Does the Nootka Lupin Facilitate or Impede Colonization and Growth of Native Birch in Iceland?

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ABSTRACT

Restoration of native birch woodlands is one of the long-term objectives for reclamation of severely degraded areas in Iceland. It is important to know whether the introduced Nootka lupin, commonly used for reclamation in Iceland, is likely to facilitate or impede the colonization and growth of birch on degraded and sparsely vegetated soils. A study on the effects of lupin on birch establishment from direct seeding and planting was initiated in 1995. It was based on identical experiments at four sites representing a range of precipitation and soils that affect the growing conditions for lupin. At each site, plots were set up inside mature lupin mats and at the edges of the lupin mats where lupin density was low. Control plots were set up on sparsely vegetated soils outside the lupin mats. In late June-early July, when the lupin was flowering, half of the lupin mat and edge plots at each site were cut. Birch was seeded or planted in the plots in late autumn the same year. Seedling emergence and survival of birch in seeded plots and survival and growth of planted birch seedlings were monitored for three growing seasons. Birch establishment was overall more successful in the edge plots than in the lupin mat and control plots, but the establishment pattern varied between sites. Success of direct seeding of birch and survival of planted birch seedlings in lupin mats was inversely correlated to the leaf area index. Birch survival and growth was higher in cut than undisturbed lupin plots. Frost heaving of birch seedlings was common in the control plots, but infrequent in the lupin plots where a sward layer, mostly of litter and mosses, covered the soil. The results demonstrate both facilitative and inhibitive effects of the lupin on birch establishment that varied between age and density of the lupin mat, environmental conditions at the study sites, and life stages of the birch plants. Because birch establishment was strongly inhibited in dense lupin stands, Nootka lupin should not be used in projects aimed at restoring birch woodlands where the site conditions favor formation of dense lupin mats.

KEYWORDS

Betula pubescens, birch, facilitation, inhibition, *Lupinus nootkatensis*, Nootka lupin, nurse species, planting, seeding, and seedling establishment

INTRODUCTION

Land degradation and soil erosion have altered Icelandic ecosystems since the country was settled over 1100 years ago. Birch (*Betula pubescens* Ehrh.) woodlands that were extensive during the mid-Holocene now cover about 1% of the land surface, which is less than 5% of the estimated woodland cover at the time of settlement (Sigurdsson, 1977). Other vegetation cover has also been reduced due to intense soil erosion that often has resulted in barren land (Arnalds *et al.*, 2001).

In recent years there has been growing interest in using birch in reclamation of eroded areas in Iceland, both in order to restore the woody structure of the ecosystems and for the long-term objective to restore some of the original birch woodlands. This usually requires re-introduction of birch or re-colonization from remnants of the old birch woodlands. The establishment and growth of birch on eroded areas is inhibited by a low nutrient status and intense frost heaving (Aradottir and Arnalds, 2001) that characterize their soils (Arnalds and Kimble, 2001). Successful birch establishment may therefore depend on cultural inputs such as fertilization, organic amendments, or establishment of vegetation cover.

Introduced Nootka lupin (*Lupinus nootkatensis* Donn ex. Sims) is a N-fixer and an effective colonizer capable of high production on nutrient deficient soils. It has been widely used in reclamation of eroded areas in Iceland. By fixing nitrogen and forming vegetation cover that reduces frost heaving, the lupin might serve as a nurse plant that facilitates the establishment of birch. On the other hand, the lupin often forms dense stands, where smaller plants are outcompeted (Magnússon *et al.*, 2001) and could therefore have the opposite effect by inhibiting birch establishment and growth.

A study on the effects of lupin on birch colonization and growth was initiated in 1995. The main objective was to assess the facilitative and inhibitory effects of lupin on birch establishment. The study was based on identical experiments at four disturbed sites with established lupin stands of known age. The experiments were designed to test the following hypotheses on birch-lupin relationship:

(1) The probability of birch establishment in the presence of lupin depends on the density of the lupin mat, which is affected by (A) site conditions and (B) the age of lupin at each point;

(2) the probability of birch establishment in lupin stands can be enhanced by artificially opening up the lupin mats (cutting).

