

Modelling climate change-driven treeline shifts: relative effects of temperature increase, dispersal and invasibility

STEFAN DULLINGER, THOMAS DIRNBÖCK* and GEORG GRABHERR
Institute of Ecology and Conservation Biology, University of Vienna, Althanstraße 14, A-1090 Vienna, Austria, and
**Federal Environment Agency, Spittelauer Lände 5, A-1090 Vienna, Austria*

Summary

1 Global warming will probably shift treelines upslope in alpine areas and towards the pole in arctic environments. However, responses of regional treelines to climatic trends over the last century do not show any clear trends. We hypothesize that these equivocal responses may partly be caused by limitation of dispersal and/or recruitment that is species-specific to particular trees with potentially expanding ranges.

2 To test this hypothesis, we established and parameterized a temporally and spatially explicit model of plant spread and analysed its sensitivity to: (a) variation in predicted climatic trends; (b) the spatial distribution of recruits around a seed source; and (c) variation in the resistance of resident non-woody vegetation to invasion. We used data from a high mountain landscape of the Northern Calcareous Alps in Austria where the treeline is dominated by *Pinus mugo* Turra, a shrubby pine.

3 Low growth rates and long generation times, together with considerable dispersal and recruitment limitation, resulted in an overall slow range expansion under various climate-warming scenarios.

4 Running the model for 1000 years predicted that the area covered by pines will increase from 10% to between 24% and 59% of the study landscape.

5 The shape of the dispersal curve and spatial patterns of competitively controlled recruitment suppression affect range size dynamics at least as severely as does variation in assumed future mean annual temperature (between 0 °C and 2 °C above the current mean). Moreover, invasibility and shape of the dispersal curve interact with each other due to the spatial patterns of vegetation cover in the region.

6 Ambiguous transient responses of individual treeline systems may thus originate not only from variation in regional climatic trends but also from differences in species' dispersal and recruitment behaviour and in the intensity and pattern of resistance of resident alpine vegetation to invasion.

Key-words: alpine treeline, climate change, dispersal, European Alps, invisibility, plant spread model

Journal of Ecology (2003) **92**, 241–252

Introduction

Predicted global warming will probably affect range sizes and the geographical distribution of biota (e.g. Grabherr *et al.* 1994; Parmesan 1996; Sturm *et al.* 2001; Thomas *et al.* 2001; Walther *et al.* 2002; Parmesan & Yohe 2003). As climatically determined ecotones, arctic and alpine treelines are assumed to be particularly sensitive to altered temperature regimes and climate warming is expected to drive treelines upslope and poleward at the expense of alpine and arctic ecosystems, respectively

(Kittel *et al.* 2000; Hansen *et al.* 2001; Theurillat & Guisan 2001). However, field studies and remote sensing analyses that have investigated recent treeline shifts in response to increasing temperatures during the last century have provided ambiguous results that span the whole gradient from rapid dynamics to apparently complete inertia (e.g. Kullman 1993; Lavoie & Payette 1994; Szeicz & MacDonald 1995; Hessl & Baker 1997; Meshinev *et al.* 2000; Cullen *et al.* 2001; Masek 2001; Motta & Nola 2001; Sturm *et al.* 2001; Klasner & Fagre 2002; Kullman 2002). Apart from variation in regional climatic trends, these equivocal findings probably result from differences between individual treeline systems. As an analogy to alien plant invasions, one may

hypothesize that dispersal capacity of tree species (e.g. Kot *et al.* 1996; Neubert & Caswell 2000; Bullock *et al.* 2002; Shigesada & Kawasaki 2002; Watkinson & Gill 2002) and competitive interactions with resident alpine vegetation (Richardson & Bond 1991; Magee & Antos 1992; Rochefort & Peterson 1996; Moir *et al.* 1999) will be major sources of variation in treeline responses to climate change.

Throughout most of the north-eastern Calcareous Alps, the treeline is currently dominated by a shrubby pine (*Pinus mugo* Turra). In an earlier study (Dirnböck *et al.* 2003), we have used an equilibrium-based static modelling approach (Guisan & Zimmermann 2000) to evaluate effects of predicted climate warming on the regional distribution of this species in some mountain ranges at the north-eastern fringe of the Alps. Results of these models suggest a considerable range expansion of *P. mugo* at only moderate levels of temperature increase. However, additional work on *P. mugo* dynamics indicated that the possible range shift might be hampered by restricted dispersal as well as by competitive inhibition of recruitment in dense grassland layers. Predicted potential distributions may thus not be achieved in the mid-term (Dullinger, Dirnböck & Grabherr 2003).

Unfortunately, most existing simulation models that explore potential range shifts and forest dynamics in response to climate change either do not represent transient dynamics (in the case of equilibrium-based, bioclimatic habitat distribution models, e.g. Guisan & Zimmermann 2000), or they disregard processes that occur beyond the boundaries of the simulation plot (in the case of gap models, e.g. Loehle & LeBlanc 1996). Models that integrate both the spatial and temporal dimensions have until now primarily been applied to the spread of alien plants (e.g. Higgins & Richardson 1996, 1999; Neubert & Caswell 2000; Shigesada & Kawasaki 2002). However, they have also been used to reconstruct Holocene vegetation dynamics (e.g. Clark 1998) and their potential for simulating possible responses of plant species to predicted climate change has been inferred from such applications (Pitelka & Plant Migration Workshop Group 1997; Clark 1998; Higgins & Richardson 1999).

We use a spatially and temporarily explicit plant spread simulator to address the relative roles of climate warming, dispersal capacity and competitive interactions with established alpine vegetation in determining the range expansion of *P. mugo*. Focusing on a 1000-year time frame, we examine how predictions of pine shrub distribution are affected by: (i) the degree of temperature increase; (ii) the shape of the dispersal curve; and (iii) the degree of invasibility of the alpine vegetation. Moreover, we examine the possible interactions among these driving processes.

Methods

STUDY SYSTEM

The study area covers the treeline ecotone and the alpine belt of Mt Hochschwab (47°34' to 47°38' latitude and

15°00' to 15°18' longitude, uppermost summit 2273 m a.s.l.), which is part of the north-eastern Calcareous Alps of Austria. The mountain range is characterized by displaced plateaus of different altitudes, with surfaces shaped by Pleistocene glaciation and karst landform development. Soils are predominantly lithic and rendzic Leptosols, as well as chromic Cambisols. Climatic conditions are temperate humid. Mean annual temperature near the summit is approximately 0–2 °C, where annual precipitation averages 2000–2500 mm with a marked peak during the growth period. The alpine areas are covered by snow for approximately 6–8 months of the year (October–May). There is much fine-scale variation in the duration of snow cover due to the rugged relief and strong winds.

