

Diallel crosses in *Picea abies* VI. Genetic variation in early reproduction in three young Norway spruce progeny trials

Tore Skrøppa^{1*}, Thomas Mørtvedt Solvin¹ and Arne Steffenrem²

¹ Norwegian Institute of Bioeconomy Research, P.O. Box 115, 1431 Ås

² Norwegian Institute of Bioeconomy Research, Skolegata 22, 7713 Steinkjer, Norway

Corresponding author: Tore Skrøppa, E-mail: tore.skrøppa@nibio.no

Abstract

Female flowering and cone production took place in three Norway spruce progeny tests at ages 17 and 20 years, each planted with full-sib families from a half diallel. The number of cones on individual trees were scored in five classes. More than 50 % of the trees produced cones, and a considerable variation was found among families for the ability to produce cones (precocity) and for the number of clones scored in classes (fruitfulness). Both traits were strongly related to tree heights and diameters at the individual and at the family level. In general, tall trees produced the highest number of cones. However, some families produced many cones even if their average heights were low. In two of the half diallels, estimates of GCA variance components for the number of cones produced had twice the value of the SCA component, indicating additive genetic inheritance of cone production. Heritability estimates of cone scores were 0.10, 0.17 and 0.23, and the genetic correlations between cone production and tree heights were 0.40, 0.50 and 0.35 in the tree half-diallels, respectively.

Keywords: *Norway spruce, half diallels, precocious flowering, cone production, tree height, genetic parameters.*

Introduction

Female flowering and cone setting in forest tree species occur when the trees have passed the juvenile period and have attained the stage of maturity. The duration of juvenility varies among species from a few to tens of years (Waring 1959, Owens and Blake 1985). In Norway spruce (*Picea abies*), the average length of the juvenile phase is 20–25 years under

natural conditions (Waring 1959). However, first flowering in this species have been observed as early as age 9–10 years (Chalupka 1972). More abundant flowering coupled with a substantial production of mature seeds typically occurs much later. Chalupka (1972) reported from the Bialowieza Primeval Forest, Poland, that cone and seed production in the spruce forest increased with tree age and attained its maximum at 110–120 years.

Weather conditions affect the initiation of flowering buds in Norway spruce. Warm and dry conditions during the second half of June and early July have been shown to promote female flowering and cone production the next summer (Lindgren et al. 1977). The between-year variation in abundance of flowering and seed crop is large and irregular in forest stands at northern latitudes and high altitudes in the Nordic countries (Andersson 1965). There is also a large variation in flowering between trees within a stand (Sarvas 1968, Hacket-Pain et al. 2019). Dominant and co-dominant trees which have the greatest exposure to sunshine and high temperatures produce more cones. Therefore, relationships are present between tree heights and diameters and their ability to flower (Chalupka and Giertych 1975). A heavy cone crop may cause loss of stem wood production in the year of seed production and some reduction in production the next couple of years, i. e. Holmsgaard and Bang (1990), Hacket-Pain et al. (2019). However, some other studies have indicated no evidence of a possible trade-off between growth-rate and reproductive success (Seiffert and Müller-Starck 2009, Avanczi et al. 2019).

Studies of flowering in Norway spruce have in most cases been made in clonal archives and seed orchards. Several studies have demonstrated variation in flowering and cone production at different levels: between sites, between years within each site, between provenances and between clones within the same provenance (e. g. Eriksson et al. 1973, Skrøppa and Tuttunen 1983, Nikkanen and Ruotsalainen 2000). The large

variation among clones in cone production implies different genetic contributions from the clones to the seed harvested in the orchard. No relationship was found between the cone production of parental clones and the height growth of their progenies in six-year-old progeny tests (Skrøppa and Tutturen 1985).

When characterizing flowering of forest trees at an early age two different factors must be distinguished (Schmidtling 1981), precocious flowering or precocity, as the early manifestation of sexual maturity, and fruitfulness, defined as the number of reproductive units. The first is a qualitative trait at a given age, while the second is quantitative.

Few results have been presented about genetic variation in precocity and fruitfulness of forest trees. Santos-del-Blanco et al. (2012) studied reproduction and growth in a young trial with populations of *Pinus pinaster* and found genetic variation among provenances for the age of first female flowering and a negative correlation between early cone production and height, most likely caused by female reproduction of less adapted provenances occurring at a lower individual height. Schmidtling (1981) showed considerable genetic variation between families for both precocity and fruitfulness in loblolly pine (*Pinus taeda* L.) and found negative correlations with growth traits. Flowering precocity was found to be highly heritable for *Eucalyptus globulus ssp. globulus* at the age of four years (Chamber et al. 1997). For Norway spruce, genetic studies of precocity and fruitfulness have not yet been published. In this paper we will present the variation and inheritance patterns of cone production found for these two traits in field trials with this species at ages between 17 and 20 years, containing families from half diallels and discuss relationships with tree heights and diameters.

