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Growth of nitrogen-fixing *Alnus incana* and *Lupinus* spp. for restoration of degenerated forest soil in northern Sweden

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Abstract

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In the interior of northern Sweden, more than 100,000 ha of previously productive forest land have degenerated soils. The presently thin humus layer and the resulting lack of mineralizable nitrogen and organic material results from strongly reduced litter production on the now almost tree-less areas. Intense forest fires in the past, as well as unfavourable forestry practices, are likely to have caused this situation. Cultivation of nitrogen-fixing plants, the native grey alder. *Alnus incana* (L.) Moench, and introduced lupins. especially *Lupinus nootkatensis* Donn, was tried in the present stydy as a means of soil restoration.

After 7 to 9 years, mesic sites with a temperature sum of >800 daydegrees during the growing season gave higher survival and better growth of *A. incana* than did drier or cooler sites. At the northernmost, coolest site, *L. nootkatensis* performed very well while *A. incana* did not. Liming and, to some extent, soil scarification improved establishment of *L. nootkatensis*.

Various amounts of alder leaves were repeatedly deposited every year to the soil in small experimental plots and the effects on soil properties were evaluated after 6 years. Nearly 1000 kg dry mass leaf litter per hectare was considered to be a realistic yearly production from dense *A*. *incana* stands. Such amouns gave a thicker humus layer with a comparably higher pH, a higher degree of base saturation, and a higher content of N_{tot} and mineralizable N.

Aspects of the biology and the handling of *A*, *incana* and *L*. *nootkatensis* are discussed, to serve as a guide in a choice between the two species for soil restoration pruposes.

Key words: Alnus, degenerated soil, humus layer, leaf litter, *Lupinus*, mineralization, nitrogen fixation, organic material, soil restoration, Sweden.

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Contents

Introduction, 3	Skällarimheden, 8
Sites and methods, 4	Riksdagsytan, 9
Sites, 4	Kiuhtisvaara, 9 Haradsheden, 9
Plant material and experimental design, 5 Alnus incana, 5 Lupinus spp., 6	Survival and growth of <i>Lupinus</i> spp., 10 <i>Skällarimheden, 10</i> <i>Kiuhtisvaara, 11</i>
Measurements, 7	Haradsheden, 11
Presence of <i>Rhizobium lupini</i> in forest soil, 7	Presence of Rhizobium lupini in forest soil, 14
Effects of adding alder leaves to the soil, 7	Effects of adding alder leaves to the soil, 15
Chemical analyses, 8	Discussion, 16
Results, 8	References, 19
Survival and growth of A. incana, 8	Acknowledgements, 20

Introduction

Degenerated forest soils are soils that have earlier been productive, but are now impoverished in terms of organic material. Such soils have a very low forest production and are expected to stay so for a long time. The soils have typically a thin humus layer of mor-type and there is thus a lack of both organic material and available nitrogen. Below the thin humus layer, typically degenerated forest soils have a rather deep, leached horizon in the podzolic profile, which indicates the previous existence of a productive, litter-producing stand. That previous litter production sustained a humus layer which was at that time much thicker than presently. Common causes of the present soil degeneration in northern Sweden are repeated, intense forest fires (Zackrisson, 1981; Engelmark, 1984), forestry practices (e.g. dimension felling, topping), and windthrow, all of which result in low litter production. The degeneration of the soil can be aggravated or preserved by intense reindeer grazing (Häggström, 1981).

Although the degenerated forest sites are not particularly dry, they are characterized by a lichen-dominated (mainly *Cladonia* spp.) ground layer and the field layer usually consists of a sparse cover of *Calluna vulgaris* (L.) Hull. and *Empetrum* spp. Furthermore, the sites are treeless or have very sparsely stocked stands of Scots pine (*Pinus sylvestris* L.) with some small birches (*Betula pendula* Roth and *B. pubescens* Ehrh.).

Today the degenerated sites are classified as nonproductive land (site productivity <1 forest cubic metre per ha and year) or nearly so. Compared to sites nearby, which are not degenerated, the soil degeneration is estimated to cause an average productivity loss of about 3 forest cubic metres per ha and year.

Degenerated mesic sites are particularly common in the interior of northern Sweden. In the two northernmost counties (Norrbotten and Västerbotten) about 100000 ha on till and about 10000 ha on sediments are classified as degenerated (Lundmark & Huss-Danell, 1981). These areas constitute about 1.5% of the total productive forest area in these two counties. In addition to the low productivity of the degenerated soils, these sites are often a problem for forestry in other respects, e.g. frost heaving, low soil temperature, ground frosts, and fungal diseases (Häggström, 1981, and references therein).

The natural regeneration of the degenerated soil can be expected to take as long as 200-300 years. It is, therefore, of great interest to find methods for more rapidly restoring the sites. We see three possibi-

lities of rebuilding a thicker, nitrogen-rich humus layer. One possibility would be to establish conifers, and add fertilizers very often in small portions or in the form of irrigation-fertilization (cf. Ingestad, 1980). Another possibility would be to add nitrogenrich organic material, e.g. peat, to the soil. A third possibility would be to use biological fertilization in the form of nitrogen-fixing plants. Nitrogen-fixing plants can utilize N_2 as nitrogen source. These plants produce leaf litter that has a higher nitrogen percentage than litter from most other species and will thus add nitrogen-rich organic material to the soil.

Of possible nitrogen-fixing species the grey alder, Alnus incana (L.) Moench, is the only native actinorhizal plant in these areas (Hultén, 1971). Alnus incana is a small, pioneering, single or multiple stemmed tree, considered hardy and able to grow on various sites (Tallantire, 1974; Schwabe, 1985). In northern Sweden it occurs on forest sites within a broad range of soil moisture and texture classes. It grows mainly on mesic and moist soil and dominating texture classes are medium sand and fine sand (Lundmark & Huss-Danell, 1981). Alnus incana can regenerate by seeds, stump sprouts and root suckers. The nitrogen-fixing root nodule endophyte, Frankia, is common in forest soil, including degenerated forest soil, in northern Sweden (Huss-Danell & Frej, 1986). Previous trials with A. incana for forest soil improvement in Sweden are very limited (Tamm, 1947; V. Söderström, pers. comm.), but nursery and field trials in Finland were very promising (Schalin, 1966).

Native legumes are very rare, and interest was focused on introduction of lupin (*Lupinus*) species. Several species (mainly *L. polyphyllus* and *L. luteus*) have been successfully used in Germany and other European countries (Mikola et al., 1983). Earlier trials with lupins in Swedish forestry are few (Tamm, 1947), but Hesselman (1917) mentions the positive effect of *L. perennis* on young Scots pine on a pine heath in southwestern Sweden. *Lupinus nootkatensis* has successfully been introduced in Iceland on eroded soil and on sandy and gravelly flats (Arnalds, 1979).

In the present investigation, the establishment, growth, and development of nitrogen-fixing A. *incana* and *Lupinus* spp. were studied on degenerated forest soil in the interior of northern Sweden. Four sites with various site characteristics were included in our study. Effects of adding alder leaves to the soil were also studied. At a later stage, the impact of successfully established nitrogen-fixing plants on the soil will be evaluated.

Sites and methods

Sites

Table 1 shows the location and climate and Table 2 gives the soil characteristics of the four sites Skällarimheden, Riksdagsytan, Kiuhtisvaara and Haradsheden. Skällarimheden, Ridsdagsytan, and Kiuhtisvaara are considered to have typically degenerated soils. Haradsheden is considered a primary lowproductive site and was included in the study for comparative purposes. Haradsheden carried a 110-year old Scots pine stand (1 100 stems ha^{-1}) but the other sites were treeless.

