eg blue sheep and

musk deer). *Betula utilis* is the most preferred tree for firewood, agricultural implements, and poles for construction work in the Manang valley. However, the species has been conserved by local conservation laws and by difficult access.

Field sampling

Vegetation

The study site was divided into 5 vertical transects, each representing both mixed and pure forests. In each transect, paired quadrats (10 m × 10 m) spaced horizontally about 100–150 m apart were sampled at every 100-m elevation increment up to the treeline (4000–4200 m). Altogether, 41 plots were sampled. In each sampling plot, the number of trees (diameter at breast height [dbh, ie at 137 cm] ≥ 10 cm), saplings (dbh < 10 cm), and seedlings were counted for each tree species, and circumference at breast height (cbh, 137 cm) was measured. Dead but erect trees were also identified and included.

Soil

Soil moisture was measured in each sampling plot by a Soil pH and Moisture Tester (Tekemura Electric Works Ltd., Japan; model: DM 15), and litter thickness by a ruler. For a detailed analysis, soil samples were collect-

TABLE 2 Density (per ha), basal area (%), and Importance Value Index (IVI) of tree species in mixed and pure *Betula utilis* forests.

Tree species	Mixed <i>Betula</i> forest (3500–3900 m)			Pure <i>Betula</i> forest (3900–4200 m)		
	D(ha ⁻¹)	BA (%)	IVI	D(ha ⁻¹)	BA (%)	IVI
<i>Betula utilis</i>	864	0.57	161.41	1207	2.2	286.87
<i>Abies spectabilis</i>	220	0.31	85.59	26	0.1	13.1
<i>Pinus wallichiana</i>	200	0.13	52.88	–	–	–
Total	1284	1.01	299.88	1233	2.3	299.97

ed from 1 of the 2 (paired) quadrats in each elevation zone of each transect. In each sampling quadrat 4 soil samples (20–30 cm depth) collected each from 4 quarters and single samples from the center were mixed and sieved to form a single soil sample; 16 such samples were collected, air dried in shade, and stored in plastic bags until laboratory analysis.

Laboratory analysis

Soil pH, organic matter (OM) content, and 3 macro nutrients (Nitrogen N, Phosphorus P, and Potassium K) were determined in the air-dried soil samples (n = 16) at the Laboratory of Soil Science Division, National Agriculture Research Council (NARC), Lalitpur. Soil pH was measured by pH meter in a 1:1 mixture of soil and distilled water; OM content by the Walkley and Black method; total N by the micro-Kjeldahl method; available P by Oslén's modified carbonate method; and available potassium (as K₂O) by flame photometer method. All these methods have been described in Gupta (2000).

Numerical analysis

From the field data, density (stems/100 m²), frequency (%), basal area (%), and the importance value index (IVI) of trees were calculated following Zobel et al (1987). The density of seedlings and saplings of tree species was also calculated. To assess regeneration status of *Betula utilis*, density–diameter curves were developed separately for mixed and pure forests. Values of density on the y-axis of the curve were expressed in logarithmic scale to decrease variation within the dataset.

Non-parametric Spearman's correlation coefficients (r) were used to estimate the relationship among elevation, forest community attributes, and soil characters. Relevant values with significant correlation (p = 0.05 and p = 0.01) are presented in Table 1. In attempting regression analysis using elevation, soil pH, soil moisture, density (tree, sapling, and seedling), and tree basal area, the data were tested for normality using the Kolmogorov-Smirnov test. Except for elevation and soil pH, other parameters did not meet the assumption of normality even after log₁₀ and square root transforma-

tions. Thus we could not perform regression analysis. Instead, we constructed scattered diagrams for the following pairs of characters: seedling and sapling density of *Betula utilis* with tree density and tree basal area of the same species, and sapling density vs tree density for *Abies spectabilis*. The regression analysis was done between elevation and soil pH (figure not shown). All statistical analyses were done using SPSS Version 10.