Summer pasturing (June to September) in the Mt Hochschwab region dates back at least to the 16th century. At least some historical livestock grazing has been documented over 30% of the study area. Since the mid-19th century, grazing intensity has decreased and much former pasture land has been abandoned, so that today only 7.5% of the study area remains as pasture for free-ranging cattle at a density of about 0.5 animals per hectare (Dullinger, Dirnböck, Greimler & Grabherr 2003).

The dominant woody plant species of the upper subalpine belt is prostrate pine (*P. mugo*). The upper limit of single *P. mugo* individuals is currently at about 1950 m a.s.l. In fact, the current subalpine belt is a mosaic of woody and non-woody vegetation. Non-woody vegetation below the treeline mainly consists of different kinds of pastures and natural grasslands, with the latter covering disturbed sites like avalanche paths and exposed ridges. Above the treeline, natural grasslands dominate with a gradual switch from *Carex sempervirens* Vill. to *Carex firma* Mygind grasslands with increasing altitude. Additionally, rock faces, scree and snowbeds are widespread from the valley bottoms to the summits.

STUDY SPECIES

Pinus mugo is an obligatory prostrate pine with adult canopy height varying between *c.* 0.3 and 2.5 m in the study area (for convenience, we use the term treeline for the upper altitudinal range margin of *P. mugo* despite its shrubby growth form). Seedling establishment seems to be inhibited by low light availability (Hafenscherer & Mayer 1986) and deep litter layers (Michiels 1993). Thus, within-stand regeneration is entirely dependent on clonal propagation by means of layering. Intensive, multidirectional layering makes clones potentially immortal and inhibits gap-phase regeneration processes in established stands (Hafenscherer & Mayer 1986), although recruitment of seedlings is common in grasslands. Seeds of *P. mugo* are primarily wind dispersed and secondary redistribution of seeds by birds and small mammals has been observed (Müller-Schneider 1986).

Table 1 Variables representing abiotic habitat conditions and sources they were derived from. DEM = digital elevation model. SOLARFLUX, NUATMOS and TAPES-G are software packages for calculating solar radiation income, topographically modified near-surface wind velocity and different topographical indices, respectively

Variable	Source	Abbreviation
Degree days	DEM, climate station data	DD
Solar radiation in May, July and September	DEM, SOLARFLUX (Dubayah & Rich 1996)	SRM, SRJ, SRS
Water balance in August	DEM, climate station data, SOLARFLUX (Dubayah & Rich 1996)	WBA
Wind speed	DEM, climate station data, NUATMOS (Ross <i>et al.</i> 1988; Bachmann 1998)	WSP
Slope inclination	DEM	SLOPE
Soil erosion potential	DEM, TAPES-G (Gallant & Wilson 1996)	EROS
Topographic wetness index	DEM, TAPES-G (Gallant & Willson 1996)	WET
Bedrock mineralogy	Geological map	GEO
Distribution of chromic Cambisols	DEM, 573 sample points	SOIL

REPRESENTATION OF ENVIRONMENTAL CONDITIONS

A digital elevation model (DEM, Austrian Mapping Agency) with a cell size of 20 m served as main input for the representation of abiotic habitat conditions (see Dirnböck *et al.* 2003 for details). The following variables were calculated (cf. Table 1):

1. Climatic conditions, represented by annual degree days (= days with a mean daily temperature > 0 °C, DD), solar radiation income at the beginning (15 May, SRM), in the middle (15 July, SRJ), and at the end (15 September, SRS) of the growth period, and site water balance in August (WBA).
2. Topography, characterized by slope inclination (SLOPE), a topographical wetness index (WET), a topographical soil erosion index (EROS), and an estimate of topographically modified near-surface wind velocity during strong, north-westerly winds (WSP).

Additionally, we provide data sets on bedrock mineralogy (GEO), spatial distribution of chromic Cambisols, and current vegetation cover. Bedrock mineralogy was derived from recently updated geological maps (scale: 1 : 50 000, Geological Survey of Austria, unpublished information). The distribution of chromic Cambisols was extrapolated from 557 sample points in the study area and adjacent mountain ranges using a binary classification tree procedure with topographical variables (altitude, slope, EROS, WET and their interactions) as predictors (misclassification rate 13%). Information on current vegetation cover, including pine shrub distribution, comes from a fine-scale vegetation map (1 : 10 000, Dirnböck *et al.* 1999) and high-resolution IR-orthophotographs (acquired on 23 July 1994, pixel resolution 25 cm). All these data sets were re-sampled to meet the resolution of the DEM.

MODEL CONCEPT AND ASSUMPTIONS

In accordance with environmental descriptors the model landscape is represented by a two-dimensional grid with a cell size of 20 m. Overall, it spans about 53 km² (131 901

cells). Pine shrub dynamics across this landscape are tracked as the changing percentage of *P. mugo* cover per individual grid cell (= site) over time. These changes result from the spatial distribution of recruits originating from a site and from the growth and mortality of individual pine shrubs growing at the respective site.

Model formulation is based on several simplifying assumptions:

1. Time passes in discrete steps. Our parameterization data demonstrate very low recruitment rates (see below). We thus decided to use a rather long time step of 50 years. Moreover, using a long time step avoids bias in recruitment rate estimation due to variable seed production and seedling survival (e.g. Clark *et al.* 1999; De Steven & Wright 2002). Although little is known about inter-annual patterns of seed production for *P. mugo*, masting behaviour is widespread among treeline species of the northern Calcareous Alps and masting frequency is very low at high elevations (e.g. > 10 years for *Picea abies* (L.) Karsten, Mayer 1976).
2. The canopy increment of an individual *P. mugo* shrub per time step is adequately represented by a growing circle. While the canopy shape is irregular, the multistem growth-form (Hafenscherer & Mayer 1986) justifies this geometrical approximation.
3. Due to intensive clonal propagation by multidirectional layering, mortality does not have an age-dependent component but is entirely due to catastrophic disturbances. The most important disturbance regimes are avalanches and extreme weather events. Such events do not cause mortality of just one individual but usually kill the whole population at a site. We thus assume mortality events to reset the canopy cover of a grid cell to 0%.
4. Recruitment and mortality of pines include a stochastic component that is due to unpredictability of annual snow fall and melting processes, unusual weather events or spatial patterns of seed and seedling predation and secondary seed dispersal (e.g. Vander Wall 1992; Greene & Johnson 1997).
5. Pine shrub populations of already densely covered cells invade neighbouring cells vegetatively. For ease

of computation, the invading front is assumed to be a straight line with a width of one cell size. We used a threshold cover of 90% to trigger this process of vegetative invasion into adjacent sites.

