

Effects of Prostrate Dwarf Pine on Norway Spruce Clonal Groups in the Treeline Ecotone of the Hrubý Jeseník Mountains, Czech Republic

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Abstract

Global temperature increase would seem likely to result in general upwards shifts of altitudinal margins of tree stands. However, range expansion of trees could be significantly affected by both negative and positive interactions with alpine shrubs in existing treeline ecotones. We examined the effects of dwarf pine (*Pinus mugo*) shrubs on the vegetative propagation and height growth of Norway spruce (*Picea abies*) trees in the treeline ecotone of the Hrubý Jeseník Mountains, Czech Republic. Here, the non-native dwarf pine was planted above timberline during the 19th and 20th centuries. In the treeline ecotone, vegetative propagation is important both for generation of clonal groups from seed-originated individuals and for persistence of such stands. We found that increasing density of dwarf pine stands strongly reduced vegetative propagation of spruce, as shown by the spruce clonal groups surrounded by dense pine having fewer layering branches and ramets than such groups outside pine stands. This has likely resulted from competitive pressure of pine causing decreased spruce layering mainly through mechanical damage and shading. In contrast, dense pine stands increased spruce height growth, presumably by providing shelter against wind and/or browsing. Our results indicate that interactions of prostrate dwarf pine and Norway spruce clonal groups include both competitive and facilitative components, which probably change in importance along climatic stress gradients.

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Introduction

The alpine treeline ecotone represents a prominent temperature-driven altitudinal boundary of forests in mountain regions (Holtmeier, 2009). Along the gradient of increasing stress due to temperature, trees lose their competitive advantage over low, prostrate shrubs (Körner, 2012). Whereas tall trees are thermally coupled with the ambient atmosphere, prostrate shrubs profit from near-ground heating of the surface air layer (Körner, 1998; Geiger et al., 2003). Therefore, direct temperature limitation of tree growth is not the only major driver of treeline ecotone dynamics, as the interaction between upright tree species and prostrate shrubs can also have a particularly strong influence (Dullinger et al., 2004; Dufour-Tremblay et al., 2012). The stress-gradient hypothesis (Callaway et al., 2002; He et al., 2013) predicts that prostrate shrubs should have prevalently competitive effects on trees in the lower part of treeline ecotone, with facilitation more common towards the tree species limit (e.g. Maestre et al., 2009).

Indeed, a range of positive and negative effects of prostrate shrubs on treeline trees has been documented. Positive effects can include protection against herbivorous insects and mammals (Dullinger et al., 2005; Grau et al., 2010), frost (Michiels, 1993), and strong winds (Vacek et al., 2012). In particular, these positive effects facilitate tree seedling survival and performance (Camarero and Gutiérrez, 1999; Gómez-Aparicio et al., 2005; Grau et al., 2010). On the other hand, prostrate shrubs compete with trees for light (Jeník and Lokvenc, 1962), nutrients, and water (Schönenberger, 1975; Weih and Karlsson, 2002; Grau et al., 2012) and can reduce tree germination success (Dullinger et al., 2005) and cool surface microclimates during the growing season (Svoboda, 2001; Köck et al., 2003). Trees can have negative effects on prostrate shrubs,

with their overstory overgrowing them, thereby likely limiting the responses of shrub species to increasing temperatures (Švajda et al., 2011; Boudreau and Villeneuve-Simard, 2012).

In the treeline ecotone, trees often occur in clonal groups (Bliss, 1971; Tranquillini, 1979; Laberge et al., 2000). Indeed, vegetative reproduction is an important strategy enabling trees to form and maintain stands in environments in which seedling growth and survival are limited by cold (Holtmeier, 2009). Thus, alpine and northern treeline ecotones often contain clonally reproduced tree groups surrounded by prostrate shrubs (Harsch and Bader, 2011; Grau et al., 2012). For example, treeline ecotones in western North American mountains contain *Abies lasiocarpa*, *Picea engelmannii*, and shrubby *Chamaecyparis nootkatensis* (Brooke et al., 1970; Arno and Hammerly, 1984); those in the Carpathians include *Picea abies* and *Juniperus communis* ssp. *alpina* (Mihai et al., 2007); and those in central Kamchatka have *Larix gmelinii* and *Pinus pumila* (Okitsu, 1998).

Norway spruce (*Picea abies* L., Karst) and dwarf pine (*Pinus mugo*, Turra) play the roles, respectively, of clonal group-forming tree and prostrate shrub species in treeline ecotones of Central Europe. There, Norway spruce is the most abundant treeline-forming species (Scotti et al., 2008; Tremł and Banaš, 2008; Hertel and Schöling, 2011). In the treeline ecotone, the reduced sexual reproduction of Norway spruce is replaced by layering, in which new ramets are generated by the rooting of plagiotropic branches of the parent tree (Kuoch and Amiet, 1970; Tranquillini, 1979; Kozłowski, 2002; Šenfěldr and Maděra, 2011; Vacek et al., 2012). Prostrate dwarf pine occurs in alpine areas of Europe from the Pyrenees to the Balkan peninsula, and is a widespread species in the altitudinal belt above the upper limit of closed forest in the eastern Alps, Sudetes, and Carpathians (Nagy et al., 2003; Úradníček et al., 2010).