Results

Distribution and community structure

The *Betula utilis* forest was present as continuous tree-line vegetation on moist, north-facing slopes interrupted by glaciers, landslides, and rocky cliffs at some places. On the dry, southwest-facing slope, 2 isolated stands were observed near the spring which had high soil moisture. Tree species richness in the forest was very low: only 3 tree species in mixed forest and 2 in pure forest (Table 2). Total tree density of these 2 forests was nearly equal, but the basal area of the pure forest (2.3%) was more than twice that of the mixed forest (1.01%). Trees were smaller in the mixed forest (dbh 10–35 cm) than in the pure forest (dbh 10–70 cm). In the pure *Betula utilis* forest, *Abies spectabilis* was present only in 7% of the sampling plots.

Betula tree density was higher than that of other species except between 3500 and 3600 m (Figure 1A). Average *Betula* tree density was higher at higher elevations. The most densely populated plots were between 3800 m and 3900 m. The density of *Abies spectabilis* increased from 3500 to 3800 m; it then decreased until it disappeared at 4000 m. The density of *Pinus wallichiana* decreased with increasing elevation (Figure 1A, Table 1, p = 0.01). The average of the total tree basal area generally increased from 3500 to 4100 m (Figure 2, Table 1, p = 0.05). In the highest elevation range trees were small with lower basal area, which represented the highest timberline in Manang.

Soil

Soil moisture increased with increasing elevation (p = 0.01) and tree basal area (p = 0.05) (Table 1). Soil was acidic to neutral (pH 5–7) (Figure 3) and soil pH

FIGURES 1A TO 1C Density of trees (A), saplings (B), and seedlings (C) of tree species in different elevation ranges.

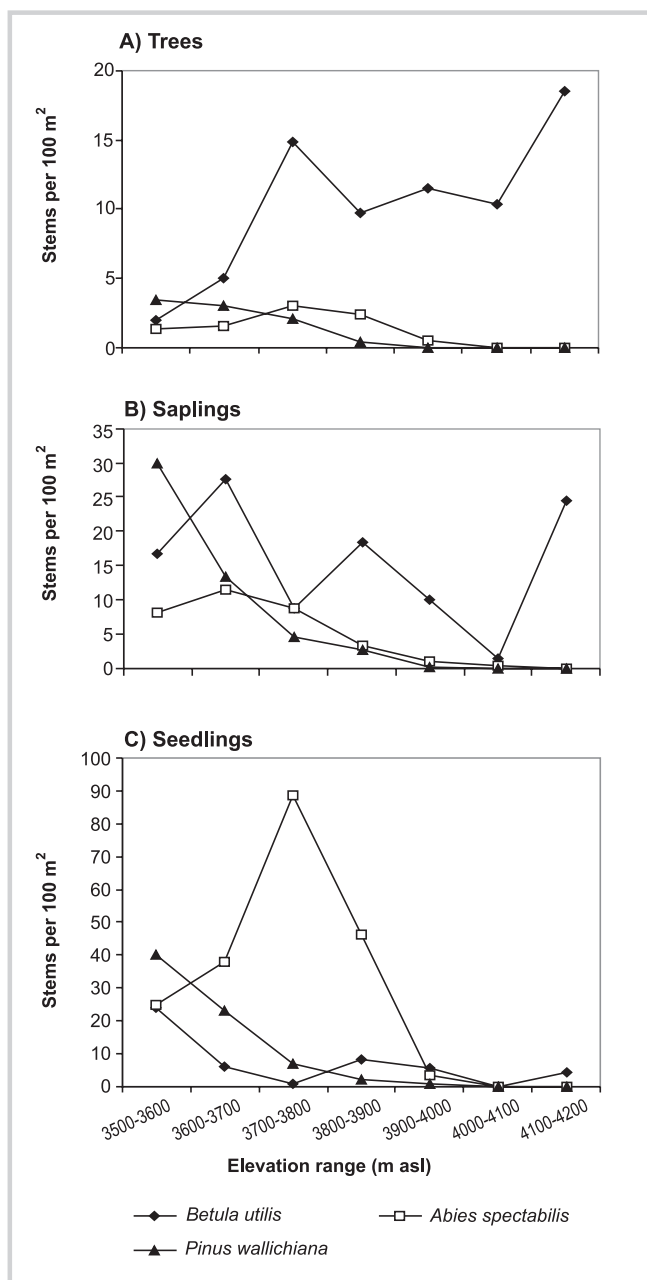


FIGURE 2 Basal area (BA) of individual tree species and of all species in different elevation ranges.

