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High stand density improves seed production in seed orchards of the masting species *Picea abies*

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Highlights

- Cone production per tree in a *Picea abies* seed orchard is independent of stand density up to at least 800 stems ha^{-1}.
- The higher the stand density, the higher per hectare cone production will be in the seed orchard.

Abstract

Reproduction in masting species is characterised by long intervals between good cone and seed production years, and only sparse reproduction between mast years. The physiological mechanisms behind masting, and how these are linked to internal resource status and external weather factors, is still a subject of scientific exploration and debate, as is the effect of climate change on masting. This study investigates cone production in one operational seed orchard in Sweden which was established with two different spacings and has since been subject to three tree thinning experiments. The spacings before thinning varied between 800 and 400 stems ha^{-1}, and then thinning reduced the stand density in all trials to half, i.e. between 400 and 200 stems ha^{-1}. In all three experiments cone production per tree was equal in un-thinned and thinned treatments, both in mast years and in non-mast years. Thus, the cone production per unit area was twice as high in the un-thinned areas. The conclusion from these experiments is that the establishment of *Picea abies* (L.) H. Karst. orchards with wide tree spacing is both a misuse of good orchard locations and bad economics.

Keywords Norway spruce; cone production; thinning
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1 Introduction

Picea abies (L.) H. Karst. exhibits masting behaviour, meaning that there are long intervals between good cone and seed production years, and between mast years they produce few or no cones and seeds. Masting, or mast seeding, is the phenomenon of synchronous seed production that varies significantly between years exhibited by conifers and other perennial plants (Pearse et al. 2016). Masting occurs in long-lived species and is most common in wind-pollinated and woody species (Herrera et al. 1998). Besides *Picea abies,* other economically important tree species that exhibit this behaviour include *Quercus robur* L., *Fagus sylvatica* L., *Picea glauca* (Moench) Voss, *Pinus nigra* J.F. Arnold and *Castanea sativa* Mill.. *Picea abies* displays strong mast year synchrony (Nussbaumer et al. 2016). The physiological mechanisms of masting and how they are linked with internal resource status and external weather factors are still the subject of scientific exploration and debate (Kelly et al. 2013; Crone and Rapp 2014; Pearse et al. 2016). The effect of climate change on masting behaviour is also unclear and needs further attention (Bogdziewicz 2022).

Most seed orchards of wind-pollinated conifers have been established at relatively similar spacing/stand densities. Zobel and Talbert (1984) give 338 stems per hectare as a suitable starting density for *Pinus taeda* L. orchards, corresponding to a spacing of 5.4 × 5.4 m between trees.

The first seed orchards of *Pinus sylvestris* L. and *Picea abies* in Sweden were established in the 1950s and 60s through grafting and usually at spacings of between 4 × 4 m and 7 × 5 m (625–285 stems ha^{-1}) and with 5 × 5 m (400 stems ha^{-1}) as the most common spacing (Hannerz et al. 2000). Werner (2010) quotes spacings of 4 × 4, 5 × 5, and 7 × 3.5 m (626–400 stems ha^{-1}) for these orchards. A second batch of *P. abies* orchards established in Sweden in the 1980s used spacings of 6–7 m between rows and 2.5–7 m between trees within a row (667–204 stems ha^{-1}).

Lindgren (1992) offers a guideline of 20 m^2 for each tree (500 stems ha^{-1}) when establishing *Picea abies* seed orchards. Plans for establishing a third generation of *P. abies* seed orchards (Rosvall et al. 2003) proposed a spacing of 7 × 4–5 m (375–286 stems ha^{-1}). In Finland the 1.5 generation *P. abies* seed orchards have been established with spacings between 250–625 stems ha^{-1} (J. Antola, pers. comm.), while in eastern Canada the recommended spacing in *P. abies* seed orchards is 5 × 6 m (333 stems ha^{-1}) (Smith and Adam 2003). In the Swedish seed orchard handbook (Almqvist et al. 2007) the recommended spacing for *P. abies* seed orchards is 200–400 stems ha^{-1}.

There are examples of seed orchards established with significantly denser spacings: for example, in New Zealand hedged seed orchards of *Pinus radiata* D. Don have been established (Sweet and Krugman 1977) and, for *P. radiata,* in even denser orchards called “Pine yards” or “Meadow orchards”, spacings of 1 × 1 to 1 × 2 m (10000 to 5000 stems ha^{-1}) have been tested (Shelbourne et al. 1989; Sweet et al. 1990). There are also examples of *Picea abies* seed orchards with rather dense spacing at 3 × 3 m (1111 stems ha^{-1}) which produce cones and seed during mast-years (Dering et al. 2014).

Almqvist and Jansson (2015) reported seed production results for *Pinus sylvestris* in an experimental seed orchard with significant differences in spacing and pruning heights. Their conclusions were that dense spacings start to produce sufficient quantities for harvest earlier, but, over the 20-year period studied, there were several combinations of stand density and pruning height that had produced equal quantities of cones.

I have been unable to find any reference to investigations into the effects of spacing or thinning on cone and seed production in *P. abies* on which to base recommendations to orchard managers when establishing new orchards or thinning established ones. Werner (1975) pointed out that the literature on the effects of thinning in seed orchards was sparse, but that it is generally recognised that, in plantations where the need for thinning has been ignored, there is a reduction in seed production which can last for many years even once thinning is carried out. A review by

Ilstedt (1982) highlights the effect of thinning on seed production in seed orchards, but references only *Pinus* species. In other masting species as *Quercus robur* spacings of 10 × 8 m (125 stems ha^{-1}) are often used and 6 × 6 m (278 stems ha^{-1}) is considered too dense (Kajba et al. 2008).

The objective of this study was to examine the effect of stand density in *Picea abies* seed orchards on the cone and seed production both on individual tree level and on an area (per hectare) level. Here, I present the results of thinning experiments in a *P. abies* seed orchard in southern Sweden on cone and seed production.

2 Material and methods

2.1 The seed orchard

The *Picea abies* seed orchard FP-512 Målilla is located in southern Sweden at 57.37 latitude, 15.85 longitude, and was established between 1993–1999. It is 22 hectares in size and was established in double-rows with four metres between the two rows and six metres between double-rows. Within each row trees were spaced 2.5 metres apart in the northern part of the orchard and 3.0 metres apart in the southern part (Fig. 1). This corresponds to 800 stems ha^{-1} and 667 stems ha^{-1}, respectively. The trees in the seed orchard comprise 237 clones and are a mixture of cuttings and grafts (produced both in a nursery and as field-grafts, grafted onto rootstocks established at the seed orchard location).