IN E. van Santen and G.D. Hill (eds). Wild and Cultivated Lupins from the Tropics to the Poles. Proceedings of the 10th International Lupin Conference, Laugarvatn, Iceland, 19-24 June 2002. International Lupin Association, Canterbury, New Zealand. ISBN 0-86476-153-8.

MATERIALS AND METHODS

The experiments were all carried out on degenerated or partially reclaimed sites where lupin had been introduced and was expanding its range (Fig. 1). The sites represent a range of precipitation and soils (Table 1) that are expected to affect growing conditions for the lupin. Table 1 shows climatic data for the nearest synoptic weather station for each site. The study sites are all at a higher elevation than the corresponding weather station and are expected to have lower annual temperatures than shown in the table. A greater annual precipitation than measured at the nearest synoptic weather station was recorded near site 1 (Icelandic Meteorological Office; http://www.vedur.is) and site 2 (Jónsson, 1986). Different stages of lupin colonization were found at each site, ranging from substrate with very sparse vegetation cover and no lupin to mature lupin stands with a dense lupin mat and a well-defined litter layer.

At each site, five areas or blocks were defined and three locations selected within each: (1) within mature lupin mats, (2) at the edge of lupin mats, and (3) control, or sparsely vegetated ground outside the lupin mats. Four plots (5.5 x 1.5 m²) were set up at each of locations (1) and (2) and randomly assigned the following treatments: (a) lupin undisturbed-birch seeded; (b)

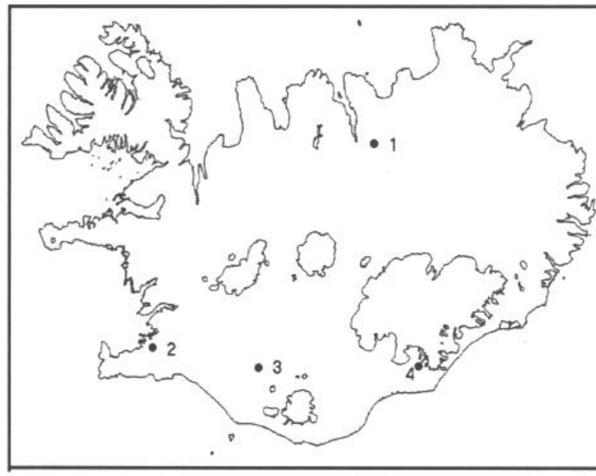

Fig. 1. Location of the study sites. Site 1: Hálsmelar in Fnjóskadalur; Site 2: Heiðmörk, near Reykjavík; Site 3: Thjórsárdalur in Arnessysla; Site 4: Svínafell in Öræfasveit.

Table 1. Location and characteristics of the study sites. Plant cover was assessed by visual estimation in four 0.2-m² quadrats within each plot.

Site no.	**1**	**2**	**3**	**4**
Location	Hálsmelar, S-Thingeyjarsysla	Heiðmörk, Gullbringusysla	Thjorsardalur, Arnessysla	Svinafell, A-Skaftafellssysla
Lat-long	65°44'N, 17°53'W	64°04'N, 21°48 W	64°06'N, 19°58'W	63°58'N, 16°52'W
Height above sea level	190-210 m	135-145 m	140-155 m	90 m
Description	Eroded, gravelly, glacial lake sediments, with remnants of birch and willow shrubland	Eroded glacial till with scattered remnants of birch and willow shrubland	Sandy lava, with sparsely vegetated tephra deposits from Hekla volcano	Glaciofluvial plain
Surface type	Lag-gravel	Lag-gravel	Coarse pumice and sand	Coarse lag-gravel and sand
Year lupine established	Before 1960	1970-1975	Around 1960	Around 1980
Plant cover outside lupine mats (control plots) in Aug. 1995 (%)				
Vascular plants	6	11	2	4
Mosses	1	7	< 1	14
Lichens	22	1	< 1	1
Annual temperature °C †				
Mean 1961-1990	3.2	4.3	3.6	4.6
1996 (June-Aug)	4.1 (10.5)	5.0 (10.3)	4.3 (10.2)	5.2 (10.1)
1997 (June-Aug)	4.0 (10.4)	5.1 (10.5)	4.4 (10.6)	5.1 (9.9)
1998 (June-Aug)	3.1 (9.1)	4.7 (10.8)	4.0 (10.8)	4.8 (9.8)
Annual precipitaiton (mm) †				
Mean 1961-1990	490	799	1117	1802
1996	435	769	1001	1663
1997	426	836	1104	2088
1998	550	751	921	1645

