Patterns of Shrub Invasion into High Mountain Grasslands of the Northern Calcareous Alps, Austria

Authors: Dullinger, S., Dirnböck, T., and Grabherr, G.

Source: Arctic, Antarctic, and Alpine Research, 35(4) : 434-441

Published By: Institute of Arctic and Alpine Research (INSTAAR), University of Colorado

URL: https://doi.org/10.1657/1523-0430(2003)035[0434:POSIIH]2.0.CO;2

Arctic, Antarctic, and Alpine Research, Vol. 35, No. 4, 2003, pp. 434–441

Patterns of Shrub Invasion into High Mountain Grasslands of the Northern Calcareous Alps, Austria

*S. Dullinger,**
T. Dirnböck,† and
*G. Grabherr**

*Institute of Ecology and Conservation Biology, University of Vienna, Althanstraße 14, A-1090 Vienna, Austria.
dull@pflaphy.pph.univie.ac.at
†Federal Environment Agency, Spittelauer Lände 5, A-1090 Vienna, Austria.
dirnboeck@ubavie.gv.at

Abstract

Both land use and expected climate change will probably cause range shifts of tree and shrub species in the European Alps. Attempts to predict the magnitude and direction of these processes will produce reliable results only if they consider both abiotic habitat conditions and biotic interactions. In this study we analyze recruitment patterns of *Pinus mugo* Turra in different grassland communities of the Northern Calcareous Alps, Austria. *Pinus mugo* is the most important invader of abandoned subalpine pastures in the area and the predominant woody plant at the current timberline. Results indicate strong dependence of colonization success on propagule pressure and differential invasibility of grassland types but only a marginal impact of local-scale site conditions, at least within the species' current altitudinal distribution limits. Because the grassland matrix at and above the current treeline is dominated by a particularly invasible grassland type, a possible climate change–driven upward movement of *Pinus mugo* shrublands may take place quite rapidly. In contrast, encroachment on abandoned subalpine pastures is frequently delayed by competition with vigorous grassland canopies.

Introduction

Global climate change is expected to alter vegetation patterns of high mountain ecosystems, especially in temperate and boreal mountains (Guisan et al., 1995; Grabherr et al., 1994, 1995; Harte and Shaw, 1995; Theurillat and Guisan, 2001). Possible range expansions of subalpine forests and shrublands will probably be one of the most important successional processes in terms of ecosystem functioning and landscape structure. Recent invasions of trees into high mountain grasslands have been reported from many parts of the world (Magee and Antos, 1992; Rochefort and Peterson, 1996; Hessl and Baker, 1997; Moir et al., 1999; Meshinev et al., 2000; Wearne and Morgan, 2001), but the impact of long-term climatic changes on these colonization processes is often difficult if not impossible to disentangle from short- or midterm climatic fluctuations (Kullmann, 1993; Szeicz and MacDonald, 1995), aperiodic disturbance events (Cullen et al., 2001), or land use changes (Motta and Nola, 2001; Didier, 2001). The latter process is especially relevant in the European Alps, where many high mountain grasslands, traditionally used for summer farming, have been abandoned during the past 150 years (Zwittkovits, 1974; Bätzing, 1991).

Recent advances in invasion ecology have demonstrated that for an organism to expand its range, it must effectively disperse propagules, cope with habitat conditions, and successfully compete within the existing biota (Richardson et al., 2000, Shea and Chesson, 2002). Various studies have demonstrated that the colonization of grasslands by tree and shrub species is strongly affected by competition with vigorous grass and herb layers (Magee and Antos, 1992; Richardson and Bond, 1991; Richardson and Higgins, 1998). Predictions of shifts in species ranges that focus exclusively on abiotic habitat conditions and that disregard biotic interactions may thus produce unreliable results (Davis et al., 1998).

In the Northern Calcareous Alps of Austria, abandoned subalpine pastures are subject to encroachment mainly by prostrate pine (*Pinus mugo* Turra). The same species dominates at the current timberline and is therefore likely to be the most important agent of probable future treeline dynamics induced by climate warming. The purpose of this study is to analyze patterns of *Pinus mugo* invasion into different high mountain grasslands of the area. We focus particularly on the following questions:

1. Do local-scale abiotic habitat conditions control recruitment success of *Pinus mugo* in high mountain grasslands?
2. Are there any differences in invasibility among the grassland communities of the area, and if so, does their current spatial distribution cause any emergent landscape-scale patterns of invasibility?

Material and Methods

STUDY AREA

The study area covers the subalpine and alpine zones of four neighbouring mountain ranges of the Northeastern Calcareous Alps in Austria (Mt. Hochschwab, Mt. Schneealpe, Mt. Rax, and Mt. Schneeberg, 15°E to 16°E and 47°30′N to 47°50′N, approximately 150 km^2; see Fig. 1). Summits vary between 1900 and 2300 m a.s.l. The mountain system is formed by mesozoic limestone and dolomite and is characterized by displaced plateaus of different altitudes. Meso- and microrelief are shaped by a variety of karst landforms such as dolines and karren. Climatic conditions are temperate humid. Mean annual temperature approximates 6–8°C in the valleys, decreasing to about 0–2°C in the summit region. Annual precipitation averages 700 mm (valleys) and 1500–2500 mm (summits), with a distinct peak during the summer season.

Summer pasturing (June–September) in the area dates back at least to the 16th century (Zwittkovits, 1974). Most of the study area has historically been influenced by livestock grazing, involving patchy forest and shrub clearing. Since the middle of the 19th century, grazing intensity has decreased and much former pastureland has become abandoned. Approximately 30% of the study area is still pastured by free-ranging cattle (farm census data 1986, Statistic Austria, unpublished). Other forms of land use are of minor importance.

Under natural conditions Norway spruce (*Picea abies*) or mixed spruce and European larch (*Larix decidua*) forests predominate in the

