SILVA FENNICA

Silva Fennica 41(2) research articles

www.metla.fi/silvafennica · ISSN 0037-5330
The Finnish Society of Forest Science · The Finnish Forest Research Institute

Seedling Establishment and Growth after Direct Seeding with *Pinus sylvestris*: Effects of Seed Type, Seed Origin, and Seeding Year

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Wennström, U., Bergsten, U. & Nilsson, J.E. 2007. Seedling establishment and growth after direct seeding with *Pinus sylvestris*: effects of seed type, seed origin, and seeding year. Silva Fennica 41(2): 299–314.

The early effects of seed type, seed origin, and seeding year on seedling emergence, survival, and growth after one to four years was quantified and examined. Two experimental series of Scots pine located at 61°N and 64°N and six orchard seed lots and six stand seed lots of adequate geographical origins in each series were used. Both series were replicated at five sites for up to five years. On average, orchard seed lots had 16% and 12% higher seedling emergence, in relation to sown germinable seeds, than stand seed lots in the northern and southern series. The survival from year 1 to year 4 was also higher for orchard seedlings than for stand seedlings; there was a 77% and 72% survival rate in the northern series and a 58% and 49% survival rate in the southern series for orchard and stand seedlings respectively. On average, after four years orchard seedlings were 26% taller in the northern series and 13% taller in the southern series. The gain in height growth for the orchard seeds was positive at all seeding years, at all sites, and at all seedling ages. If survival was calculated to the height of a four-year-old seedling, the survival of orchard seedlings increased by 3% in the northern and 1% in the southern series as the result of the higher growth of orchard seedlings. Using orchard seeds resulted in 6 percent units higher growth gain when the clear cuts were regenerated with direct seeding than with plants using the same seed material. Changes in the ranking of seed lots and seed types at different sites and seeding years for seedling emergence is an effect of external factors such as grazing and foraging that cannot be related directly to the tested factors.

Keywords direct seeding, orchard seed, Scots pine, stand seed
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Received 8 September 2006 **Revised** 24 January 2007 **Accepted** 12 April 2007
Available at http://www.metla.fi/silvafennica/full/sf41/sf412299.pdf

1 Introduction

Scots pine (*Pinus sylvestris* L.) is a native species in Sweden that ranges from 55°30´ N in the south to 68°30´ N in the north (Skogen ... 1990). In Sweden, the latitude and altitude is negatively correlated to the temperature sum and the growing period at any given location (Morén and Perttu 1994). The survival of the local provenance of Scots pine is also negatively correlated to latitude and altitude as shown by Eriksson et al. (1980) and Person (1994). The latitudinal origin of a Scots pine seed lot is important for survival and growth (Eiche 1966, Remröd 1976, Eriksson et al. 1980, Persson 1994). Survival is positively correlated and growth is negatively correlated to the latitudinal origin of a seed lot at any location. The altitudinal origin is though of minor importance for survival and growth (Persson and Ståhl 1993, Persson 1994). For volume production in northern Sweden, the gain in survival rate by using Scots pine seeds from more northern origins outweighs the loss in height growth. In operational forestry, stand seed of Scots pine is therefore usually southerly transferred 1–3 degrees in northern Sweden.

Seed maturation in Scots pine is positively correlated to the temperature sum (Almqvist et al. 1998). Cone production is higher in southern Sweden than in the northern Sweden and higher at lower altitudes than at higher altitudes (Hagner 1958). To increase seed quality and crop, seed orchards are located at mild locations on agricultural land. Clones from a seed orchard in northern Sweden originate from higher altitudes and latitudes than the location of the orchard; in mid and southern Sweden the clones originate from approximately the same latitude (Hannerz et al. 2000). To further improve quality and crop, seed orchards are also planted with wide spacing and are typically treated with fertiliser, herbicides, and grass cuttings. In general, seeds matured on orchard grafts are better developed, have higher seed weight, and higher germination rates than stand seeds of the same clone origin (Simak and Gustafsson 1954).

Pollen from outside sources, background pollination, has a great impact in Scots pine seed orchards. Approximately 40% of the pollen in mature Swedish orchards originate from outside sources (Yazdani and Lindgren 1991). Contamination with local pollen in south transferred seed orchards means genetic loss in hardiness compared to progenies from local stands at the clone origin (Nilsson 1991).

The clones in Swedish seed orchards originate from selected trees. The expected genetic gain of using orchard seed is approximately 8% when regeneration is made with plants (Andersson 1996). When regeneration is made with direct seeding, the gain seems to be higher. Orchard seedlings are approximately 20–25% taller than a corresponding stand seed five years after seeding (Wennström et al. 1999, 2001).

For a seed to become a mature tree, it must survive many hazards. These hazards tend to be more frequent in the beginning than in the end of the life cycle. The critical period starts even before germination with predation of seeds, followed by the germination phase that usually allows only less than half of the viable seed to emerge, predation on germinants and seedlings, mortality due to weather effects, etc. (Nystrand and Granström 1997a, Winsa and Bergsten 1994, Engelmark et al. 1998, Wennström et al. 1999). At the end of the life cycle, the mortality in mature cultured forests is below 0.6% per year of the total stem number (Øyen 2000).

High quality orchard seed – seeds with high seed weight and high germination rates and capacity – is beneficial to use in comparison with poor or average quality stand seed to overcome the hazards associated with emergence and early survival (Winsa and Bergsten 1994). In fact, the positive effect on direct seeding could be very high resulting in a four-fold increase in seedling emergence (Winsa and Bergsten 1994). Because orchard seeds normally have higher seed weight than stand seeds, even if the germination capacity at optimal conditions is equally high, we hypothesise that orchard seeds in general should result in increased seedling emergence and establishment after direct seeding of Scots pine, i.e., also when the germination capacity is high for both types.

This study quantifies and examines the effect of seed type on seedling emergence and survival, and on early seedling growth at different sites and seeding years. To also quantify the effect of latitudinal origin, the seed lots were chosen to represent a latitudinal gradient. The experiment was repeated for six years in two climatically different regions on clear-cuts of different ages. Nursery-grown seedlings from the same seed material were also planted at four sites to make comparison with planting possible.

2 Materials and Methods

In 1995, two series of experiments were started: a northern series (N) near the forest research station at Vindeln, (64°15´N., 225–260 m.a.s.l.) and a southern series (S) near the forest research station at Siljansfors (61°00´N., 260–410 m.a.s.l.), hereafter referred to as northern and southern series of experiments. In each series, one new site was established on a "fresh" clear-cut each spring from 1995 to 1999. At each series, six orchard seed lots and six stand seed lots were tested. Seeding was repeated yearly in June at each site until 2000 (Tables 1 and 2). An extra orchard seed lot (O7) was included in the northern series from 1997.

