

Seedling recruitment of *Larix decidua* and *Picea abies* along an elevational gradient across a treeline ecotone in the Swiss Alps



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Per te, Mami.

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Summary

This Master's thesis is part of the Global Treeline Range Expansion Experiment, a globally distributed collaborative project, aiming at testing the factors that limit seedling recruitment near treeline and contributing to a widely supported prediction of future treeline expansion in response to current climate warming. The study was conducted at three experimental sites along an elevational gradient at the research site Stillberg near Davos (Grisons, Switzerland): a subalpine Larch-Spruce forest, a dense short-grown alpine shrub and herb vegetation at the treeline, and an alpine meadow. In 2013, a full factorial experiment has been established at each site with randomly assigned experimental plots. On half of the plots, seeds from low and high elevation provenances of two conifer species, *Larix decidua* and *Picea abies*, were seeded in two consecutive years (2013 and 2014). Furthermore, a substrate treatment (soil surface scarification) and a post-dispersal seed and seedling predator exclosure treatment (cages) were applied on half of the plots. Seedling recruitment was assessed by measuring germination, survival and growth. Seedlings were measured in October 2013 and four times from June to September 2014. Germination and survival were analysed with generalized linear mixed models and growth with linear mixed models.

In this treeline ecotone, seedling recruitment was influenced by different site conditions. At the treeline and alpine site, recruitment occurred, whereas at the forest site almost no seeds germinated. The lack of recruitment at the forest site was mainly due to the inhibiting effect of the understorey vegetation with strongly reduced light availability at the soil surface. Seed source was considerably limiting, as no natural recruitment was found without seeding at any of the sites. Bare ground facilitated recruitment by reducing the competing effect of vegetation, indicating substrate limitation, especially at the treeline site. Other factors slightly influenced recruitment, such as predation, seed species and provenance, and interannual variation. Although seed source and substrate limitations are determining the early seedling stages in this treeline ecotone, also other factors might become important in later tree life stages and contribute to future treeline expansion in response to climate change.

Riassunto

Questa tesi di Master è parte del Global Treeline Expansion Experiment, un progetto collaborativo distribuito in tutto il mondo, il cui scopo è testare i fattori che limitano la sementazione in prossimità del limite del bosco e contribuire a una più precisa previsione del suo avanzamento in risposta al cambiamento climatico in corso. Lo studio è stato condotto lungo un gradiente altitudinale presso il sito di ricerca svizzero Stillberg, vicino a Davos nel Canton Grigioni, in tre stazioni sperimentali: un bosco subalpino di larici e pecci, una densa vegetazione di basse erbe e arbusti al limite degli alberi, e un prato alpino. L'esperimento fattoriale completo è iniziato nel 2013 e per ogni stazione sono state assegnate casualmente delle parcelle. In metà di esse sono stati seminati, in due anni consecutivi (2013 e 2014), semi provenienti da basse e alte quote di due specie di conifere, *Larix decidua* e *Picea abies*, e nell'altra metà non si è eseguita nessuna semina. Inoltre nelle parcelle o è stato applicato un trattamento del substrato (eliminazione della superficie), o/e l'esclusione di predatori di semi e di semenzali (cestini), nelle diverse combinazioni. La sementazione e la sopravvivenza sono state analizzate con modelli misti lineari generalizzati e la crescita con modelli misti lineari.

La sementazione è stata influenzata dalle diverse condizioni delle tre stazioni. Al limite degli alberi e nel prato alpino la sementazione è avvenuta, mentre nella stazione del bosco quasi nessun seme ha germinato. La mancata sementazione nel bosco era dovuta all'effetto inibitorio della vegetazione del sottobosco con una disponibilità di luce molto ridotta sulla superficie del terreno. Nelle parcelle non seminate, si è osservata una mancata sementazione naturale in ciascuna delle tre stazioni; indicando una chiara limitazione dovuta alla mancanza di fonte di semi. La terra nuda ha facilitato la sementazione riducendo la concorrenza dello strato erbaceo e arbustivo; questo dimostra un'evidente limitazione del substrato, specialmente nella stazione al limite degli alberi. Gli altri fattori, come la predazione, la specie e la provenienza dei semi, e la variazione annuale, hanno influenzato leggermente la sementazione. Sebbene la fonte di semi e il substrato germinativo siano due fattori determinanti per la sementazione, anche altri fattori potrebbero diventare importanti in stadi successivi delle rinnovazione (attecchimento e crescita) e contribuire a un futuro avanzamento del limite del bosco nel contesto del cambiamento climatico.

Zusammenfassung

Diese Masterarbeit ist Teil des Global Treeline Range Expansion Experiments. Ein weltweites Kooperationsprojekt mit dem Ziel die Faktoren zu testen, welche die Ansamung der Keimlinge an der Waldgrenze limitieren und zu einer besser unterstützten Vorhersage der künftigen Ausdehnung der Waldgrenze, als Folge der Klimaerwärmung, beizutragen. Diese Arbeit wurde an drei experimentellen Standorten entlang eines Höhengradienten in der Versuchsfläche Stillberg in der Nähe von Davos (Graubünden, Schweiz) durchgeführt: in einem subalpinen Lärchen-Fichtenwald, einer dichten alpinen Kraut- und Strauchvegetation an der Baumgrenze, und in einem alpinen Rasen. 2013 wurde ein faktorielles Experiment an jedem Standort mit willkürlich zugewiesenen experimentellen Plots etabliert. Auf der Hälfte der Plots wurden Samen von hohen und tiefen Höhenlagen von zwei Nadelbaumarten, *Larix decidua* und *Picea abies*, in zwei aufeinanderfolgenden Jahren ausgesät (2013 und 2014). Weiter wurden eine Substratbehandlung (Schürfung der Bodenoberfläche) und eine Behandlung mit Ausgrenzung von Samen- und Keimlingherbivoren (Körbchen) auf der Hälfte der Plots angelegt. Die Ansamung wurde im Oktober 2013 und vier Mal zwischen Juni und September 2014 aufgenommen. Keimung und Überleben wurden mit generalisierten linearen gemischten Modellen und Wachstum mit linearen gemischten Modellen analysiert.

In diesem Waldgrenzen-Ökoton wurde die Ansamung durch die verschiedenen Standortbedingungen beeinflusst. An der Baumgrenze und am alpinen Standort hat die Ansamung erfolgt, während im Wald fast kein Samen gekeimt hat. Die fehlende Keimung im Waldstandort ist auf die hemmende Wirkung der Bodenvegetation und die damit verbundene starke reduzierte Lichteinstrahlung an der Bodenoberfläche zurückzuführen. Die Samenquelle war deutlich limitierend mit keiner natürlichen Ansamung ohne Aussaat an allen drei Standorten. Freiliegender Boden hat die Ansamung erleichtert durch reduzierte Konkurrenzvegetation, was auf Substratlimitierung, besonders am Standort der Baumgrenze, hindeutet. Obwohl Limitierungen durch Samenquelle und Substrat bestimmend für die Ansamung sind, können andere Faktoren, wie Frass, Samenherkunft, und interannuelle Variabilität, in späteren Lebensphasen der Bäume entscheidend werden und zu einer künftigen Ausdehnung der Waldgrenze im Zusammenhang mit dem Klimawandel beitragen.

1. Introduction

An increase in global mean temperature of 0.7°C has been observed over the last century and further warming (of up to 4°C) is projected for the future (IPCC, 2013). Since ecosystems at high latitudes and at high elevations are often temperature limited, they are particularly susceptible to the changing climate. Many limits of plant species ranges and of vegetation zones are determined by temperature. Therefore, it is predicted that these range limits will shift with the on-going global warming (Lenoir et al., 2008) and many examples of shifting ranges as well as increased plant species diversity on alpine summits have already been described (Engler et al., 2011; Frei et al., 2010). Similarly, it has been demonstrated that treelines have shifted north- and upwards (Devi et al., 2008; Esper and Schweingruber, 2004; Kullman, 2002; Moiseev and Shiyatov, 2003) and, in the further support, dendrochronological studies showed increased tree growth during recent decades (Esper et al., 2002; Paulsen et al., 2000).

1.1. Treeline definition and types

The treeline ecotone is the transition zone where trees reach their (upper or poleward) distribution limit. It is one of the most obvious biogeographical range limit and is a dynamic boundary that has been shifting repeatedly for 10'000ds of years (Körner, 2012). Treeline is a phenomenon that occurs in different regions of the world and in different forms (Holtmeier, 2009). Although these forms are a continuum, four treeline types are commonly classified: diffuse, abrupt, island and krummholz (Harsch and Bader, 2011). Whether the treeline is a sharp line or a transition zone stretched along several meters depends on the scale considered (Körner, 2012). For many years, treelines have fascinated humans who tried to clarify the reasons for treeline formation and position (Malanson et al., 2011).

1.2. Treeline limiting factors

Different types of treelines are limited by different factors (Harsch and Bader, 2011). Important limiting factors include climatic conditions (e.g. average- and extreme temperatures, precipitation, duration of snow cover), site conditions (substrate, competition by other vegetation), herbivores and seed sources (distance to nearest seed trees and provenances of seeds) (Harsch and Bader, 2011). The natural treeline position is mainly determined by temperature (Körner, 2012). Globally, the treeline forms at an elevation where the mean

growing season temperature is 5 – 7°C (Körner and Paulsen 2004; Körner 2012). This relatively narrow temperature range is the lower limit for tree growth, below this limit the assimilates of the photosynthesis are not stored (Körner and Paulsen, 2004). Thus, under climate warming, the treeline position will no longer be in equilibrium with climate and therefore, will have a tendency to shift, aiming at a new equilibrium. However, a certain time is required to allow for a treeline shift, because: a) a good seed year has to be followed by favourable years for seedling establishment to allow (successful) recruitment; b) a seedling above treeline needs time to grow and to become a sapling and then an adult tree; c) the short-grown alpine shrub and herb vegetation may profit as well from milder climatic conditions and might limit tree seedling recruitment through competition; d) increasing mean temperature represents also changes in winter temperature that are hardly relevant for tree growth. As a consequence of these conditions, shifts of treeline position can lag behind climatic changes by some decades (Körner, 2012).

Climate change has already contributed to treeline shifts in the past and is strongly assumed to have an even stronger influence in the future (Körner, 2012); however, the effect of future climate change is still controversial (Körner, 2012). Global warming related to climate change will probably affect regions at high altitudes and latitudes more strongly, because heat deficiency characterises the vegetation in these regions, which slows down physiological processes (Harsch et al., 2009). Thus, even a slight increase in temperature can induce treeline advances to a higher altitudes and latitudes (Holtmeier and Broll, 2005).

1.3. Seedling recruitment

Seeds of all conifer species are of a similar morphological structure. They are winged, with a micropyle at the opposite end of the wing and a coat. Inside the coat, the embryo with a radicle is embedded in the female gametophytic tissue (Powell, 2009). Seeds of most conifers, including *Larix decidua* and *Picea abies*, are anemochorous. They are dispersed over short or long distances by wind (Williams, 2009).

Seedling recruitment consists of seed germination, survival and growth of seedlings (Leck et al., 2008) and is the most vulnerable phase in the life of trees (Smith et al., 2009). The definition for ‘seedling’ of a tree species varies in the literature. In this thesis, an individual of a tree forming species is referred to as seedling in the first few years from germination, when it is commonly smaller than 15 cm (adapted from Körner (2012)).

As seedling growth consists of dry matter accumulation, seedlings need to form new tissue from cells produced by the meristem. Root and shoot elongation occur only above a certain temperature limit, which lies between 4 and 7°C, but is usually around 5°C (Körner, 2012). A lack of suitable warm conditions may lead to seedling mortality. Survival of the first winter is a crucial challenge for seedlings, as less than 5% -20% of in situ sown seeds survive (Castanha et al., 2012; Germino et al., 2002; Körner, 2012). Transplanted seedlings have a slightly higher survival rate: on average one third of the seedlings survive the first winter (Barbeito et al., 2012; Munier et al., 2010). In addition, two other important causes of mortality are predation and desiccation. Minor causes are fungal attack, physical damage, competition among seedlings, and competition with the alpine shrub and herb vegetation (Leck et al., 2008).

Tree seedlings are of relatively small stature and nested among other plants or boulders. Therefore, they experience a similar microclimate as other mountain plants with near surface temperatures that are significantly higher than air temperatures several meters above ground (Körner, 2012; Körner and Paulsen, 2004). Profiting from such enhanced temperatures, tree seedlings may exist several hundred metres above the treeline (Körner, 2012; Lenoir et al., 2009; Zurbriggen et al., 2013).

However, climate is not the only driver determining recruitment. Non-climatic factors are also important for tree seedling recruitment with seed limitation being one of the most important (Brown et al., 2014). Seed limitation can be caused by limitation of seed source, of seed dispersion, and by seed predation (Leck et al., 2008). Seed source limitation can be due to lower seed production, i.e. small seed crops (Körner, 2012; Trant and Hermanutz, 2014). Conifers tend to produce small seed crops (or even no seeds) for a certain number of years and then, suddenly in one year, they produce a large seed crop in a wide area, a phenomenon named masting (Roland et al., 2014). Besides the rarity of seed years, further effects on seed source should be considered: seed production close to the treeline is lower than in forests, namely seed production per cone usually decreases with approaching the treeline, and an exceptionally large seed crop does not always correspond to a large number of viable seeds (Brown et al., 2014). Seed source limitation, mainly due to a lack of viable seeds, i.e. empty, seeds rather than limited seed production, is considered fundamental for upwards colonisation (Brown and Vellend, 2014) and may impede a treeline shift in pace with climate warming. Given that seeds are produced and viable, they have to be dispersed to allow recruitment, but

seed dispersal decreases with distance from the mother tree (Brown and Zobel, 1988) and is mostly constrained within 100 m (González de Andrés et al., 2014). Predation of seeds can occur before and after dispersal. Pre-dispersal seed predation takes place when seeds, still in cones, are eaten by animals, mainly by squirrels and birds, and can affect up to half of all seeds (Peters et al., 2003). Post-dispersal seed predation takes place when seeds are successfully dispersed, but then eaten by animals before they can germinate. Post-dispersal seed predation can be divided in predation by invertebrates, small mammals, large mammals, and birds. All forms of seed and seedling predation by granivores and herbivores, respectively, generally might be a critical bottleneck constraining germination and its exclusion may enhance recruitment (Brown et al., 2014; Brown and Vellend, 2014; Cairns et al., 2007; Cairns and Moen, 2004; Castro et al., 1999; Côte et al., 2005; Côté et al., 2003; Itô and Hino, 2004; Ravolainen et al., 2011). Furthermore, seed origin may influence recruitment success, with seeds of a given provenance or species being better adapted to particular site conditions (Leck et al., 2008).

Moreover, suitable substrate is necessary for treeline expansion (Brown and Vellend, 2014). Removing the dense short-grown alpine shrub and herb vegetation (a treatment hereafter referred to as scarification) can strongly enhance earliest life stages of trees, as it competes with seedlings and might be even more important than climate limitation (Barbeito et al., 2012; Körner, 2012). Additional treeline limiting factors can be: tissue loss through mechanical damage, soil pathogens, insect outbreak cycles, negative carbon balance, slow growth, and land use change (Brown and Vellend, 2014; Körner, 2012).

1.4. Global Treeline Expansion Experiment

As successful recruitment is a crucial part of treeline expansion under warming climate, it is important to extend our knowledge about seedling recruitment and some studies have already been conducted (Holtmeier, 2009; Munier et al., 2010). While many studies have focussed on adult trees, less is known so far about seedling recruitment (Bansal and Germino, 2010; Holtmeier, 2009; Maher et al., 2005; Smith et al., 2003) and particularly the non-climatic factors influencing it (Brown et al., 2013). To address these questions the Global Treeline Range Expansion Experiment (hereafter referred to as G-TREE) was started in 2013 as a global initiative for testing the factors influencing seedling recruitment at and near the treeline. The general objectives of G-TREE are to determine where and under what circumstances treeline expansion can occur and to permit predictions about future treeline

expansion (Brown et al., 2013). Thus, the key aim of G-TREE is to disentangle seed limitations from substrate limitation on treeline recruitment. To this purpose a straightforward experimental design with seeding and substrate-altering treatments has been implemented on experimental sites in alpine and Arctic treeline ecotones distributed worldwide. All seeding trials follow an identical field protocol (Brown et al., 2013) and experimental sites have so far been established in Australia, Canada, France, Norway, Scotland, Russia, Spain, Sweden, Switzerland, the United States, and Venezuela. These sites allow a broad geographic coverage of both latitudinal and altitudinal treelines. In the Swiss Alps, a G-TREE site was set up in the Dischma valley near Davos in the vicinity of the Stillberg treeline research site. The evaluation of the first two years of this experiment is the topic of this Master's thesis. Thus, the following experimental description applies to both, the whole G-TREE Experiment and this Master's thesis.

Artificial seeding allows identifying seed source limitation for colonisation of populations beyond the range edge, whereas a substrate treatment allows assessing suitability of seed beds following disturbance. Additional aims are to test effects of site, species, seed origin, herbivory, and impacts of annual variation on treeline recruitment. The experiment was conducted at three sites across the treeline ecotone: below the (current) treeline in forest, at the treeline, and above the treeline in the alpine zone. Seeds of the two species *Larix decidua* and *Picea abies* were used in the seeding treatment to determine species differences in recruitment, with the former species having a pioneer character and a higher altitudinal distribution limit than the latter (Brändli, 1998). Of each species, two provenances of regional seeds were sown: one from near the treeline (species range edge – i.e. high elevation) and the other from a fully forested area (species range interior – i.e. low elevation). Effects of post-dispersal seed and seedling predation were investigated by protecting half of the experimental plots with predation exclosures. The seeding was applied in two consecutive years: 2013 and 2014.

In this Master's thesis the following specific research questions are addressed:

1. Research question 1: Is seedling recruitment site dependent?
2. Research question 2: Is seed source a limiting factor in this treeline ecotone?
3. Research question 3: Does post-dispersal seed and seedling predation influence seedling recruitment?

4. Research question 4: Are there species and provenance differences in seedling recruitment?
5. Research question 5: Does substrate limit seedling recruitment?
6. Research question 6: Does interannual variability influence seedling recruitment?

2. Material and Methods

2.1. Study site

The Swiss G-TREE experiment is located in the treeline ecotone ranging from 1900 – 2400 m a.s.l. (below and above treeline) of the North-Eastern slope of the Dischma valley, community Davos, canton Grisons, Switzerland. Three sites studied are along an elevational gradient at the research site Stillberg (Figure 2.1).

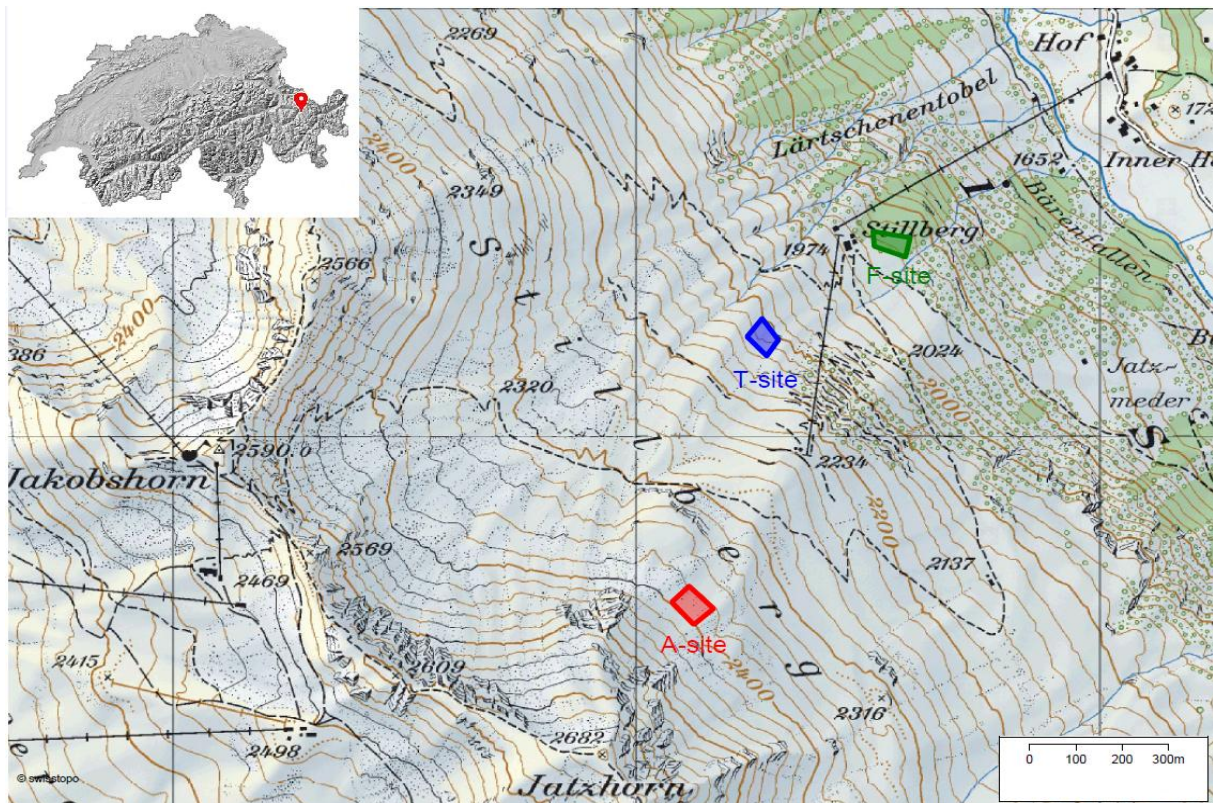


Figure 2.1: Location of the study site. The red polygon represents the Alpine site at 2400 m a.s.l., the blue polygon represents the Treeline site at 2100 m a.s.l., and the green polygon represents the Forest site at 1900 m a.s.l. © Bundesamt für Landestopographie swisstopo, 2007 (www.map.geo.admin.ch).

The lowest site (hereafter referred to as forest site and F-site, respectively) lies in a subalpine Larch-Spruce forest (*Larici-Picetum*) with dwarf shrubs (Zurbriggen et al., 2013). Compared to the other two sites, the forest site has on average the lowest vegetation cover and the highest litter cover (29.0 ± 17.0 % and 76.3 ± 15.6 %, respectively) (Appendix I). At the forest site, few competing vegetation species with large leaves like *Adenostyles sp.*, *Achillea macrophylla*, and *Cicerbita alpina* make up the understory (Appendix II). Under snow cover in winter, soil temperature at 5 cm depth remained constant and was slightly higher than the expected 0°C at the soil surface (Appendix 0). The middle site (hereafter referred to as

treeline site and T-site, respectively) lies within dense short-grown alpine shrub and herb vegetation in a long-term alpine treeline research site (Barbeito et al., 2012). Compared to the other two sites, the treeline site has on average the lowest rock and mineral soil covers (0.1 ± 0.7 % and 0.4 ± 2.2 %, respectively) and the highest moss cover (52.0 ± 27.6 %) (Appendix I). In both 2013 and 2014, both forest and treeline sites present minor oscillations over time than the alpine site (Appendix III). The highest site (hereafter referred to as alpine site and A-site, respectively) lies in an alpine meadow. Compared to the other two sites, the alpine site has the highest vegetation cover (63.9 ± 12.3 %) and the highest rock cover (10.7 ± 8.7 %) (Appendix I). Assuming that temperature stays constant as long as the snow cover soil, the snow last at the alpine site longer than at the treeline and forest sites; as consequence the vegetation period starts later at the alpine site and is thus shorter. The highest temperature over the whole period June 2013 – September 2014 was recorded in July 2013 at the A-site. In July 2013 temperature stays above 8°C and in August 2014 above 7°C at all three sites. At the beginning of July 2013 temperature fall twice below 5°C and in September below 4°C August 2014 below 6°C at the alpine site (Appendix III). On average, the alpine site was the site with the lowest soil temperature (Appendix 0).

