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Temperature, precipitation and biotic interactions as determinants of tree seedling recruitment across the tree line ecotone

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Abstract

Seedling recruitment is a critical life history stage for trees, and successful recruitment is tightly linked to both abiotic factors and biotic interactions. In order to better understand how tree species distributions may change in response to anticipated climate change, more knowledge of the effects of complex climate and biotic interactions is needed. We conducted a seed sowing experiment to investigate how temperature, precipitation and biotic interactions impact recruitment of Scots pine (*Pinus sylvestris)* and Norway spruce (*Picea abies)* seedlings in southern Norway. Seeds were sown into intact vegetation and experimentally created gaps .To study the combined effects of temperature and precipitation, the experiment was replicated across twelve sites, spanning a natural climate gradient from boreal to alpine and from sub-continental to oceanic. Seedling emergence and survival were assessed 12 and 16 months after sowing, respectively, and above-ground biomass and height was determined at the end of the experiment. Interestingly, very few seedlings were detected in the boreal sites, and the highest number of seedlings emerged and established in the alpine, indicating that low temperature did not limit seedling recruitment. Site precipitation had an overall positive effect on seedling recruitment, especially at intermediate precipitation levels. Seedling emergence, establishment and biomass were higher in gap plots compared to intact vegetation at all temperature levels. These results suggest that biotic interactions in the form of competition may be more important than temperature as limiting factor for tree seedling recruitment in the sub- and low-alpine zone of southern Norway.

Key words: seed-sowing experiment – climate gradients – biotic interactions – *Picea abies* – *Pinus sylvestris*

Introduction

All populations depend on successful recruitment for their long-term persistence. Recruitment is thus a key life history event that involves several phases and processes: flowering, pollination, seed maturation, seed dispersal, seed germination and survival of seedlings, all of which are influenced by both abiotic (e.g. climatic) conditions and biotic interactions (Grubb 1977; Kitajiama and Fenner 2000; Turnbull et al. 2000; Bansal and Germino 2010). In harsh environmental conditions such as the alpine it can take a long time from seedling emergence to establishment. Thus, for trees in this environment, abiotic and biotic conditions affecting seedlings must prevail for several seasons to assure successful recruitment (Juntunen and Neuvonen 2006). Knowledge of the relative importance of abiotic and biotic factors affecting early life-stages and variation across ecotones is thus paramount to understand the recruitment dynamics of tree species in various environments.

Abiotic factors are often considered the most important determinants of plant recruitment in climatically harsh and cold environments, and seedling establishment has been shown to be strongly affected by both temperature and precipitation in these habitats (Smith 1994; McCarty 2001). In general, increasing temperature is assumed to favour plant recruitment in low-temperature environments (Fenner and Thompson 2005). In boreal conifer trees (e.g. *Pinus* and *Picea* species), germination typically peaks at temperatures slightly above 20 °C, while periods with temperatures below 15°C during the growing season limit seed germination (Black and Bliss 1980; but see Milbau et al. 2009). Precipitation is also known to have a direct positive effect on seedling establishment in dry environments, and drought can lower seedling survival drastically (McCarty 2001; Walther et al. 2002). However, the effects of precipitation on recruitment are hard to predict as these depend on the amount, timing and predictability of the rainfall (Fay and Schultz 2009).

Biotic interactions also play a key role in tree seedling emergence, establishment and survival (Ohlson and Zackrisson 1992; Hörnberg et al. 1997). A recent study on alpine plants found that once a plant seedling has germinated in a suitable microhabitat, biotic interactions become one of the major drivers of establishment success (Olsen and Klanderud 2014). Accordingly, seedling responses to neighbouring vegetation are an important aspect of regeneration and possibly of the ensuing structure of tree stands and forests (Maher and Germino 2006). However, the effects of biotic interactions are themselves known to vary with abiotic conditions. The stress-gradient hypothesis proposed by Bertness and Callaway (1994) suggests that the magnitude of biotic interactions differ along gradients of abiotic environmental stress: facilitation and competition are expected to dominate at high and low stress levels, respectively (Callaway et al. 2002). Hence, competition should be more important as a determining factor for recruitment in habitats with warm and wet conditions compared to habitats that are relatively cold and dry, where facilitative interactions more likely prevail.