Each site consists of ten blocks. In each block, one plot of each seed lot, randomly organised, was sown each year. At the second, third etc. seeding occasion, seeding was repeated in an adjacent row within each block. Due to lack of space at sites 1 and 6 all seed-lots were not represented at the seeding in year 2000. The results from the seeding year 2000 at site 1 and 6 were therefore not included in this analysis.

Scarification was done at the time of seeding. In the northern series, removal of the humus layer was done using a clearing saw equipped with a rotating tiller (Eco-cultivator) and when necessary accomplished by hand using a mattock. The sites in the southern series were generally stonier, so all scarification was made by hand using mattocks. In 1995, the first seeding year, the scarification at site 6 was not made as planned and therefore the results are excluded in the calculations.

The scarified plot area was 35 to 50 cm square. Seeds, 36 (6×6) in each plot, were sown in microsite indentations with 4-cm target spacing in the scarified plots, with exception of site 6, a very stony site, where only 9 (3×3) seeds in each plot were sown. Microsite indentations (Bergsten

Table 1. Site description of the northern and southern series.

No.	Series	Lat.	Alt.	T-sum[a]	Site index[b]
1	N	64°15´	260	824	T23
2	N	64°17´	235	843	T22
3	N	64°16´	240	839	T21
4	N	64°18´	225	850	T21
5	N	64°18´	245	833	T22
6	S	60°54´	325	972	T18
7	S	61°04´	405	896	T17
8	S	60°50´	310	988	T16
9	S	60°56´	375	928	T18
10	S	61°13´	260	1007	T19

a) Expected temperature sum, when the mean day temperature has reached +5°C (Morén and Perttu 1994)
b) Expected dominant height (m) at an age of 100-years (Hägglund and Lundmark 1981)

1988) were made with a special tool consisting of contiguous square pyramids with 4×4 cm bases and a height of 2 cm. All plots were well marked with plastic sticks in each of the four corners of the plot.

The number of dead and living seedlings was assessed the first autumn after growth cessation. After the second growth period, only living seedlings were assessed. The height of the tallest seedling in each plot was measured after growth cessation starting in 1997.

Seedling establishment was calculated as the proportion of established seedlings in relation to the number of sown germinable seeds. The percentage of germinated seeds and fresh not germinated seeds was analysed on a germination table (Jacobsen´s apparatus) (International... 1996). Survival was calculated as the number of living seedlings in year 4 in relation to the number of living seedlings in year 1. Occasional survival values higher than 100% (i.e. increase of seedlings) were counted as 100%. Height measurement was assessed on the tallest seedling in each plot.

One-year-old nursery-grown seedlings, from the very same seed-material, were planted at sites 1, 2, 6, and 7 in 1996 simultaneous with seeding. Seedlings were planted within the same blocking, but not in direct connection to the seeded plots, with the same scarification technique as the seeded plots. Seedling height and survival were assessed yearly from 1997.

Table 2. Seed data of used seed-lots.

No	Seed lot	Orch. lat.(a	Clon. lat.(b	Mean origin(c	Mat. yr.	G14 (d	FEG (e	GE (f	1000–sw(g	Series	Plant establ. yr. 1 (%)	Survival yrs. 1–4	Height yr. 1 (mm)	Height yr. 4 (mm)
O1	Orchard, 123 Klocke	62°54´	67°42´	66°36´	1984	95.8	1.0	87.5	6.24	N	40.5	71.3	19.3	286
O2	Orchard, 1 Skaholma	63°48´	67°00´	66°18´	1994	98.3	0.5	95.7	6.14	N	42.5	77.4	18.4	282
O3	Orchard, 401 Hortlax	65°18´	66°18´	66°00´	1992	87.0	7.0	91.4	5.82	N	37.3	78.2	20.6	292
O4	Orchard, 4 Skatan	63°48´	65°42´	65°12´	1994	99.5	0.0	98.7	5.97	N	40.9	75.4	28.3	283
O5	Orchard, 10 Östteg	63°48´	65°06´	64°48´	1994	99.3	0.0	97.7	6.40	N	43.1	77.1	19.9	289
O6	Orchard,18 Brån	63°54´	64°24´	64°20´	1994	99.5	0.5	92.0	6.24	N	41.8	83.3	20.3	307
O7	Orchard, 605 Sävar	63°54´	65°35´	64°00´	1994	97.0	0.8	94.6	6.05	N	(h	(h	(h	(h
S1	Stand, 67°00´ 100 m.a.s.l.	–	–	–	1988	92.5	4.8	93.0	4.98	N	36.0	76.8	13.9	234
S2	Stand, 66°30´ 300 m.a.s.l.	–	–	–	1988	94.0	2.7	88.0	4.78	N	36.9	76.9	15.1	227
S3	Stand, 66°00´ 300 m.a.s.l.	–	–	–	?	87.8	7.2	37.6	4.99	N	29.7	71.2	11.8	230
S4	Stand, 65°10´ 300 m.a.s.l.	–	–	–	1986	79.3	10.0	64.7	3.13	N	32.4	65.2	16.6	189
S5	Stand, 64°20´ 300 m.a.s.l.	–	–	–	1992	91.8	3.2	86.1	4.70	N	35.1	71.9	15.5	237
S6	Stand, 63°07´ 250 m.a.s.l.	–	–	–	1993	93.8	0.8	91.2	4.12	N / S	41.3 / 38.9	66.7 / 57.6	16.3 / 14.7	259 / 105
S7	Stand, 61°40´ 500 m.a.s.l.	–	–	–	1992	88.0	6.8	61.9	4.86	S	37.5	61.5	15.8	115
S8	Stand, 60°54´ 290 m.a.s.l.	–	–	–	1994	98.8	0.2	99.2	3.73	S	46.4	45.5	17.5	143
S9	Stand, 60°40´ 250 m.a.s.l.	–	–	–	1962	57.8	7.5	54.1	3.84	S	31.6	44.6	13.4	123
S10	Stand, 59°50´ 110 m.a.s.l.	–	–	–	1984	82.3	14.8	61.7	5.32	S	43.6	41.0	18.7	113
S11	Stand, 59°40´ 150 m.a.s.l.	–	–	–	1994	98.0	0.2	97.2	3.64	S	46.2	42.3	17.4	125
O8	Orchard, 433 Tällby	61°36´	63°00´	62°30´	1993	95.5	0.2	97.4	6.20	S	45.6	61.6	19.6	132
O9	Orchard, 28 Solvarbo	60°24´	63°42´	61°18´	1995	96.3	1.8	88.3	7.45	S	44.1	57.5	22.3	117
O10	Orchard, 442 Sollerön	60°30´	60°54´	61°18´	1993	97.5	0.0	99.2	5.70	S	47.5	60.9	18.2	125
O11	Orchard, 493 Askerud	61°00´	59°53´	60°54´	1983	99.5	0.0	95.7	6.01	S	45.7	60.9	19.7	167
O12	Orchard, 452 Öhn (i	60°30´	60°12´	60°36´	1982	97.0	2.0	93.0	4.56	S	45.9	53.5	18.4	138
O13	Orchard, 40 Dömle (i	59°36´	60°54´	60°30´	1995	85.8	0.8	87.2	4.82	S	44.9	52.5	18.7	137

