

## Timing of Seed Dispersal in *Pinus sylvestris* Stands in Central Sweden

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The objective of the study presented here was to describe the variation in timing of seed dispersal from Scots pine (*Pinus sylvestris* L.) seed trees in central Sweden. Seeds were collected in traps at two sites, for three years at one, and four years at the other. The traps were emptied from March to August each year at 1–2 week intervals during the main period of seed dispersal. The annual seed fall varied between 200 000 and 1.6 million seeds per hectare. The seed fall started in mid to late April, shortly after the heat sum had started to accumulate. The most intensive seed fall took place in early to mid May. The peak period, when 50% of the total seed dispersal occurred, lasted for 18–28 days at the different sites and years. The variation in timing among years seemed to be mainly due to climatic factors – high temperatures promoted seed dispersal, for instance. The results may be useful for planning the time of scarification to optimise the natural regeneration of Scots pine. The data suggest that scarification in the spring, no later than mid-May, would generally create a good seed-bed for most of the current year's seeds, whereas scarification in late May or June would bury a large proportion of this cohort.

**Keywords** natural regeneration, Scots pine, seed fall

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## 1 Introduction

The success of natural regeneration of Scots pine (*Pinus sylvestris* L.) depends on the amount and quality of the released seed and the conditions at the site during germination and seedling establishment. In most conditions seedling establishment is greatly improved by soil scarification (Hagner 1962). The positive effects of scarification on natural regeneration decrease with time as the vegetation and litter cover increases, the amount of moisture and soil temperature falls, and the soil surface hardens (as reviewed in Karlsson 2000). The best conditions for natural regeneration occur if the scarification is done shortly before a rich seed-fall, especially in areas where scarcity of germinable seeds limits the success of regeneration (Karlsson and Örlander 2000). This suggests that soil scarification in the spring, immediately preceding a rich seed fall, could be a successful strategy for promoting the natural regeneration of Scots pine. However, the general recommendation in modern Swedish forestry handbooks is to scarify in the autumn, well before the expected seed fall (Jäghagen and Sandström 1994, Bräf 1995, Enström 1996). The main argument in favour of this advice is that the seed fall might occur early in the spring, when scarification is prevented by snow cover. However, the scientific support for this recommendation is weak since there have been few investigations of the timing of seed dispersal in Fennoscandia. Heikinheimo (1932, 1937) studied seed dispersal in Finland and found that the Scots pine seed was mainly released in May and June, after the snow melted. It was only in exceptional cases, in Finnish Lapland, that the seed was released on snow-covered ground. In Norway, north of latitude 69°, Scots pine seed was found to be released in June and the first half of July (Bergan 1981). The only relevant Swedish study to our knowledge was a two-year pilot survey in northern Sweden (Västerbotten), reported by Hesselman (1939), which indicated that most of the seed was released in May and early June, after the snow cover had melted.

The objective of the present study was to obtain data on the timing of Scots pine seed dispersal in central Sweden to help plan scarification schedules designed to promote natural regeneration in this region. For this purpose we used seed traps

to measure the seed fall in Scots pine stands at two sites in Central Sweden over a period of 3–4 years.

## 2 Materials and Methods

The study was conducted in Scots pine shelterwood stands at two locations in central Sweden, at Garpenberg (lat 60°16'N, long 16°11' E, 170 m a.s.l.) and Knivsta (lat 59°43' N, long 17°49' E, 30 m a.s.l.). The former was a Scots pine dominated mixed stand (93% Scots pine, 7% Norway spruce) with mature (120 years old) trees and a spacing varying between about 6–10 m (100–250 trees per hectare) after harvesting, which took place in 1988. The one in Knivsta was also a Scots pine dominated mixed stand (80% Scots pine, 5% Norway spruce, 15% aspen and birch) with a density of 120 trees per hectare. The Scots pine seed trees were on average 130 years old at breast height, and the stand was released about 15 years before the study started.

