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Effects of pruning and stand density on cone and pollen production in an experimental *Pinus sylvestris* seed orchard

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Highlights

- Pollen production of *Pinus sylvestris* began at the same age for all studied stand density and pruning height combinations but increased more rapidly at higher densities.
- Treatments with dense spacing increased seed production earlier.
- Many combinations of stand density and target height gave comparable levels of seed production, yielding a wide range of viable management options.

Abstract

Seed orchards are the link between tree breeding and reforestation. This paper presents data on cone, seed and pollen production and seed quality gathered over 21 years in a *Pinus sylvestris* (L.) experimental seed orchard containing plots with 14 different combinations of stand density and targeted pruning height. The treatments' stand densities ranged from 267 to 4000 stems ha^{-1}, and the target graft heights ranged from 2 to 6 meters. Pollen production began at the same orchard age for all studied combinations of stand density and target height but the level of pollen production per hectare increased more rapidly in treatments with higher stand densities. In treatments with dense spacing, cone and seed production initially increased more rapidly than in treatments with wider spacing, thereby providing an earlier return on investment and a shorter seed production lag time. However, the levels of cone and seed production in such treatments over the entire study period were not appreciably different to those achieved in treatments with wider spacing and higher target height. The treatments did not differ substantially with respect to seed quality. These results show that comparable levels of seed production can be obtained with different combinations of stand density and target height, giving seed orchard owners and managers a wide range of viable management options.

Keywords seed orchard management; crown management; spacing; seed production
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1 Introduction

Seed orchards are the production populations of breeding programmes that produce improved seed for regeneration. In Sweden, 90 percent of the *Pinus sylvestris* (L.) seed used in plant production originates from Swedish seed orchards (Swedish Forestry Agency 2013). When establishing seed orchards, owners and managers require information on the crop's development and annual variation in size and fertility to select optimal stand densities and pruning regimes.

Seed and pollen production in seed orchards have been studied extensively. However, most of these investigations only considered data from one or a few commercial seed orchards gathered over a limited number of years (Griffin 1982; Ying et al. 1985; Fries 1994; Burczyk and Chalupka 1997; Matziris 1997). Some studies have followed flowering and seed production over longer periods in individual seed orchards of conifers such as *P. sylvestris* (Kroon et al. 2009), *Picea abies* (L.) Karst. (Nikkanen and Ruotsalainen 2000), *Pinus taeda* (L.) (Schmidtling 1983), *Pseudotsuga menziesii* (Mirbel) Franco. (El-Kassaby et al. 1989), and *Tsuga heterophylla* (Raf.) (Ross 1989). These efforts yielded valuable information on the general progression of fruitfulness over time but provided limited insights into the effects of different management regimes on traits important for seed production.

Various authors have compiled production data from existing seed orchards in order to predict the future performance of new orchards (Ilstedt and Eriksson 1982; Hannerz et al. 2000). These compilations provide useful information on the influence of soil properties and climate on seed production but provide no information on the effects of different management regimes.

As an orchard develops, its trees may become too tall for efficient management. This makes management activities in the orchard excessively time-consuming and expensive, and may reduce the effectiveness of activities such as supplemental mass pollination or protection from insects and fungus. Crown pruning is therefore widely used to control the trees' height growth. Several pruning and crown management experiments in a wide range of conifer species have been reported and reviews of the literature data have been published (Werner 1975; Owens and Blake 1987; Ho and Schooley 1995). Unfortunately, most of these experiments examined relatively few treatments over comparatively short periods of time, making it difficult to generalize their results.

The initial spacing in clonal seed orchards is normally wide enough to give crowns full exposure to sunlight for 15 to 20 years without any need for roughing. In addition, the spacing must be such that there is room for machines to operate without being so wide as to compromise the efficiency of land use. The most commonly used spacings in soil-based seed orchards are 5 to 7 metres between rows and 4 to 7 metres within rows, giving stand densities of 200–500 trees per hectare. There are also more dense orchard designs with up to several thousand trees per hectare (Setiawati and Sweet 1996) .

Little is currently known about the development of cone and pollen production from year to year in conifer seed orchards with different initial stand densities and pruning regimes. To address this deficiency, we studied an experimental *P. sylvestris* seed orchard containing 14 different combinations of initial stand density and pruning regime. The investigation's objectives were to analyse the effects of initial stand density and adopted pruning regime on 1) the onset of pollen production; 2) the development of cone and pollen production over time; and 3) the quality of the produced seed.

2 Material and methods

2.1 The experimental seed orchard

Drögsnäs experimental seed orchard was established in 1990. The seed orchard is located in central Sweden, at 59°37´N, 12°56´E and 80 m a.s.l. The orchard site extends over approximately 5 ha and the effective area (i.e. the area of the experimental plots) is 2.7 ha. Some tree mortality occurred during the years after planting (1991–1995); the dead trees were replaced with new grafts. Grafts that died after 1995 have not been replaced.

2.2 Trial design

The trial was established with three replicates of each treatment. Fourteen different combinations of stand density and targeted pruning height were investigated (Table 1). The plot size was variable: treatments with wider spacing had larger plots to accommodate an adequate number of stems. The trial initially included an additional two treatments with a target pruning height of 7 meters but these plots were excluded from this analysis because their grafts grew and developed much more slowly than those of the other plots. It is not clear why this happened, but it means that comparisons between the results for these treatments and the others may not be particularly informative for any of the studied variables.