a) Location of the orchard
b) Mean clone origin
c) Exp. hardiness of the collected seed in the orchard in comparison of stand seed lots
d) Germination capacity after 14 days at Jacobsen´s apparatus (8 h 30°C, 16 h 20°C)
e) Fresh but not germinated seed after 14 days.
f) Germination energy (7/14 days)
g) weight of 1000 seeds
h) No mean value, the seed lot was not included in years 1995 and 1996
i) Size fractionated seed lot. The fraction with smaller seeds is used in the experiment

2.1 Statistical Analyses

Within the northern and southern series, seedling establishment in relation to sown germinable seeds, survival of living seedlings and height of the tallest seedling in each plot was analysed using model:

$$y = \mu + S + B(S) + Y + S\times Y + Y\times B(S) + T + S\times T + Y\times T + L(T) + S\times L(T) + Y\times L(T) + e \quad (1)$$

where y is the response variable, μ = overall mean, S = effect of site, B(S) = effect of block within site, Y = effect of seeding year, T = effect of seed type, L(T) = effect of seed lot within seed type, and *e* = random residual. Other effects are interaction effects. A fixed effect model, with Y×B(S) as a random plot residual, was used.

Estimates of seed type and seed lot effects on seedling establishment for individual sites and seeding years were obtained using models:

$$y = \mu + B + T + L(T) + e \quad (2)$$

$$y = \mu + B + L + e \quad (3)$$

where y is the response variable, μ = overall mean, B = effect of block, T = effect of seed type, L and L(T) = effects of seed-lot, and *e* = random residual.

The effect of seed type on height of planted seedlings was analysed using model:

$$y = \mu + S + B(S) + T + S\times T + L(T) + S\times L(T) + e \quad (4)$$

where y is the response variable, μ = overall mean, S = effect of site, B(S) = effect of block within site, T = effect of seed type, L(T) = effect of seed lot within seed type, S×T and S×L(T) are interactions effects, and *e* = random residual.

Linear regression analysis of field results (seedling emergence, seedling establishment, seedling height, and survival) on seed data (germinable seeds, 1000-sw, and latitude) was used to eliminate differences between seeding year × seed lot combinations using dummy variables. This was used to estimate individual overall relationships between seed data and field results for both seed types at each experimental series.

The statistical analyses were carried out using the SAS procedure of general linear models (SAS/STAT™... 1988). Log transformations [log((p + 0.5)/(1.5 – p))] were used for analyses of proportions (Sabin and Stafford 1990).

3 Results

3.1 Seedling Emergence and Establishment in Relation to Sown Germinable Seeds

In the northern series, direct seeding with orchard seed resulted in higher seedling establishment (on the average 17% year 1 and 28% year 4) than seeding with stand seed at years 1–4 (Table 3). Effects of site and seeding year were significant at all ages as well as the interaction between site and seeding year. Interactions between site and seed type at years 1 and 2 and interactions between seeding year and seed type years 1 to 4 were also significant. There were significant interactions of seed lot (within seed type) with seeding year at all ages. Interactions between seed lot and site were all insignificant.

In the southern series, direct seeding with orchard seed resulted in (12% year 1 and 36% year 4) higher seedling establishment than seeding with stand seed at years 1 to 4 (Table 3). The site effect was significant at all ages. The effect of seeding year and the interaction between site and seeding year were significant at years 1 to 3. The interactions of seed type × site and seed type × seeding year were insignificant at all ages. Seed lot effects were significant at years 1 and 2, probably because of seed lot O5 showed the poorest results. Seed lot × seeding year interactions were smaller than in the northern series and significant only at year 2.

In sites and seeding years, the use of orchard seed compared to stand seed positively influenced the first year seedling establishment in 1996 at sites 1, 2, 6, and 7, in 1997 at sites 2, 3, and 6, in 1999 at sites 3, 4, 7, and 10, and in 2000 at sites 2, 3, 4, and 10 (Fig. 1). Close to significant values ($p<0.07$) were also recorded at sites 2 and 8 in 1999. If the predated seedlings, recorded at site 9, were included, the positive influence of using orchard seeds on plant establishment was also significant in 1999 and 2000. In 2000 at site 5, however, the influence of using orchard seed