The meteorological station Stillberg, at 2090 m a.s.l., recorded a mean annual air temperature of 2.0°C and an annual precipitation sum of 1150 mm over the period 1975-2005. The growing season lasts from the End of May until the End of September (Rixen et al., 2012). The snow cover lasts from mid of October to the end of May, although snowfall can occur throughout the year (Walder, 1983). In 1975, an afforestation program at the Stillberg (Bebi et al., 2009) has contributed to a remarkable upward shift of the treeline position, as the trees were planted up to an elevation of 2200 m a.s.l.. Currently, the anthropogenic treeline lies at 2100 m a.s.l. (Barbeito et al., 2012). Thus, the forest site is located ca. 200 m below and the alpine site 300 m above the current treeline (Table 2.1).

Table 2.1: Position, elevation and mean annual temperature at the forest, treeline, and alpine G-TREE site.

G-TREE site	longitude [Swiss Grid]	latitude [Swiss Grid]	altitude [m a.s.l.]	mean soil annual temperature [$^\circ\text{C}$]
forest	2785500	1183500	1930	5.7 ± 4.0
treeline	2785340	1183220	2100	5.4 ± 3.7
alpine	2785090	1182570	2390	5.3 ± 5.2

2.2. Ecology of the analysed tree species

The G-TREE experiment at Stillberg was conducted with two species: *Larix decidua* and *Picea abies*. In this subchapter the ecology of both study species are described.

2.2.1. *Larix decidua* MILL.

Larix decidua MILL. (hereafter referred to as *L. decidua* or larch, respectively) is most common in four fragmented regions across Europe. The subarea with the most extended abundance is located in the Alps, whereas *L. decidua* only occurs in small regions of the Carpathians, Sudetes and Poland (Figure 2.2). In the Western Alps, *L. decidua* grows in the subalpine and alpine zone within an elevation range of 1'300 and 2'400 m a.s.l., whereas in the Eastern Alps its range also extends to the sub montane zone with 300 m a.s.l. as lower and 1'600 m a.s.l. as upper range limit. *L. decidua* forms mixed stands with Norway Spruce, Swiss stone pine, European silver fir and European beech depending on the altitude but sometimes occur as well in pure stands (Schütt et al., 2006).

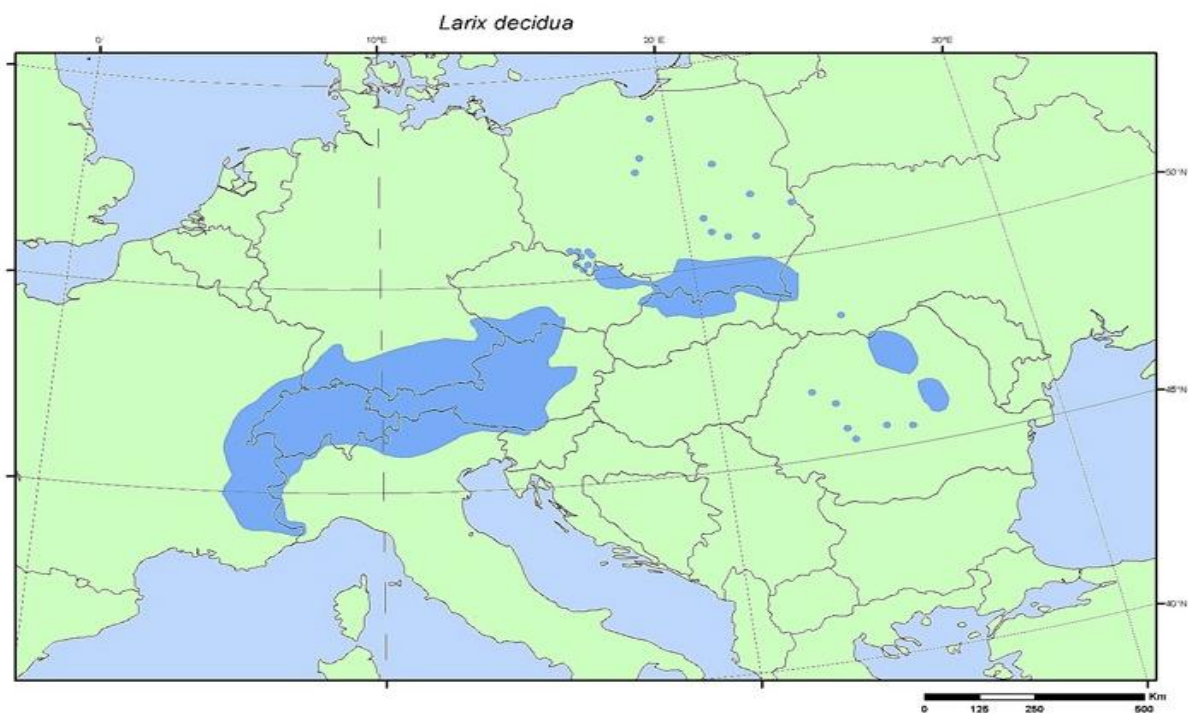


Figure 2.2: Distribution map of European Larch (*L. decidua*) (Source: EUFORGEN).¹

¹ Modified from European Forest Genetic Resource Programme <http://www.euforgen.org> (14th January 2015).

L. decidua is a light-demanding tree species, which does not tolerate lateral and direct shading and thus suffers from tree competition, especially in closed stands. Due to its pioneer character, this tree species colonises disturbed soils surfaces and open land (Brändli, 1998; Matras and Pâques, 2008) created by avalanches, mudflows, forest fires, or livestock farming (Schütt et al., 2006). Its habitat preferences is nutrient-rich, rather dry soil with a high water retention capacity, while the pH is not relevant as it can grow on both acidic and basic soil (Schütt et al., 1984). *L. decidua* grows in regions of continental climate (Schütt et al., 2006). *L. decidua* is the only defoliating European conifer species. Needles are arranged in clusters of 40 to 50 on short shoots, while they are singly arranged on long shoots. The flowering period is at the beginning of spring (March/April), before new needles appear. Female flowers are red-pink, male flowers are greenish-yellow (Schütt et al., 1984). This tree species is anemochorous, meaning that pollen is dispersed by wind. The ovate, brown, and smaller than 4 cm cones of *L. decidua* contain on average 40 to 60 seed scales, respectively seeds, and can stay on the tree for two to three years after seed dispersal. The winged seeds are 3 to 5 mm long and triangular. Sexual reproduction starts at the age of 15 years, although with the production of mainly not viable seeds. In closed stands at high elevation, trees produce seeds only mainly from the age of 30 years. The process of seed production is not annual, but takes place every seven to ten years at high elevation and every three to four years at low elevation. More than half of the produced seeds can be empty (without embryo) and not viable (Matras and Pâques, 2008; Professur für Waldbau und Professur für Forstschutz & Dendrologie der ETHZ, 2002). Cones of mid- and high-region of the crown present more viable seeds and the highest quantity of cones belongs to the dominant trees in a stand. Seeds ripen in seven to eight months, but although they are mature in fall (October/November) they are dispersed by wind, rodents and birds only in the following spring with the opening of the seed scales. Because of the reduced opening of the seed scales, a portion of seeds remain in the cones (Schütt et al., 2006). Seeds risk to be eaten by birds and insects (Brown and Vellend, 2014), when still in the cones or on the soil surface and they may be affected by pathogens and insects. Seeds remain viable for a period up to ten years. Under suitable conditions germination is initiated, the seeds do not need to be covered by soil (Schütt et al., 2006). Germination can occur already three days after sowing (Trevisan et al., 1990). After three to four weeks, about half of the seeds germinate; two weeks later all the viable seeds germinated (Schütt et al., 2006). The embryo is equipped with relatively large amount of reserves, but they are quickly used (within two weeks completely depleted) (Trevisan et al., 1990).

Cotyledons carry out photosynthesis already one week after germination, although they are still enclosed in the seed tissues and seed reserves last for another week (Schütt et al., 2006; Trevisan et al., 1990). Seedlings of *L. decidua* have on average six cotyledons, which die and fall after the first autumn with the first leaves. During the following vegetation period, new spiral-arranged needles are formed (Schütt et al., 2006).

2.1.1 *Picea abies* (L.) KARST.

The natural distribution of *P. abies* (hereafter referred to as *P. abies* or spruce, respectively) ranges from the Arctic Circle to the mountainous regions of Central and Eastern Europe (Schütt et al., 1984). The most extended region covers large parts of Scandinavia, the east coast of the Baltic Sea and Russia. Smaller and more fragmented distributions in Central Europe, mainly in the Alps and Carpathians, as well as spots in the Balkan region complement the natural range of this tree species (Figure 2.3). *P. abies* does not occur exclusively within its natural (distribution) range, because it is also planted and cultivated in West Europe, North America, and Japan (Schütt et al., 2006). The elevational distribution of *P. abies* ranges from mountain and sub alpine level to lowlands.

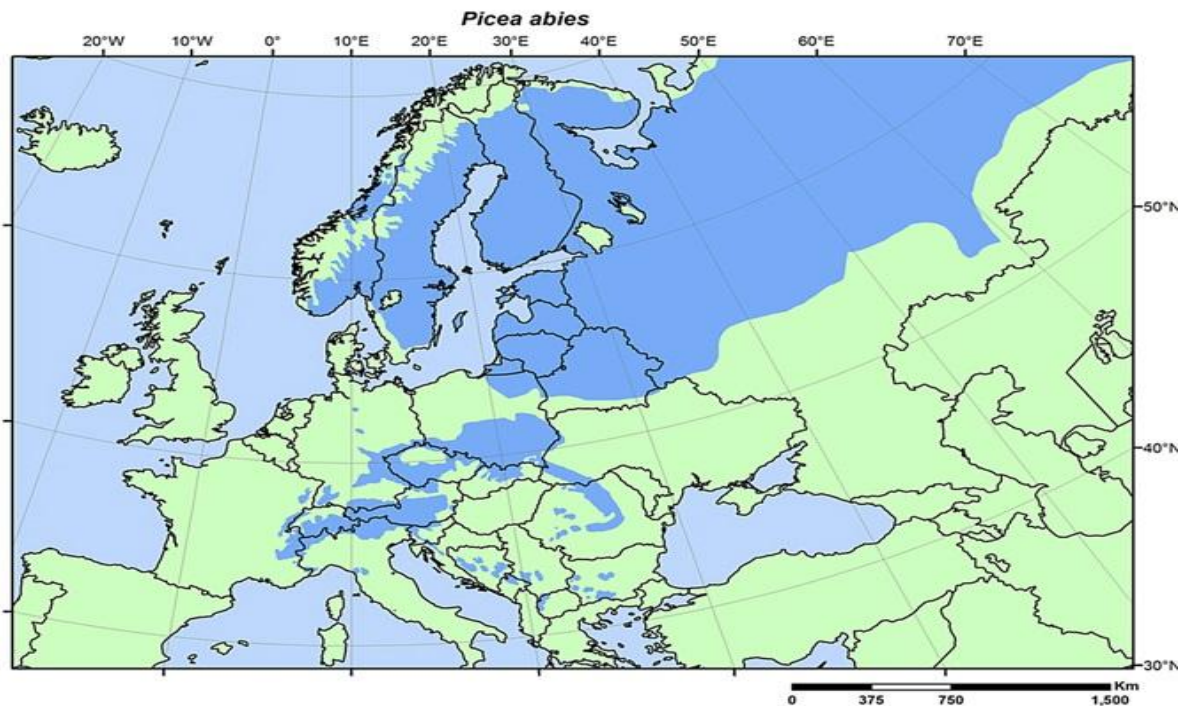


Figure 2.3: Distribution map of Norway spruce (*P. abies*) (Source: EUFORGEN).²

² Modified from European Forest Genetic Resource Programme <http://www.euforgen.org> (14th January 2015).

P. abies mainly occurs in continental climate (Schütt et al., 2006). It grows both in open and closed stands mixed with other conifers as well as deciduous species. While shady conditions are well tolerated by juvenile trees (Skrøppa, 2003), adult trees show a reduced shading tolerance (Professur für Waldbau und Professur für Forstschutz & Dendrologie der ETHZ, 2002). Moist soil and humid air conditions provide optimal growth conditions (Professur für Waldbau und Professur für Forstschutz & Dendrologie der ETHZ, 2002). Concerning soils, *P. abies* occurs in acidic fresh clay with pH between 4 and 5 (Schütt et al., 1984). Needles of *P. abies* are long-living (five to seven years at low elevation and up to 12 years at high elevation) and of variable length between 1 and two cm, depending on climate, habitat, population, crown and shoot region, and tree age. *P. abies* is wind-pollinated. The pollination occurs between neighbour trees, as well as with more distant trees. Seed dispersal mainly occurs in proximity of mother trees (Skrøppa, 2003). This monoecious species has red to yellow male flowers and red to green female flowers, which flower between April and June together with the formation of new needles (Professur für Waldbau und Professur für Forstschutz & Dendrologie der ETHZ, 2002). The brown and pendent cones are 8 to 16 cm long at low elevation and decrease with altitude, reaching a size of less than 8 cm at timberline. The seed scales can be up to 2.5 cm long and 1.8 cm large. Cone maturation takes place between September and November, and seed dispersal can last up to April (Schütt et al., 2006). Trees start to produce seeds at the age of 30-50 years in open stands and at the age of 60-70 years in closed stands. Seed production cycles occur only every seven to eight years at high elevation and every three to four year at low elevation (Professur für Waldbau und Professur für Forstschutz & Dendrologie der ETHZ, 2002). Up to 95% of seeds per cone are viable and remain viable for three to four years. Seeds of *P. abies* can be eaten by birds such as spotted woodpecker and by small mammals such as squirrel and bank vole (Schütt et al., 2006). In addition, they are threatened by insects and fungi. The former like *Laspeyresia strobilella* L. and *Lasiomma anthracina* can eat seeds while the latter can cause a reduction of seed viability by affecting cones (Schütt et al., 2006). Under suitable conditions, seeds begin to germinate after two to five weeks. Young seedlings have seven to nine cotyledons (Schütt et al., 2006).

2.3. Data collection

2.3.1. Experimental design

The experimental design consists of three sites, two seeding treatments, two substrate treatments, two species, two elevation provenances, two years of seeding, two predator

exclosure treatments, and five plot replicates per site resulting in a total of 60 plots and 960 subplots (Table 2.2, Appendix IV).

Table 2.2: Variables describing the experimental design.

factor name	factor name used in R	levels of factors
site	site	forest, treeline, and alpine site
plot*	plot-number	101 to 161
seeding treatment	seeded	seeded or unseeded
substrate treatment	scarified	scarified or unscarified
species	species	<i>L. decidua</i> or <i>P. abies</i>
provenance	provenance	low or high elevation provenance
year of seeding	year	2013 or 2014
predator exclosure treatment	cage	with cage or without cage

*Please, notice that plot is not a treatment, but a random factor.

In summer 2013, three experimental sites of the G-TREE experiment were set up at the Stillberg (Figure 2.1). At each site, five plots replicates of four seed source and substrate treatment combinations were implemented resulting in a total of 20 randomly assigned 45 cm wide and 2.24 m long plots per site. These treatment combinations were applied at site level and consist of: 1) seeded (seeded and unscarified), 2) scarified (scarified and unseeded), 3) seeded and scarified, and 4) full control (unseeded and unscarified) plots. The scarification treatment was applied using a hand-cultivator by removing surface plant litter, as well as mosses and lichens, but leaving vascular plants rooted in the soil. For the seeding treatment, 12'000 seeds per species and provenance were sown, resulting in a total of 48'000 seeds per application year. Seeds were equally spread (across the respective subplot). Each plot consisted of 16 subplots containing different seed sources and years of implementation (Figure 2.4). Subplots are 22.5 cm wide and 28 cm long.

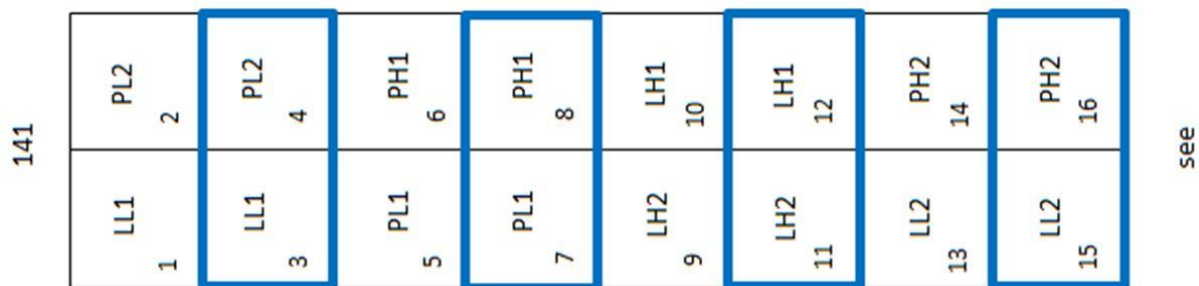


Figure 2.4: Plot set up description using the example of “seeded” A-Site plot 141. The first letter indicates the tree species, the second letter the provenance and the number refers to the year of seeding; e.g. PL2: *P. abies*, low elevation provenance, seeded in the second year (2014). In blue, subplots with cages (post-dispersal seed and seedling predator exclosures). Please, consider that the picture has been rotated 90° left, due to representation reasons.

In summer 2013, four different types of seeds were sown in half of the plots (only seeded and seeded and scarified plots): *L. decidua* from low elevation provenance, *L. decidua* from high elevation provenance, *P. abies* with low elevation provenance, and *P. abies* with high elevation provenance (Table 2.3).

Table 2.3: Overview of the provenances of the sown seeds, including abbreviation (seed code), species, provenance, elevation of seed origin location, location of seed origin, year of collection, exposition of seed origin, and thousand grain weight (TGW).

seed code	species	provenance	elevation of seed origin [m a.s.l.]	location of seed origin	year of collection	exposition of seed origin	TGW [g]
LL	<i>L. decidua</i>	low	1350	Wiesen	1995	SW	8.5
LH	<i>L. decidua</i>	high	1760	Celerina	1970	N	7.3
PL	<i>P. abies</i>	low	1000	Küblis	1985	N	6.8
PH	<i>P. abies</i>	high	1960	Sertig	1983	E	6.8

In 2014, the seeding procedure was implemented on the other half of the subplots, again with seeds of both species and provenances. For both years, seeds were obtained from the Swiss Federal Institute for Forest, Snow and Landscape Research WSL (hereafter referred to as WSL) in Birmensdorf, Switzerland, where they were stored at 5°C. In addition, half of the subplots per plot were covered by predator exclosures, in form of durable and stable metallic cages of 45 cm by 28 cm. A metal cage always covered two adjacent subplots (Figure 2.4). The cage is known to exclude the following predators: mice, ungulates, mountain hares, and birds, whereas burrowing animals, i.e. voles, are probably not prevented from entering (Schütz, 2013).

2.3.2. Seedling recruitment response variables

Germination, survival, and growth are the three seedling recruitment response variables measured and together describe recruitment of seedlings (Leck et al., 2008). In this experiment growth is represented by seedling height. The germination process was surveyed at the end of the first vegetation period (October 2013) and three times during the second vegetation period (July, August, and September 2014), resulting in a total of four surveys. Seeds were considered germinated and counted when the radicle was visible, i.e. seed coat penetration occurred. The winter survival of seedlings germinated from seeds sown in 2013 was assessed in June 2014, after snow melt, and again in July, August, and September 2014. Seedlings were considered still alive and counted when they presented green parts, i.e. photosynthetic activity. No distinction was made between dead seedlings, i.e. no green parts,

but still visible and seedlings that had disappeared because of snow, wind, predators, etc. In addition to counting germinated seeds and surviving seedlings, height of 10 randomly chosen seedlings per plots (when fewer seedlings than 10 then of each seedlings) was measured. Three height measurements were taken in July, August, and September 2014, together with the germination surveys. Two different heights were measured: a) the height from the soil surface to the shoot tip, b) the height from the soil surface to the tip of the longest needles for seeds germinated in 2013 and of the longest cotyledon for seeds germinated in 2014. Both heights were measured, because the shoot can elongate in case of light deficiency (Brang, 1995). In plots with predator exclosures, cages were removed to easily measure seedling height, and then placed again. For each plot, all observations regarding germination, survival, and growth were recorded on a separate field protocol (Appendix V).

2.4. Data compilation

A correction for seed viability was needed, as not all 200 sown seeds in each plot with seeding treatment were viable. The effective number of viable seeds may differ between species and provenances. Thus, this aspect should be considered for each recruitment response variable and model. The number of viable seeds can be estimated by viability tests. Seed viability was determined at the WSL in Birmensdorf. Viability was assessed by sowing seeds into Petri dishes containing agar and by incubating them at an appropriate temperature. The number of germinated seeds was checked till no germination occurred anymore. Then a cutting test was performed to control for empty seeds (Millenium Seed Bank, 2014). WSL-viability was assessed every two years since seed harvest providing constant viability values (A. Burkart, WSL, personal communication), giving a long term reliability of this viability. The viability, as well as the expected number of viable seeds for both years, is listed in Table 2.4.

Table 2.4: Overview of the amount of seeds sown per subplot, viability in percent and viable seeds per subplot.

seed code	sown seeds [#]	WSL-viability [%]	expected viable seeds [#]
LL	200	28	56
LH	200	11	22
PL	200	74	148
PH	200	61	122

Recruitment response variables had to be processed further in order to calculate the measures related to germination, survival, and growth processes. Data exploration was performed with the variables listed in Table 2.5.