All plots featured a central subplot containing the same 8 clones but the treatments had different number of replicates of each clone due to variation in the plots' sizes. The clones' ramets were randomized in each plot. All measurements were acquired within these central subplots. The central subplots were surrounded by a row of grafts in which 18 different clones were represented. The surrounding grafts were treated in the same way as those in the corresponding central subplot.

2.3 Soil and vegetation treatment

The same soil and vegetation treatments were applied to all plots throughout the experiment. The growth of grass in the plots was controlled and the trees were protected against pine weevil, moles and roe deer. The plots were fertilized with 200 grams of 11-5-18 NPK fertilizer per graft at seed orchard age 5.

Table 1. The combinations of spacing and target graft height in the studied treatments within the experimental seed orchard.

		Target height of grafts (m)						
Stems ha^{-1}	Spacing (m)	2	3	4	5	6	Plot size (m)	No. grafts in each central plot
4000	2.5 × 1.0	A					15 × 15	52
2000	5.0 × 1.0	C					15 × 15	16
1600	2.5 × 2.5	B					15 × 15	13
1333	5.0 × 1.5	D					15 × 15	8
889	7.5 × 1.5	F					15 × 30	16
800	5.0 × 2.5		E				15 × 30	16
667	7.5 × 2.0		G	H			15 × 30	10
533	7.5 × 2.5		I		K	L	15 × 30	8
267	7.5 × 5.0			M	N	O	30 × 30	8

2.4 Pruning regime

The pruning of trees in plots with target graft heights of 2 meters (treatments A, B, C, D and F) began at seed orchard age 5. All grafts with heights of 2 meters or more were pruned just above the branch whorl closest to 1.8 meters. In addition, the leading shoots on the branches were pruned. In subsequent years the grafts were pruned annually, allowing their height to increase by 5–10 cm per year.

For treatments with target graft heights of 3 metres (E, G, I), pruning began at seed orchard age 5 and focused on grafts with heights of 2 meters or more. The top was pruned just above the first branch whorl above 2 metres. In addition, the leading shoots on the branches were pruned. In subsequent years, the grafts' heights were allowed to increase by 20 cm annually until they reached the target height of 3 meters. Thereafter the grafts were pruned annually, allowing their heights to increase by 5–10 cm per year.

For treatments with target heights of 4 to 6 meters (H, K, L M, N, and O), pruning began when the grafts were one metre below their target height (at seed orchard ages of 6, 8 and 9, respectively). The tops were pruned just above the first branch whorl above the target height minus one metre, along with the leading shoots on the branches. In subsequent years, the grafts were allowed to grow by 20 cm each year until they reached their target height, after which they were pruned annually and allowed to gain 5–10 cm of height each year.

2.5 Data collection

2.5.1 Graft height development

Graft height was measured annually in the autumn just before pruning on all grafts between seed orchard age 6 and 21 except at age 15. The height was defined as the distance between the top of the highest shoot and the ground.

2.5.2 Pollen production

Pollen production was recorded annually for all grafts from seed orchard age 9 as a binary variable (i.e. pollen production observed or not observed). From seed orchard age 12 the amount of pollen on a subset of grafts was estimated using the method of Eriksson and Jansson (1987). This method involves selecting three branches per graft, counting how many pollen clusters they bear, and measuring the average cluster length. The graft's total number of branches is then counted and used to estimate its total pollen cluster length. The pollen mass per graft is estimated as the product of the total length of the pollen clusters and a constant representing the pollen mass of 1 cm clusters of strobili as reported by Koski (1975). In each plot, one graft of each clone was sampled for this purpose. The pollen production per hectare was calculated as the product of the estimated value per graft and the treatment's planned stand density.

2.5.3 Cone production

Cone production was measured annually on all grafts from seed orchard age 6 to age 21. The volume of the cones and the total number of cones produced by each graft was recorded. Cone production per hectare was calculated by multiplying the estimated value per graft by the treatment's planned stand density.

2.5.4 Seed quality

The recorded seed quality traits were the number of filled and empty seeds per cone, percentage of filled seeds per cone, and 1000-grain mass.

All cones from each plot were bulked and one sample per plot was used to measure two seed quality parameters annually: the 1000-grain mass (at orchard ages 6–15 and 17–21) and the number of filled seed per cone (at orchard ages 6–15 and 18–21). At orchard ages 6–10 and 12–13, seed quality was assessed based on the entire bulk sample. At ages 11 and 14–21, subsamples of 2 litres per plot were used.

2.5.5 Seed production per hectare

Seed production per hectare was calculated for each treatment by combining the estimated number of cones per graft, number of filled seeds per cone, 1000-grain mass, and planned stand density per hectare. Separate calculations were performed for each treatment and year. For years without data on the number of filled seeds per cone (seed orchard ages 16 and 17) or 1000-grain mass (age 16), averages of the years with data for each treatment were used.