The distribution and altitudinal limits of Norway spruce and dwarf pine have been strongly influenced by past agricultural activities such as grazing, grass mowing, burning, and logging (Dirnböck and Grabherr, 2000; Sitko and Troll, 2008). Thus, treeline ecotones were shifted downwards and dwarf pine stand distribution became more scattered between the 11th and 18th centuries (Tremml et al., 2008). Later, from the second half of the 19th century through the mid-20th century, dwarf pine was frequently planted in deforested or steeply sloping mountain areas to protect soil against mass movement and surface erosion (Bukovčan, 1960; Hošek, 1964; Souček and Špulák, 2011; Roštinský et al., 2013). This occurred in the Hrubý Jeseník Mountains (eastern part of the Sudetes Mountains) where the pine was planted as a non-indigenous species on summit forest-free areas. There, some Norway spruce clonal groups are surrounded by dwarf pine stands of known planting date, whereas others are not. This provides a special opportunity to examine the effects of prostrate dwarf pine on dynamics of Norway spruce clonal groups by comparing the spruce groups inside and outside dwarf pine stands.

To date, the literature on interactions between Norway spruce and dwarf pine only reflects examination of the effects of the pine on spruce sexual reproduction and height growth (Dullinger et al., 2005). Studies of similar tree–shrub systems from alpine treeline ecotones indicate both competition among species of different sizes and different competition strategies and facilitation through protective effects of shrubs at early life stages of tree seedlings on extreme sites (Anthelme et al., 2003; Takahashi, 2003; Grau et al., 2012). However, no published study has investigated the effect of prostrate shrubs on vegetative reproduction of treeline trees. Since vegetative reproduction is important for the persistence and spread of spruce at its upper distributional limit, in the present study we examine (1) the influence of dwarf pine stand density on indicators of spruce clonal group vegetative reproduction ability, and (2) the effect of distance from dwarf pine shrubs on actual spruce vegetative reproduction.

Material and Methods

STUDY SITES

Our study sites (Praděd, Keprník, Větrná Louka, and Vysoká Hole) are situated on the highest peaks of the Hrubý Jeseník Mountains, and comprise all the locations on these mountains in which spruce groups and planted dwarf pine co-occur (see Fig. 1). The Hrubý Jeseník Mountains reach their maximum elevation at Mount Praděd, at 1492 m a.s.l. (Fig. 1). The climate is relatively cold and humid, with the summit areas characterized by annual precipitation of around 1400 mm and average temperature around 1.1 °C (Tolasz et al., 2007). The mountain tops of the Hrubý Jeseník Mountains are among the windiest locations in Europe (Migala, 2005).

The highest elevations are thought to have been naturally forest-free (Jeník, 1961), but the extent of alpine meadows was significantly enlarged by human activities (Novák et al., 2010), e.g. grass mowing, cattle grazing, and woodland burning and logging. The average altitude of the upper limit of closed forest is 1300 m a.s.l. Above this, scattered Norway spruce groups occur. Spruce groups typically consist of one seed-originated parent tree accompanied by variable numbers of its ramets. Indeed, within these groups, trees of clonal origin clearly dominate, accounting for 90–95% of the trees (Šenfěldr and Maděra, 2011). Therefore, we term the spruce groups “clonal groups.” Nevertheless, sparse

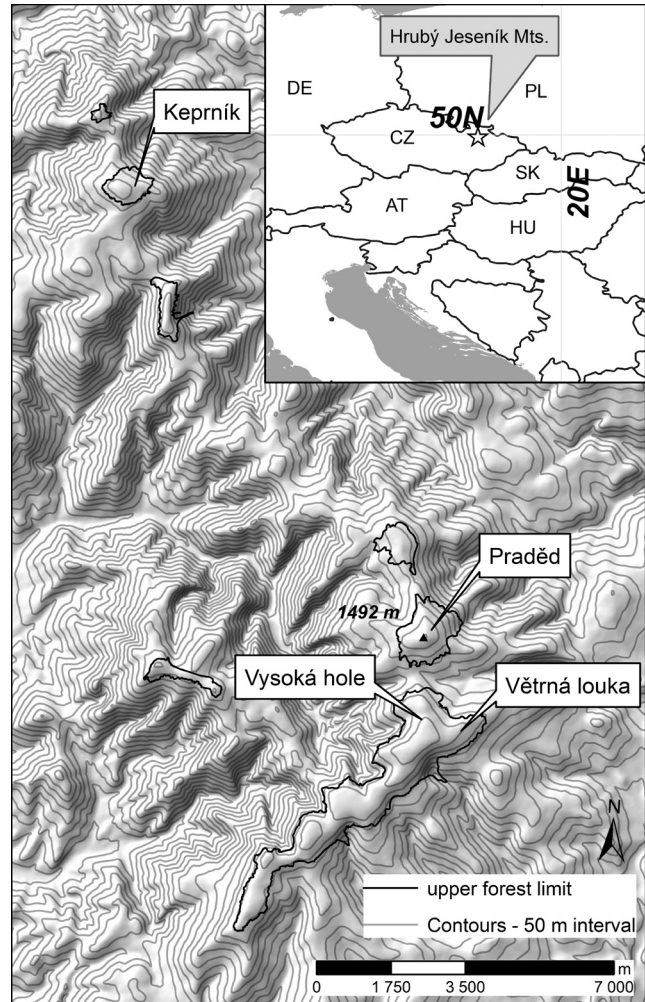


FIGURE 1. Topographic map showing location of study sites and elevation of the upper forest limit in the Hrubý Jeseník Mountains; inset shows position of the Hrubý Jeseník Mountains in Europe.

sexual reproduction is present at treeline, with seedlings of height 10–80 cm at a density of 25–39 specimens per hectare found at the study sites (Šenfěldr and Maděra, 2011).

