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Seed rain and environmental controls on invasion of *Picea abies* into grassland

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Abstract Although changes in land-use, climate, and the spread of introduced tree species have increased the global importance of tree invasions into grasslands, our ability to predict any particular invasion is limited. To elucidate mechanisms driving tree invasions of grasslands, we studied in detail how seed dispersal and fine-scale environment control the expansion of an introduced *Picea abies* Karst. (Norway spruce) population into Western Carpathian grassland. We mapped invading trees and measured tree size, fecundity, seed rain, seedling density, plant community composition, and light and soil environment within a 200 × 60 m belt across the invasion front. Maximum likelihood estimates of dispersal kernels suggested peak seed deposition directly underneath tree crowns where germination was poor, but mean dispersal distances were sufficiently large to generate overlapping seed shadows from multiple trees that saturated the invasion front with seeds further away from seed-dispersing trees. Partial Mantel tests indicated that germinant density was affected considerably less by seed rain than by moss cover ($r = 0.54$), overstory tree influence ($r = -0.32$), soil moisture ($r = 0.21$), grass cover ($r = -0.15$), and diffuse radiation ($r = 0.13$). However, these variables were not independent but formed complex multivariate gradients within the invasion front. Moss cover and soil moisture were negatively correlated with overstory tree influence and the resulting gradient clearly affected germinant density (partial Mantel $r = 0.45$). In contrast, positively correlated light and grass cover defined a gradient related weakly to germinant density (partial Mantel $r = 0.05$) as it integrated opposing effects of these variables on germinants. Seedlings had similar environmental associations, but except for the lasting positive effects of moss these tended to weaken with seedling size. Although a few seedlings may establish and survive in the more adverse environment of the outer edges of the invasion front, a significant population expansion may require a gradual build-up of the critical density of invading trees to reduce grass cover and facilitate germination on moist mossy seedbeds within uncolonized areas. Thus, *Picea abies* appears more likely to spread within temperate grasslands by gradual expansion of

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its population frontier rather than by advanced groups.

Keywords Colonization · Dispersal kernel · Ecotone · Mountain meadow · Norway spruce · Recruitment limitation

Introduction

Invasions of trees into grassland communities have been studied as an increasingly global ecological phenomenon in Europe (Prévosto et al. 2003; Doležal et al. 2004; Marie-Pierre et al. 2006), North America (Magee and Antos 1992; Miller and Halpern 1998; Dovčiak et al. 2005; League and Veblen 2006), and the southern hemisphere (Richardson et al. 1994; Higgins and Richardson 1998; Kitzberger et al. 2000). Trees influence aboveground net primary productivity, nutrient cycling, and root turnover in grasslands (Reich et al. 2001), and grassland conversions into forests may play an important role in the regulation of global climate by changing carbon storage in trees and soils (Ceulemans and Mousseau 1994; Jackson et al. 2002) and by changing surface albedo (Bonan et al. 1992). Despite the global significance of tree invasions into grasslands, our ability to predict any particular invasion is still rudimentary.

Although tree seedling recruitment is critical for the dynamics of tree–grass systems (Prach et al.1996; Higgins et al. 2000; Jeltsch et al. 2000) and forests (Clark et al. 1999; Caspersen and Saprunoff 2005), field-based models of seedling recruitment are currently available only for forests (Pacala et al. 1993). Seedling recruitment is a function of seed rain density and environmental factors that influence seed germination and seedling growth and survival (Houle 1995, 1998; Clark et al. 1999; LePage et al. 2000; Camarero et al. 2005); both seed rain and environment in open grassland differ considerably from those in closed forest.

First, grasslands tend to be generally unsuitable habitat for tree seedlings due to the intense competition from grassland species and interference from grassland litter (Prach et al. 1996; Li and Wilson 1998), absence of mycorrhizal fungi (Dickie and Reich 2005), and unsuitable microclimatic conditions (De Steven 1991). As a consequence, tree seedling recruitment may occur as infrequent regeneration pulses during short and difficult-to-predict temporal windows of opportunity represented by periods of favorable climate or disturbance to dominant grassland vegetation (Higgins et al. 2000; Jeltsch et al. 2000; Dovčiak et al. 2005). Second, grassland community characteristics, the abundance of mycorrhizal fungi, microclimate, and seed rain density tend to form complex gradients of correlated variables that covary with the distance to forest edge and interact to create spatial widows of opportunity for a tree invasion (Magee and Antos 1992; Chen et al. 1999; Dickie and Reich 2005; Dovčiak et al. 2005). Third, once established, trees have a greater range of environmental tolerance than seedlings (regeneration niche, Grubb 1977) and can further facilitate an invasion by moderating microclimate, excluding grassland vegetation, altering the character of litter, soil, and soil microbial community (Finegan 1984; Asselin et al. 2001; Siemann and Rogers 2003; Pagès et al. 2003; Griffiths et al. 2005), and eventually also by providing additional seed rain (storage effect, Warner and Chesson 1985). Thus, even a sporadic and spatially restricted recruitment (invasion) pulse may ultimately lead to a successful invasion on timescales broad enough to accommodate tree maturation (and self-facilitation of the invasion) and climate variability (temporal opportunity windows).

The sporadic and patchy character of tree recruitment poses difficulties for direct field studies of tree invasions; such studies would need to investigate both broad-scale seed rain patterns and fine-scale processes that influence seedling recruitment over impractically long time intervals. Thus, the majority of field studies of tree invasions into grasslands tend to be retrospective analyses of existing invasion fronts and use the distance to forest edge as a partial surrogate for seed rain (e.g., Magee and Antos 1992; Miller and Halpern 1998; Riege and Del Moral 2004). Measuring the distance to forest edge, as opposed to quantifying seed rain, is simple and it can be done quickly at a large number of sites. However, the relationship between seed rain density and distance to forest edge may vary widely even within a single site (and even more so across many sites), and thus using distance as a surrogate for seed rain may mask important invasion mechanisms and pathways (Dovčiak et al. 2005). At the same time, understanding invasion mechanisms, rather than mean invasion trends, is necessary for predicting if and how a tree invasion may occur at any particular grassland.