2.6 Statistical analyses

Statistical analyses of height development and the production of cones and pollen were performed using the Proc Mixed module of SAS (version 9.4) based on the following model:

$$y_{ijkl} = \mu + b_i + c_j + d_k + cd_{jk} + cf_{jl} + e_{ijkl} \quad (1)$$

where
y_{ijkl} = dependent variable, e.g. cone volume at age 10
μ = overall mean
b_i = fixed effect of block
c_j = fixed effect of treatment
d_k = random effect of clone
f_l = fixed effect of year
e_{ijkl} = residual, $(N(0, \sigma_e^2))$

For the seed quality traits, the Proc Mixed module of SAS was used with the following model because only plot-level data were available:

$$y_{ijk} = \mu + b_i + c_j + cf_{jk} + e_{ijk} \quad (2)$$

where
y_{ijk} = dependent variable, e.g. 1000-grain mass at age 10
μ = overall mean
b_i = fixed effect of block
c_j = fixed effect of treatment
f_k = fixed effect of year
e_{ijk} = residual, $(N(0, \sigma_e^2))$

For both models (Eq.1 and Eq. 2), an autoregressive spatial covariance structure on residuals was used to account for the dependence between repeated measurements, $\sigma_e^2\rho^w$. The parameter σ_e^2 stands for the variance of an observation, ρ for the correlation between adjacent observations on the same subject, and w for the time interval between two measurements. Tukey-Kramer adjusted significance levels were used for multiple comparisons.

3 Results

3.1 Height development

Pruning increased the differences in graft height between treatments with different target heights. By orchard age 12, all treatments had reached heights that necessitated pruning (Fig. 1).

3.2 Pollen production

Pollen production started simultaneously in all treatments (Table 2). By orchard age 12, more than 80 percent of the grafts in the experiment were producing pollen (data not shown).

Treatments with relatively dense spacing achieved a pollen production of around 20 kg ha^{-1} or more at an orchard age of 12 or 13, while those with wider spacings achieved this level of production at a seed orchard age of 15 to 16 (Table 2). The 20 kg ha^{-1} threshold is widely used as an indicator of adequate pollen production (Koski 1975).

The variance component for clone was 14.8 percent and the interaction between treatment and clone accounted for 6 percent of the random variation. There was no significant effect of treatment on pollen production and no interaction between treatment and year ($p = 0.43$ and 0.33 respectively).

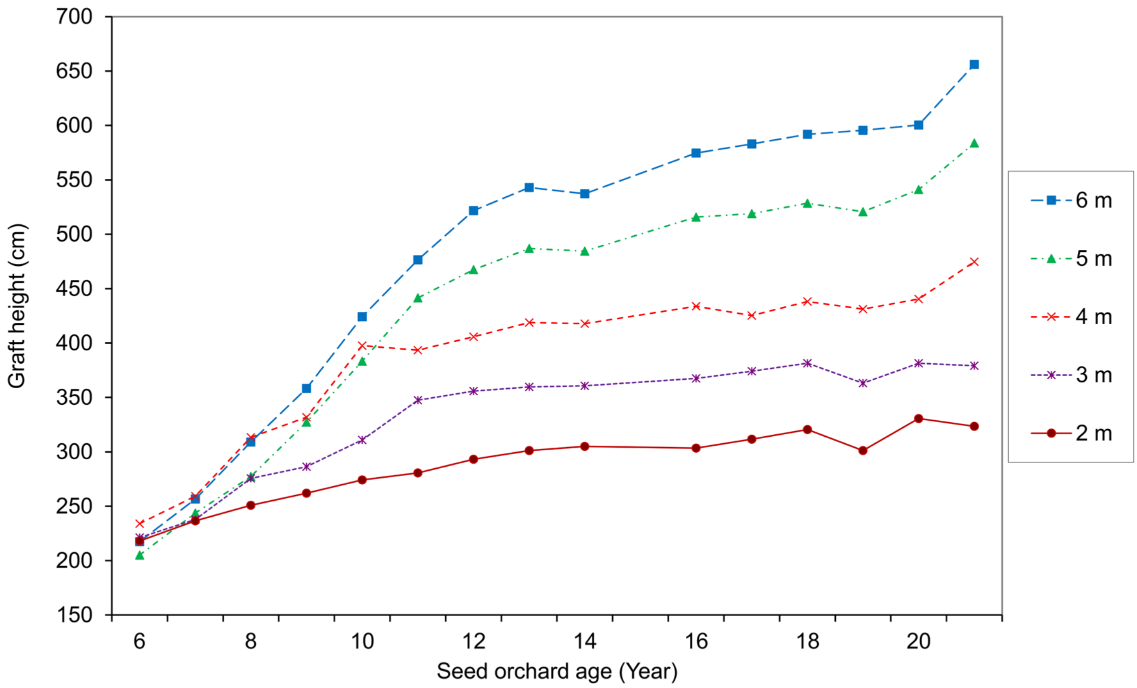

Fig. 1. Graft height before pruning in the autumn each year for treatments with different target heights.

Table 2. Percentage of pollen-producing grafts (seed orchard age 9–11) and pollen production per year (seed orchard age 12–20) in the different treatments.