Skällarimheden has a slight north slope and a severe exposure to northerly winds. The latest conifer stand, thinned in 1943, was damaged by windthrow

Table 1. Location and climate of the study sites. T_{sum} (= temperature sum), precipitation and humidity refer to growing season

Study site	Latitude. longitude. altitude (m a.s.l.)	Growing season (No. of days with mean temperature $>+5^{\circ}$ C)	T _{sum} (day- degrees)	Precipi- tation (mm)	Humidity (mm)
Skällarimheden	66.5 °N. 20.2 °E, 280	135	825	300	+50
Riksdagsytan	66.3 °N, 20.0 °E, 415	134	690	300	+50
Kiuhtisvaara	67.7 °N. 23.4 °E. 300	130	670	250	+25
Haradsheden	66.1 °N. 20.9 °E, 60	140	975	300	+ 50

Table 2. Soil properties of the study sites at start of the experiments. A_0 = organic horizon, A_1 = humus-mixed mineral soil, A_2 = leached horizon. pH-values within brackets are weighted values. Ground vegetation type and reference values refer to the corresponding non-degenerated dwarf-shrub type in northern Sweden. From each site 4–6 samples (from together 60–120 different points) of the humus layer have been collected and analysed

	Profile ch	aracteristic	s			Humus laye	er			
Study site	Moisture class	Material type	Texture (<i>domi-</i> <i>nating</i> particle size)	Base mine- ral index	horizon	Thick- ness (cm)	Organic material (ton- ha ⁻¹)	рН _{(Н2} О)	N _{tot} (kg ha ⁻¹)	Ground vegetation type
Skällarimheden	mesic	morainic	<i>fine</i> and medium sand	13	podzol 3.2	$\begin{array}{ccc} A_0: & 0.4 \\ A_1: & 0.7 \\ sum: 1.1 \end{array}$	3.61 4.63 8.24	3.81 3.90 (3.88)	60 66 126	lichen type
Riksdagsytan	mesic	morainic	<i>medium</i> and fine sand	7	podzol 3.8	$A_0: 1.4 A_1: 1.2 sum: 2.6$	14.21 11.11 25.32	3.90 4.08 (4.03)	272 137 409	lichen type
Kiuhtisvaara	mesic	morainic	medium sand	11	podzol 4.6	$A_0: 2.2 A_1: 0.8 sum: 3.0$	16.67 7.41 24.08	4.21 4.22 (4.22)	271 275 546	lichen type
Haradsheden	dry	late glacial sediment	<i>medium</i> and fine sand	9	podzol 2.8	$A_0: 0.8 A_1: 0.9 sum: 1.7$	4.67 3.88 8.55	4.06 4.38 (4.34)	79 64 143	lichen type
Reference	mesic	morainic	<i>fine</i> and medium sand	12	podzol 5-6	$\begin{array}{rrrr} A_0: & 5 & -6 \\ A_1: & 0.5-2 \\ sum: 5.5-8 \end{array}$	5 - 10	3.8-4.2 4.0-4.4 (3.9-4.3)	500-600 100-200 600-800	Vaccinium myrtillus type

and had to be clear-felled in 1949 (F. Ebeling, pers. comm.). Further information about the site is given in Huss-Danell (1986b).

Riksdagsytan is on a southeast slope. The latest tree stand was clearfelled in 1939 and remaining seed-trees were removed in 1953. In 1953, 14000 pine seedlings per ha were found, but this number decreased gradually to only 100 seedlings per ha in 1978 (F. Ebeling, pers. comm.). Considerable amounts in the soil of charcoal fragments from Norway spruce (*Picea abies* (L.) Karst.) indicate that this species largely influenced the site until a very intense forest fire in 1652 (O. Zackrisson, pers. comm.). The latest forest fire was dated to 1693.

The Kiuhtisvaara site is on a SSE slope. The strongly stratified pine forest was clear-felled in 1947, and topping and notching were performed in 1954 and 1955, respectively (S. Winsa, pers. comm.). The few seed-trees were felled in the early 1970s. At the beginning of the present study, a field layer covered 80% of the ground and was composed of *Calluna vulgaris* (L.) Hull. (75%), *Empetrum hermaphroditum* Hagerup (15%), *Vaccinium vitis-idaea* L., *V. uligino-sum* L., *V. myrtillus* L., *Arctostaphylos uva-ursi* (L.) Spreng. and *A. alpina* (L.) Spreng. The bottom layer covered 65% of the ground. Lichens (mainly *Cladonia* spp.) constituted two thirds and mosses (mainly

Pleurozium schreberi (Brid.) Mitt. and *Dicranum* sp.) one third of the bottom layer.

The Haradsheden site has been strongly influenced by frequent forest fires in the past. Fire has been recorded about every 50 years from before 1274 until 1715. The latest fire occurred in 1847 (O. Zackrisson, pers. comm.). The field layer at the site in 1977 covered about 20% of the ground, and was dominated by *V. vitis-idaea* while *C. vulgaris*, *E. hermaphroditum* and *A. uva-ursi* formed a minor part of the field layer. About 80% of the ground had a bottom layer and this was composed of reindeer-grazed *Cladonia* spp. and only few plants of mosses (*Polytrichum juniperinum* Hedw., *Pleurozium schreberi*).

Plant material and experimental design

Alnus incana

The experimental design for alder plantings is given in Table 3. In 1977–1979 naturally occurring seedlings of *A. incana* were collected, mainly from roadcuts (Table 3). The plants were about 0.2 to 0.5 m high and were all nodulated. The root system was kept as intact as possible, but the amount of soil adhering the root system varied. Nursery plants were used in 1979 (Table 3). They were raised and inoculated as described elsewhere (Huss-Danell, 1986b).

Table 3. Experimental design of alder plantings at the study sites. Square spacing was used, except on ploughed soil where plants were placed at uniform distances along the furrows. F = fenced plot to exclude moose (Alces alces (L.)) and reindeer (Rangifer tarandus (L.)). P = ploughed soil. R = roadside plants. N = nursery grown plants of A. incana. ¹66.1 °N 20.9 °E ²65.6 °N 22.3 °E ³67.6 °N 23.4 °E

Site	Plot size	Planting	Planted ald	ers		
Plot	$(m \times m)$	year	No.	Provenance	Туре	
Skällarimheden				·····.		
9, F	16.5×33	1977	210	Harads ¹⁾	R	
7, F	16.5×16.5	1979	100	Harads	Ν	
11	30×75	1979	1 000	Harads	Ν	
12	18×75	1979	580	Luleå ²⁾	Ν	
Riksdagsytan	20 ×25	1978	500	Harads	R	
Kiuhtisvaara						
1	30×30	1979	125	Harads	Ν	
11	30×30	1979	125	Harads	Ν	
12	30×30	1979	125	Kihlanki ³⁾	R	
3. P	30×30	1979	125	Harads	Ν	
13. P	20×30	1979	125	Harads	Ν	
7. P	$30' \times 30$	1979	125	Kihlanki	R	
17. P	20×30	1979	125	Kihlanki	R	
Haradsheden						
4. F	10×10	1977	100	Harads	R	
14, F	10×10	1977	100	Harads	R	
7. F	10×10	1979	100	Harads	Ν	
9. F	10×10	1979	100	Harads	Ν	
17	18×75	1979	900	Harads	N	
18	12 ×75	1979	600	Luleå	N	

The plants were 1.5 years old, on average 0.3 m high, and had a small amount of peat adhering to the root systems at planting. All plantings were made in mid-September when the alders were dormant and leaf shedding had begun.

Lupinus spp.

The experimental designs for lupin plantings and sowings are given in Tables 4 and 5, respectively. One annual (*Lupinus luteus* L. cv. Lima) and three perennial lupins (*L. arcticus* S. Wats., *L. nootkatensis* Donn and *L. polyphyllus* Lindl.) were studied. Seeds of *L. luteus* and *L. polyphyllus* were obtained commercially (Weibull Trädgård AB, Landskrona, Sweden). Seeds of *L. arcticus* were collected at Frances Lake, Yukon, Canada (61.4°N, 129.6°W) by Prof. M. Hagner, Umeå. Seeds of *L. nootkatensis* were obtained from Västerbotten's county forestry board (provenance Lawing, Kenai, Alaska, USA) and from H. Bjarnason, Reykjavik, Iceland (provenance Point Packenham, Prince William Sound, Alaska).