† Data for nearest synoptic weather station (Icelandic Meteorological Office; http://www.vedur.is

lupin undisturbed-birch planted; (c) lupin cut-birch seeded and (d) lupin cut-birch planted. At location (3) outside the lupin mats, plots were seeded and planted with birch. At site number three, an additional treatment was included in all locations, i.e. seeding of birch into seeding cones (Cercone from AB CERBO, Sweden, height 8 cm, bottom diameter 6 cm, top opening diameter 1.7 cm).

The cutting of plots took place between 29 June and 8 July 1995. At that time the lupin had started to flower in all plots, except for a couple of blocks at site 1 where snowmelt was late in the spring of 1995. The cutting time was selected with the objective to maximize the disturbance of the lupin stands and was based on earlier studies showing that lupin cut at this time would show less regrowth than if cut earlier or later (Sigurdsson *et al.*, 1995). The vegetation was cut as close to the ground as possible with a weedcutter and the litter was left on the ground.

Each study plot had 20 seeding/planting spots set out on a regular grid 50 cm apart from each other and 50 cm from the edge of the plot. The birch was seeded by a Panama Direct Seeder (Panama Pump Company, Hattiesburg, Mississippi, USA) that placed 45 ± 3 seeds (n=20) at each seeding spot, which gave about 34 live seeds per seeding spot. Fewer seeds were placed in the cones at about 15 ± 1 seeds per cone. The birch seedlings used for planting were grown in 100 cm^3 containers for one growing season. The birch was seeded and planted between Sept. 26 and Oct. 11 1995.

Seedling emergence and survival of birch in the seeded plots and survival, growth, and frost heaving of planted birch seedlings were monitored for three years. In August 1995 and 1997, the vegetation cover was estimated in four randomly distributed, 0.2 m^2 quadrats in each plot. Density of lupin stems in three size categories: mature, juvenile, and young (first year seedlings) were recorded in the same quadrats and the maximum height of lupin in the mature and juvenile categories was measured. A graded pin was used to measure thickness of the moss and litter layer at 5 points in each quadrat. Leaf area index was measured annually, late in the growing season, with Li-Cor LAI 2000.

Plots were the experimental units and data were computed as a mean per plot or a percentage of plants or seeding spots per plot. The results are presented as the mean ($\pm$ 1 standard error) of the five plots in each treatment within a location. The success of birch establishment was measured as the percentage of seeding or planting spots that had a live birch plant $\geq$ 1 year old in 1998. Birch establishment in undisturbed lupin plots was compared among sites with ANOVA, using the site-block interaction as an error term. Success of birch establishment among locations (undisturbed plots) and among cutting treatments in edge and lupin mat plots was compared by separate ANOVAs. Data was arcsine transformed where needed to comply with requirements of normal distribution. Pearson correlations were calculated for the relationship between LAI of lupin mat plots (undisturbed and cut) and birch establishment by seeding or planting. The edge and control plots were not included in these correlations because of possible confounding effects of frost heaving.

RESULTS

Characteristics of the lupin mat and the sward layer in the study plots in 1995 are shown in Fig. 2. Average height of lupin stems in undisturbed plots was greatest at sites 3 and 4 and lowest at site 1 (Fig. 2A). Height of lupin in edge plots was always lower than in lupin stands, reflecting the younger age of the lupin there, and height of lupin in cut plots was always less than in corresponding undisturbed plots (Fig. 2A). Leaf area index (LAI)