The recordings were taken over four years at Garpenberg (1993–1996) and three years at Knivsta (1996–1997 and 1999). At Garpenberg, the seed traps consisted of three plastic trays with a catch area of 0.14 m<sup>2</sup> (37.5 × 37.5 cm) placed on the ground, 50 m apart in the stand. The traps were put out in early March each year, and the seed was collected on seven to nine occasions between then and the following August. At Knivsta, the seed traps consisted of circular bag nets, each with a catch area of 0.25 m<sup>2</sup>, tied on poles about 1 metre above ground level. Ten traps were evenly distributed in the stand at an average distance between them of 10 m. The traps were positioned differently each year. The traps were placed out in late February, and the seed was collected on 12–14 occasions between then and August each year. The trapped seed was separated according to tree species.

The distribution of the seed dispersal was analysed with respect to the time of year and weather. The seeds were registered separately for each trap at Knivsta. At Garpenberg, however, the seed data from the three traps were pooled for each sampling occasion. Therefore, we could calculate the errors of the estimated seed amounts for each year

**Table 1.** Mean and maximum temperatures and precipitation (total amount and number of days in which it fell) for the months March–June at the meteorological stations Ultuna and Falun during the studied years.

Variable	Year	Month			
		March	April	May	June
<b>Ultuna</b>					
Mean temp., °C <sup>a)</sup>	1996	-1.9	5.0	7.9	14.4
	1997	1.3	3.5	8.5	15.6
	1999	0.9	6.5	9.3	16.3
	Normal <sup>e)</sup>	-1.1	3.9	10.2	15.0
Max. temp., °C <sup>b)</sup>	1996	8.6	20.8	22.8	24.3
	1997	12.4	15.7	20.5	27.2
	1999	12.9	17.7	23.8	27.0
Precip., mm <sup>c)</sup>	1996	26	14	58	44
	1997	16	22	58	95
	1999	44	83	15	33
	Normal <sup>e)</sup>	26	30	33	46
Precip., days <sup>d)</sup>	1996	14	4	12	11
	1997	12	16	11	15
	1999	22	18	10	9
<b>Falun</b>					
Mean temp., °C <sup>a)</sup>	1993	-0.5	4.8	12.2	11.5
	1994	-1.5	5.3	9.2	13.0
	1995	-0.1	2.1	8.4	15.1
	1996	-2.1	4.0	7.2	14.3
	Normal <sup>e)</sup>	-2.1	3.1	9.8	14.7
Max. temp., °C <sup>b)</sup>	1993	11.2	26.4	27.6	24.3
	1994	9.1	18.6	21.6	26.2
	1995	10.9	17.5	25.9	27.7
	1996	10.1	17.5	23.6	25.0
Precip., mm <sup>c)</sup>	1993	3	24	25	71
	1994	40	34	16	38
	1995	53	83	67	60
	1996	9	20	72	42
	Normal <sup>e)</sup>	32	38	45	58
Precip., days <sup>d)</sup>	1993	4	9	11	20
	1994	14	12	7	16
	1995	16	15	13	16
	1996	8	10	11	15

a) Monthly mean temperature

b) Monthly maximum temperature

c) Total precipitation per month (snow and rain)