Table 2.5: Seedling recruitment variables.

variable	abbreviation	unit	description
assessed in 2013 and 2014			
any germination	anygerm	factor	either 0 germination (no seeds germinated) or 1 germination (one or more seeds germinated)
no. of germinated seeds	germpos	#	total number of germinated seeds
no. of ungerminated seeds	germneg	#	total number of germinated seeds as difference between the expected viable seeds and germpos
percentage of germinated seeds	germpos-percent	%	percentage of germinated seeds, where the total number of expected viable seeds equals 100%
percentage of ungerminated seeds	germneg-percent	%	percentage of ungerminated seeds, as difference between 100% and germpos-percent
assessed in 2014			
any survival	anysurvival	factor	either 0 survival (no seedlings survived first winter) or 1 survival (one or more seedlings survived first winter)
no. of surviving seedlings	survivalpos	#	total number of surviving seedlings after first winter, corresponding to germpos in June 2014
no. of dead seedlings	survivalneg	#	total number of dead seedlings after first winter, as difference between germpos in October 2013 and germpos in June 2014
percentage of surviving seedlings	survivalpos-percent	%	percentage of surviving seedlings, where germpos in October 2013 equals 100%
percentage of dead seedlings	survivalneg-percent	%	percentage of dead seedlings, as difference between 100% and survivalpos-percent
any growth	anygrowth	factor	either 0 growth (no height increment) or 1 growth (height increment, independently from the number of seedlings)

2.5. Statistical analysis

Statistical analysis and visualization of data were performed with the software R (R for Windows, Version 3.1.0) (R Development Core Team, 2014), a program for statistical computing. All data was analysed with generalized linear mixed-effects models and linear mixed-effects models (hereafter referred to as GLMMs and LMMs, respectively) (Pinheiro and Bates, 2000). The GLMMs were fitted with the function *glmer* in the *lme4* package (Bates et al., 2014) and LMMs with the *lmer* function of the same package. GLMMs are modern statistical methods. The use of GLMMs in environmental sciences and ecology began only

recently (Zuur et al., 2012). Consequently, little literature is available about their use in these research areas (Zuur et al., 2009).

2.5.1. Random effects

Plot and two subplot structures were entered as random effects in the models in order to avoid the correlation within these units, which leads to pseudo-replication (Crawley, 2007; Zuur et al., 2009). The two subplot structures were subplot row and subplot pair. First, in the experimental design predator exclosure treatment was not fully randomized, because two adjacent subplots shared a metallic cage. These two subplots were correlated, for instance if a mouse would feed under one of the cages, would likely affect both subplots under this specific cage. A variable named “subplot-row” was introduced to handle this dependency. This variable groups the two horizontally adjacent subplots that share a cage (Figure 2.5). Second, as a consequence of the experimental design, two subplots with the same treatment combination (species, provenance and year of sowing) are always located next to each other, like a vertically orientated pair. Together they represent a split-subplot of which one half has the seed and seedling predator exclosure treatment (with cage) and the other half does not have it (without cage). Subplot-pair accounted for the high correlation within this pair. This new variable represents the vertically orientated pairs of subplots with the same species, provenance and sowing year combination whereof one subplot is covered with a cage and the other one is not (Figure 2.5).

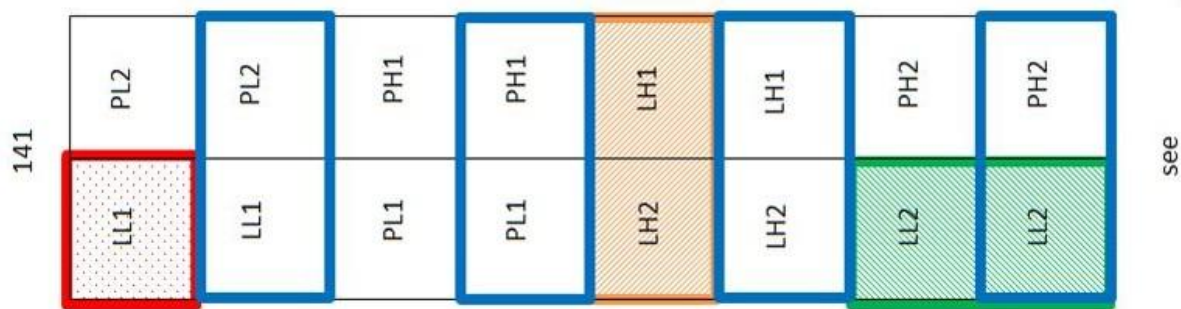


Figure 2.5: Example of subplot coding for plot 141 at the A-site with treatment “seeded”. Subplot represents the smallest unit in the experiment, where 200 seeds were sown (marked in red). In blue, pairs of subplots sharing a cage (seed and seedlings predator exclosure treatment). An example for subplot-row (horizontally paired subplots) is marked in orange. In green, subplot-pair (vertically paired subplots). Please, consider that the picture has been rotated 90° left, due to representation reasons.

2.5.2. GLMMs und LMMs Models for Recruitment Response Variables

Due to the presence of random effects, generalized linear models (GLMs) and linear models (LMs) were not applicable, leading to the use of generalized mixed models (GLMMs) and linear mixed models (LMMs) for data evaluation (Zuur et al., 2009).

The random effects describe the structure of the experimental design (e.g. difference among plots). Thus, variances of random effects were considered to determine the proportion of the total variance in the model that is explained by a given random effect. Significances of fixed effects were estimated by using likelihood ratio tests (hereafter referred to as LRTs) (Pinheiro and Bates, 2000). For the fixed effects, the significance level α was reduced from 5% to 1% (Appendix VI) because *P*-values from LRTs tend to be anti-conservative, i.e. more significant than in reality (Pinheiro and Bates, 2000). For the interactions of fixed effects, the *P*-values calculated from LRTs are considered to be neither conservative nor anti-conservative. Thus, the significance level α was kept at 5% (Appendix VI).

2.5.2.1. Part I: GLMMs for germination

The germination percentage represented as proportion data was analysed with the *glmer* function in the *lme4* package (version 1.1-7) and *binomial* distribution (link *logit*) in a GLMM. The proportion of germination occurred (germination positive) to not germinated seeds (germination negative) was used as the response variable in these models. Only plots with seeding treatment were evaluated, due to the fact that no seedlings were found on unseeded plots. For test purposes, a model with data from all three sites was fitted and then compared to the model with data only from alpine and treeline sites giving quite similar results (Appendix VII). Thus, the model with data from all three sites was preferred. The fitted GLMM-model can be compared with analyses of other G-TREE experiment worldwide (Brown, 2014).

The generalized linear mixed model, as well as the linear mixed models, fitted for Part I includes data of seeds sown in both 2013 and 2014. In 2013, seeds were sown approximately 1-1.5 months later than in 2014. Thus, the survey of October 2013 is comparable with the one of September 2014 because the germination span is similar between 2013 and 2014 (3.5-4 months). For fitting the full models, the following explanatory variables were chosen: site, cage, seed species, seed provenance, scarification, and year. Initially, a full model was fitted with all explanatory variables included as single fixed effect terms and as all two-way

interactions plus all three random effect terms (“subplot-row”, “subplot-pair”, and “plot-number”). The full model was reduced with the function *drop1* of the package *stats* by dropping each non-significant interaction at time. No single effect could be reduced, as all explanatory variables were in at least one significant interaction. After model reduction, the final model included all the significant fixed effects terms, all significant interactions and the random effect terms (Frei et al., 2014). The final reduced model for germination with all sites is the following:

```
mfinal_germ_glmer <- glmer(germpos, germneg) ~ site + cage +
species + provenance + scarified + year + (1 | subplot-row) + (1 |
subplot-pair) + (1 | plot-number) + site:scarified + site:year +
cage:provenance + cage:year + species:provenance +
provenance:year, family = binomial, control =
glmerControl(optimizer = "bobyqa"), data = gtree)
```

Both AIC and BIC values were reduced by fitting the model: 1502.2 and 1631.5 for the full model and 1484.5 and 1563.8 for the final reduced model (AIC and BIC, respectively). Likelihood ratio test (LRT) was performed to assess the significance of the fixed effect terms, which was represented by *P*-values from Chi-square statistic and was determined in three steps: 1) a new model was fitted without all interactions containing the chosen fixed effect term; 2) this new model was fitted without the chosen fixed effect term; 3) the two new models were compared using the function *anova* of the *stats* package.

2.5.2.2. Part II: GLMMs for survival

The generalized linear mixed model fitted for Part II includes only data of seeds sown in 2013, as the ones sown in 2014 had not experienced the first winter at the time of the data analysis yet. Solely data of the treeline and alpine sites was considered, since at the forest site only four seeds germinated in 2013 (Appendix VIII), of them none survived. To fit the full model, the following explanatory variables were chosen: site, cage, seed species, seed provenance, and scarification.

Similarly to Part I, generalized linear mixed model (GLMMs) in Part II was performed with *glmer* function in *lme4* package (version 1.1-7) and *binomial* distribution (link *logit*), reduced and evaluated according to Zuur et al. (2009). Analogously to the germination process, survival was analysed as proportion data: either survival occurred (survival positive) or not (survival negative). The final reduced model for survival with all sites is the following:

```
mfinal_survival_glmer <- glmer(cbind(survivalpos, survivalneg) ~  
site + species + provenance + scarified + (1 | subplot-row) + (1 |  
subplot-pair) + (1 | plot-number) + site:species +  
provenance:scarified, family = binomial, control =  
glmerControl(optimizer = "bobyqa"), data = gtree)
```

Both AIC and BIC values were reduced by model reduction: 293.9 and 348.8 for the full model and 284.6 and 313.4 for the final reduced model (AIC and BIC, respectively).

2.5.2.3. Part III: LMMs for growth

In Part III, linear mixed models (LMMs) were fitted for all sites and for only the treeline and the alpine sites (excluding forest site). Results were similar (Appendix VII) and thus, the model without forest site was kept, due to the exiguous number of seedlings growing at the forest site (Appendix VIII). As growth measure seedling total height in September 2014 was preferred to the growth rate of the period July 2014 to September 2014, because the few observations in July precluded the computation of the growth rate. To fit the full model, the following explanatory variables were chosen: site, cage, seed species, seed provenance, scarification, and year. Model reduction and evaluation was performed analogously to Part I and Part II, according to Zuur et al. (2009). The final reduced model for growth with all sites was the following:

```
mfinal_growth_lmer <- lmer(September_tl_mean ~ site + cage +  
provenance + scarified + (1 | subplot-row) + (1 | subplot-pair) +  
(1 | plot-number) + cage:scarified, REML=FALSE, data = gtree)
```

Both AIC and BIC values were reduced by fitting the model: 203.3 and 300.5 for the full model and 186.7 and 220.1 for the final reduced model (AIC and BIC, respectively).

3. Results

This chapter is structured in three subchapters: germination of seeds, winter survival of one-year-old seedlings, and growth of seedlings. Each subchapter is divided in two sections. The first section focuses on the model results for germination, with data of all three sites, and for winter survival and growth, with data only of alpine and treeline sites (Table 3.1). Although the fitted model for germination included data from all sites, the exiguous number of germinated seeds at the forest site has to be considered (only 11 germinated seeds in total, Appendix VIII). In 2013, none of the *L. decidua* seeds and only four *P. abies* seeds germinated at the forest site (Appendix VIII). None of the seedlings survived the first winter. Thus, winter survival at the forest site was not analysed. Analogously, the growth analysis considered only the treeline and alpine sites.

The model factors are presented in the same sequence as the hypotheses: site, predator exclosures (cage), species, provenance, scarification, and year. The second section focuses on the temporal development of germination, survival, and growth over summer 2014, illustrating the main trends. The sum of the random effect terms accounted for 29%, 63% and 28% of the total variance of germination, survival and growth, respectively (Appendix IX).

3.1. Part I: Germination of seeds

3.1.1. Germination across all sites

No germination occurred in unseeded plots whereas on seeded plots on average 4.7 ± 0.4 % of the sown seeds germinated (Appendix X). Because of this lack of germination in unseeded plots, the results presented were based on seeded plots only. The forest site showed only very little germination with 0.1 ± 0.04 % (mean \pm standard error) of all viable seeds and germination was significantly higher at the treeline and alpine site ($P_{\text{site}} < 0.001$, Table 3.1), where 5.9 ± 0.8 % and 8.0 ± 0.8 % seeds germinated, respectively (Appendix X). Post-dispersal seed and seedling predation significantly affected germination ($P_{\text{cage}} < 0.001$), with 4.1 ± 0.5 % germinated seeds without and 5.2 ± 0.6 % with cages. *L. decidua* germinated clearly better than *P. abies*, with germination percentages of 6.4 ± 0.7 % and 2.9 ± 0.4 %, respectively ($P_{\text{species}} < 0.001$). Significantly more seeds from low elevation provenances than from high elevation provenances germinated (6.9 ± 0.7 % and 2.4 ± 0.3 %, respectively; $P_{\text{provenance}} < 0.001$). Germination was not significantly influenced by scarification ($P_{\text{scarified}} = 0.027$), with

3.9±0.5% and 5.4±0.6% seeds germinating on non-scarified and on scarified plots, respectively. The total number of germinated seeds did not significantly differ between years ($P_{\text{year}} = 0.647$) with 4.2±0.6% germination in 2013 and 5.1±0.6% in 2014.

Table 3.1: Main effects of site, cage, species, provenance, scarified and year, as well as their interactions for the final reduced models of germination, survival, and growth, respectively.

	germination		survival		growth	
	χ^2	P	χ^2	P	χ^2	P
<i>main effects</i>						
site	75.807	<0.001***	2.699	0.100	28.009	<0.001***
cage	15.631	<0.001***	4.366	0.037(*)	0.532	0.466
species	24.332	<0.001***	0.057	0.811	0.095	0.758
provenance	37.079	<0.001***	1.072	0.301	9.822	0.002*
scarified	4.855	0.028(*)	12.712	<0.001**	1.088	0.297
year	0.210	0.647	—	—	5.837	0.016(*)
<i>interactions</i>						
site × cage	0.023	0.989	0.141	0.707	0.789	0.374
site × species	1.418	0.492	4.138	0.042*	0.294	0.588
site × provenance	0.646	0.724	0.123	0.726	0.102	0.749
site × scarified	8.435	0.015*	2.548	0.110	1.711	0.191
site × year	90.498	<0.001***	—	—	5.457	0.019*
cage × species	1.544	0.214	0.516	0.472	0.355	0.552
cage × provenance	6.424	0.011*	1.504	0.220	0.042	0.837
cage × scarified	0.063	0.801	0.446	0.504	4.849	0.028*
cage × year	5.115	0.024*	—	—	1.283	0.257
species × provenance	16.018	<0.001***	1.080	0.299	1.308	0.253
species × scarified	0.642	0.423	0.000	0.986	0.030	0.863
species × year	1.871	0.171	—	—	1.362	0.243
provenance × scarified	0.585	0.444	6.973	0.008**	1.141	0.286
provenance × year	0.872	0.350	—	—	0.344	0.558
scarified × year	4.519	0.034*	—	—	0.244	0.621

The germination model was based on all three sites, whereas survival and growth models only on the treeline and the alpine site. Values and symbols are χ^2 -values, P -values and significances, respectively from likelihood ratio tests of mixed-effect models. The significance levels for main effects were corrected for anti-conservative P -values ($\alpha = 0.01$) whereas for interactions not ($\alpha = 0.05$). Degrees of freedom are two for site and its interactions, and one for the other main effects and their interactions.

Germination was slightly influenced by the interaction of site with scarification ($P_{\text{site} \times \text{scarified}} = 0.015$, Table 3.1, Figure 3.1a). At the treeline, seeds significantly profited from scarification (3.5±0.7% on unscarified plots and 7.8±1.4% on scarified plots); but not at the forest site (0.0±0.0% and 0.2±0.1%, respectively) and alpine site (8.2±1.2% and 7.8±1.1%, respectively) (Appendix XI). Germination was strongly influenced by the interaction of site and year ($P_{\text{site} \times \text{year}} < 0.001$, Figure 3.1b). At the treeline, seeds sown in 2013 germinated significantly more

than those sown in 2014 ($9.6 \pm 1.4\%$ and $2.2 \pm 0.5\%$, respectively); whereas at the alpine site the opposite was the case ($3.1 \pm 0.5\%$ in 2013 and $12.9 \pm 1.3\%$ in 2014). At the forest site, few seeds germinated independently of the year ($0.1 \pm 0.0\%$ in 2013 and $2.2 \pm 0.1\%$ in 2014).

Germination was slightly influenced by the interaction of provenance with predator exclosures ($P_{\text{cage} \times \text{provenance}} = 0.011$, Figure 3.1c). With cages, the difference in germination between seeds of low and high elevation provenances was slightly greater ($7.9 \pm 1.1\%$ vs. $2.6 \pm 0.5\%$) than without cages ($6.0 \pm 0.9\%$ vs. $2.2 \pm 0.4\%$). Germination was slightly influenced by the interaction of predation exclosures with year ($P_{\text{cage} \times \text{year}} = 0.237$, Figure 3.1d). On plots without cages, seeds sown in 2014 germinated better than those sown in 2013 ($4.6 \pm 0.7\%$ and $3.6 \pm 0.7\%$, respectively).

Germination was strongly influenced by the interaction of species with provenance ($P_{\text{species} \times \text{provenance}} < 0.001$, Figure 3.1e). *L. decidua* seeds from the low elevation provenance germinated significantly better than those from the high elevation provenance ($10.6 \pm 1.2\%$ and $2.2 \pm 0.5\%$, respectively) and better than *P. abies* seeds from both provenances ($3.3 \pm 0.5\%$ and $2.5 \pm 0.4\%$, respectively). Germination was influenced by the interaction of scarification with year ($P_{\text{scarified} \times \text{year}} = 0.034$, Figure 3.1f). On unscarified plots, seeds sown in 2014 germinated significantly better than those sown in 2013 ($4.6 \pm 0.8\%$ and $3.2 \pm 0.5\%$, respectively).

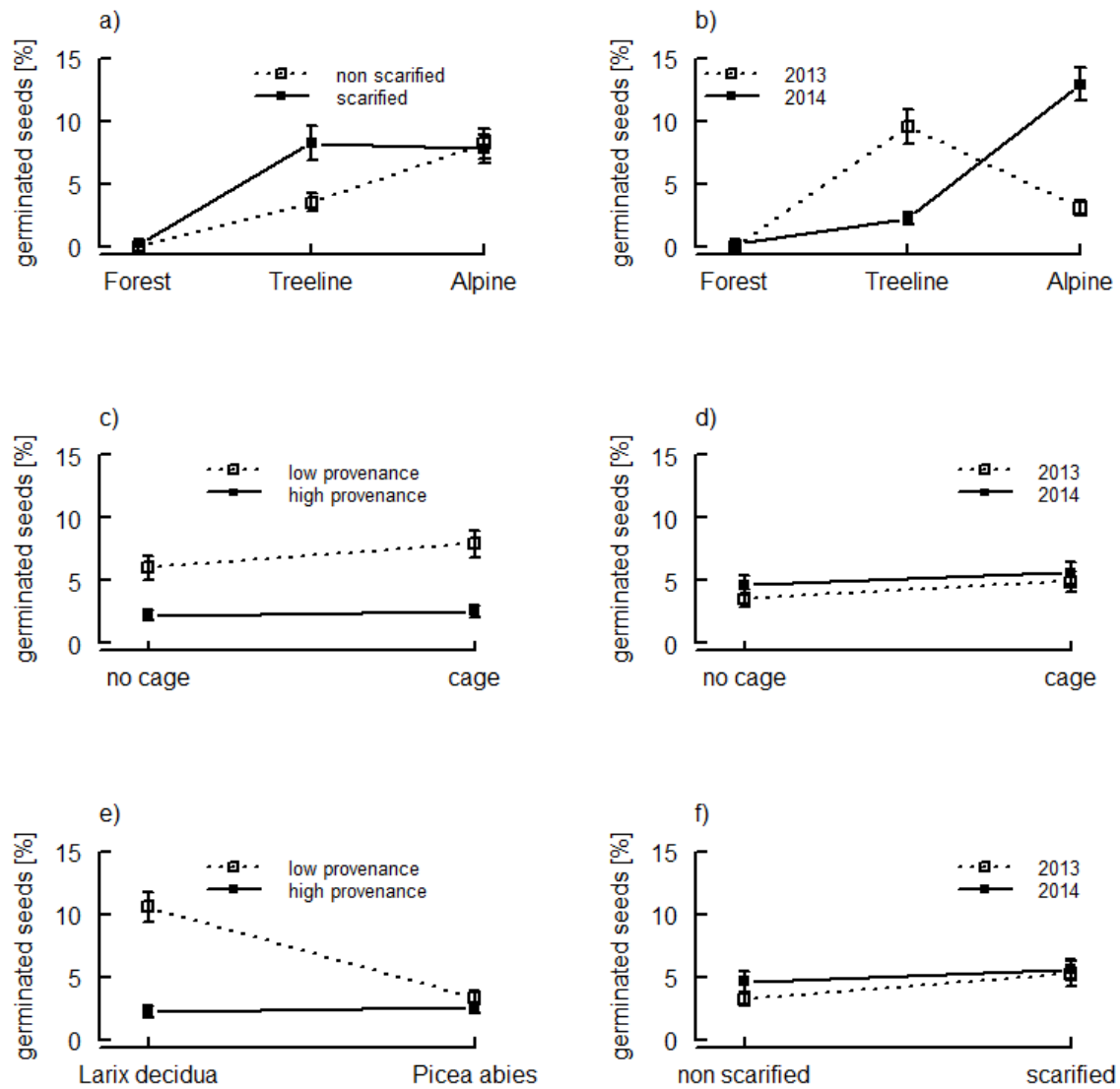


Figure 3.1: Significant two-way interactions for germination as percentage of germinated seeds: site × scarified (a), site × year (b), cage × provenance (c), cage × year (d), species × provenance (e), and scarified × year (f). Error bars indicate standard errors of trait means.

All other interactions were non-significant. The post-dispersal seed and seedling predation exclosures combined with site ($P_{\text{site} \times \text{cage}} = 0.988$, Table 3.1, Figure 3.2a) showed lower germination at the treeline than at the alpine site on plots without cages ($5.2 \pm 1.1\%$ and $7.0 \pm 1.1\%$, respectively) as well as on plots with cages ($6.6 \pm 1.2\%$ and $9.0 \pm 1.2\%$, respectively) (Appendix XI). The combination of site and species did not significantly influence germination ($P_{\text{site} \times \text{species}} = 0.492$, Figure 3.2b) with fewer germinated seeds at the treeline than at the alpine site for *L. decidua* ($7.9 \pm 1.35\%$ and $11.1 \pm 1.39\%$, respectively) as well as for *P. abies* ($3.9 \pm 0.8\%$ and $4.9 \pm 0.6\%$, respectively). Similarly, site combined with provenance did not significantly influence germination ($P_{\text{site} \times \text{provenance}} = 0.724$, Figure 3.2c) with lower

germination at the treeline than at the alpine site for seeds from low elevation provenances ($9.0 \pm 1.4\%$ and $11.6 \pm 1.3\%$, respectively) as well as for seeds from high elevation provenances ($2.8 \pm 0.6\%$ and $4.3 \pm 0.7\%$, respectively).