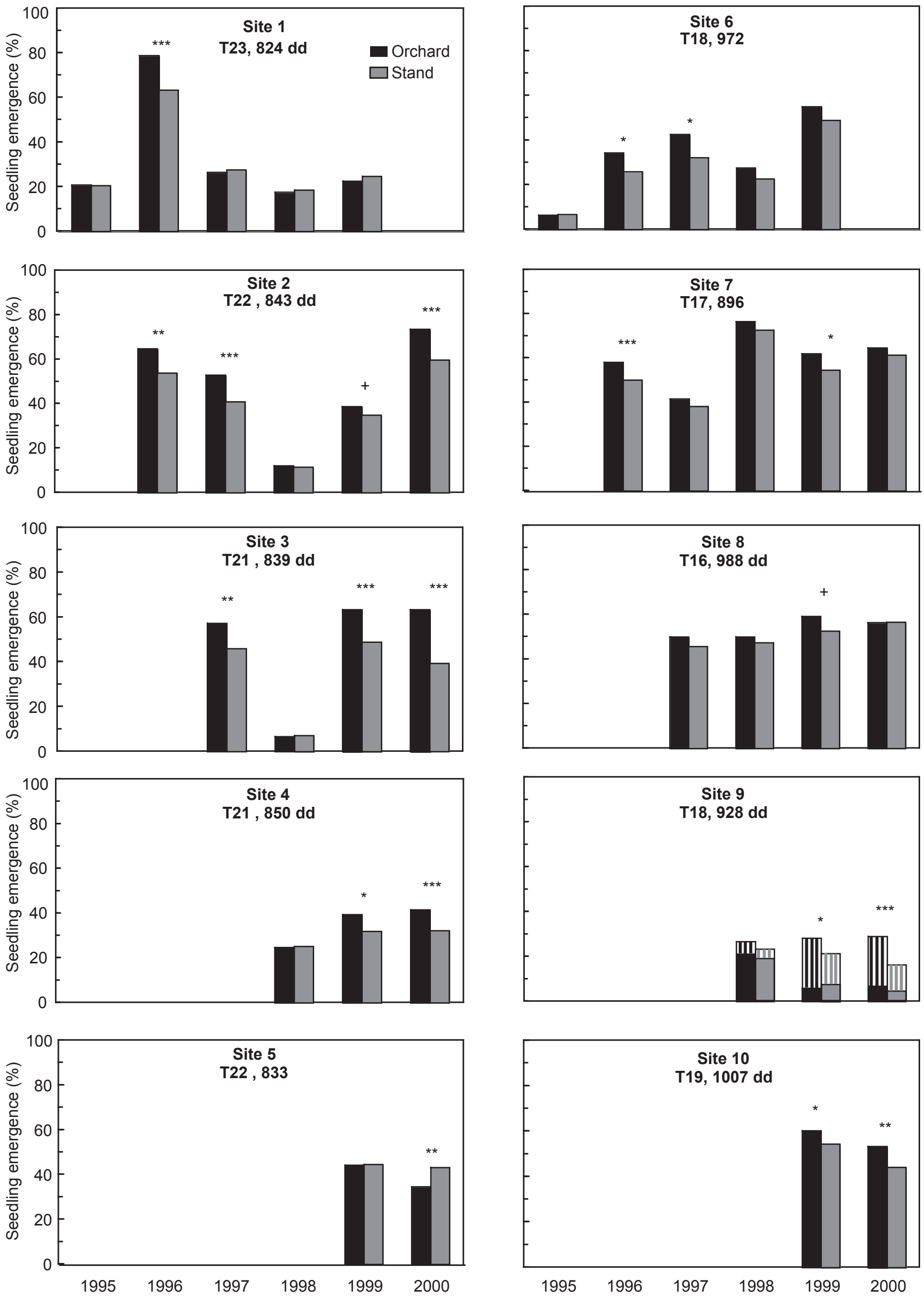

Fig. 1. Seedling emergence at the first autumn after seeding in relation to sown germinable seeds of orchard (black bars) and stand (grey bars) seedlings years 1995 to 2000. Significant differences between seed types are marked with: *** = $p < 0.001$, ** = $p < 0.01$, * = $p < 0.05$, and + = $p < 0.10$. At site 9 browsed seedlings are included in the figure and marked with vertical bars. The significance levels at site 9 represent seedling emergence including browsed seedlings. Site index and expected T-sum for the sites are presented in each figure. Seed lot O7 was not included in years 1995 and 1996 and was therefore excluded.

Table 3. Results from analysis of variance model 1 of seedling establishment (=proportion of living seedlings in relation to sown germinable seeds) 1 to 4 years after seeding, and seedling survival from year 1 to year 4. S = site, Y = seeding year, T = seed type, L = seed lot. All effects are not shown. Bold labels indicate significant value, $p < 0.05$.

Series	Age after seeding	Number of				Significance levels Effect									Mean (%)	
		Plots	Sites	Years	R²	S	Y	S×Y	T	S×T	Y×T	L(T)	S×L(T)	Y×L(T)	Orch.	Stand
N	1	2443	5	6	0.61	**0.019**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.006**	0.085	**<0.001**	40.9	35.2
N	2	1916	5	5	0.65	**0.004**	**<0.001**	**<0.001**	**0.002**	**0.020**	**<0.001**	**0.039**	0.088	**0.005**	34.6	32.0
N	3	1268	4	4	0.67	**0.010**	**<0.001**	**<0.001**	**<0.001**	0.602	**<0.001**	0.101	0.636	**0.002**	28.2	24.3
N	4	749	3	3	0.54	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.270	**0.031**	0.060	0.446	**0.043**	37.6	29.9
N	1 to 4	694	3	3	0.41	**0.002**	**<0.001**	0.537	**0.042**	0.186	0.883	0.289	0.300	0.785	77.0	71.5
S	1	2154	5	5	0.57	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.205	0.890	**<0.001**	0.103	0.098	45.6	40.8
S	2	1672	5	4	0.55	**<0.001**	**<0.001**	**<0.001**	**0.001**	0.075	0.735	**0.003**	0.224	**0.052**	34.6	29.9
S	3	1076	4	3	0.54	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.529	0.242	0.462	0.529	0.206	28.7	23.4
S	4	600	3	2	0.37	**0.017**	0.183	0.088	**<0.001**	0.455	0.877	0.376	0.117	0.245	25.5	18.7
S	1 to 4	565	3	2	0.41	**0.002**	**0.005**	0.954	**0.004**	0.186	0.883	0.289	0.143	0.270	57.8	48.9

compared to stand seed was significantly negative. The seedling establishment in 2000 at site 5 was negatively correlated to seed weight.

The differences between seed lots were larger in years with medium to good seedling emergence results (Fig. 2). For example, in 1998 in the northern series, the conditions for seedling emergence were poor and the difference between seed lots was not significant. Large changes in the ranking of seed lots were observed at different seeding years in the sites.

The coefficient of variation (standard deviation in relation to the mean value) for seedling establishment after four years within seed lots, sites, and seeding years was smaller for orchard seed lots than for stand seed lots. The coefficient of variation was 51 and 63 in the northern series, and 77 and 92 in the southern series for orchard and stand lots respectively. Also the number of zero plots, i.e. plots with no seedlings, was smaller for orchard seed lots than for stand seed lots with 4% and 8% in the northern and 26% and 44% in the southern for orchard and stand seed lots respectively.

The seedling emergence was positively correlated with the percentage of germinable seeds in the seed lots, with exception of stand seedlings in the northern series and orchard seedlings in the southern series (Fig. 3). The influence was weak and explained only 0.0 to 4.9% of the variation. Seed weight did not influence seedling emergence although the influence within orchard seed lots in the northern series was significantly positive. The seed weight range within orchard seed lots in the northern series was narrow. The latitudinal origin had a weak negative influence on seedling emergence. The latitude explained only less than 1% of the variation.

The seedling establishment 4 years after seeding was positively influenced by the percentage of germinable seeds in the seed lot in the northern series, but not in the southern. The percentage of germinable seeds explained 1.5–4.2% of the variation. Seed weight and latitude of origin did not influence seedling establishment 4 years after seeding.

No correlation between seedling emergence and clear-cut age, site index or meteorological data (cumulative T-sum and precipitation) could be detected (data not shown).