Dwarf pine was planted on these mountains during the 19th and 20th centuries, mostly between 1874 and 1928, at spacings of 1.25 × 1.25 m to 2 × 2 m square (Hošek, 1964). This species now covers 179.2 ha (6.8%) of the area above the upper limit of closed forest (Tremml et al., 2010). Since designation of the Šerák-Keprník and Praděd nature reserves in 1955, both Norway spruce populations and dwarf pine stands have developed spontaneously, without any direct human intervention. Of particular conservation concern, dwarf pine stands rapidly expanded into surrounding alpine grasslands, leading to a loss of rare alpine plants and insects (Kuras et al., 2001; Tremml et al., 2010; Zeidler et al., 2012).

FIELD DATA COLLECTION

To examine the effects of dwarf pine density on spruce clonal growth characteristics, we distinguished three types of pine stands (see Fig. 2) based on pine canopy cover: no pine

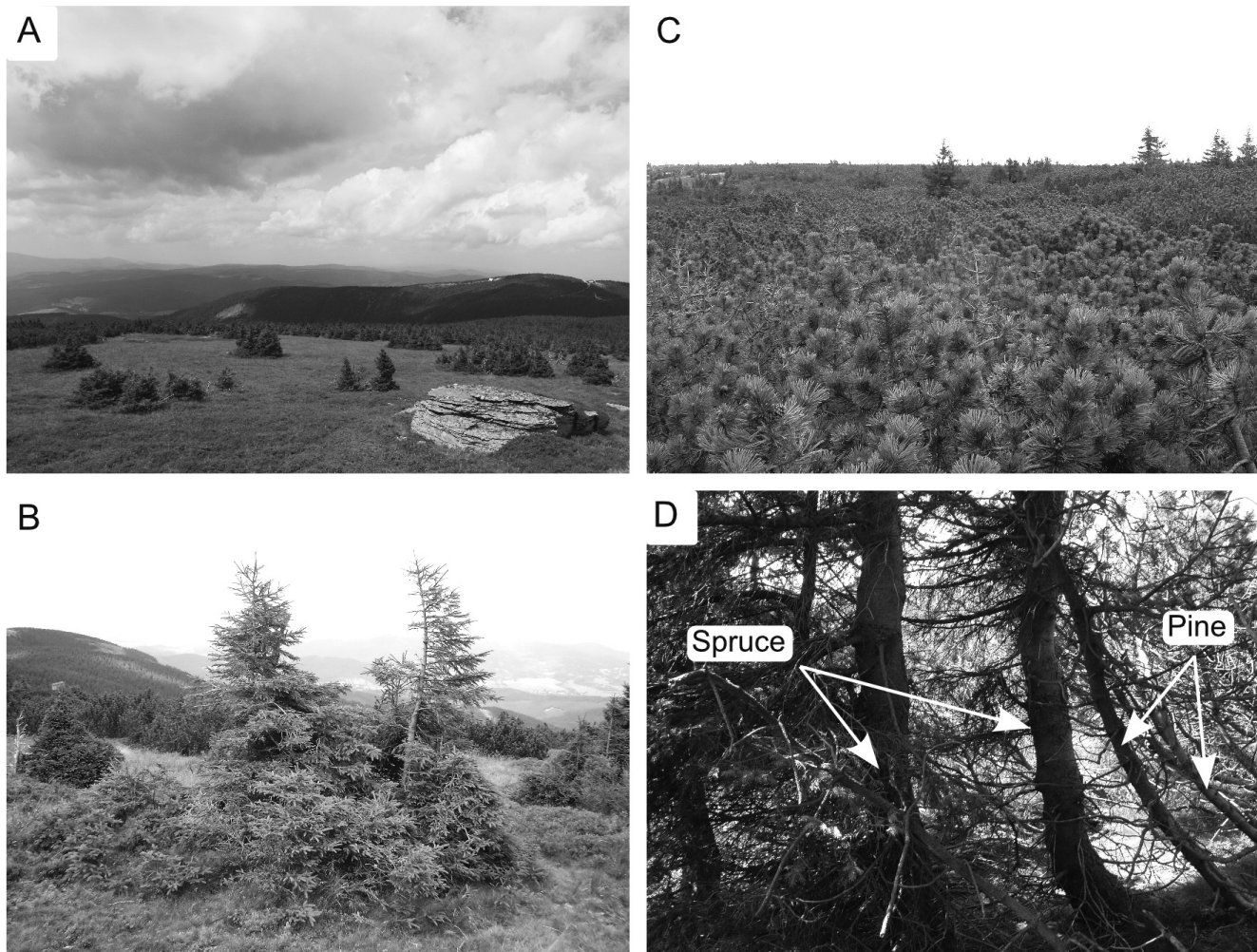


FIGURE 2. Photographs showing (A) extensive clonal spruce groups in a no-pine plot; (B) detail of a clonal group with layering branches growing in a no-pine plot; (C) spruce groups growing in a dense pine stand; and (D), close mechanical contact of pine with spruce resulting in absent layering branches in a dense pine stand.

presence (type “no-pine”), sparse pine (pine cover 20–70%; type “sparse”), and dense pine (pine cover 70–100%; type “dense”). Precise information about dwarf pine cover was obtained from orthorectified images with 0.25 m resolution, using supervised classification followed by manual error correction. Although we searched for all types of stands at each site, two sites lacked dense pine stands (Praděd and Větrná Louka) and one lacked sparse pine stands (Vysoká Hole) (Table 1). Cover of dwarf pine stands was usually related to their age, with some deviations caused by site factors and rates of seedling establishment (Tremblé et al., 2010).