Bare-root plants of L. nootkatensis were obtained

from the forest nurseries of Norrbotten's ad Västerbotten's county forestry boards. At Skällarimheden very tiny plants or pieces of root system from the lupin were planted, while plants used at Kiuhtisvaara and Haradsheden were up to 4 years old an very vigorous. Potted three-week-old plants of *L. nootkatensis* and *L. polyphyllus* were raised in peat in a greenhouse and planted at Haradsheden. Lupins were planted in June or September (Table 4).

At Kiuhtisvaara and Haradsheden, sowing was also tried (Table 5). Lupin seeds were inoculated with *Rhizobium* immediately before sowing by adding soil from growing lupins to the seeds. At Kiuhtisvaara, sowing was done on the ploughed soil by dropping some 10-15 seeds in each seed spot and covering the seeds with about 2 cm mineral soil. At Haradsheden, various treatments and sowings of the seed spots were tried in mid-June or mid-September (Table 5). In untreated plots the lichen mat was removed from the seed spots, the seeds were dropped into the more or less undisturbed mineral soil, and the lichens replaced and trampled firmly on the soil. In one plot

Table 4. Experimental design of lupin plantings at the study sites. Spacing as in Table 3. F = fenced plot (see Table 3). P = ploughed soil

Site Plot	Lupin species	Plot size $(m \times m)$	Planting time	No. of plants
Skällarimheden 10. F	L. nootkatensis	10.5×10.5	Sept. 1977	36
Kiuhtisvaara 6. P	L. nootkatensis	30 ×30	Sept. 1979	125
Haradsheden 1, F	L. polyphyllus	20 ×20	June 1977	20
2. F 3, F	L. nootkatensis L. nootkatensis	$\begin{array}{ccc} 20 & \times 20 \\ 20 & \times 20 \end{array}$	June 1977 June 1977	20 20
16	L. nootkatensis	20×20	Sept. 1977	25

Table 5. Experimental design of lupin sowings at the study sites. Spacing as in Table 3. F = fenced plot (see Table 3). L = limed seed spots. M = mixed mineral soil. P = ploughed soil

Site Plot	Lupin species	Plot size $(m \times m)$	Sowing time	No. of seed spots	
Kiuhtisvaara					
8, P	L. articus	30×30	Sept. 1979	125	
15, P	L. articus	20×30	Sept. 1979	125	
4, P	L. nootkatensis	30×30	Sept. 1979	125	
16, P	L. nootkatensis	20×30	Sept. 1979	125	
Haradsheden					
1. F	L. arcticus	20×20	Sept. 1979	72	
6. F	L. luteus	10×10	June 1977	100	
13, F, L	L. luteus	10×10	June 1977	100	
12. F	L. nootkatensis	10×10	June 1977	100	
6, F	L. nootkatensis	10×10	Sept. 1979	100	
5, F, L	L. nootkatensis	10×10	June 1977	134	
15, F, M	L. nootkatensis	10×10	Sept. 1979	100	
15. F	L. polyphyllus	10×10	June 1977	110	
11, F, L	L. polyphyllus	10×10	June 1977	134	

the mineral soil was mixed thoroughly by hand to 5-10 cm depth before dropping the seeds and replacing the lichen mat. In limed plots 0.25 kg lime (dolomite) was mixed into the mineral soil of each seed spot, which corresponds to about 3350 kg lime ha⁻¹ if calculated over an entire plot.

Measurements

Survival and height of the alders and length of the longest current year's shoot were recorded in mid-September. The presence of root suckers and flowers, as well as browsing or other damage, was noted.

Survival, plant height, presence of pods, and sometimes the number of shoots per plant, were recorded for lupins in mid-September. Seed germination during the year of revision (seedlings in the cotyledonary stage), as well as grazing or other damage of the lupins, were also noted.

Spreading of *L. nootkatensis* was studied at Skällarimheden. Seed production and numbers of self-sown seedlings were estimated. Such seedlings were examined for presence of root nodules.

Presence of Rhizobium lupini in forest soil

The presence of lupin root nodule bacteria in forest soil (Table 6) was studied to determine the future need for inoculation of lupin seeds. Soil was collected aseptically with a spoon and immediately put into new, sealed plastic bags. After cold transportation and storage (≤ 4 days), the soil was transferred aseptically into sterilized culture tubes (7 replicate tubes per soil). The tubes were closed with cellulose stoppers and contained some sterile perlite. Surface-sterilized (30% H₂O₂ for 2×20 minutes, 3×10 minutes sterile distilled water) seeds of L. nootkatensis were added aseptically to the culture tubes. Tubes treated in the same way, but containing only sterile perlite and a low-N nutrient solution, served as controls for surface-sterility of seeds and for aseptic handling of the growth system. To test that the growth system permitted nodulation, tubes with soil from a lupin plant were sown with L. nootkatensis and otherwise treated as tubes with soil samples. All tubes were kept in a growth chamber (17 h light at 25°C, 7 h dark at 15°C) and later on in a greenhouse (day-light supplemented to 17 h light; temperature about 20°C) and were watered aseptically with sterile distilled water when needed. After four months the lupin root systems were carefully examined for presence of root nodules.

Effects of adding alder leaves to the soil

A field experiment with simulated leaf litter fall was carried out to give an indication of possible soil improvement by alder. Leaves were stripped from a naturally growing stand of *A. incana*, dried (about

Table 6. Summary of sites where forest soil samples were collected and analysed for presence of Rhizobium lupini. Sampling was made in mid-September 1984. Soil was collected to 10 cm depth from 5-6 spots randomly within 5×5 m

Site Plot	Latitude longitude: m above sea level	Site characteristics	Soil pH _(H2O)
Skällarimheden 40 m from edge of plot No. 10 150 m from edge of plot No. 10 200 m from edge of plot No. 10	66.5 °N 20.2 °E; 280 280 280	degenerated forest soil (see Tables $1-2$)	4.5 4.6 4.4
Riksdagsytan	66.3 °N 20.0 °E; 410	(see Tables 1-2)	3.8
Haradsheden plot No. 16 200 m from lupin plots	66.1 °N 20.9 °E; 60 55	(see Tables 1–2)	4.4 4.7
Vidsel	65.8 °N 20.6 °E; 55	Pinus sylvestris, Calluna vulgaris, Vaccinium vitis-idaea, Cladonia spp. Nephroma arcticum, Peltigera aphthosa; podzol on sediment	4.0
Ersmark	64.9 °N 20.9 °E; 30	clear-felled area; V. vitis-idaea, V. myrtillus, Deschampsia flexuosa, Pleurozium schreberi; podzol on till	3.9

	Amoun	t of element	added (kg	ha ⁻¹)	
Leaf dry mass added (kg·ha ⁻¹ ·year ⁻¹)	500	750	1 000	2 000	3 000
Element					
Ν	88	132	176	352	529
Р	5.7	8.6	11.4	22.9	34.3
Ca	46.2	69.2	92.4	185	277
К	32.4	48.6	64.8	130	195
Mg Mn	4.2	6.3	8.5	16.9	29.2
Mň	0.72	1.06	1.42	2.84	4.26

 Table 7. Amounts of mineral elements added to the soil via yearly supply of alder leaves to experimental plots at

 Haradsheden. Values are the 6-year total for the 6-year-period 1978–1983

45°C), broken up and mixed. Amounts corresponding to 500, 750, 1000, 2000 and 3000 kg dry mass per ha were laid in small plots (1.5 by 1.5 m) at Haradsheden in mid-September every year from 1978–1983. As the leaves were in pieces, they were efficiently caught in the lichen mat. Subsamples of the dried leaves (stored at -20° C) were analysed for mineral content (Table 7). In mid-September 1984 soil samples (one composite sample per plot) were collected and kept frozen during transportation to Uppsala.