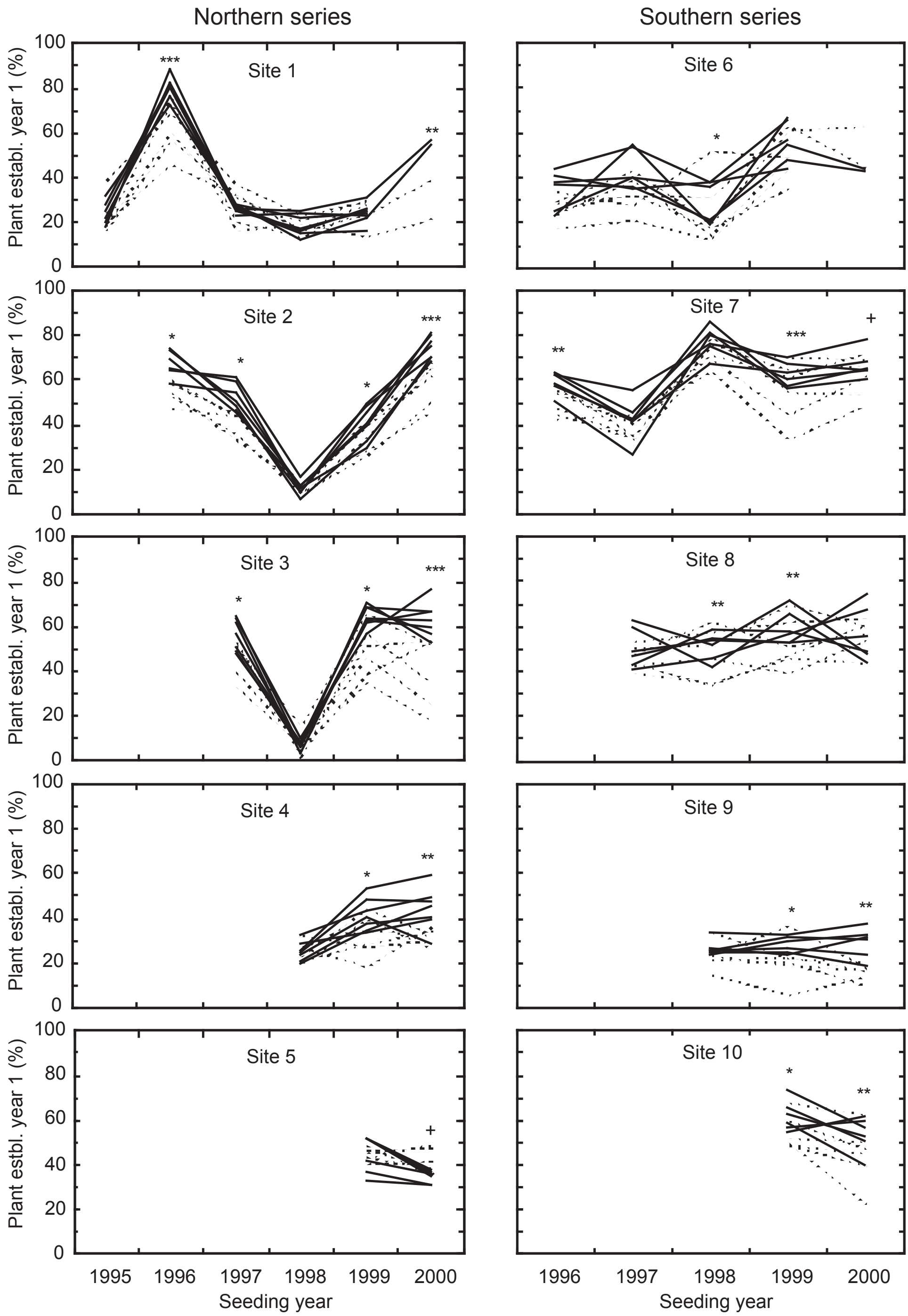

Fig. 2. Seedling emergence in relation to sown germinable seeds of orchard seed lots (solid lines) and stand seed lots (broken lines) at the first autumn after seeding from 1995 to 2000. Significant differences between seed lots are marked with: *** = p < 0.001, ** = p < 0.01, * = p < 0.05, and + = p < 0.10. The figure is based on least square means.