In each study site, at similar altitudes, we randomly placed 4 to 9 circular 30-m-diameter sample plots in each pine stand type (no-pine, sparse, dense). In each of these plots, data were recorded from all clonal spruce groups and solitary spruce trees. For study design simplicity, each solitary tree was treated as a clonal group. For each clonal group, the number of layering branches, the total number of trees, and the height of the highest tree in the group (maximum tree height) were recorded. Additionally, to detect possible effects of dwarf pine on juvenile spruce stem-breaks, for each tree growing in the dense and no-pine plots, we recorded the presence/absence of multiple

stems, up to the height of 130 cm (roughly corresponding to the average height of dwarf pine stands).

Next, we randomly chose two spruce clonal groups on each plot for age structure analysis. Two groups per plot were sufficiently representative because across sites, the average number of clonal groups per plot was 3.8 ± 0.8 SD; ($n = 60$). Within each of these groups, all trees were cored using a Pressler borer. Cores were taken from the stem base (5 to 20 cm above ground). Tree rings were measured on a positioned table. If off-center cores were collected, we used the age correction method employing the mean annual width of the five rings nearest the pith (Batllori and Gutiérrez, 2008). Coring height correction was based on mean height growth rate of seedlings and juvenile ramets (height 10–200 cm; Šenfeldt, Tremblé—unpublished data). We considered the following three variables derived from age structure analysis: mean age, age of the oldest tree, and number of juvenile ramets (i.e. 20 years old or younger).

The numbers of layering branches and juvenile ramets can serve as indicators of spruce vegetative reproduction intensity, as groups with relatively high vegetative reproduction are characterized by numerous juvenile ramets and layering branches and by low mean age. Additionally, the overall number of trees

TABLE 1
Basic characteristics of sample plots in the four study sites above upper forest limit in the Hrubý Jeseník Mountains.

Study site	Type of pine stands	Pine stand age	Number of plots	Overall number of trees	Mean altitude of plots (m a.s.l.) \pm SD	Inclination (%)	Aspect
Keprník	no-pine	—	8	129	1378.3 \pm 11.0	38	SE
	sparse	130	7	119	1400.7 \pm 9.5	33	E
	dense	90	9	50	1388.0 \pm 16.5	35	E
Praděd	no-pine	—	6	329	1435.0 \pm 21.6	38	NE
	sparse	130	6	153	1441.3 \pm 17.6	40	NE
	dense	—	—	—	—	—	—
Větrná Louka	no-pine	—	4	181	1378.8 \pm 3.8	22	E
	sparse	50	4	114	1390.8 \pm 4.0	15	E
	dense	—	—	—	—	—	—
Vysoká Hole	no-pine	—	7	277	1400.8 \pm 8.2	21	E
	sparse	—	—	—	—	—	—
	dense	90	9	156	1402.9 \pm 3.9	11	E

within a group provides an indicator of long-term vegetative reproduction ability (Kuoch and Amiet, 1970). The maximum tree height within each clonal group was recorded to evaluate effects of pine presence on spruce height growth.

Further, we assessed the effect of the distance between dwarf pine margins and spruce group crown margins (hereinafter referred as “distance to pine”) on the presence/absence of spruce layering branches. Spruce groups were placed in four distance classes: 0–1 m, 1–3 m, 3–5 m, and 5–7 m, with the corresponding mid-range values of 0.5 m, 2 m, 4 m, and 6 m used in the analysis. The distances to the nearest dwarf pine margin were evaluated in the four cardinal directions, and only those spruce groups having distance values within these classes in all four directions were regarded as suitable for analysis. At each site (excluding Keprník), 10 such clonal groups in each distance class were chosen, and the presence or absence of layering branches in each of the clonal groups was recorded.

DATA ANALYSIS

The data from our sample plots had a hierarchical structure (sample plot/clonal group/tree). To avoid pseudoreplication and simplify analyses (Murtaugh, 2007), we generally used within-plot average values for analyses at the plot level. The exception was the probability analysis of the relationship between distance to pine and layering branch occurrence, due to its different sampling design.

In analyzing our data, we first performed principal component analysis (PCA) to evaluate the relationships among studied spruce clonal group characteristics and also the effect of pine stand type (no-pine/sparse/dense) on the whole set of spruce clonal group characteristics. Data were scaled to unit variance before using PCA. To assess the effect of pine stand type, we fitted this factor onto the first two main components of the ordination. Its significance was tested using a permutation test.

To test differences within studied clonal spruce group characteristics (mean age, age of the oldest tree, maximum height,

number of layering branches, and number of juvenile ramets), we used linear mixed effect (LME) models with restricted maximum likelihood (REML), treating pine stand type as a fixed effect and site as a random effect. To evaluate the significance of site effects, we also fitted a simpler model with only pine stand type (i.e., with no random effect) using generalized least squares (GLS) REML estimation. We used likelihood ratio tests and Akaike’s Information Criterion (AIC) to compare this GLS model with the more complex LME model (see Zuur et al., 2009). To account for heteroscedasticity of our dependent variables, we did square-root transformation of all dependent variables except age of the oldest tree. Because maximum height was correlated with mean age, a separate analysis of a subset of trees of similar age (60–80 years) was conducted. This allowed us to evaluate the effect of pine stand type on maximum height independent of mean age.

The effect of distance to pine on the probability of spruce layering was analyzed using generalized linear models (binomial family and probit link function) with distance to pine as the explanatory variable and probability of layering as the dependent variable. WALD Z was used to evaluate the significance of distance to pine.