			Percent grafts with pollen (%)			Pollen production (kg ha^{-1} yr^{-1})									
Code	Target height (m)	Stems ha^{-1}	9	10	11	12	13	14	15	16	17	18	19	20	Average±StdErr
A	2	4000	28	0	79	15.7	16.1	10.1	28.3	52.8	12.5	24.8	19.5	44.2	24.9±1.6
C	2	2000	26	0	88	11.8	19.3	11.3	49.0	52.4	28.9	23.7	27.8	38.2	29.2±1.7
B	2	1600	29	0	72	20.0	37.5	22.8	27.4	63.9	27.1	60.8	42.1	58.7	40.0±1.9
D	2	1333	35	0	85	12.2	16.6	17.0	39.5	43.4	33.6	39.6	26.7	20.4	27.7±1.3
F	2	889	22	0	83	12.9	12.4	13.0	35.1	45.7	49.1	37.4	50.4	57.2	34.8±2.0
E	3	800	24	0	69	10.8	21.4	26.9	34.5	88.3	91.3	73.4	69.2	69.9	54.0±3.4
G	3	667	11	0	73	9.1	23.1	16.5	25.5	54.1	66.3	49.3	51.9	42.5	37.6±2.2
H	4	667	33	0	77	15.9	30.8	28.5	38.3	66.8	58.2	39.8	53.1	71.8	44.8±2.1
I	3	533	13	0	71	10.4	21.7	17.7	26.9	44.6	68.6	40.9	51.7	44.9	36.4±2.1
K	5	533	11	0	53	3.5	12.3	4.0	29.6	65.6	57.4	41.7	46.6	62.3	35.9±2.7
L	6	533	19	0	70	10.7	29.7	23.5	46.4	81.0	91.6	32.4	62.9	73.8	50.3±3.1
M	4	267	45	0	74	9.0	20.1	14.5	19.2	65.6	55.3	32.7	46.9	39.1	33.6±2.2
N	5	267	11	0	63	1.4	8.2	9.1	21.3	59.4	68.5	49.5	55.2	74.6	38.6±3.2
O	6	267	32	0	78	6.4	18.7	12.3	32.1	55.3	64.4	51.8	53.9	55.5	38.9±2.4
	Average±StdErr		24	0	74	10.7±0.3	20.6±0.6	16.2±0.5	32.4±0.6	59.9±0.9	55.2±1.7	42.7±1.0	47.0±1.0	53.8±1.2	37.6

3.3 Cone production

For cone size, the variance component for clone was large (53.8 percent) and the interaction between treatment and clone was small, accounting for 1.5 percent of the total random variation. There was no significant treatment effect on cone size and no significant interaction between treatment and year ($p = 0.25$ and 0.26 respectively).

Cone size varied between years and treatments (Fig. 2) but tended to increase over time. In particular, cones from early crops were appreciably smaller than those from later crops.

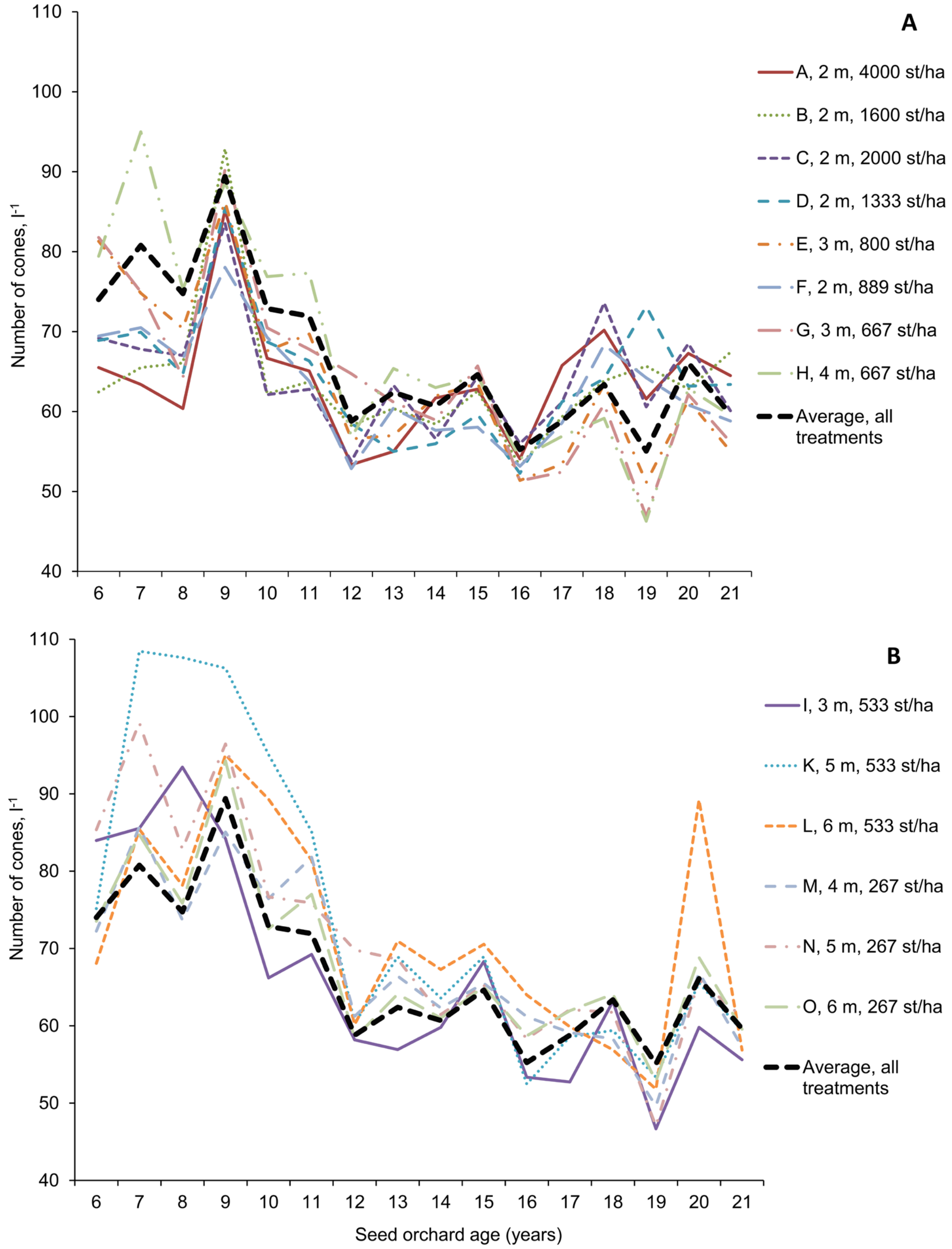

Fig. 2. Cone size, measured as number of cones per litre, from seed orchard age 6 to 21. In A: treatment A–H. In B: treatment I–O. Average for all treatments in both A and B.