d) Number of days per month with precipitation >0 mm

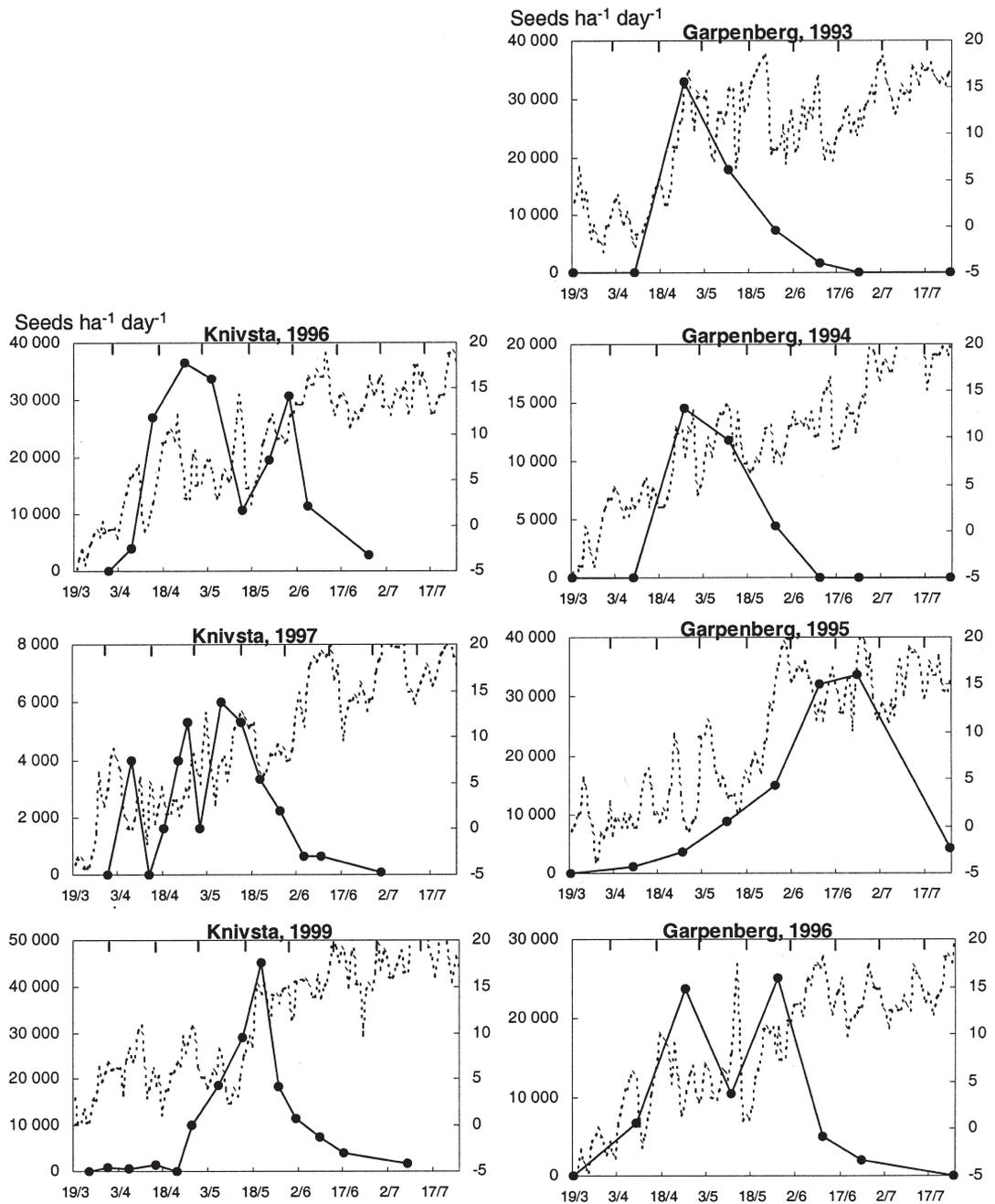
e) Average during the reference period 1961–1990

only at Knivsta. With respect to the few traps and the absence of error estimates at Garpenberg, the calculated total amount of seed per hectare should be interpreted with caution.

Heat sums with a threshold of +5 °C (Sarvas 1967), starting on January 1st, were calculated for

each year and site. Weather data were collected from the meteorological stations in Ultuna, Uppsala, located 20 km from Knivsta, and in Falun, 50 km from Garpenberg.

The weather varied considerably among the studied years (Table 1, Fig. 1). Some marked



**Fig. 1.** Daily seed fall per hectare (solid line, left y-axis) and daily mean temperature (broken line, right y-axis). Each point represents the average daily seed fall between two observations. Note the difference in scales on the left y-axes.

deviations from normal weather patterns are mentioned here. In the last week of April and early May of 1993 the weather was exceptionally warm. In contrast, in 1995 spring temperatures were low, while precipitation was high in most of April and May, totalling 150 mm for the two months compared with 83 mm during an average year. The precipitation occurred as snow, resulting in 20 cm snow cover as late as mid-May in Falun. Early spring 1996 was unusually dry and warm, with periods of maximum temperatures above 15 °C in early- and mid-April at both Ultuna and Falun. However, May 1996 was both chilly and rainy. In 1997, the heat sum started to build up early at Ultuna, due to a warm spell in late March–early April, but the weather patterns were more normal later in the year. There was also a warm period in late March–early April 1999, but the rest of April was chilly and rainy, and there were no further warm periods until the later part of May that year.