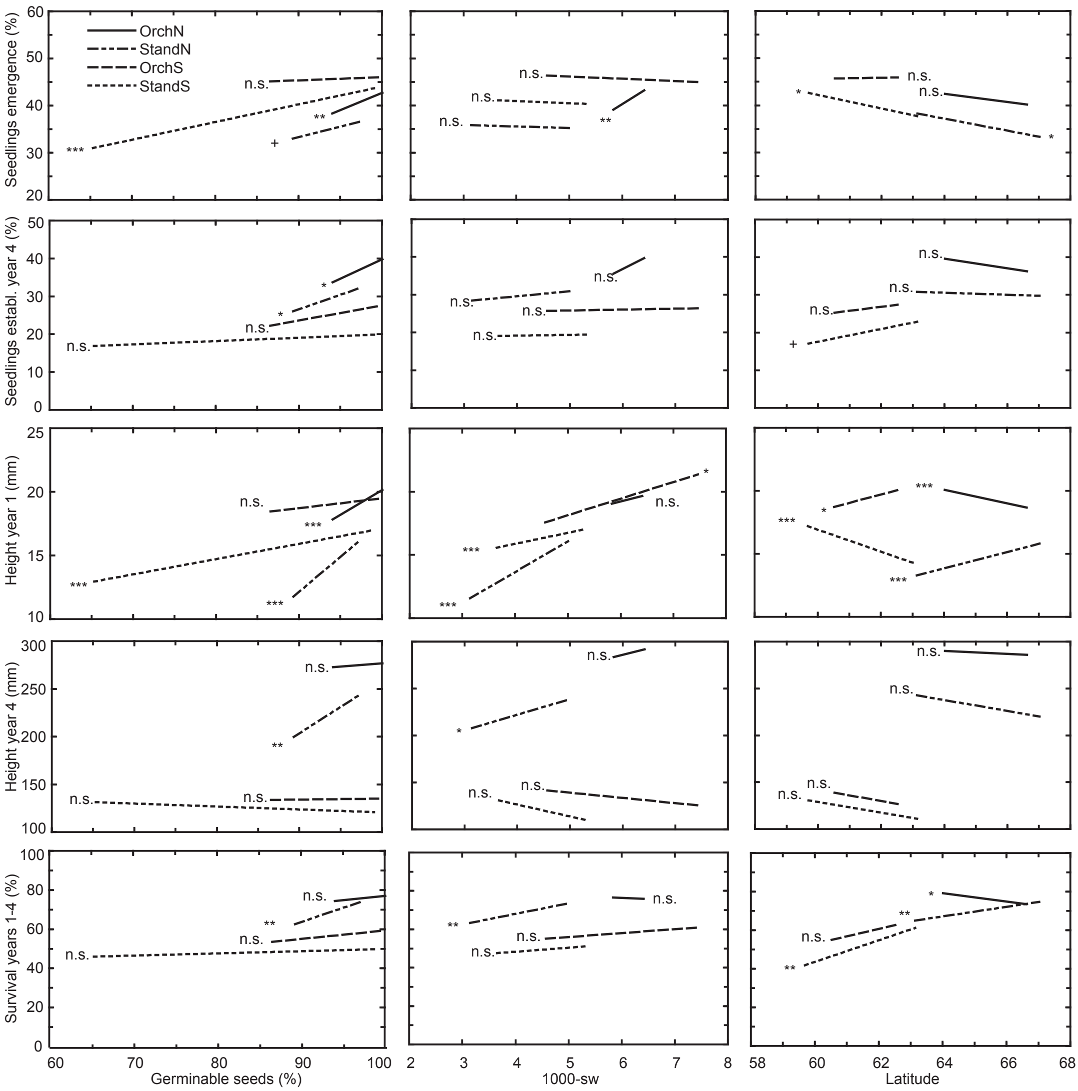

Fig. 3. The correlation between seed data (germinable seeds, seed weight, and latitude origin) to seedling emergence, seedling establishment year 4, survival from year 1 to year 4 and height of the tallest seedling years 1 and 4. The figures are based on mean values for each seed lot for each site and seeding year. The length of each line represents the range of the x-axis. Note that both series are included in the figures but cannot be directly compared.

3.2 Survival

The survival from year 1 to year 4 was higher in the northern series than in the southern series, 77% of the orchard seedlings and 72% of the stand seedlings that were alive at year 1 in the northern series were still alive at year 4 (Table 3). In the southern series, 58% of the orchard seedlings and 49% of the stand seedlings were still alive at year 4. The difference between seed types was significant in both experiments. In addition, effects of site and seeding year were significant in both experiments. All interactions were insignificant. However, at site 7 (p=0.034) and site 9 (p=0.001) in the southern series there was significantly higher mortality of orchard seedlings than stand seedlings the first summer (data not included). Browsing, probably by weevils, mainly caused the mortality at site 9.

The coefficient of variation for survival was lower for orchard seed lots than for stand seed lots in both series with 29 and 35 in the northern series and 55 and 72 in the southern series for orchard and stand seed lots respectively.

The survival between years 1 and 4 of stand seedlots originating from northern origins was higher than for seed lots of southern origin in both series (Fig. 3). In the northern series orchard seedlings with southern origin had higher survival than those with northern origin. The survival was not influenced by the percentage of germinable seeds or seed weight with exception of stand seedlings in the northern series, where survival was positively influenced by percentage of germinable seeds and seed weight. Neither was survival correlated to the number of seedlings in the plot in year one.

3.3 Height of the Tallest Seedling in Each Plot

The use of orchard seed compared to stand seed increased the first year's height of the tallest seedling in each plot by 31% and 19% in the northern and southern series respectively (Table 4). The increase did not change in the years when calculated on the same seedlings years 1 and 3 (data not included). The use of orchard seed, instead of stand seed, significantly increased height growth in each plot for years 1 to 4 after seeding in the northern series and at years 1 and 2 after seeding in the southern series (Table 4). However, the effect of using orchard seed compared to stand seed was positive at all sites, at all seeding years, and at all seedling ages in both series (data not included). There was a significant difference between sites at all ages in both series, with exception of year 3 in the southern series. The height was also influenced by seeding year at all ages, with exception of years 3 and 4 after seeding in the southern series. The interaction of site and seeding year (years 1–3 in the northern series and year 1 in the southern series) significantly

Table 4. Effects of site (S), seeding year (Y), seed type (T), and seed lot (L) on the height of the tallest seedling in each plot 1 to 4 years after seeding. All effects/interactions including site and seeding year are calculated as random effects. B(S) and B×Y(L) were excluded from the table due to low interest. Bold labels indicate significant value, $p < 0.05$.

	Age after	Number of				Significance levels Effect									Mean (%)	
Series	seeding	Plots	Sites	Years	R^2	S	Y	S×Y	T	S×T	Y×T	L(T)	S×L(T)	Y×L(T)	Orch.	Stand
N	1	1969	5	4	0.56	**0.002**	**<0.001**	**<0.001**	**<0.001**	**0.039**	**0.004**	**<0.001**	**0.022**	**0.016**	19.5	14.8
N	2	1683	5	4	0.46	**0.009**	**<0.001**	**0.035**	**<0.001**	0.056	0.527	**<0.001**	0.536	0.403	42.4	31.7
N	3	1122	4	4	0.53	**0.004**	**<0.001**	**0.047**	**<0.001**	0.092	0.202	0.079	0.454	0.112	129	97.6
N	4	704	3	3	0.43	**<0.001**	**0.053**	0.735	**<0.001**	0.126	0.238	**0.036**	0.880	0.265	287	230
S	1	1690	5	4	0.55	**0.002**	**<0.001**	**<0.001**	**<0.001**	0.625	0.247	**<0.001**	0.200	0.565	19.5	16.3
S	2	1406	5	4	0.39	**0.038**	**<0.001**	0.243	**<0.001**	0.463	0.082	**<0.001**	0.251	0.389	30.1	25.1
S	3	850	4	3	0.30	0.678	0.391	0.096	0.102	0.354	0.159	0.748	0.522	0.831	67.4	57.7
S	4	484	3	2	0.35	**0.004**	0.075	0.802	0.124	0.707	0.516	0.515	0.440	0.847	136	120

Table 5. Planted seedlings: Effects of Site (S), Seed-lot (L) and Seed-type (T) on plant height years two to five. OrchA and StandA represent sites 1 and 6, OrchB and StandB represents sites 2 and 7 respectively. Effects of B(S) were excluded from the table due to low interest. Bold labels indicate significant value, $p < 0.05$.