Table 3. Cone production (hl ha^{-1}) for the combinations of spacing and target graft height in the experimental seed orchard. First figure is cone production from age 6 to 13 and second figure is cone production for the whole studied period (age 6 to 21).

		Target height of grafts (m)				
Stems ha^{-1}	Spacing (m)	2	3	4	5	6
4000	2.5 × 1.0	105 / 177				
2000	5.0 × 1.0	73 / 183				
1600	2.5 × 2.5	90 / 193				
1333	5.0 × 1.5	60 / 144				
889	7.5 × 1.5	41 / 132				
800	5.0 × 2.5		55 / 223			
667	7.5 × 2.0		44 / 168	64 / 230		
533	7.5 × 2.5		41 / 159		31 / 238	51 / 237
267	7.5 × 5.0			37 / 181	38 / 232	46 / 252

For cone production, the variance component for clone was 9.0 percent, and the interaction between treatment and clone accounted for 5.2 percent of the total random variation. The interaction between treatment and year had a significant effect on cone production ($p<0.0001$) but the treatment did not ($p=0.36$).

In treatments with high stand densities, cone production increased faster than in those with wider spacing. However, over the entire study period (up to age 21), combinations with wide spacings and high target heights had the greatest total cone production (Table 3).

3.4 Seed quality

There was a significant effect on number of filled seeds per cone of the interaction between treatment and year ($p<0.0001$) but no significant effect of treatment ($p=0.26$). The average number of filled seeds per cone varied from year to year (between 8.1 and 23.2), with an average of 17.4 filled seeds per cone over all treatments and years. The differences between treatments within the same year were relatively small (data not shown).

There was a significant effect on seed mass of treatment and of the interaction between treatment and year ($p<0.0001$ for both).

The seed mass was lower during the first few crop years but stabilized at around 6.0–6.5 gr (1000 seeds)$^{-1}$ from orchard age 10 and onwards (Table 4).

3.5 Seed production per hectare seed orchard

The orchard's seed production per hectare was calculated by combining the estimated number of cones per graft, number of filled seeds per cone, 1000-grain mass, and planned stand density per hectare. Treatments with high stand densities and low target heights exhibited rapid early increases in seed production but treatments with lower stand densities and higher target heights exhibited the greatest cumulative seed production over the studied period (Table 5). Seed production during the studied period varied from 88 kg ha^{-1} for Treatment F (889 Stems ha^{-1}, 2 m target height), which corresponds to 5.5 kg ha^{-1} yr^{-1}, up to 172 kg ha^{-1} for Treatment O (267 Stems ha^{-1}, 6 m target height), which corresponds to 10.8 kg ha^{-1} yr^{-1}, (Fig 3a and Fig. 3b).

Table 4. Seed mass (g (1000 seeds)$^{-1}$) for the seed production from seed orchard age 6 to 21 for the different treatments.

	Seed orchard age[1)]															
Treatment	6	7	8	9	10	11	12	13	14	15	17	18	19	20	21	Aveage±StdErr
A, 2 m, 4000 Stems ha^{-1}	6.4	6.3	6.1	5.8	7.0	6.3	7.2	6.7	6.3	6.8	6.8	6.8	6.5	6.2	6.2	6.5±0.03
C, 2 m, 2000 Stems ha^{-1}	5.7	5.9	5.8	5.3	6.7	6.1	6.9	6.8	6.1	6.6	6.8	6.1	6.7	5.9	5.9	6.2±0.03
B, 2 m, 1600 Stems ha^{-1}	6.4	6.2	6.0	5.7	6.9	6.2	6.7	6.5	6.2	7.0	6.8	6.6	6.3	5.9	6.0	6.4±0.03
D, 2 m, 1333 Stems ha^{-1}	6.3	6.0	6.7	5.7	7.0	6.7	7.3	6.8	6.5	6.8	6.6	6.6	7.3	5.9	6.4	6.6±0.03
F, 2 m, 889 Stems ha^{-1}	6.2	6.1	5.9	6.0	7.4	6.9	7.4	7.1	6.1	7.0	7.2	7.0	6.7	6.3	6.3	6.6±0.03
E, 3 m, 800 Stems ha^{-1}	5.8	5.8	6.1	5.5	7.4	6.4	7.2	6.7	6.4	6.6	6.9	6.4	6.7	6.0	6.3	6.4±0.04
G, 3 m, 667 Stems ha^{-1}	5.7	5.7	6.0	5.9	7.0	6.5	6.8	6.8	6.4	6.7	7.3	6.4	6.8	5.9	6.2	6.4±0.03
H, 4 m, 667 Stems ha^{-1}	5.3	5.0	5.5	5.9	6.2	5.9	6.5	6.3	5.4	7.0	6.7	6.5	7.0	5.8	6.3	6.1±0.04
I, 3 m, 533 Stems ha^{-1}	5.3	5.6	6.0	5.7	7.1	6.6	7.0	6.6	6.2	6.2	6.8	6.0	6.3	5.9	6.5	6.3±0.03
K, 5 m, 533 Stems ha^{-1}	5.4	5.0	5.1	5.6	5.9	5.9	6.6	6.4	5.4	6.5	6.8	6.7	5.9	6.0	6.5	6.0±0.04
L, 6 m, 533 Stems ha^{-1}	5.7	5.3	5.6	5.0	6.0	5.3	6.0	6.1	5.2	5.8	6.1	5.8	6.7	5.2	5.2	5.7±0.03
M, 4 m, 267 Stems ha^{-1}	5.2	4.8	5.7	5.3	6.2	6.0	6.8	6.7	5.6	6.6	6.7	6.0	6.2	5.9	6.3	6.0±0.04
N, 5 m, 267 Stems ha^{-1}	5.3	4.9	5.6	5.3	6.2	5.8	6.3	6.2	5.3	5.9	6.8	6.3	6.3	5.4	6.1	5.9±0.04
O, 6 m, 267 Stems ha^{-1}	5.8	5.0	5.9	5.5	6.5	6.0	6.1	7.0	5.9	6.2	6.5	6.3	6.4	5.5	6.1	6.0±0.03
Average ±StdErr	5.8 ±0.03	5.5 ±0.04	5.9 ±0.03	5.6 ±0.02	6.7 ±0.04	6.2 ±0.03	6.8 ±0.03	6.6 ±0.02	5.9 ±0.03	6.6 ±0.03	6.8 ±0.02	6.4 ±0.02	6.6 ±0.03	5.8 ±0.02	6.2 ±0.02	6.2