In this study we investigated the interactive effects of climate and biotic interactions on the recruitment and growth of two common boreal tree species, Scots pine (*Pinus sylvestris* L.*)* and Norway spruce (*Picea abies* (L.) Karst.) in southern Norway. Seeds of both species were sown into intact vegetation and bare-ground gaps. Scots pine and Norway spruce are dominant forest tree species within the boreal zone of Eurasia and both species are native to Norway and known for their wide ecological range (Ohlson and Zackrisson 1992; Seppä et al. 2009). Creating experimental gaps in natural and semi-natural habitats is a standard method for examining the importance of biotic interactions from neighbouring plants (Aarssen et al 1990) and has proven useful for studying interspecific interactions (Diaz et al. 2003). The experiment was replicated within a unique climate "grid" consisting of a natural temperature gradient (alpine-boreal) repeated over four levels of precipitation (continental-oceanic) (see Meineri et al. 2013, 2014). The climate grid encompasses the tree line ecotone, in which dynamics of upward tree migration has been extensively studied in a climate warming perspective (Kozlowski et al. 1991; Kullman 2002; Körner and Paulsen 2004; Holtmeier and Broll 2005). Despite comprehensive studies of the tree line ecotone, knowledge is still lacking on the relative importance of abiotic and biotic factors as determinants of tree recruitment in alpine and sub-alpine environments. Understanding the factors impacting successful recruitment is a fundamental step towards understanding tree line dynamics in a changing climate.

We have addressed the following questions: 1) How does the emergence, establishment and growth of pine and spruce seedlings vary with temperature and precipitation? 2) How do biotic interactions from the standing vegetation sward impact seedling recruitment and growth? 3) How does the effect of biotic interactions vary along the climate gradient? We expected higher seedling emergence and establishment under warm and wet conditions. Further, we hypothesized that the effect of gap formation (i.e. release from biotic interactions) on seedling emergence and establishment would become increasingly positive with increasing temperature, in accordance with the stress-gradient hypothesis. For cold sites we expected to find a negative gap effect, as neighbouring plants may provide shelter from harsh environmental conditions such as wind, drought and frost (Maher and Germino 2006). As climatic conditions are likely to have a significant impact on plant allocation, we examined the biomass of seedlings at the end of the experiment. We expected seedlings to grow taller and heavier with increasing temperature and precipitation. Finally, we hypothesized that seedlings in intact vegetation, experiencing more intense competition for light, would invest relatively more in height growth than seedlings in gaps.

Methods

Study area, study species and experimental design

The seed sowing experiment was conducted within a unique climate grid consisting of a natural temperature gradient replicated four times along a precipitation gradient stretching from the relatively continental inland towards the oceanic coast in southern Norway (see map in Supplementary Material, Fig. S1). The grid allows for the independent combination of three levels of summer temperature [means of the four warmest months: 6.5°C (alpine), 8.5°C (sub-alpine) and 10.5°C (boreal)] with four levels of precipitation [600 mm, 1200 mm, 2000 mm and 2700 mm] across twelve sites (Fig. S1 and Table 1; see also Meineri et al. 2013, 2014).

The twelve study sites were all located in semi-natural grasslands on calcareous bedrock supporting high fine-scale plant diversity. The four alpine sites were situated in the low-alpine zone, the four sub-alpine sites at or just below the tree line, and the boreal sites were situated in or near forested areas. In this paper the term tree line refers to the transition from the uppermost closed forest to the treeless alpine vegetation (Körner and Paulsen 2004; Batllori et al. 2009). Besides their climatic attributes, sites were selected to keep vegetation type, geology and land-use as constant as possible to facilitate comparison among sites. The mean vegetation height in the sites increased with increasing temperature from 6.5 cm in the alpine sites to 9.7 cm in the sub-alpine and 15.3 cm in the boreal sites (Olsen et al. submitted). Further details on vegetation characteristics and site selection criteria are described in Meineri et al. (2013, 2014).

Five experimental blocks were established in each of the study sites, with four study plots of 25 × 25 cm positioned in a grid within each block. These four plots were randomly assigned to one of two vegetation treatments for each of the species: controls with intact vegetation and gaps where vegetation and roots were removed. In total there were 240 study plots; 120 for each species.

In spring 2010, 50 seeds were sown in each plot. All seeds used in the experiment were bought from the public seed supplier "Skogfrøverket" in Lillehammer, Norway, and stored at -20 °C prior to sowing. Seeds were scattered evenly on the bare soil of the gap plots and onto the intact vegetation in the control plots. To prevent seeds from being blown or washed away from the gap plots seeds were pressed down a few millimetres into the soil surface, but not covered. Sites were fenced to prevent animal trampling and disturbance, and the grassland sward was cut approximately 5 cm above ground level in late August to mimic biomass removal by abundant free-roaming domestic and wild ungulates in the area. Otherwise seedlings were left undisturbed.

Seedling recruitment was assessed by recording seedling emergence, establishment and growth. The number of seedlings was counted 5, 12 and 16 months after sowing. Due to low over-winter mortality (<5%) we defined the emergence phase as the first 12 months after sowing, followed by the establishment phase from 12 to 16 months. After the last count (16 months after sowing) the aboveground part of all seedlings was harvested. The harvested seedlings were stored in paper bags and dried at 80°C until constant weight. The height (total length from the original emerging point to the apical meristem) and aboveground dry-weight biomass of all seedlings were measured individually.