In order to improve our current understanding of mechanisms behind tree invasions into grasslands, we studied the relative roles of broad-scale seed rain and fine-scale environmental limitations, and their composite influences on seedling recruitment across the invasion front of an introduced Norway spruce (*Picea abies* Karst.) population that has been invading an adjacent grassland since the 1950s. To achieve this goal, we integrated studies of seedling demography, seed dispersal, and environmental factors such as light, soil, and plant community characteristics to answer the following questions: (1) How do individual reproducing trees influence seed rain patterns within the invasion front? (2) How well does the composite seed rain pattern from all reproducing trees correlate with seedling density? (3) What are the environmental factors that correlate best with seedling density? (4) What are the main environmental gradients across the invasion front and how well do they relate to seedling recruitment? and (5) Do different seedling life stages differ in their environmental associations (regeneration niches)?

Methods

Study area

The study site is a grassland ~100 ha in area located within the forest matrix of the Poľana Biosphere Reserve in the western Carpathian Mountains, central Slovakia (Príslopy Pass, 48°38′10″ N, 19°25′11″ E, ~900 m above sea level). The grassland contributes significantly to the biodiversity of the reserve, which is dominated by European beech (*Fagus sylvatica* L.) and silver fir (*Abies alba* Mill.) with typical beech-fir forest understory communities. The grassland is dominated by grasses *Avenula adsurgens*, *Brachypodium pinnatum* and *Nardus stricta*, locally by low shrub *Vaccinium myrtilus* with a smaller component of scattered short shrubs of *Juniperus communis* and herbaceous grassland species (Ujházy 2003; Hrivnák and Ujházy 2005). Mean July temperatures in the area reach ~14°C, mean January temperatures are *ca.* −6°C, the annual precipitation is ~900–1,200 mm, and snow cover lasts >100 days (Ministry of Environment of the Slovak Republic 2002). The soils are mostly deep and fertile cambisols overlaying andesite lava flows (Hraško et al. 1980).

The grassland originated in the 19th century after forest clearance, and it was utilized as a hay meadow with an annual mowing regime. In the 1890s, *Picea abies* was planted along the north-facing forest margin within a strip ~20 m wide. Reflecting a Europe-wide trend in abandonment of the use of montane grasslands due to intensifying agriculture, mowing and hay production were replaced by cattle grazing in the early 1950s, and the grassland was completely abandoned in the 1980s (cf. Ujházy 2003). The planted *Picea abies* population began to invade the grassland in the 1950s, and the invasion was well under way by 1975 (Gömöry et al. 2006). A part of the invaded area (~10% of the grassland) was restored by manual removal of invading trees to preserve biodiversity and communities associated with grasslands, but the remaining area contains a well-developed invasion gradient ranging from the original open grassland to areas fully colonized by *Picea abies*.

Field measurements

Transect establishment

In 2003, we established a 200 × 40 m permanent belt transect approximately perpendicularly to contour lines and to the forest edge so that the transect crossed the strip of planted *Picea abies* and the adjacent area that was originally uninvaded grassland (and was not impacted by the restoration treatment or the dirt road present within the grassland). The transect crossed all stages of stand development from the strip of planted trees (now >100 years old and starting to break up due to mortality), across a young spruce stand with a closed canopy (now ~50 years old), to a relatively open grassland with scattered junipers and young spruce trees. The position of the border between planted trees and original grassland was identified using historical aerial photographs that revealed that the lower 160 m of the transect was originally a grassland. We mapped and measured several variables across transect in 2003 and 2004.

Tree and seedling measurements

In 2003, we established and mapped a 10 × 10 m grid within the transect using an electronic tachymeter (ELTA-4, Carl-Zeiss Jena, Germany), and recorded the position (*x, y, z* coordinates), breast-height diameter (dbh, at 1.3 m height) and height of all trees >1.3 m tall (Fig. 1a). The position and height of all invading seedlings (>1-year-old and ≤1.3 m tall) were recorded within the lower 160 m (original grassland) portion of transect in April 2004 before the growth flush of the ground-layer vegetation (Fig. 1b). We characterized seed source by estimating tree fecundity as the number of cones produced in 2003 using binocular counts on each tree of individual cones (if ≤30 cones/tree) or cone groups (if >30 cones/tree; cone group ~10 cones). In addition, we estimated fecundity and recorded the spatial position, dbh, and height for cone-bearing trees within 10 m on either side of the belt transect (thus extending the belt width to 60 m for seed source mapping; Fig. 1c). No reproducing trees were found below the lower edge of transect.