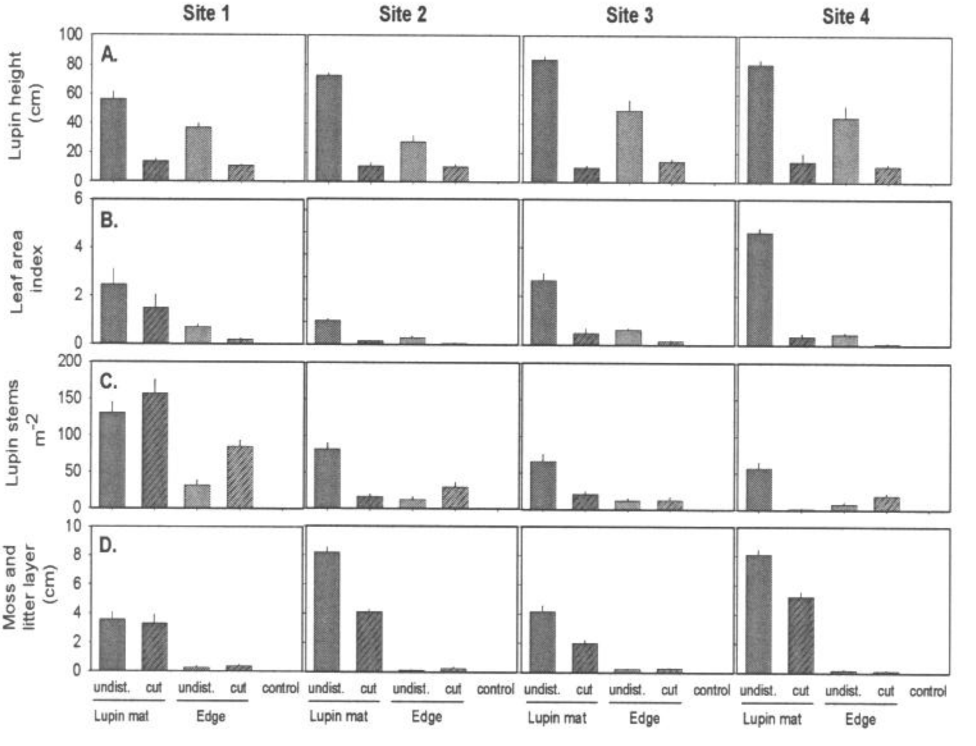

Fig. 2. Some characteristics of lupin and sward layer in the experimental plots in August 1995. A. Height of lupin, B. leaf area index (LAI); C. density of mature lupin stems; D. the depth of moss and litter layer. The bars represent the average of five plots within each site. Vertical lines show 1 SE. Dark-gray bars indicate lupin mats, light-gray bars indicate edge plots and white bars indicate control plots. Solid bars fills are for undisturbed plots and hatched bars for cut plots.

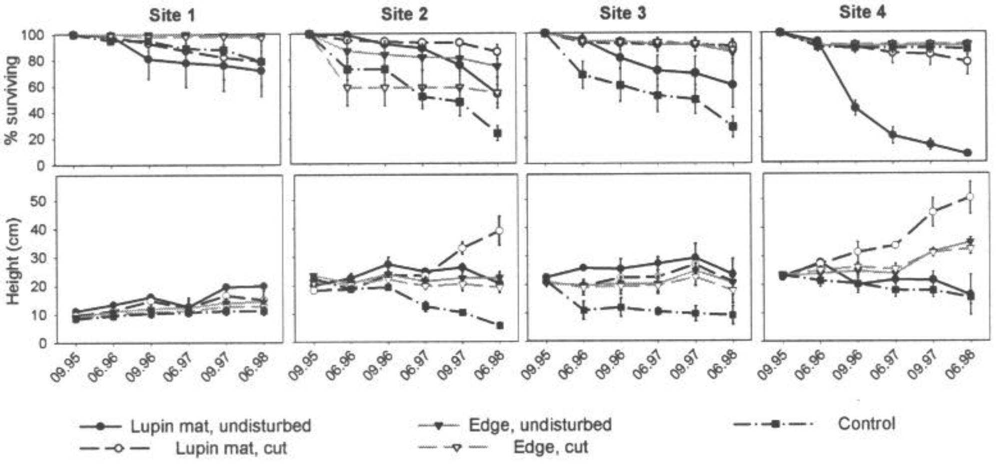

Fig. 3. Survival (top) and growth (bottom) of planted birch seedlings in the experimental plots, from time of planting in Sept.-Oct. 1995 to June 1998. The points show the mean (and 1 SE) of five plots with 20 plants each. Height data includes measurements of life plants only.