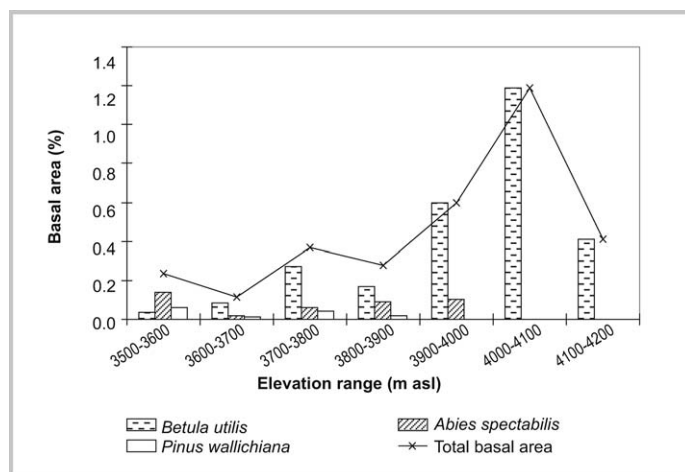
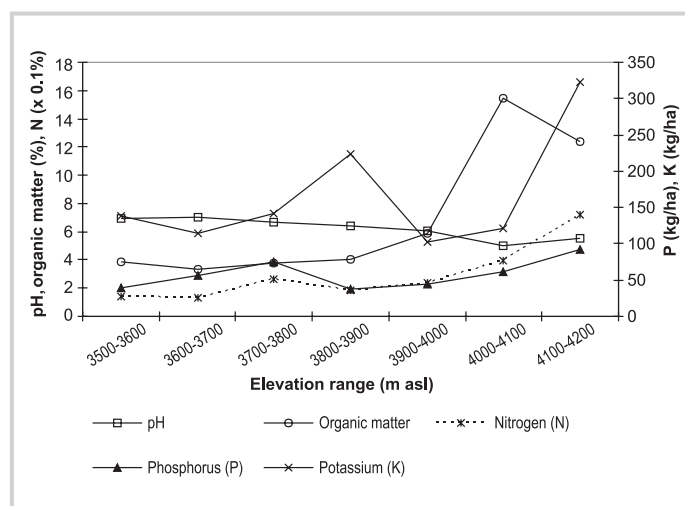


FIGURE 3 Soil pH, total nitrogen (N, × 0.1%), available phosphorus (P₂O₅, kg/ha), and available potassium (K₂O, kg/ha) of soil samples collected from different elevations. Each value is the mean of triplicate samples, except those for the last 2 elevation ranges, which are the values of single soil samples.



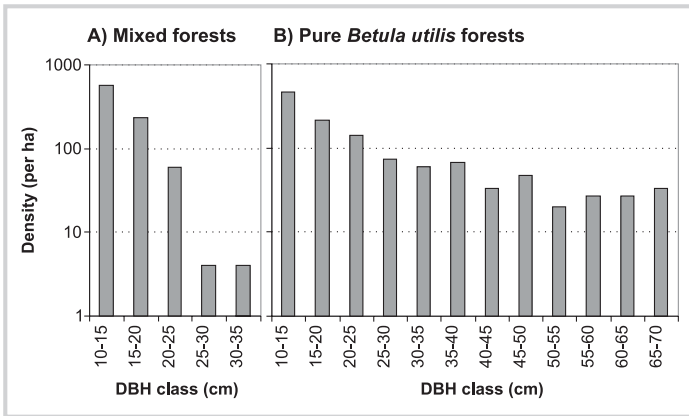
declined with increasing elevation ($R^2 = 0.72$, $p < 0.001$, diagram not shown). Soil OM ranged from 1.74 to 15.41%; total N from 0.1 to 0.7%; available P from 11 to 92 kg/ha; and available K from 57 to 322 kg/ha. All these soil characteristics generally had high values at high elevations (Figure 3) but the relation between them and elevation was not significant except for OM and N (Table 1). Soil nitrogen increased with increasing elevation ($p = 0.05$) and the *Betula utilis* pure forest had higher soil N (0.367%) than the mixed forest (0.184%).

Thus, the edaphic condition became better (higher soil moisture, OM, and N) in the pure *Betula* forest at higher elevation. On undisturbed plots of the pure forest, litter thickness on the forest floor was up to 25 cm but it was relatively thin (up to 10 cm) in the mixed forest.