1) No data for seed orchard age 16 available.

Table 5. Seed production (kg ha^{-1}) for the combinations of spacing and target graft height in the experimental seed orchard. First figure is seed production from age 6 to 13 and second figure is seed production for the whole studied period (age 6 to 21).

		Target height of grafts (m)				
Stems ha^{-1}	Spacing (m)	2	3	4	5	6
4000	2.5 × 1.0	67 / 115				
2000	5.0 × 1.0	44 / 109				
1600	2.5 × 2.5	55 / 122				
1333	5.0 × 1.5	41 / 97				
889	7.5 × 1.5	28 / 88				
800	5.0 × 2.5		39 / 148			
667	7.5 × 2.0		30 / 111	44 / 153		
533	7.5 × 2.5		27 / 98		22 / 158	37 / 158
267	7.5 × 5.0			27 / 116	22 / 128	29 / 172

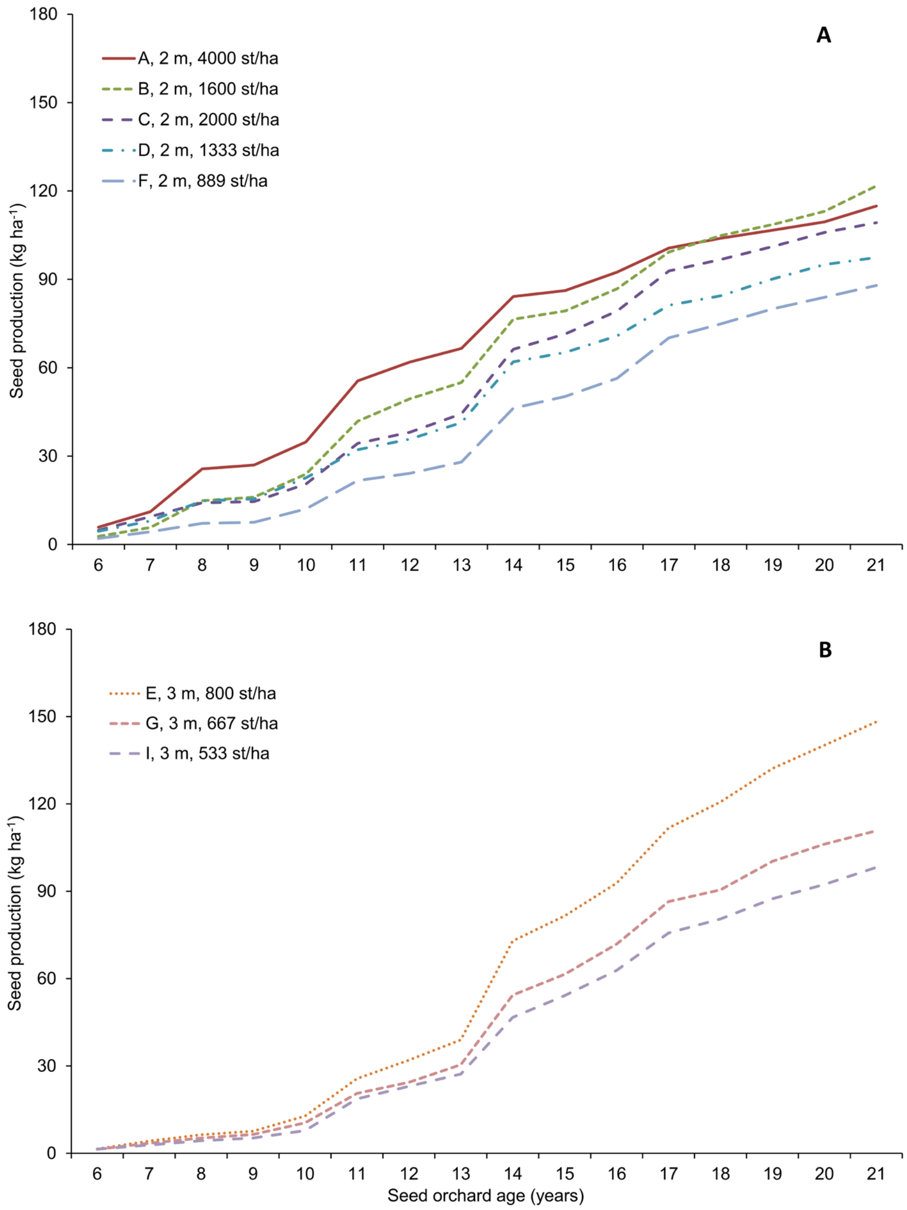

Fig. 3a. Cumulative seed production per hectare from seed orchard age 6 to 21 (kg ha^{-1}) in treatments with A: target height of 2 metres, and B: target height of 3 metres.