Results

Survival and growth of A. incana

Skällarimheden

Alders at Skällarimheden survived very well (Fig. 1). In all plots the survival was 84-92% after 7 to 9 years. There were no differences in survival between provenances or between plant types (roadside or nursery plants) used. Nor was there any difference between fenced and non-fenced plots. The height increase of the alders was constantly about 0.23 m per year (Fig. 2). The length of the top shoot (longest shoot of the current year's growth) of the alders was very similar to that of naturally occurring young *A*. *incana* nearby, indicating that the growth of the planted alders at Skällarimheden was very much determined by the environmental conditions at the site.

Skällarimheden is the only study site where regeneration of *A. incana* has so far been recorded. In plot no. 7 there were on average 0.02, 0.07 and 0.23 root suckers per living alder 5, 6 and 7 years after planting, respectively. In plot no. 9 there were on average 0.03, 0.11, 0.40 and 0.56 root suckers per living alder 6, 7, 8 and 9 years after planting. In plot no. 9 both female and male flower buds were found on 2.6, 0.5 and 11.9% of the alders 7, 8 and 9 years after plant-

Chemical analyses

Fresh samples were used for determination of ammonium and nitrate and air-dry samples for other analyses. N_{tot} was determined as Kjeldahl-N, ammonium and nitrate were determined according to Sveriges Standardiseringskommission (1976 *a*, *b*, *c*), and mineralizable nitrogen was determined after 9 weeks of incubation (Nômmik 1976). Determinations of C_{tot} followed Nômmik (1971) and analyses of cations and base mineral index followed Brown (1943) and Tamm (1934), respectively.

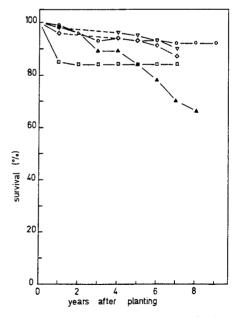


Fig. 1. Survival of *A. incana* planted at Skällarimheden (open symbols) and at Riksdagsytan (filled symbol). \bigcirc , plot no. 9; \square , plot no. 7; \diamondsuit , plot no. 11; \bigtriangledown , plot no. 12; \blacktriangle , Riksdagsytan. Further details on experimental design are given in Table 3.

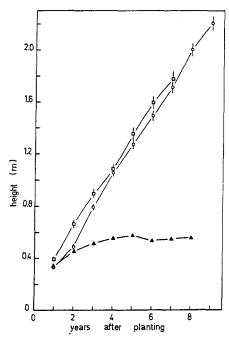


Fig. 2. Height of *A. incana* planted at Skällarimheden and at Riksdagsytan. Symbols as in Figure 1. $\bar{x} \pm SE$ given, unless SE is smaller than the symbol.

ing. Also, in plot no. 7 flower buds were found on 1.2% of the alders after 7 years. No self-sown alder seedlings have yet been observed.

Riksdagsytan

At Riksdagsytan, the survival of the alders gradually decreased to 66% after 8 years (Fig. 1). The plot was not fenced, and a few of the deaths are ascribed to reindeer (plants broken near the ground, parts of the bark removed, uprooted plants). The growth of the alders was very slow (Fig. 2). During their second season at the site, the alders increased their height by nearly 0.1 m, but during the following years, only by 0.01 to 0.06 m per year. Some of the alders with dead tops survived by sprouting new shoots near the ground. This phenomenon lowers the mean value for height of living alders. Except during the very first years, the alders at Riksdagsytan always gave a less vigorous impression than those at Skällarimheden. although the variation among individual alders was considerable at Riksdagsytan.

Kiuhtisvaara

At Kiuhtisvaara, the survival of the alders was initially fairly high, ranging from 62 to 97% in the various plots (Table 8). The survival was somewhat higher in ploughed than in untreated plots but no differences between provenances were seen. Some of the deaths

Table 8. Development of planted alders at Kiuhtisvaara. Height values are $\bar{x}\pm SE$. P = ploughed soil

	Drou	Surviva	l (%) after	Height (m) after 6 years ¹⁾	
Plot	Prov- enance	l year	6 years ¹⁾		
1	Harads	62.4	12.0	0.26 ± 0.04	
11	Harads	85.6	8.0	0.23 ± 0.03	
12	Kihlanki	70.4	4.8	0.03 ± 0.01	
3. P	Harads	92	17.6	0.17 ± 0.02	
13. P	Harads	85.6	11.2	0.10 ± 0.02	
7. P	Kihlanki	96.8	18.4	0.14 ± 0.02	
17. P	Kihlanki	88.8	28.8	0.09 ± 0.01	

¹⁾ Revision on 20th June 1985, i.e. nearly 6 years after planting.

among the alders were probably due to reindeer damage, since several uprooted plants were found. During the third year after planting, the survival decreased to less than 40%, as judged from a superficial inventory. One possible explanation is that in early June of the third year, there was a rapid shift from daily maximum temperatures as high as about 20°C to daily minimum temperatures below 0°C (data from the Swedish Meteorological and Hydrological Institute, Station Pajala: Anonymous, 1986). Living plants had only tiny brownish-green leaves and usually only small, basal shoots. During the sixth growing season at the site, about 5-30% of the planted alders were alive (Table 8). The survival rate was higher in ploughed than in untreated plots. The height of the alders was, however, on average lower than at planting. Often, the tops had died and measured heights were due to basal sprouts with mostly tiny leaves. Alders planted very close to a boulder or a fallen log were often more vigorous than more exposed plants, which suggests that the microclimate of the alders was important at the site. No differences in vigour were observed between alders planted on west-facing and east-facing slopes of the furrows in the ploughed plots. In plots with untreated soil, roadside plants of the provenance Kihlanki (very close to the site Kiuhtisvaara) had poorer survival and plant height than nursery-grown alders of the provenance Harads (from a more southerly area at lower altitude). However, within ploughed plots there were no clear differences between the two provenances.

Haradsheden

At Haradsheden, the survival of the alders (Fig. 3) decreased to about 70% during the first two years and then more slowly to about 60% after 7 years and nearly 50% after 9 years. There were no differences in survival between alders of the two provenances or the

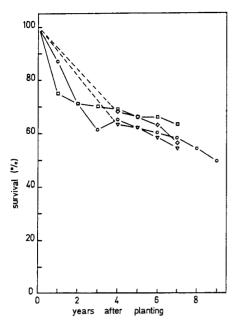


Fig. 3. Survival of *A. incana* planted at Haradsheden. \bigcirc , plots no. 4+14; \Box . plots no. 7+9; \diamondsuit , plot no. 17; \bigtriangledown , plot no. 18. Further details on experimental design are given in Table 3.

two types of plants (roadside or nursery-grown) or between alders in fenced and non-fenced plots. The height increase (Fig. 4) was initially faster in plots no. 7 and 9 (nursey-grown plants) than in plots no. 4 and 14 (roadside plants), but was then similar in all plots studied. The alders usually had fairly large but thin leaves on the slender shoots. Because of this, the alders gave a slight impression of being shade plants at the site.

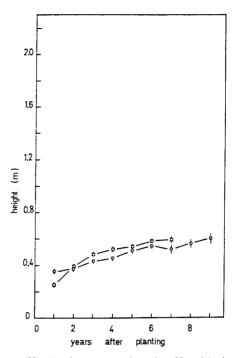


Fig. 4. Height of *A. incana* planted at Haradsheden. Symbols as in Fig. 3. $\bar{x} \pm SE$ given, unless SE is smaller than the symbol.

Survival and growth of Lupinus spp.