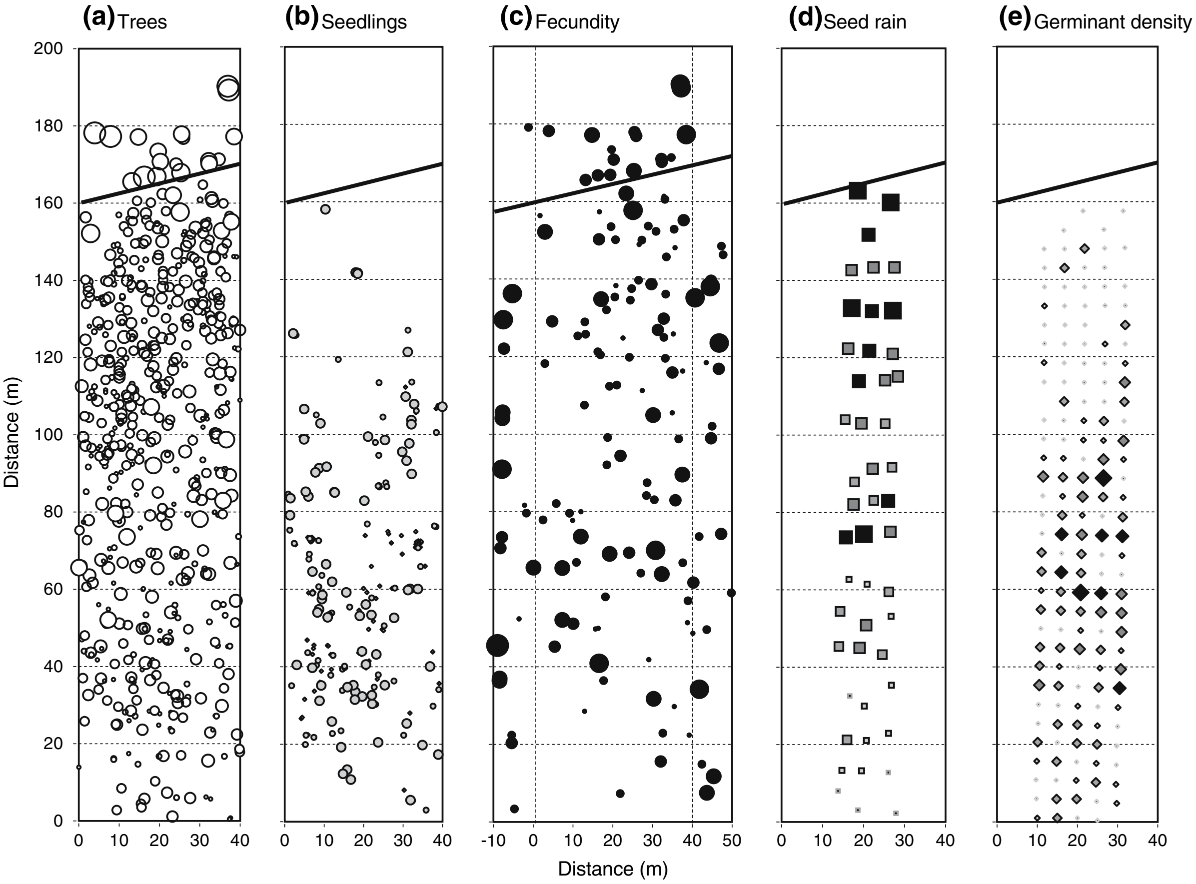


Fig. 1 *Picea abies* demography across the invasion front: (**a**) locations of trees >1.3 m tall, (**b**) locations of seedlings (>1-year-old, ≤1.3 m tall), (**c**) fecundity (number of cones per tree), (**d**) observed seed rain density in seed trap (number of seeds per m^2), (**e**) density of germinants (<1-year-old) on vegetation plots (number of germinants per m^2). Sizes of symbols correspond to (**a**) tree breast-height diameter (range 1–95 cm), (**b**) seedling height class (class 1 <20 cm, class 2 = 20–50 cm, class 3 = 50–130 cm), (**c**) fecundity (range 1–410 cones), (**d**) seed rain density (0–744 seeds per m^2), and (**e**) germinant density (0–38 germinants per m^2). The slanted line at ~160–170 m marks the edge between the strip of planted trees and the original grassland. Note that seedlings (**b**), seed rain (**d**), and germinants (**e**) were studied only within the original grassland, while fecundity (**c**) was studied within a broader 60 m wide belt to improve the accuracy of the seed rain model. Further details are provided in *Methods*

Seed rain density

Seed rain was sampled using 50 seed traps ($30 \times 30 \times 8$ cm metal frames with a 1×1 mm polyethylene mesh bottom) that were placed near the mapped grid points within the 20 m wide central strip along the axis of the belt transect (thus all seed source trees were mapped and measured within $\geq$20 m around each seed trap; Fig. 1d vs. c). Seed traps were placed in February 2004 before cones opened and seeds were collected and counted biweekly. The seed dispersal season was short ($\sim$3 weeks) and finished in mid April.

Ground-layer vegetation

The density of germinants (individuals < 1-year-old that originated from the measured seed rain) as well as the percent cover of all herb, shrub, and moss species in the ground layer were recorded on a fine-scale 5×5 m grid of 147 circular 0.5 m^2 vegetation plots established within the 20 m wide central strip of the transect where seed rain was measured (Fig. 1e). In addition, we characterized plant community composition within 5×5 m quadrats centered on the vegetation plots by estimating the percentage of the area occupied by plant community types identified in a related ordination study of the transect plant communities (*Trifolium medium–Brachypodium pinnatum*, *Phyteuma spicatum–Agrostis capillaris, Knautia arvensis–Avenula adsurgens*, *Prunella vulgaris–Ajuga reptans*, *Platanthera bifolia–Avenella flexuosa, Antennaria dioica–Nardus stricta*, *Vaccinium myrtillus*, *Hylocomium splendens*, and *Jungermannia leiantha–Plagiomnium affine* agg.; Hrivnák and Ujházy 2005).

Physical environment

Soil samples were taken from the center of each vegetation plot (Fig. 1e) from the uppermost mineral horizon from 5 cm to 10 cm depth. Gravimetric moisture was determined from fresh samples. Half of each sample was air-dried and used for measurement of soil acidity (pH-H_20, pH-KCl), soil organic matter content (using standard Tyurin titrimetric method), and total nitrogen (using standard Kjeldahl wet oxidation). At each vegetation plot, canopy light transmission was characterized using vertical hemispherical photographs taken 20 cm above the soil surface with a Nikon Coolpix 5400 digital camera equipped with a fisheye FC-E9 objective. Canopy openness (*CO*, the percentage of open sky seen from beneath the forest canopy), and the amount of direct (R_{DIR}) and diffuse (R_{DIF}) solar radiation transmitted by the canopy were estimated from the photographs using Gap Light Analyser 2.0 (Frazer et al. 1999).