6. Rock faces lack appropriate space and soil substrate to support a dense *P. mugo* canopy. According to our field experience we set the maximum value of pine shrub cover in rock habitats to 10%.

7. Besides seed availability and climatic constraints, pine shrub colonization of debris cones is mainly controlled by mechanical stress. Successful invasion is thus only possible if the site is positioned on a ridge or if there is a neighbouring cell above the focal site that provides shelter as a result of existing dense pine cover. These rules produce the typical colonization pattern of pine shrubs on debris cones, i.e. propagating downhill in a conical fashion.

The model starts from the current distribution of pine shrub populations across the landscape. Initially, all currently occupied sites are assigned a cover of 100% and an age of 100 years. The model first calculates the fecundity of the population at each site as a function of the age of the individuals and of environmental conditions. Sites with populations above a certain threshold of fecundity (see below) are defined as seed sources. Next, it determines the number of newly germinating recruits per individual site during one time step. Year of germination is chosen randomly. The canopy cover of all individuals at a site increases by a site-specific growth rate independently of age (Michiels 1993). The resulting increase in pine shrub cover per site is augmented by vegetative invasion from neighbouring cells. The model proceeds by simulating catastrophic mortality events. A random number generator (0–1, uniform distribution) is used and, for each cell, this number is compared with the site-specific probability of occurrence of such an event. If the number is greater than this probability for a given site, its pine shrub cover is reset to 0%. Lastly, the model re-calculates the age of each *P. mugo* population at the end of the time step. Age of a population is represented as a cover-weighted mean of the age of all its individuals.

PARAMETER ESTIMATION

Recruitment, growth, fecundity and mortality functions were estimated using data collected at 140 plots (each 20 × 20 metre) in the study area and on adjacent mountain ranges. Selection of plots was based on a stratified random sampling design (Dullinger, Dirnböck & Grabherr 2003). For growth and fecundity parameters we additionally used 196 pine shrub individuals selected during random walks in the same areas.

Recruitment, dispersal functions and invasibility

The site-specific 50-year recruitment rate was determined by counting the number of individuals younger than 50 years on each plot (see Dullinger, Dirnböck &

Grabherr 2003 for methods of age determination). We fitted a recruitment kernel to these data using the distance (two-dimensional Euclidean distance) to the nearest pine shrub stand (= grid cell with a pine shrub cover > 10% as determined from aerial photographs) as predictor. Two alternative statistical models were applied: a negative exponential and a restricted cubic spline with four knots. Restricted cubic splines are third-order polynomials within intervals of the predictor forced to be smooth at the joining points (= knots) and constrained to be linear in the tails (Stone & Koo 1985; Harrell 2001).

In simulation runs, stochastic variation in the number of recruits per site was implemented by drawing a random number from an exponential distribution for each site with the site-specific recruitment rate (determined from the recruitment kernel) as the respective mean. We used an exponential distribution to mimic the error pattern in fitted recruitment kernels for plots 0 and 20 m from the nearest seed source. Subsequently, the predicted number of recruits per site and time step was weighted by two alternative invasibility layers. These layers were derived from the vegetation map. The first one assumed equal invasibility (weighting factor = 1) across all types of alpine vegetation (but holding forests and snowbeds uninvasible), the second one assigned each plant community a specific invasibility value. These were calculated as the ratio between observed recruitment rates in individual plant communities and expected rates under a null model of equal invasibility using the same parameterization data set as for demographic variables and vary between 0.1 and 2.1 for the plant communities of the study area (see Dullinger, Dirnböck & Grabherr 2003 for details).

Growth

The vegetative growth rate of 231 individuals was measured as the mean length-increment of a randomly selected major branch between 1996 and 1999. This growth rate was regressed against abiotic environmental conditions using ordinary least-squares regression. Both linear and non-linear effects were considered. Non-linear effects were tested for by restricted cubic splines with four knots. Moreover, we tested for all two-way interactions among predictors. Model and predictor significances were obtained from the Wald test statistic assuming a chi-square distribution with one degree of freedom (Harrell 2001). The full model was reduced by backward elimination, knot reduction and linearization, respectively (threshold *P*-value 0.05). The final coefficient of determination was corrected for possible overfit by means of bootstrapping (1000 re-samples with replacement).

Fecundity

Using the number of cones produced by an individual as an indicator, each pine shrub was assigned an ordinal fecundity value on a four-level scale (0–3). Fecundity

Table 2 Regression functions for parameterizing the demographic processes of the *Pinus mugo* spread model. LS = least squares regression; LR = logistic regression; PO = proportional odds regression. For each multiple regression function only significant predictors are listed. Distance = distance to nearest pine shrub stand; Damage = probability of climatic damage; Age = age of pine shrub individual. For abbreviations of abiotic habitat variables see Table 1. *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$. R^2 - and Somer's D_{xy} -values were corrected for possible overfit by bootstrapping (1000 resamples). exp = exponential recruitment kernel; rcs = restricted cubic spline recruitment kernel. Regression equations and coefficients are listed in Appendix S1, date used for establishing regression models are given in Appendix S2 (see Supplementary Material)

	Model type	Predictors	R^2 -orig	R^2 -corr	D_{xy} -orig	D_{xy} -corr	P
Recruitment_EXP	LS	Distance***	0.62	0.59	–	–	< 0.0001
Recruitment_RCS	LS	Distance***	0.88	0.85	–	–	< 0.0001
Growth	LS	DD*** Damage*** SOIL* WET* SRJ*	0.49	0.44	–	–	< 0.0001
Fecundity	PO	Age*** GEO*** Damage *** SRM** DD*	0.57	0.54	0.80	0.79	< 0.0001
Mortality	LR	EROS*** WET*** DD** SLOPE*	0.27	0.24	0.69	0.66	< 0.0001
Occurrence of damage	PO	DD*** SRJ*** Age*** SLOPE* WET*	0.4	0.38	0.7	0.68	< 0.0001

was regressed against environmental conditions, age of the individual and occurrence of damage (see below) by means of a proportional odds model (= ordinal logistic regression model, Harrell 2001) using the same procedure as for the growth function. Instead of least-squares R^2 we report Nagelkerke's R^2 and Somer's D_{xy} as a measure of concordance between regression model predictions and data (Table 2).