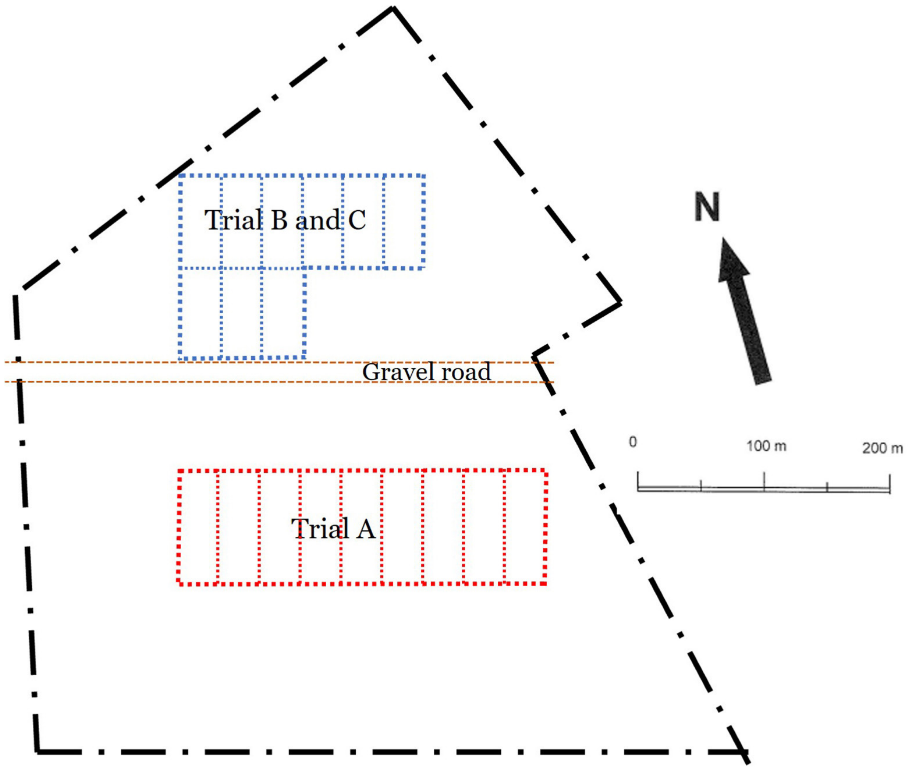

Fig. 1. Overview of seed orchard FP-512 Målilla, Sweden (57.37 latitude, 15.85 longitude) with the location of the three trials, each with nine blocks. Trial A was active throughout the studied period, Trial B was active until 2016, and Trial C began in 2017.

The entire seed orchard was top pruned at a height of approxemately 3 metres in the autumn of 2006 (i.e., all trees taller than 3 m were topped to 3 m). In the autumn of 2013, the northern part of the seed orchard was top pruned to a height of approx. 4.5 metres.

In the spring of 2017, the northern part (north of the gravel road) was thinned by removing one of the two rows in each double-row, changing the spacing to 10 × 2.5 m, corresponding to 400 stems ha^{-1}. In 2018 the southern part of the orchard was similarly thinned, changing the spacing to 10 × 3.0 m, which corresponds to 333 stems ha^{-1}.

The seed orchard has been harvested by the owners on six occasions. On each occasion the whole seed orchard was harvested. In 2007, a total of 16 550 litres of cones were collected, resulting in 105.28 kg of seed. In 2017, 56 560 litres of cones gave 463.28 kg in seed. In 2019, 28 500 litres of cones resulted in 191.16 kg of seed. In 2020, 24 400 litres of cones gave 2.2 kg of seed. In 2021, 49 600 litres of cones gave 16.6 kg of seed. Finally, in 2022, the total collection resulted in 344 000 litres of cones that yielded 354.8 kg of seed.

2.2 Design of the trials

The experimental plots were established in the autumn of 2007 in areas demonstrating high survival and even development of the orchard trees, to minimise within-block variation. At the start of the trial, the trees were on average 2.5 m high and 10 cm in diameter at breast height ($D_{1,3}$). In 2020/21 the trees in the northern part were, on average, 11.4 m high and had an average $D_{1,3}$ of 21 cm. In the southern part the corresponding figures were a height of 11.3 m and a $D_{1,3}$ of 22 cm.

Initially, two thinning experiments were established which aimed to explore the effect of thinning on seed production: Trial A, south of the gravel road which crosses the orchard in an east-west direction, and Trial B to the north of the road. Each trial comprised 9 blocks (Fig. 1). Trial A covered 3.6 ha, and Trial B 3.0 ha. The trials were designed as randomised block trials using two different thinning regimes (not thinned and thinned). In the thinned plots every second tree in each of the double-rows was removed (Fig. 2, part I).