The post-dispersal seed and seedling predator exclusions did not significantly interact with species ($P_{\text{cage} \times \text{species}} = 0.214$, Figure 3.2d) with lower germination on plots without cages than on plots with cages for *L. decidua* ($5.6 \pm 0.9\%$ and $7.1 \pm 1.1\%$, respectively) as well as for *P. abies* ($2.6 \pm 0.5\%$ and $3.3 \pm 0.5\%$, respectively). Predator exclusions did not significantly interact with substrate treatment ($P_{\text{cage} \times \text{scarified}} = 0.801$), as slightly fewer seedlings germinated on unscarified plots than on scarified plots without cages ($3.5 \pm 0.7\%$ and $4.7 \pm 0.8\%$, respectively) as well as with cages ($4.3 \pm 0.7\%$ and $6.1 \pm 1.0\%$, respectively).

Within species, germination did not significantly differ between substrate treatments ($P_{\text{species} \times \text{scarified}} = 0.423$, Figure 3.2d) with fewer germinated seeds on unscarified plots than on scarified ones for *L. decidua* ($5.3 \pm 0.9\%$ and $7.4 \pm 1.1\%$, respectively) as well as for *P. abies* ($2.5 \pm 0.4\%$ and $3.4 \pm 0.6\%$, respectively). Within species, there was no significant interannual variation of germination ($P_{\text{year} \times \text{species}} = 0.171$, Figure 3.2f) with lower germination in 2013 than in 2014 for *L. decidua* ($6.7 \pm 1.0\%$ and $7.1 \pm 1.0\%$, respectively) as well as for *P. abies* ($2.8 \pm 0.5\%$ and $3.1 \pm 0.5\%$, respectively).

Germination was not significantly influenced by the interaction of scarification with provenance ($P_{\text{provenance} \times \text{scarified}} = 0.444$, Figure 3.2e) with lower germination on unscarified plots than on scarified plots for seeds from low elevation provenances ($6.0 \pm 0.9\%$ and $7.9 \pm 1.1\%$, respectively) as well as from high elevation provenances ($1.8 \pm 0.4\%$ and $2.9 \pm 0.5\%$, respectively). Within provenances, no significant interannual variation of germination was observed ($P_{\text{provenance} \times \text{year}} = 0.35$, Figure 3.2h) with fewer germinated seeds in 2013 than in 2014 from low elevation provenances ($6.7 \pm 1.0\%$ and $7.2 \pm 1.0\%$, respectively) as well as from high elevation provenances ($1.8 \pm 0.4\%$ and $3.0 \pm 0.5\%$, respectively).

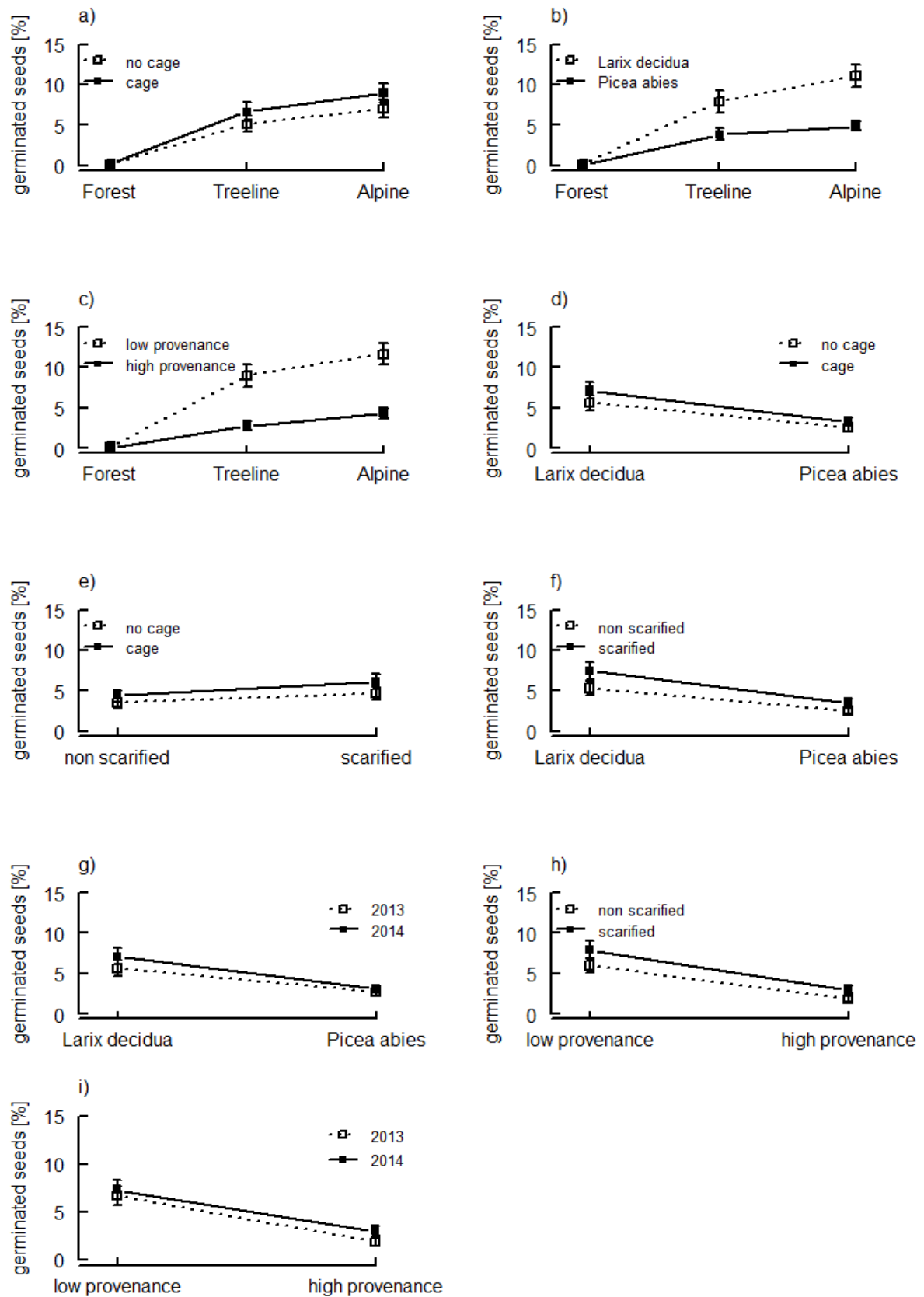


Figure 3.2: Non significant two-way interactions for germination as percentage of germinated seeds: site \times cage (a), site \times species (b), site \times provenance (c), cage \times species (d), cage \times scarified (e), species \times scarified (f), species \times year (g), provenance \times scarified (h), provenance \times year (i). Error bars indicate standard errors of trait means.

3.1.2. Germination during summer 2014

The percentage of germinated seeds sown in June 2014 was quite constant over summer 2014, at the forest and treeline site, whereas at the alpine site it increased and was particularly high in September (Figure 3.3a, Appendix XII). However, the small germination of seeds sown in 2014 at the forest site should be considered (7 germinated seeds, cf. Appendix VIII). The positive effect of the post-dispersal seed predator exclosures became evident towards the end of the summer, with germination under cages being slightly higher than without cages (Figure 3.3b). *L. decidua* germinated better than *P. abies*, with the difference becoming larger through the summer (Figure 3.3c). Similarly, the provenance difference increased over time, with seeds from low elevation provenances germinating better than from high elevation provenance (Figure 3.3d). Germination did not show clear differences due to substrate (Figure 3.3e).

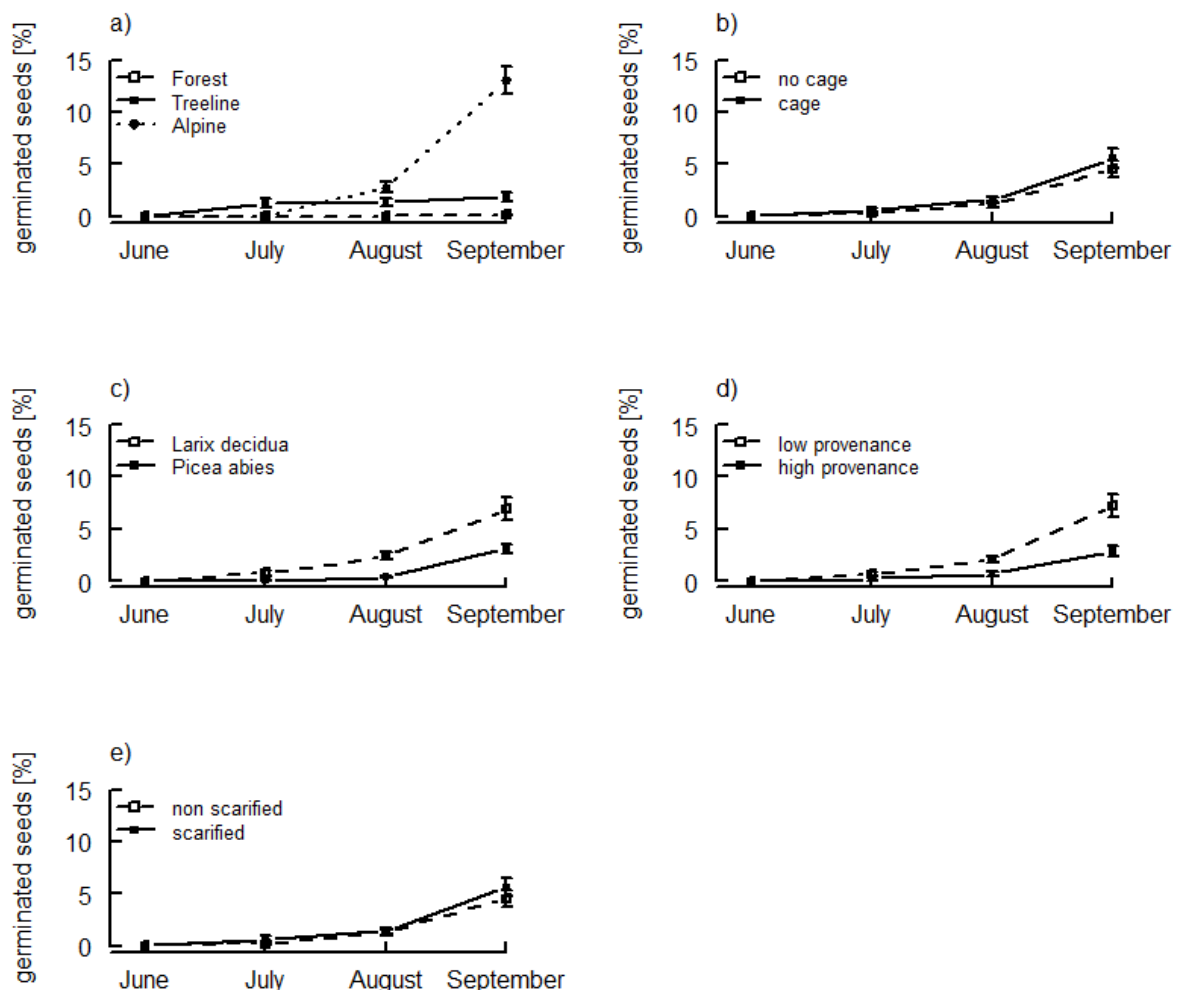


Figure 3.3: Germination during summer 2014 of seeds sown in June 2014: site (a), cage (b), species (c), provenance (d), scarified (e). Error bars indicate standard errors of trait means.

3.2. Part II: Winter survival of seedlings

3.2.1. Winter survival at treeline and alpine sites

Of all seeds germinated in 2013, $28.8 \pm 3.6\%$ seedlings survived the first winter (Appendix X). Survival was not significantly influenced by site ($P_{\text{site}} = 0.100$, Table 3.1). At the treeline site, $37.6 \pm 5.1\%$ seedlings and at the alpine site $17.4 \pm 4.6\%$ survived the first winter (Appendix X). The predator exclosures slightly influenced survival ($P_{\text{cage}} = 0.037$), without cages $33.5 \pm 5.7\%$ seedlings whereas with cages $24.7 \pm 4.6\%$ seedlings survived the first winter. Between species, no significant difference resulted ($P_{\text{species}} = 0.810$), as $28.3 \pm 5\%$ of *Larix decidua* and $27.1 \pm 4.9\%$ of *Picea abies* that had germinated in 2013 survived. No significant difference in provenance was observed ($P_{\text{provenance}} = 0.300$), with $31.9 \pm 4.2\%$ seedlings from low elevation provenance and $23.0 \pm 6.5\%$ from high elevation provenance surviving the first winter. The substrate treatment was decisive for survival ($P_{\text{scarified}} < 0.001$), as on scarified plots $44.1 \pm 5.4\%$ seedlings survived in contrast to $13.2 \pm 3.7\%$ on unscarified plots.

Survival significantly differed in the combination of site and species ($P_{\text{site} \times \text{species}} = 0.042$, Table 3.1, Figure 3.4a). At the treeline, slightly more seedlings of *P. abies* than of *L. decidua* survived ($40.7 \pm 7.6\%$ and $34.0 \pm 7.2\%$, respectively), whereas at the alpine site slightly more seedlings of *L. decidua* than of *P. abies* survived ($21.6 \pm 6.7\%$ and $12.9 \pm 6.0\%$, respectively) (Appendix XI). Substrate treatment significantly interacted with seed provenance ($P_{\text{provenance} \times \text{scarified}} = 0.008$, Figure 3.4b), with higher survival for seedlings from low than from high elevation provenances on unscarified plots ($17.3 \pm 5.0\%$ and $3.3 \pm 2.9\%$, respectively) and little provenance differences on scarified plots ($43.6 \pm 5.9\%$ and $40.2 \pm 10.9\%$, respectively).

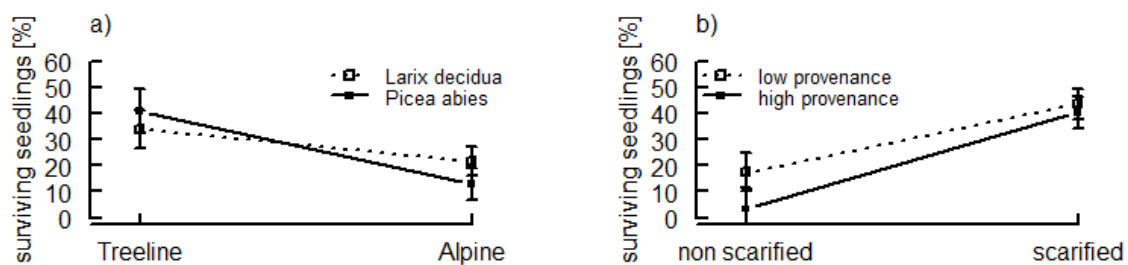


Figure 3.4: Significant two-way interactions for survival as percentage of surviving seedlings: site \times species (a) and provenance \times scarified (b). Error bars indicate standard errors of trait means.

The effect of site combined with the post-dispersal seed and seedling predator exclosures did not significantly influence survival ($P_{\text{site} \times \text{cage}} = 0.707$, Table 3.1, Figure 3.5a); with more surviving seedlings at the treeline than at the alpine site on plots without cages ($44.2 \pm 7.5\%$ and $18.4 \pm 7.7\%$, respectively) as well as with cages ($31.4 \pm 7.0\%$ and $16.5 \pm 6.3\%$, respectively)

(Appendix XI). Site combined with provenance did not significantly affect survival ($P_{\text{site} \times \text{provenance}} = 0.726$, Figure 3.5b); with more surviving seedlings at the treeline than at the alpine site from seeds from low elevation provenances ($40.2 \pm 5.8\%$ and $21.4 \pm 6.0\%$, respectively) as well as from seeds from high elevation provenances ($32.8 \pm 7.3\%$ and $8.9 \pm 4.3\%$ respectively). The combination of site and scarification did not significantly influence survival ($P_{\text{site} \times \text{scarified}} = 0.110$, Figure 3.5c); with more surviving seedlings on unscarified than on scarified plots at the treeline ($13.7 \pm 5.3\%$ and $59.8 \pm 6.2\%$, respectively) as well as at the alpine site ($12.5 \pm 5.2\%$ and $22.5 \pm 7.4\%$, respectively).

Species-specific survival was not significantly influenced by the presence of cages ($P_{\text{cage} \times \text{species}} = 0.472$, Figure 3.5d); with higher survival without cages than with cages of *L. decidua* seedlings ($32.6 \pm 7.8\%$ and $24.4 \pm 6.5\%$, respectively) as well as of *P. abies* seedlings ($31.7 \pm 8.3\%$ and $23.3 \pm 6.8\%$, respectively). The provenance-specific survival was not significantly influenced by the post-dispersal seed and seedling predator exclosures ($P_{\text{cage} \times \text{provenance}} = 0.220$, Figure 3.5e); with more surviving seedlings without cages than with cages from seeds from low elevation provenances ($36.5 \pm 6.4\%$ and $25.4 \pm 5.2\%$, respectively) as well as from seeds from high elevation provenances ($24.2 \pm 7.2\%$ and $20.5 \pm 6.0\%$, respectively). Survival did not significantly differ in the interaction of substrate treatment and predator exclosures ($P_{\text{cage} \times \text{scarified}} = 0.504$, Figure 3.5f); with more surviving seedling without cages than with cages on unscarified plots ($15.8 \pm 6.4\%$ and $10.3 \pm 4.0\%$, respectively) as well as on scarified plots ($45.9 \pm 8.4\%$ and $38.9 \pm 6.9\%$, respectively).

Species and provenance did not significantly influence survival ($P_{\text{species} \times \text{provenance}} = 0.299$, Figure 3.5g); with seedlings surviving better from seeds from low elevation provenances than from high elevation provenances for *L. decidua* ($29.0 \pm 5.5\%$ and $26.4 \pm 11.9\%$, respectively) as well as for *P. abies* ($32.1 \pm 6.1\%$ and $20.2 \pm 10.6\%$). Within species, substrate treatment did not significantly influence survival ($P_{\text{species} \times \text{scarified}} = 0.986$, Figure 3.5h); with fewer surviving seedlings on unscarified plots than on scarified ones for *L. decidua* ($15.4 \pm 5.2\%$ and $40.2 \pm 7.7\%$, respectively) as well as for *P. abies* ($10.4 \pm 5.5\%$ and $44.5 \pm 7.6\%$, respectively).

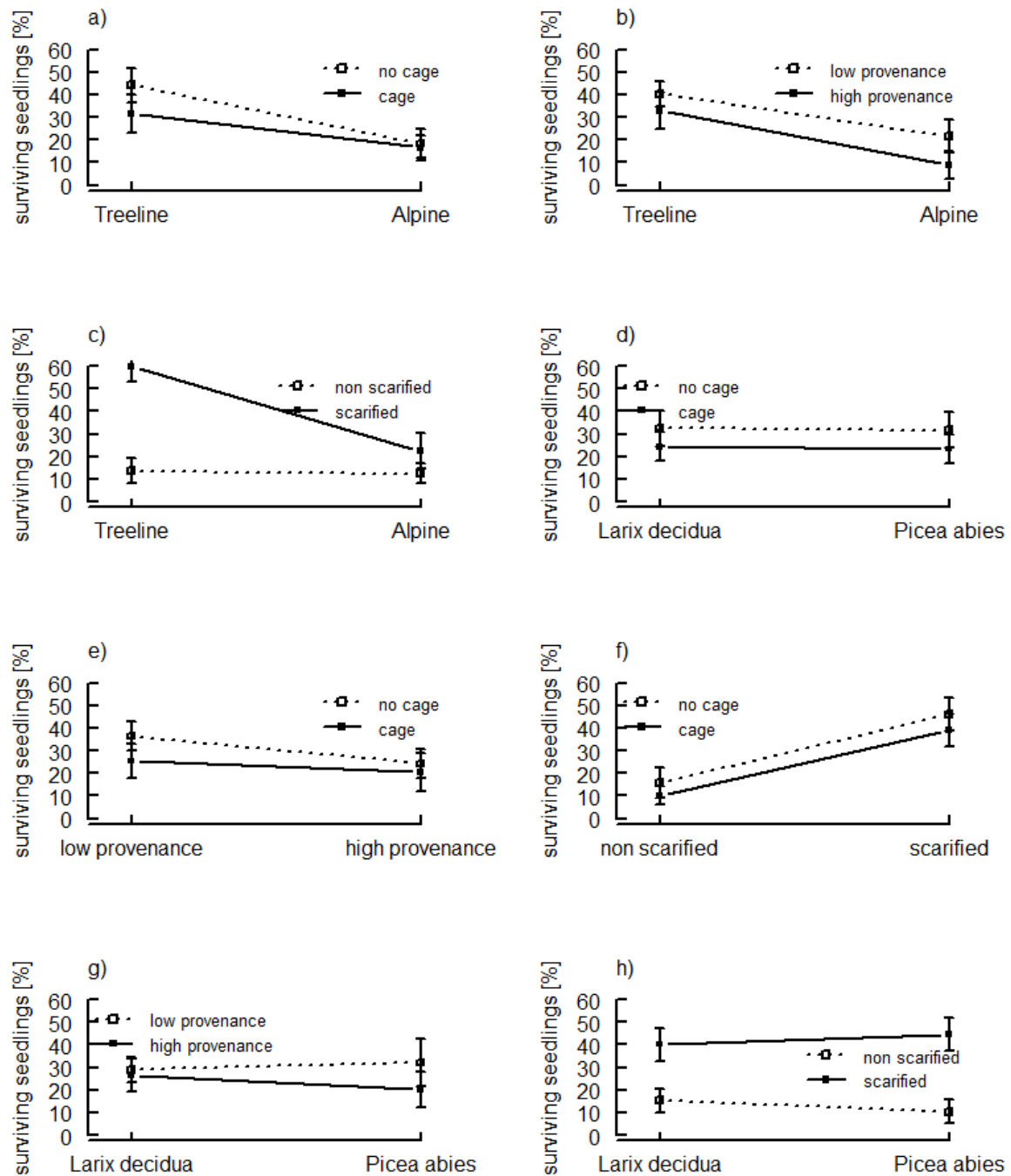


Figure 3.5: Non significant two-way interactions for survival as percentage of surviving seedlings: site × cage (a), site × provenance (b), site × scarified (c), cage × species (d), cage × provenance (e), cage × scarified (f), species × provenance (g), species × scarified (h). Error bars indicate standard errors of trait means.

3.2.2. Survival during summer 2014

Most seedlings that survived the first winter and were still alive at the beginning of the second vegetation period (June 2014) survived till the end of the second vegetation period (September 2014) (Figure 3.6, Appendix XIII). Seedlings survived better at the treeline than at the alpine site, after winter and during the whole summer 2014 (Figure 3.6a). Seedling

survival without cages was slightly higher than with cages at the beginning of the second vegetation period (June 2014), whereas during summer the difference became smaller (Figure 3.6b). No difference in survival between species was found immediately after snow melt, whereas during the summer *P. abies* showed a slightly higher mortality compared to *L. decidua* (Figure 3.6c). Seedlings from low elevation provenances survived slightly better than those from high elevation provenances after the winter as well as during the summer (Figure 3.6d). On scarified plots, seedling survival was higher than on unscarified plots. This difference seems to become larger through the summer (Figure 3.6e).