All statistical analyses were carried out using R statistical environment version 2.14 (R Development Core Team, 2011). The ‘vegan’ package (Oksanen et al., 2012) was used for multivariate analysis, the ‘nlme’ package (Pinheiro et al., 2013) for LME and GLS, and the ‘lattice’ package (Sarkar, 2008) for boxplot construction.

Results

PRINCIPAL COMPONENT ANALYSIS

Data on 380 clonal spruce tree groups comprising 1508 trees were collected from a total of 60 plots at the four sites (Table 1). The PCA ordination diagram for the six clonal spruce group characteristics showed a clear trend from the dense pine stand type to the no-pine stand type along the first principal

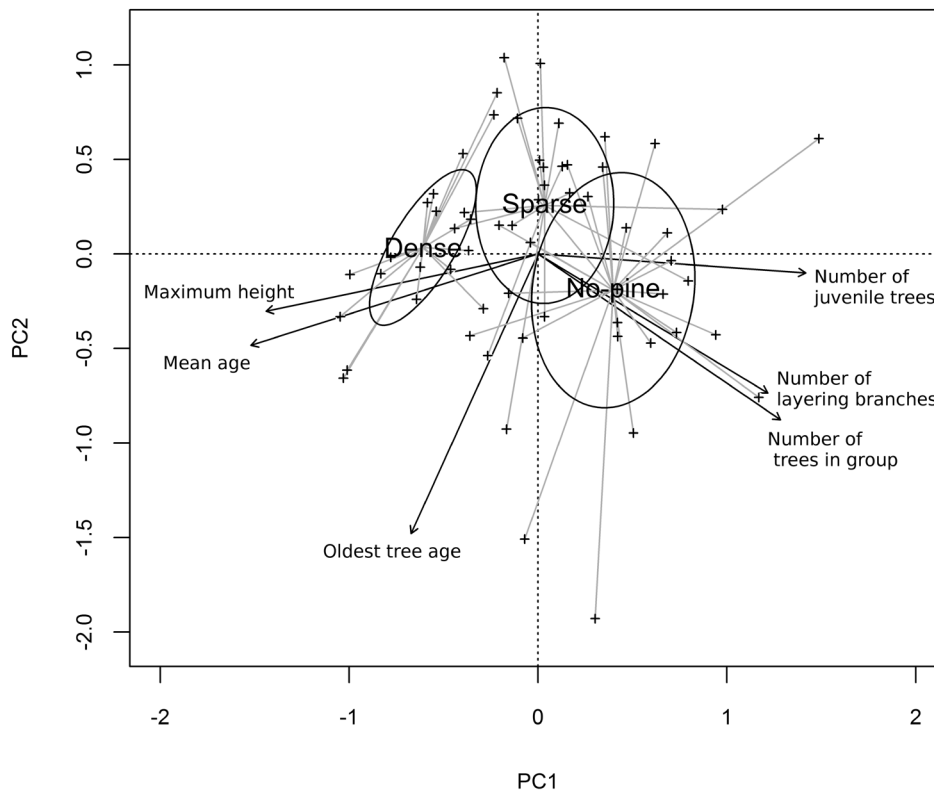


FIGURE 3. Principal component analysis (PCA) ordination plot showing projections of sample plot and clonal spruce groups characteristics. Sample plots in different pine stand types (dense, sparse, no-pine) are distinguished using a spider plot. Dispersion ellipses for pine stand types are plotted using standard deviations of point scores. The first PCA axis explains 52% of variance, and the second explains 20% of variance.

component (Fig. 3). The effect of pine stand type on the studied characteristics was significant ($p < 0.001$). The numbers of juvenile ramets, layering branches, and trees in a group were positively correlated with the first principal component and tended to be higher in no-pine stands. In contrast, maximum height and mean age were negatively correlated with the first principal component and tended to be higher in dense pine stands. The ages of the oldest trees tended to be greater in dense stands than in sparse stands, with this variable distinct in that it was correlated with the second principal component, standing apart from the other variables. The ordination plot showed also strong positive correlations between maximum height and mean age and between number of trees in a group and number of layering branches.

DIFFERENCES IN AGE-RELATED VARIABLES AND TREE HEIGHT

At all sites and in all pine stand types, the spruce populations were younger than the surrounding pine stands (compare pine stand age in Table 1 and age of oldest spruce tree in Fig. 4). The age differences between the spruce (oldest tree in group, indicating establishment date) and surrounding pine stands ranged from 10 (dense pine, Keprník sites) to 60 years (sparse pine, Praděd site). Thus, most of the spruces have been growing, since their early ontogenetic stages, inside gradually closing pine stands.

The effect of pine stand type was significant for all variables except the age of the oldest spruce (Table 3). In contrast, a site did not have a significant effect on any studied variable (Table 2). Mean

TABLE 2

Evaluation of site effects on clonal spruce group characteristics; likelihood ratio test and Akaike's Information Criterion (AIC) were used to compare simpler model without site effect (fitted using generalized least squares [GLS]) and model with site linear mixed effect (LME). Results show site effects that were not significant in any case.