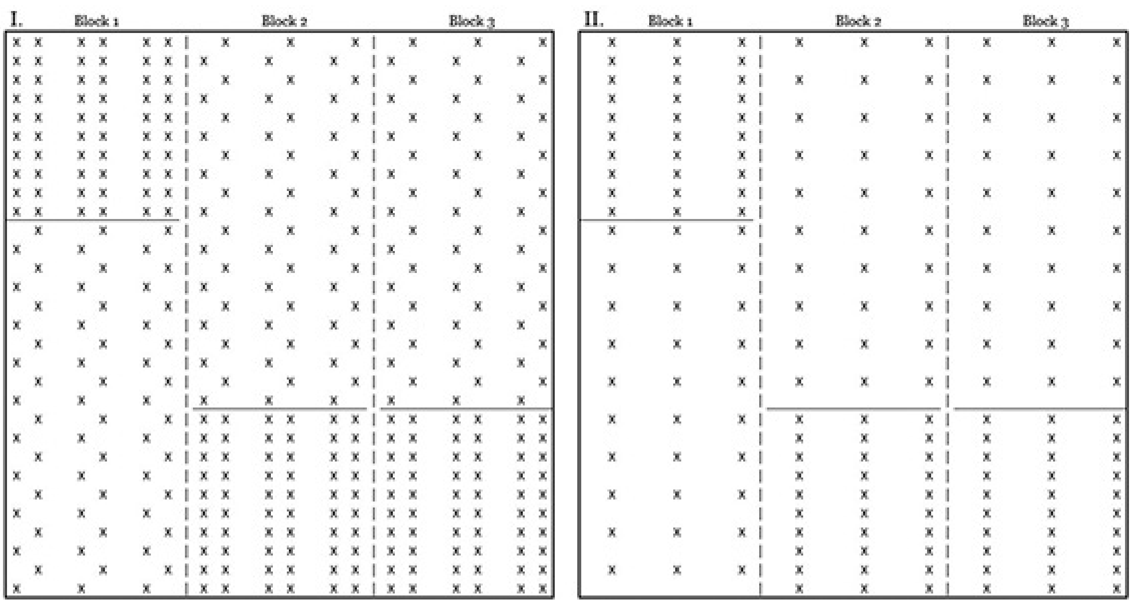

Fig. 2. Thinning trials in the *Picea abies* seed orchard FP-512 Målilla, Sweden. I. – Layout of the plots in three blocks (of nine) each in Trials A and B. II. – Layout of the plots in three blocks (of nine) in Trial C.

Table 1. Treatments in the three thinning trials in the *Picea abies* seed orchard FP-512 Målilla in Sweden (57.37 latitude, 15.85 longitude).

Trial		Treatments	Cone data for years
Trial A	Not thinned	667 stems ha^{-1}	2011, 2016, 2017, 2019–2022
	Thinned	333 stems ha^{-1}	
Trial B	Not thinned	800 stems ha^{-1}	2011, 2016
	Thinned	400 stems ha^{-1}	
Trial C	Not thinned	400 stems ha^{-1}	2019–2022
	Thinned	200 stems ha^{-1}	

In 2017, the orchard owner thinned the northern part, including the area of Trial B. This then became a new trial, Trial C, comprising the same 9 blocks but with each now demonstrating two treatments: not thinned (400 stems ha^{-1}) and thinned (200 stems ha^{-1}) (Fig. 2, part II; Table 1).

When the southern part of the orchard was thinned in 2018 the experimental plots in Trial A were excluded, and thus the experiment could continue uninterrupted.

2.3 Data collection and manipulation

In 2011 the number of cones per tree in the central double-row of each plot was scored, and in 2016 the number of cones per tree in the central double-row of each plot was counted. In 2017 the cones were collected from all trees on each plot in Trial A, and the volume (in litres) of healthy cones (which were collected for seed extraction) per row was recorded. In 2019 the volume of healthy cones for Trial A and C was collected in the same way. In 2020–2022 data of the volume of healthy and bad cones were measured for each row on each plot in Trial A and C. In the years 2011, 2016, 2017 and 2020 the number of living trees per row in all plots were counted.

The scoring of cones per tree in the data collections in 2011 were transferred to numbers as shown in Table 2. We used a conversion rate of 10 cones per litre (cones l^{-1}) and the stand density on each plot (200, 333, 400, 667 and 800 stems ha^{-1}, respectively) to calculate the volume of cones per hectare (hl ha^{-1}), based on 10 cone samples from *Picea abies* seed orchards in south- and central Sweden (U. Wennström, pers. comm.).

In 2022 a sample of 30 healthy cones was collected from each plot in Trials A and C. Before extracting seeds, samples from un-thinned and thinned plots in three blocks were pooled, resulting in six samples from each of the two trials. Data about cone and seed quality were collected for each sample.

Table 2. In the thinning trials A and B in the *Picea abies* seed orchard FP-512 Målilla, data collection 2011. Scoring classes for number of cones per tree and the number used for each class in the statistical analyses.

Cone scoring class	Number used	Cone scoring class	Number used
0	0	41–80	60
1–10	5	81–160	120
11–20	15	161–320	240
21–40	30	>320	480

2.4 Statistical analyses

Statistical analyses of volume of cones per tree (l tree^{-1}) and volume of cones per hectare (hl ha^{-1}) were performed using the Proc GLM module of SAS (version 9.4), based on the following model:

$$y_{ijk} = \mu + b_i + c_j + d_k + bc_{ij} + bd_{ik} + e_{ijk} \quad (1)$$

where:
y_{ijk} = Dependent variable, e.g., volume cones per hectare
μ = overall mean
b_i = fixed effect of year
c_j = fixed effect of block
d_k = fixed effect of treatment
e_{ijk} = residual, $(N(0,\sigma_e^2))$

Tukey-Kramer adjusted significance levels were used for multiple comparisons.

3 Results

3.1 Trial A

The statistical model fits the data very well both for volume of cones per tree and for, volume of cones per hectare with model F-values (and p-values) of 22.2 (< 0.0001) and 20.3 (< 0.0001), respectively, and r-square values of 0.964 and 0.962, respectively.

The volume of fresh cones per tree varied considerably between years: 2017 and 2019 can be considered mast years, and 2022 as a semi-mast year. There were no statistically significant differences ($p<0.05$) between lower and higher stem densities in any year except 2017, when plots with higher stand density (667 stems ha^{-1}) yielded higher numbers of cones per tree (Fig. 3). For total cones produced per tree, higher stand density (667, stems ha^{-1}) produced 4 percent more cones per tree, although this result was not statistically significant ($p<0.05$).

In terms of the volume of fresh cones produced per hectare of seed orchard, there were large and statistically significant ($p<0.001$) differences between the stand densities in the two mast years, the semi-mast year, and in total production over the years studied (Fig. 4). For the total volume of cones produced per hectare, higher stand density (667 stems ha^{-1}) produced 105 percent more fresh cones per hectare. There was no difference in cone production per hectare between stand densities in non-mast years.

For the years 2020 to 2022, bad cones (those so damaged by insects and/or fungus that they were not sent for seed extraction) were also collected. The volume of bad cones per tree was larger in the denser stands than in the more widely spaced stands in two of the years (2021 and 2022), although this was only statistically significant in 2022 (Fig. 5).

The difference between spacings in terms of total volume of cones per hectare was greater when also bad cones were taken into consideration (Fig. 6).