The seed fall, expressed as the proportion ( $Y$ ) of total seed fall at day  $X$  each year followed a sigmoid pattern that was well explained by the logistic function  $Y = 1 / (1 + b \cdot \exp(-rX))$  ( $R^2$  varied from 0.92 to 0.99 for the different years and sites). This function can be rewritten as  $\ln(1/Y - 1) = \ln(b) - rX$ , where  $\ln(b)$  and  $r$  are the

regression coefficients. With regression analysis, the periodicity of the seed fall was described with the days when 10, 25, 50, 75 and 90% of the seed fall had occurred (D10, D25 etc.). The length of the period with the peak seedfall was also estimated for each year and site (D75–D25).

The seedfall also showed a sigmoid pattern in relationship to heatsum. Several non-linear functions were tested to describe the relationship, but none was found to be stable enough to sufficiently explain seedfall at all different sites and years. A modelling approach to heatsum was therefore not justified.

### 3 Results

A few seeds were found in early April at Knivsta but the main seed fall never started before mid-April at any of the sites Knivsta and Garpenberg (Table 2). The estimated time when 10% of the seeds were released varied from 13 April to 14 May (Table 2). The most intensive seed fall generally took place in early-mid May, the number of seeds released per hectare per day peaking at more than 40 000 in mid-May during rich seed years (Fig. 1). The time at which 50% of all the annual

**Table 2.** Estimated dates when 10, 25, 50, 75 and 90% of the total seedfall had occurred (D10, D25 etc.), length of the peak period when 50% of the seed was released (D75–D25), total number of seeds collected per hectare  $\times 1000$ , and the standard error of that estimate (standard error could not be estimated at Garpenberg). The dates were estimated with a logistic model based on the observed proportion of released seeds as dependent on day of observation. Finally, the  $R^2$  from the logistic regression model is shown.

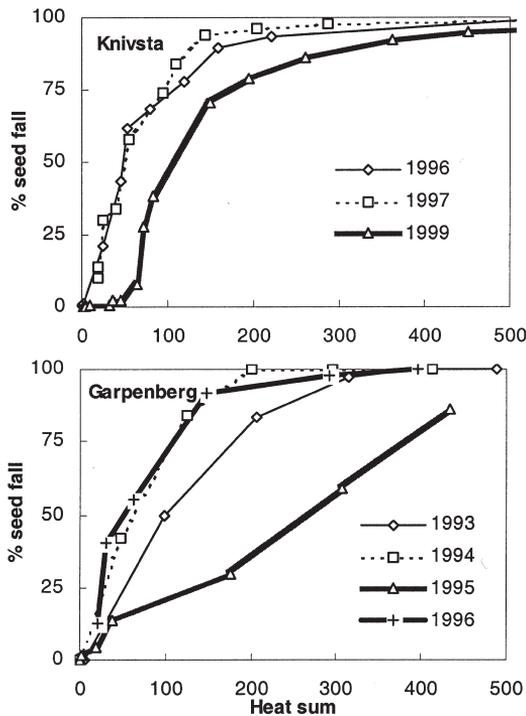
	Garpenberg				Knivsta		
	1993	1994	1995	1996	1996	1997	1999
D10 <sup>a)</sup>	13 Apr	17 Apr	14 May	17 Apr	22 Apr	15 Apr	2 May
D25 <sup>a)</sup>	23 Apr	26 Apr	28 May	28 Apr	2 May	25 Apr	12 May
D50 <sup>a)</sup>	3 May	5 May	11 June	10 May	11 May	6 May	21 May
D75 <sup>a)</sup>	13 May	14 May	24 June	22 May	21 May	17 May	31 May
D90 <sup>a)</sup>	23 May	23 May	8 July	2 June	31 May	28 May	9 June
D75–D25, days <sup>b)</sup>	20	18	27	23	20	22	19
Total seed fall ha <sup>-1</sup> $\times 1000$	900	500	1 500	1 100	1 600	200	1 100
Std error <sup>c)</sup>	-	-	-	-	49	25	82
$R^2$ <sup>d)</sup>	0.99	-	0.99	0.97	0.92	0.99	0.98