of undisturbed plots was greatest at site 4 (Fig. 2B) and lowest at site 2. However, the low LAI at site 2 in 1995 is probably an underestimate as it was measured late in the season when the lupin foliage had started to wilt. In 1996 and 1997, the lupin plots at site 2 had a greater LAI than at sites 1 and 3 (not shown). LAI was lower in cut plots and edge plots than in the undisturbed lupin plots (Fig. 2B). Site 1 had overall greatest density of mature lupin stems and higher stem density in cut than undisturbed plots (Fig. 2C). At the other three sites, density of mature lupin stems was greatly reduced by the cutting. Both undisturbed and cut lupin plots had a layer of mosses and litter, but this layer was limited in the edge plots and usually not present in the control plots (Fig. 2D).

In 1998, survival of planted seedlings was overall greater in edge plots than in undisturbed lupin or in control plots ($F_{location}$=23.7; P <0.001), but survival in lupin mats and control plots varied greatly between sites (Fig. 3). At sites 2 and 3 survival of planted birch seedlings was lowest in the control plots, but at site 4 survival was lowest in undisturbed lupin plots (Fig. 3). Survival of planted seedlings in undisturbed lupin plots decreased with time and was lowest at site 4 where only 7% of the planted seedlings were left in 1998, but highest at site 1 (F_{site}=5.0; P=0.02). The effect of cutting the lupin on the survival of planted birch seedlings was significant ($F_{cutting}$=10.4; P=0.02), but there was also a strong interaction between cutting and location (F_{cxl}=17.1; P <0.001), as the effect of cutting was more pronounced in the lupin mats than in the edge plots. Survival of planted seedlings in lupin plots (cut and undisturbed) in 1998 was negatively correlated with the 1995 LAI (r =-0.68; P <0.001; n=37), and correlation with the 1997 LAI was even stronger (r =-0.82; P <0.001; n=40). Survival of planted birch seedlings in control plots at sites 2 and 3 was under 30%, with most of the mortality occurring in the winter. High winter mortality was also observed in cut edge plots at site 2 during the first winter after planting (Fig. 3). Frost heaving of planted seedlings was common in plots with high winter mortality, that is, in control and edge plots at sites 2 and 3 (Fig. 4). On the other hand, frost heaving was rarely observed at site 4 (Fig. 4) where the substrate was coarse gravel on glaciofluvial plain, and it was uncommon in lupin plots that had a moss and litter layer (Figs. 2D and 4).

In 1998 the average height of planted seedlings in control plots was less than at the time of planting except at site 1 (Fig. 3). Growth of planted birch seedlings was in most cases greater in the presence of lupin than in the control plots (Fig. 3). Seedling growth was greatest in cut lupin plots at sites 2 and 4, where the seedlings had more than doubled their planting height by 1998 (Fig. 3).

Seedling emergence was similar in all location-cutting combinations at sites 1 and 2 and was observed in 40-70% of seeding spots there (Fig. 5). At site 3, seedling emergence was very low (<1-20% of seeding spots) and was mostly limited to the lupin plots. Seeding in cones at site 3, on the other hand, resulted in much greater seedling emergence, which was greatest in the lupin plots and least in the control plots (Fig. 5). Seedling emergence was also greatest in the cut and undisturbed lupin plots at site 4.

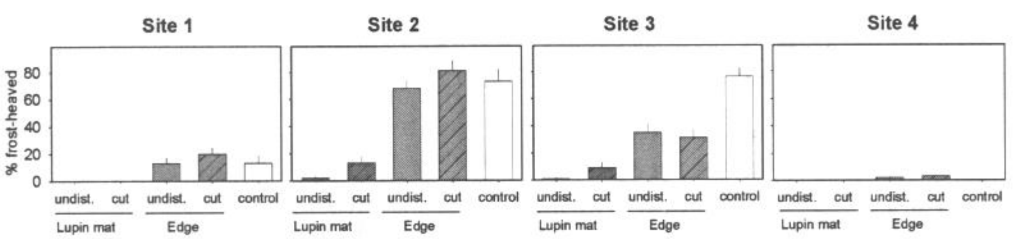

Fig. 4. Frost heaving of birch seedlings during the first winter after planting. The bars show the percentage of planted seedlings that were frost heaved. Colors and hatchment of bars are the same as in Fig. 2.