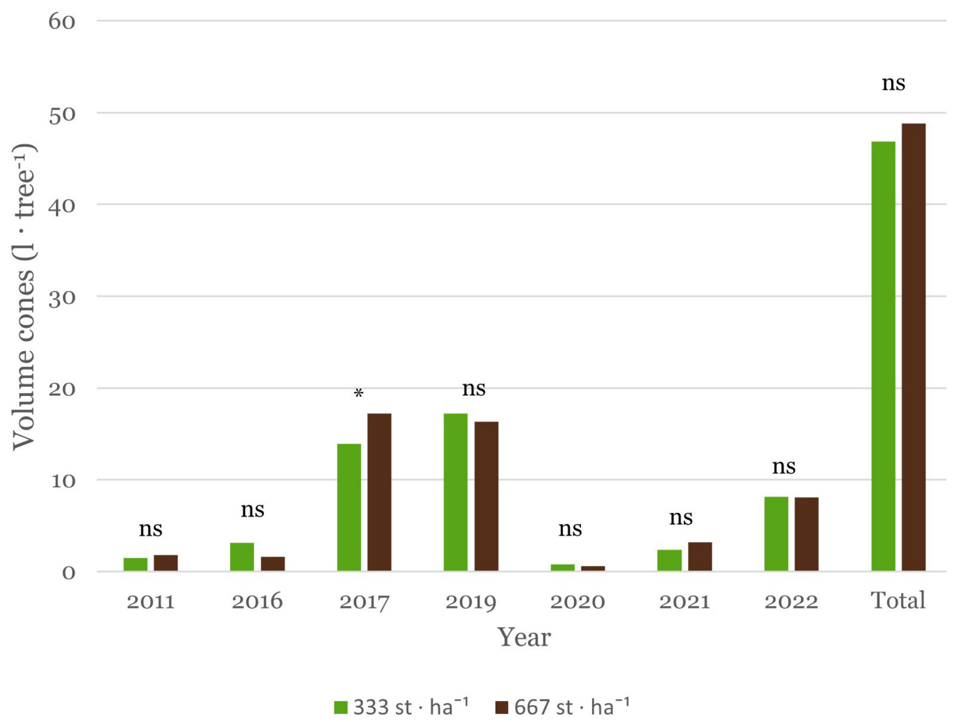

Fig. 3. In thinning Trial A in the *Picea abies* seed orchard FP-512 Målilla, Sweden. The volume of fresh cones per tree (l tree^{-1}) in Trial A. Significance levels above the bars: ns – not statistically significant ($p < 0.05$); * – statistically significant ($p < 0.05$).

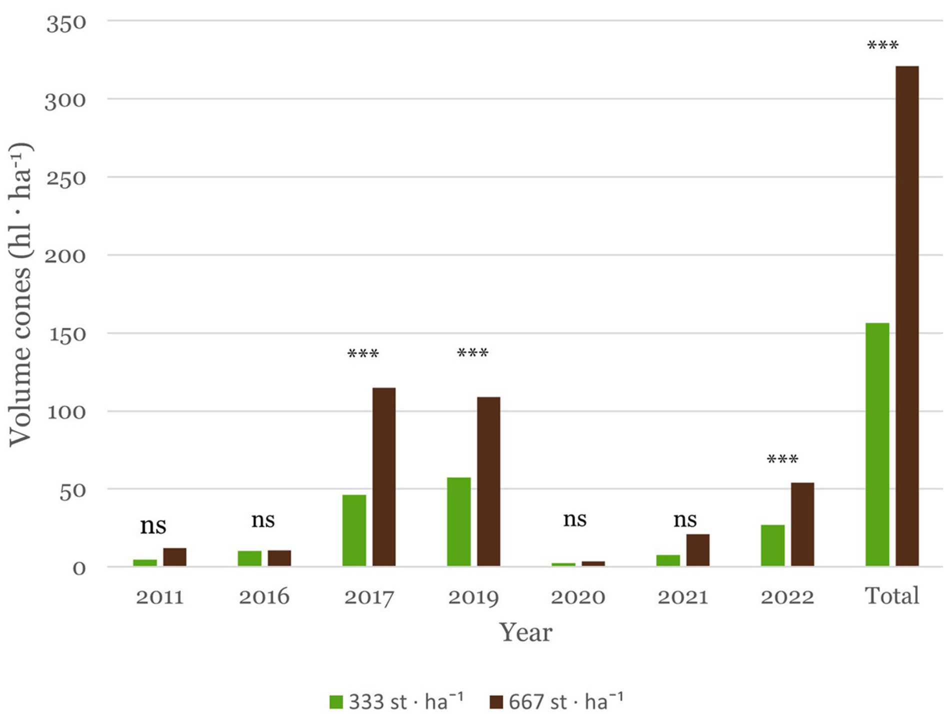

Fig. 4. In thinning Trial A in the *Picea abies* seed orchard FP-512 Målilla, Sweden. The volume of fresh cones per hectare (hl ha^{-1}) in Trial A. Significance levels above the bars: ns – not statistically significant ($p < 0.05$); *** – statistically significant ($p < 0.001$).