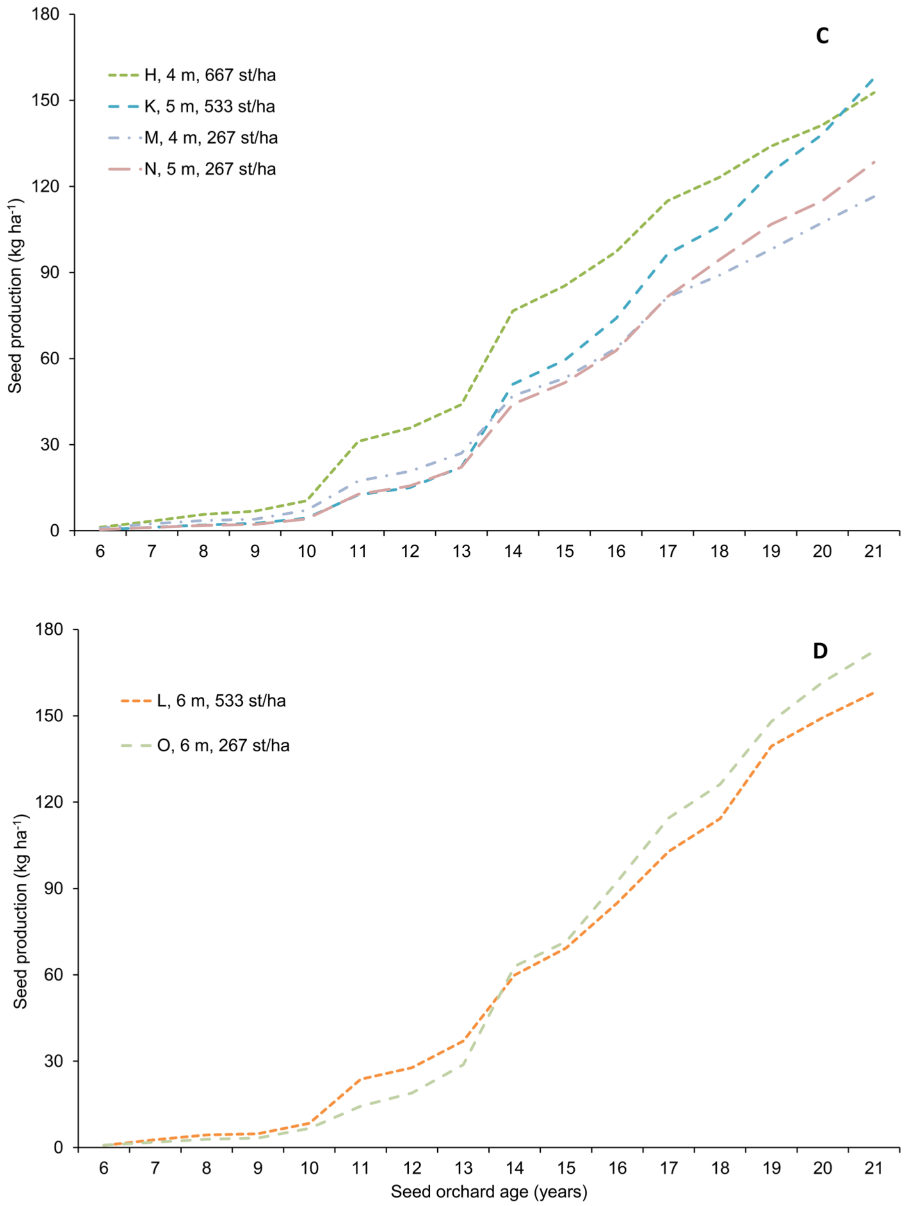

Fig. 3b. Cumulative seed production per hectare from seed orchard age 6 to 21 (kg ha^{-1}) in treatments with C: target heights of 4 and 5 metres, and D: target height of 6 metres.

4 Discussion

4.1 Experimental conditions

The statistical analyses showed that the clones differ with respect to all of the studied cone and pollen variables, with variance components ranging from 9 to 54 percent of the total random variation. The clones were expected to differ with respect to important traits, so efforts were made to ensure an even balance of clones between treatments when the experiment was established.

The experimental design includes combinations of high stand density with low target height and lower stand densities with higher target heights. There is consequently some confounding between the effects of stand density and target height, reducing the scope for their separation. The trial included several combinations of spacing and target height that might be encountered in operational seed orchards. Therefore, its results may be useful for guiding seed orchard management decisions.

There were large differences between years for most of the studied treatments, and also rank changes between treatments between years; both of these trends are reflected in the significant observed interactions between treatment and year. The treatment by year interactions also explain the non-significant treatment effects for most variables: the interaction terms captured most of the treatment differences. However, by considering the cumulative effects of the different treatments over multiple years, it was possible to draw conclusions relevant to seed orchard management.