In the simulation model the population of a site was defined a seed source if its predicted fecundity value was greater than 1.

Mortality

We used the distribution of dead individuals across our sampling plots to estimate the site-specific risk of adult mortality by means of logistic regression. The procedure of regression analysis was the same as for growth and fecundity functions.

In the simulation model, the site-specific probability of finding a dead individual was set as the site-specific adult mortality per time step. This somewhat arbitrary definition was found to produce realistic spatio-temporal mortality patterns in exploratory simulation runs. Avalanche paths, which are unlikely ever to support closed *P. mugo* cover on account of frequent severe disturbance, do not become overgrown, whereas the establishment and persistence of closed populations at less exposed sites is not affected.

Furthermore, we adapted the concept usually applied to mortality routines in forest gap model formulations

(Keane *et al.* 2001) and defined sites with predicted growth rates lower than the minimum observed in our parameterization data set to be not suitable for permanent *P. mugo* establishment. In the simulation, this was realized by resetting the population of all such sites to 0% cover after each time step.

For all individuals we also recorded occurrence of damage due to climatic constraints (frost desiccation, snow-ice abrasion) on a four-level ordinal scale. Occurrence of damage turned out to be a significant predictor in both growth and fecundity models. We thus introduced the site-specific probability of damage (estimated by means of a proportional odds model, cf. Table 2) to the growth and fecundity functions, interpreting it as a weighted interaction term of individual age and abiotic site conditions.

SIMULATION RUNS AND EVALUATION OF THE EFFECTS OF TEMPERATURE RISE, DISPERSAL AND INVASIBILITY ON PINE SHRUB EXPANSION

A factorial design was established combining four different climatic scenarios with the two distance-dependent recruitment functions (exponential and restricted cubic spline) and the two alternative invasibility patterns (homogenous and varied).

As *P. mugo* performance in parameterization plots did not show any significant effect of water balance (cf. Table 2), climatic scenarios only took account of temperature rise. A baseline scenario assumed that current temperature conditions remain unchanged (overall mean

annual temperature in the study area for 1995–98, calculated by linear regression of data from nearby meteorological stations against altitude and geographical longitude: 1.2 °C). Scenario 2 was derived from simulation outputs of the global circulation model ECHAM4 (Roecker *et al.* 1996) downscaled for Austria by Lexer *et al.* (2001). According to this scenario, a 0.65 °C increase in mean annual temperature might be expected for the study area by the year 2050 (means for 2035–65 vs. 1961–95), but temperature is assumed to remain constant thereafter. Scenario 3 is as scenario 2, but with a further increase to +1.2 °C above current mean temperature in total by the year 2100, and scenario 4 has a further increase to +2 °C by the year 2150. The different scenarios were incorporated into the model by adapting the degree day-values of all sites according to the assumed temperature regime.

Overall, this $2 \times 4 \times 2$ combination of fixed effects yields 16 different scenarios in a fully orthogonal design. Ten replicates of each combination of treatments were run. For each time step of each replicate run, we recorded the total percentage of pine shrub cover, the elevation of the uppermost population and the maximum distance from an existing seed source at which a new recruit had established. To focus exclusively on climate change effects and to exclude the confounding influence of unpredictable changes in land use, all scenarios were run under the assumption that cattle grazing and logging will cease instantaneously. To minimize edge effects we applied the model to the whole landscape (131 901 sites, 52.7 km²), but results are reported only for the area above 1700 m a.s.l. (84 827 sites, 33.9 km²). ANOVA was used to test for main effects and interactions of climate scenario, recruitment kernel and invasibility on the recorded response variables. Assumptions of ANOVA were evaluated using diagnostic plots (normal probability plots, e.g. Ellison 2001) and calculating Cochran's C for homogeneity of variances.

Results

PARAMETERIZATION OF RECRUITMENT, GROWTH, FECUNDITY AND MORTALITY FUNCTIONS

With an average of about 0.0005 individuals m⁻² year⁻¹, recruitment of *Pinus mugo* is generally sparse even where seed sources are available within a radius of 20 m, and declines sharply to 7.6×10^{-6} or 5.9×10^{-5} individuals m⁻² year⁻¹ at 100 m, depending on the recruitment kernel used. The main differences between the two recruitment functions are that the restricted cubic spline-model predicts higher recruitment in the immediate vicinity of a seed source and has a longer tail, whereas the exponential model simulates more recruits at intermediate distances (50–300 m, see Fig. 1). Both functions provide significant fits to the data though residual variance is considerably lower for the more flexible restricted cubic spline kernel (see Table 2).

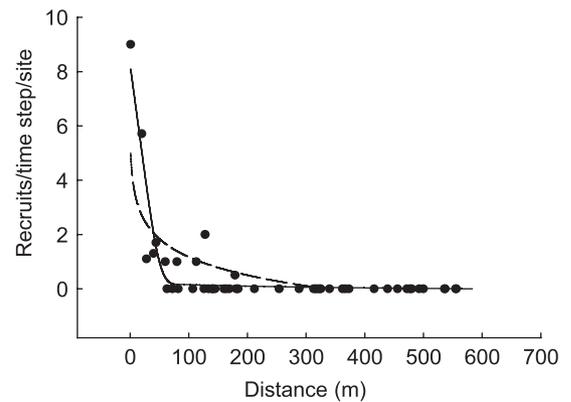


Fig. 1 Recruitment kernel of *Pinus mugo* fitted to data from 140 field plots. Solid line: restricted cubic spline function. Dashed line: negative exponential function. Each site is 400 m², the time step is 50 years. Distance = distance to the nearest site with *P. mugo* cover > 10%. Points represent average recruitment intensities at each distance.

Mean annual growth is extremely slow, with a 4-year average of only about 5 cm year⁻¹ (minimum 1.5 cm year⁻¹, maximum 12.9 cm year⁻¹). Of the abiotic site conditions, variation in growth rate is most sensitive to temperature (see Table 2, Fig. 2).

Fecundity levels were primarily controlled by age of individuals: pine shrubs usually do not start cone production until they are about 15–20 years old and high fecundity rates (ordinal fecundity value 3) are rarely achieved by individuals younger than 50 years. Fecundity becomes independent of age after 80 years and is affected only slightly by temperature (Table 2, Fig. 2).