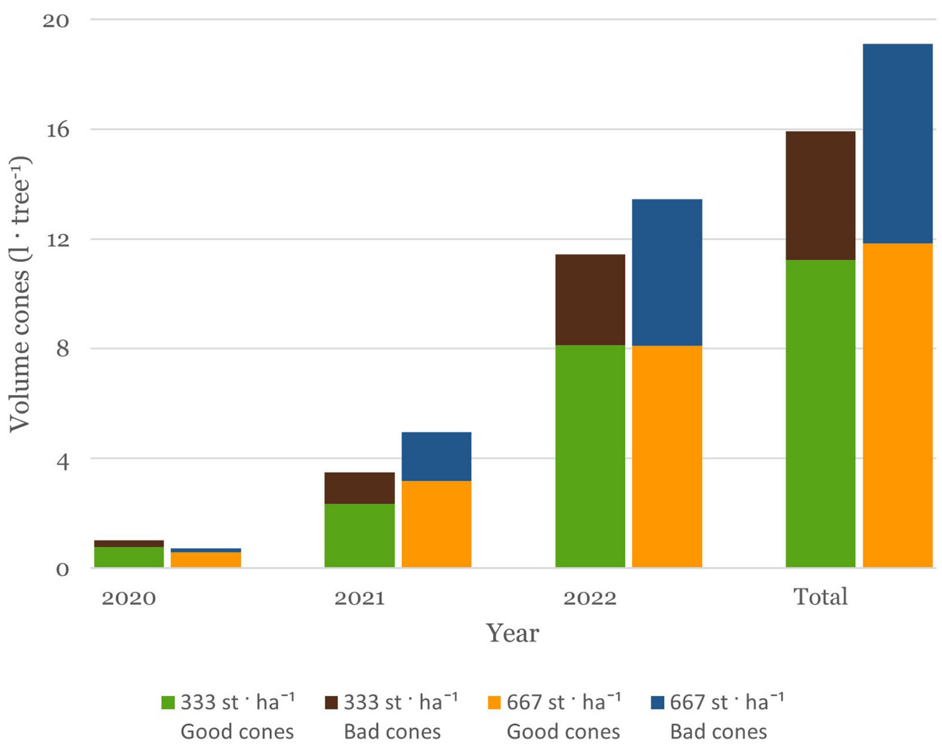

Fig. 5. In thinning Trial A in the *Picea abies* seed orchard FP-512 Målilla, Sweden. The total volume cones per tree (l tree^{-1}) divided into good and bad cones in Trial A for the years 2020–2022.

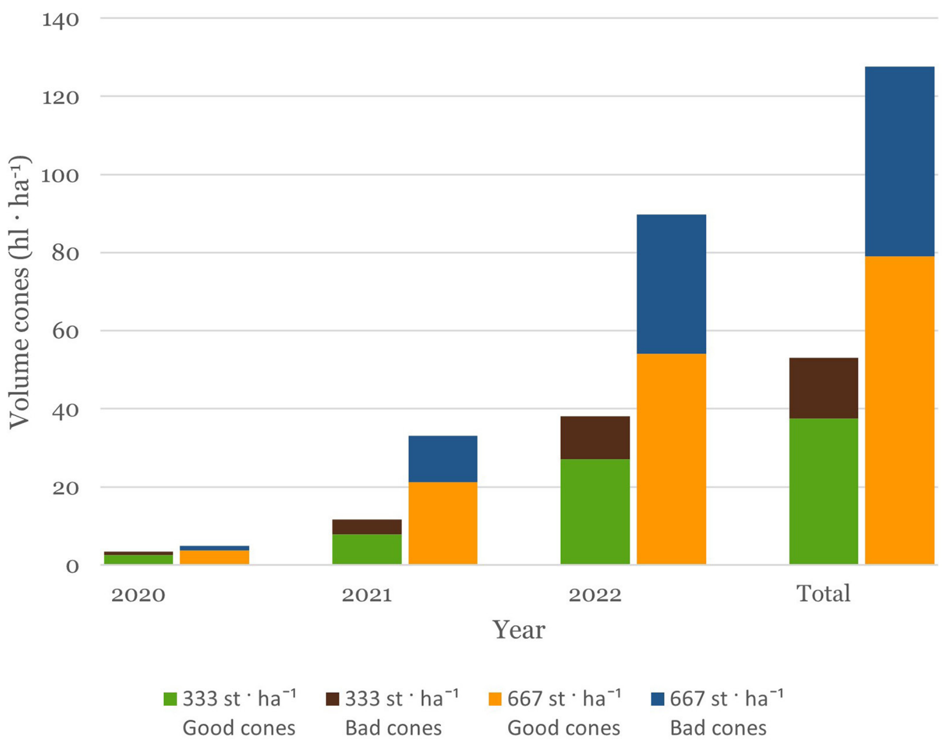

Fig. 6. In thinning Trial A in the *Picea abies* seed orchard FP-512 Målilla, Sweden. The total volume of cones per hectare (hl ha^{-1}) divided into good and bad cones in Trial A for the years 2020–2022.

3.2 Trial B

The statistical model fits the data very well both for volume of cones per tree and for volume of cones per hectare, with model F-values (and *p*-values) of 11.6 (< 0.0001) and 10.2 (< 0.0001), respectively, and r-square values of 0.933 and 0.924, respectively.

The volume of cones per tree varied considerably between the two years, although neither of them can be considered mast years. There were no statistically significant differences ($p<0.05$) between the lower and higher stem density in either of the two years studied or in the total volume of cones produced per tree (Fig. 7).

In 2011, there was a statistically significant difference ($p<0.001$) between higher (800 stems ha^{-1}) and lower density (400 stems ha ha^{-1}) stands in terms of volume of cones produced per hectare. The higher density stand produced 96% more over the two years studied (Fig. 8).

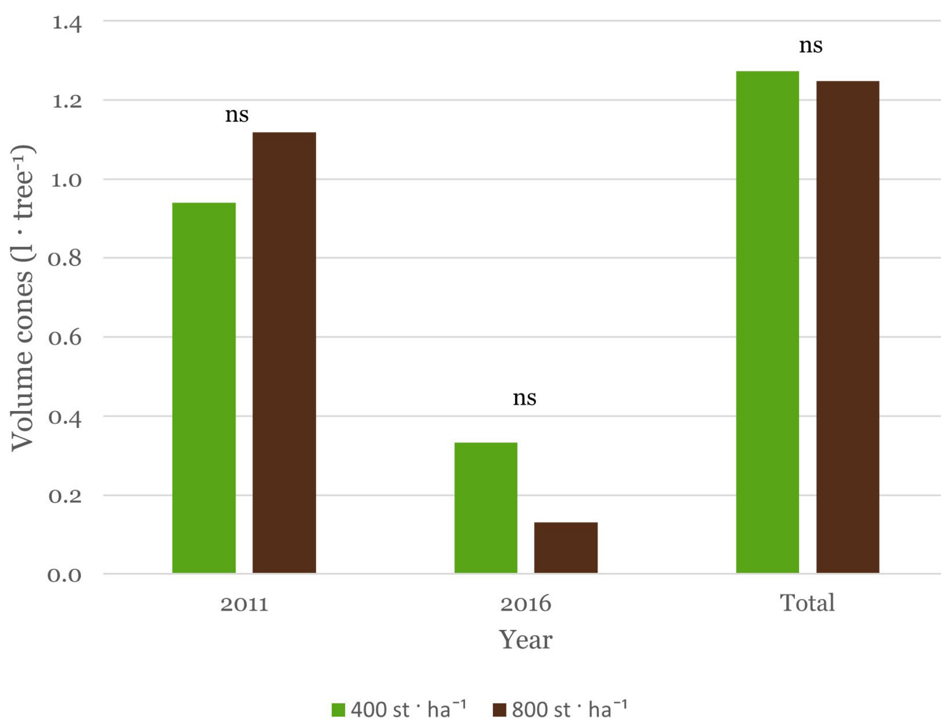

Fig. 7. In thinning Trial B in the *Picea abies* seed orchard FP-512 Målilla, Sweden. The volume of cones per tree (l $tree^{-1}$) in Trial B. Significance levels above the bars: ns – not statistically significant ($p < 0.05$).