Statistical analyses

Effects of climatic variables and creation of gaps on tree seedling emergence, establishment and growth were examined using linear mixed-effects models. The boreal sites were omitted from these analyses due to the very low numbers of seedlings that emerged (Fig. 1). Temperature (from cold to warm: alpine, sub-alpine), precipitation (from dry to wet: 1-4) and treatment (gap versus intact vegetation) were used as fixed factors. To account for the nested design, we estimated random intercepts for blocks nested in sites. Poisson distributions were used for seedling emergence and establishment, and normal distributions were found suitable for seedling height and biomass variables. Likelihood ratio (LR) tests were used to select the final models. Markov Chain Monte Carlo (MCMC) estimation with 10.000 iterations was used to assess variable significances for the models assuming normal distribution. Separate mixed-effects models were run for each tree species. All statistical analyses were performed in R version 2.15.2 (R Development Core Team 2012) using R Studio Version 0.96.331 (RStudio, Inc). We used the package lme4 (Bates et al. 2012) for the mixed effects models and LanguageR (Baayen 2011) for the Markov Chain Monte Carlo estimations.

Results

Overall, emergence and growth patterns were similar for pine and spruce. In total 1226 pine seedlings and 1138 spruce seedlings emerged during the first 12 months. Numbers of emerged seedlings per plot ranged from 0 to 41 for pine, and from 0 to 44 for spruce, with a median of 9 and 10, respectively. After 16 months, at the end of the second growing season, 900 pine and 922 spruce seedlings had established and were harvested.

The number of emerged seedlings in intact vegetation decreased with increasing temperature and increased with precipitation (Fig. 1a and b). Mean seedling emergence per plot was 2-3 times higher in alpine than sub-alpine sites for both species (Fig. 1a and b). Seedling emergence increased with site precipitation regardless of site temperature, but more strongly in sub-alpine (pine: coef=1.98, $p<0.01$ for precipitation level 3 and coef=1.73, $p<0.01$ for precipitation level 4; spruce: coef=1.49, $p<0.01$ for precipitation level 3 and coef=1.63, $p<0.01$ for precipitation level 4) than in alpine (pine: no significant difference, $p>0.05$ for all precipitation levels; spruce: coef=0.66, $p<0.01$ for precipitation level 3 and coef=0.4, $p<0.05$ for precipitation level 4) sites (Table 2), resulting in less pronounced differences between temperature levels at high precipitation. The creation of gaps increased mean seedling emergence of both species (Fig. 1a and b), although there was substantial variation between sites. The gap treatment strongly increased emergence at intermediate precipitation levels in both alpine and intermediate sites (pine: coef=0.90, $p<0.001$ for precipitation level 2 and coef=0.91, $p<0.001$ for precipitation level 3; spruce: coef=0.62, $p<0.05$ for precipitation level 2 and coef=0.74, $p<0.01$ for precipitation level 3), () and was especially pronounced for pine at intermediate temperature and precipitation (coef=3.54, $p < 0.01$ for precipitation level 2) (Table 2). Gap plots in the sub-alpine sites with medium high site precipitation (level 3) had the highest number of seedlings per plot for both species (Fig. 1a and b). Almost no seedlings emerged in the boreal sites in neither gap nor intact vegetation plots (Fig. 1a and b).

The patterns for establishment followed the same overall trends as for emergence. The mean number of established seedlings per plot in intact vegetation was higher in alpine than in sub-alpine sites (Fig. 1c and d), although most pronounced for pine (coef=-2.58, $p < 0.001$) (Table 2). Pine seedling establishment increased significantly with site precipitation in the intermediate temperature sites (coef=1.51, $p<0.05$ for precipitation level 3 and coef= 3.05, $p<0.001$ for precipitation level 4), but not in the alpine sites ($p > 0.05$ for all precipitation levels) (Table 2), resulting in smaller differences in establishment between temperature levels at high site precipitation. For spruce establishment there was no interactive effect of temperature and precipitation on establishment, and seedling establishment increased with site precipitation at both temperature levels (coef=1.17, $p<0.05$ for precipitation level 2, coef=2.01, $p<0.001$ for precipitation level 3 and coef=1.19, $p<0.05$ for precipitation level 4) (Table 2). For both species there was a tendency towards a peak in establishment at intermediate site precipitation (Fig. 1c and d). Overall, the creation of gaps almost doubled mean seedling establishment for both species (Fig. 1c and d). The effect of gap was higher on establishment than emergence, but there was substantial variation among sites. The gap treatment increased seedling establishment of pine in the alpine (coef=0.66, $p<0.05$ for precipitation level 2, coef=0.88, $p<0.01$ for precipitation level 4), with a similar, although more pronounced, pattern in the sub-alpine sites (coef=3.78, $p<0.01$ for precipitation level 2) (Table 2). Seedling establishment of spruce in gaps followed the same trend as for pine, but was not significant ($p>0.05$ for all tests) (Table 2). Very few seedlings had established in the boreal sites (Fig. 1c and d), which was expected due to the low emergence, but a few "late emergents" were detected in the last survey and were included in the establishment counts.