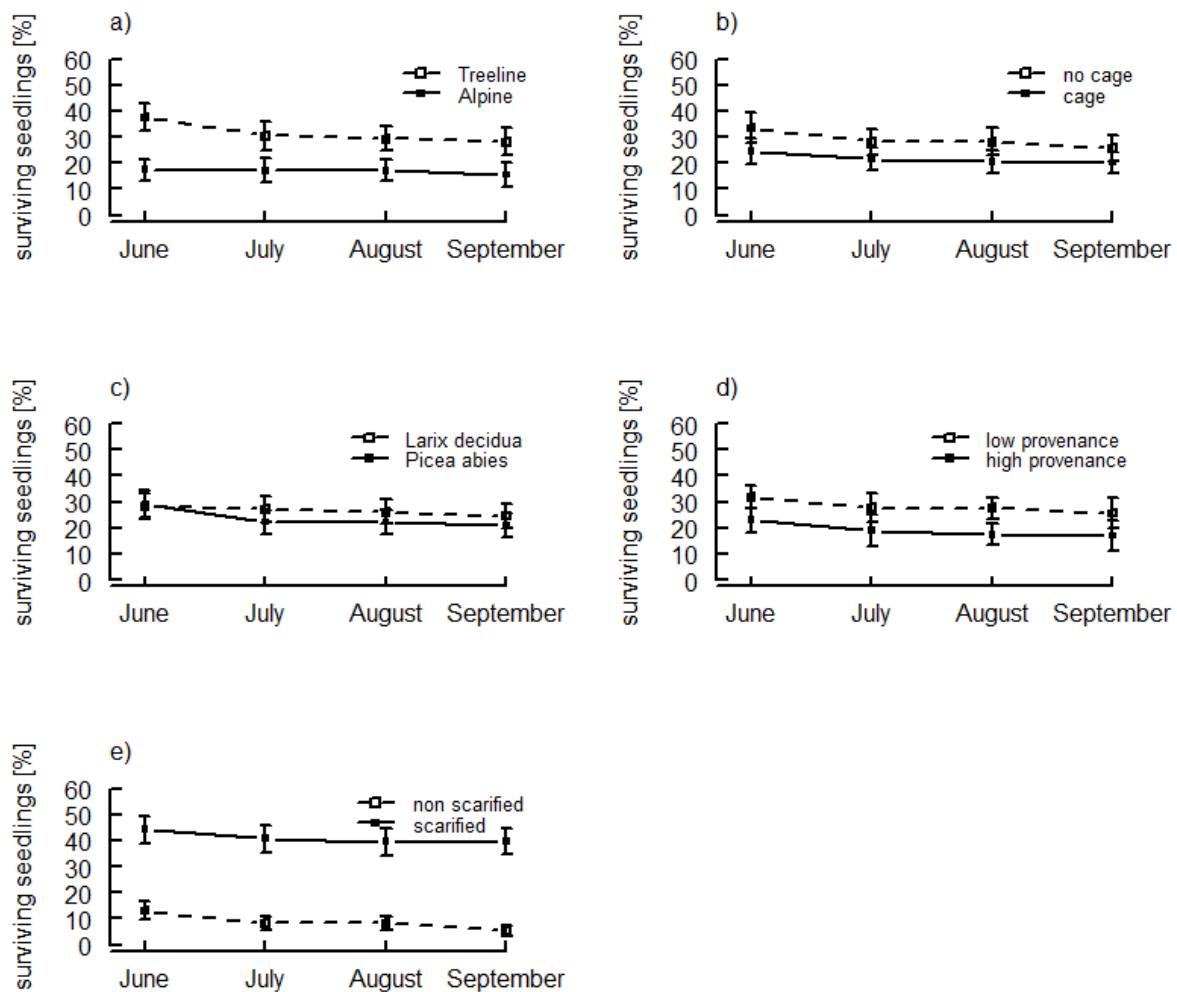


Figure 3.6: Seedling survival during summer 2014 of seeds sown in June 2013: site (a), cage (b), species (c), provenance (d), scarified (e). Error bars indicate standard errors of trait means.

3.3. Part III: Growth of seedlings

3.3.1. Growth of seedlings at treeline and alpine sites

In September 2014, seedlings were on average 2.9 ± 1.0 cm long (Appendix X). Growth was strongly influenced by site ($P_{\text{site}} < 0.001$, Table 3.1). In September 2014, seedlings reached a mean total height of 3.8 ± 0.1 cm at the treeline site and 2.3 ± 0.1 cm at the alpine site (Appendix X). Thus, seedlings at the alpine site were significantly shorter than at the treeline site, independently of cage, species, provenance, scarification and year (Figure 3.7a, Figure 3.8f-i). The seedling predator exclosures are not decisive for growth ($P_{\text{cage}} = 0.466$), as the difference in average total height was minimal: 2.9 ± 0.1 cm without and 3.0 ± 0.1 cm with predator exclosure. Total height did not significantly differ between species, as *Larix decidua* seedlings were on average 3.0 ± 0.1 cm and *Picea abies* seedlings 2.8 ± 0.1 cm high ($P_{\text{species}} = 0.758$, Table 3.1). Seedlings from low elevation provenances were significantly taller than those from high elevation provenances ($P_{\text{provenance}} = 0.002$). Mean total height was 3.1 ± 0.1 cm and 2.6 ± 0.1 cm for seeds from low and high elevation provenances, respectively. Total height was not significantly different between substrate treatments ($P_{\text{scarification}} = 0.297$). On scarified plots, seedlings were 2.8 ± 0.2 cm and on unscarified plots 3.0 ± 0.1 cm high. Two-year-old seedlings were on average slightly taller than one-year-old seedlings, 3.4 ± 0.1 cm and 2.8 ± 0.1 cm, respectively ($P_{\text{year}} = 0.016$, Figure 3.8g).

Year, i.e. age of seedlings, interacted significantly with site ($P_{\text{site} \times \text{year}} = 0.019$, Table 3.1, Figure 3.7a). In September 2014, seedling height at the treeline was higher than at the alpine site for two-year-old seedlings (3.8 ± 0.1 cm and 2.6 ± 0.1 cm, respectively) as well as for one-year-old seedlings (3.9 ± 0.2 cm and 2.2 ± 0.1 cm, respectively) (Appendix XI). The interaction of substrate treatment with seed and seedling predator exclosure treatment significantly affected growth ($P_{\text{cage} \times \text{scarified}} = 0.028$, Figure 3.7b). On unscarified plots, seedlings were shorter on plots without cages than on those with cages (2.8 ± 0.2 cm and 2.9 ± 0.2 cm, respectively) whereas on scarified plots there was no difference (3.0 ± 0.2 cm for both predator exclosure treatments).

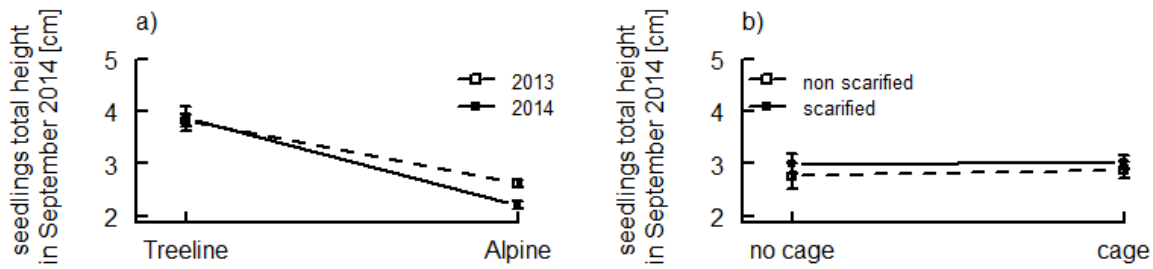


Figure 3.7: Significant two-way interactions for growth as total height in September in centimetres: site \times year (a) and cage \times scarified (b). Error bars indicate standard errors of trait means.

Besides the above mentioned, all other interactions did not significantly influence seedling growth. At the treeline seedlings were taller than at the alpine site on plots without cages (3.7 ± 0.2 cm and 2.4 ± 0.1 cm, respectively) as well as on plots with cages (3.9 ± 0.1 cm and 2.2 ± 0.1 cm, respectively) ($P_{\text{site} \times \text{cage}} = 0.374$, Table 3.1, Figure 3.8a). Seedlings were taller at the treeline than at the alpine site for *L. decidua* (3.9 ± 0.2 cm and 2.4 ± 0.1 cm, respectively) as well as for *P. abies* (3.8 ± 0.1 and 2.2 ± 0.1 cm, respectively). ($P_{\text{site} \times \text{species}} = 0.588$, Figure 3.8b). Seedlings from seeds from low elevation provenances were taller than those from high elevation provenance at the treeline (3.9 ± 0.1 cm and 3.6 ± 0.1 cm, respectively) as well as at the alpine site (2.4 ± 0.1 cm and 2.1 ± 0.1 cm, respectively) ($P_{\text{site} \times \text{provenance}} = 0.749$, Figure 3.8c). At the treeline, seedlings were taller on unscarified plots than on scarified ones (4.5 ± 0.2 cm and 3.7 ± 0.2 cm, respectively) whereas at the alpine site there was no difference (2.3 ± 0.1 cm on both substrate treatments) ($P_{\text{site} \times \text{scarified}} = 0.191$, Figure 3.8d).

Seedlings of *L. decidua* were 3.0 ± 0.2 cm high both with and without cages, whereas seedlings of *P. abies* were 2.9 ± 0.2 cm and 2.8 ± 0.1 cm long with and without cages ($P_{\text{cage} \times \text{species}} = 0.552$, Figure 3.8e). Seedlings from seeds from low elevation provenances were taller than those from high elevation provenances on plots with cages (3.1 ± 0.2 cm and 2.6 ± 0.1 cm, respectively) as well as on plots without cages (3.1 ± 0.2 cm and 2.5 ± 0.1 cm, respectively) ($P_{\text{cage} \times \text{provenance}} = 0.837$, Figure 3.8f). One-year-old seedlings were 2.8 ± 0.2 cm and 2.7 ± 0.2 cm high with and without cages, respectively; whereas two-year-old seedlings were 3.4 ± 0.2 cm high independently of the presence of cages ($P_{\text{cage} \times \text{year}} = 0.999$, Figure 3.8g).

Seedlings from low elevation provenances were taller than from high elevation provenances for *L. decidua* (3.2 ± 0.2 cm and 2.6 ± 0.2 cm, respectively) as well as for *P. abies* (3.0 ± 0.1 cm and 2.6 ± 0.2 cm, respectively) ($P_{\text{species} \times \text{provenance}} = 0.253$, Figure 3.8h). *L. decidua* seedlings were 3.1 ± 0.2 cm and 3.0 ± 0.1 cm high whereas *P. abies* seedlings were 2.5 ± 0.1 cm and 3.0 ± 0.1 cm high, on non-scarified and on scarified plots, respectively ($P_{\text{species} \times \text{scarified}} = 0.863$,

Table 3.1, Figure 3.9a). One- and two-year-old *L. decidua* seedlings were 2.9 ± 0.2 cm and 3.3 ± 0.2 cm high whereas *P. abies* seedlings were 2.6 ± 0.1 cm and 3.5 ± 0.1 cm high, respectively ($P_{\text{species} \times \text{year}} = 0.243$, Figure 3.9b).

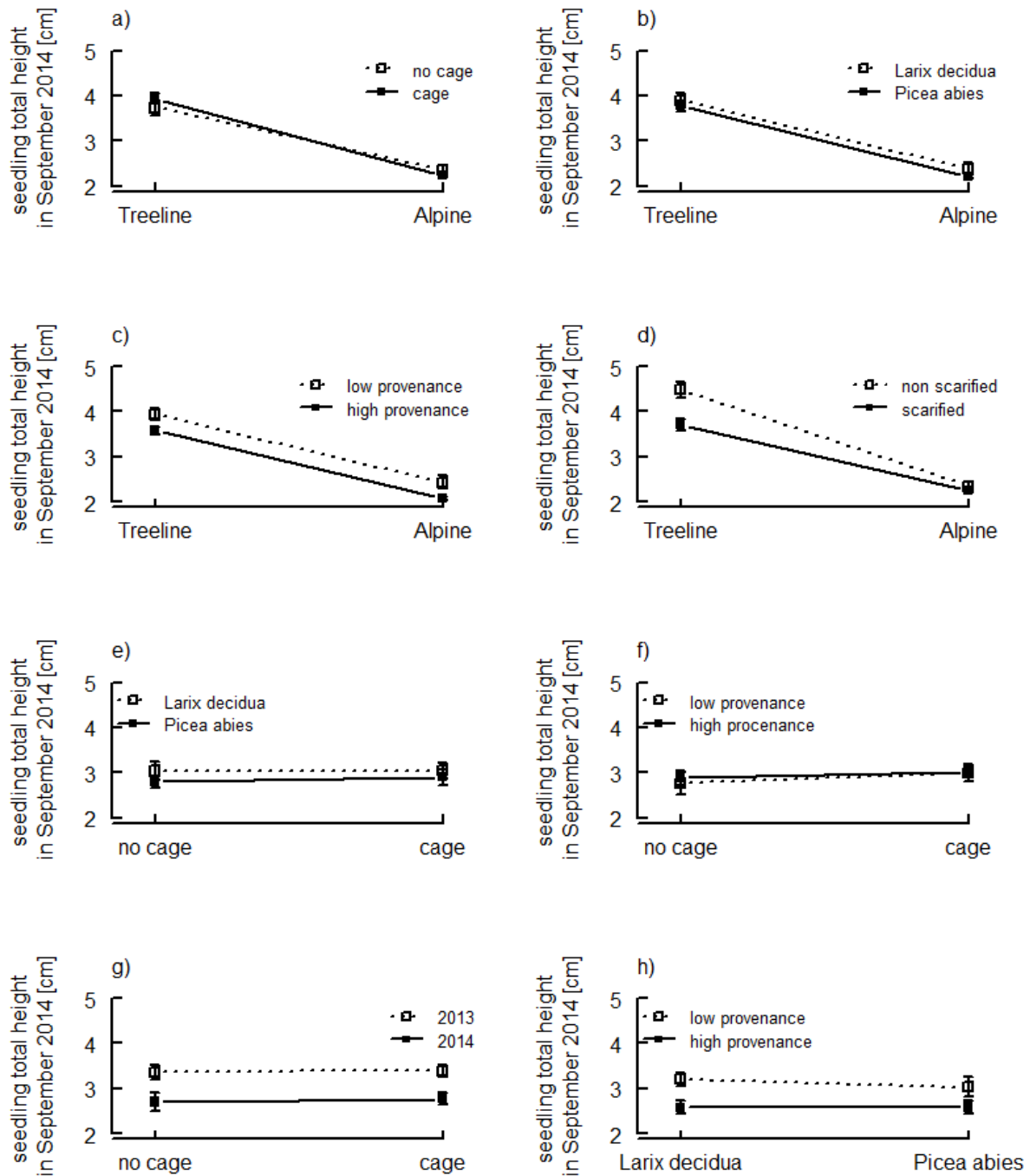


Figure 3.8: Non significant two-way interactions for growth as seedling total height in September 2014 [cm]: site × cage (a), site × species (b), site × provenance (c), site × scarified (d), cage × species (e), cage × provenance (f), cage × year (g), species × provenance (h). Error bars indicate standard errors of trait means.

Seedlings from seeds from low elevation provenance were taller than from those from high elevation provenances on unscarified plots (3.1 ± 0.2 cm and 2.0 ± 0.1 cm, respectively) as well as on scarified plots (3.2 ± 0.2 cm and 2.8 ± 0.1 cm, respectively) ($P_{\text{provenance} \times \text{scarified}} = 0.286$, Figure 3.9c). One- and two-year-old seedlings from low elevation provenances (3.0 ± 0.2 cm and 3.4 ± 0.2 , respectively) were taller than those from high elevation provenances (2.4 ± 0.1 cm and 3.3 ± 0.2 , respectively) ($P_{\text{provenance} \times \text{year}} = 0.558$, Figure 3.9d).

Two-year-old seedlings were taller than one-year-old ones on unscarified plots (3.4 ± 0.4 cm and 2.7 ± 0.2 cm, respectively) as well as on scarified plots (3.4 ± 0.2 cm and 2.8 ± 0.2 cm, respectively) ($P_{\text{scarified} \times \text{year}} = 0.621$, Figure 3.9e).

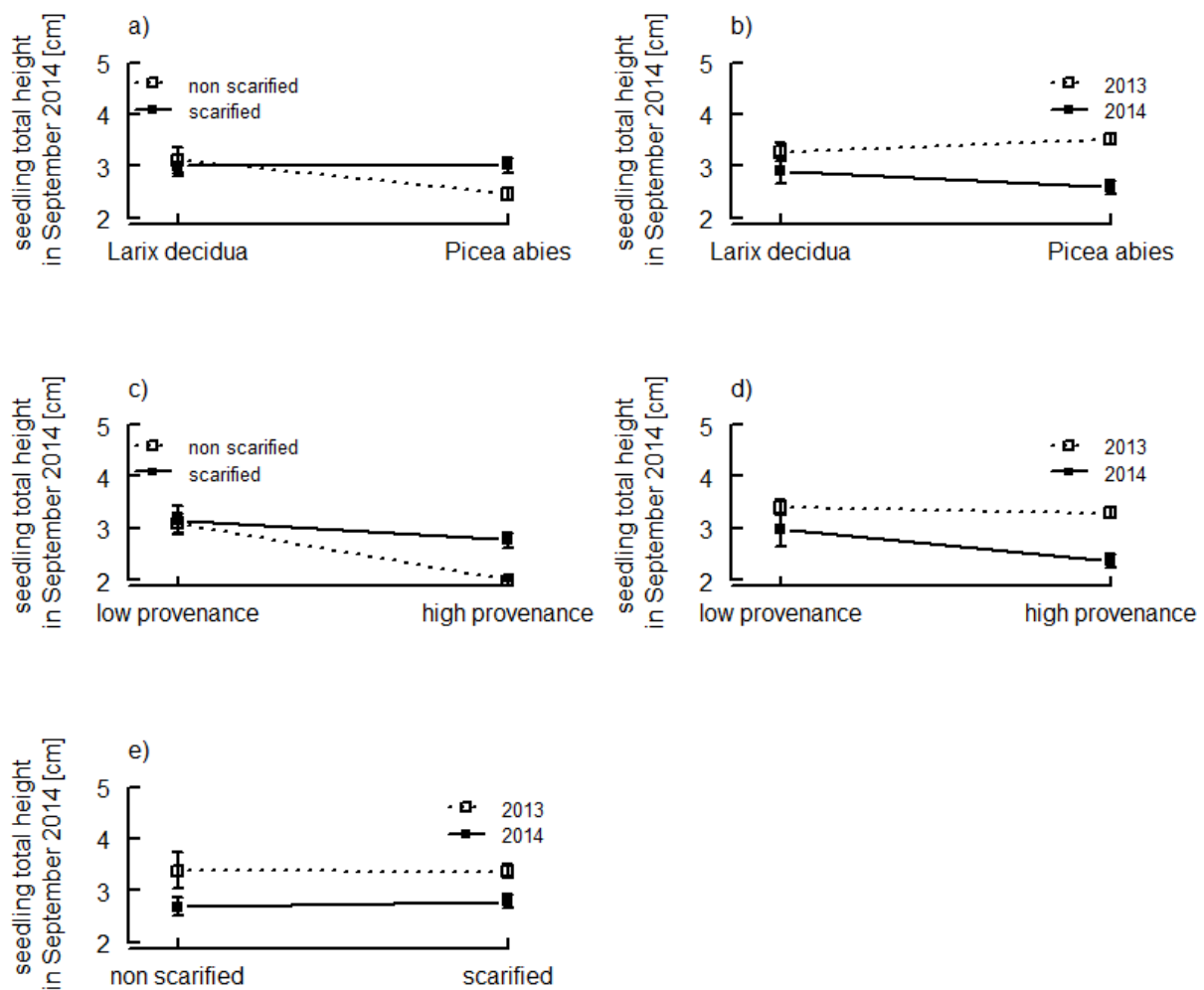


Figure 3.9: Non significant two-way interactions for growth as seedlings total height in September 2014 [cm]: species × scarified (a), species × year (b), provenance × scarified (c), provenance × year (d), scarified × year (e). Error bars indicate standard errors of trait means.

3.3.2. Growth of seedlings during summer 2014

At the treeline, seedlings grew during summer, especially in the last month, whereas at the alpine site the mean total length of seedlings did not increase (Figure 3.10a, Appendix XIV). The seedling predator exclosures did not affect seedling growth (Figure 3.10b). Seedlings of *P. abies* were taller than those of *L. decidua* at the beginning of the summer, but later on a reversed difference was observed (Figure 3.10c). Growth differences between provenances became more evident over the summer, with taller seedlings from low elevation provenances than those from high elevation provenances in September 2014 (Figure 3.10d). At the beginning of the summer seedlings were taller on scarified plots than those on unscarified plots, whereas at the end of the summer the opposite was the case (Figure 3.10e). Two-year-old seedlings were taller than one-year-old ones over the whole summer 2014 (Figure 3.10f).

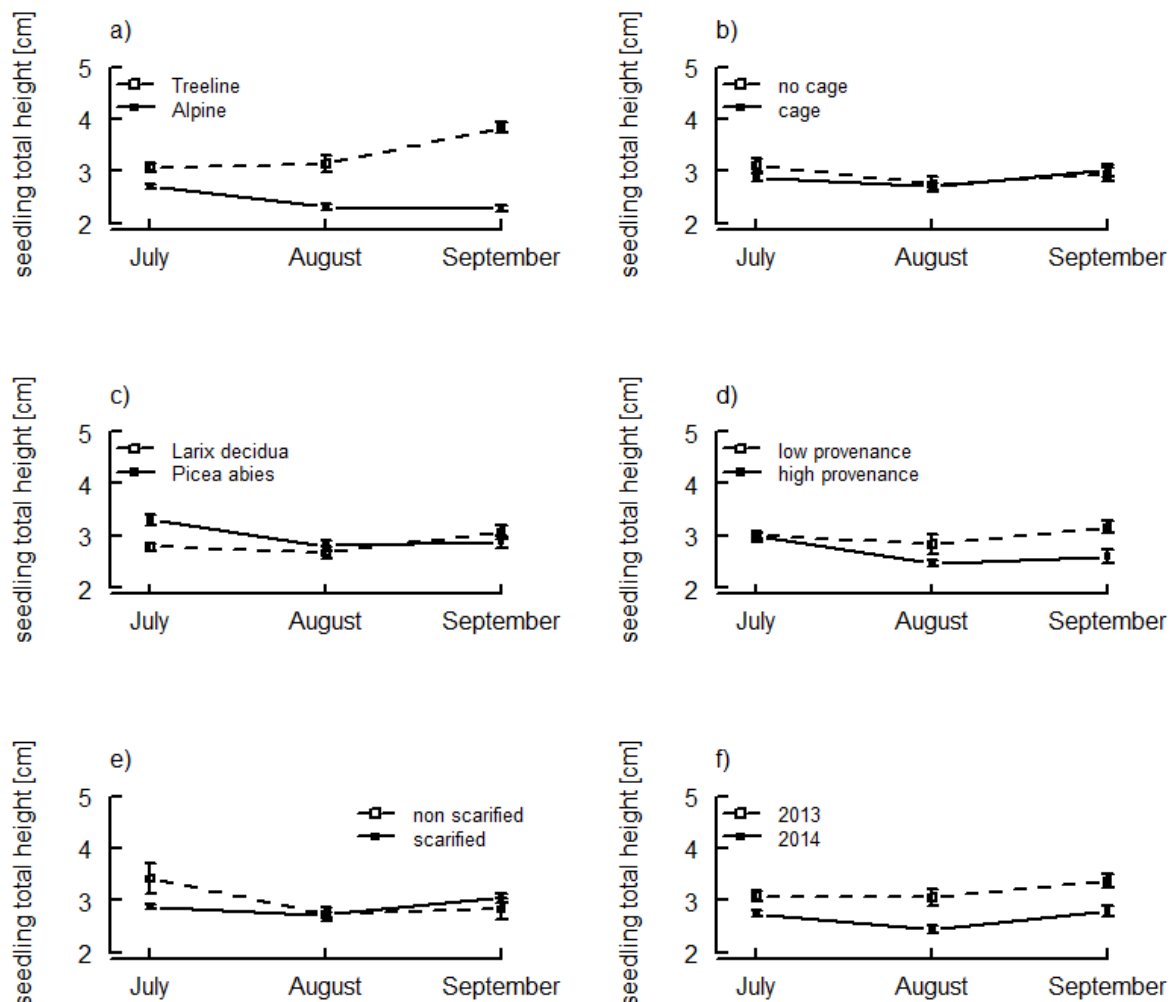


Figure 3.10: Seedling growth during summer 2014: site (a), cage (b), species (c), provenance (d), scarified (e), year (f). Error bars indicate standard errors of trait means. The knick after July is due to new germinated seedlings being measured in the ten casually chosen seedling.