Regeneration

The density–diameter curve of the tree population of *Betula utilis* both in mixed and pure forests nearly resembled a reverse J-shape (Figure 4). Thus, in general both forests were regenerating, although regeneration was higher in the mixed forest. The distribution of trees as well as saplings and seedlings was not uniform among the sampling plots; there were no trees on 23% of the sample plots, saplings on 8% of the plots, and seedlings on 60%. The average sapling density in the

FIGURES 4A AND 4B Density–diameter curve of *Betula utilis* in mixed (A) and pure (B) *Betula utilis* forests. Density is in logarithmic scale.

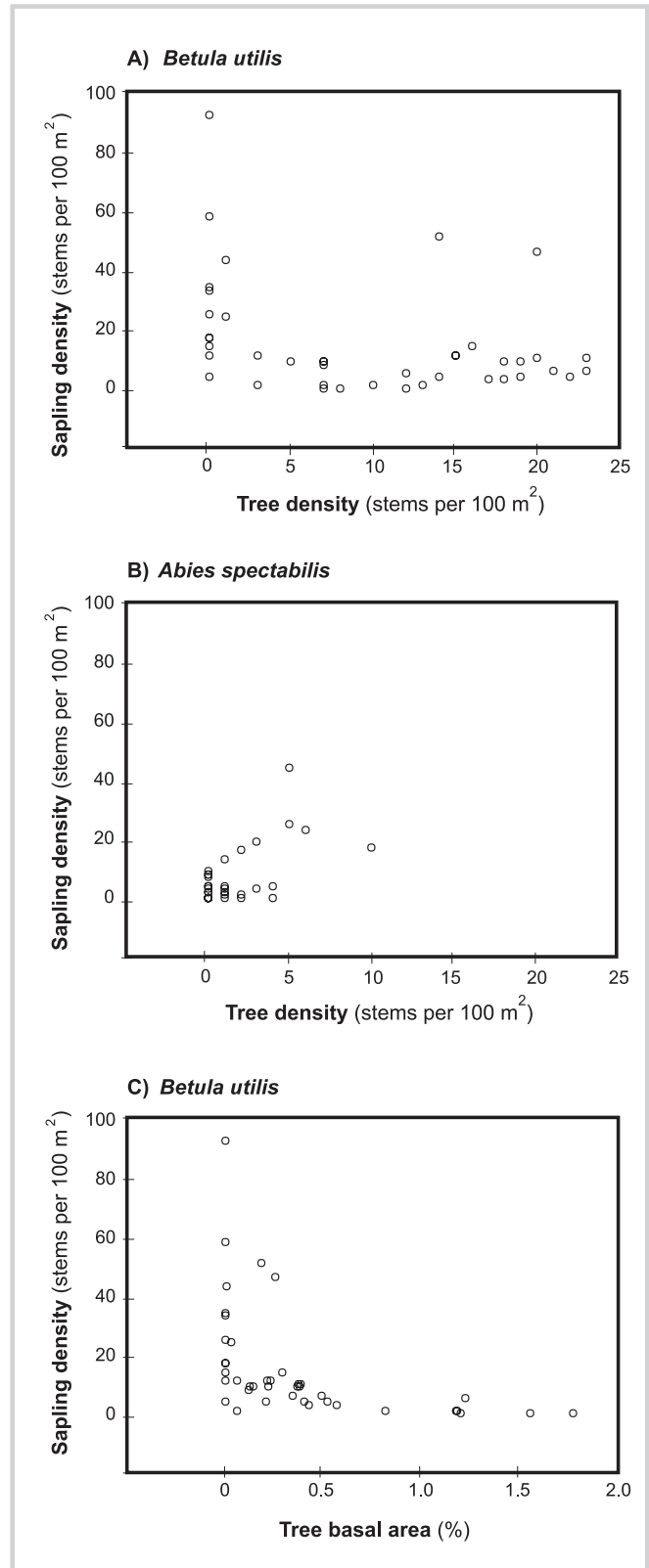


pure forest (9.13 stems/100 m²) was lower than it was in the mixed forest (17.24 stems/100 m²) but the seedling density was nearly equal in these 2 forests (3.73 and 4.08 stems/100 m², respectively). The sapling density of *Betula utilis* was highest at 3600–3700 m and lowest at 4000–4100 m, but it did not show any regular pattern of change with elevation (Figure 1B). The density of *Betula utilis* seedlings was highest at the lowest elevation, but it was absent at 4000–4100 m (Figure 1C), where basal area (BA) was highest (Figure 2), with large trees and closed canopy. However *Betula utilis* seedlings were found up to 4250 m.