Topography is the most important factor controlling adult mortality (Table 2). Average mortality is low (2–3%), with high values spatially clustered on exposed ridges, steep slopes with high erosion potential and risk of avalanches, and at the base of slopes where snow accumulates. Among climatic variables, temperature is again the most effective predictor. However, in contrast to growth and fecundity functions, its effect is non-linear with lowest mortality (i.e. the highest survival probability) at intermediate DD-values (Fig. 2).

SIMULATION RUNS AND EVALUATION OF THE EFFECTS OF TEMPERATURE RISE, DISPERSAL AND INVASIBILITY ON PINE SHRUB EXPANSION

Pine shrubs currently cover 10% of the study area. Within the next 1000 years the model predicts *P. mugo* to increase its cover to between 24% and 59% depending on the degree of climatic warming, the assumed shape of the recruitment kernel and the invasibility matrix used in simulation runs (Fig. 3). Within-scenario variance of predicted values is generally low.

As expected, the rate of pine shrub expansion increases with rising temperatures. The effect of higher temperature is most pronounced when comparing the baseline

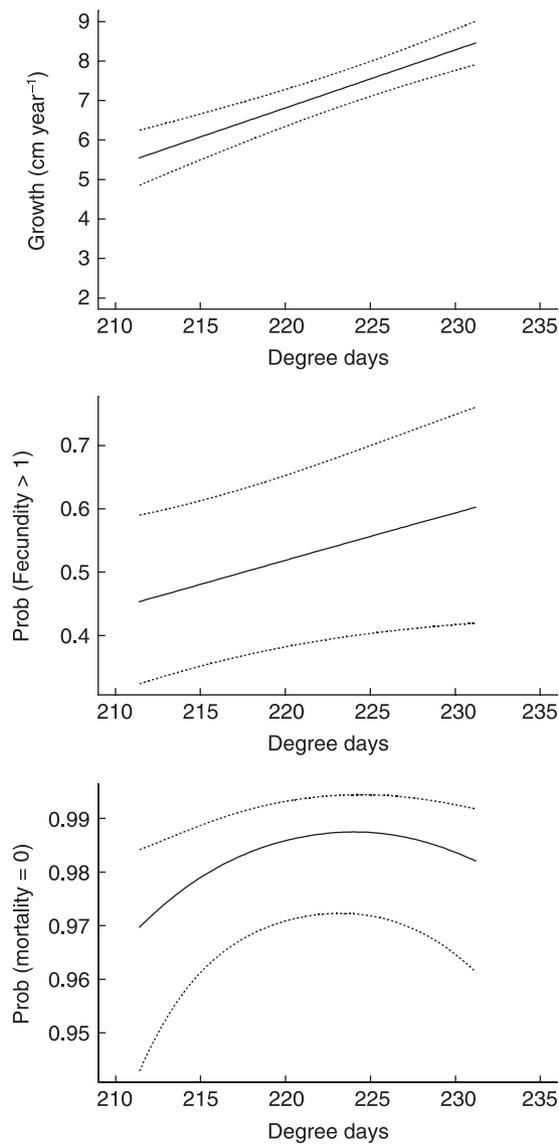


Fig. 2 Partial effects of temperature (number of days with mean temperature > 0 °C per year) on growth, fecundity and mortality of *P. mugo* in multivariate regression models (cf. Table 2). Dashed lines represent 95% confidence intervals. Additional predictors are set to the following values. *Growth*: damage = 0, SOIL = 1, SRJ = 27.1 MJ, WET = 5.94. *Fecundity*: age = 40, damage = 0, SRM = 25.8 MJ, GEO = limestone. *Mortality*: WET = 5.9, EROS = -0.27 , SLOPE = 18.5° . For abbreviations see Table 1.

Table 3 Effects of climate change scenario (ClimScen), shape of the recruitment kernel (RecrKern), spatial invasibility pattern (Invas) and their interaction terms on the area predicted to be covered by *P. mugo* in 1000 years time (= Area), the uppermost position of *P. mugo* individuals after 1000 years (= Altitude), and the maximum distance from a seed source at which a new recruit is predicted to establish during one time step (= MaxDistance). Results of fixed-effects factorial ANOVA. d.f. = degrees of freedom

Treatment	d.f.	Area		Altitude		Max Distance	
		F-value	P	F-value	P	F-value	P
ClimScen	3	26150	< 0.0001	530	< 0.0001	5.3	0.001
RecrKern	1	32568	< 0.0001	1817	< 0.0001	0.2	0.65
Invas	1	8020	< 0.0001	929	< 0.0001	123.4	< 0.0001
ClimScen : RecrKern	3	900	< 0.0001	8	0.0005	3.2	0.02
ClimScen : Invas	3	181	< 0.0001	23	< 0.0001	3.5	0.02
RecrKern : Invas	1	4241	< 0.0001	347	< 0.0001	112.4	< 0.0001

scenario with an assumed increase of 0.65 °C and lowest when switching from a $+1.2$ °C scenario to a $+2$ °C scenario (Fig. 4a).

Assuming an exponential recruitment kernel results in considerable acceleration of pine shrub spread. After 1000 years, simulation runs with an exponential kernel predict that *P. mugo* will cover an area nearly 50% larger on average than simulations with a restricted cubic spline-kernel (Fig. 4b). Similarly, spatially varied invasibility of the resident vegetation facilitates pine spread (an additional increase of about 30% in the area covered by *P. mugo* after 1000 years, compared with the homogenous model, Fig. 4c).

ANOVA results demonstrate that all main effects and all interactions significantly affect model predictions. ANOVA coefficients are highest for the $+0.65$ °C climate scenario and the recruitment function used (Fig. 5). The interaction between shape of the recruitment kernel and invasibility pattern is especially pronounced, whereas all others are of minor importance.

The uppermost position of *P. mugo* individuals shifts from the present value (1935 m a.s.l.) to between 2076 m and the highest peak of the model area (2273 m a.s.l.) depending on the scenario considered. Main effects and interactions change model predictions in a similar way to that observed for the area covered by pine shrubs. Again, the most pronounced interaction is that between recruitment kernel and invasibility pattern (Table 3).

Figure 6 illustrates why this latter interaction is salient in both cases. If an exponential kernel is used, the maximum distance of a new recruit from the nearest seed source is only marginally influenced by the way invasibility is modelled. In contrast, when applying a restricted cubic spline kernel, this maximum distance is strongly affected by the invasibility pattern.