Skällarimheden

The development of planted L. nootkatensis at Skällarimheden was very good (Fig. 5). The survival was very high and the plants reached their final height and number of stems per plant after 4 years. After 5 years each plant covered on average an area nearly 1 m in diameter. Two years later it was no

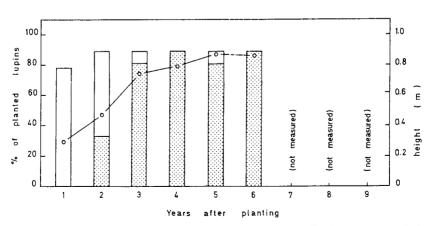


Fig. 5. Survival, height and flowering of *L. nootkatensis* planted at Skällarimheden. Total bars show survival and dotted areas of bars show lupins with pods. Curve shows \bar{x} for height of lupins (SE smaller than the symbols).

longer possible to distinguish between original and self-sown lupin plants within the plot. The ground was completely covered by lupin shoots. After 8 years the ground-layer (mostly lichens) had more or less disappeared under the very dense lupin cover. The above-ground biomass of one average-sized plant in mid-September 1983 (6 years after planting) was 584 g dry mass, containing 4.3 g Kjeldahl-N. This corresponds to 2 595 kg dry mass \cdot ha⁻¹ and 19 kg N \cdot ha⁻¹ at a spacing of 1.5 by 1.5 m.

Flowering and seed production began in the second year, and from the fourth year and onwards all fullsized plants produced seeds. The seed production per plant was estimated after 6 and 7 years (one plant per year). In the first sample, 28 out of the 46 shoots had on average 24.1 pods containing on average 8.7 seeds. In the second sample, the plant had 70 shoots with pods. On each shoot there were 18.4 ± 1.3 ($\bar{x} \pm$ SE; range 1–49) pods containing 7.1 \pm 0.1 (range 1–11) seeds. This gives averages of 5871 and 9145 seeds produced by the two plants, respectively. The potential for generative reproduction by *L. nootkatensis* at Skällarimheden was thus very high.

Self-sown plants of L. nootkatensis were first observed after 3 years, when a total of 43 seedlings was found within the plot (Lundmark and Huss-Danell 1981). One year later 40.3 and 44.4 seedlings m^{-2} (2) random samples) were found within the plot. Assuming that this density was valid for the entire plot, a total of about 4700 self-sown lupins should have been produced in the plot $(10.5 \times 10.5 \text{ m})$. This figure seems reasonable with regard to the preceding year's seed production in the plot. In that year, a total of 32 plants had on average 9.2 shoots bearing pods. Assuming that each such shoot had 20 pods containing 8 seeds (cf. above) the total seed production would have been 47 100 seeds, which is 10 times the estimated number (4700) of self-sown lupins in the plot the following year.

Kiuhtisvaara

At Kiuhtisvaara, planted *L. nootkatensis* had 99.2 and 95.2% survival 1 and 3 years after planting, respectively. All plants flowered in the third year. By this time, the plants had also reached what seems to be their final size (about 0.8 m high and some 40 shoots per plant) in northern Sweden. Sown plants of *L. nootkatensis* also developed well (Table 9). As an example, 80% of the seed spots contained plants 3 years after sowing. These plants were on average 0.7 m high and had a large number of pod-bearing shoots. By their sixth growing season at Kiuhtisvaara, both planted and sown *L. nootkatensis* had developed tremendously. Older plants (planted or sown in 1979) often covered an area 0.5-1.5 m in diameter. Under the dead lupin shoots from previous years, mosses had often occupied the bare soil of the ploughed furrows. Seed production had been high, as judged from the large number of remnants of pod-bearing shoots and from the innumerable self-sown lupins found at the site. The self-sown lupins had established in the bare mineral soil, as well as in the untreated soil between ploughed furrows. Also selfsown plants had become old and large enough to produce seeds.

Germination of L. arcticus was poorer than that of L. nootkatensis at Kiuhtisvaara. Only 10 and 40% of original seed spots in the two L. arcticus plots contained plants during the sixth year, compared to about 80% for L. nootkatensis (Table 9). Plants of L. arcticus were smaller than plants of L. nootkatensis. During the sixth year, plants of L. arcticus in the original seed spots covered an area about 0.5 m in diameter. Self-sown plants were very numerous, but were more often situated close to an old plant than was the case for self-sown plants of L. nootkatensis at the site.

Haradsheden

At Haradsheden, the survival of planted *L. nootkatensis* was initially 65 to 95% but decreased during the following years to 0, 8 and 10% in plots no. 2 (Fig. 6), 3 (Fig. 7), and 16, respectively. The average height of the plants reached only about 0.3-0.5 m and the number of shoots per plant was commonly 1 to 10. The devlopment was thus not as good at Haradsheden as at Skällarimheden and Kiuhtisvaara. Shoots with pods did not occur every year in all three plots. So far, only one self-sown plant has been found. Planted *L. polyphyllus* survived only the first summer at the site.

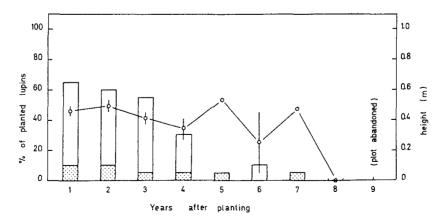
Seeds of *L. arcticus* did not germinate sufficiently to establish at Haradsheden (Table 9). The annual lupin *L. luteus* germinated very well (Table 9) but was very heavily grazed, presumably (fenced plots, sharp bites, droppings) by mountain hare (*Lepus timidus L.*) A few plants reached the flowering stage, but none produced seeds before freezing. *Lupinus luteus* was not able, therefore, to establish at Haradsheden.

Seeds of *L. polyphyllus* also germinated very well at Haradsheden (Table 9). After one growing season, plants were found in all seed spots in the limed plot and in 75% of the seed spots in the untreated plot. Some seeds also germinated during subsequent years.

Study site Plot	Lupin species	Years after sowing	Frequency of seed spots with plants (%)	Plant height (m)	No. of shoots per seed spot with plants	No. of shoots with pods per seed spot with plants
Kiuhtisvaara						
8	<i>L</i> . <i>a</i> .	$\frac{1}{6^{1)}}$	3.2 10.4	-	_	-
15	L.a.	$\frac{1}{6^{1}}$	48.8 38.4	0.05 ²)	-	
4	L.n.	$ \frac{1}{3} _{6^{1}} $	86.4 80.0 88.0	$0.20^{2})$ $0.71\pm0.01^{3})$	53.2 ± 3.4^{3}	$\frac{1}{22.2\pm2.1^{3)}}$
16	L.n.	$\frac{1}{6^{1}}$	48.8 79.2	0.10 ²⁾	-	-
Haradsheden		0				
1	L.a.	1 2	6.9 0	0.01 ± 0	1.0 ± 0	0 0
		2 3	0	(plot abandoned)		
6	L.1.	1	94.0	0.09. gr	–. gr	0. gr
		$\frac{1}{2}$	0	0	0	0
		3	0	(plot abandoned)		
11	<i>L.p.</i>	1	100.0	0.11 ± 0.01	-	0
		2 3 4 5	59.3	0.06 ± 0.01	-	0
		3	13.4	0.07 ± 0.01	-	0
		4	2.2	0.05 ± 0.01	-	0
			3.0	0.12 ± 0.01	-	0
		6	2.2 2.2	0.11 ± 0.05	-	0
		7		0.05 ± 0.02	-0	0
		8 9	$\begin{array}{c} 0\\ 0\end{array}$	0 (plat shandanad)	0	0
12				(plot abandoned)		0
13	L.l.	1	100.0	0.12, gr	–. gr 0	0. gr
		$\frac{2}{3}$	0		U	0
		3	0	(plot abandoned)		
15	<i>L.p.</i>	1	74.5	0.06 ± 0.01	-	0
		2	13.6	0.04 ± 0.01		0
		3	5.5	0.06 ± 0.01	-	0
		1 2 3 4 5	0	0	0	0
		5	0	(plot abandoned)		

Table 9. Development of sown lupins on degenerated forest soil. Lupin species: L.a. = Lupinus arcticus, L.1. = L. luteus, L.n. = L. nootkatensis, L.p. = L. polyphyllus. Years after sowing means No. of growing seasons. $\bar{x} \pm SE$ given. – = not determined. gr = grazed

¹⁾ Revision on 20th June instead of mid-September ²⁾ estimated value ³⁾ determined on a subsample of n = 10.