Seed dispersal model

Seed shadows (seed dispersal kernels) can be derived using inverse modeling when both seed dispersal and tree fecundity are estimated using maximum likelihood methods from tree spatial locations, tree height, tree basal area (or other fecundity surrogate), and observed spatially referenced seed (or seedling) densities (e.g., Ribbens et al. 1994; Sato and Hiura 1998; Clark et al. 1999; LePage et al. 2000). With a few modifications (such as using direct estimates of fecundity), we adopted the approach of Sato and Hiura (1998) because it incorporates mechanisms behind wind seed dispersal (Greene and Johnson 1989).

Assuming that seeds are isotropically and lognormally distributed around the maternal tree, the number of seeds $f(x)$ at a distance x from the maternal tree can be estimated as

$$f(x) = \left(S/\sqrt{2\pi} \cdot \sigma x\right) \cdot \mathrm{e}^{-(\log x - m)^2/2\sigma^2} \tag{1}$$

where S is the number of seeds produced by a maternal tree and is directly proportional to the number of cones C ($S = a \cdot C$, where a is a constant—average number of seeds per cone); m is a function of the release height h ($m = \log(b \cdot h)$, where b is a constant); and σ is a constant. Because cones were concentrated in the uppermost third of the tree crown, we estimated release height h as 5/6 of the tree height plus the altitudinal difference (z_{diff}) between the tree base and the seed trap. The parameters m and σ determine the shape of the dispersal curve, and they can be interpreted within the framework of the mechanistic dispersal model of Greene and Johnson (1989); m as a function of release height, average horizontal wind speed, and seed descent speed, and σ *as* the standard deviation of the logarithm of horizontal wind speed (Sato and Hiura 1998). Seed density per unit area at distance x from a seed source tree can then be obtained by dividing $f(x)$ by $2\pi x$:

$$g(x) = \left(S/\sqrt{8\pi^3}\cdot\sigma x^2\right)\cdot \mathrm{e}^{-(\log x-m)^2/2\sigma^2} \tag{2}$$

As seed shadows of individual trees may overlap, the total expected seed density in the j-th seed trap E_j located at the distance x_{ij} from the i-th maternal tree can be calculated as

$$\begin{aligned} E_j &= \sum\nolimits_i g_{ij}(x_{ij}) \\ &= a\cdot\sum_i C_i\cdot \mathrm{e}^{-(\log x-\log b-\log h_i)^2/2\sigma^2}/\sqrt{8\pi^3}\cdot\sigma\cdot x_{ij}^2 \end{aligned} \tag{3}$$

Assuming that the number of seeds in a trap (count variable) follows a Poisson distribution, the likelihood L_j of observing O_j seeds when a mean of E_j seeds are expected in the j-th trap is

$$L_j = \frac{\mathrm{e}^{-E_j}E_j^{O_j}}{O_j!} \tag{4}$$

The log likelihood for a set of n traps is the sum of the logarithms of likelihoods given by Eq. 4. We maximized log likelihood to obtain the best estimates of the parameters b and σ using a grid search with both parameters ranging from 0.1 to 5 in 0.1 increments. The range of starting values for parameter estimates was biologically and meteorologically plausible and allowed for locations of seed dispersal peaks at various distances from seed dispersing trees. The average number of seeds per cone a was set such that $\sum_j E_j = \sum_j O_j$. Since the maximum log likelihood values were observed for $b \in \langle 0.4, 0.5\rangle$ and $\sigma \in \langle 0.8, 1.1\rangle$, we subsequently refined the parameter estimation within these intervals with 0.001 increments for both b and σ. Maximum likelihood routines were programmed in Turbo Basic. The goodness of fit of the model was assessed using product–moment correlation coefficient and linear regression between the observed and predicted seed rain densities (PROC GLM; SAS 1988). Mean dispersal distance (MDD) was calculated following Ribbens et al. (1994).

Derived variables and statistical analyses

Response variables

To express the progress of the invasion into the grassland, we chose the density of germinants (<1-year-old) and three seedling height classes (<20 cm, 20–50 cm, and 50–130 cm tall) as the main response variables. However, while we measured germinant density directly on the 0.5 m^2 vegetation plots, less abundant seedlings were individually mapped. Thus, we divided the belt transect into 5 × 5 m quadrats centered on the vegetation plots and calculated the density of each seedling height class within each quadrat.

Influence of overstory trees

We summarized the potential competitive influences of many surrounding individual trees on the density of germinants by calculating tree influence potential as a single plot-level statistic for each vegetation plot (*IP*, Kühlmann et al. 2001). *IP* is an index calculated for any particular point on the forest floor from the sizes of all trees within the local neighborhood weighted by their distance from that point. We used $IP_{BA} = \sum_i BA_i \mathrm{e}^{-r_i}$, where BA_i is the basal area of i-th tree within the 5-m-neighborhood of the vegetation plot, and r_i is the distance between the the i-th tree and the center of the vegetation plot. The 5 m neighborhood size approximately corresponds to the crown size of an average adult tree in this study. Since seedlings were dispersed across 5 × 5 m quadrats, we expressed the influence of overstory trees as their total basal area within a local neighborhood of each quadrat (from quadrat center to $\leq$5 m from quadrat edges).