Discussion

Results of this simulation study indicate that while pine shrubs will invade and displace current alpine vegetation under future climate change scenarios, they are likely to do so rather slowly. This inertia is due to recruitment and dispersal limitation as well as to long

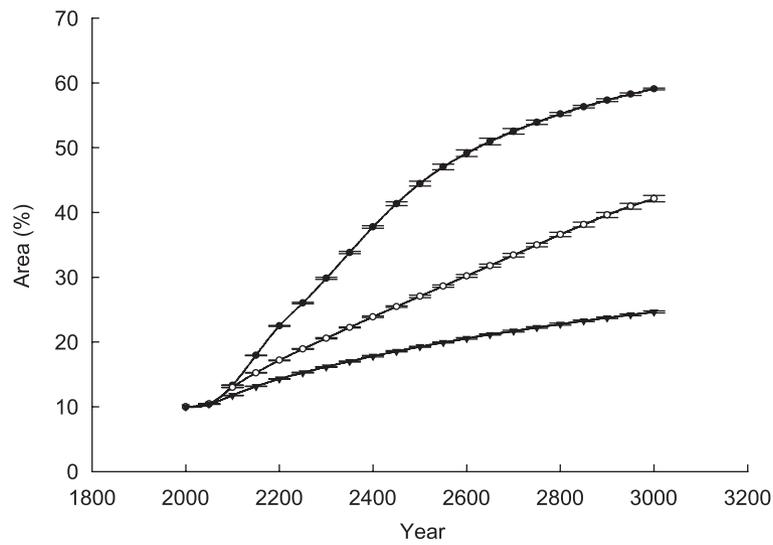
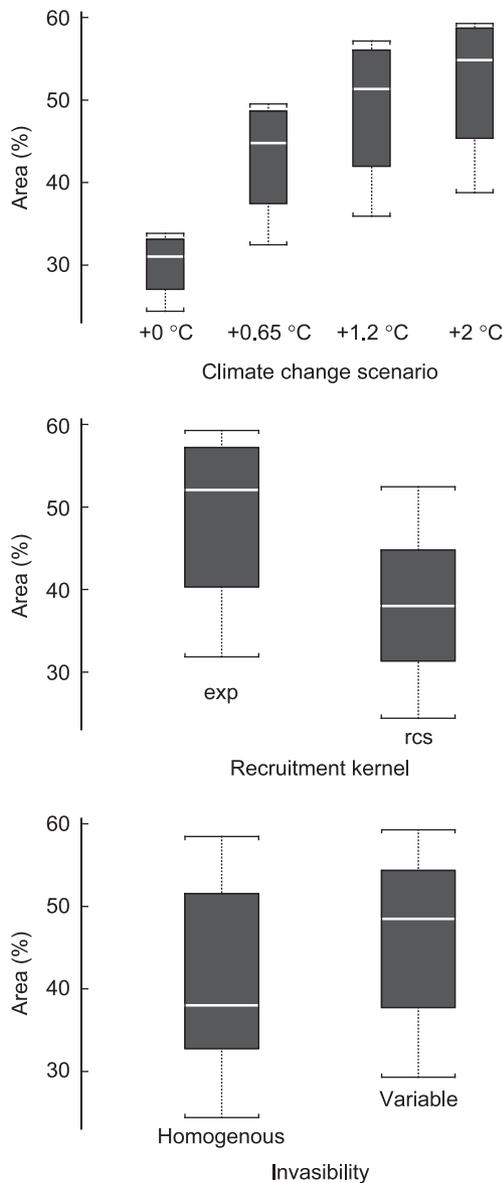


Fig. 3 Predicted increase of the area covered by *P. mugo* during the next 1000 years. Maximum, minimum and median of 160 model runs. Error bars represent standard deviations.



generation times and slow growth rates. Although our estimates of growth rates and generation times agree with values reported in Schroeter (1926) and Michiels (1993), comparable data on the intensity and spatial pattern of *P. mugo* recruitment in subalpine and alpine environments are lacking. In general, recruitment limitation seems to be a widespread phenomenon in temperate forests (Clark *et al.* 1998, 1999), but the number of recruits detected in our study is particularly low. Ribbens *et al.* (1994), for example, have defined recruitment limitation as occurring where the expected number of recruits drops below one individual $m^{-2} year^{-1}$. Mayer (1976) reports 0.1–0.5 successful recruitment events $m^{-2} year^{-1}$ for *Picea abies* in gaps of subalpine spruce forests, which are dominant below the pine shrub belt in our study area. Moreover, the initially low rate declines sharply with distance from seed sources. As seed dispersal distance is closely linked to seed release height (e.g. Nathan & Muller-Landau 2000), we assume that this sharp decline in recruitment is caused by narrow seed shadows of the low growing pine shrubs.

Nevertheless, despite such a slow response, pine shrub cover of the model landscape is predicted to increase considerably over the next 1000 years. With climatic conditions unchanged (control scenario) most of this range expansion is due to encroachment onto summer farms, both those abandoned during the last 150 years and those set as abandoned for the

Fig. 4 Effects of climate change scenario, shape of the recruitment kernel and spatial pattern of invasibility on the area predicted to be covered by *P. mugo* 1000 years from the present day. Boxes show the limits of the middle half of all simulation results, lines inside the boxes represent the median, and lines to the top and the bottom of each box highlight minima and maxima predicted under the respective variable value. exp = exponential recruitment kernel; rcs = restricted cubic spline recruitment kernel.

with favourable recruitment conditions. Assuming differential invasibility strengthens the effect of the thin but longer tail of the restricted cubic spline kernel due to the region-specific spatial distribution of habitats suitable for recruitment.

Although invasibility of resident vegetation has long been recognized as a major factor controlling alien plant spread (Richardson & Bond 1991; Wiser *et al.* 1998; Shea & Chesson 2002), its possible impact on the rate of altitudinal treeline shifts driven by climate change has been largely ignored. However, there is evidence that resident vegetation may strongly affect rates of woody plant encroachment into non-forest subalpine habitats (Magee & Antos 1992; Rochefort & Peterson 1996; Moir *et al.* 1999; Dullinger, Dirnböck & Grabherr 2003). Competition with herbaceous vegetation was also invoked as a possible explanation for regionally observed, unexpectedly slow expansion of boreal forests into arctic tundra in recent decades (Masek 2001). Such encroachment processes probably resemble the invasion of exotic pine species into native non-forest vegetation (Richardson & Higgins 1998; Higgins *et al.* 2001). Our results confirm this functional similarity. Like the interaction of dispersal and invasibility patterns, the accelerating effect of spatially varied invasibility is due to the particular spatial arrangement of plant communities: easily invadable communities dominate at and above the current treeline (Dirnböck *et al.* 1999). Under predicted climate warming scenarios, it is exactly this altitudinal belt where most of the terrain that can be newly colonized by *P. mugo* is concentrated.