The success of direct seeding was measured by the proportion of seeding spots that had ≥ 1-year-old live seedlings in 1998. Seeding success was greatest at site 1, both overall and in undisturbed lupin plots. No live seedlings were found by 1998 in undisturbed lupin plots at sites 2 and 4, in spite of the high seedling emergence recorded there (Fig. 5). The success of seeding in cut and undisturbed lupin plots was not significantly correlated with the LAI in 1995 ($r=-0.16$; $P=0.29$), but negatively correlated with the LAI in 1996 ($r=-0.42$; $P=0.002$) and 1997 ($r=-0.53$; $P<0.001$). The effect of location on seeding success was significant ($F=4.3$; $P=0.02$) and was greatest in undisturbed edge plots and lowest in the control plots. However, relative seeding success in control *vs.* undisturbed lupin plots varied between sites (Fig. 5).

DISCUSSION

The results demonstrate both facilitative and inhibitive effects of lupin on birch establishment and growth. The success of direct seeding and planting of birch was generally greater in edge plots than in control plots (Figs. 3 and 5), indicating facilitation of birch establishment by lupin on the sparsely vegetated substrates characterizing the study sites. On the other hand, success of direct seeding and planting of birch was low in dense lupin mats, indicating inhibition of birch establishment by lupin. Comparable interplay between facilitation and inhibition caused by competitive interactions has been described by many authors (Morris and Wood, 1989; del Moral, 1993; Walker, 1993; Chapin *et al.*, 1994; Bellingham *et al.*, 2001) and ascribed to various factors, including physical factors and life stages of both the benefactors and beneficiaries (Callaway and Walker, 1997).

To evaluate hypothesis 1A, i.e. that the probability of birch establishment depends on lupin density which, in turn, is affected by site conditions, birch establishment in undisturbed lupin mats was compared among the four sites. Birch establishment in undisturbed lupin mats varied between sites (Figs. 3 and 5) and was lowest at site 4, which had the highest LAI and the second greatest lupin height (Fig. 2). In contrast, the birch establishment rate in undisturbed lupin mats was greatest at site 1, which had the lowest mean LAI and lupin height. These results support the hypothesis and indicate that the probability of birch establishment in lupin mats decreased with increased density of the lupin mats. Magnusson *et al.* (2001) found that the lupin did not form as thick, dense, and long-lived thickets at inland sites in North-Iceland as in other areas of the country and attributed this to the drier climate in the North. In this study, a similar pattern was observed, i.e. mean annual precipitation at the weather station closest to site 4, which had highest LAI in mature lupin stands, was more than three times greater than at the weather station nearest to site 1, which had the lowest LAI in mature lupin stands (Table 1).

Comparison of birch establishment in undisturbed lupin mats and undisturbed edge plots gives an evaluation of hypothesis 1B, i.e. that the age of the lupin stand affects density of the lupin mat (cf. Magnusson *et al.*, 1995) and hence, birch establishment. Survival of planted birch seedlings was always lower in undisturbed lupin mats than in undisturbed edge plots (Fig. 3) that had less lupin height, LAI, and density of mature lupin stems than the lupin mats (Fig. 2). The same pattern was observed for success of seeding at sites 2 and 4, but the overall level was very low (Fig. 5). On the other hand, success of seeding was very similar in lupin mats and edge plots at sites 1 and 3, where it was respectively high and low (Fig. 5). Finally, seeding success was greater in the mature lupin plots than in the edge plots when seeded in cones at site 3 (Fig. 5), where the stabilization of pumice and sand by the lupin may have outweighed the disadvantages of the lupin cover. Morris and Wood (1989) have reported a similar pattern of facilitation by diffuse lupin