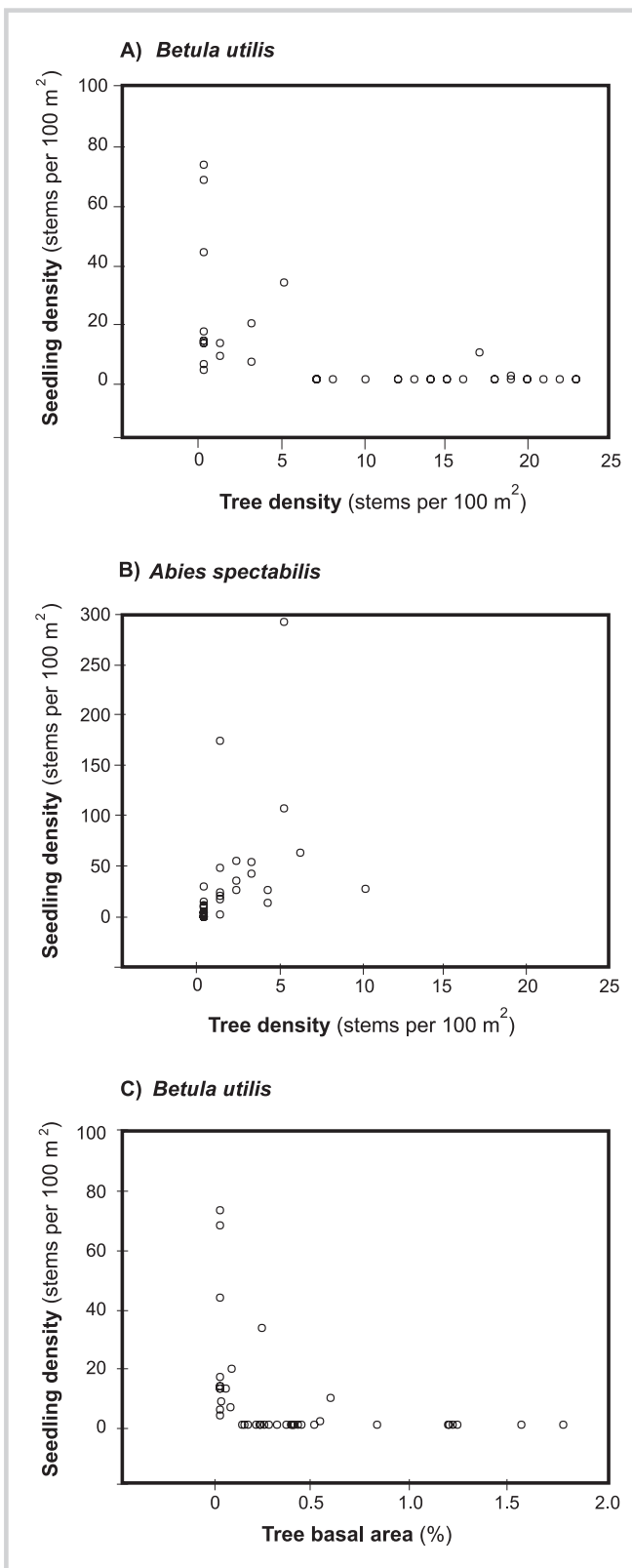
The sapling density of *Betula utilis* was high on those plots where tree density and basal area (the surrogate of canopy cover) were low (Figures 5A and 5C). On plots with BA > 0.6%, saplings were either absent or had very low density, and plots with the highest sapling density had no trees. Plots with *Betula utilis* seedling density ≥ 40 stems/100 m² had no trees, whereas on plots with tree density ≥ 20 stems/100 m² and BA > 0.6%, seedlings were absent (Figures 6A and 6C). Between 3900 and 4000 m in the 3rd transect, *Betula utilis* seedlings were absent inside the tree canopy, but at 20 m horizontal distance from the forest edge, seedling density was 68 stems/100 m². Similarly, between 4100 and 4200 m *Betula utilis* saplings and seedlings were common outside the tree canopy (forest edge) and above (up to 50 m altitude distance) the treeline (density: 9 and 11 stems/100 m², respectively). Here seedlings were growing amongst the thicket of thorny shrubs. Between 3800 and 4000 m in the 5th transect the forest had been damaged by fire over 40 years earlier and the stand floor was exposed to direct sunlight. In these stands saplings and seedlings were well represented (density: 11 stems/100 m² and 25 stems/100 m², respectively).