			LS-means (cm) Seed type within site				Significance levels Effect					
Year	Series	R^2	OrchA	StandA	OrchB	StandB	S	T	S×T	L(T)	S×L(T)	Obs
2	N	0.258	21.8	22.3	17.8	17.5	**<0.001**	0.770	0.361	**<0.000**	0.623	555
3	N	0.237	39.8	36.7	33.7	31.3	**<0.001**	**0.005**	0.698	**0.049**	0.437	539
4	N	0.144	50.8	44.3	44.0	44.7	**<0.001**	0.220	0.090	0.508	0.773	524
5	N	0.179	80.0	72.1	69.3	64.4	**<0.001**	**0.001**	0.427	0.330	0.892	514
2	S	0.292	15.9	15.1	12.6	11.3	**<0.001**	**0.052**	0.710	**0.002**	0.231	299
3	S	0.189	19.5	19.7	16.7	16.5	**<0.001**	0.994	0.814	0.099	0.059	389
4	S	0.190	28.2	27.2	25.4	25.0	**0.034**	0.572	0.799	0.069	0.056	383
5	S	0.250	39.7	35.7	39.3	36.6	0.891	**0.045**	0.706	**0.019**	**0.011**	379

influenced the height growth. The interaction of site and seed type and seeding year and seed type was significant in year 1 in the northern series. There were significant differences between seed lots (within seed types) for years 1, 2, and 4 in the northern series and in years 1 and 2 in the southern series. The interactions between seed lot and site and between seed lot and seeding year were insignificant, except for the first year after seeding in the northern series.

Orchard seedlings were more even in size. The coefficient of variation for height of the tallest seedling in each plot in year 4 was 31 and 35 in the northern series, and 61 and 69 in the southern series for orchard and stand seedlings respectively.

The percentage of germinable seeds and seed weight was positively correlated to seedling height year 1, Fig. 3. The influence was slightly stronger for seed weight where 1–41% of the variation was explained by seed weight while 2–33% of the variation was explained by the percentage of germinable seeds. For year 1, the height was significantly influenced by latitude of origin; however, the influence was a bit confusing. The latitude positively influenced height for stand seedlings in the northern series and orchard seedlings in the southern series. For orchard seedlings in the northern series and stand seedlings in the southern series, the opposite relationship was found.

3.4 Plants

Orchard seeds produced seedling heights 9% greater than stand seed after 5 years in both series when the regeneration was made with plants (Fig. 4). The gain was significant at years 3 and 5 in the northern series and at years 2 and 5 in the southern series (Table 5). There were significant differences between the two sites in the northern series (years 2–5) and between the sites in the southern series (years 2–4). The seed lots were significantly different in the northern series at years 1 and 2 after planting and after years 1 and 5 in the southern series. Seed lots within seed types differed significantly in rank at the two sites in the southern series five years after planting. When the regeneration was made with direct seeding, sown the same date as the plants were planted, the gain in height growth from using orchard seed compared of stand seed was 15% after 5 years in both series.

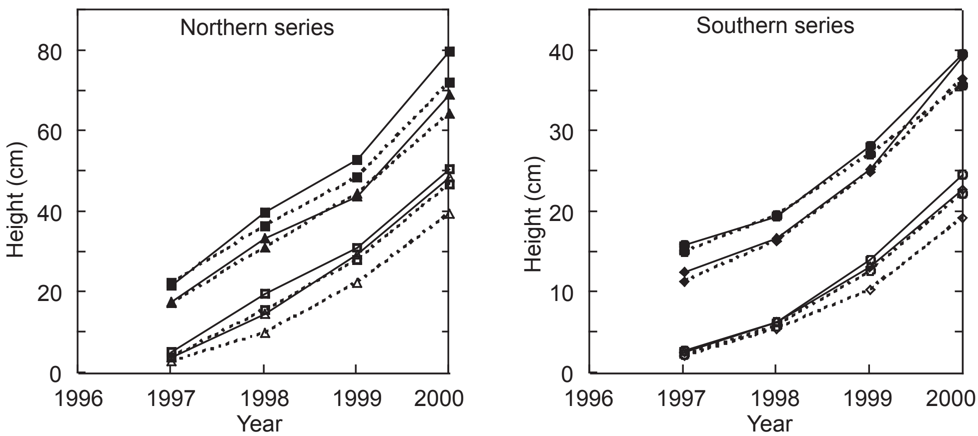

Fig. 4. Height development (cm) of seedlings, directly seeded and planted in 1996 at sites 1 (squares) and 2 (triangle) in the northern series and sites 6 (circles) and 7 (diamonds) in the southern series. Solid symbols represent planted seedlings and hollow symbols represent directly seeded seedlings. Solid lines represent orchard seedlings and broken lines represent stand seedlings. The figure is based on least square means.

4 Discussion

4.1 Seedling Emergence, Establishment and Predation

The higher seedling establishment in relation to sown germinable seeds of using orchard seed compared to stand seeds agrees with earlier investigations (Winsa and Bergsten 1994, Wennström et al. 1999, 2001). It seems that in some years and at some sites the effect of seed type was insignificant or even that use of stand seed compared to orchard seed positively influenced seedling emergence. A possible reason could be high seed and seedling predation. Birds are important seed predators on scarified clear-cuts (Vaartaja 1950, Heikkilä 1977, Bergsten 1985). Birds rely on vision when foraging (Nystrand and Granström 1997b). Orchard seeds and seedlings are larger than stand seed and seedlings and are therefore easier to find and more cost efficient to predate. Seed predation by birds in these experiments is probably higher than in practical seeding because birds are quick to learn (Morris 1979) and can fly from plot to plot (well marked with plastic sticks) to find seeds in each microsite indentation. Predation is a problem in practical seeding although probably less significant since seeds are sown one by one in rows with wider spacing between seeds and also the microsite indentations are abundant in relation to seeds which makes seed predation less cost efficient for the predator.

In 1995, while seeding site 1 we observed *Fringilla coelebs* (L.) finches flying from plot to plot predating from the well marked sown plots. At site 5 in year 2000, seedling establishment was negatively correlated to seed weight, which could be an indication of predation. At site 9 we noted browsed seedlings leaving a stump with no growth potential. The stumps were assessed and the larger orchard seedlings were significantly more browsed than stand seedlings (Fig. 1). Weevil predation is a probable cause.

The changes in ranking of seed types between seeding years and of seed lots between seeding years and sites indicate that the causes for poor or good seedling emergence varies from year to year. In one year, seed lots that can germinate in low temperature have an advantage. In another year, however, seed lots with small seeds are less likely to be eaten by birds and in another year seed lots with fast germination rates during a suitable weather period gives the highest emergence. On average, orchard seed lots with high germination capacity, fast germination, and high seed weight are advantageous to use in relation to stand seed lots.

Orchard seed lots did not only germinate better than stand seed lots, the seedlings were also more evenly distributed. The coefficient of variation for seedling establishment was lower for orchard seed lots than for stand seed lots in both series. In addition, the number of zero-plots for orchard seed lots was almost half the number for stand seed lots. The weak correlation between clear-cut age, T-sum, weather data, and seedling emergence was probably a result of more than the tested factors involved. Examples of other factors that could influence seedling emergence include predation, fungi damage, early frost, splash effects from intensive rain that can transport seeds out of the plots, etc. Shorter dry periods, not detectable in this investigation, can be very sensitive to a seed that is just about to emerge.