Both pine and spruce seedling height varied along the climate gradients. Spruce seedlings were significantly taller in sub-alpine compared to alpine sites (coef=7.12, $p<0.01$), and pine showed a similar non-significant response ($p>0.05$) (Fig. 2a and b). There were few significant effects of site precipitation on height growth (Table 3). Seedlings were generally shorter in gaps than in intact vegetation in both sub-alpine and alpine sites (pine: coef=-1.2, $p<0.05$ for precipitation level 2 and coef=-5.8, $p<0.01$ for precipitation level 3; spruce: coef=-4.14, $p<0.05$ across all precipitation levels) (Fig. 2a and b and Table 3). The few spruce seedlings found in the boreal sites (the late emergents) were among the tallest seedlings sampled (Fig. 2b).

Spruce seedling biomass was higher in sub-alpine compared to alpine sites (coef=0.88, $p< 0.05$), while no significant difference was found for pine ($p > 0.05$), and there were few significant effects of site precipitation on biomass (Fig. 2c and d and Table 3). Pine seedlings in gap plots had higher biomass than those growing in intact vegetation in the sub-alpine sites (coef=0.75, $p<0.01$) (Table 3), with a similar tendency in the alpine (Fig. 2c). Spruce seedlings in gaps had higher biomass at both temperature levels (coef=0.26 $p < 0.05$) (Table 3), with a tendency for greater differences in sub-alpine sites (Fig. 2d).

Discussion

Contrary to our expectations, more tree seedlings emerged and established in the cold alpine sites compared to the sub-alpine and boreal sites, indicating that low temperatures did not restrict seedling recruitment of pine and spruce in the low-alpine zone in this study. This was an unexpected finding, as the alpine sites are located well above the current tree line. Very few seedlings were found in the boreal sites, which is surprising as these locations were characterized by well-developed conifer stands and should in principle provide suitable microhabitats for tree seedling emergence and establishment. Our findings contradict previous studies showing a dominant role of temperature for successful establishment of trees (Tranquillini 1979; Payette 1985; Kullman and Engelmark 1990; Grace et al. 2002; Juntunen and Neuvonen 2006). Nonetheless, our results are in line with studies (e.g. Maher et al. 2005; Batllori et al. 2009; Milbau et al. 2009) suggesting that other factors, such as biotic interactions and precipitation, may be more important than low temperature as determinants of successful tree seedling emergence and establishment also in alpine zones.

Site precipitation was an important factor for tree seedling recruitment within our study system, with higher emergence and establishment at sites with intermediate and high precipitation. Soil moisture is important for initiating germination mechanisms (e.g. Ibanez et al. 2007), and our findings align with previous studies showing a positive effect of precipitation on seedling recruitment (McCarty 2001; Walther et al. 2002). The tendency for a unimodal relationship with a decline in establishment in sites with the lowest and highest precipitation may be due to drought in the dry continental end of the precipitation gradient, and by hypoxic soil conditions in the wet oceanic end. Seedling survival at medium-high precipitation sites may also be enhanced by high winter precipitation. While frost-heaving has been reported to be among the most common causes of seedling damage and mortality during the first winter, insulation by a deep snow cover can enhance winter survival (Erefur et al. 2008). The high over-winter survival of seedlings found in this study may thus be a result of a protective snow cover during winter.

Whereas site temperature and precipitation was found to have an effect on tree seedling recruitment success, interactions with the established vegetation also affected recruitment across the tree line ecotone in this study. Gaps generally promoted seedling emergence and establishment in both sub-alpine and alpine sites, as more seedlings were found in gaps compared to intact vegetation. Our findings are in line with previous studies showing a clear benefit from gaps on recruitment (Berkowitz et al. 1995; Gray and Spies 1996; Munier et al. 2010). Gap formation in the form of vegetation removal can influence seedling recruitment by reducing aboveground competition and thereby increasing light availability, but also by enhancing temperature fluctuations and nutrient levels (Graae et al. 2011). We did not measure resource levels or microclimatic conditions in this study, and our experiment thus cannot determine the mechanism behind the positive effect of gaps on seedling recruitment. However, seedlings in gap plots were shorter than seedlings in intact vegetation, yet had higher biomass, suggesting that removal of surrounding vegetation reduced competition for light. In intact vegetation with intense competition for light seedlings potentially invest relatively more in height growth at the expense of stability tissue like thicker stem and roots (Norgren 1996). Thus, it seems that decreased competition, with a corresponding increase in light availability, may override potential negative effects of gap such as increased vulnerability to injuries and damage (Munier et al. 2010) and drought- and temperature-related stress (Smith et al. 2003).