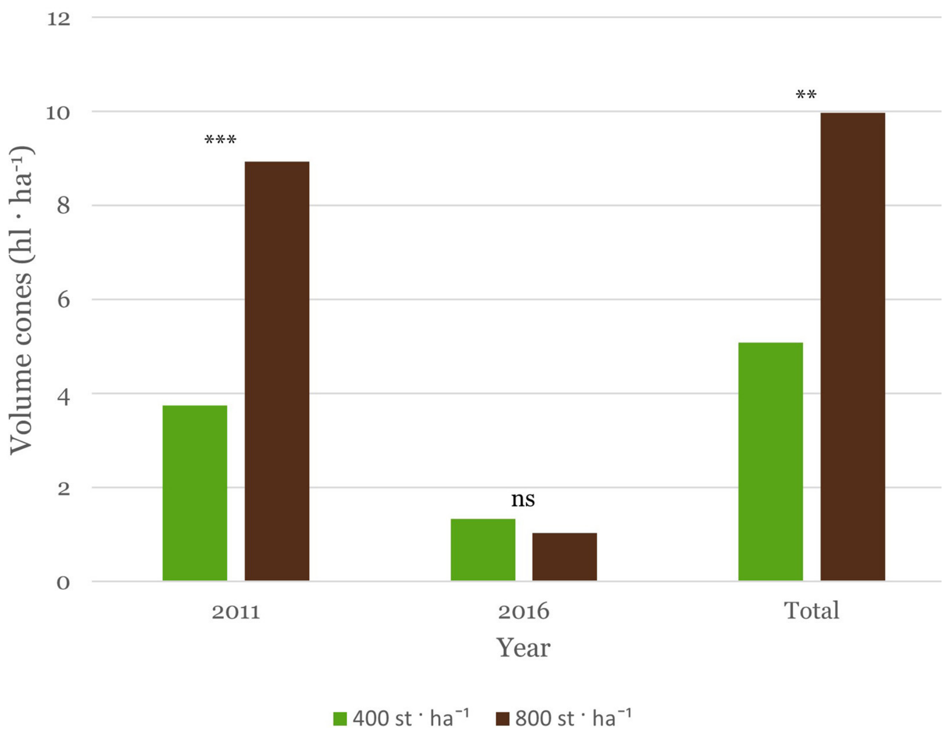

Fig. 8. In thinning Trial B in the *Picea abies* seed orchard FP-512 Målilla, Sweden. The volume of cones per hectare (hl ha^{-1}) in Trial B. Significance levels above the bars: ns – not statistically significant ($p < 0.05$); ** – statistically significant ($p < 0.01$) ; *** – statistically significant ($p < 0.001$).

3.3 Trial C

The statistical model fits the data well both for volume of cones per tree and for volume of cones per hectare, with model F-values (and *p*-values) of 45.5 (< 0.0001) and 30.0 (< 0.0001), respectively, and r-square values of 0.982 and 0.979, respectively.

The volume of fresh cones per tree varied considerably between the years. There were no statistically significant differences ($p<0.05$) between lower and higher stem density stands in any of the studied years or in the total volume of cones produced per tree (Fig. 9).

There were large and statistically significant ($p<0.001$) differences between the stand densities in the volume of fresh cones produced per hectare in 2022, and in the total production over the years studied (Fig. 10). For the total volume of cones produced per hectare the higher stand density (400 stems ha^{-1}) produced 102% more cones per hectare over the years studied.

In 2020–2022, bad cones also were collected. The volume of bad cones per tree was greater in the denser than in the wider spacing in 2022 only, and the difference was statistically significant ($p<0.001$), (Fig. 11).

The difference between spacings in terms of total volume of cones per hectare was greater when bad cones were taken into consideration (Fig. 12).

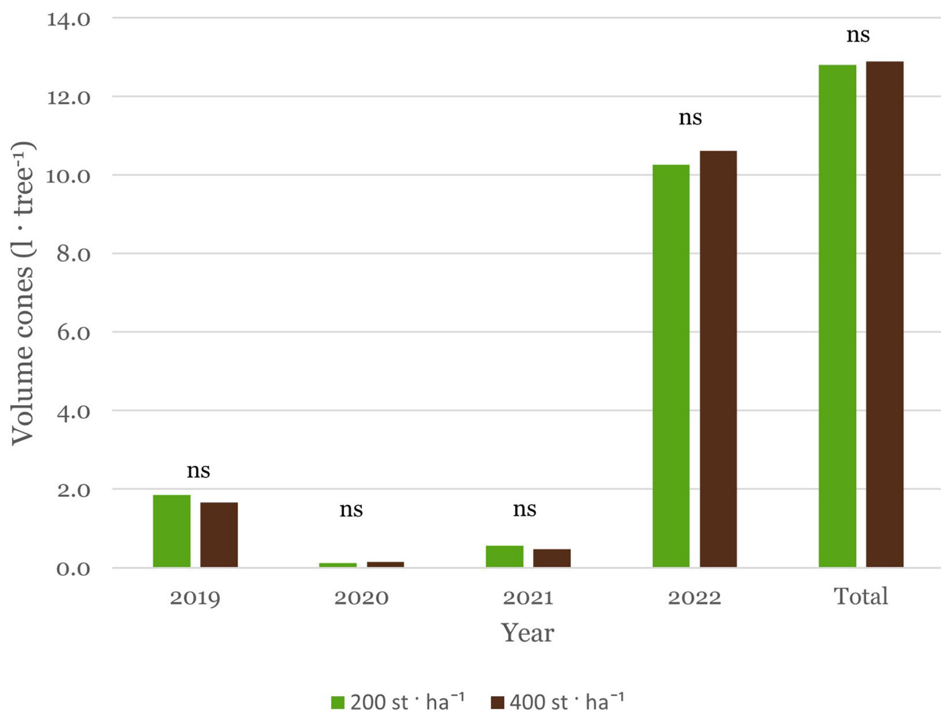

Fig. 9. In thinning Trial C in the *Picea abies* seed orchard FP-512 Målilla, Sweden. The volume of cones per tree (l $tree^{-1}$) in Trial C. Significance levels above the bars: ns – not statistically significant ($p < 0.05$).