<sup>a)</sup> Day when 10%, 25% etc. were released as estimated with the logistic function.

<sup>b)</sup> Extension of the period in days when 50% of the total seed release occurred (D75–D25)

<sup>c)</sup> Standard error of means of total seed fall ha<sup>-1</sup>.

<sup>d)</sup> Degree of determination ( $R^2$ ) for the logistic regression



**Fig. 2.** Accumulated seed fall at Knivsta and Garpenberg. Proportion (percent) of all seeds collected at different heat sums.

seed had been released occurred in early-mid May at both sites and all years, with the exception of Garpenberg 1995 as an extreme outlier with a seed dispersal that occurred about one month later than the other years (Table 2). The peak period, when 50% of the total seed amount was released, extended over a period of 18 to 28 days at the different sites and years, with an average of 21 days (standard error 3 days). Most of the seed fall (90% of total) had occurred by the end of May or early June, again with Garpenberg 1995 as an outlier (Table 2). For both studied sites and all years seed dispersal began shortly after the heat sum of the current year had started to accumulate (Fig. 2). However, heat sum failed to improve the prediction of seed fall compared to the use of calendar days. The main reason was the year 1995 in Garpenberg. The periods by which 50% of the seed had fallen corresponded to heat sums of 50 to 100 degree-days at both sites and at all years

except at Garpenberg in 1995, when the heat sum was over 250 degree-days (Fig. 2).

The total annual seed fall varied between 200 000 and 1.6 million seeds per hectare (Table 2), with standard errors at the Knivsta site from 25 000 to 82 000, or 3–12.5% of the mean. Standard errors could not be calculated for the Garpenberg site.

## 4 Discussion

### 4.1 Variation among Years

This study demonstrates that seed dispersal in Scots pine stands in central Sweden starts in late April and peaks in early-mid May in most years. The variation in timing among years is probably mostly due to variations in weather conditions. The relatively long sampling interval, one-two weeks during the main seed fall, does not allow the seed fall to be analysed with respect to short term weather conditions, e.g. specific days with favourable temperature, wind and humidity. However, the variation among years allows several conclusions to be drawn by comparison to average weather patterns (Table 1, Fig. 1).

The results suggest that, generally, seed dispersal commences shortly after the temperature rises above 5 °C and heat sum starts to accumulate. The exceptional year at Garpenberg, 1995, provided an example of the dependence of seed fall on warm and dry weather. In this case the heat sum started to accumulate in late April (Fig. 2), stimulating the commencement of seed fall. However, this was followed by a period of low temperatures and high precipitation, causing seed fall to lag behind in comparison to other years. The precipitation in April and May that year was 80% above the normal level (Table 1).

The observations from 1996 at Garpenberg and Knivsta and 1997 at Knivsta further supported the hypothesis that seed fall can start in April during periods with warm weather, but be interrupted by poor weather conditions and resume when conditions become favourable again (Fig. 1). April 1996 was much warmer than normal at both sites, and April 1997 was warm at the beginning of the month. May 1996 and May 1997 (to a lesser

degree) were considerably colder and wetter than normal. Two warm days occurred in mid-May 1996 (Fig. 1), which were probably not enough to promote seed fall, especially since one of them coincided with rain and the preceding and following days were very cold. It was not until late May that temperatures rose again in 1996 and seed fall reached a new peak. The observations from 1993 and 1999 showed that the peak seed fall period is short during years when temperatures rise quickly and remain high. The relatively late seed fall in 1999, despite periods with high temperatures in April, was probably due to the high precipitation that also occurred this month. All these results support the idea that seed dispersal is promoted by high temperatures. Hesselman (1939) also suggested that seed dispersal is promoted by short-term periods of warm, dry weather.