Characteristic	AIC GLS	AIC LME	Likelihood ratio	<i>p</i> -value
Mean age	458.6	460.6	6.45e-8	0.500
Trees in group	108.8	110.8	1.97e-8	0.500
Layering branches	134.6	136.6	1.70e-8	0.500
Juvenile trees	116.2	118.2	2.39e-8	0.500
Age of oldest tree	205.7	207.7	3.56e-8	0.500
Height max	659.2	660.5	0.612	0.217

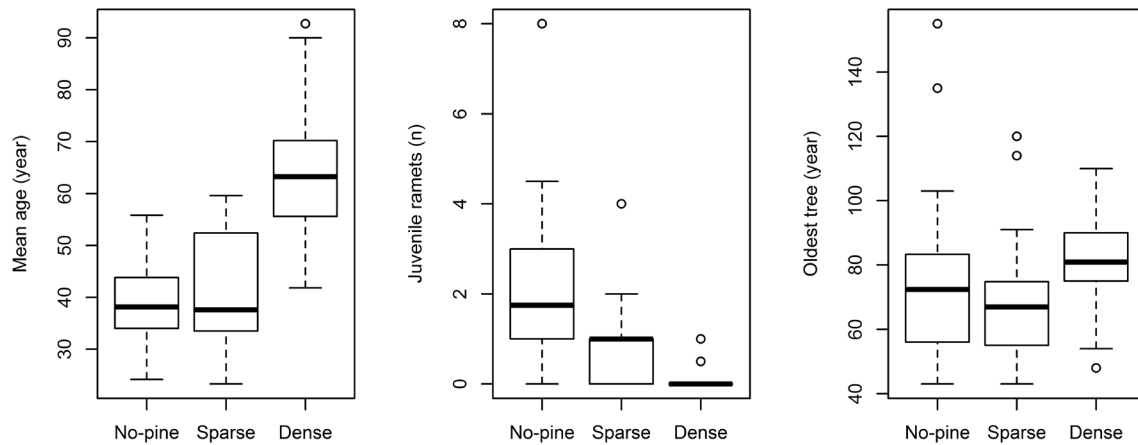


FIGURE 4. Boxplots of mean age, number of juvenile ramets (20 years old or younger), and age of the oldest tree for spruce groups in each pine stand type (dense, sparse, no-pine). The horizontal line in each box represents the median; the hinges represent the 25th and 75th percentiles; the whiskers represent 1.5 times the interquartile range; open circles represent values outside this interval.

spruce age was greater in dense pine stands than in no-pine stands and sparse pine stands (Fig. 4). The number of juvenile ramets showed the opposite trend. It was lower in dense pine stands (with almost no juveniles) and higher in no-pine stands (on average, two juvenile ramets per spruce clonal group) (Fig. 4). The age of the oldest tree tended to be higher in dense pine stands, but this trend was not significant (Fig. 4). Overall, the oldest tree was 155 years old, and it was found in a no-pine stand at Keprník (Fig. 4). Stem breaks were more frequent in no-pine plots (55%) than dense pine plots (20%; $p < 0.001$, t -test). The maximum height of spruce trees in dense pine stands was significantly greater than those of no-pine and sparse pine plots (Table 3, Fig. 5). The height findings were similar to the trend for mean age, which is not surprising, as maximum tree height was correlated with mean age ($r = 0.75$). However, this trend was also found in the subset of spruce trees of similar age (60–80 years, $n = 28$). In this subset, trees in dense pine stands were significantly taller (mean height [cm]: 441 ± 72 SD) than trees in no-pine stands (mean height [cm]: 367 ± 56 SD; $F = 7.4$, $p < 0.01$).

NUMBER OF TREES AND NUMBER OF LAYERING BRANCHES

The numbers of trees and layering branches were both significantly affected by pine stand type (Table 3), showing similar

trends to the number of juvenile ramets: numbers low in dense pine, higher in sparse pine, and even higher in no-pine stands (Fig. 5). At the site level, the average number of trees per group ranged from 3 at Keprník (dense pine stand) to 11 at Praděd (no-pine stands). Layering branches occurred in 41–80% of the clonal spruce groups in no-pine stands, in 20–39% in sparse pine stands, and in 6–14% in dense pine stands. The highest number of layering branches for a single clonal spruce group was 20 in a no-pine stand at Praděd (Fig. 5).

EFFECT OF DISTANCE TO PINE ON LAYERING PROBABILITY

The probability of layering, calculated as the number of spruce clonal groups having layering branches divided by total number of spruce groups in the distance class, was significantly affected by the distance between the spruce group crown and dwarf pine crown margin ($p < 0.001$; Wald Z value = -5.603). None of the spruce groups in the distance class 0–1 m had any layering branches, resulting in zero layering probability in this distance class. The probability of layering increased with increasing distance to pine: from 17% in the 1–3 m distance class, to 43% in the 3–5 m class, and finally to 67% in the 5–7 m class (Fig. 6).

TABLE 3

Effects of pine stand type (referred to as “pine” in table) on clonal spruce group characteristics. Because site effect was not significant, F and p -values from only GLS models are shown. Pine stand type had significant effects on all studied characteristic except the age of the oldest tree.

Variable	Predictor	d.f.	F	p -value
Mean age	pine	2; 58	35.481	<0.001
Trees in group	pine	2; 58	26.781	<0.001
Layering branches	pine	2; 58	21.012	<0.001
Juvenile trees	pine	2; 58	19.366	<0.001
Age of oldest tree	pine	2; 58	1.447	0.244
Height max	pine	2; 58	15.918	<0.001