Our simulation model does not consider possible climate change effects on recruitment. Pine shrub spread is likely to be driven mainly by exceptionally favourable years for recruitment (Kullman 1993), the frequency of which may increase with climate warming. This could considerably accelerate range expansion driven by climate change. However, our parameterization data set provides little evidence for major effects of temperature on local-scale recruitment intensity during the last 50 years (Dullinger, Dirnböck & Grabherr 2003). When controlling for distance to seed sources, differences in recruitment success between lower subalpine and treeline populations were only marginally significant during this time span. Nevertheless, we cannot exclude the possibility that exceptionally extended periods of warmer summers may produce threshold effects on recruitment intensity at and above the current treeline that may cause our simulation results for *P. mugo* to be underestimates. However, even enhanced recruitment of *P. mugo* under climate warming would not diminish the codominant effect of dispersal and competition on its spread.

In conclusion, the results of this modelling study suggest that patterns and rates of transient treeline dynamics that are driven by climate change may be idiosyncratic. Species will not only vary in their response to increasing temperatures in terms of their growth rates,

as they may also possess different dispersal capacities and competitive abilities during their recruitment phase. Our study demonstrates that these species-specific traits may affect future range dynamics as much as, if not more than, variation in regional climatic trends. Moreover, they interact with each other and with spatial vegetation patterns. This further complicates the task of accurately predicting transient treeline dynamics driven by climate change.

Acknowledgements

We are grateful to M. Steinkellner, G. Mandl, G. Bryda and R. Tscheliesnig for meteorological, geological and land use data, to J. Greimler, I. Schmidberger, N. Sauberer and T. Englisch for field data collection, and to N. Zimmermann and A. Bachmann for GIS software. D. Moser, M. Abensperg-Traun, L. Haddon and two anonymous referees provided helpful comments on earlier versions of the manuscript. The study was funded by the Austrian Federal Ministry for Education, Science and Culture and the Water Department of the Viennese administration.

Supplementary material

The following material is available from <http://www.blackwellpublishing.com/products/journals/suppmat/JEC/JEC872/JEC872sm.htm>

Appendix S1 Parameter values and regression equations for models of recruitment, growth, fecundity, mortality and probability of damage of *Pinus mugo*.

Appendix S2 Data used for regression models of growth, fecundity, mortality and probability of damage of *Pinus mugo*.

References

- 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.
- Bullock, J.B., Moy, I.L., Pywell, R.F., Coulson, S.J., Nolan, A.M. & Caswell, H. (2002) Plant dispersal and colonization processes at local and landscape scales. *Dispersal Ecology* (eds J.M. Bullock, R.E. Kenward & R.S. Hails), pp. 279–302. Blackwell Scientific, Oxford.
- Clark, J.S. (1998) Why trees migrate so fast. Confronting theory with dispersal biology and the paleorecord. *American Naturalist*, **152**, 204–224.
- Clark, J.S., Beckage, B., Camill, P., Cleveland, B., HilleRis-Lambers, J., Lichter *et al.* (1999) Interpreting recruitment limitation in forests. *American Journal of Botany*, **86**, 1–16.
- Clark, J.S., Macklin, E. & Wood, L. (1998) Stages and spatial scales of recruitment limitation in southern Appalachian forests. *Ecological Monographs*, **68**, 213–235.
- Cullen, L., 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.