According to the stress-gradient hypothesis, the role of competition should decrease relative to facilitation with decreasing abiotic stress, and facilitation should therefore be more important in alpine than in sub-alpine and boreal habitats (Callaway et al. 2002). Our findings indicate that the positive effect of gaps on seedling emergence and establishment, which could be due to lower competition, was relatively more important than any facilitative effect of surrounding vegetation at all temperature levels, including the alpine. Nonetheless, the difference in biomass between seedlings in gaps vs. intact vegetation was larger in sub-alpine compared to alpine sites, which may suggest that competition intensity increased with increasing temperature. Vegetation height increased with increasing temperature, further suggesting that competition is more intense at high temperatures. Even gaps were overgrown in some boreal sites (L. Tingstad, pers. obs.), which may explain the almost complete lack of tree seedling recruitment in these sites.

Our findings suggest that competition may limit seedling emergence and establishment of pine and spruce at the tree line ecotone, as indicated by the positive effect of gap formation on recruitment, although the strength of the interactions seemed to vary with temperature and to a lesser degree with precipitation. The finding that low temperature was not a limiting factor for the emergence and establishment of pine and spruce seedlings, could indicate that climate warming may not directly influence seedlings in the sub- and low-alpine zone of southern Norway. However, climate warming may affect growth and survival of trees at later life stages. Previous studies have detected tree seedlings above the tree line that rarely become mature, upright trees (Körner and Paulsen 2004; Körner 2012). Seedlings in our study had a mean height of 2.45 cm and may have experienced a thermal advantage of being short and hence sheltered by surrounding vegetation. Thus, although climate warming may not enhance seedling recruitment *per se*, it may increase the number of seedlings growing into tall trees, which can in turn lead to altitudinal advancement of the tree line. Climate warming may also indirectly affect tree seedling recruitment by altering biotic interactions. The role of competition in plant communities has been shown to increase with increasing temperature (Klanderud 2005; Olsen and Klanderud 2014), and our findings suggest that more intense competition in a warmer climate may, at least locally, reduce tree seedling emergence and establishment. Disturbance, i.e. the formation of gaps, may thus become an increasingly important factor influencing tree seedling recruitment also in alpine habitats, with a potential impact on future tree line position.

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Legal statement: We hereby declare that this manuscript is the outcome of our original work and that data and manuscript have been submitted to this journal only. The authors declare that they have no conflict of interest

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Table 1: Altitude and climatic characteristics of the twelve study sites. The sites were divided into three habitat types based on elevation a.s.l. and designated as alpine (Alp), sub-alpine (Sub) or boreal (Bor), within which four precipitation categories (1-4) were denoted based on mean annual precipitation (mm). Mean temperature of the four warmest months (tetraterm) (°C) and precipitation data were provided by the Norwegian Meteorological Institute

Site	Altitude	Temperature	Precipitation
	m a.s.l.	*tetraterm,°C*	*mm (mean annual)*
Alpine			
Alp1	1208	6.17	596
Alp2	1097	6.45	1321
Alp3	1213	5.87	1925
Alp4	1133	6.58	2725
mean	*1162*	*6.50*	
Sub-alpine			
Sub1	815	9.14	789
Sub2	700	9.17	1356
Sub3	770	8.77	1848
Sub4	780	8.67	3029
mean	*766*	*8.50*	
Boreal			
Bor1	589	10.33	600
Bor2	474	10.50	1161
Bor3	436	10.60	2043
Bor4	476	10.78	2923
mean	*493*	*10.50*	

Table 2: Model coefficients, standard errors (SE) and p-values of mixed effects models examining the effects of climate and gap formation on seedling emergence and establishment. Temperature is represented by sub-alpine ("Sub") and precipitation by category number 2, 3 and 4 from dry to wet. Model coefficients reflect contrasts with the temperature category "Alp", the precipitation category "1", and the treatment category "intact vegetation" which are included in the intercept. * = p < 0.05, ** = p < 0.01, *** = p < 0.001. ns= not significant.