1523-0430/03 $7.00

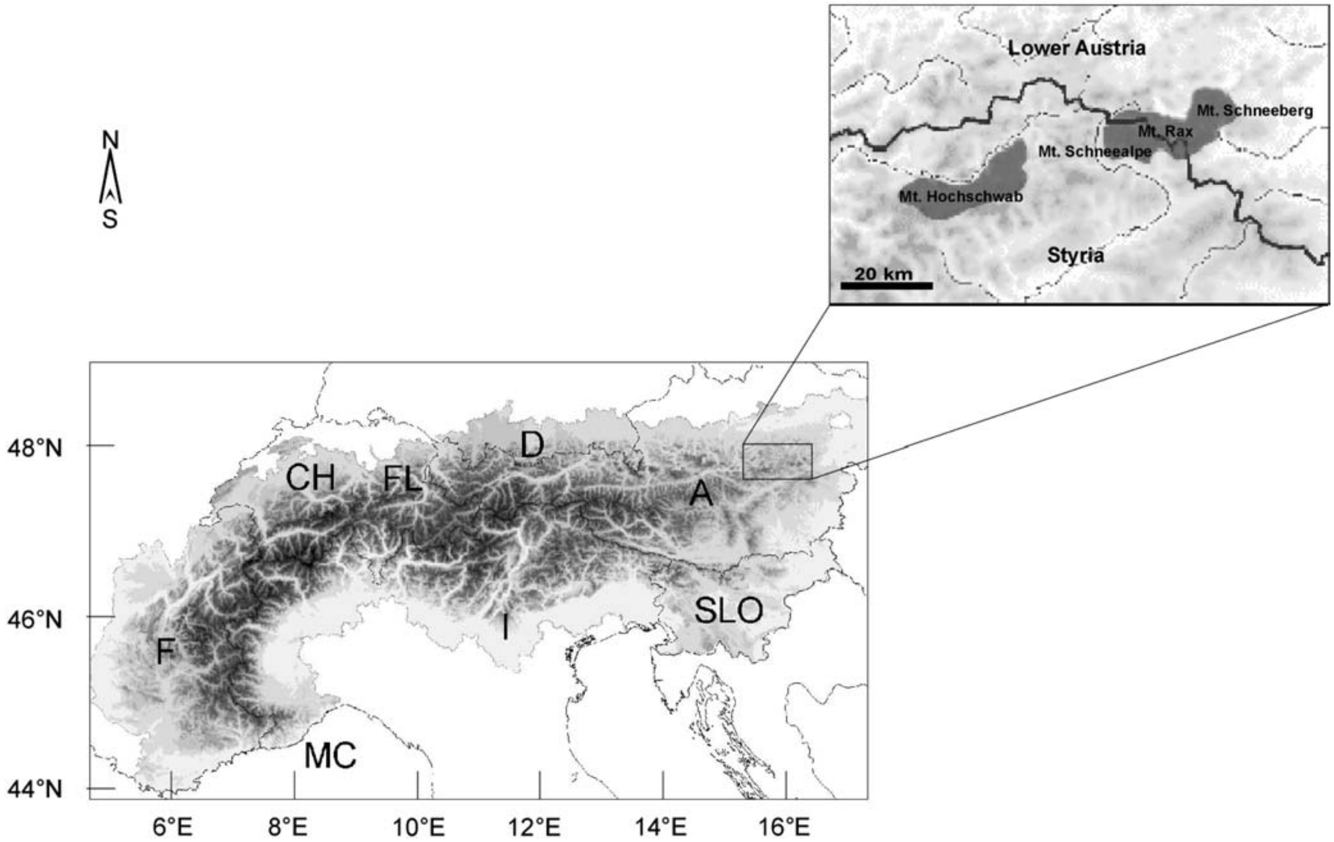

FIGURE 1. Geographical position of the study area. Only the Alps are represented by topographical shadings (A = Austria, CH = Switzerland, D = Germany, F = France, FL = Liechtenstein, I = Italy, MC = Monaco, SLO = Slovenia).

lower parts of the subalpine belt, and prostrate pine (*Pinus mugo*) shrubland predominates at the current treeline ecotone between around 1750 m and 1900 m a.s.l. The subalpine belt today is a mosaic of woody and nonwoody vegetation, with spruce and spruce-larch forests rarely occurring above 1600 m a.s.l. Nonwoody vegetation below the treeline consists mainly of different kinds of pastures and natural grasslands, with the latter covering disturbed sites such as avalanche paths and exposed ridges or abandoned pastures as a first step of secondary succession. Less frequently, tall herb communities (*Adenostyles alliaria*, *Aconitum napellus*) and fens (*Carex nigra*, *C. rostrata*) occur. Above the treeline, natural grasslands are dominating. Rock faces, scree, and snowbeds are widespread, ranging from the valley bottoms up to the summits.

SPECIES

Pinus mugo Turra has an obligatory prostrate growth form. Maximum canopy heights of 5 m have been reported (Richardson and Rundel, 1998), but in the study area plant height usually varies between 0.3 and 2.5 m. The geographical range of the species spans the mountains of eastern Europe (Willis et al., 1998). Within its natural range it is most frequent in treeline ecotones, where it establishes monodominant, dense, and extensive shrublands. For convenience, we use the term “treeline” for the upper altitudinal range margin of *Pinus mugo* despite its shrubby growth form. Seedling establishment seems to be inhibited by low light availability (Hafenscherer and Mayer, 1986) and deep litter layers (Michiels, 1993). Thus, within-stand regeneration is entirely dependent on clonal propagation by means of layering. However, recruitment of seedlings in grasslands and other open habitats is widespread. The species is well known for being a successful woody pioneer in naturally disturbed sites or fallow pastures of subalpine regions (Ellenberg, 1988; Michiels, 1993). Moreover, recent observations suggest that it is as effective an invader of new habitats outside its natural range as many other species of the genus (Richardson and Higgins, 1998). Seeds of *Pinus mugo* are primarily wind dispersed. Secondary distribution of seeds by birds and small mammals has been observed (Müller-Schneider, 1986).

ENVIRONMENTAL DATA

Environmental information on the study area was provided by means of a raster-based Geographical Information System (GRID-module of ARC-Info 7.1: see Table 1). Grid cell size was uniformly 20 × 20 m according to the resolution of the Digital Elevation Model (DEM) (Austrian National Mapping Agency) used. Based on meteorological station data and the DEM, we derived envelopes for abiotic habitat variables that are known to influence the performance of high mountain plants (Körner, 1999). Temperature was represented by Degree Days (number of days with a mean $>0°C$). Degree Days were calculated by means of lapse rates for altitude and geographical longitude according to data from 20 meteorological stations in or near the study area. Solar radiation was calculated for the early (15 May), the mid (15 July), and the late growing period (15 September) with the program SOLARFLUX (Dubayah and Rich, 1996) assuming clear sky conditions. SOLARFLUX accounts for relief shading and topographic position. Potential evapotranspiration (PET) was estimated for August using the formula of Turc (1961). PET calculations were restricted to August because in the humid and snow-rich climate of the study area we expected that occasional water stress would not occur before late summer. Topography was represented by slope inclination, a topograhic wetness index (WET), and a topographic soil erosion index (EROS). Both indices were calculated by means of the program package TAPES-G (Gallant and Wilson, 1996). WET computes topographically controlled average soil moisture conditions based on elevation, flow direction, drainage area, and slope fields (Barling et al., 1994). EROS estimates the spatial distribution of soil erosion and deposition potential using the same topographic variables (Wilson and Gallant, 1996). As we assumed snow-ice abrasion during winter to influence the performance of *Pinus mugo* we simulated near surface wind velocities using the diagnostic wind field model NUATMOS (Version 5N: Ross et al., 1988) that was integrated into a GIS by Bachmann (1998). NUATMOS was initialized assuming strong winds (22 m s^{-1}) from the main wind direction during winter (northwest = 280°). Information on snow distribution was available from 11 classified satellite images of a subarea comprising one-third of the study area (Mt. Schneealpe and western parts of Mt. Rax, acquired between February and June 1998, 1999, and 2000, resolution 20 m). From these data we extrapolated a snow cover index applying a binary classification tree with solar radiation, wind velocity, elevation, and topographical indices as predictor variables (misclassification error = 8%: Dirnböck et al., 2003).