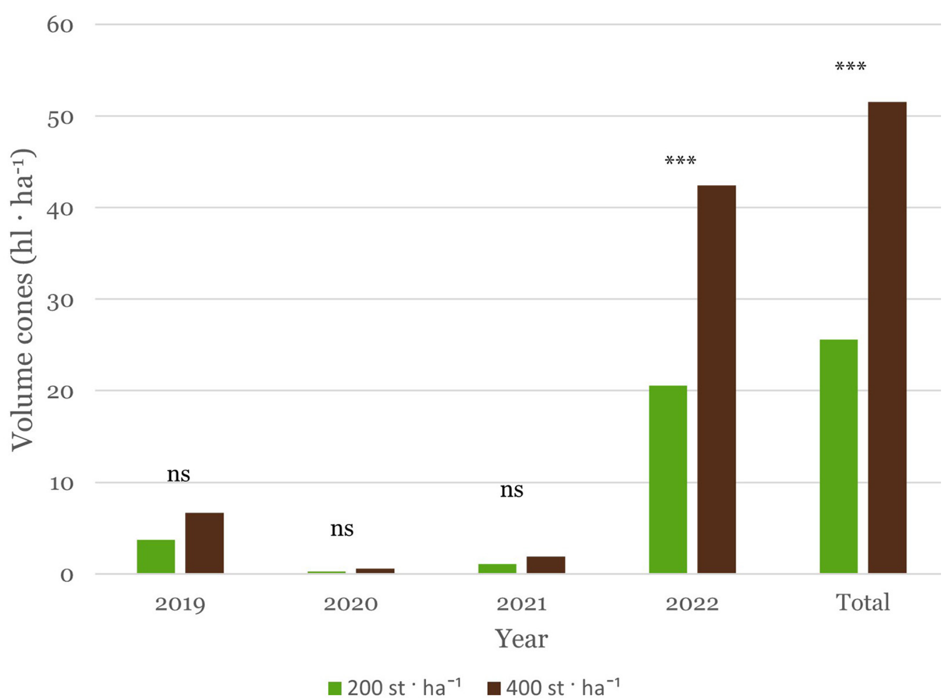

Fig. 10. In thinning Trial C in the *Picea abies* seed orchard FP-512 Målilla, Sweden. The volume of cones per hectare (hl ha^{-1}) in Trial C. Significance levels above the bars: ns – not statistically significant ($p < 0.05$); *** – statistically significant ($p < 0.001$).

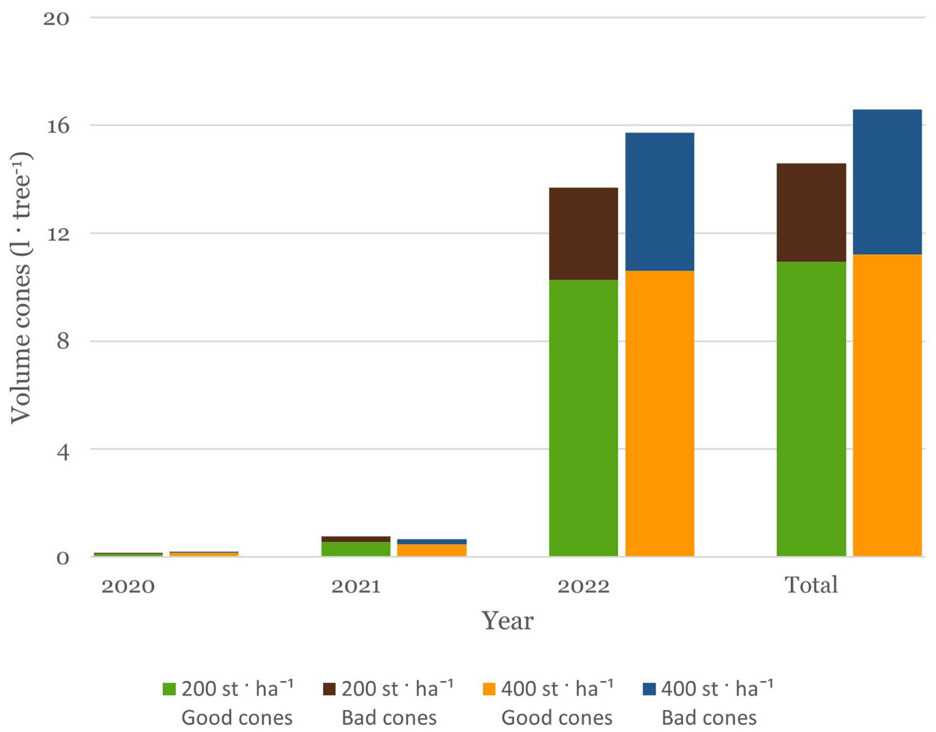

Fig. 11. In thinning Trial C in the *Picea abies* seed orchard FP-512 Målilla, Sweden. The total volume cones per tree (l tree^{-1}) divided into good and bad cones in Trial C for the years 2020–2022.