	PINE						SPRUCE					
	Emergence (# seedlings)			Establishment (# seedlings)			Emergence (# seedlings)			Establishment (# seedlings)		
	Coefficient	*SE*	P	*Coefficient*	*SE*	P	*Coefficient*	*SE*	P	*Coefficient*	*SE*	P
Intercept	2.89	0.27	***	2.41	0.29	***	2.43	0.24	***	0.74	0.39	**
Temperature												
Sub	-2.68	0.52	***	-2.58	0.61	***	-1.41	0.46	**	-0.87	0.66	ns
Precipitation												
2	-0.35	0.38	ns	-0.33	0.42	ns	0.21	0.34	ns	1.17	0.50	*
3	-0.13	0.38	ns	0.41	0.40	ns	0.66	0.34	**	2.01	0.49	***
4	0.26	0.37	ns	-0.71	0.43	ns	0.4	0.20	*	1.19	0.51	*
Treatment												
Gap	-0.47	0.17	**	-0.06	0.18	ns	-0.43	0.20	*	0.34	0.38	ns
Interactions												
Gap × 2	0.90	0.22	***	0.66	0.26	*	0.62	0.24	*	0.30	0.42	ns
Gap × 3	0.91	0.22	***	0.33	0.23	ns	0.74	0.24	**	0.10	0.41	ns
Gap × 4	0.13	0.22	ns	0.88	0.28	**	0.33	0.25	ns	0.04	0.44	ns
Gap × Sub	0.34	0.55	ns	-0.16	0.71	ns	20.30	6743.10	ns	0.44	0.67	ns
Sub × 2	-1.64	1.19	ns	-1.28	1.24	ns	0.26	0.59	ns	-1.75	0.98	ns
Sub × 3	1.98	0.66	**	1.51	0.74	*	1.49	0.56	**	0.42	0.78	ns
Sub × 4	1.73	0.66	**	3.05	0.76	***	1.63	0.57	**	1.38	0.79	ns
Sub × 2 × Gap	3.54	1.16	**	3.78	1.25	**	15.58	1599.10	ns	0.81	0.93	ns
Sub × 3 × Gap	0.27	0.59	ns	1.19	0.75	ns	17.11	1599.10	ns	0.28	0.70	ns
Sub × 4 × Gap	0.69	0.59	ns	-0.28	0.77	ns	16.99	1599.10	ns	-0.54	0.72	ns

Table 3: Model coefficients, standard errors (SE) and p-values of mixed effects models examining the effects of climate and gap formation on seedling height and aboveground biomass. Temperature is represented by sub-alpine (“Sub”) and precipitation by category number 2, 3 and 4 from dry to wet. Model coefficients reflects contrasts with the temperature category “Alp”, the precipitation category “1”, and the treatment category “intact vegetation” included in the intercept. * = p < 0.05, ** = p < 0.01, *** = p < 0.001. ns= not significant. “-“ indicates variables removed during model selection