Influence of understory vegetation

We characterized the establishment environment for germinants on the vegetation plots by defining three vegetation cover variables: (i) the total moss cover (mainly *Hylocomium splendens, Rhytidiadelphus squarrosus, Plagiomnium* spp., and *Pleurozium schreberi*) as a surrogate for potentially suitable germination microsites (c.f. St. Hilaire and Leopold 1995; Delach and Kimmerer 2002), and the cover of

(ii) *Vaccinium* spp. and (iii) grasses (*Brachypodium pinnatum, Avenula adsurgens*, and *Calamagrostis arundinacea*) as surrogates for microsites in plant communities potentially structured by intense competition (c.f. De Steven 1991; Siemann and Rogers 2003). For seedling density within the 5 × 5 m quadrats, we approximated these three vegetation cover variables (total moss, *Vaccinium*, and grasses) by calculating their expected average values for each quadrat from the proportions of the plant community types and their mean cover values in each type (Hrivnák and Ujházy 2005).

Gradients within the invasion front

We studied the underlying multivariate relationships among the variables using factor analysis (Reyment and Jöreskog 1997; Hirzel et al. 2002). Variable sets related to germinant and seedling densities were studied separately since variables were measured or derived either for vegetation plots or for quadrats. We ran analyses with the number of factors increasing from two to seven; the best results were achieved using three factors which explained >90% of total variance while providing the lowest interpretable number of factors (the first two factors explained >70% of total variance). Factors were extracted using principal component analysis with the squared multiple correlations of each variable with all other variables used as a prior communality estimate. The orthogonality of axes was preserved using varimax rotation (PROC FACTOR; SAS 1988).

Mantel tests

Since the data were not spatially independent, we used partial Mantel tests to correlate germinant density with seed rain, and germinant and seedling densities with plant community and environmental variables, and with their linear combinations (factor scores) that described the main gradients present within the invasion front. These tests yield partial correlation coefficients between the matrix of differences in response and predictor variables while controlling for the effect of the matrix of spatial distances among plots (Smouse et al. 1986). The significance of the partial correlation coefficients was tested using 100,000 random permutations. The calculations were performed using the program *zt* (Bonnet and Van de Peer, Ghent University, Belgium).

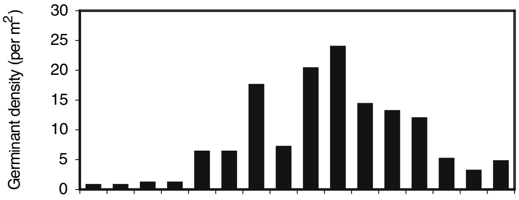
Results

Patterns of invasion

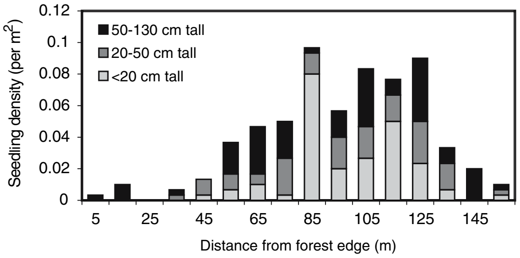
The density of germinants and seedlings varied along the invasion gradient; it was lowest at the forest edge where the canopy of previously established trees was dense, somewhat higher in the relatively open grassland, and highest approximately in the center of the invasion front (Fig. 2). Although germinants and seedlings were distributed equally relative to the forest edge (mean distances to forest edge 95.7 m and 94.6 m; Fig. 2), their fine-scale spatial patterns progressively diverged with size-class. Germinant density was positively correlated with the density of seedlings <20 cm tall (partial Mantel $r = 0.28$, $P < 0.0001$), weakly positively correlated with the density of seedlings 20–50 cm tall ($r = 0.07$, $P < 0.0001$), and not correlated with the density of seedlings 50–130 cm tall ($r = 0.02$, $P < 0.20$).

Seed rain patterns

The mean seed rain density was 245 (SE ± 25) seeds m^{-2} (i.e., >50 times greater than mean germinant density) but there was a tendency for seed rain to decrease with distance from forest edge ($r = -0.94$, $P < 0.0001$) as reproducing trees were spaced further apart far from the forest edge (Fig. 1c). Depending on tree height and fecundity, the peak seed deposition from any reproducing tree occurred between 0.5 m and 2.1 m from that tree (i.e., directly under its crown) and rapidly decreased with distance to produce short mean dispersal distances between 4.3 m and 17.4 m (Fig. 3). The seed dispersal model produced a good fit between the observed (O) and predicted (E) seed rain densities ($r = 0.77$, $O = -3.92 + 1.02 \cdot E$), predicted seed rain was unbiased (t-test: intercept = 0, $t = -0.115$, $P < 0.91$), and the relationship between the observed and predicted seed rain was that of identity (t-test: slope = 1, $t = -0.131$, $P < 0.90$). The model



(a) Germinants



(b) Seedlings

Fig. 2 Distribution of germinants (**a**) and seedlings (**b**) across the invasion front. Average densities were calculated in successive 10 m wide bands starting immediately adjacent to the planted strip of *Picea abies* and ending at the outer edge of the invasion front at 160 m

performed equally well across the invasion gradient, as the regression residuals did not correlate with the distance to the forest edge ($r = 0.19$, $P < 0.21$).

Environmental patterns

Environmental variable sets related to germinant and seedling densities showed similar multivariate patterns; the two factor analyses explained similar proportions of variance and resulted in similar environmental gradients. The strongest gradient in the vegetation plot variable set for germinants was dominated by increasing light and grass cover with distance from the forest edge (factor 1, ~40% of variance); the second most important gradient predominantly characterized the decreasing tree influence potential and increasing moss cover (factor 2, ~33% of variance); and the weakest gradient was related mainly to soil acidity (factor 3, ~17% of variance) (Table 1). In comparison, the strongest gradient in the environmental variable set for seedlings was dominated by decreasing tree basal area and increasing grass cover with distance from the forest edge (factor 1, ~41% of variance) followed by light gradient (factor 2, ~32% of the variation) and soil acidity gradient (factor 3, ~21% of the variation) (Table 2).