4. Discussion

Our G-TREE experiment at Stillberg, Davos, aims at investigating important treeline limiting factors. Our results showed that seedling recruitment in our treeline ecotone is influenced by complex interactions among factors.

4.1. Site dependent seedling recruitment

Our experiment was set up with three sites along an elevational gradient in the treeline ecotone. This allowed us to study whether elevation dependent factors are limiting seedling recruitment across treeline. The sown seeds germinated at all three sites. At first sight, it might be surprising that most germination occurred at and above treeline but not below treeline. The extremely low recruitment at the forest site is expected to be caused by the dense cover of competing understorey vegetation that probably prevented the germination of seeds. This inhibiting effect of the understorey vegetation for germination was probably mainly due to the strongly reduced light availability at the soil surface and not to e.g. the competition for nutrients. This result coincides with the findings of Imbeck and Ott (1987), who studied regeneration of *P. abies* with transplanted and natural seedlings in Lusiwald near Davos-Laret, a subalpine spruce forest rich in tall forbs (*Piceto-Adenostyletum*) not far from our study site. They found that less than 5% of naturally germinated seedlings survived the first winter on sites with dense cover of competing understory vegetation whereas potted spruce seedlings suffered less from this inhibiting effect because their surrounding vegetation was cut regularly. Our finding is also in agreement with Cranston and Hermanutz (2013), who found lower survival of one-year-old transplanted *P. mariana* seedlings in highly shaded plots. Moreover, Manson et al. (2004) described decreasing survival with increasing canopy cover for *L. decidua* and *Picea* spp. in an experiment on shade tolerance of transplanted seedlings in Southern Scotland.

Another negative aspect for germination depending on the understorey vegetation is the timing of these rapidly growing tall forbs (Imbeck and Ott, 1987): in spring, almost no understorey vegetation occurred, whereas later on it became abundant. Thus, some sown seeds may have germinated early in the season, but then died during summer through competition for light. Similarly, we observed that the few naturally germinated seedlings at the forest site died between June and November 2013 (details not shown).

In our experiment seedlings at the alpine site were significantly smaller than at the treeline and forest sites. A similar finding was described by Munier et al. (2010), who found that seedling height of *Picea mariana* decreased significantly from their experimental forest and treeline sites to the alpine site. They attributed this seedling height reduction to the more intense and direct radiation at the alpine site. Growth could also be reduced by low mean temperatures at the alpine site and by the risk of extreme temperatures. Low temperatures can induce frost events, in which upper soil layers freeze and frost heave by a few centimetres causes (irreparable) root damage. Besides possible growth constraints at the alpine site related to the lower temperature, possible growth enhancement at the treeline should be considered. Seedlings germinated in mossy substrate (or more generally, on unscarified plots) suffer from limited light conditions and thus, invest energy in shoot elongation (Cranston and Hermanutz, 2013). Once seedlings have grown beyond the vegetation layer (approximately, from the third growing season on mossy treeline substrate), they are surrounded by a completely different environment, i.e. more windy, drier, colder or warmer (Maher et al., 2005; Smith et al., 2003) and thus the difference in seedling height between alpine and treeline might become smaller (Cranston and Hermanutz, 2013).

Seedlings of *L. decidua* and *P. abies* have higher altitudinal distribution limits than adult trees of the same species, as Lenoir et al. (2009) observed that seedlings have on average a 69 m higher range limit than adults of 17 European tree taxa in an experiment with several sites from lowland to the subalpine vegetation belt across France. According to Körner (2012), this difference in range limits between seedlings and adult trees might be due to the enhanced temperatures close to the ground from which seedlings profit whereas adult trees are exposed to lower air temperatures. Thus, the upper limit of adult trees is usually lower than the one of seedlings (Körner, 2012). In contrast, Rabasa et al. (2013) found such a difference between seedling and adult tree ranges only for *Abies alba*, but not for the other six species observed, *P. abies* even showed an opposite pattern in their study on climate-driven changes in plant distribution across Europe. Körner (2012) argues that seedlings nested into appropriate shelter position may do well several hundred metres above treeline (Körner, 2012). He suggests that such seedling occurrence above treeline has to be considered carefully and must not be interpreted as treeline advance in relation to climate warming, because they can be injured and killed by environmental factors such as wind, frost events, snow movements, drought, herbivores, and pathogens (Körner, 2012). Successful seedling recruitment at a certain site does not necessarily mean that these seedlings will grow to adult trees (Körner, 2012).

However, according to Vitasse et al. (2012), such seedling occurrence above treeline represents the potential for an upward expansion of trees in the Alps as in response to ongoing climate warming because climate warming might reduce temperature limitation for tree growth at elevations above the current treeline.

As expected seedling recruitment was not strongly affected by climate, although this factor is likely to become more important in later tree life stages. Furthermore, seedling recruitment varied along an elevational gradient from forest to treeline up to the alpine site mainly due to non-climatic factors. Site affected seedling recruitment in our experiment by different light conditions, dependence depending on the competing understorey vegetation which resulted resulting in no successful recruitment at the forest site, by temperature variations among microsites and along the elevational gradient. Nevertheless the interactions of site with other factors could be even more relevant.

4.2. Seed source limits germination

The observation of no natural recruitment in combination with germination on seeded plots in our experiment indicates seed source limitation according to Turnbull et al. (2000). Our finding coincides with the finding of Munier et al. (2010), who observed seed source limitation for *Picea mariana* in a seed addition experiment in the Mealy Mountains (Labrador, Canada). Seed source limitation is relatively common and was for example observed in dwarf shrubs and perennial herbs by Lindgren et al. (2007) in a seed addition experiment in Ammarnäs (Lapland, Sweden).

To overcome this first bottleneck for recruitment, viable seeds must be produced (Leck et al., 2008). The viability of possible locally produced seeds was not assessed, but the viability of the seeds used in the seeding treatment was determined (cf. Table 2.4). In line with our viability values for *L. decidua*, Kosinski (1987) found that usually less than 30% of seeds were viable and the rest was empty in a study on the seed production of the same species in Poland. Our viability values for *P. abies* were clearly higher than the average of 10% found by Johnstone et al. (2009) for *Picea mariana* in interior Alaska (USA). In our experiment, the sown seeds were less viable then at the moment of seed collection due to the storage over long time (A. Burkart, WSL, personal communication). David (2002) found that the longer seeds are stored, the less they germinated and the longer it took to reach 15% germination in a study on effects of prolonged storage on germination of *L. decidua* seeds from Sudeten and Poland.

Seed source limitation seems thus to be a relevant contributing factor for seedling recruitment near treeline, although other factors are probably even more important.

4.3. Minor influence of post dispersal seed and seedling predation on seedling recruitment

Although seed source limitation can be an important constraint to seedling recruitment, produced seeds need to be successfully dispersed and then both, seeds and seedlings, not eaten by predators (Leck et al., 2008). In this experiment seed dispersal and pre-dispersal seed predation were not studied, but post-dispersal seed and seedling predation by large mammals and birds was. Post-dispersal seed and seedling predation had only minor influence on seedling recruitment in our study system. In contrast the literature provides several examples of enhanced seedling recruitment due to predator exclosures. Dulamsuren et al. (2013) found that post-dispersal predation was an important constraint to germination for *Pinus sylvestris* in an experiment on seedling emergence and establishment in the Khentei Mountains (Mongolia). Côte et al. (2005) found that up to 19% of seeds might be eaten by invertebrates (*Myrmica* spp, *Pterosichus* spp., *Formica* spp.) and up to 12% of seedlings eaten mainly by slugs in an experiment on invertebrate predation of post-dispersal seeds and seedlings of *Picea mariana* in a boreal forest close to Lac-Saint-Jean (Quebec, Canada). Small rodents were also a source of seed and seedling predation for *Picea mariana*, as found by Côté et al. (2003) in an experiment on post-dispersal predation. Castro et al. (1999) found an even higher percentage of post-dispersal predation: up to 96% of seeds of *Pinus sylvestris* were eaten by rodents and birds in an experiment on seed predation and dispersal in Sierra Nevada and Sierra de Baza (Spain). Brown and Vellend (2014) observed that seeds and seedlings were present in plots under cages but not in control plots, whereby the most likely seed predators were voles in an experiment on *Acer saccharum* in Parc national du Mont Mégantic (Quebec, Canada). Analogous results were found also in Asia and South America: Itô and Hino (2004) found that the presence of large and small mammals reduced recruitment of *Abies homolepsis* in an experiment on mice and deer exclosures in a subalpine mixed forest of Mt. Odaigahara (Japan). Furthermore, Marcora et al. (2013) observed lower survival and growth in control plots than in plots with grazing exclosure for transplanted *Polylepis australis*, *Maytenus boaria* and *Escallonia cordobensis* in an experiment on seedling establishment in Sierras Grandes (Argentina). Large herbivores, i.e. ungulate, cattle, may be another source for seedling damage and mortality through grazing (Cairns and Moen, 2004). Thus, animal activity may

affect treeline, and seedling recruitment can be strongly constrained by biotic factors such as herbivores in form of post-dispersal seed predation as well as of seedlings predation (Cairns et al., 2007).

In our treeline system, ungulates (mainly red deer and chamois) were potentially present at all three sites whereas, sporadically during summer, horses and cows grazed in the vicinity of our alpine and treeline site. Grazing by cattle was prevented at all three sites, but with different types of fences; whereas grazing by ungulate could not be prevented. The minor influence of predation on seedling recruitment found in our treeline system could be explained by the following aspects. The used cages were intended to exclude predating mammals and birds. However they did not ensure an exclusion of invertebrates as they were too coarsely meshed to prevent ants, other insects and slugs from entering. Invertebrates might contribute significantly to herbivory (Côte et al., 2005; Dulamsuren et al., 2013), but their effect was not tested with our predator enclosure treatment. The used cages were also not able to prevent digging animals such as voles from feeding on seeds and seedlings. Furthermore, our results might be influenced by the fact that the cages were positioned on uneven soil surface and remaining small gaps might have enabled mice and small rodents feeding under the cages. Hence, the combination of these different aspects may have led to the reduced importance of post-dispersal seed and seedling predation in our experiment, although elsewhere herbivores can be a relevant constraint to seedling recruitment near treeline.

4.4. Minor role of seed origin

Besides the decisive role of seed limitation (source, dispersal and predation), also seed origin could contribute to successful seedling recruitment near treeline. Recruitment success may differ between species and provenances. In our treeline system, *L. decidua* showed higher survival than *P. abies* at the alpine site, whereas at the treeline the inverse pattern occurred. In line with this observation, Trant and Hermanutz (2014) found that recruitment of larch increased with decreasing temperature whereas recruitment of spruce was positively correlated with temperature in a study on treeline dynamics of *Larix laricina*, *Picea glauca*, *Picea mariana* and *Abies alba* in the Mealy Mountains (Labrador, Canada). Thus, larch is performing better in cold environments typical for alpine sites, indicating that *L. decidua* might be better adapted to high elevation than *P. abies* and might survive better at high elevation. This finding might be reflected in the different upper range limits of these two species in the Alps (2'100 and 1'800 m a.s.l., respectively, Brändli (1998) and Zurbriggen et

al. (2013)). In addition to the altitudinal range, the pioneer character of the analysed species might have contributed to species differences. However, contrary to the expectation, *L. decidua* did not profit more from scarification than *P. abies*, in our experiment. *P. abies* commonly occurs in closed stands and therefore is less sensitive to competition and light deficits in contrast to the pioneer species *L. decidua* that preferably colonises open stands and bare ground (Brändli, 1998).

In contrast to species, seedlings from low elevation provenances survived better than those from high elevation provenances on unscarified plots whereas on scarified plots no difference in survival was observed. This might be because seeds produced at low elevation are already adapted to competition as they originated from closed stands whereas seeds produced at high elevation are better adapted to open forest stands and respectively more disturbed soils (Leck et al., 2008).

In our experiment, seedlings from low elevation provenances are taller than those from high elevation provenances. Similar results were shown by Castellanos-Acuña et al. (2013), for *Pinus devoniana* in an experiment on altitudinal variation of provenances in México and similar patterns were observed by Brown and Vellend (2014) for *Acer saccharum*. The reduced growth of seedlings from high elevation provenances could be a strategy to increase resistance to frost damage and thus survival as adaptation to high elevation sites (Vitasse et al., 2009). Likewise, Oleksyn et al. (1998) found that seedlings from high elevation provenance have higher chlorophyll and carotene concentrations, as well as higher net photosynthetic capacity of *P. abies* in a study on cold adaptation of different provenances in the Carpathian and the Sudety Mountains (Poland). According to Oleksyn et al. (1998), the reduced growth observed in *P. abies* seedlings from high elevation provenance might also be caused by higher respiration rates and higher root allocation.

In our experiment, *L. decidua* from low elevation provenance germinated more than seeds from high elevation provenance, whereas *P. abies* did not show significant germination differences due to seed provenance. Such provenance dependent differences coincide with the findings of Singh et al. (2006), who observed the same pattern for *Celtis australis* in an experiment on seed provenance variation along an elevational gradient from 550 to 1980 m a.s.l. in Central Himalaya (India). The authors attributed these germination differences to genetic characteristics of the source population and to the environment of seed production. In less favourable environments, reduced resources are available for fruiting and producing

seeds, resulting in reduced seed size and seed reserves (Singh et al., 2006). In our experiment, seeds of *L. decidua* from low elevation provenance were collected in a location with south-west exposition whereas the other three seed origins were from north and east exposed slopes. This may have resulted in seed reserve differences, with seeds of *L. decidua* from low elevation provenance being on average 14% heavier than the ones from high elevation provenance and also on average 20% heavier than seeds of *P. abies* from both provenances (Table 2.3). Hence, the larger seed reserves of low elevation *L. decidua* can explain its enhanced germination. Although only few species and provenance differences were observed in our study system, they may become more evident in future when seedlings grow above the vegetation layer and face other recruitment constraints.

4.5. Substrate limitation

Even though seed (source) limitation is particularly relevant near treeline, suitable substrate as seedbed is decisive for seedling recruitment by allowing the germination and successive thrive of those seeds reaching the soil. The higher germination on scarified plots at the treeline site than at the forest and alpine sites is likely influenced by the dense and thick moss layer covering the soil surface at the treeline site. Hunziker and Brang (2005) showed that a deep and dense moss mat impeded germination of *P. abies* seeds because it prevented seedlings from reaching the soil surface after bailing out the energy reserves from the female gametophytic tissue (Holtmeier, 2009; Leck et al., 2008; Powell, 2009). In contrast to the substrate limitation at the treeline site, seedbed for germination was not likely limiting at our alpine site because of the less dense vegetation cover with a relatively high proportion of rock and bare ground. Our findings are in agreement with Motta et al. (1994), who observed higher germination on scarified surfaces than on mossy surfaces for *P. abies* in an experiment on mossy seedbed and recruitment in Sedrun (Grisons, Switzerland); and with Munier et al. (2010), who found significantly enhanced germination on scarified plots, at the treeline as well as at the alpine and forest sites in an experiment on *Picea mariana* seedlings in the Mealy Mountains (Labrador, Canada). This might arise from reduced competition on scarified surfaces and from exposed mineral soil providing a particularly favourable seedbed for spruce recruitment (Munier et al., 2010). Nonetheless, other aspects like pathogens and variation in nutrient availability could also be important for seedling growth (Hunziker and Brang, 2005).

Similarly to germination, survival was also higher on scarified than on non-scarified plots at our treeline site. Hébert et al. (2006) found similar results in an experiment on scarification

and water relations of *Picea mariana* and *Pinus banksiana* in Mistassibi River and Péribonka Lake (Québec, Canada). They related the positive effect of scarification on survival to the higher water availability in soil, as the interception and competition by vegetation were reduced. However, in our treeline system the positive effect of scarification on survival may be due to the reduced water availability on scarified substrate, as the mossy substrate was partially too wet leading to rotten seedlings (details not shown). Even though these findings are in contrast to the findings of Wheeler et al. (2011), who observed a lower survival of one year old *Picea mariana* seedlings on bare ground (81.7%) than on plots covered with *Pleurozium* (moss) (93.3%) whereas survival on plots covered with *Cladonia* (lichens) was even lower (81.1%). This contrary result could be due to the common expectation that vegetation cover protects seedlings from adverse wintery environmental conditions such as wind, snow, and frost. This finding could arise because mosses and lichens protect seedlings from low temperature extremes that often occur on scarified soil during cold periods and nights when an insulating snow cover is absent (Wheeler et al. (2011). Hence, Wheeler et al. (2011) hypothesise that soil temperatures under moss and lichen seedbeds might be higher than on scarified surfaces during the winter half year and lower during the summer half year. In fact a distinction is needed between short growing vegetation, such as moss and lichens, and tall shrubs such as *Rhododendron*. In our experiment, the former seems to reduce seedling recruitment and the latter to enhance it. Shrubs (mainly *Rhododendron*) characterizing our treeline site may protect seedlings, by reducing the cooling effect of cold winds and the related heat loss. As a consequence, the soil surface is warmer at the treeline than at the alpine site, which might have contributed to the fact that more seedlings survived at the treeline than at the alpine site (where shrubs are absent). This may coincide with (Grau et al., 2013), who observed enhanced survival of *Pinus uncinata* seedlings on unscarified plots in a transplantation experiment with *Rhododendron* scarification, artificial warming and nutrient addition in the central Pyrenees.

Thus, at our treeline site, moss and shrubs are likely to have opposite effects on seedling recruitment. Moss may have reduced seedling recruitment by influencing the water availability; whereas shrubs may have enhanced it by providing more suitable microclimate conditions. Hence, the presence of bare soil generally enhanced seedling recruitment, indicating a substrate limitation and suggested how substrate disturbance may contribute to reduce the competing effect of vegetation.

4.6. Interannual variability partially influenced recruitment

Although only two years were analysed, the study provides already strong evidence that interannual variability is be relevant for recruitment since germination and growth were affected by year. Differences in survival could not be assessed, because data of the second winter were not yet recorded. In our experiment, in a cold and wet year (2014) more germination occurred at the alpine site, whereas in a “normal” year (2013) at the treeline site. Our result might be caused by drought, as few seeds germinated in 2013 because under “normal” climatic conditions insufficient moisture may have prevented germination start at the alpine site. In 2014, the wet weather could have provided enough moisture for germination at the alpine site, which is characterized by dryer soil, less moss and a shorter-grown vegetation layer. This could have led to germination occurring at the alpine site till the end of the summer and being in September 2014 even higher than in July and August. Our result is in contrast to the finding of Castanha et al. (2012), who observed highest germination at their alpine site in an exceptionally warm summer (2009) in a study on seedling recruitment of *Pinus flexilis* and *Picea engelmanni* across a treeline ecotone in the Rocky Mountains (Colorado, USA). This result might be due to the fact that high temperature enhanced germination at the alpine site by leading to early snow melt and a long growing season while it has constrained germination at the forest site because of dry conditions (Castanha et al., 2012).

In our experiment, on unscarified plots, seeds sown in 2014 germinated more numerous than seeds sown in 2013, possibly reflecting the colder and wetter summer of that year. This finding is in contrast with the observation of Munier et al. (2010) that seedling emergence was significantly higher in warmer years. Our finding might arise from the fact that the constraint is not water availability, but water surplus in the particularly wet year 2014 leading to rotten seeds. Thus, in this situation the effect of the surrounding vegetation (moss, lichens, herbs, and shrubs) is positive, due to higher interception, absorption, and evaporation than on bare soil. The opposite situation could have occurred in the normal year 2013, where water supply was lower, leading to competition for water between seeds and surrounding vegetation and thus, facilitating germination on scarified plots. While the positive effects of other ground vegetation on water availability seems to prevail, it should also be considered that some seeds were removed by water flowing down during intense and long rain events and that wet weather conditions might have increased the risk of seeds and seedlings to rot. In September

2014, two-year old seedlings were, as expected, significantly taller than one-year old seedlings at the alpine site. The different seedling size depending on seedling age is, for example, in line with Burschel et al. (1997), who expected seedlings to grow faster with increasing age. In contrast to this expectation, Hunziker (2005) found decreasing growth rates with age. Assuming constantly favourable environmental conditions, a possible explanation is that chamois browsed taller seedlings more often than shorter ones (Hunziker and Brang, 2005). In our experiment, the lack an increasing seedling height is influenced by the measurements that were taken on different individuals/seedlings at the different times.

In our experiment, seedlings that survived the first winter survived till the end of the second vegetation period. This finding coincides with the findings of Batllori et al. (2009) who found that summer survival after the first winter was 100% for *Pinus uncinata* in an experiment on recruitment of transplanted seedlings in the Pyrenees. This confirms the hypothesis that first winter is one of the major bottle necks for seedling recruitment, as it bears the greatest risk to survival (Körner, 2012).

As expected, in our treeline system seedling recruitment is influenced by interannual variation. Surprisingly, germination seems not to be limited by cold and wet weather conditions at high elevations and age-dependent difference in seedling height is remarkable only at high elevations. The effect of year on survival and growth is partially limited, as they were not yet analysed for seeds sown in 2014. For this reason, the G-TREE experiment at Stillberg is kept until the end of summer 2015. However, maintaining it for several more years, together with the continuation of the multiple recruitment surveys within a single growing season would provide data on the complete seedling phase and on seedling development on a finer scale. Long-term observation of seedling recruitment is in fact extremely worthwhile as evidenced by Munier et al. (2010), who conducted re-assessments of a similar experiment after five and ten years.