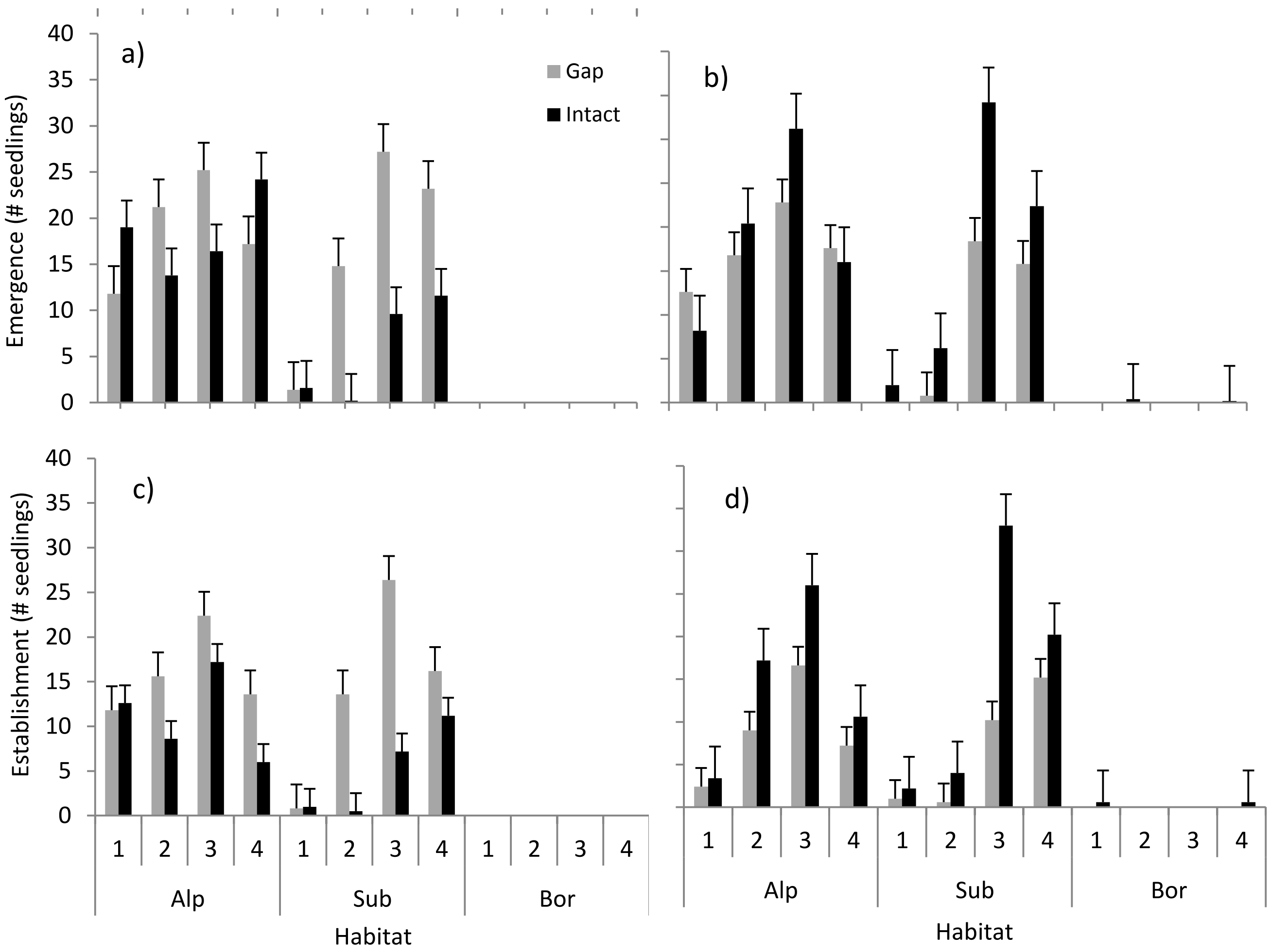
	PINE						SPRUCE					
	Height (mm)			Aboveground biomass (g*100)			Height (mm)			Aboveground biomass (g*100)		
	Coefficient	*SE*	P	*Coefficient*	*SE*	P	*Coefficient*	*SE*	P	*Coefficient*	*SE*	P
Intercept	22.90	1.48	***	0.10	0.02	***	23.02	2.28	***	1.29	0.39	**
Temperature												
Sub	-2.70	2.70	ns	-0.30	0.20	ns	7.12	1.76	**	0.88	0.34	*
Precipitation												
2	-1.01	2.10	ns	-0.09	0.21	ns	-0.32	2.70	ns	-0.80	0.50	*
3	3.50	2.10	*	0.01	0.20	ns	-0.16	2.50	ns	-0.50	0.49	ns
4	-5.40	2.20	ns	-0.20	0.20	ns	-3.13	2.60	ns	-0.60	0.49	ns
Treatment												
Gap	-2.56	1.58	ns	0.09	0.14	ns	-4.14	1.52	*	0.26	0.10	*
Interactions												
Gap × 2	-1.20	2.30	*	-	-	-	-	-	-	-	-	-
Gap × 3	-5.80	2.20	**	-	-	-	-	-	-	-	-	-
Gap × 4	1.50	2.40	ns	-	-	-	-	-	-	-	-	-
Gap × Sub	14.90	3.20	ns	0.75	0.24	**	-	-	-	-	-	-
Sub × 2	11.20	4.40	ns	0.09	0.30	ns	-	-	-	-	-	-
Sub × 3	4.40	3.60	ns	0.40	0.30	ns	-	-	-	-	-	-
Sub × 4	12.30	3.60	ns	1.39	0.35	**	-	-	-	-	-	-
Sub × 2 × Gap	-17.90	4.80	ns	-	-	-	-	-	-	-	-	-
Sub × 3 × Gap	-12.50	4.10	ns	-	-	-	-	-	-	-	-	-
Sub × 4 × Gap	-17.30	4.10	ns	-	-	-	-	-	-	-	-	-

Figure legends:

Fig. 1 Observed patterns of tree seedling emergence and establishment in the twelve study sites in response to presence (intact vegetation) or absence (gap) of vegetation: a) pine seedling emergence, b) spruce seedling emergence, c) pine seedling establishment and d) spruce seedling establishment. Habitat types correspond to the temperature gradient: alpine (Alp), sub-alpine (Sub) and boreal (Bor). The precipitation gradient is indicated with numbers 1-4 from dry to wet (see Table 1). Bars show means ± SE, N=5