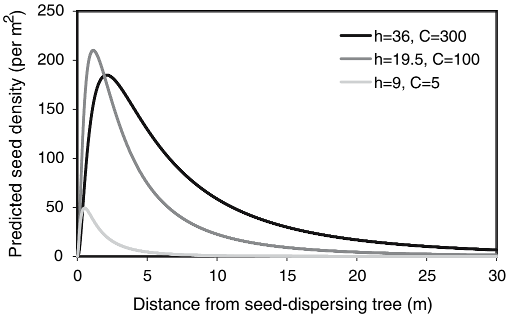


Fig. 3 Seed dispersal kernels for three individual trees that differ in height h (m) and fecundity C (number of cones). Maximum likelihood estimates of dispersal kernel parameters were $a = 32.9$, $b = 0.484$, and $\sigma = 1.028$ (Eq. 3). The three depicted kernels illustrate seed dispersal from the smallest ($h = 9$, $C = 5$), average ($h = 19.5$, $C = 100$), and largest ($h = 36$, $C = 300$) seed-dispersing tree within the invasion front

Germinant niche

Germinant density (mean ± SE; 4.6 ± 0.6 germinants m^{-2}) was only weakly positively related to seed rain which was on average >50 times greater and appeared to saturate vegetation plots with seeds. In contrast, several environmental variables were related to germinant density better than seed rain (Table 3). Overstory tree influence potential had the most negative effects on germinant density, thus negating positive effects of nearby trees as the seed source (c.f., Fig. 3). Shading by overstory trees could explain their negative effects only partially: germinant density correlated weakly positively with diffuse radiation and canopy openness but weakly negatively with direct radiation (Table 3). Relative to light variables, germinant density was more positively related to soil moisture (Table 3), which was negatively correlated with tree influence potential (partial Mantel $r = -0.38$, $P < 0.0001$). However, of all variables, germinant density was most positively related to moss cover (Table 3), which was positively correlated with soil moisture (partial Mantel $r = 0.39$, $P < 0.0001$). In contrast, grass and *Vaccinium* cover appeared to influence germinant density negatively (Table 3). The main multivariate gradient driving the germinant density was that of increasing moss cover with decreasing tree influence potential (factor 2) while the strongest environmental gradient (factor 1) had only weak influence on germinant density as it integrated

Table 1 Correlations between extracted factors and the original environmental variables related to germinant densities on vegetation plots. Loadings >0.5 are in bold

Variable	Factor 1	Factor 2	Factor 3	Communality[g]
CO[a]	**0.89**	0.40	−0.03	0.96
R_{DIF}[b]	**0.87**	0.42	0.00	0.93
R_{DIR}[c]	**0.77**	0.21	0.18	0.67
Grass cover	**0.65**	0.31	0.15	0.55
Distance[d]	**0.52**	0.48	−0.32	0.61
Moss cover	0.24	**0.64**	−0.05	0.47
IP_{BA}[e]	−0.27	**−0.89**	0.04	0.86
pH-H_2O	−0.12	0.08	**0.85**	0.74
pH-KCl	0.03	0.03	**0.82**	0.68
Moisture	0.01	0.31	0.23	0.15
Seeds[f]	−0.21	−0.42	−0.07	0.22
Total N	0.21	0.17	−0.11	0.08
Vaccinium cover	0.11	0.06	0.04	0.02
Organic C	−0.05	0.04	−0.11	0.02
Proportion of variance explained	0.40	0.33	0.18	

[a] Canopy openness

[b] Transmitted diffuse solar radiation

[c] Transmitted direct solar radiation

[d] Distance from the edge of forest (planted strip)

[e] Tree influence potential

[f] Predicted seed rain density

[g] Portion of the variance of the original variables explained by the factors

mainly the positive effects of diffuse radiation and canopy openness with the negative effects of grass cover (Table 3, Fig. 4).

Seedling niche

Seedlings <0.2 m tall were most negatively related to tree basal area and grass cover, and they were positively related to light, but these relationships weakened as seedlings increased in height to >0.5 m (Table 4). In contrast, moss cover was related positively to seedling density similarly well across height classes (Table 4). Soil variables (including moisture) tended to be correlated positively with seedlings 0.5–1.3 m tall but unrelated or negatively related to seedlings <0.5 m tall. Both main multivariate gradients (related to tree basal area, grass cover, and light) correlated equally positively with the density of seedlings <0.2 m tall, suggesting that the overall positive effects of high light and low overstory basal area outweigh the negative effects of grass cover at this seedling life-stage (Table 4, Fig. 5). However, both gradients became less significant as seedlings increased in size, reflecting weaker relationships of taller seedlings to light and tree basal area. The weak gradient related to soil pH (factor 3) did not show a clear pattern.

Table 2 Correlations between extracted factors and the original environmental variables related to seedling densities on quadrats. Loadings >0.5 are in bold

Variable[a]	Factor 1	Factor 2	Factor 3	Communality
Distance	**0.92**	0.19	−0.10	0.89
Tree basal area	**−0.83**	−0.29	0.01	0.77
Grass cover	**0.65**	0.08	0.09	0.58
R_{DIF}	0.45	**0.88**	0.02	0.98
CO	0.49	**0.87**	0.01	0.99
R_{DIR}	0.36	**0.61**	0.18	0.53
Moss cover	0.46	0.39	0.03	0.21
pH-H_2O	−0.16	0.00	**0.83**	0.71
pH-KCl	−0.06	0.05	**0.81**	0.66
Vaccinium cover	0.19	0.14	−0.08	0.05
Total N	0.20	0.05	−0.04	0.07
Moisture	−0.08	0.26	0.21	0.12
Organic C	−0.05	−0.02	−0.12	0.02
Proportion of variance explained	0.41	0.32	0.21	