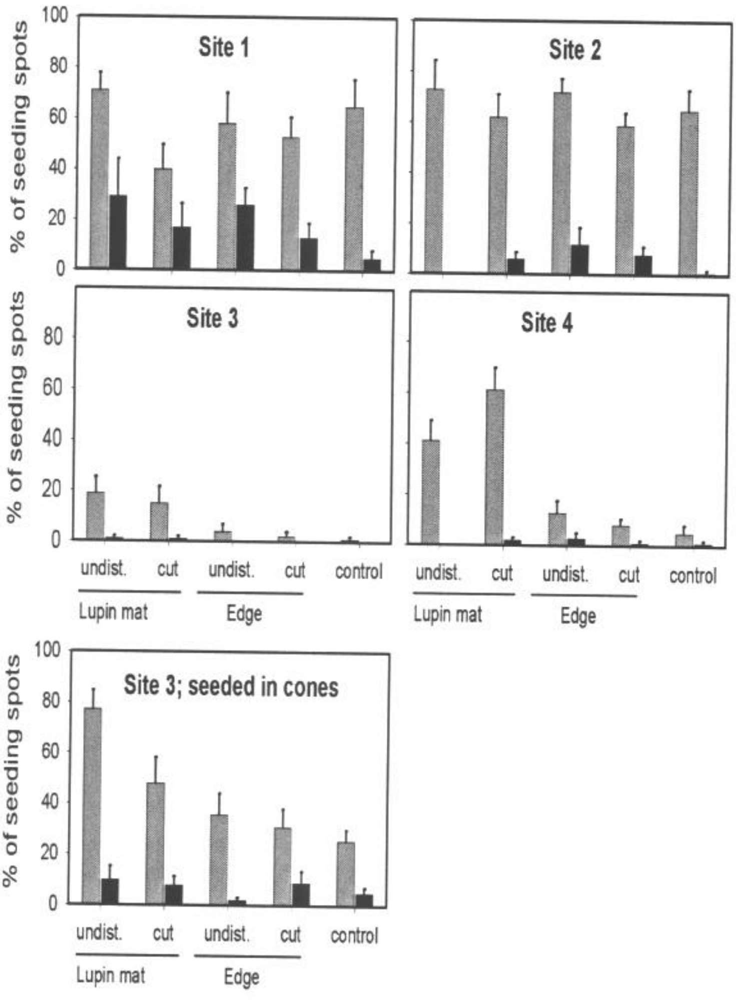

Fig. 5. Seedling emergence and seeding success of birch in the experimental plots. The bars show the percentage of seeding spots where seedling emergence of birch was observed (gray bars) and seeding spots that had live seedlings ≥ 1 year old in 1998 (black bars). Each bar represents the mean of five plots with 20 seeding spots each. Vertical lines show 1 SE.

(*Lupinus lepidus*) and inhibition in dense lupin patches on Mt. St. Helen.

The cutting of lupin reduced its height and LAI at all sites and reduced the density of mature stems at sites 2-4 (Fig. 2). At site 1, cut lupin plots had slightly higher density of mature lupin stems two months after cutting (Fig. 2), and it was the only site where average lupin height, LAI, and stem density were comparable in cut and undisturbed lupin plots two years later (not shown). The inconsistency in lupin reaction to cutting between sites can be attributed to difference in lupin phenology at the time of cutting, (cf. Sigurdsson *et al.*, 1995). The lupins at sites 2-4 were in full flower when cut, but at site 1, the flowering had barely started in three out of five replications. Survival and growth of planted birch seedlings was generally higher in cut than undisturbed lupin plots (Fig. 3). This supports the hypotheses that birch establishment can be enhanced by opening up the lupin stands. Birch survival in cut and undisturbed lupin plots was negatively correlated with plot LAI, which further demonstrates the inhibitory effects of dense lupin mats on birch. The pattern of seeding success for birch was not as clear as that for survival of planted seedlings, but nevertheless it showed a significant negative correlation with the 1997 LAI.