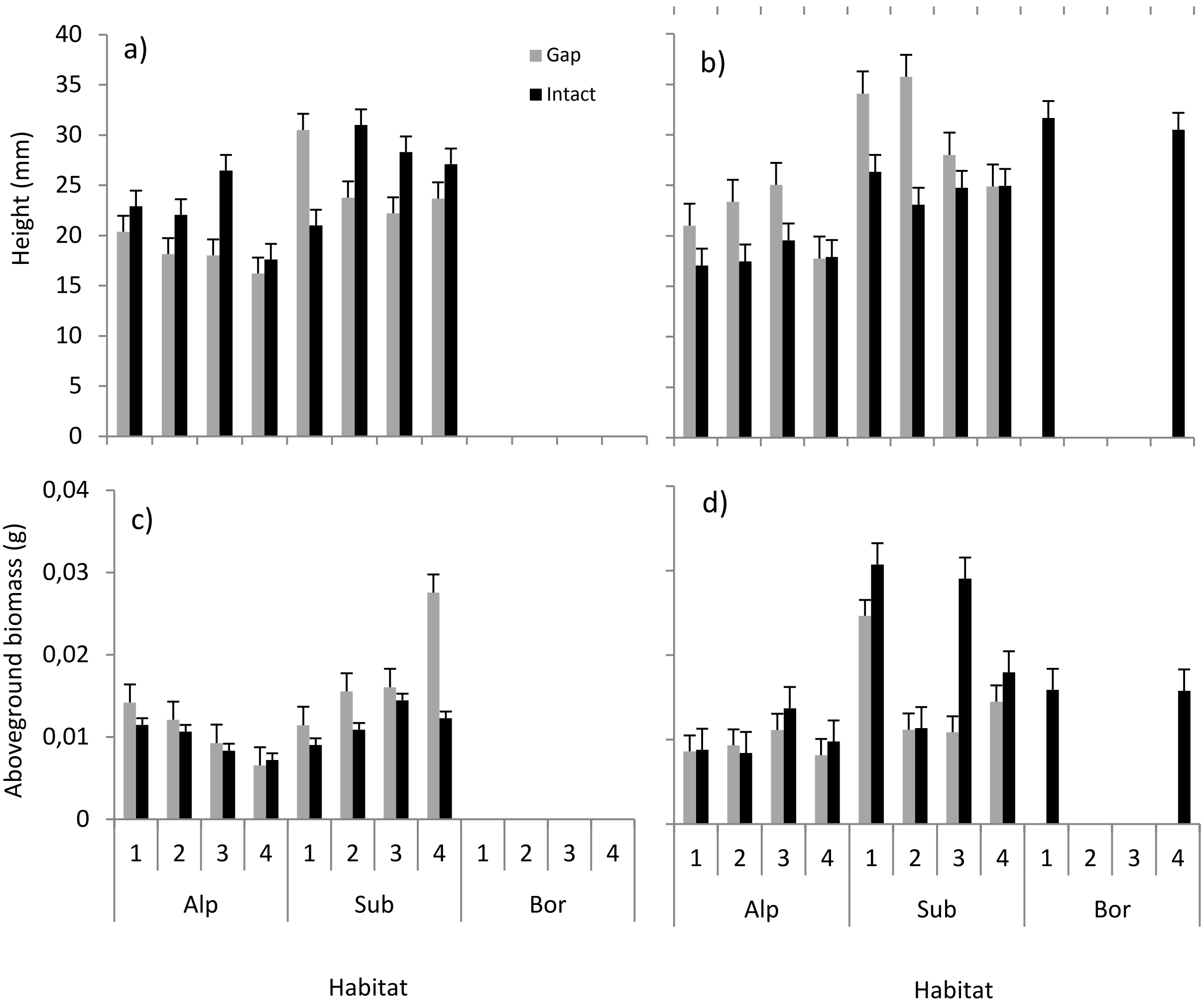
Fig. 2 Observed patterns of tree seedling height and aboveground biomass in the twelve study sites in response to presence (intact vegetation) or absence (gap) of vegetation: a) pine seedling height, b) spruce seedling height, c) pine seedling biomass, d) spruce seedling biomass. Habitat types correspond to the temperature gradient: alpine (Alp), sub-alpine (Sub) and boreal (Bor). The precipitation gradient is indicated with numbers 1-4 from dry to wet (see Table 1). Bars show means ± SE. N=5

Figure 1



a)
b)
c)
d)
Gap
Intact
Emergence (# seedlings)
Establishment (# seedlings)
0
5
10
15
20
25
30
35
40
1
2
3
4
Alp
Sub
Bor
Habitat

Figure 2



a)
b)
c)
d)
Gap
Intact
Height (mm)
Aboveground biomass (g)
40
35
30
25
20
15
10
5
0
0,04
0,03
0,02
0,01
0
1 2 3 4 1 2 3 4 1 2 3 4
Alp
Sub
Bor
Habitat