[a] See Table 1 for variable abbreviations

Discussion

The success and speed of tree migrations or invasions can be influenced by propagule pressure (Křivánek et al. 2006) related to the shape of seed dispersal kernels and spatial distribution of seed source (Clark 1998; Clark et al. 2001; Bullock et al. 2006), but also by properties of the substrate or local environment that influence seedling establishment and survival (Geritz et al. 1984; LePage et al. 2000; Manning et al. 2005). In our study, the grassland invasion by *Picea abies* was limited considerably more so by fine-scale environmental conditions than by seed rain, but favorable environments were not randomly arranged relative to seed source. Instead, fine-scale environments were aligned along multivariate gradients related to previously established trees that decreased

Table 3 Partial Mantel correlations between environmental variables and germinant density

Variable[a]		*r*
Seeds		0.06***
IP_{BA}		−0.32***
Light	*CO*	0.08**
	R_{DIR}	−0.06**
	R_{DIF}	0.13***
Soil	Moisture	0.21***
	pH-H_2O	0.07*
	pH-KCl	*ns*
	Organic C	*ns*
	Total N	0.05**
Vegetation	Moss cover	0.54***
	Grass cover	−0.15***
	Vaccinium	−0.08***
FA[b] axes	F1 (+light, +grass)	−0.05*
	F2 (−IP_{BA} , +moss)	0.45***
	F3 (+pH)	*ns*

ns = non-significant, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$

[a] See Table 1 for variable abbreviations

[b] Factor analysis; individual factors are given as F1–3. The original variables with the highest loadings are listed in brackets with a sign indicating loading direction

Table 4 Partial Mantel correlations between environmental variables and seedling density

Variable[a]		*r* by seedling height class (m)		
		<0.2	0.2–0.5	0.6–1.3
Tree basal area		−0.18***	−0.13***	*ns*
Light	*CO*	0.12***	0.13***	0.06*
	R_{DIR}	0.20***	0.12***	*ns*
	R_{DIF}	0.10***	0.12***	*ns*
Soil	Moisture	*ns*	*ns*	0.14***
	pH-H_2O	*ns*	−0.11***	0.09***
	pH-KCl	−0.06**	−0.22***	0.12***
	Organic C	*ns*	0.03*	0.05*
	Total N	−0.05**	−0.06**	*ns*
Vegetation	Moss cover	0.23***	0.13***	0.19***
	Grass cover	−0.23***	*ns*	*ns*
	Vaccinium	0.07**	*ns*	0.08**
FA axes	F1 (−BA[b], +grass)	0.16***	*ns*	*ns*
	F2 (+light)	0.14***	0.13***	0.08**
	F3 (+pH)	0.04*	−0.17***	0.12***

ns = non-significant, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$

Seedlings were not analyzed relative to measured seed rain since they did not originate from it

[a] See Tables 1 and 3 for variable abbreviations

[b] Tree basal area

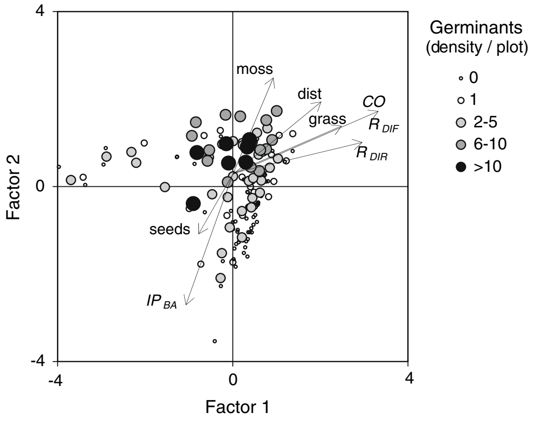


Fig. 4 Ordination of vegetation plots relative to the main factors and original environmental variables (Table 1). Plot symbols (circles) are scaled with germinant density, and vectors indicate the magnitude and direction of the loadings of the original environmental variables. For clarity, only the main variables are depicted (loadings |*r*| > 0.5, communality >0.2). The first two factors explained >73% of total variance

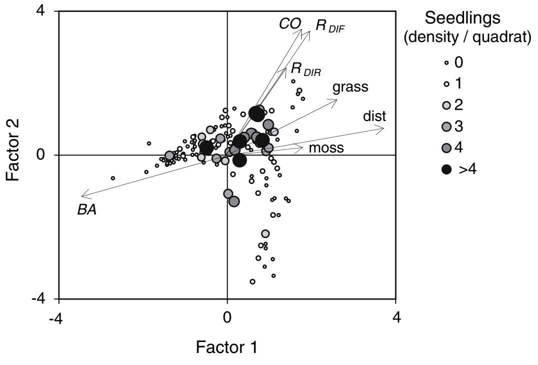


Fig. 5 Ordination of seedling quadrats relative to the main factors and original environmental variables (Table 2). Quadrat symbols (circles) are scaled with seedling density, and vectors indicate the magnitude and direction of the loadings of the original environmental variables. For clarity, only the main variables were depicted (loadings |*r*| > 0.5, communality >0.2). The first two factors explained >72% of total variance

in density and basal area with the distance from the forest edge. Thus, the engineering effects (feedbacks) of forest trees on fine-scale environment (Jones et al. 1994) influenced invasion patterns and they appear to have a potential to influence invasion speed as suggested by recent theoretical studies (Cuddington and Hastings 2004; Levine et al. 2006).