Frost heaving of planted birch seedlings seemed to be one of the major causes of their winter mortality in control and edge plots at sites 2 and 3 (Fig. 4). On the other hand, little frost heaving was observed at site 1 and hardly any at site 4 (Fig. 4). Several factors that affect frost heaving could contribute to these differences between sites, including differences in soil moisture, soil texture, snow cover, and frequency of frost-thaw cycles (Heidman, 1976; Bergsten *et al.*, 2001; Matsuoka, 2001). The occurrence of frost heaving in lupin mats at sites 2 and 3 was much lower than in control and edge plots. The lupin and the moss and litter layer formed in lupin mats probably acted as a thermal insulator that inhibited diurnal freeze-thaw action (cf. Matsuoka, 2001) and, therefore, frost heaving of the planted seedling. Other studies have shown that frost heaving of planted seedlings can be reduced by an organic surface layer or by planting in vegetation instead of bare ground (Aradottir and Gretarsdottir, 1995; Oddsdottir *et al.*, 1998; Bergsten *et al.*, 2001). The results from the current study indicate that facilitation through formation of plant cover and moss and litter layer reduced the rate of frost heaving in lupin mat and edge plots compared to the control (Figs. 2 and 4).

Height of planted birch seedlings was greater in the presence of lupin than in control plots, except at site 1 where seedling height in all treatment-location combinations was similar and in undisturbed lupin plots at sites 2 and 4, where the lupin mat was very dense (Fig. 3). Top kill was common in the planted seedlings of control plots, and by 1998 their average height was less than at the time of planting at all sites except site 1 (Fig. 3). Slow or negative growth during the establishment phase is commonly observed on exposed sites in Iceland (Aradottir and Gretarsdottir, 1995; Aradottir *et al.*, 1997), but in this study the negative growth observed in the control plots was not duplicated in the presence of lupin, except for the very dense lupin mats. Facilitation of birch growth was especially pronounced in cut lupin plots at sites 2 and 4, and indicated that cutting dense lupin mats could be a useful preparation for afforestation practices. At site 3, the birch seedlings were browsed by a group of sheep in the fall of 1997, causing a decrease in average seedling height from the Sept. 1997 measurement to the June 1998 measurement (Fig. 3).

The facilitative and inhibitory effects of lupin on birch establishment are the outcome of different processes (cf. Walker, 1993). Nitrogen fixers can, for example, facilitate establishment of later colonizers by providing a shady, moist microenvironment that favors seedling emergence, as seen by high seedling emergence in lupin plots in this study (Fig. 5). Nitrogen content of soil increases where lupin colonizes barren and partly vegetated areas (Magnusson *et al.*, 2001), and the increased nitrogen can facilitate growth of birch seedlings (Fig. 3). In this study, the lupin cover and the associated litter and moss layer reduced the rate of frost heaving. By sheltering the birch seedlings from wind, the lupin may also have affected their growth. The inhibitory effects on both planted and seeded birch were most pronounced where the lupin mat was dense and were probably mostly related to competition for light and/or space. Also, in tall lupin mats the stems often subside in late summer and their weight can press down small birch seedlings growing near them. If the weight of lupin stems and litter push the birch seedlings into more or less vertical position, the competitive effects of lupin will become even more severe in successive years. This pattern was observed at site 4 and to a lesser degree at site 2, resulting in successively smaller stature and survival of the birch seedlings (Fig. 3). In plots where the lupin mat had been cut and thus opened up before planting, competition was reduced and survival and growth of birch was facilitated.

This study shows that lupin can be used as a nurse species for birch on degraded soils with sparse vegetation cover, given that the lupin patches are not too dense or, if they are, are opened up by cutting or other means. As the lupin is an aggressive and invasive exotic species (Magnússon *et al.,* 2001), it should be used with caution, and where it can form dense mats, its inhibitive effects on birch establishment and growth are expected to outweigh the facilitative effects. The Nootka lupin should, therefore, not be used in reclamation projects aimed at restoring birch woodlands under conditions where it can form dense stands.

ACKNOWLEDGEMENTS

This research was supported by grants from the Icelandic Technical Fund, Agricultural Productivity Fund of Iceland, and the Nordic Forest Research Cooperation Committee. Most of the fieldwork was conducted in association with the Icelandic Forest Research Station at Mogilsá with the assistance of Járngerdur Grétarsdóttir and Tumi Traustason. Contributions by Borgthor Magnusson and Sigurdur Magnusson during the initial stage of the project are gratefully acknowledged. Ólafur Arnalds and Kristín Svavarsdóttir gave valuable comments on the manuscript. The Icelandic Forest Service, Reykjavik Forest Association, and landowners at Svinafell granted access to the experimental areas.

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