Besides climatological and topographical descriptors we derived information on bedrock material from a geological map of the study area (scale 1:50,000: Geological Survey of Austria, unpublished). Bedrock mineralogy was compiled into 4 classes: limestone, dolomite, Quatenary sediments, and eolian deposits (Tertiary loams). Spatial land use information comes from cadastral maps combined with historical and actual farm census data covering the time span between 1770 and 2000. We used time since pasture abandonment as a measure for land use impact, setting the concrete values to the difference in years between the date of the most recent document reporting a parcel to be used and the year 2000.

For the whole study area a map of *Pinus mugo* shrubland was produced by visual interpreation of infrared and black-and-white orthophotos (scale 1:5000–1:10,000). Using this map we calculated the distance of each sampling plot (see below) to the next *Pinus mugo* stand as well as the deviation of compass direction of this proximate shrubland patch from the main wind direction (northwest = 280°) during seed-release period (October: Müller-Schneider, 1986). These two variables should provide an estimate of seed input into each sampling plot.

SAMPLING DESIGN

Selection of field plots was based on a stratified random sampling design. Our stratification considered land use, Degree Days, PET, the wetness index, and geology (see Table 1). Concerning land use, sampling was restricted to former pastures not yet overgrown by *Pinus mugo* shrubland or *Picea abies–Larix decidua* forests. Areas actually used for summer farming were not considered; neither were those that have never been used at all. Continuous variables were categorized into classes, and each possible combination of values was defined as a separate stratum. Sampling was restricted to strata larger than 4 ha, resulting in a total of 99 relevant strata. Each stratum had to be sampled by at least 1 plot, strata larger than 40 ha by 2, and some very large ones (>400 ha) by 3 sample plots. Plot locations were selected randomly. A total of 140 plots were selected this way, each 20 × 20 m in size. Plots were localized in the field by means of a GPS (GARMIN E-TREX^{c}, mean Root Mean Square Error: 7.5 m).

DATA COLLECTION

All living and dead individuals of *Pinus mugo* in each study plot were sampled (698 individuals in total). Besides attributes not considered in this study, we recorded each individual's origin (seed or layer), vitality (dead or alive), height, diameter (mean of largest and smallest diameter), and the vegetation type in which it had germinated (rock, scree, or particular grassland type). Small individuals (diameter <0.5 m) were aged by counting bud scares if readily visible (n = 196). If larger individuals were present on the plot, a maximum of 3 of them (largest, smallest, and median) were sectioned as close to the root collar as possible, and rings were counted under a stereoscope (14× magnification) after grinding the surface (n = 116). For each individual sectioned, a growth rate was calculated by dividing the length of the sectioned branch by its ring count. The age of all remaining individuals (n = 386) was estimated as a function of their diameter, height, and the average growth rate of the sectioned individuals on the respective plot (linear regression, $R^2 = 0.69$).

TABLE 1

Minimum, maximum, mean, and standard deviation of numerical environmental variables at 140 sampling plots and number of plots in each class of bedrock material (Lime = limestone; Dol = dolomite; QS = Quatenary sediments; ED = eolian deposits)

Variable	Min	Max	Mean	StdDev
Degree days	197	246	222	12
Radiation 15 May (MJ/m^2)	10.95	28.92	24.3	4.05
Radiation 15 July (MJ/m^2)	13.54	29.73	25.56	3.63
Radiation 15 September (MJ/m^2)	3.126	23.19	14.97	5.84
PET August	1.07	4.65	2.85	0.79
Slope inclination (°)	1	53	23	11
Wetness index	2.83	13.02	6.24	1.84
Soil erosion index	−8.22	35.37	0.92	5.24
Wind speed (m s^{-1})	3.74	45.2	16.02	7.06
Snow cover index	0.301	0.502	0.385	0.074
Time since pasture abandonment (yr)	40	180	96	48
Distance to seed source (m)	20	937	161	207
Deviation from main wind direction (°)	1	316	156	101
	Lime	Dol	QS	ED
Geology (number of plots)	77	39	20	4

For each plot we further recorded the percentage cover of all tree and shrub species present and the percentage cover of all nonwoody vegetation types. For the dominant nonwoody vegetation type (mainly grasslands) we recorded some structural attributes (canopy height and canopy cover) and documented the species composition by means of a 30-m^2 relevé according to Braun-Blanquet (1964). Relevés were assigned to plant communities according to Mucina et al. (1993a, 1993b) and Grabherr and Mucina (1993).

As some grassland types hardly predominated on the sampling plots, their structural properties were poorly represented. To extend information on mean structural attributes of all major grassland communities of the area, we used an additional data set of 1116 relevés done in the course of mapping the area's subalpine and alpine vegetation during the years 1994–1999 (Greimler and Dirnböck, 1996; Dirnböck and Greimler, 1997; Dirnböck et al., 1998, 1999; Dullinger et al., 2001). All relevés come from the same area and have been done in the same way as on the plots of this study by the authors themselves. Mean canopy height and canopy cover of the respective communities in this larger data set were then used to analyze correlation between vegetation structure and invasibility.

DATA ANALYSIS

Dependence of recruitment patterns on abiotic habitat conditions was tested by means of multivariate regression analysis. As response

TABLE 2

Comparison of the full multivariate model of Pinus mugo *recruitment rate (10 linearly fitted numerical variables, a categorical one with 4 classes, and a numerical one fitted by a restricted cubic spline function with 4 knots: see Fig. 2) and a univariate one using distance to seed source as the only predictor. Corrected R^2 values come from bootstrap validation (1000 resamples). The F-test was calculated based on corrected R^2 values*

	df	R^2—original	R^2—corrected	*P*
Full model	16	0.47	0.33	<0.0001
Univariate model	1	0.31	0.3	<0.0001
$F_{15,123}$		0.367		>0.05

variable we used the recruitment rate (= RR, in recruits per year) at each plot during the last 50 yr, i.e., the number of recruits younger than 50 yr divided by 50. We restricted the analysis to this time span because we could not decide unambiguously if some older individuals had come from one seedling or from two or more that had merged. All abiotic habitat variables including distance to and direction of next seed source as well as land use information were included in the model. Solar radiation was represented by calculations for only 15 July because May, July, and September values were closely correlated and the midseason gradient proved to have the highest predictive power. Distance to seed source was log-transformed prior to analysis to account for the well-known exponential decrease of seed rain density with distance from the propagule source (Nathan and Muller-Landau, 2000). Nonlinear effects were tested for by using restricted cubic spline functions with 4 knots (Harrell, 2001). Cubic spline functions were introduced separately for each variable to avoid seriously overfitting the model. The final model comprised all nonlinear terms that proved significant. Goodness of fit (R^2) was validated by bootstrapping (1000 resamples, function *validate* implemented in the Design-library of S-Plus 2000 for Windows; see Harrell [2001] for details). The final multivariate model was compared to a univariate one containing only the single most important variable by means of an F-test for the comparison of nested models.