The changes in ranking of seed lots between seeding years and sites demonstrate the need of replicates at different sites and years in field experiments. The two series are also a good example of the need of field experiments. The best seed lot in the laboratory is not always the best in the field experiment.

4.2 Seedling Survival

The higher survival rates for orchard seedlings compared to stand seedlings agree with earlier investigations (Winsa and Bergsten 1994). The higher survival of orchard seedlings could be explained by the higher growth of orchard seedlings because survival seemed to be correlated positively to the height of the tallest seedling. The difference in survival between sites was expected (Winsa and Bergsten 1994, Wennström et al. 1999). Differences in survival between seeding years have as far as we know not been shown in earlier studies of direct seeding with pine. The connection is most likely since mortality is highest during the first years (Kinnunen 1992). For example, health of plants is highly dependent on weather conditions, such as frost heaving, which is one of the main causes for mortality (Winsa and Bergsten 1994, 1995). The higher mortality in the southern series could be an effect of frost heaving. A permanent snow cover protects seedlings from frost heaving injuries (Bergsten et al. 2001). In northern Sweden, the snow starts in November and stays until May; in southern Sweden, the snow will come and go several times during winter, therefore the number of occasions for frost heaving injuries would be higher in the southern than in the northern series.

Seedling survival, as expected (Andersson 1996), was correlated positively to latitude of origin. In the northern series, however, orchard seedling survival was negatively correlated to latitude of origin. The survival for orchard seedlings in the northern series was generally high. Because seedlings with southern origin in the northern series were slightly taller than the northern ones and frost heaving injury is related to the mechanical strength (Schramm 1958), it is likely that survival of orchard seedlings in the northern series was correlated to seedling size rather than climatic adaptation. Mortality in northern Sweden, caused by climatic adaptation, usually occurs when seedlings are tall enough to break the snow cover (Engelmark et al. 1998). A contributory cause of mortality is that the seed lot O1 from seed orchard Klocke, with the most northern origin, was an early collection from a young orchard with probably low internal pollen production. Because the clones are transferred 4° of latitude south, high levels of background pollination might have dramatically affected the geographical distribution of gene origin of the Klocke seed lot. Excluding O1 from the dataset, however, does not change the major results.

Normally survival is correlated to a time. If we had correlated survival to a certain height, e.g., the size of a 4-year-old stand seedling, the survival of the taller orchard seedlings would increase approximately 3 per cent units in the northern series and 1 per cent units in southern series (data not included).

4.3 Seedling Growth

The gain in height growth using orchard seed is well documented (Ackzell and Lindgren 1994, Winsa and Bergsten 1994, Wennström et al. 1999, 2001). The height gain from the use of orchard seeds in these experiments was indeed general; the effect was positive at all sites, at all seeding years, and at all seedling ages in both series. The higher gain in height growth of using orchard seed compared to stand seed for direct seeding is probably a result of a better seed physiology (Simak and Gustafsson 1954, Wennström et al. 2002) and higher genetic gain (Danell 1993).

The higher gain in height growth in orchard seeds in the northern series compared to the southern series (24% and 13% after four years respectively) could be an effect of smaller differences in seed weight between seed types in the southern series (c.f. Wennström et al. 2002). Orchard seed lots in the northern series had 38% higher seed weight than stand seed lots. In the southern series, the difference between seed types was only 15%. The tallest seedlings in each plot were slightly more even in size for orchard seed lots than for stand seed lots in both series. This could be an effect of smaller variation in seed weight in orchard seed lots than in stand seed lots (Wennström et al. 2002).

The correlation between seed traits and first year's growth was strong. Both the percent of germinable seed in the seed lot and the seed weight positively influenced first year seedling height and explained a large part of the variation. At an age of 4 years, correlations between seed traits and seedling height were low. Wennström et al. (2002) showed a strong and long lasting influence of seed weight, within seed lots, in a direct seeding experiment. A weak, but concordant, negative correlation of latitude of origin on height growth indicates that genetic differences between seed lots were the dominant factor in these experiments that influenced seedling growth after four years.

4.4 Seeded vs. Planted Seedlings

Orchard seeds, compared to stand seeds, resulted in a gain in height that was positive in direct seeding and planting. Orchard seeds used for planted seedlings were 9% higher in both series, which is close to the expected genetic gain (8%) for used seed lots at the experimental sites (Andersson 1996). The relative gain in height growth after five years of orchard seed was 6 per cent units larger when the regeneration was made with direct seeding. A higher gain of using orchard seed for direct seeding compared to planting is also suggested by Ackzell and Lindgren (1994).

The higher growth in the northern compared to the southern series is confusing. Both planted and seeded seedlings are almost double in size in the northern series. This contradicts earlier results (Andersson 1996). Difference in site index, T22 and T18 in the northern and southern series respectively, can partly explain the difference. The higher mortality in the southern series could indicate that seedlings in the southern series suffer from damage caused by such conditions as frost heaving.

As shown in Fig. 4, sown seedlings (the tallest seedling in each plot) was only 1½ year after planted seedlings in height growth. Direct seeding can, with advantage, be accomplished in direct connection to harvest while a clear-cut rest is often used for commercial planting forestry to avoid damage from *Hylobius abietis*. Clear-cut rest minimises the growth difference between the two methods. Mineral soil patches though, is not the optimal scarification method for planting. If the plants were planted on e.g. mounds, the difference between planting and seeding would be greater (Örlander et al. 1990).

5 Conclusions

The study shows that direct seeding with orchard seed compared to stand seed from similar geographic origin increases seedling emergence and survival. The effect of orchard seed on seedling emergence is less significant or negative in years with poor conditions for seedling emergence. Seed predation is one possible cause for poor results. The gain in height growth from orchard seed compared to stand seed was consistent and is larger when the regeneration is made with direct seeding than with plants.

Orchard seed lots generally have higher germination capacity than stand seed lots, the seedling emergence in relation to sown germinable seeds is higher, the survival is higher, and the seedlings are more evenly distributed with less zero-plots. In addition, the need to over-dose (to minimise zero plots) will be reduced. The result is that when direct seeding with orchard seed, seed dosage can be considerably reduced and therefore future pre-commercial thinning cost will be reduced as compared to direct seeding with stand seed.

The large differences of the effect of seed type at different seeding years and sites and the changes in ranking between seed lots at different seeding years within sites indicate that the impact of external factors, such as predation, can not directly be related to the tested factors.

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