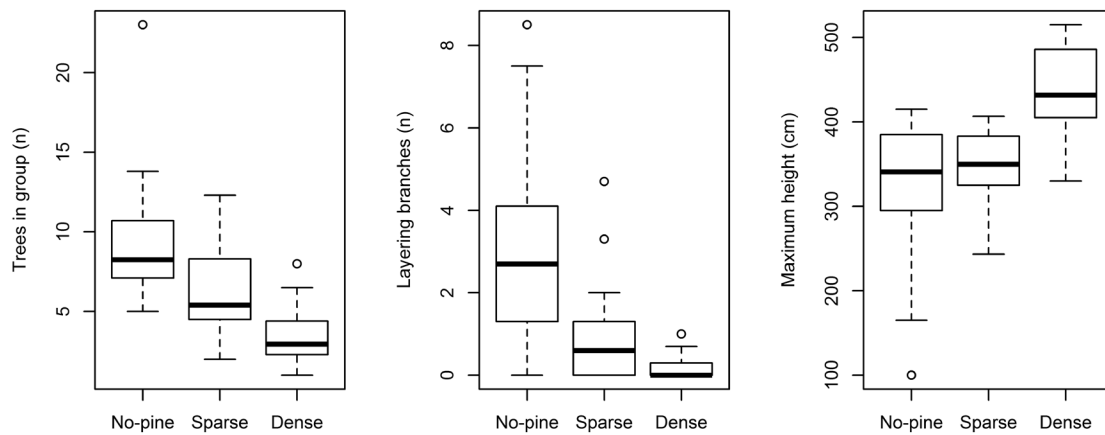


FIGURE 5. Boxplots of number of trees in a clonal group, number of layering branches, and maximum height for spruce groups in each pine stand type (dense, sparse, no-pine). The horizontal line in each box represents the median; the hinges represent the 25th and 75th percentiles; the whiskers represent 1.5 times the interquartile range; open circles represent values outside this interval.

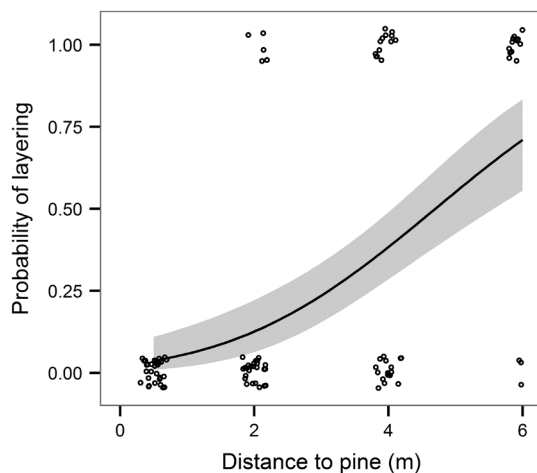


FIGURE 6. Spruce branches layering probability in relation to distance between spruce tree crown and pine shrub crown margins. Layering probability is gradually increasing from zero to 67% with increasing distance to pine. Gray area is within 95% confidence intervals. Small circles (slightly jittered to avoid overplotting) represent the observed values.

Discussion

Our results clearly show that vegetative propagation of spruce was strongly affected by the density of surrounding dwarf pine stands. In particular, this was demonstrated by the spruce populations in pine stands being older, with fewer juveniles, than the spruce groups surrounded by alpine meadows. Furthermore, in dense pine stands the reduced occurrence of layering branches indicated the lower potential for vegetative propagation (see Kuoch and Amiet, 1970; Schönenberger, 1981; Tranquillini, 1979).

We suggest that the scarcity of layering branches probably resulted from a combination of the competitive pressure of closely occurring pine (causing light deficiency, Soukupová et al., 2001; Wild and Wildová, 2002; Dullinger et al., 2005) and increased branch mortality from prolonged snow cover and wetter

microclimate in pine stands (Culek, 2012). Indeed, both the snow cover prolongation and increased moisture can lead to fungal infection (Vacek et al., 2012). The mortality of actual or potential layering branches could also be increased by mechanical damage from prostrate branches of dwarf pine (see Fig. 2, part D). In fact, we have observed high dieback of spruce branches in dense pine stands in the study area. The relative importance of the various explanatory phenomena is likely to differ among the distance classes, as they would operate over different distances. Thus, mechanical damage would likely have been especially important in the class of shortest distances to pine margins (0–1 m), thereby at least partly explaining the zero layering probability found for that class. However, at this distance, shading (Wild and Wildová, 2002; Dullinger et al., 2005) and snow cover prolongation (Culek, 2012) also likely contributed to the extremely low layering probability. The reduced layering probability of spruces even at relatively large distances from pine (3–5 m), about 25% less than for those in meadows, can probably be ascribed largely to snow prolongation and to a lesser degree to shading. Apparently, none of these mechanisms would operate at distances greater than 6 m, as no effect on spruce layering was observed.

Layering success is also known to be affected by ground vegetation (Arno and Hammerly, 1984; Vacek et al., 2012), waterlogging (Vacek et al., 2012), and soil moisture scarcity, but none of these is likely to have substantially influenced our observed outcomes. In particular, increasing dwarf pine cover is characterized by increasing dominance of ground vegetation cover by *Avenella flexuosa* (Zeidler et al., 2012). However, ground vegetation dominated by this species is associated with very low mortality of spruce layering branches (Vacek et al., 2012). Therefore, such a change in vegetation cover could not underlie the inhibitory effect we found of dwarf pine on spruce layering (if anything, it would have reduced the strength of this effect). Similarly, mortality of juvenile ramets is higher in waterlogged areas (Vacek et al., 2012), but our sites were not waterlogged (as shown by the absence of hygrophilous vegetation). Too little soil moisture can also limit vegetative reproduction of some woody species in alpine areas (e.g., *Salix* and *Rhododendron* at sites in the Alps having substrate that does not retain water), with adventitious root development strongly dependent on available soil moisture

(Körner, 2003). However, in our study system, there is unlimited water availability in the root zone soil substrate during the entire growing season (Šenfeldr et al., 2013).