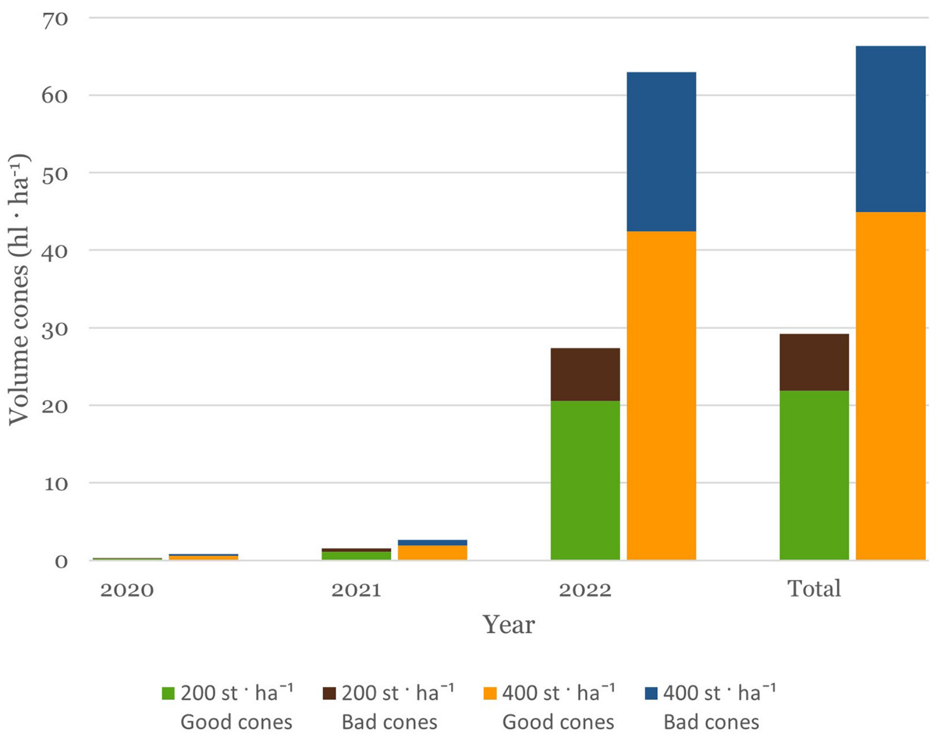

Fig. 12. In thinning Trial C in the *Picea abies* seed orchard FP-512 Målilla, Sweden. The total volume of fresh cones per hectare (hl ha^{-1}) divided into good and bad cones in Trial C for the years 2020–2022.

Table 3. In the thinning trials A and C in the *Picea abies* seed orchard FP-512 Målilla. Cone and seed quality data. Cones collected in autumn 2022. Traits with statistically significant differences ($p < 0.05$) are marked in bold.

Trial	Treatment	Cones per liter	Cone lenght (cm)	Seeds damaged by insects (%)	Empty seeds (%)	Filled seeds (%)	1000 seeds weight (gr)	AP (%) [1]	Filled seeds per cone	Seeds per Kg
A	Thinned	7.3	11.8	0.3	0.5	99.2	7.34	96	179	138 787
A	Not thinned	7.7	11.7	0.9	1.7	97.4	7.43	97	185	135 088
C	Thinned	8.0	11.5	0.9	1.0	98.1	**7.09**	96	**174**	**141 142**
C	Not thinned	7.7	11.5	0.6	1.4	98.0	**6.82**	97	**196**	**146 642**

[1] AP – anatomic potential, a value corresponding to germination capacity (Simak 1980).

3.4 Cone and seed quality in Trial A and C

There were no large and statistically significant differences in any trait between the two spacings in either of the trials, apart from in Trial C where the dense spacing yielded lower seed weight and a higher number of seeds per cone and per Kg (Table 3). This result was statistically significant ($p < 0.05$).

4 Discussion

The fact that *Picea abies* is a masting species must be taken into consideration in all decisions regarding seed production in seed orchards. It is clear from the data presented here that the mast years accounted for most of the seed production in these orchards, and therefore how orchard trees behave during the masting years should guide all seed orchard management operations, starting with establishment.

The Målilla seed orchard studied here experienced three mast years in a 16-year period (in 2007, 2017, and 2019) and one semi-mast year (2022). This equates to an average of four to five years between mast years. With such long intervals between good seed production years, it becomes essential that, in those years, the orchard produces especially high yields and that the orchards are managed in a way that facilitates this. The data from seven years of cone production in Trial A includes two mast years and one semi-mast year, and those years represent 84% and 87% of all cones produced in the low and high stand density plots, respectively. The single most productive year accounted for 37% and 36% of total production of fresh cones per hectare over the years studied.

Together, the three trials include a range of stand densities, from 200 to 800 stems ha^{-1}, which covers the normal range of stand densities used in *Picea abies* seed orchards. In all three trials, trees in higher density stands produced the same volume of cones per tree as those in lower density stands. Within this range (200–800 stems ha^{-1}) stand density seems to have little effect on the volume of cones produced per tree. If new seed orchards are established at lower densities, or orchards are thinned during the production phase, this can only be justified for other reasons, such as accessibility for machinery.

The larger volume of damaged cones in the denser spacings, both per tree and per hectare, is probably due to the increased density of food resources for pathogens. The observation that the difference is even larger for total production of cones per hectare than for fresh cones highlights the scope for increasing seed production even further in orchards with high stand density.

Cone and seed quality assessment did not reveal any major differences, which confirms that spruce can produce high quality seed in dense spacings, at least up to 667 stems ha^{-1}.

Stand density also may affect synchronisation of male and female flowering. Nikkanen (2001) found that wide spacing in promoted better reproductive synchronisation between female and male flowering in a *Picea abies* seed orchard. Better synchronisation would enhance pollination between the clones in the orchard and thus reduce the level of pollen contamination. This is an important aspect even if the contamination levels in *P. abies* seed orchards are lower than in orchards of *Pinus sylvestris* (Heuchel et al. 2022). Different aspects of stand density in *P. abies* seed orchards need to be further studied to have better information to base management decisions in operational seed orchards on.

Based on the results presented here, we conclude that the denser the spacing the higher per hectare production capacity of a seed orchard will be, at least up to 800 stems ha^{-1}. Finding good locations to establish seed orchards is difficult, and the larger the location needs to be the harder it becomes. Many management costs are also area dependent, for example fencing, grass management, root pruning for flower stimulation, and individual tree management activities as transport time between trees increases. Establishing a *Picea abies* seed orchard with wide spacing is therefore both a misuse of a good orchard location and bad economics.

5 Conclusions

Based on the results presented here the following conclusions can be drawn:

- The fact that *Picea abies* is a masting species needs to be taken into consideration in seed orchard management.
- Cone production per tree in a *Picea abies* seed orchard is independent of stand density up to at least 800 stems ha^{-1}.
- The higher the stand density, up to at least 800 stems ha^{-1}, the higher per hectare cone production will be in the seed orchard.
- Establishment of *Picea abies* seed orchards with wide tree spacing is both a misuse of good orchard locations and bad economics.

Declaration of openness of research materials, data, and code

Data and code can be made available by a reasonable request by email to the author.

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