Role of seed rain

Although seed rain can influence forest dynamics (Ribbens et al. 1994; Clark et al. 1999; LePage et al. 2000; Asselin et al. 2001) and tree invasions into grasslands (Prévosto et al. 2003; Camarero et al. 2005; Dovčiak et al. 2005), it was only weakly positively correlated with the density of germinants in our study. Overall seed rain was high and it saturated germination microsites, which appeared to limit germinant density more than seed rain. The influence of individual seed producing trees was limited as the seed saturation was due to overlapping tails of seed shadows of multiple seed producing trees; the majority of seeds from any individual seed-dispersing tree was deposited directly underneath its crown into an environment least favorable for germinants. Although germinant density was most negatively related to tree influence potential, mean dispersal distances for mature trees were long enough (~17 m) to avoid the negative effects of maternal trees and generate overlapping seed shadows within the uncolonized (more open) areas of the invasion front. Although seed rain may vary among years due to the variation in seed production and wind regime, similar mean dispersal distances were found in studies of conifers of comparable seed size and morphology (~24 m for *Picea glauca* and *Picea sitchensis* and 14.5 m for *Abies lasiocarpa*, LePage et al. 2000; ~16 m for *Pinus strobus*, Ribbens et al. 1994), and spatial genetic analyses of parent–offspring relationships within our study area suggest that previous invasion waves were also characterized by short modal distances (D. Gömöry, unpublished data).

Initial role of environment

Germinant density in our study was related considerably less to the seed rain from which the germinants originated than to several variables that characterized the environment into which the seeds were deposited. Germinant density was by far most closely related to moss cover (positively), followed by tree influence potential (negatively), followed by soil moisture (positively), grass cover (negatively), and diffuse light (positively). However, these variables were not independent; moss cover (and soil moisture) was negatively related to overstory tree influence and these variables together formed an environmental gradient which influenced germinant densities considerably more so than the orthogonal gradient defined by positively associated light and grass cover. Forest tree establishment and recruitment is often determined by interactions of variables rather than by the effects of any single variable (McKinley and Van Auken 2005) and such variables are frequently correlated and form complex environmental gradients; for example, overstory may influence tree regeneration (Frelich et al. 1993; Dovčiak et al. 2003), but also herbaceous plant communities (Frelich et al. 2003; Thomsen et al. 2005) and nutrient cycling (Reich et al. 2001). In our study, moss in uncolonized areas within the invasion front provided the best germination seedbed, while highly open areas with high direct light and high grass cover had low density of germinants. Thus, while our results further support the positive effects of moss as a germination seedbed (e.g., St. Hilaire and Leopold 1995; McLaren and Janke 1996; Delach and Kimmerer 2002) and the negative effects of dense grass cover (De Steven 1991; Siemann and Rogers 2003), it explicitly places these effects in the context of multivariate environmental gradients that can be encountered across invasion fronts. Moss in our study provided not only moister and thus more suitable seedbed, but it also occurred in areas that experienced relatively less shading by trees but that were shaded sufficiently enough that the competition from grass was decreased. In other studies, germination was increased on moss patches, likely due to greater moisture, but the survival of germinants was not (St. Hilaire and Leopold 1995; Delach and Kimmerer 2002). On the other hand, Parker et al. (1997) found that the survival of germinants that experienced a brief drought treatment was greater on moss seedbeds compared to other seedbeds. Such positive initial effects of moss can be considerably enhanced if germinants encounter less competition from grass and experience light levels sufficient for their subsequent recruitment to larger size-classes, as they did in this study.

Role of environment in seedling recruitment

Although germinant and seedling densities did not differ in their broad-scale patterns relative to the forest edge, seedling regeneration niche appeared to gradually shift as seedling fine-scale patterns and environmental associations progressively diverged with increasing size-class. Such changes in regeneration niche over time (Grubb 1977) may lead to discordant spatial patterns of tree size-classes structured by different regeneration bottlenecks (Dovčiak et al. 2001, 2003; Gratzer and Raib 2004). The only variable in our study that was related to seedling density equally well across all size-classes was moss cover, suggesting lasting positive effects of moss seedbed (Gratzer and Raib 2004; Kupferschmid and Bugmann 2005). On the other hand, the initial associations of small seedlings (<0.2 m tall) with light (positive), and tree basal area and grass cover (negative), became progressively weaker or disappeared as seedlings increased in size, while the role of positive effects of soil variables increased for tall seedlings (>0.5 m). Thus, our study confirms that light, overstory trees, and grass may affect seedlings (Smith and Olff 1998; Davis et al. 1999, 2005; Pagès et al. 2003), but it suggests that these effects may be different in different seedling life-stages (size classes). Although only a few seedlings may establish in areas with high grass cover, they appear less prone to competition from grass once they reach a critical size (~20 cm height). On the other hand, larger seedlings may become limited by soil resources in areas that were originally favorable for seedling establishment (Barot et al. 1999; Dovčiak et al. 2003). Although the differences in seedling regeneration niches were not sufficiently large to cause different broad-scale seedling patterns in our study, even small differences could potentially influence invasion patterns on the large spatio-temporal scales typically involved in tree population spread, for example, in tree migrations.

Patterns of invasion

While tree invasions into grasslands tend to be limited by some combination of seed rain and environment (Rouget and Richardson 2003; Dovčiak et al. 2005), our study suggests that the expansion of at least some invasion fronts that already contain new reproducing individuals may be limited by environmental constraints on seedling establishment much more so than by seed rain. Although a few reproducing trees may occur at the edge of the invasion front (adjacent to open grassland) and contribute to seed rain there, their impact on tree population spread may be minimal due to the negative effects of dense grass cover on germination and the survival of germinants and small seedlings. Instead, a complete invasion is more likely further back from the edge where previously established trees reach a critical threshold density (phase transition, Milne et al. 1996) to sufficiently modify the environment (for example, to suppress the competition from grass) and thus facilitate further invasive spread (an intermediate scenario to ‘‘pushed’’ versus ‘‘pulled’’ invasions, Levine et al. 2006). Thus, our study lends support to the theory that, in the absence of extreme climatic events or disturbance, populations of wind dispersed tree species (such as *Picea abies*) may spread into grasslands by expanding their population frontiers rather than by the establishment of small advanced groups far ahead of the population frontier (invasion by extremes; Clark et al. 2001).

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