5. Conclusion

The G-TREE experiment at Stillberg Davos showed that seedling recruitment was strongly influenced by different site conditions along an elevational gradient (forest, treeline and alpine site). Reduced light availability at the forest site prevented recruitment whereas seedlings germinated and survived at and above treeline, in both years of seeding. Thus, seedling recruitment was not temperature limited in this alpine treeline ecotone. Overall the experiment showed evidence for seed source limitation with no successful natural recruitment at any of the sites and for substrate limitation with facilitated recruitment on bare ground. Avalanches, trampling and digging by animals are important disturbance events in our treeline ecotone, which create favourable seed beds. Thus, such irregularly occurring disturbances are essential to enhance the potential for seedling recruitment. Also treeline limiting factors underlie irregular cycles for example masting years or outbreaks of predators with the former leading to increased seed production and the latter to increased post-dispersal seed and seedling predation. Maintaining the Stillberg experiment for a longer time period will allow a more comprehensive analysis of these irregularly occurring driving factors for seedling establishment. Thereby also other effects, such as differences in species and provenances, might become more visible in later tree life stages considering the importance of adult trees for treeline formation and contribute to future treeline expansion in response to climate change. Finally, together with the findings of the global G-TREE initiative, this study will help to disentangle the importance of the different treeline limiting factors and their interacting effects, contributing to a widely supported prediction of future treeline expansion.

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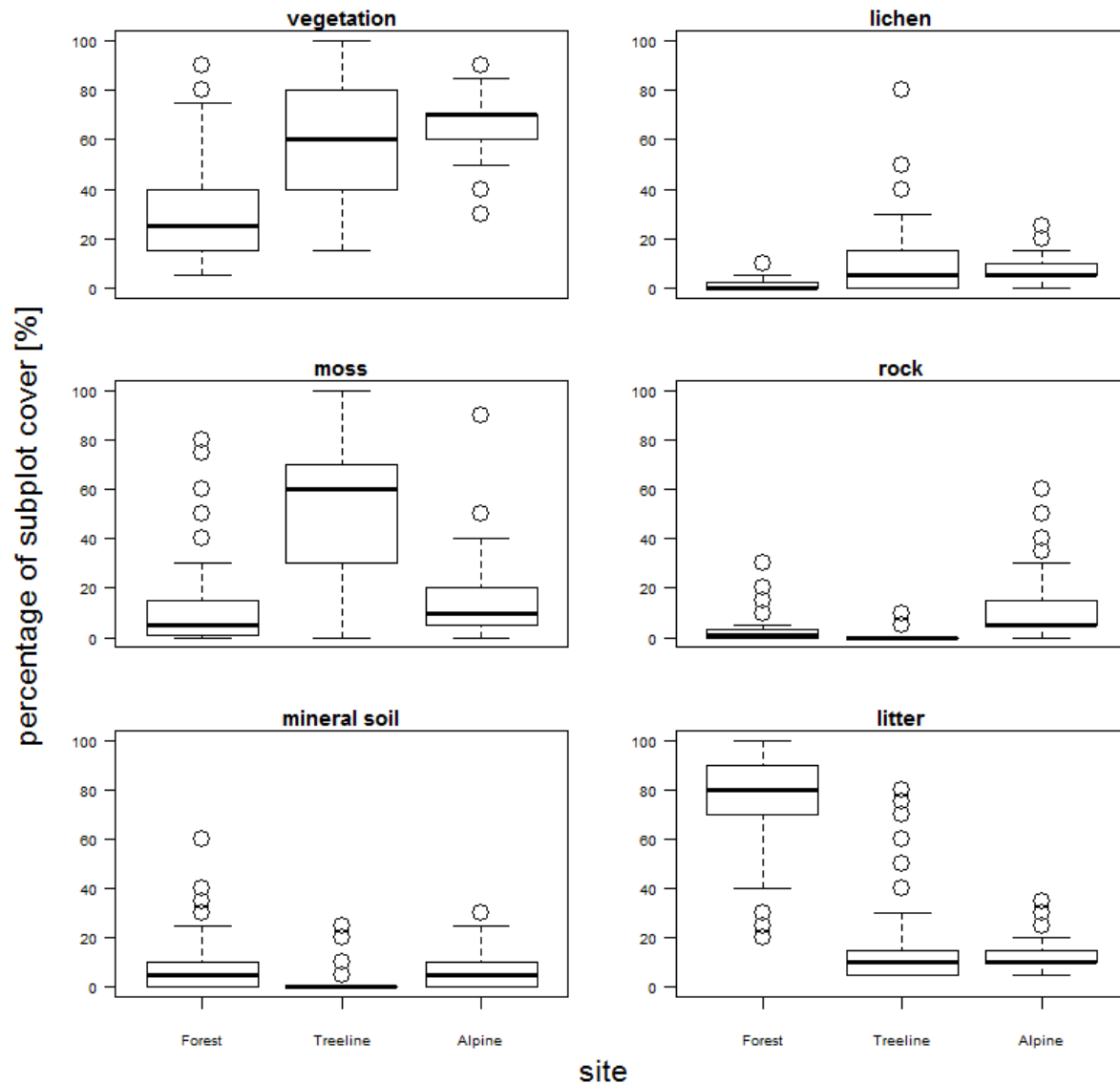
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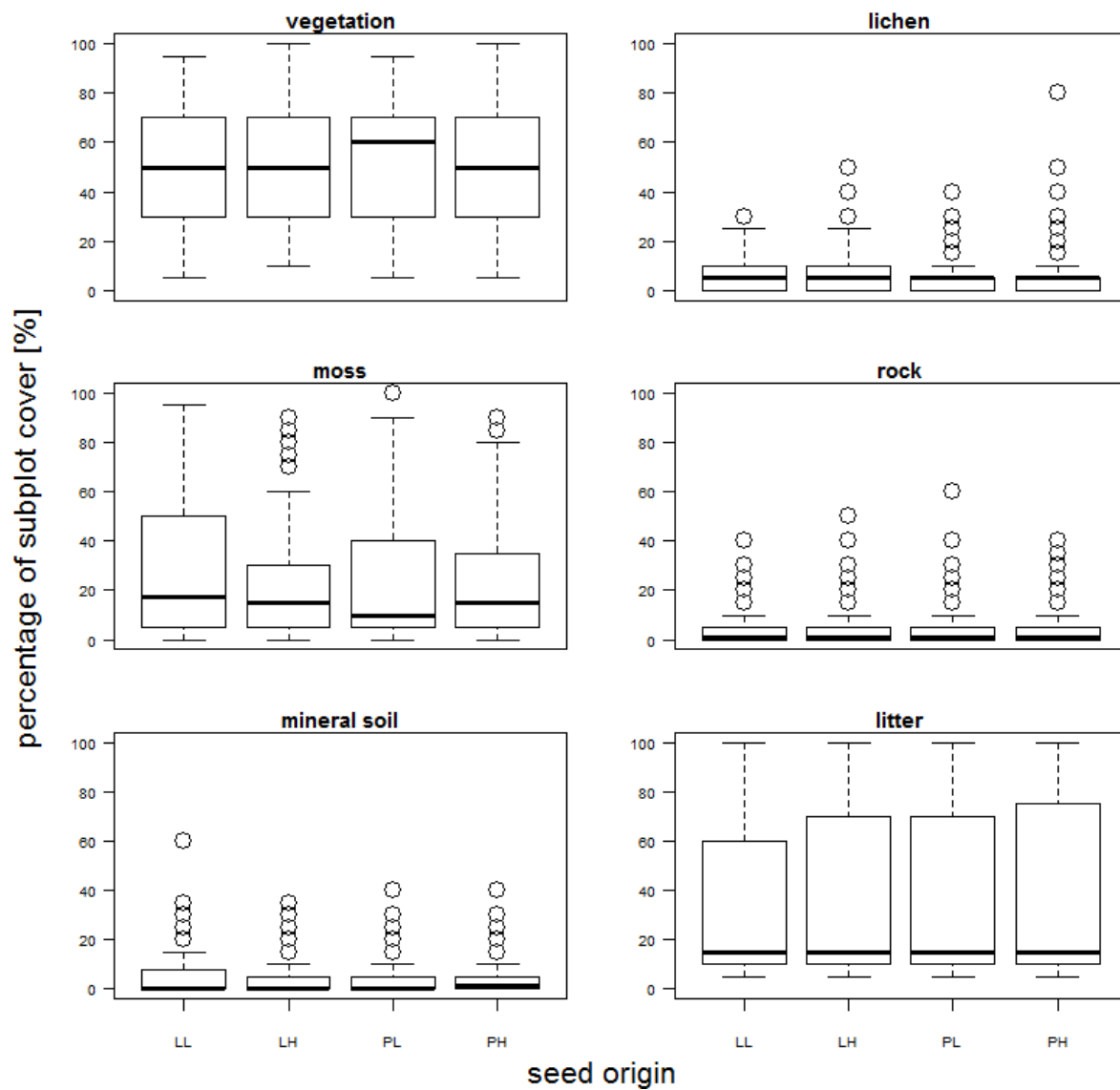
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Appendix

I. Subplot cover



Percentage of vegetation, lichen, mosses, rock, mineral soil, and litter covering subplots at the forest, treeline, and alpine site, respectively. There was less vegetation cover at the forest than at the treeline and alpine site, where it was on average above 60%. Lichen cover was tendentially low at all three sites, although with higher variation at the treeline site. Moss cover was on average around 60% at the treeline site and thus clearly higher than at the forest and alpine sites. Rock cover was minimal, but at alpine site some subplots showed a higher proportion of rocks. Mineral soil was on average less than 10% at all three sites. Litter cover was significantly higher at the forest than at the treeline and alpine site, although at the forest site some subplots showed an exceptionally high proportion of litter. Vegetation and litter cover showed inverse trends: at the forest site the former was low and the latter high, at the treeline and alpine site the opposite was the case.



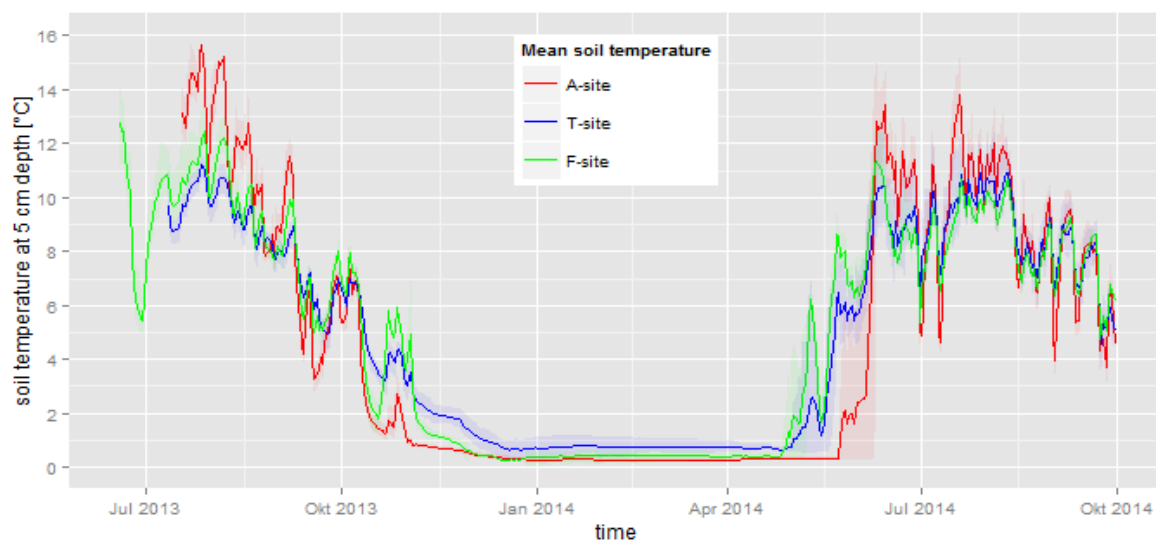
Percentage of vegetation, lichen, moss, rock, mineral soil, and litter covering subplots sown with *L. decidua* from low elevation and high elevation provenances and *P. abies* from low and high elevation provenances, respectively. The percentage of subplot cover did not significantly differ between subplots sown with different species and provenances.

II. Competing vegetation

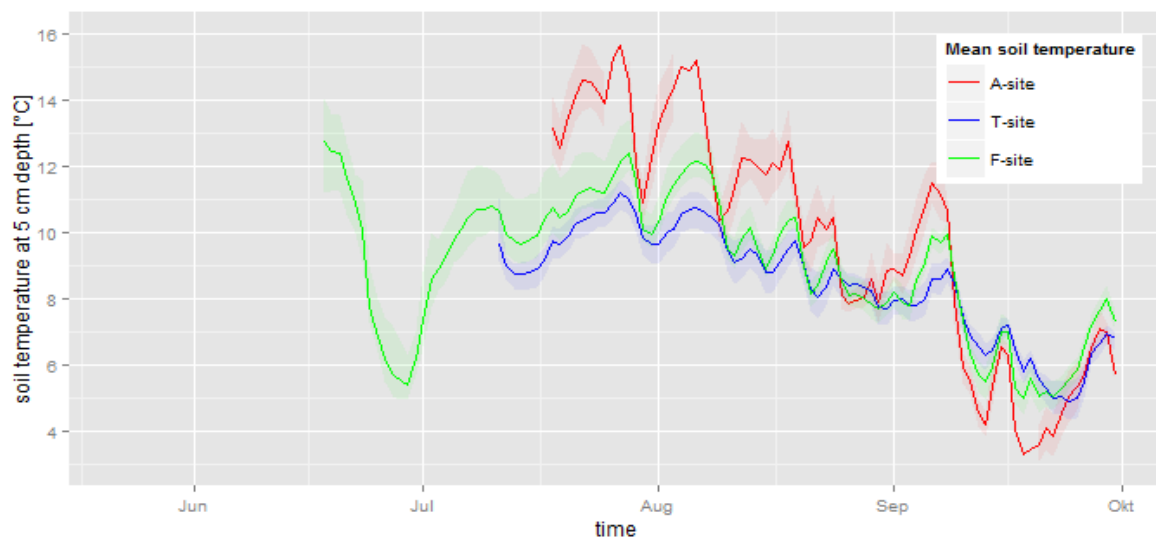
Competing vegetation of some herbaceous species per site. At the forest site, fewer species were found but with larger leaf dimensions, i.e. *Adenostyles* sp., *Achillea macrophylla*, and *Cicerbita alpina*.

forest site	treeline site	alpine site
<i>Adenostyles alliariae</i>	<i>Empetrum nigrum</i>	<i>Cirsium spinosissimum</i>
	<i>Calluna vulgaris</i>	<i>Pulsatilla alpina</i> s.l.
	<i>Cetraria islandica</i>	<i>Phyteuma hemisphaericum</i>
<i>Adenostyles alpina</i>	<i>Rhododendron ferrugineum</i>	<i>Campanula scheuchzeri</i>
<i>Adenostyles leucophylla</i>	<i>Vaccinium vitis-idaea</i>	<i>Senecius incanus</i> ssp. <i>Carniolicus</i>
<i>Solidago virgaurea</i>	<i>Vaccinium myrtillus</i>	<i>Arnica montana</i>
<i>Achillea macrophylla</i>	<i>Luzula sylvatica</i>	<i>Alchemilla xanthochlora</i>
<i>Homogyne alpina</i>	<i>Homogyne alpina</i>	<i>Gentiana punctata</i> (gentiana
<i>Cicerbita alpina</i>	<i>Lycopodium annotinum</i>	<i>purpurea</i> agg.)
<i>Stellaria nemorum</i>	<i>Dicranum scoparium</i>	<i>Mysotis alpestris</i> (evtl. <i>Mysotis</i>
<i>Veratrum album</i>	<i>Solidago virgaurea</i>	<i>arvensis</i>)
<i>Peucedanum ostruthium</i>	<i>Carex</i> ssp.	<i>Pyrola minor</i>
<i>Deschampsia cespitosa</i>	<i>Festuca rubra</i>	<i>Leontodon helveticus</i>
<i>Athyrium distentifolium</i>	<i>Hylocomium splendens</i>	<i>Bartsia alpina</i>
<i>Oxalis acetosella</i>	<i>Hylocomium umbratum</i>	<i>Ligusticum mutellina</i>
<i>Calamagrostis villosa</i>	<i>Rhytidiadelphus triquetrus</i>	<i>Vaccinium uliginosum</i>
<i>Dryopteris dilatata</i>	<i>Thuidium tamariscinum</i>	<i>Potentilla aurea</i>
<i>Luzula sylvatica</i>	<i>Vicia sepium</i>	<i>Homogyna alpina</i>
<i>Valeriana montana</i>	<i>Chaerophyllum villarsii</i>	<i>Leucanthemopsis alpina</i>
[...]	<i>Melampyrum pratense</i>	<i>Festuca halleri</i> agg.
	<i>Foliose lichens</i>	<i>Euphrasia minima</i>
	[...]	<i>Salix retusa</i>
		<i>Juncus trifidus</i>
		<i>Phleum alpinum</i>
		<i>Poa alpina</i>
		<i>Anthoxanthum odoratum</i>
		<i>Helictotrichum versicolor</i>

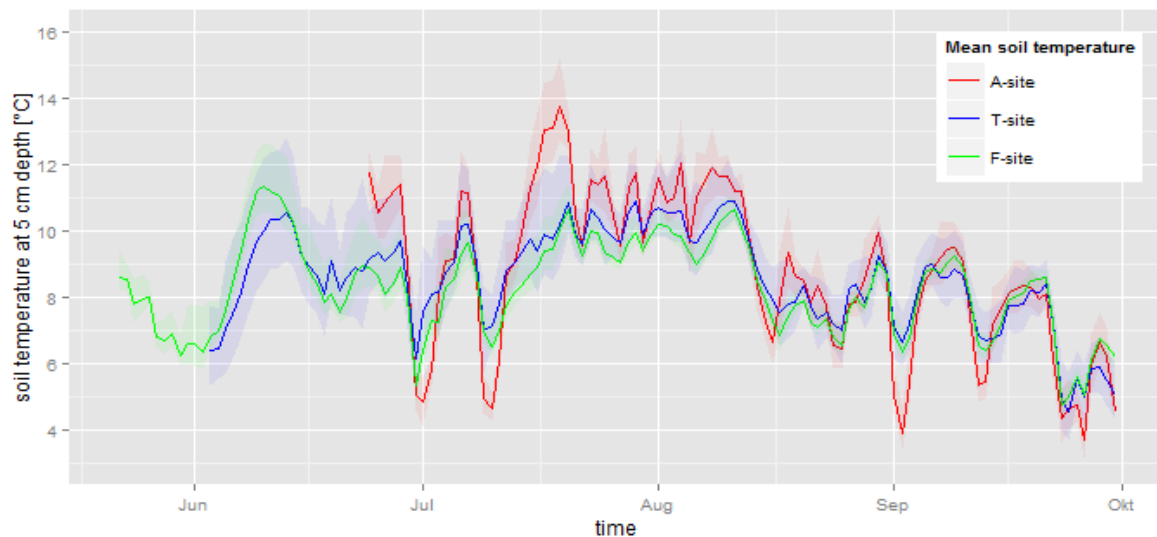
III. Soil temperature per site



Soil temperature measured at 5 cm depth in degree Celsius from the sowing date in 2013 until 30. September 2014. Lines represent daily mean temperatures; shadows represent daily minima and maxima temperatures. The red line shows the temperature for the alpine site (2400 m a.s.l.), the blue line shows the temperature for the treeline site (2100 m a.s.l.), and the green line shows the temperature for forest site (1900 m a.s.l.). Data starts from sowing time: at the alpine site 17.7.2013, the treeline site 11.7.2013, and the forest site 16.6.2013 (first year of sowing) and at alpine site 25.6.2014, treeline site 3.6.2014, and forest site 22.5.2014 (second year of sowing). Under the winter snow cover, soil temperature at 5 cm depth remained constantly and was slightly higher than the expected 0°C at the soil surface. Considering that temperature stayed constant as long as the snow covered the soil, the snow lasted longer at the alpine than at the treeline and forest site. As a consequence, the vegetation period started later at the alpine site and was thus shorter.



Soil temperature measured at 5 cm depth in degree Celsius from the sowing date in 2013 until 30. September 2013. Data starts from sowing time: at the alpine site 17.7.2013, treeline site 11.7.2013, and forest site 16.6.2013. The highest temperature over the whole period June 2013 – September 2014 was recorded in July 2013 at the alpine site. The temperature oscillations at the treeline and forest site were smaller than at the alpine site. In July 2013 temperature stayed above 8 °C and in August 2014 above 7°C at all three sites.