Materials and methods

Trials and measurements

Two field trials with full-sib families of Norway spruce were established in 1976 and a third trial in 1979. The families in each trial formed a half diallel from controlled crosses in a complete diallel design, each made in 1973 in a natural population (Skrøppa and Tho 1990). The three half diallel trials will be denoted as Diallel 1, planted in 1976, Diallel 2, planted in 1979, and Diallel 3, planted in 1976. Two of the diallels were generated from 10 parents and one from 9 parents. In each population, trees standing more than 50 m apart were randomly chosen among the trees having both female and male flowers and were crossed in all possible combinations. The trials were planted with 2 m spacing in four-tree family plots randomly distributed in 12 complete blocks. Two of the field trials were established at sites with climatic conditions not very different from the origins of the natural population and the third at a somewhat milder site (Table 1, Solvin et al. 2024).

All families from the full diallels were tested in short-term trials where height and diameter were measured until age ten years from seed (Skrøppa et al. 2023). In the field trials, heights

were measured at different intervals (Solvin et al. 2024). In this study, height and diameter at breast height measured in 1994 in all three half diallels, and in 2001, 2003 and 2005 in Diallels 1, 2 and 3, and of diameter in 2013 in Diallels 2 and 3, respectively, will be used in calculations. Measurements of shoot elongation were made in the field trials during two growing seasons (1980 and 1981), at dates early in the summer and at dates closer to the end of the growing season (Solvin et al. 2024.) Proxies for growth start and growth cessation were calculated as the proportion of leader shoot growth completed at the two dates. Low values indicate late shoot growth start and late growth cessation.

During the early summer of 1995 both female and male flowering occurred in the trials, and cones developed during the summer and early autumn. The age of the trials since planting was then 20, 17 and 20 years, for Diallels 1, 2 and 3, respectively. In the late autumn that year trees in the three trials were scored for the number of cones in the following classes:

- 0: no cones
- 1: 1 – 10 cones
- 2: 11 – 20 cones
- 3: 21 – 40 cones
- 4: more than 40 cones.

The flowering was most likely initiated by high temperatures during the month of July the previous year. In 1994, the mean temperature of July across the three sites was 18.7°C compared to the mean temperature of 14.4°C for the same month for the reference period 1961-1990 (MET Norway (Lussana et al. 2019)). Mean temperatures for the months of June and August were below or equal to the temperature for the reference period.

Cones were collected from 105 trees at Bjugstad and Nygård and germination tests were made of 12 seed lots. The germination percentage was 50 % for one seed lot and was above 70 % for the other lots.

Calculations

Cone scoring was done on 1274, 1181 and 1396 trees in diallels 1, 2 and 3 respectively. Chi-square tests were made for testing the homogeneity among full-sib families for precocity and fruitfulness. For each of the five scoring classes calculations were made of mean values of heights and diameters in 1994 and for the height and diameter increments in the period until the next measurement. Correlation coefficients were estimated between tree heights and cone score of individual trees and between mean height and cone score of half-sib families.

The cone score of each tree was transformed to normal scores within each block by the Blom transformation (SAS 2003). The transformed scores were analysed in a mixed model in the software ASReml-R (Butler 2009, Gilmour et al. 2006) by the following model:

$$Y_{ijkl} = \mu + GCA_i + GCA_j + SCA_{ij} + P_{ijk} + E_{ijkl}$$

Table 1

Locations of the long-term field trials and the origin of the parents, with key climatic characteristics. Climatic values are averages across the period 1961-1990. Climatic data from MET Norway (Lussana et al. 2019).

	Latitude	Longitude	Altitude	Mean annual temperature	Temperature sum degree days	Number of full-sib families
<u>Diallel 1: 10 x 10</u>						
Trial (Bjugstad)	60°47'	10°36'	370 m	2.2 °C	920	45
Origin	60°58'	10°56'	500 m	1.1 °C	740	
<u>Diallel 2: 10 x 10</u>						
Trial (Nygård)	60°47'	10°39'	240 m	2.9 °C	1070	45
Origin	60°50'	10°38'	270 m	2.5 °C	1000	
<u>Diallel 3: 9 x 9</u>						
Trial (Løten)	60°43'	11°35'	470 m	1.5 °C	850	36
Origin	60°47'	11°50'	300 m	2.0 °C	960	

where μ is the general mean, GCA_i and GCA_j are the general combining ability of parent i and j respectively, SCA_{ij} is the specific combining ability of the crossing of parent i and j , P_{ijk} and E_{ijk} are random effects of plot and residual, respectively. The random effects are assumed to be independently distributed with expectations 0 and respective variance components. Estimates of variance components and their standard errors were calculated and the narrow sense heritability, $h^2=4 \sigma_{GCA}^2 / \sigma_P^2$, where σ_{GCA}^2 is the variance of the GCA and σ_P^2 is the total phenotypic variance. BLUP estimates of the GCA effects were also calculated. Similar analyses were earlier made of the height, diameter and of the shoot elongation measurements (Solvin et al. 2024). Genetic correlations between traits were calculated in bivariate analyses of pairs of traits in ASReml-R analyses.