For evaluating dependence of recruitment patterns on the "host community," we established a null model based on the assumption of equal recruitment rate in each of the major grassland communities of the study area. The expected number of recruits in any one of these grassland types under the null model was calculated as

$$(n*(A_i/A_s))/A_s \tag{1}$$

where n = the total number of recruits, A_i = the proportional area of the *i*th community, and $A_s = \sum A_i$. Significant deviation of the observed distribution of recruits among grassland communities from the expected one under the null model was tested for by means of a χ^2 test.

We used the ratio of observed versus expected number of recruits in any one grassland community as an index of its invasibility. The dependence of this index on structural properties (mean canopy height, mean canopy cover) and on the position of the different communities on environmental gradients was examined by means of univariate regression models. For each variable, original and log-transformed values were tested separately. Position on environmental gradients was calculated as an area-weighted mean of the respective habitat variable in our sampling plots, i.e., by calculating for each grassland community

$$(p_{i,j}*v_{a,j})\Big/\sum p_{i,j} \tag{2}$$

where $p_{i,j}$ = proportion of community *i* on the area of plot *j* and $v_{a,j}$ = value of variable *a* on plot *j*. Moreover, we tested the dependence of the invasibility index on the mean age of recruits in a grassland community to control for a possible bias due to an age-dependent decrease of mortality: if mortality should have a peak during the first years or decades following germination, then uneven transition probabilities among age classes will result in higher invasion rates for communities with younger recruits. This relationship was tested by means of a univariate regression model using the mean age of recruits in the patches of a community as predictor of its respective index of invasiblity.

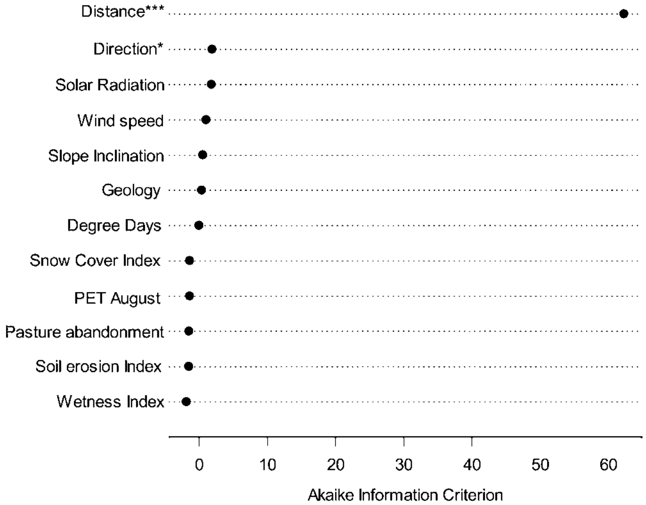

FIGURE 2. Akaike Information Criterion (AIC) for predictor variables in a multivariate regression model of Pinus mugo *recruitment rate in high mountain grasslands of the Northern Calcareous Alps. AIC was adjusted to χ^2 values of the respective variables derived from a Wald test of the multivariate model (cf. Harrell, 2001). Distance = distance to seed source; Direction = deviation of compass direction of the next seed source from the prevailing wind direction during the main seed release period (October); PET = potential evapotranspiration; Pasture abandonment = time since pasture abandonment. *** = $P < 0.0001$, * = $P < 0.05$.*

Finally, we attempted to analyze landscape-scale patterns of invasibility using the current distribution of grassland types across the study area as an indicator. This current spatial distribution was derived from vegetation maps (scale 1:10,000: Greimler and Dirnböck, 1996; Dirnböck and Greimler, 1997; Dirnböck et al., 1998, 1999; Dullinger et al., 2001). We calculated the proportional area of each grassland community of the overall grassland matrix in altitudinal steps of 100 m. The proportions were multiplied by the respective indices of invasibility, and the sum of these values was used as an estimate of the overall invasibility of the grassland matrix of each altitudinal belt.

Nomenclature follows Adler et al. (1994). ARC-Info (7.1) was used to analyze spatial data and S-Plus 2000 for all statistical calculations.

Results

The multivariate regression model of RR against abiotic habitat variables and land use history is highly significant but explains only 33% of the overall variance in RR when using a bootstrap validation correcting for model overfit (Table 2). It has just two significant predictors: distance to seed source and deviation of compass direction of the next seed source from the prevailing wind direction during seed release (Fig. 2). Solar radiation in July ($P = 0.05$) and wind velocity ($P = 0.07$) are marginally nonsignificant, with wind velocity having a significant nonlinear effect. However, compared to the impact of propagule pressure, local-scale abiotic habitat conditions seem to

TABLE 3

χ^2 statistic comparing the observed number of Pinus mugo *recruits in 10 predominant grassland types of the study area to an expected number under a neutral model assuming equal distribution of recruits among these grassland communities. Expected numbers were calculated with respect to the proportional area of each grassland type in the sampling plots. Obs/Exp = Ratio of observed and expected number of recruits*

Grassland type	Area (m^2)	Observed	Expected	Deviance	Obs/Exp
Carex firma grassland	1018	61	28	37	*2.18*
Carex sempervirens grassland	6188	264	173	48	*1.53*
Leontodon hispidus–Crepis aurea pasture	583	20	16	1	*1.25*
Agrostis alpina–Festuca pumila grassland	1243	29	35	1	*0.83*
Calamagrostis varia grassland	408	7	11	2	*0.61*
Carex ferruginea grassland	846	9	24	9	*0.38*
Nardus stricta pasture	320	2	9	5	*0.22*
Deschampsia cespitosa pasture	2013	11	56	36	*0.19*
Helictotrichon parlatorei grassland	1433	2	40	36	*0.05*
Tall herb communities	420	0	12	12	*0.00*
	14,472	*405*	*405*	*188*	
χ^2				188	
Degrees of freedom				9	
P value				<0.001	

have little influence on recruitment success (Fig. 2). The predominant importance of seed input is confirmed by the comparison between the full model and a univariate one using distance to seed source as the only predictor of RR (Table 2). No significant ($P > 0.05$) improvement of fit can be achieved by adding habitat information provided by the 11 additional predictors in the Full Model.