The *Abies spectabilis* sapling density was highest at 3600–3700 m and that of *Pinus wallichiana* at 3500–3600 m; it then declined at high elevations for both species (Figure 1B). The sapling density of *Abies spectabilis* increased with increasing tree density

FIGURES 5A TO 5C Scatter diagrams showing variation of sapling density with tree density and basal area. Scales are not equal in the different figures.



FIGURES 6A TO 6C Scatter diagrams showing variation of seedling density with tree density and basal area. Scales are not equal in the different figures.



($p = 0.05$, Table 1; Figure 5B). Between 3700 and 3800 m, *Abies spectabilis* seedling density was the highest but that of *Betula utilis* was the lowest (for the elevation ranges where its seedlings were present). On a few plots between 3700–3800 m the forest stand was dominated by *Betula utilis* (density: *Betula* 18 stems/100 m²; *Abies* 6 stems/100 m²) but *Betula utilis* seedlings were absent, whereas *Abies spectabilis* seedling density was 248 stems/100 m². In the same stands *Abies spectabilis* stumps were frequently encountered (density: 9 stems/100 m²). Seedlings of *Abies spectabilis* and *Pinus wallichiana* were absent above 4000 m.

Herbivory and treeline

Subalpine *Betula utilis* forests and upslope alpine meadows were the main grazing areas for livestock and wildlife (eg musk deer and blue sheep). Signs of browsing were observed on seedlings and saplings, particularly near the forest edge. The treeline in our study site was the abrupt or anthropo-zoogenic type (see Ellenberg 1988), where large trees of *Betula utilis* in closed stands changed to treeless alpine vegetation without the krummholz zone (ie a transition zone with dwarf, twisted, and shrub-like individuals); but in some transects seedlings and small saplings were growing amongst the thickets of thorny *Caragana* spp. above the treeline.

Discussion

Betula utilis forms a continuous treeline on the north-facing slope of the valley where the soil receives snowmelt water from high mountains (> 7000 m asl) covered by permanent snow, and soil moisture increased with elevation ($p < 0.001$). On the dry, south-facing slope of the valley, with seasonal (winter) snow on the hilltop, *Betula utilis* was present in a few moist pockets. Horizontal distribution of *Betula utilis* in the Manang valley thus appears to be governed by soil moisture, which in turn is controlled by aspect and water sources.

Increasing soil moisture with elevation may be due to the combined effect of the increasing tree canopy cover, decreasing temperature, and decreasing distance from snowmelt water sources. High litter accumulation and soil OM decrease soil pH (Biswas and Mukherjee 1994). The soil pH followed a similar trend; it also decreased with increasing elevation in the present study ($p = 0.001$). Since decrease in pH with increasing elevation ($r = -0.785$, $p < 0.05$) was also reported for treeline soil in African mountains (Fetene et al 2006), this trend may be a common feature of treeline soil. The edaphic condition (soil moisture, OM, N) of forest soils was better at high elevations (Figure 3), which appears to be favorable for the establishment of early successional deciduous broadleaved species like *Betula utilis*.