Figs. 6-7. Survival, height and flowering of *L. nootkatensis* planted in plots no. 2 (Fig. 6) and no. 3 (Fig. 7) at Haradsheden. Total bars show survival and dotted areas of bars show lupins with pods. Curves show height of lupin plants with $\tilde{x} \pm SE$ given (unless SE is smaller than the symbol). gr = grazed.

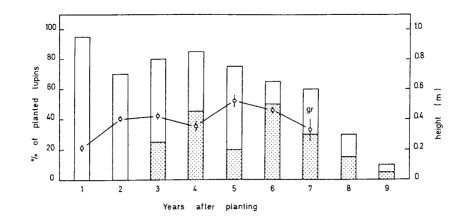


Fig. 7.

Fig. 8.

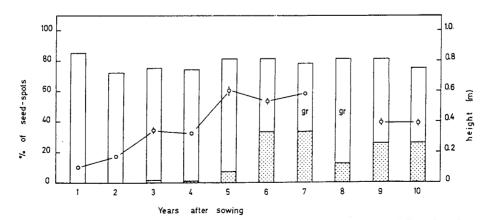
In spite of this, the number of seed spots with lupins decreased rapidly from year to year. After 4 years *L. polyphyllus* was no longer found in the untreated plot and after 8 years the species was not observed at the site at all. The average height of the plants was seldom more than 0.1 m and flowers and pods were never observed. *Lupinus polyphyllus* was thus not able to establish at Haradsheden.

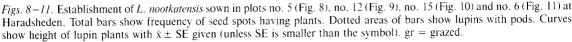
Sown *L. nootkatensis* developed very well in the limed plot at Haradsheden (Fig. 8). About 80% of the seed spots had plants during all 10 years. The average plant height increased gradually from about 0.1 m after 1 growing season to about 0.6 m after 5 years. Pod-bearing plants were observed from the third year onwards. After 7 and 8 years a large number of lupins had such a size that adjacent plants touched each other (spacing of seed spots was 1×1 m), but in the two following years plants were again smaller. Self-sown lupins were observed in the plot from the seventh year and onwards.

Development of sown L. nootkatensis was less successful in the untreated plot (Fig. 9) which was start-

ed at the same time as the limed plot (Fig. 8). About 65% of the seed spots produced plants in the first growing season. This frequency gradually decreased to only 3% after 10 years. The plant height (<0.25 m) was also inferior to that of lupins in the limed plot. Shoots with pods were found only occasionally 6, 7, and 9 years after sowing. No self-sown lupin plants have been observed so far.

The superior development of *L. nootkatensis* in the limed plot might be due to the lime, the mixing of mineral soil which was done at liming or both. To study the importance of mixing the mineral soil, a new pair of plots was sown with *L. nootkatensis* in September 1979 (Table 5). In one plot the mineral soil in the seed spots was mixed as in the limed plot, but without adding lime. Seed spots in the other plot were left untreated. After 1 year 62 and 48% of the seed spots had plants in the treated (Fig. 10) and untreated (Fig. 11) plots, respectively. A few years later the survival of plants in the two plots was fairly similar. The lupins were taller in the treated plot 1-4 years after sowing. It thus seems that mixing the





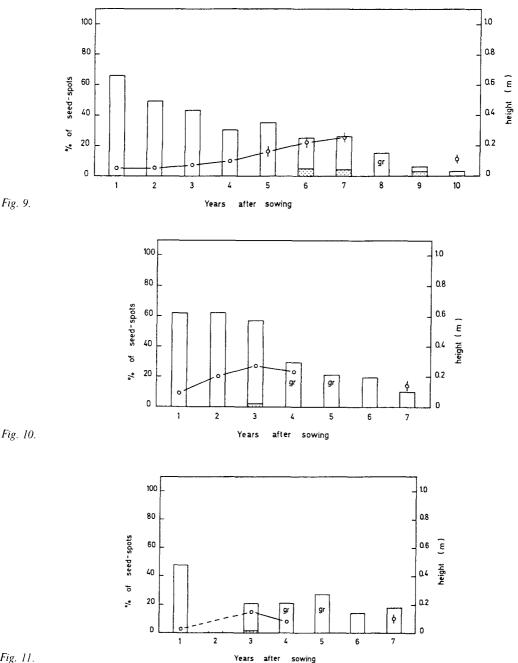


Fig. 11.

mineral soil was of positive value during the first years at the site, but can not completely explain the positive effect of adding lime into the mineral soil at sowing.

Except for the heavy grazing on L. luteus, damage to lupins was generally small. Mostly only the leaf lamina was nibbled off from the petiole, but shoots were otherwise intact. However, in some years (especially 1983 and 1984) grazing reduced height and seed production in several lupin plots at Haradsheden. The grazing was mainly ascribed to mountain hare.

Presence of *Rhizobium lupini* in forest soil

That limited spread of the nitrogen-fixing bacterium R. lupini occurs in forest soil was seen at Skällarimheden. There, nodulation was examined on self-sown L. *nootkatensis* 0-5 m outside the edge of the lupin plot. In 1983, 14 out of 21 examined seedlings were nodulated. In 1984, 1985, and 1986 all examined seedlings beyond the cotyledonary stage (n = 64, 183, and 650, respectively) were nodulated.

In the culture tubes containing collected forest soil (Table 6), some 30 lupin seedlings per soil sample developed. The seedlings had several true leaves and the cotyledons were all senescent at harvest of the experiment. All seedlings growing in forest soil and all seedlings growing in tubes with sterile perlite lacked nodules. In contrast, seedlings growing in lupin soil were all nodulated, which is good evidence that the growth system used did permit nodulation to occur if there was a sufficient number of infective R. *lupini* in the soil. Apparently the studied forest soils did not contain a detectable number of infective R. *lupini*.

Effects of adding alder leaves to the soil

The yearly supply of alder leaves to experimental plots at Haradsheden affected the lichen-rich ground layer. After 6 years the lichen thalli (*Cladonia* spp.) were larger in all plots supplied with alder leaves than in control plots. In the plot "2000", the lichen-dominated ground layer also contained some mosses (*Pohlia nutans* (Hedw) Lindb. and *Polytrichum juniperinum*) and some single plants of *Deschampsia flexuosa* (L.) Trin. In the plot "3000", about 70% of the area was still covered by *Cladonia* spp., while about 20 and 10% of the area was covered with remnants of alder leaves and with mosses (see above), respectively. In addition, there were a few plants of *D. flexuosa*.

Table 10 shows the effects on soil characteristics. The depth of the humus layer was 0.5 cm in control plots but 1.5 cm in plots that had received 1000-3000 kg dry mass leaves ha⁻¹. The pH of the humus layer increased in plots receiving at least 750 kg dry mass leaves ha⁻¹ and was more than one unit higher in the plots "2000" and "3000" than in the control

plots. Additions of ≥ 1000 kg dry mass leaves ha^{-1} had doubled the dry mass of the humus layer.

Carbon as a percentage of dry mass in the humus layer varied, but total mass of carbon per ha was increased over the control in all plots, and in the plots "2000" and "3000" it reached values twice as high as in the control plots (Table 10). The N-percentage of the humus layer was 0.65% in control plots, but gradually increased to 1.38% of dry mass in the plot "3000". There was a large effect on total amount of N in the plots. While control plots contained some 100 kg N_{tot} ha⁻¹, the plots given alder leaves contained from 150 to 470 kg N_{tot} ha⁻¹. Amounts of NH_4^+ were less than 1 kg·ha⁻¹ in control plots, but 2-3 kg·ha⁻¹ in the plots "500" and "750", and as high as 20-30kg ha-1 in the plots "2000" and "3000". Traces of nitrate were seen only in the plots "2000" and "3000". The proportion of N_{tot} that could be mineralized (= available N) was very low (<1%) in control plots. In the plots "500" and "750", this value had increased to 1-2% and in the plots "2000" and "3000" it was as high as 5-8%.