While testing the influence of the "host community" on recruitment patterns, we accounted for the influence of seed input by holding distance to seed source constant; i.e., we restricted our analysis to sampling plots immediately adjacent to established *Pinus mugo* shrublands. The χ^2-statistic, using only these 50 immediately adjacent plots, reveals a highly significant deviance of the observed distribution of recruits among the different grassland communities from an equal distribution expected under the null model (Table 3). Apart from tall herb communities, which seem to be completely resistant to *Pinus mugo* invasion, the index of invasibility differs by almost two orders of magnitude. *Carex firma* swards turn out to be by far the most invasible grassland community of the study area, followed by *Carex sempervirens* grasslands and *Leontodon hipidus–Crepis aurea* pastures. Besides tall herb communities, *Pinus mugo* had particular difficulty establishing in *Nardus stricta* and *Deschampsia cespitosa* pastures as well as *Helictotrichon parlatorei* grasslands.

Univariate regression analysis of the invasibility index against structural properties or position of the respective grasslands on environmental gradients reveals that soil erosion potential is the only significant environmental predictor of invasibility (Fig. 3). However, the main factor controlling the differential recruitment success of *Pinus mugo* seems to be the canopy structure of the respective grassland community. Both canopy height and canopy cover are significantly correlated with the invasibility index. For EROS and canopy height, logarithmic transformation improves the model fit, indicating a nonlinear relationship with recruitment rates. There is no indication for any bias of the results due to a dependence of the invasibility index on the mean age of recruits in a community.

Area statistics derived from the vegetation map demonstrate considerable variability in the composition of the grassland matrix among different altitudinal steps (Fig. 4). The most obvious trend is a nearly linear increase of the proportion of *Carex firma* grasslands between 1500 and 2200 m a.s.l., and these grasslands in turn proved to be most invasible in the preceding analysis. Plotting the overall invasibility index of each altitudinal belt against the current distribution of *Pinus mugo* shrublands demonstrates that invasibility does not match the current *Pinus mugo* distribution but is highest at and above its present altitudinal range margin.

Discussion

Our results show that patterns of *Pinus mugo* recruitment in high mountain grasslands of the Northern Calcareous Alps are mainly a function of propagule pressure and the differing invasibility of the respective "host communities." In contrast, there is little indication of a major impact of abiotic habitat conditions on recruitment success. This is surprising given the well-known influence especially of temperature on the germination behavior of alpine plants (Körner, 1999). However, meteorological stations measure air temperature at 2 m above ground, and it is well known that, in alpine regions in particular, temperature conditions at the soil surface, especially in dense canopies of herbaceous or dwarf shrub vegetation, may deviate considerably from the temperature 2 m higher (Geiger, 1965; Cernusca, 1975, 1976). Moreover, habitat conditions of the seedbed should be measured at the scale of the regeneration niche (Grubb, 1977), which may cover only a few square centimeters. Microtopographic variation as well as neighboring plants (e.g., Moen, 1993) may strongly influence climatic patterns at this scale. Lack of correlation between recruitment success and the abiotic environment in our study may therefore be partly due to a deviance of microclimatological patterns from local-scale gradients. Additionally, the presumably crucial influence of temperature (Körner, 1999) on the position of the current upper-altitudinal-range margin of *Pinus mugo* may be masked by partial collinearity with propagule pressure, because for sampling plots above the current treeline there is a close negative correlation between decreasing Degree Days and increasing distance to seed source. It is thus hardly possible to disentangle the relative roles of dispersal limitation and temperature thresholds in determining the lack of recruitment success above the current treeline. However, what we may unambiguously conclude from our results is that within current distribution limits, local-scale environmental gradients have little impact on *Pinus mugo* colonization of high mountain grasslands.

The predominant impact of propagule pressure on colonization success is a simple consequence of basic models of population dynamics (Silvertown and Lovett Doust, 1993). Holding mortality constant, an enhanced seed input must increase recruitment rates. However, as a consequence, application of a null model of equal recruitment rates among grassland types may be biased by differing

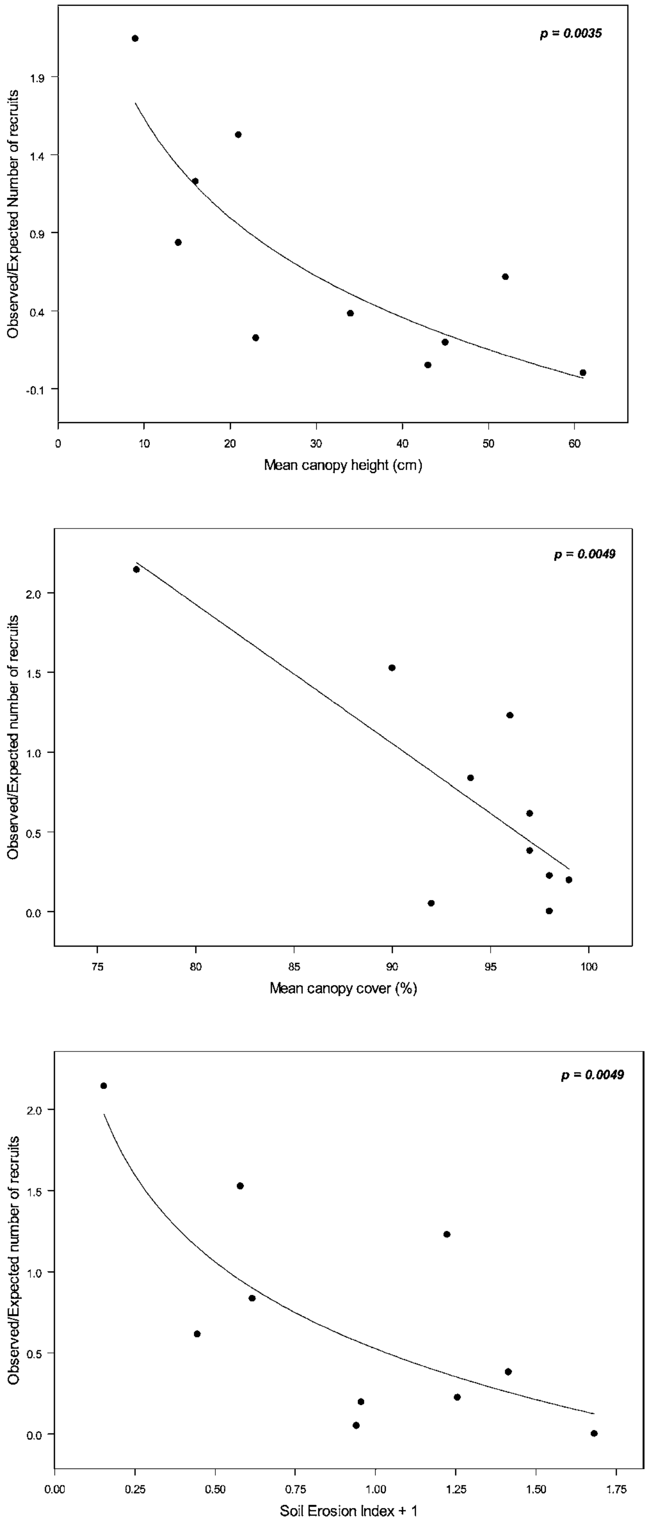

FIGURE 3. Univariate regression models using the index of invasibility of the 10 predominant grassland types of the study area as response and their canopy structure, respectively, using their position on different environmental gradients as predictors. Models for Degree Days, solar radiation, potential evapotranspiration, slope inclination, wetness index, wind velocity, snow cover index, land use, geology, and mean age of recruits in the respective communities are not shown. They all have P *values >0.1.*