The data doesn't allow to separate the effects of site and years, since only the year 1996 was common for the two sites. This particular year, though, showed a very strong similarity between the sites (Table 2 and Fig. 1). The estimated time of 50 and 75% seed fall differed only one day between them.

#### 4.2 Abundance of Seed Fall

This study was not designed to measure the total abundance of the annual seed fall, and especially the numbers from Garpenberg should be interpreted with caution. However, the figures are in good agreement with other studies in Sweden. Karlsson and Örländer (2000) found a range of between 20 000 and 640 000 seeds per hectare over a seven year period in a sparse seed tree stand in central Sweden (60–84 trees/hectare), while Beland et al. (2000) found that between 430 000 and 2 380 000 seeds/hectare fell in shelterwoods in southern Sweden with 160–200 trees per hectare.

#### 4.3 Silvicultural Implications

In contrast to information contained in many forestry handbooks ((Jäghagen and Sandström 1994, Braf 1995, Enström 1996), the main part of the seed dispersal occurred after the snow cover had

disappeared. The period of snow cover ends, on average, on April 12 in Falun and on April 14 in Ultuna, the meteorological stations representing Garpenberg and Knivsta, respectively (Eriksson 1990). The probability of snow cover occurring after April 15 in Falun and Ultuna is 13 and 17 percent, respectively. The snow usually disappears earlier on flat land, where the meteorological stations are located, than in the forest (Eriksson 1990). Nevertheless, the results indicate that seed fall on snow-covered ground is a very rare event in central Sweden. Sixty years ago Hesselman (1939) stressed that foresters commonly but mistakenly believe that Scots pine seeds are shed onto snow – probably because Norway spruce seeds are often dispersed in the winter – and the misconception persists today.

The relative benefits of scarification in the autumn or spring need to be further investigated. In practice, spring scarification during the relatively short period between snow melt and seed dispersal might be hampered by technical problems, such as the forest floor being waterlogged. There may also be logistic conflicts since, for instance, the machines needed to pull the scarification equipment may also be required for hauling timber in logging areas. On the other hand, completely fresh scarification, just before seed fall, may enhance germination. The porous soil surface is full of small depressions after scarification, into which the seed can fall and be covered through micro-erosion of the soil. A thin cover of organic compounds or mineral soil protects the seeds against predators and moisture stress, and improves germination (Björ 1971, Heikkilä 1977, Bergsten 1988). However, radical scarification may create deep depressions, in which the seed may be buried and killed (Söderström 1979). The results obtained using freshly scarified soil should also be compared with those obtained using autumn-prepared soil that has frozen and thawed over the winter, which makes the soil more compact and increases capillary movement of soil water. The latter factor has been shown to have a strong influence on seedling emergence rates after direct seeding of Scots pine seeds (Winsa 1995). The success of germination and establishment will probably depend on several factors besides time of scarification, such as soil type, weather conditions, geographical location and method of scarification.

In order to take advantage of all of the naturally dispersed Scots-pine seed, sites should be freshly prepared no later than April, before the bulk of the seed fall. However, the number of seeds released after mid-May was still high in this study (50 000 to 1.5 million per hectare), which shows that even sites prepared in mid-May will receive large numbers of seeds in most years. If scarification is done in late May or June a large part of the newly fallen seeds will be buried, and a large proportion of those that have already germinated will probably be killed.

#### 4.4 Conclusions

Most of the Scots-pine seed dispersal in central Sweden takes place in May, after the snow cover has disappeared. This allows for scarification to be executed during the relatively short period between the snow melting and early-mid May. However, more studies are needed to determine more precisely the effects of scarifying in various ways in the autumn, spring or early summer, on the success of natural regeneration of Scots pine. These studies should also cover the effects of various soil types, climatic conditions and yearly variations.

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