- De Steven, D. & Wright, J. (2002) Consequences of variable reproduction for seedling recruitment in three neotropical tree species. *Ecology*, **83**, 2315–2317.
- 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**, 401–418.
- Dubayah, R. & Rich, P.M. (1996) GIS-based solar radiation modeling. *GIS and Environmental Modeling* (eds M.F. Goodchild, L.T. Steyaert & B.O. Parks), pp. 129–134. John Wiley & Sons, New York.
- Dullinger, S., Dirnböck, T. & Grabherr, G. (2003) Patterns of shrub invasion into high mountain grasslands of the Northern Calcareous Alps (Austria). *Arctic, Antarctic and Alpine Research*, **35**, 434–441.
- Dullinger, S., Dirnböck, T., Greimler, J. & Grabherr, G. (2003) A resampling approach for evaluating effects of pasture abandonment on subalpine plant species diversity. *Journal of Vegetation Science*, **14**, 243–252.
- Ellison, A.M. (2001) Exploratory data analysis and graphic display. *Design and Analysis of Ecological Experiments*, 2nd edn (eds S.M. Scheiner & J. Gurevitch), pp. 37–62. Oxford University Press, Oxford.
- 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.
- Grabherr, G., Gottfried, M. & Pauli, H. (1994) Climate effects on mountain plants. *Nature*, **369**, 448.
- Greene, D.F. & Johnson, E.A. (1997) Secondary dispersal of tree seeds on snow. *Journal of Ecology*, **85**, 329–340.
- Guisan, A. & Zimmermann, N.E. (2000) Predictive habitat distribution models in ecology. *Ecological Modelling*, **135**, 147–186.
- Hafenschärer, J. & Mayer, H. (1986) Standort, Aufbau, Entwicklungsdynamik und Verjüngung von Latschenbeständen im Karwendeltal/Tirol. *Schweizer Zeitschrift für Forstwesen*, **137**, 177–203.
- Hansen, A.J., Neilson, R.P., Dale, V.H., Flather, C.H., Iverson, L.R., Currie, D.J. *et al.* (2001) Global change in forests: response of species, communities, and biomes. *Bioscience*, **51**, 765–779.
- Harrell, F.E. (2001) *Regression Modeling Strategies*. Springer, New York.
- Hessl, A.E. & 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.
- Higgins, S.I. & Richardson, D.M. (1996) Modeling invasive plant spread: the role of plant–environment interactions and model structure. *Ecology*, **77**, 2043–2054.
- Higgins, S.I. & Richardson, D.M. (1999) Predicting plant migration rates in a changing world: the role of long-distance dispersal. *American Naturalist*, **153**, 464–475.
- Higgins, S.I., Richardson, D.M. & Cowling, R.M. (2001) Validation of a spatial simulation model of a spreading alien plant population. *Journal of Applied Ecology*, **38**, 571–584.
- Hoch, G., Popp, M. & Körner, C. (2002) Altitudinal increase of mobile carbon pools in *Pinus cembra* suggests sink limitation of growth at the Swiss treeline. *Oikos*, **98**, 361–374.
- Keane, R., Austin, M., Field, C., Huth, A., Lexer, M.J., Peters, D. *et al.* (2001) Tree mortality in gap models: application to climate change. *Climatic Change*, **51**, 509–540.
- Kittel, T.G.F., Steffen, W.L. & Chapin, F.S. III (2000) Global and regional modelling of arctic-boreal vegetation distribution and its sensitivity to altered forces. *Global Change Biology*, **6**, 1–18.
- Klasner, F.L. & Fagre, D.B. (2002) A half century of change in alpine treeline patterns at Glacier National Park, Montana, U.S.A. *Arctic, Antarctic, and Alpine Research*, **34**, 49–56.
- Kot, M., Lewis, M.A. & van den Driessche, P. (1996) Dispersal data and the spread of invading organisms. *Ecology*, **77**, 2027–2042.
- Kullman, L. (1993) Pine (*Pinus sylvestris* L.) tree-limit surveillance during recent decades, Central Sweden. *Arctic and Alpine Research*, **25**, 24–31.
- Kullman, L. (2002) Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. *Journal of Ecology*, **90**, 68–77.
- Lavoie, C. & Payette, S. (1994) Recent fluctuations of the lichen-spruce forest limit in subarctic Quebec. *Journal of Ecology*, **82**, 725–734.
- Lexer, M.J., Hönninger, K., Scheifinger, H., Matulla, Ch, Groll, N., Kromp-Kolb, H. *et al.* (2001) The sensitivity of the Austrian forests to scenarios of climatic change. *Monographien des Umweltbundesamt Wien*, **132**, 1–132.
- Loehle, C. & LeBlanc, D. (1996) Model-based assessments of climate change effects on forests: a critical review. *Ecological Modelling*, **90**, 1–31.
- Magee, T.K. & Antos, J.A. (1992) Tree invasion into a mountain-top meadow in the Oregon Coast Range, USA. *Journal of Vegetation Science*, **3**, 485–494.
- Masek, J.G. (2001) Stability of boreal forest stands during recent climate change: evidence from Landsat satellite imagery. *Journal of Biogeography*, **28**, 967–976.
- Mayer, H. (1976) *Gebirgswaldbau – Schutzwaldpflege*. Fischer, Stuttgart.
- Meshinev, T., Apostolova, I. & 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**, 1–300.
- Moir, W.H., Rochelle, S.G. & Schoettle, A.W. (1999) Micro-scale patterns of tree establishment near upper treeline, Snowy Range, Wyoming, U.S.A. *Arctic, Antarctic, and Alpine Research*, **31**, 379–388.
- Motta, R. & Nola, P. (2001) Growth trends and dynamics in sub-alpine forest stands in the Varaita Valley (Piedmont, Italy) and their relationships with human activities and global change. *Journal of Vegetation Science*, **12**, 219–230.
- Müller-Schneider, P. (1986) Verbreitungsbiologie der Blütenpflanzen Graubündens. *Veröffentlichungen des Geobotanischen Instituts der ETH, Stiftung Rübel*, **85**, 1–263.
- Nathan, R. & Muller-Landau, C. (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology and Evolution*, **15**, 278–285.
- Neubert, M.G. & Caswell, H. (2000) Demography and dispersal: calculation and sensitivity analysis of invasion speed for structured populations. *Ecology*, **81**, 1613–1628.
- Parmesan, C. (1996) Climate and species' range. *Nature*, **382**, 765–766.
- Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.
- Pitelka, L.F. & Plant Migration Workshop Group (1997) Plant migration and climate change. *American Scientist*, **85**, 464–473.
- Ribbens, E., Silander, J.A. & Pacala, S.W. (1994) Seedling recruitment in forests: calibrating models to predict patterns of tree seedling dispersion. *Ecology*, **75**, 1794–1806.
- Richardson, D.M. & Bond, W.J. (1991) Determinants of plant distribution: evidence from pine invasions. *American Naturalist*, **137**, 639–668.
- Richardson, D.M. & Higgins, S.I. (1998) Pines as invaders in the southern hemisphere. *Ecology and Biogeography of Pinus* (ed. D.M. Richardson), pp. 450–473. Cambridge University Press, Cambridge.

- Rocheftort, R.M. & 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.
- Roecker, E., Oberhuber, J.M., Bacher, A., Christoph, M. & Kirchner, I. (1996) ENSO variability and atmospheric response in a global coupled atmosphere-ocean GCM. *Climate Dynamics*, **12**, 737–754.
- Ross, D.G., Smith, I.N., Manins, P.C. & Fox, D.G. (1988) Diagnostic wind field modeling for complex terrain: model development and testing. *Journal of Applied Meteorology*, **27**, 785–796.
- Schroeter, C. (1926) *Das Pflanzenleben der Alpen*. Albert Raustein, Zürich.
- Shea, K. & Chesson, P. (2002) Community ecology theory as a framework for biological invasions. *Trends in Ecology and Evolution*, **17**, 170–176.
- Shigesada, N. & Kawasaki, K. (2002) Invasion and the range expansion of species: effects of long-distance dispersal. *Dispersal Ecology* (eds J.M. Bullock, R.E. Kenward & R.S. Hails), pp. 350–373. Blackwell Scientific, Oxford.
- Stone, C.J. & Koo, C.Y. (1985) *Additive Splines in Statistics. Proceedings of the Statistical Computing Section ASA: 45–48*. American Statistical Association, Washington, DC.
- Sturm, M., Racine, C. & Tape, K. (2001) Increasing shrub abundance in the Arctic. *Nature*, **411**, 546–547.
- Szeicz, J.M. & 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. & 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. *et al.* (2001) Ecological and evolutionary processes at expanding range margins. *Nature*, **411**, 577–581.
- Vander Wall, S.B. (1992) The role of animals in dispersing a 'wind-dispersed' pine. *Ecology*, **73**, 614–621.
- Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C. *et al.* (2002) Ecological responses to recent climate change. *Nature*, **416**, 389–395.
- Watkinson, A.R. & Gill, J.A. (2002) Climate change and dispersal. *Dispersal Ecology* (eds J.M. Bullock, R.E. Kenward & R.S. Hails), pp. 410–430. Blackwell Scientific, Oxford.
- Wiser, S.K., Allen, R.B., Clinton, P.W. & Platt, K.H. (1998) Community structure and forest invasion by an exotic herb over 23 years. *Ecology*, **76**, 2071–2081.

Received 22 May 2003

revision accepted 4 November 2003

Handling Editor: Malcolm Press