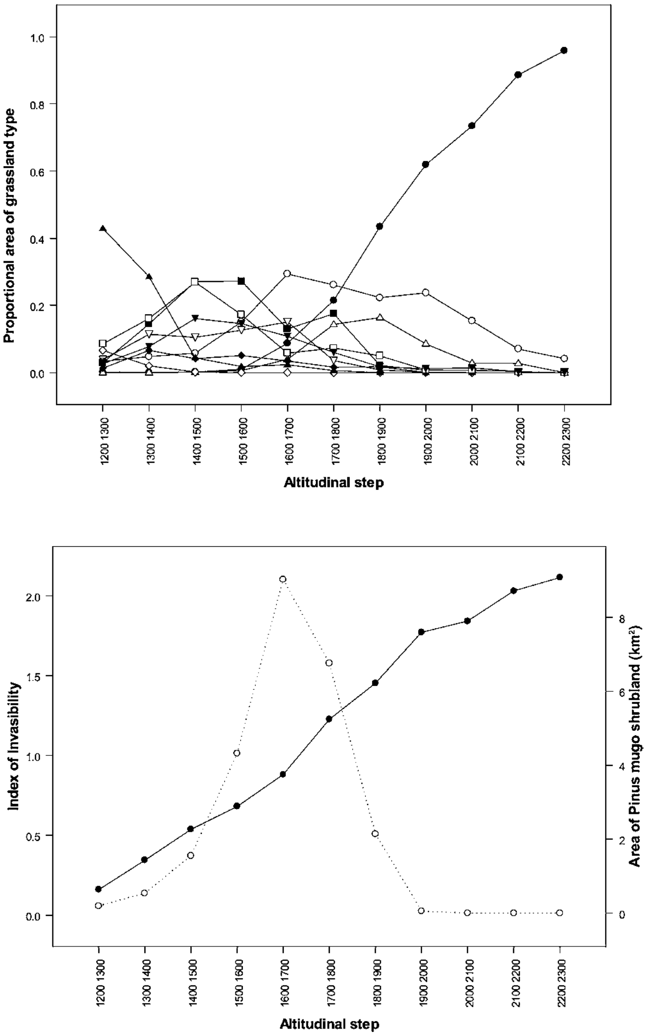

FIGURE 4. (top) Proportional area of the 10 predominant grassland communities of the study area in altitudinal steps of 100 me. ● = Carex firma *grassland; (○) =* Carex sempervirens *grassland; (♦) =* Carex ferruginea *grassland; (◇) =* Calamagrostis varia *grassland; (▲) = Tall herb communities; (△) =* Agrostis alpina–Festuca pumila *grassland; (▼) =* Deschampsia cespitosa *pasture; (▽) =* Helictotrichon parlatorei *grassland; (■) =* Leontodon hispidus–Crepis aurea *pasture; (□) =* Nardus stricta *pasture. (bottom) Index of invasibility of the overall grassland matrix (= sum of the proportional areas of the 10 predominant grassland types weighted by their respective index of invasibility (= solid line) and current distribution of* Pinus mugo *shrublands (= dotted line) in altitudinal steps of 100 m.*

seed input. Although we have held distance to seed source constant, homogeneous seed input over the whole area of a 20 × 20-m sampling plot is quite unlikely to occur. Short-distance seed dispersal kernels are usually exponential in shape (Nathan and Muller-Landau, 2000), with the majority of seeds deposited within a few plant heights of the source (Bullock and Clarke, 2000). Besides stochastic events and differential fecundity of neighboring *Pinus mugo* stands, the very size of the plots will thus cause a gradient of seed rain density from the immediate edge of the propagule source to the opposite border of the plot. Hence, comparison of recruitment data among grassland types will be biased if some of them show a systematic trend to occur closer to the edge of *Pinus mugo* shrublands. In fact, such habitat preferences are known for *Deschampsia cespitosa* and *Carex ferruginea* grasslands (e.g., Greimler and Dirnböck, 1996), which probably profit from enhanced water and nutrient supply at shrubland edges (Holtmeier and Broll, 1992). However, contrary to expectation, these communities have a very low index of invasibility. Thus, nonrandom differences in seed input are unlikely to be responsible for the deviance of observed recruitment patterns from the null model.

The relationship between invasibility index and grassland canopy structure suggests that colonization success of *Pinus mugo* is controlled by varying intensities of competition in the respective "host communities." Accordingly, competitive interactions with nonwoody plants, notably grasses, have been demonstrated to be a key factor not only in controlling pine invasions in different habitats and parts of the world (Richardson and Bond, 1992; Richardson and Higgins, 1998) but also in colonization of subalpine grasslands by other tree species (Magee and Antos, 1992). Experimental tests will be necessary to determine the limiting resource, but given the comparatively high light requirements of seedlings of different *Pinus* species (Keeley and Zedler, 1998), and of *Pinus mugo* in particular (Hafenscherer and Mayer, 1986; Michiels, 1993), shading by dense and high grassland canopies may be supposed to be the most important factor. Additionally, there is a significant relationship between the invasion index of a community and its position on a gradient of soil erosion potential. Considering the low explanatory power of EROS in the abiotic habitat model, this correlation is possibly coincidental and does not indicate a mechanistic process. However, topsoil erosion may in fact facilitate *Pinus mugo* recruitment as heavy litter seems to inhibit successful seedling establishment (Michiels, 1993). A similar inhibitive effect of thick litter layers was demonstrated for *Picea abies* in central European montane grasslands (Prach et al., 1996).

As a consequence of grassland communities' differential invasibility, the current spatial distribution will variegate *Pinus mugo* colonization rates in different parts of the landscape. Considering possible climate change effects, the predominance of highly invasible *Carex firma* grasslands at and above the current treeline is particularly remarkable. If climate warming relaxes the environmental constraints that limit *Pinus mugo*'s current altitudinal distribution, an effect that has been hypothesized to depend on exceeding certain thresholds (Paulsen et al., 2000), a consecutive range expansion into former alpine grasslands may take place quite rapidly. Such an accelerated upward movement of *Pinus mugo* shrublands may pose a major threat to populations of many herbaceous alpine species if they are unable to change their ranges at comparable rates (Theurillat and Guisan, 2001; Thomas et al., 2001). In contrast, even under the favorable climatic conditions of lower subalpine regions, *Pinus mugo* will probably colonize the vigorous high-growing grasslands of many abandonend pastures at quite low rates. The results of this study suggest that biotic interactions will have a major impact on land use and climate change–driven successional dynamics that may shape the vegetation cover of many temperate and boreal high mountain landscapes during the next decades and centuries.