On the southern declivity of the central and eastern Himalayas, *Betula utilis* was found below the treeline at lower elevations (about 3000 and 3400 m, respectively) (Singh and Singh 1992). In the dry valleys the treeline itself is higher than on the southern declivity (Stainton 1972). The question is why *Betula utilis* has been distributed up to higher elevations on the north face of the main Himalayas rather than on the south. This could be attributed to different patterns of rainfall and moisture gradients. The north-facing slope of the main Himalayas receives only a small part of the monsoon rain and the main source of soil moisture is snowmelt water from high mountains. Dry soil on the valley floor (3300–3400 m) and on lower parts of the slope (3300–3600 m) is suitable for conifers like *Pinus wallichiana* but not for *Betula utilis*. From this belt to the treeline, soil temperature may not be low enough to prevent tree growth but the soil is sufficiently moist to support the growth of *Betula utilis*. Survival of most birch species depends on adequate moisture and nutrients (Carlton and Bazzaz 1998), which were higher at higher elevations in the present study. Soil moisture plays a greater role in distribution of *Betula utilis*; this was also supported by 2 further observations: *Betula utilis* descended down to the valley floor along moist watercourses; and it was virtually absent on the dry south-facing slope of the valley.

Tree species richness declined near the treeline and mono-dominant forest stands of *Betula utilis* were present between 3900 and 4200 m. However, this kind of pure *Betula utilis* forest was found at lower elevations (around 3100 m) elsewhere, eg on the southern slope of Kumaon Himalaya (Singh and Singh 1992) where BA of *Betula utilis* (ie 0.093%) was very low in comparison to our study (Table 2). *Betula utilis* appeared to be the only broadleaved, deciduous tree species which can form mature, pure stands, forming the treeline up to 4200 m in dry valleys of the trans-Himalayan region. In the mixed forest of *Betula utilis* at lower elevations, 2 other associated conifer species shared slightly < 50% IVI (Table 2) and their recruits were abundant (Figures 1B and 1C). At this elevation, seedlings of *Abies spectabilis* were most abundant and were growing under deep shade.

The coexistence of *Betula utilis* with conifers in this mixed forest appears to be related to large-scale disturbance such as clear cutting, an observation similar to Mori and Takeda (2004) in subalpine forests of central Japan. In the past, timber demands from local people were mainly met by *Abies spectabilis* and its pure stand virtually disappeared from the study area except at a limited site (eg near Millereppa cave in Braka). Thus the mixed forest of *Betula utilis* at lower elevations with smaller individuals (Figure 4A) and lower BA (Table 2) might have developed after large-scale clear cutting of

Abies spectabilis trees in the past. Open forest left after clear cutting became suitable for seed germination and seedling establishment of *Betula utilis*. Similar observations were also made by Catovsky and Bazzaz (2000), Peterson and Pickett (2000), and Grime (2001) for other early successional species. Few mature trees of *Abies spectabilis* that survived after clear cutting served as a seed source for abundant growth of seedlings and saplings under the canopy of *Betula utilis* at lower elevations (Figures 1B and 1C). Shade-tolerant species, when grown to tall trees, will cast deep shade and replace shade-intolerant species (Grime 2001). Thus in future, the mixed forest of *Betula utilis* at low elevations may be replaced by shade-tolerant, slow-growing *Abies spectabilis*. The present distribution of tree species along elevation gradients (Figure 3) showed that *Pinus wallichiana* and *Abies spectabilis* could not expand beyond 4000 m and *Betula utilis* will continue to be a dominant species at higher elevations.

There was continuous regeneration of *Betula utilis* in both the mixed forest at lower elevations and the pure forest at higher elevations (Figure 4). The mixed forest was young with smaller individuals and might have developed after clear cutting of large *Abies spectabilis* trees. Removal of canopy trees increased light intensity to the forest floor and reduced litter accumulation, which is suitable for seed germination and seedling establishment of early successional *Betula* spp. (Carlton and Bazzaz 1998; Grime 2001). Thus human activities such as timber harvesting have reduced tree BA, and changed species composition and the seral stage of the forest. Fire damage (> 40 years ago) exposed mineral soil, which might be suitable for seed germination and seedling survival of *Betula utilis*, similar to *Betula alleghaniensis* (Peterson and Pickett 2000). The sites exposed to direct sunlight are more suitable than the deep-shaded forest floor for seedling growth of *Betula* spp., provided that moisture and nutrients are adequate (Marquis 1965; Carlton and Bazzaz 1998). This was expressed as high seedling and sapling densities on these treeless but moist plots (Figures 5 and 6) in the present study. Mature trees growing near such sites might have provided seeds for germination in such open stands.