In the control plots, the degree of base saturation was about 30% in the humus layer (Table 10). In plots supplied with alder leaves, the value increased with increasing amounts of added leaves, reaching 65% in the plot "3000". Calcium and magnesium contributed most to this increase, as judged from analyses of single elements (data not shown).

For the mineral soil (Table 10), the effects of adding alder leaves to the soil were not as pronounced as for the humus layer. The amount of NH_4^+ was zero in control plots, but 4–6 kg·ha⁻¹ in the plots "500" and "750", and 11–12 kg·ha⁻¹ in the plots "2000" and "3000". The proportion of N_{tot} that could be mineralized was also zero in control plots, but 1.5–2.5% in the plots "500" and "750", and 3–5% in the plots "2000" and "3000". The degree of base saturation increased from about 10–15% in control plots to about 25% in plots supplied with alder leaves.

Plot	Soil horizon	Depth (cm)	рН	Dry mass (ton ha ⁻¹)	C _{tot} (% dry mass)	C_{tot} (ton \cdot ha ⁻¹)	N _{tot} (% dry mass)	N _{tot} (kg ·ha ⁻¹)	$NH_4^+ (kg ha^{-1})$	$NO_3^- (kg ha^{-1})$	Minerali- zable N (% of N _{tot})	Degree of base satu- ration (%)
0,	$ B/S A_0 0-5 5-10 10-20 Sum $	0.5	4.20 4.18 4.26 5.33 5.32	8.26 14.2 913 721 1567 3223	41.78 20.82 0.88 0.79 0.38	3.451 2.956 8.034 5.696 5.955 26.092	0.626 0.627 0.049 0.032 0.015	51.7 89.0 447 231 235 1054	0.71 0 -	- 0 - -	0.80 0 -	 10.8 17.1 19.6
02	$\begin{array}{c} B/S \\ A_0 \\ 0-5 \\ 5-10 \\ 10-20 \\ Sum \end{array}$	0.5	4.23 4.24 4.76 5.36 5.34	9.76 16.7 785 1 290 1 465 3 566	41.50 24.07 0.68 0.57 0.27	4.050 4.020 5.338 7.353 3.956 24.717	0.583 0.671 0.036 0.019 0.011	56.9 112 283 245 161 858	0.10 0 - -	0 0 -	0.09 0 -	- 32.0 15.3 13.9 17.8
500	$B/S = A_0 = 0$ 0 - 5 = 5 5 - 10 = 10 - 20 Sum	0.7	4.44 4.26 5.25 5.26 5.42	7.48 19.8 666 706 1518 2917	44.70 26.40 1.14 0.56 0.22	3.344 5.227 7.592 3.954 3.340 23.457	1.240 0.769 0.041 0.017 0.010	92.8 152 273 120 152 790	 4.00 	- 0 - -	1.34 1.47 _	- 33.9 24.3 15.1 17.5
750	$B/S = A_0 = 0$ 0 - 5 = 5 5 - 10 = 10 - 20 Sum	1.0	4.76 4.40 5.22 5.41 5.42	8.72 19.0 593 681 1476 2778	45.57 31.86 1.53 0.55 0.21	3.973 6.053 9.073 3.746 3.100 25.945	$\begin{array}{c} 1.346 \\ 0.890 \\ 0.040 \\ 0.018 \\ 0.008 \end{array}$	117 169 237 122 118 763	- 3.00 5.93 - -	- 0 - -	1.78 2.50 -	- 34.2 25.3 25.4 17.9
1 000	$B/S = A_0 = 0$ 0 - 5 = 5 5 - 10 = 10 - 20 Sum	1.5	4.75 4.54 5.12 5.49 5.50	10.76 39.8 713 692 1365 2821	45.19 15.50 0.59 0.67 0.53	4.862 6.169 4.207 4.636 7.234 27.108	$\begin{array}{c} 1.325 \\ 0.843 \\ 0.030 \\ 0.026 \\ 0.015 \end{array}$	143 336 214 180 205 1078	- 1.39 2.85 - -	- 0 - -	0.41 1.33 -	42.1 19.3 20.2 15.1
2 000	$B/S = A_0 = 0 - 5 = 5 - 10 = 10 - 20$ Sum	1.5	4.76 5.33 5.56 5.58 5.44	8.82 34.5 779 954 2 180 3 956	43.34 22.04 1.16 0.68 0.28	3.821 7.604 9.036 6.487 6.104 33.052	1.257 1.213 0.048 0.029 0.013	111 418 374 277 283 1463	- 31.95 10.91 - -	0.38 0 - -	7.73 2.92 -	- 51.3 35.5 14.5 14.5
3 000	$B/S A_0 0-5 5-10 10-20 Sum$	1.5	5.27 5.42 5.40 5.57 5.50	8.22 34.2 773 749 1 491 3 055	45.27 20.98 0.82 0.58 0.29	3.721 7.175 6.339 4.344 4.324 25.903	2.135 1.371 0.032 0.020 0.016	175 469 247 150 239 1280	21.72 12.37 _	0.82 0 - -	4.81 5.01	65.2 22.7 26.9 23.7

Table 10. Soil characteristics resulting from six years annual deposition of alder leaves in experimental plots at Haradsheden. Plot designations refer to dry mass $(kg \cdot ha^{-1})$ alder leaves supplied every year. Soil horizon 0-5, 5-10 and 10-20 refer to mineral soil at 0-5, 5-10 and 10-20 cm depth, respectively. - = not determined

Discussion

In the present study, successful establishment of A. *incana* depended on site factors. Skällarimheden, with good development of alder, is more fine-textured than the other three sites (Table 2). The climate of the sites seemed to be another important factor. The poor survival of *A*. *incana* at Kiuhtisvaara might

be due to the cooler climate there as compared to Skällarimheden (Table 1). Also, Riksdagsytan has a cooler climate than Skällarimheden due to the higher altitude of Riksdagsytan. In spite of the limited number of sites we have studied, we can not at present recommend planting A. incana on mesic sites with T_{sum} lower than ca 800 day-degrees. Soil nutrients are also of importance for the development of alders. This is judged from a related study at Skällarimheden, where growth and the production of leaf litter and leaf litter nitrogen was enhanced by liming as well as by NPK-fertilization (Huss-Danell, 1986b). At Haradsheden, alders were planted in an old Scots pine stand. Competition for light, water and nutrients (other than N) might have been negative for the development of alders there. Alders lose a large part of their nutrients in the yearly leaf litter fall (Saarsalmi et al. 1985) while pines keep their needles for several years and may, therefore, conserve their nutrients better than alders.

The survival and growth of *A. incana* were not much influenced by fencing the plots or by use of different provenances or types of plants. On the other hand, it is likely that variation in early survival among plants at a site could be due to the amount of soil adhering to the root system at planting. A larger clod of soil (roadside plants) or nutrient-rich peat (nursery plants) would give a better mechanical protection of the roots at planting and also a richer nutrient supply during the first season(s). In a separate study at Skällarimheden (Huss-Danell, 1986b), it was shown for nursery-raised alders that root growth was much greater than shoot growth the first year after planting, which indicates that these plants had to adjust to a nutrient-poor soil.