4.2 Height development

The differences between treatments with different target heights increased over time, as expected. The height development data showed that it was possible to manage trees' height growth so as to ensure that they reached their target heights and then grew by only 5 to 10 cm per year thereafter (note that Fig. 1 shows the height before pruning in autumn each year). This demonstrates that there are no biological constraints that require seed orchard managers to plan for target heights of more than two meters for at least the first 21 years of the orchard's life.

4.3 Pollen production

The onset of pollen production occurred at around the same time in all of the treatments (Table 2), suggesting that stand density has little effect on the onset of pollen production by grafts. The greatest pollen production during the early years of the experiment (up to 15 years after establishment) occurred in treatments with relatively high stand densities (533–1600 Stems ha^{-1}). After that, all treatments produced pollen at levels above the 20 kg ha^{-1} threshold suggested by Koski (1975), and most of the treatments produced twice that level almost every year.

4.4 Cone production

The cones produced by the grafts were smaller during the first few crop years, i.e. up to seed orchard age 11. The largest cones during these first coning years were produced in treatments with low target heights and high stand densities. From age 12 and onwards, the cone size stabilised at around 60 cones per litre and there was relatively little year-to-year variation. The cone sizes observed in this work are consistent with those reported for previous studies conducted in Swedish *P. sylvestris* seed orchards (Almqvist et al. 1995; Almqvist et al. 1996; Almqvist 1998; Eriksson et al. 1998).

Treatments with dense spacing will reach levels of production that warrant harvesting more quickly than those with less dense spacing, and will provide a greater total production during the first years after the orchard's establishment. They will thus give the orchard owner a more rapid return on investment and deliver increased genetic gains in operational plantations at an earlier stage. Treatments with over 1000 stems ha^{-1} produced on average 82 hl ha^{-1} of cones from age 6 to 13 whereas treatments with 533 or 267 stems ha^{-1} produced on average 41 hl ha^{-1} of cones during the same period of time.

4.5 Seed quality

The number of filled seeds varied between years, but the within-year variation between treatments was small. Similar patterns were observed for seed weights but with a somewhat greater variation between treatments within the same year. In addition, seed weights tended to be lower during the first 4 production years (seed orchard ages 6–9). The numbers of filled seeds and seed weights were within the limits of normal variation for seed orchard seeds of *P. sylvestris* (Almqvist et al. 1995; Almqvist et al. 1996; Almqvist 1998; Eriksson et al. 1998). All of the tested treatments were thus capable of producing high quality seed.

4.6 Seed production per hectare seed orchard

The production levels obtained in this study of seed production from production between orchard ages of 6 and 21 were higher than those previously reported in the literature. The average per-hectare production in the relatively young seed orchard examined in this work varied between 5.5 and 10.8 kg (ha yr)$^{-1}$. For comparative purposes, three unpruned Turkish *Pinus sylvestris* seed orchards with spacings between 204 and 277 Stems ha^{-1} and orchard ages between 11 and 20 years produced 2.1, 1.3 and 3.5 kg ha^{-1}, respectively, in a single year (Bilir et al. 2008). Based on results reported by Prescher et al. (2005), seed production levels of between 4.3 to 19.1 kg ha^{-1} yr^{-1} were achieved in six periodically pruned (no more detailed information on the pruning regime was available) Swedish *Pinus sylvestris* seed orchards with orchard ages of 20 to 44 years and spacings of 130 to 350 Stems ha^{-1}. In a compilation of seed production data for most of the first generation Swedish *Pinus sylvestris* seed orchards Hannerz et al. (2000) reported an average seed production level of 5.5 kg ha^{-1} yr^{-1} for seed orchards in their production ages. In an analysis of future seed supply of *Pinus sylvestris* from seed orchards in Sweden, Almqvist et al. (2010) used production levels of 5.5 and 6.5 kg ha^{-1} yr^{-1} for northern and southern Sweden, respectively. The rather high production reported in this study indicates that more intensive management of operational seed orchards will probably increase production.

Like cone production, seed production initially increased most rapidly in treatments with more dense spacings. Treatments with over 1000 Stems ha^{-1} produced on average 52 kg ha^{-1} of seed from age 6 to 13 while treatments with 533 or 267 Stems ha^{-1} produced on average 27 kg ha^{-1} of seed over this period.

Comparable levels of total seed production were achieved with many different combinations of stand density and target height. As such, seed orchard owners and managers have a wide range of viable management options. The earlier start of seed production achieved at higher stand densities would give orchard owners a more rapid return on investment at the cost of a greater initial investment. Therefore, the optimal stand density and target height will depend on the orchard owner's priorities. Economic calculations should be performed to determine optimal target heights and densities for different types of owner. The production data reported herein will be valuable in clarifying the biological limitations on seed production when performing such calculations.

5 Conclusions

The following conclusions can be drawn from the results of this study:

Pollen production started at the same seed orchard age for all studied combinations of stand density and target height. However, pollen production increased more rapidly in treatments with higher stand densities.

Treatments with dense spacing will reach production levels that warrant harvesting earlier than treatments with lower stand densities. However, over the studied period, many treatments achieve similar levels of cone and seed production regardless of their planned stand density or target height.

There were only small differences in seed quality traits between the different treatments.

Many different combinations of stand density and target height can yield comparable levels of seed production, so seed orchard owners and managers have a wide range of viable management options.

Management strategies that use dense initial spacings and low target heights followed by thinning and an increased target height will probably have the greatest per hectare production over time.

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Total of 26 references.