Sapling and seedling distribution of *Betula utilis* was spatially heterogeneous, which may be relatively common under natural conditions, as with *Betula alleghaniensis* (Houle 1998). Spatial heterogeneity in sapling and seedling distribution appeared to be determined by light availability caused by variation in canopy cover (here we used BA as surrogate of canopy cover). The stands with the highest sapling and seedling densities (Figures 5 and 6) of *Betula utilis* had no tree canopy because seed germination and seedling survival of *Betula* spp. are restricted to the local areas where mineral soil remains exposed (Grime 2001).

Low germination of small seed such as of *Betula* spp. under low light and high humidity conditions prevailed in such closed stands and can also lead to high seedling mortality due to fungal attack. Low seed germination and seedling survival have been confirmed by the experimental manipulation of light intensity available to seedlings; low light reduced seedling emergence of birch (*Betula* spp.) by 43%, seedling growth by 99%, and survival by 94% (Catovsky and Bazzaz 2000). The abundant growth of saplings and seedlings near the open edges of such forest stands indicated that the seed source was not the limiting factor for low recruitment in closed canopy stands. According to Carlton and Bazzaz (1998) lack of birch regeneration can be attributable to poor seedling growth and survival rather than inadequate seed dispersal. Low light and thick litter may be the major constraints for seedling establishment of *Betula utilis* under its own canopy. In experimental seed dispersal of 3 birch species, none of the seedlings survived in the forest understory (Carlton and Bazzaz 1998). Poor seedling recruitment in the understory has been reported for undisturbed old-growth alpine forest in central Japan (Mori and Takeda 2004) and undisturbed mixed forest of interior British Columbia, Canada (Coates 2002). Partially open canopy, caused by self-thinning (natural death), natural disturbance, or manual removal of selected old trees, could increase light availability on the forest floor and reduce litter accumulation. This may increase the seedling survival of *Betula utilis* under its own canopy and induce regeneration. Present results support the argument that abundant natural regeneration of old-growth forest can be obtained after partial cutting (Vetaas 2000; Coates 2002; Shrestha et al 2004).

Treeline without krummholz zone, as at our study site, was a characteristic of the anthropo-zoogenic type (see Ellenberg 1988) where large trees of *Betula utilis* in closed stands changed over to treeless alpine vegetation. Although the treeline is traditionally considered as a thermally limited ecotone, and soil temperature as responsible for setting the treeline location worldwide (Koerner 1998), livestock and/or natural herbivory also has signifi-

cant influences on the position and structure of treelines (Cairns and Moen 2004). An 'abrupt' treeline of *Betula utilis* in Manang appears to be—at least partly—due to herbivory of wildlife and/or livestock. Alpine mat was the main pasture where livestock grazing pressure was high. The *Betula utilis* forest was the major habitat of musk deer and blue sheep in this region, which feed on young leaves of *Betula utilis* (first author's personal observation). It appears that high herbivory pressure in this region limited the upslope migration of *Betula utilis*, similar to the Scandinavian mountain birch (*Betula pubescens*) treeline (Cairns and Moen 2004). When protected from browsing (eg by thicket of thorny *Caragana* spp.), seedlings and saplings of *Betula utilis* survived above the present treeline.

Conclusions

The upper distribution limit of *Betula utilis* was higher on the north-facing declivity of the main Himalayas than on the south-facing one. The treeline-forming pure forest of *Betula utilis* was mature but mixed forest at lower elevations was young, which might have developed after large-scale clear cutting of *Abies spectabilis* trees. *Betula utilis* mixed forest may be replaced again by slow-growing, shade-tolerant *Abies spectabilis*. In general, *Betula utilis* was regenerating in both pure and mixed forests. However, the distribution of seedlings and saplings was spatially heterogeneous and appeared to depend on tree basal area (or canopy cover). The stands with the highest density of *Betula utilis* seedlings and saplings had no trees, whereas seedlings were absent where tree density and BA exceeded 20 stems/100 m² and 1.0%, respectively. It was apparent that *Betula utilis* seedlings could not thrive under closed *Betula* canopy even if seeds produced were viable. Partial canopy opening may induce seedling establishment and hence continuous regeneration of *Betula utilis* in mature stands. The treeline formed by *Betula utilis* was of the anthropo-zoogenic type, without a krummholz zone. It appears that herbivory pressure in this region shaped the treeline and limited the upslope migration of *Betula utilis*.

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