Acknowledgments

We are grateful to Andi Bachmann, who gave us access to his GIS application of NUATMOS; to M. Steinkellner for meteorological; G. Mandl and G. Bryda for geological, and J. Jansa for snow cover data; to M. Abensperg-Traun and Connie Oehring for linguistic improvement; and to J. Greimler and D. Moser for valuable criticism. J. Greimler, I. Schmidsberger, N. Sauberer, and T. Englisch helped with fieldwork. Financial support came from the Water Department of the City of Vienna and the Austrian Federal Ministry for Education, Culture, and Science.

References Cited

Adler, W., and Oswald, K., Fischer, R., 1994: *Exkursionsflora für Österreich*. Stuttgart: Ulmer. 1180 pp.

Bachmann, A., 1998: *Coupling NUATMOS with the GIS ARC/Info.* Final Report for MINERVE 2. Department of Geography of the ETH Zürich, Division of Spatial Data Handling. 13 pp.

Barling, R. D., Moore, I. D., and Grayson, R. B., 1994: A quasi-dynamic wetness index for characterizing the spatial distribution of zones of surface saturation and soil water content. *Water Resources Research,* 30: 1029–1044.

Bätzing, W., 1991: *Die Alpen: Entstehung und Gefährdung einer europäischen Kulturlandschaft.* München: C. H. Beck. 286 pp.

Braun-Blanquet, J., 1964: *Pflanzensoziologie*, 3rd ed. Wien: Springer. 865 pp.

Bullock, J. M., and Clarke, R. T., 2000: Long distance seed dispersal by wind: measuring and modelling the tail of the curve. *Oecologia,* 124: 506–521.

Cernusca, A., 1975: Standörtliche Variabilität und Engergiehaushalt alpiner Zwergstrauchbestände. *Verhandlungen der Gesellschaft für Ökologie, Wien*, 9–21.

Cernusca, A., 1976: Energy exchange within individual layers of a meadow. *Oecologia (Berlin),* 23: 141–149.

Cullen, L., and Stewart, G. H., Duncan, R. P., Palmer, G., 2001: Disturbance and climate warming influences on New Zealand *Nothofagus* tree-line population dynamics. *Journal of Ecology,* 89: 1061–1071.

Davis, A. J., and Jenkinson, L. S., Lawton, J. L., Shorrocks, B., Wood, S., 1998: Making mistakes when predicting shifts in species range in response to global warming. *Nature,* 391: 783–786.

Didier, L., 2001: Invasion patterns of European larch and Swiss stone pine in subalpine pastures in the French Alps. *Forest Ecology and Management,* 145: 67–77.

Dirnböck, T., Greimler, J., 1997: Subalpine-alpine Vegetationskartierung der Raxalpe, Nordöstliche Kalkalpen. *Linzer Biologische Beiträge,* 29: 299–339.

Dirnböck, T., Greimler, G., Grabherr, G., 1998: Die Vegetation des Zeller Staritzen Plateaus (Hochschwab, Steiermark) und ihre Bedeutung für den Quellschutz. *Mitteilungen des Naturwissenschaftlichen Vereins der Steiermark,* 128: 123–183.

Dirnböck, T., Dullinger, S., Gottfried, M., Grabherr, G., 1999: Die Vegetation des Hochschwab (Steiermark): alpine und subalpine Stufe. *Mitteilungen des Naturwissenschaftlichen Vereins der Steiermark,* 129: 111–251.

Dirnböck, T., Dullinger, S., Grabherr, G., 2003: A regional impact assessment of climate and land-use change on alpine vegetation. *Journal of Biogeography,* 30: 401–417.

Dubayah, R., and Rich, P. M., 1996: GIS-based solar radiation modeling. *In* Goodchild, M. F., Steyaert, L. T., and Parks, B. O. (eds.), *GIS and Environmental Modeling*. New York: Wiley, 129–134.

Dullinger, S., and Dirnböck, T., Grabherr, G., 2001: Die subalpine und alpine Vegetation der Schneealpe, Steiermark. *Mitteilungen des Naturwissenschaftlichen Vereins der Steiermark*, 83–128.

Ellenberg, H., 1988: *Vegetation ecology of central Europe.* Cambridge: Cambridge University Press. 731 pp.

Gallant, J. C., Wilson, J. P., 1996: Tapes-G: a grid based terrain analysis program for the environmental science. *Computers and Geoscience,* 22: 713–722.

Geiger, R., 1965: *The Climate Near the ground.* Cambridge, MA: Harvard University Press. 277 pp.

Grabherr, G., Mucina, L., 1993: *Die Pflanzengesellschaften Österreichs. Teil II.* Jena: Gustav Fischer. 523 pp.

Grabherr, G., Gottfried, M., and Pauli, H., 1994: Climate effects on mountain plants. *Nature,* 369: 448.

Grabherr, G., and Gottfried, M., Gruber, A., Pauli, H., 1995: Patterns and current changes in alpine plant diversity. *In* Chapin, F. S., and Körner, C. (eds.), *Arctic and Alpine Biodiversity: Pattern Causes and Ecosystem Consequences.* New York: Springer, 167–181.

Greimler, J., and Dirnböck, T., 1996: Die subalpine und alpine Vegetation des Schneebergs, Niederösterreich. *Linzer Biologische Beiträge,* 28: 437–482.

Grubb, P. J., 1977: The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Review,* 52: 107–145.

Guisan, A., and Holten, J. I., Spichiger, R., Tessier, L. (eds.), 1995:

Potential Ecological Impacts of Climate Change in the Alps and Fennoscandian Mountains. Genève: Conservaitoire and Jardin Botaniques de Genèves. 194 pp.

Hafenscherer, J., and Mayer, H., 1986: Standort, Aufbau, Entwicklungsdynamik und Verjüngung von Latschenbeständen im Karwendeltal/Tirol. *Schweizerische Zeitschrift für Forstwesen,* 137: 177–203.

Harrell, F. E., Jr., 2001: *Regression Modeling Strategies.* New York: Springer. 568 pp.

Harte, J., and Shaw, R., 1995: Shifting dominance within a montane vegetation community: results of a climate-warming experiment. *Science,* 267: 876–880.

Hessl, A. E., and Baker, W. L., 1997: Spruce and fir regeneration and climate in the forest-tundra ecotone of Rocky Mountains National Park, Colorado, U.S.A. *Arctic and Alpine Research,* 29: 173–183.