In contrast to hampering the vegetative reproduction of spruce, dense pine stands positively affected spruce height growth. As shown by the lower ages of spruce groups compared to their surrounding pine stands, many of these spruces have been growing in gradually increasing pine cover. The improved height growth in the dense pine stands might be related to decreased browsing pressure from herbivores (Rao et al., 2003; Russell and Fowler, 2004; Dullinger et al., 2005) and/or lower wind abrasion of aboveground biomass in the juvenile ontogenetic phases. The latter explanation in particular is supported by our finding of lower numbers of broken stems in dense pine plots in comparison to no-pine plots. Protection against frost (Michiels, 1993) might also have played a role. We suggest that these benefits accelerated height growth at least until the shrub layer was overtopped, with the added growth retained such that trees that lacked this protection as juveniles would not catch up. We do not believe that the higher spruce growth was the result of competition for light and growing space with pine, because we find no differences in spruce tree slenderness coefficients between dense pine and no-pine plots (not shown). In most cases, gaps in pine stands were probably large enough for the juvenile phase of the oldest trees in a group not to experience light deficiencies. According to Wild and Wildová (2002), the negative effect of pine on low-stature plants is manifested only within a ca. 0.4- to 0.6-m-wide buffer zone along the pine margin. In our study, it appears that the benefit from sheltering by dwarf pine outweighed possible suppression due to competition for light and nutrients. These findings are in contrast to results from the eastern Alps, where poorer height growth was found in pine stands than in meadows. This dissimilarity is probably related to stronger effects (abrasion, breaks) of wind on alpine/subalpine ecosystems in the Sudetes than in the Alps (see Trembl et al., 2012). Besides strong winds, high population densities of browsers (red deer [*Cervus elaphus*]) in the treeline areas of the Sudetes might be key height growth-limiting factors for Norway spruce in its early ontogenetic stages. Our finding of a positive effect of dwarf pines on spruce height growth along with a negative effect on vegetative propagation is consistent with the overall view that interactions between treeline species can have both positive and negative components (Callaway and Walker, 1997; Song et al., 2010).

At the upper forest limit in the study area, the spruce trees occur as “competitive stress tolerators” (C-S strategists, sensu Brzeziecki and Kienast, 1994) in dense sexual populations, reaching heights of about 10 m (Trembl, 2007). There, the pine-spruce interaction is mainly competitive, and, as documented from many areas, spruce is gradually overgrowing pine stands (Jeník and Lokvenec, 1962; Dullinger et al., 2005; Švajda et al., 2011; Šenfeldr et al. 2012). In the upper part of the treeline ecotone, this interaction switches to at least partly facilitative, with pine, representing strong “stress tolerators” (S – strategist, sensu Brzeziecki and Kienast, 1994) benefitting the height growth of spruce at its range limit (Körner, 2012). However, this facilitative role is ambiguous, since spruce layering is suppressed. This pattern is consistent with special cases of the stress-gradient hypothesis (Maestre et al., 2009) posed by competition between C-S and S strategists (Wang et al., 2008). In our study system, different spruce morphotypes are represented by high stature sexual populations and low stature clonal populations (Schöb et al., 2013). Moreover, changes between competition and facilitation can also occur during the ontogenies of interacting species (Miriti, 2006). Taking these

considerations into account, the pine-spruce interactions along the alpine treeline ecotone can be understood within the framework of the stress-gradient hypothesis (Callaway et al., 2002).

Most treelines in Europe have recently been subjected to forest and shrub invasion following the cessation of mountain agriculture, along with climate amelioration (Anthelme et al., 2003; Gehrig-Fasel et al., 2007). Generally, for upward shifts of island-form, wind-affected treelines, as found in the study area, the combination of both sexual and vegetative reproduction is needed (Holtmeier, 2009; Šenfeldr and Maděra, 2011). Our findings suggest that potentially quick upward expansion of forest within the zone adjacent to the current upper forest limit is likely to be slowed by closed dwarf pine stands, since they hamper both seedling recruitment of spruce (Dullinger et al., 2005) and spruce layering. In the upper part of the treeline ecotone at climatically extreme sites, the interactions are complex as shown by our documentation of both facilitative and competitive effects of dwarf pine on spruce establishment and growth. Future scenarios of spruce-dwarf pine interactions will strongly depend on the texture of dwarf pine stands and the availability of space for spruce germination (Wild and Winkler, 2008). Moreover, although interactions of spruce and dwarf pine within the treeline ecotone may follow their current patterns, they will probably also depend on differing individual responses of both species to climate change (Walther et al., 2002).

Conclusions

Our results show that tree-shrub interactions at wind-affected treelines significantly determine dynamics of clonal tree groups. We found that the distance between spruce trees and surrounding dwarf pine proved to be a key limiting factor of the spruce’s vegetative reproduction. As a result of strong competitive pressure of dwarf pine, the numbers of layering branches and juvenile spruce ramets decreased with increasing pine stand density. On the other hand, spruce height growth was facilitated in dense pine stands. This study indicates that both competition and facilitation between shrubs and trees will influence dynamics of the alpine treeline ecotone. The expansion of spruce coverage will probably be slowed significantly at sites with dense dwarf pine stands adjacent to the current upper forest limit. At climatically more extreme sites, facilitative interactions should also be considered. Similar patterns of interactions between shrubs and trees are likely to occur at treelines involving other tree and shrub species. Thus, the results of this study can contribute to the understanding of processes driving treeline dynamics, not only in the particular study system, but also more generally, especially in the context of treeline responses to climatic change.

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