Among the lupins, L. nootkatensis was the only successful species in the comparative study at Haradsheden, and at Kiuhtisvaara L. nootkatensis performed better than did L. arcticus. In Alaska and British Columbia, where L. nootkatensis is native, the plants are 0.4 to 1 m tall at favourable locations and barely 0.1 m in areas of severe exposure (Dunn & Gillett, 1966). The size of L. nootkatensis in northern Sweden is thus in good accordance with values from the areas where the species is native. In the experiments at Haradsheden, the establishment of sown L. nootkatensis was facilitated by liming and, to some extent, also by soil scarification. It is commonly argued that liming is a positive factor for development of legumes, although it varies between species and soil conditions (Munns, 1977). The lime effect on legumes has been ascribed to specific effects of Ca²⁺-ions on the infection and nitrogen fixation processes, to raised pH-values in the soil, and to increased availability of other nutrients, especially phosphorus (Dixon & Wheeler, 1983). The soil scarification was expected to give more favourable temperature conditions and decreased root competition from the vegetation already present. Shading was a negative factor for development and nitrogen fixation of *L. arboreus* (Sprent, 1973; Sprent & Silvester, 1973). The more successful development of lupins at the open sites Skällarimheden and Kiuhtisvaara than at the shaded site Haradsheden is in good agreement with that observation. However, Haradsheden also differed in having a pine stand competing with the lupins for water and nutrients.

Alders in a reproductive stage were found only at Skällarimheden, but so far, propagation has only been by root suckers and not through seedlings. The alders that were raised in the nursery were thus 7 years old when the first individuals formed root suckers and 9 years old when flowering for the first time. For the more heterogeneously-aged roadside plants, the corresponding ages were ≥ 8 and ≥ 9 years, respectively. Lupinus nootkatensis, on the other hand, very soon (2-4 years) reached an impressive sexual reproduction potential. These reproduction habits should be considered when conifers are to be planted in plots with A. incana and L. nootkatensis. At open sites, like Skällarimheden or Kiuhtisvaara, the conifers should be planted early, probably already before the lupin. Otherwise the thick mat of lupin shoots will compete too much with the conifer plants. In alder plantations, however, we do not see the same need for an early planting of conifers. The alders grow merely in height rather than in width. and will thus give more space for conifers than the easily spreading L. nootkatensis. Most likely the alders must later on be removed by cleaning, while it might be possible to outcompete lupins by shading. Such outcompeting by shading is being practised in plantations of Pinus radiata having an understorey of L. arboreus in New Zealand (Gadgil, 1983). Lupinus nootkatensis seemed able to produce a large seed-bank in the soil. Some of these seeds are expected to germinate after many years when the conditions for seed germination become favourable. During the course of this study, seeds sown at Haradsheden in 1977 germinated every year, including 1985, that is after 8 years. Such late germination is, of course, an advantage in that the lupin can recover at a site when the conifer stand is thinned (Gadgil, 1983). However, it may become difficult to get rid of the species from a site where it has been introduced.

When making a choice between A. incana and L.

nootkatensis for soil restoration, we see advantages and disadvantages with both species. Lupinus nootkatensis seemed hardier than A. incana (Kiuhtisvaara). Alnus incana is native in the area while L. nootkatensis is an introduced species. Lupins, in general, are poisonous (Davis, 1982; Hatzold et al., 1982; Schoeneberger et al., 1982) and L. nootkatensis is claimed to have a rather high alkaloid content (Arnalds, 1979). Sheep kept on a diet of L. nootkatensis lost weight and became ill (Arnalds, 1979). The high reproductive potential of L. nootkatensis may make it difficult to keep the species within a designated area. The alder gives, in addition to its soil improvement, some production of wood for fuel or pulp, but the lupins do not. Lupins are easier and cheaper to etablish as they can be sown directly at the site. So far, we can only recommend establishment of A. incana by planting. The lupins need, however, to be inoculated with the proper type of Rhizobium since this organism was apparently absent from the studied forest soils. A similar experience was also reported from Iceland (Arnalds, 1979). Freezing and low pH of soil are likely to impair survival and growth of rhizobia (Lindström et al., 1985; Lindström & Myllyniemi, 1987). Inoculation of lupins is easily done by mixing the seeds with a R. lupini-culture, with soil, or with crushed root nodules from a site with nodulated lupins. The lack of R. lupini opens the possibility to introduce strains with high nitrogen fixation capacity (Caradus & Silvester, 1979. As to A. incana, on the other hand, infective and nitrogen-fixing Frankia was found in all studied types of forest soils, including the degenerated soil at Skällarimheden (Huss-Danell & Frej, 1986), and inoculation of the alder seedlings in the nursery is therefore not neccessary. However, inoculation of alders in the nursery eliminates the time needed for nodulation in the field, and the alders can start their growth more rapidly. Inoculation is simply done by watering the alder seedlings with a suspension of pure cultures of Frankia, a suspension of soil or a suspension of crushed root nodules from nodulated alders (Berry & Torrey, 1985; Périnet et al. 1985; Huss-Danell, 1986b).

The simulated supply of alder leaves to the experimental plots at Haradsheden gave a clear effect on the soil characteristics as early as 6 years later. The results give some indications about possible beneficial effects of alder plantations. We regard 500 to 1 000 kg dry mass of leaf litter per ha to be a realistic supply from a dense alder stand. This judgement is based on data from the shoot litter traps operated in natural alder stands near the study sites at Skällarimheden and Haradsheden (Lundmark & Huss-Danell,

1981). Another basis for the judgement is a separate study at Skällarimheden, where the best performing A. incana plots (planting pits were limed at planting) produced 440-710 kg dry mass leaf litter ha⁻¹ year⁻¹ as early as 6 years after planting (Huss-Danell, 1986b). Depending on the age, density and soil characteristics of the stands, Schalin (1966) found the yearly leaf litter production from A. incana in Finland to be 450-3100 kg dry mass per ha. From Alaska, van Cleve et al. (1971) reported a yearly foliage production of $1\,600-2\,100$ kg per ha for A. incana ssp. tenuifolia. A yearly leaf litter fall of 500-1000 kg dry mass per ha would correspond to about 10-25 kg N pe ha and year. This value is similar to the estimate of the above-ground litter nitrogen produced by fullsized lupins at a spacing of 1.5 by 1.5 m at Skällarimheden (19 kg N \cdot ha⁻¹ \cdot year⁻¹). In addition to the aboveground production of litter, a considerable belowground production of litter from both A. incana and L. nootkatensis also takes place. The ratio between above-ground an below-ground litter production is not known. In laboratory experiments, young, nitrogen-fixing. A. incana released almost all of its nitrogen in the form of shoot litter (Huss-Danell, 1986a). However, in nature, the root system is influenced by stress factors such as drought and freezing, and by micro-organisms and animals. It is likely that production of root litter, and possibly also root exudates, is higher under such conditions (Hale et al., 1978).

The simulated supply of alder leaves at Haradsheden was done repeatedly over only 6 years, and a longer period would, of course, increase the effects. On the other hand, green leaves were used rather than leaf litter and the nitrogen percentage was higher (nearly 3% of dry mass) than in more or less leached leaf litter collected from planted alders at Skällarimheden (mostly 2-2.5% of dry mass; Huss-Danell, 1986b). The important effect of the supply of alder leaves was the build-up of a thicker humus layer with a comparably higher pH, a higher degree of base saturation, and a higher content of carbon and nitrogen (Table 10). Additions of ≥1000 kg dry leaves ha-1 increased the organic material and Ntot in the humus layer to values approaching reference values for non-degenerated dwarf-shrub sites in northern Sweden (cf. Table 10 and Table 2). This build-up of the humus layer increases the soil biological activity and, consequently, gives higher capacity for the humus layer to deliver available nitrogen and other nutrients to plant roots. We can thus conclude that the planting of alder will be an effective means for soil restoration. To what extent a conifer (pine) plantation can utilize the improved soil conditions will be judged from future experiments. Pot experiments with conifers showed beneficial effects of alder, both from the alder root system (Virtanen, 1957) and from alder leaf litter (Mikola, 1958). It will also be important to find proper management systems, so that the microclimatic effects of alder are fully utilized without too much competition between alders and conifers for light, water and nutrients (other than N) at a site.

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