Holtmeier, F. K., and Broll, G., 1992: The influence of tree islands and microtopography on pedoecological conditions in the forest-alpine tundra ecotone on Niwot Ridge, Colorado Front Range, U.S.A. *Arctic and Alpine Research,* 24: 216–228.

Keeley, J. E., and Zedler, P. H., 1998: Evolution of life histories in *Pinus*. *In* Richardson, D. M. (ed.), *Ecology and Biogeography of Pinus*. Cambridge: Cambridge University Press, 219–250.

Körner, C., 1999: *Alpine Plant Life*. New York: Springer. 338 pp.

Kullmann, L., 1993: Pine (*Pinus sylvetris* L.) tree-limit surveillance during recent decades, Central Sweden. *Arctic and Alpine Research,* 25: 24–31.

Magee, T. K, and Antos, J. A., 1992: Tree invasion into a mountain-top meadow in the Oregon Coast Range, USA. *Journal of Vegetation Science*, 3: 485–494.

Meshinev, T., Apostolova, I., and Koleva, E. S., 2000: Influence of warming on timberline rising: a case study on *Pinus peuce* Griseb. in Bulgaria. *Phytocoenologia*, 30: 431–438.

Michiels, H. G., 1993: Die Stellung einiger Baum- und Straucharten in der Struktur und Dynamik der Vegetation im Bereich der hochmontanen und subalpinen Waldstufe der Bayrischen Kalkalpen. *Forstliche Forschungsberichte München*, 135. 300 pp.

Moen, J., 1993: Positive versus negative interactions in a high alpine block field: germination of *Oxyria digyna* seeds in a *Ranunculus glacialis* community. *Arctic and Alpine Research,* 25: 201–206.

Moir, W. H., Rochelle, S. G., and Schoettle, A. W., 1999: Microscale patterns of tree establishment near upper treeline, Snowy Range, Wyoming, U.S.A. *Arctic, Antartic, and Alpine Research,* 31: 379–388.

Motta, R., and Nola, P., 2001: Growth trends and dynamics in subalpine forest stands in the Varaita Valley (Piedmont, Italy) and their relationships with human activities and global change. *Journal of Vegetation Science,* 12: 219–230.

Mucina, L., Grabherr, G., and Ellmauer, T., 1993a: *Die Pflanzengesellschaften Österreichs.* Teil I. Jena: Gustav Fischer. 578 pp.

Mucina, L., Grabherr, G., and Wallnöfer, S., 1993b: *Die Pflanzengesellschaften Österreichs.* Teil III. Jena: Gustav Fischer. 353 pp.

Müller-Schneider, P., 1986: Verbreitungsbiologie der Blütenpflanzen Graubündens. *Veröffentlichungen des Geobotanischen Institutes der Eidg. Techn. Hochschule, Stiftung Rübel*, 85. 263 pp.

Nathan, R., and Muller-Landau, C., 2000: Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology and Evolution,* 15: 278–285.

Paulsen, J., Weber, U. M., and Körner, Ch., 2000: Tree growth near treeline: abrupt or gradual reduction with altitude? *Arctic, Antarctic, and Alpine Research,* 32: 14–20.

Prach, K., Leps, J., and Michálek, J., 1996: Establishment of *Picea abies*-seedlings in a central European mountain grassland: an experimental study. *Journal of Vegetation Science,* 7: 681–684.

Richardson, D. M., and Bond, W. J., 1991: Determinants of plant distribution: evidence from pine invasions. *American Naturalist,* 137: 639–668.

Richardson, D. M., and Higgins, S. I., 1998: Pines as invaders in the southern hemisphere. *In* Richardson, D. M. (ed.), *Ecology and Biogeography of Pinus.* Cambridge: Cambridge University Press, 450–474.

Richardson, D. M., and Rundel, P. W., 1998: Ecology and biogeography of *Pinus*: an introduction. *In* Richardson, D. M. (ed.), *Ecology and Biogeography of Pinus.* Cambridge: Cambridge University Press, 3–48.

Richardson, D. M., Bond, W. J., Richard, W., Dean, J., Higgins, S. I., Midgley, G. F., Milton, S. J., Powrie, L. W., Rutherford, M. C., Samways, M. J., and Schulze, R. E., 2000: Invasive alien species and global change: A south African perspective. *In* Mooney, H. A., and Hobbs, R. J. (eds.), *Invasive Species in a Changing World.* Washington, DC: Island Press, 303–350.

Rochefort, R. M., and Peterson, D. L., 1996: Temporal and spatial distribution of trees in subalpine meadows of Mount Rainier National Park, Washington, U.S.A. *Arctic and Alpine Research,* 28: 52–59.

Ross, D. G., Smith, I. N., Manins, P. C., and Fox, D. G., 1988: Diagnostic wind field modeling for complex terrain: model development and testing. *Journal of Applied Meteorology,* 27: 785–796.

Shea, K., and Chesson, P., 2002: Community ecology theory as a framework for biological invasions. *Trends in Ecology and Evolution,* 17: 170–176.

Silvertown, J. W., and Lovett Doust, J., 1993: *Introduction to Plant Population Biology,* 3rd ed. Oxford: Blackwell. 210 pp.

Szeicz, J. M., and MacDonald, G. M., 1995: Recent white spruce dynamics at the subarctic alpine treeline of north-western Canada. *Journal of Ecology,* 83: 873–885.

Theurillat, J.-P., and Guisan, A., 2001: Potential impact of climate change on vegetation in the European Alps: a review. *Climatic Change,* 50: 77–109.

Thomas, C. D., Bodsworth, E. J., Wilson, R. J., Simmons, A. D., Davies, Z. G., Musche, M., and Conradt, L., 2001: Ecological and evolutionary processes at expanding range margins. *Nature,* 411: 577–581.

Turc, L., 1961: Évaluation de besoins en eau d'irrigation, évapotranspiration potentielle, formule simplifiée et mise en jour. *Annales Agronomiques,* 12: 13–49

Wearne, L. J., and Morgan, J. W., 2001: Recent forest encroachment into subalpine grasslands near Mount Hotham, Victoria, Australia. *Arctic, Antarctic, and Alpine Research,* 33: 369–377.

Willis, K. J., Bennet, K. D., and Birks, H. J. B., 1998: The late Quaternary dynamics of pines in Europe. *In* Richardson, D. M. (ed.), *Ecology and Biogeography of Pinus.* Cambridge: Cambridge University Press, 107–121.

Wilson, J. P., and Gallant, J. C., 1996: EROS: a grid based program for estimating spatially-distributed erosion indices. *Computers and Geosciences,* 22: 707–712.

Zwittkovits, F., 1974: *Die Almen Österreichs.* Zillersdorf: Selbstverlag. 419 pp.

Ms submitted July 2003