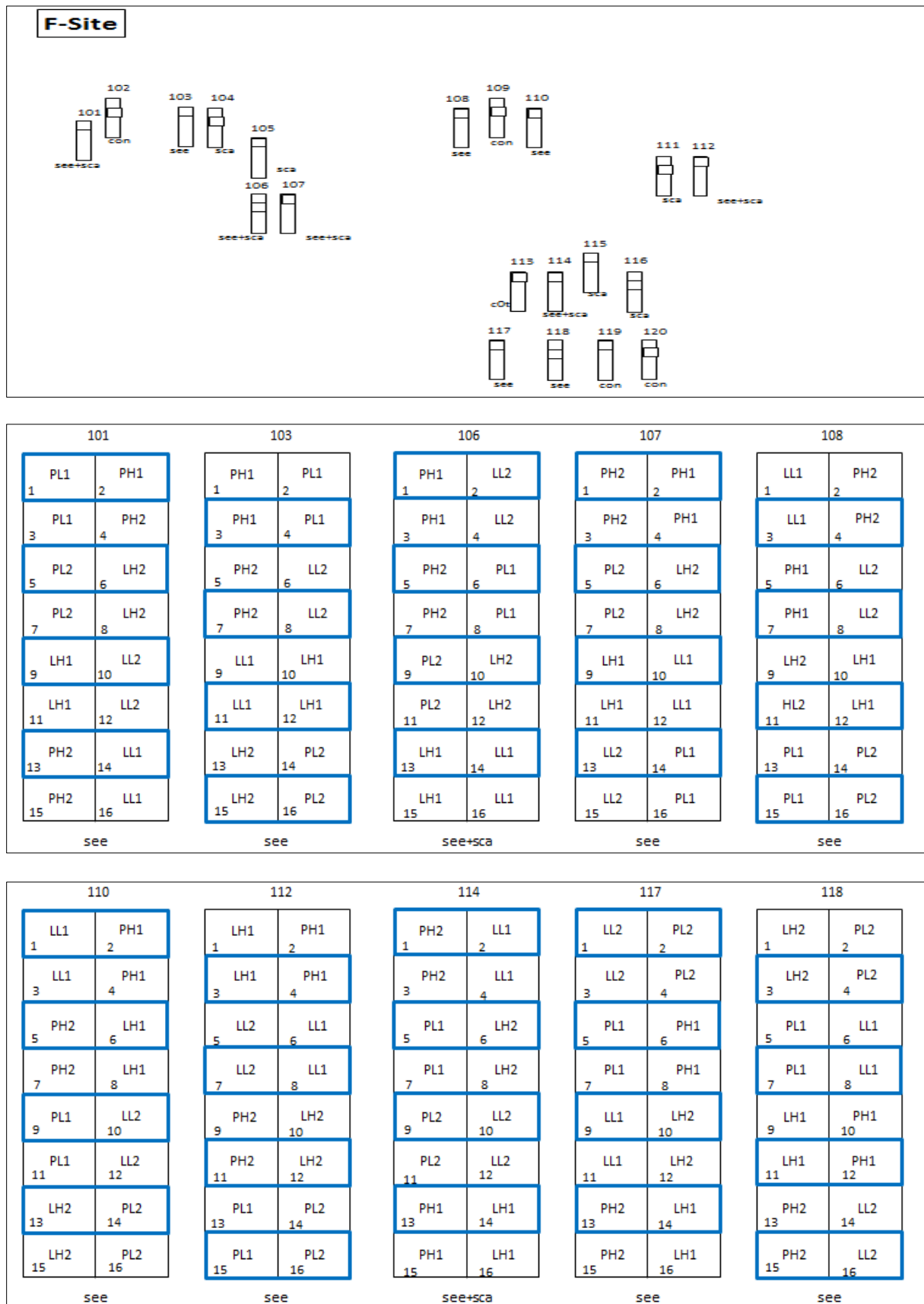


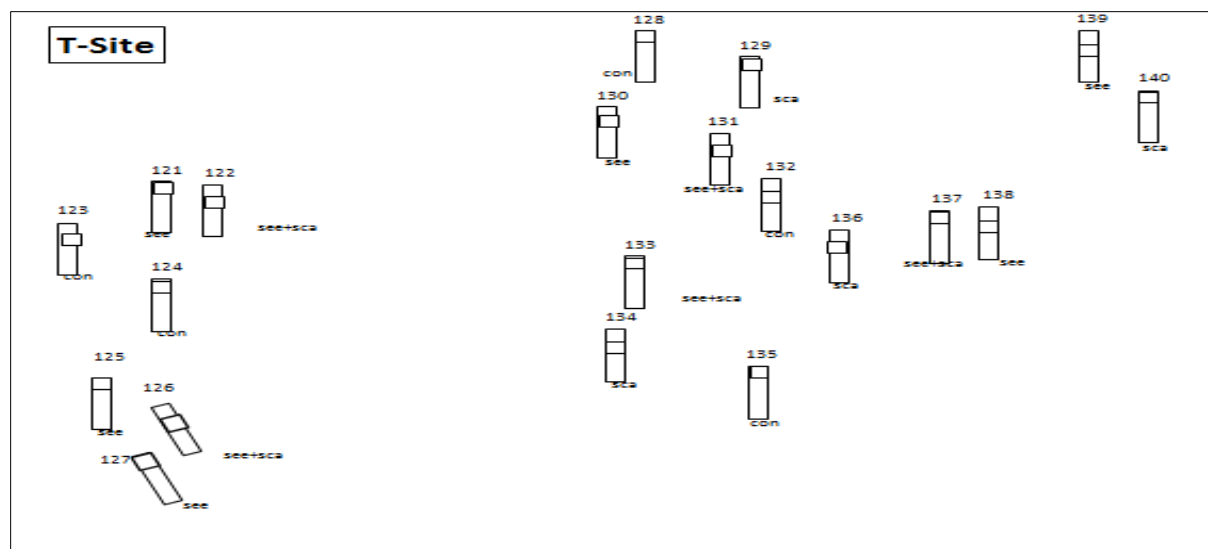
Trend of the soil temperature measured at 5 cm depth in degree Celsius from the sowing date in 2014 until 30. September 2014. Data starts from sowing time: at the alpine site 25.6.2014, treeline site 3.6.2014, and forest site 22.5.2014. As in 2013, the temperature oscillations at the treeline and forest site were smaller than at the alpine site. At the beginning of July 2014, temperature fell below 5°C twice, below 6°C in August 2014 and below 4°C in September at the alpine site.

Overview of monthly mean soil temperatures [°C] and standard deviations per site from June 2013 to September 2014.

year	month	forest site [°c]	treeline site [°c]	alpine site [°c]
2013	June	8.8±3.0	NA	NA
	July	10.4±1.0	9.9±0.8	14.2±1.9
	August	9.7±1.4	9.2±0.9	11.2±2.2
	September	7.0±1.6	6.8±1.2	6.6±2.5
	October	4.8±1.9	4.8±1.3	3.2±2.2
	November	1.4±1.0	2.1±0.5	0.7±0.1
	Dezember	0.4±0.1	0.8±0.2	0.4±0.1
2014	January	0.4±0.1	0.8±0.1	0.3±0.1
	February	0.4±0.1	0.8±0.1	0.3±0.1
	March	0.4±0.1	0.8±0.1	0.3±0.1
	April	0.5±0.2	0.7±0.1	0.3±0.1
	May	4.8±2.4	3.3±2.0	0.7±0.7
	June	8.7±1.5	8.6±1.4	9.2±3.7
	July	8.8±1.2	9.4±1.1	9.9±2.5
	August	8.6±1.3	9.0±1.3	9.4±1.8
	September	7.3±1.3	7.2±1.3	6.9±1.8

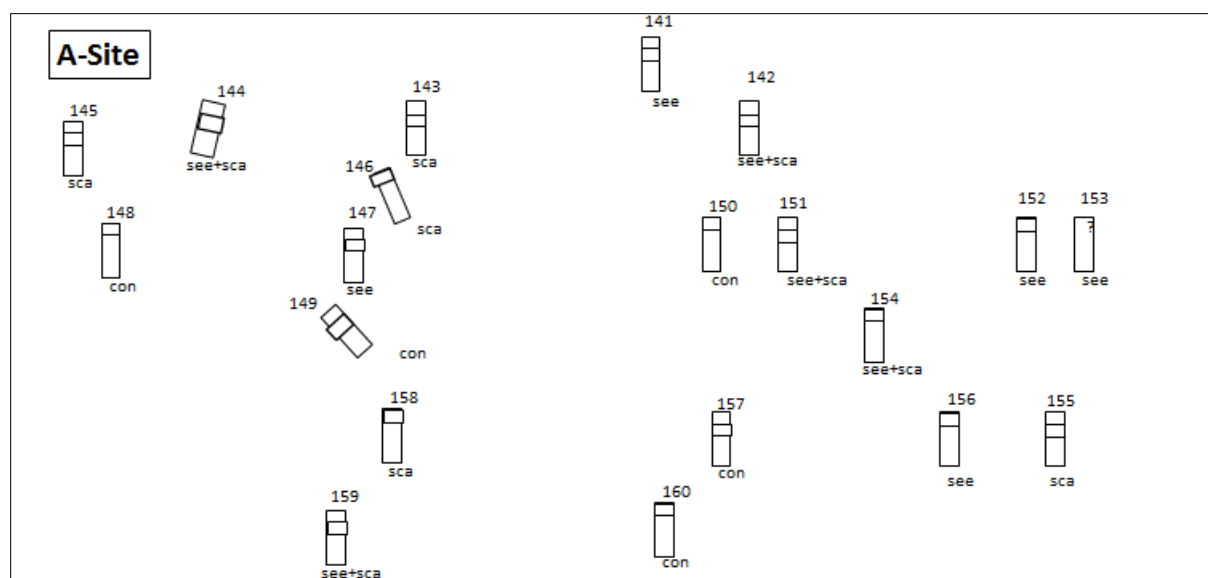
IV. Experimental Design





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6	LL2	6	PL2	6	LH2	6	PH2	6	LH2
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V. Field Protocol 2014

Site: A T F					Survey date:				
Plot number:					Seeded: YES NO Scarified: YES NO				
subplot number	cage	# seedlings	seedling shoot length [cm]	seedling total length (with cotyledons) [cm]	subplot number	cage	# seedlings	seedling shoot length [cm]	seedling total length (with cotyledons) [cm]
1					2				
3					4				
5					6				
7					8				
9					10				
11					12				
13					14				
15					16				
Remarks:									

VI. Significance classes for fixed effects and interactions

Significance classes for fixed effects and interactions, respectively.

<i>P</i> -value for single fixed effects	<i>P</i> -value for interactions	notation	interpretation
$p > 0.01$	$p > 0.05$	n.s.	not significant
$0.01 \geq p > 0.001$	$0.05 \geq p > 0.01$	*	weakly significant
$0.001 \geq p > 0.0001$	$0.01 \geq p > 0.001$	**	strongly significant
$0.0001 \geq p$	$0.001 \geq p$	***	very strongly significant

VII. Main effects and interactions of the alternative models

Main effects of site, cage, species, provenance, scarified and year, as well as their interactions, for the final reduced models of germination, survival, and growth, respectively. Germination model is based only on the treeline and alpine sites, whereas the growth model on all three sites. Values and symbols are χ^2 -values, P -values and significances, respectively from likelihood ratio tests of mixed-effect models. The significance levels for fixed effects are corrected for anti-conservative P -values ($\alpha = 0.01$) whereas for interactions not ($\alpha = 0.05$). Degrees of freedom are two for site and its interactions, and one for the other main effects and their interactions.

	germination		growth	
	χ^2	P	χ^2	P
<i>Main effects</i>				
site	5.754	0.016(*)	35.175	< 0.001
cage	15.557	< 0.001	0.740	0.390
species	24.229	< 0.001	0.014	0.905
provenance	34.735	< 0.001	10.896	0.001**
scarified	3.042	0.081	0.893	0.345
year	0.057	0.812	5.929	0.015(*)
<i>Interactions</i>				
site \times cage	0.009	0.926	0.786	0.675
site \times species	0.038	0.846	0.427	0.808
site \times provenance	0.375	0.540	4.767	0.092
site \times scarified	6.042	0.014*	1.301	0.522
site \times year	88.867	< 0.001	5.372	0.068(*)
cage \times species	1.413	0.235	1.216	0.270
cage \times provenance	5.606	0.018*	0.013	0.909
cage \times scarified	0.048	0.827	5.293	0.021*
cage \times year	5.451	0.020*	1.317	0.251
species \times provenance	18.847	< 0.001	1.373	0.241
species \times scarified	0.380	0.538	0.029	0.865
species \times year	1.002	0.317	1.367	0.242
provenance \times scarified	0.413	0.520	0.274	0.601
provenance \times year	1.178	0.278	0.547	0.459
scarified \times year	3.547	0.060(*)	0.623	0.430

VIII. Germination at the forest site

Overview of the sown seeds germinated at the forest site.

plot number	cage	species	provenance	scarified	year	germpos [#]	germneg [#]	germpos [%]	germpos [%]
p101	nocage	<i>Larix decidua</i>	high	sca	2014	1	21	4.55	95.45
p101	nocage	<i>Larix decidua</i>	low	sca	2014	1	55	1.79	98.21
p106	cage	<i>Picea abies</i>	low	sca	2014	1	147	0.68	99.32
p106	nocage	<i>Picea abies</i>	low	sca	2014	1	147	0.68	99.32
p107	cage	<i>Larix decidua</i>	low	sca	2014	1	55	1.79	98.21
p108	nocage	<i>Picea abies</i>	low	nosca	2013	1	147	0.68	99.32
p110	cage	<i>Picea abies</i>	low	nosca	2013	1	147	0.68	99.32
p112	cage	<i>Picea abies</i>	low	sca	2013	1	147	0.68	99.32
p112	nocage	<i>Picea abies</i>	high	sca	2013	1	121	0.82	99.18
p114	cage	<i>Larix decidua</i>	low	sca	2014	2	54	3.57	96.43
p117	cage	<i>Picea abies</i>	low	nosca	2014	1	147	0.68	99.32

IX. Random effects

Variance and standard deviation of the three random effects subplot_row, subplot_pair, and plot_number for final reduced models of germination, survival, and growth.

random effect	germination		survival		growth	
	var	std. dev.	var	std. dev.	var	std. dev.
subplot-row	2.25	1.50	0.06	0.24	0.00	0.06
subplot-pair	0.23	0.48	1.76	1.33	0.06	0.25
plot-number	0.01	0.11	1.17	1.08	0.20	0.45

X. Mean values for germination, survival, and growth

Mean germination percentages at all three sites, winter survival percentages and growth in centimetres of seedlings at the treeline and alpine sites for the main effects.

main effect	level	germination	survival	growth
site	forest	0.1±0.0	—	—
	treeline	5.9±0.8	37.8±5.1	3.8±0.1
	alpine	8.0±0.8	17.4±4.6	2.3±0.1
cage	no cage	4.1±0.5	33.5±5.7	2.9±0.2
	cage	5.2±0.6	24.7±4.6	3.0±0.1
species	<i>Larix decidua</i>	6.4±0.7	28.3±5.0	3.0±0.1
	<i>Picea abies</i>	2.9±0.3	29.2±5.2	2.8±0.1
provenance	low	6.9±0.1	31.9±4.3	3.1±0.1
	high	2.4±0.3	23.0±6.5	2.6±0.1
scarified	unscarified	3.9±0.5	13.2±3.7	2.8±0.2
	scarified	5.4±0.6	44.1±5.4	3.0±0.1
year	2013	4.2±0.6	27.7±3.5	3.4±0.1
	2014	5.1±0.6	—	2.7±0.1
overall mean	—	4.7±0.4	28.8±3.6	2.9±1.0

XI. Mean values of interactions for germination, survival, and growth

Mean germination percentages of all three sites, winter survival percentages and growth in centimetres of seedlings from the treeline and alpine sites, for the two-way interactions.

interaction	level	germination	survival	growth
site × cage	forest × no cage	0.1±0.1	—	—
	forest × cage	0.1±0.1	—	—
	treeline × no cage	5.2±1.0	44.2±7.5	3.7±0.2
	treeline × cage	6.6±1.2	31.4±7.0	3.9±0.1
	alpine × no cage	7.0±1.1	18.4±7.7	2.3±0.1
	alpine × cage	9.0±1.2	16.5±6.3	2.2±0.0
site × species	forest × <i>Larix decidua</i>	0.2±0.1	—	—
	forest × <i>Picea abies</i>	0.1±0.0	—	—
	treeline × <i>Larix decidua</i>	7.9±0.1.3	34.0±7.2	3.9±0.2
	treeline × <i>Picea abies</i>	3.9±0.8	40.7±7.6	3.8±0.1
	alpine × <i>Larix decidua</i>	11.1±1.4	21.6±6.7	2.4±0.1
	alpine × <i>Picea abies</i>	4.9±0.6	12.9±6.0	2.2±0.1
site × provenance	forest × low	0.2±0.1	—	—
	forest × high	0.1±0.1	—	—
	treeline × low	9.0±1.4	40.2±5.8	3.9±0.1
	treeline × high	2.8±0.6	32.8±7.3	3.6±0.1
	alpine × low	11.6±1.3	21.4±6.0	2.4±0.1
	alpine × high	4.3±0.7	8.9±4.3	2.0±0.0
site × scarified	forest × unscarified	0.0±0.0	—	—
	forest × scarified	0.2±0.1	—	—
	treeline × unscarified	3.5±0.7	13.7±5.3	4.5±0.2
	treeline × scarified	8.3±1.4	59.8±6.2	3.7±0.2
	alpine × unscarified	8.2±1.2	12.5±5.2	2.3±0.1
	alpine × scarified	7.8±1.1	22.5±7.4	2.6±0.1
site × year	forest × 2013	0.1±0.0	—	—
	forest × 2014	0.2±0.1	—	—
	treeline × 2013	9.6±1.4	37.6±5.1	3.8±0.1
	treeline × 2014	2.2±0.5	—	3.9±0.2
	alpine × 2013	3.1±0.5	17.4±4.6	2.6±0.1
	alpine × 2014	12.9±1.3	—	2.2±0.1

continued.				
interaction	level	germination	survival	growth
cage × species	no cage × <i>Larix decidua</i>	5.6±0.9	32.6±7.8	3.0±0.2
	no cage × <i>Picea abies</i>	2.6±0.5	31.7±8.3	2.8±0.1
	cage × <i>Larix decidua</i>	7.1±1.1	24.4±6.5	3.0±0.2
	cage × <i>Picea abies</i>	3.3±0.5	23.3±6.8	2.9±0.2
cage × provenance	no cage × low	6.0±0.9	36.5±6.7	3.1±0.2
	no cage × high	2.2±0.4	24.2±7.2	2.5±0.1
	cage × low	7.9±1.1	25.4±5.2	3.1±0.1
	cage × high	2.6±0.5	20.5±6.0	2.6±0.1
cage × scarified	no cage × unscarified	3.5±0.7	15.8±6.4	2.8±0.2
	no cage × scarified	4.7±0.1	45.9±8.4	3.0±0.2
	cage × unscarified	4.3±0.7	10.3±4.0	2.9±0.2
	cage × scarified	6.1±1.0	38.9±6.9	3.0±0.2
cage × year	no cage × 2013	3.6±0.7	31.1±5.5	3.4±0.2
	no cage × 2014	4.6±0.7	—	2.7±0.2
	cage × 2013	4.9±0.8	23.8±4.4	3.4±0.2
	cage × 2014	5.6±0.9	—	2.8±0.2
species × provenance	<i>Larix decidua</i> × low	10.6±1.3	29.0±5.5	3.2±0.1
	<i>Larix decidua</i> × high	2.2±0.5	26.4±11.9	2.6±0.2
	<i>Picea abies</i> × low	3.3±0.5	32.1±6.1	3.0±0.1
	<i>Picea abies</i> × high	2.5±0.4	20.2±10.6	2.6±0.1
species × scarified	<i>Larix decidua</i> × unscarified	5.3±0.9	15.4±5.2	3.1±0.2
	<i>Larix decidua</i> × scarified	7.4±1.1	40.2±7.7	3.0±0.1
	<i>Picea abies</i> × unscarified	2.5±0.4	10.4±5.5	2.5±0.1
	<i>Picea abies</i> × scarified	3.4±0.6	44.5±7.6	3.0±0.1
species × year	<i>Larix decidua</i> × 2013	5.7±1.0	28.3±5.0	3.3±0.2
	<i>Larix decidua</i> × 2014	7.1±1.0	—	2.9±0.2
	<i>Picea abies</i> × 2013	2.8±0.5	27.2±5.3	3.5±0.1
	<i>Picea abies</i> × 2014	3.1±0.5	—	2.6±0.1
provenance × scarified	low × unscarified	6.0±0.9	17.3±5.0	3.1±0.2
	low × scarified	7.9±1.1	43.6±5.9	3.2±0.2
	high × unscarified	1.8±0.4	3.3±2.9	2.0±0.1
	high × scarified	2.9±0.5	40.2±10.9	2.8±0.3
provenance × year	low × 2013	6.7±1.0	30.4±5.8	3.4±0.2
	low × 2014	7.3±1.0	—	3.0±0.2
	high × 2013	1.8±0.4	22.3±6.4	3.3±0.2
	high × 2014	7.1±0.5	—	2.4±0.1
scarified × year	unscarified × 2013	3.2±0.5	12.7±3.6	3.4±0.4
	unscarified × 2014	4.6±0.8	—	2.7±0.2
	scarified × 2013	5.3±1.0	42.4±5.3	3.4±0.2
	scarified × 2014	5.6±0.8	—	2.8±0.2

XII. Germination during summer 2014

Mean percentages of germinated seeds relative to viable seeds sown in July 2014, during summer 2014.

main effect	level	June	July	August	September
site	forest	NA	0	0	0
	treeline	NA	1.3±0.4	1.3±0.1	1.9±0.4
	alpine	NA	0	2.8±0.1	13.1±1.4
cage	no cage	NA	0.3±0.2	1.2±0.3	4.5±0.1
	cage	NA	0.5±0.2	1.6±0.3	5.5±0.1
species	<i>L. decidua</i>	NA	0.8±0.3	2.4±0.4	7.0±0.1
	<i>P. abies</i>	NA	0.1±0.1	0.3±0.1	3.1±0.1
provenance	low	NA	0.7±0.2	2.0±0.4	7.2±0.1
	high	NA	0.2±0.2	0.7±0.2	2.8±0.1
scarification	unscarified	NA	0.2±0.1	1.3±0.3	4.5±0.1
	scarified	NA	0.6±0.3	1.5±0.9	5.6±0.1
year	2014	NA	0.4±0.1	1.4±0.2	5.0±0.1

XIII. Survival during summer 2014

Mean percentages of surviving seedlings relative to the germinated seedlings in October 2013 during summer 2014, with data from seeds sown in 2013 (two-year-old seedlings).

main effect	level	June	July	August	September
site	forest	NA	NA	NA	NA
	treeline	37.6±5.1	30.5±4.7	29.4±4.6	28.2±4.7
	alpine	17.4±4.6	17.1±4.6	17.1±4.6	15.5±4.5
cage	no cage	33.5±5.7	28.2±5.3	28.1±5.3	25.6±5.3
	cage	24.7±4.7	21.6±4.3	20.5±4.1	20.1±4.2
species	<i>L. decidua</i>	28.3±5.0	27.2±4.9	26.1±4.7	24.5±5.0
	<i>P. abies</i>	29.2±5.2	22.2±4.7	22.1±4.7	20.1±4.5
provenance	low	31.9±4.3	27.7±4.1	27.5±4.1	25.7±4.1
	high	23.0±6.6	18.9±6.0	17.4±5.6	17.0±5.8
scarification	unscarified	13.2±3.7	8.25±2.7	8.3±2.7	5.3±2.3
	scarified	44.1±5.4	40.7±5.3	39.5±5.2	39.7±5.2
year	2013	28.8±3.6	24.5±3.4	24.0±3.3	22.7±3.3

XIV. Growth of seedlings during summer 2014

Mean seedling total height in cm during summer 2014, with data from seeds sown in 2013 and 2014 (one-year-old and two-year-old seedlings).

main effect	level	July	August	September
site	forest	NA	NA	NA
	treeline	3.1±0.1	3.1±0.1	3.8±0.1
	alpine	2.7±0.1	2.3±0.1	2.3±0.1
cage	no cage	3.1±0.1	2.7±0.1	2.9±0.1
	cage	2.9±0.1	2.7±0.1	3.0±0.1
species	<i>L. decidua</i>	2.8±0.1	2.7±0.1	3.0±0.1
	<i>P. abies</i>	3.3±0.1	2.8±0.1	2.9±0.1
provenance	low	3.0±0.1	2.8±0.1	3.2±0.1
	high	3.0±0.1	2.5±0.1	2.6±0.1
scarification	unscarified	3.4±0.2	2.7±0.2	2.8±0.2
	scarified	2.9±0.1	2.7±0.1	3.0±0.1
year	2013	3.1±0.1	3.1±0.1	3.4±0.1
	2014	2.7±0.1	2.4±0.1	2.8±0.1