Results

The percentage of trees bearing cones (mean precocity) were 57.9, 65.8 and 51.5 in the three half diallels, respectively. The number of trees in each cone score class is shown in Table 2. The chi-square tests for testing the homogeneity among full-sib families of the distribution of trees with cones (precocity) and of number of trees in each cone score class (fruitfulness) showed significance in all three diallels ($p < 0.0001$). Thus, there were family differences both for the frequencies of trees having cones and for the frequencies in the different cone score classes. The ranges of variation in precocity for half-sib families were from 50 to 74 %, 54 to 78 % and 35 to 63 % in the three diallels, respectively. The estimated correlation coefficients between these percentages and the mean cone score of the half-sib families were 0.91, 0.95 and 0.97.

The mean heights of the trees scored were 630, 495 and 399 cm in the three trials, respectively. In all three trials, trees with no cones (class 0) had lower mean heights than those in the other classes, and there was an increasing mean height

with the number of cones in the class (Table 2). In general, the tallest trees in each half-sib family produced the highest number of cones. At the individual tree level, ignoring family relationships, the correlation coefficients between tree height and cone score were 0.50, 0.54 and 0.57 in the three half-diallels, respectively.

The trend in height growth with the cone classes is illustrated in Figure 1 based on mean height increments in the period before flowering. In the next increment period, this trend was not present, especially in particular in Diallel 2 and 3. Analyses of diameter increments confirm the results from the height increments (Figure 2). However, diameter measurements at ages 36 and 40 in Diallels 2 and 3 showed that the differences in diameter means among cone classes observed at the early age were kept.

At the half-sib family level, a close relationship between mean cone score and mean tree height was present in Diallel 2 (Figure 3). In both Diallel 1 and 2, the half-sib family with the lowest mean tree height had a cone class score above the mean and thus deviated from the general relationship between tree height and cones production. Similarly, in Diallel 3 two half-sib families with low height means had a high cone score. In these four families the mean tree heights were between 5 and 10 % lower than the corresponding means of the whole trial. The trees in these families had a high ability of cone production even if they were not among the dominant trees in the trial.

In the mixed model analysis of transformed cone scores, the estimates of the GCA and SCA variance components were of similar size in Diallel 1 (Table 3). In the two other diallels the GCA variance component estimates had twice the values of the SCA component, indicating predominantly additive genetic inheritance of cone production. The estimates of heritability were 0.10, 0.14 and 0.20 in the three half diallels.

Table 2
Number of trees in each cone score class (N) and mean heights 1994 of the trees in each class.

Cone class	Diallel 1		Diallel 2		Diallel 3	
	N	Height cm	N	Height cm	N	Height cm
0	536	549	404	402	678	325
1	291	637	396	506	455	441
2	141	686	153	552	202	506
3	278	737	216	601	60	551
4	28	786	12	658	1	
Total	1274	630	1181	495	1396	399

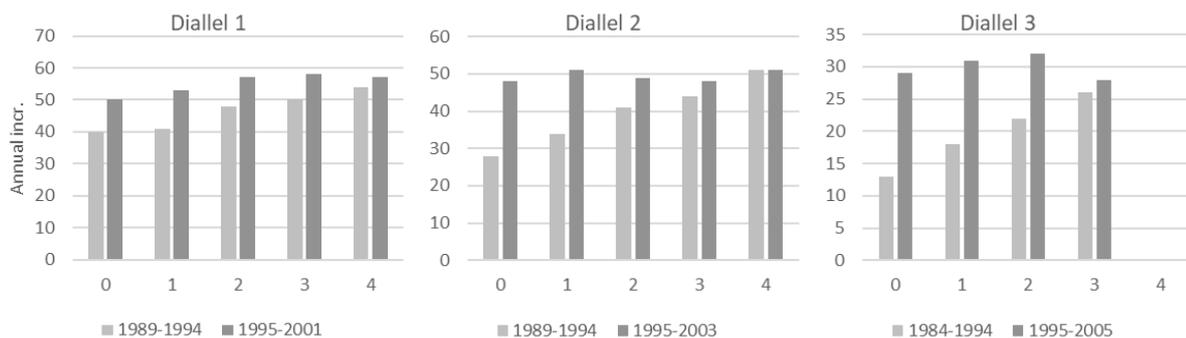


Figure 1
Mean annual height increment (cm) in each cone class in the periods between measurements for Diallels 1, 2 and 3.

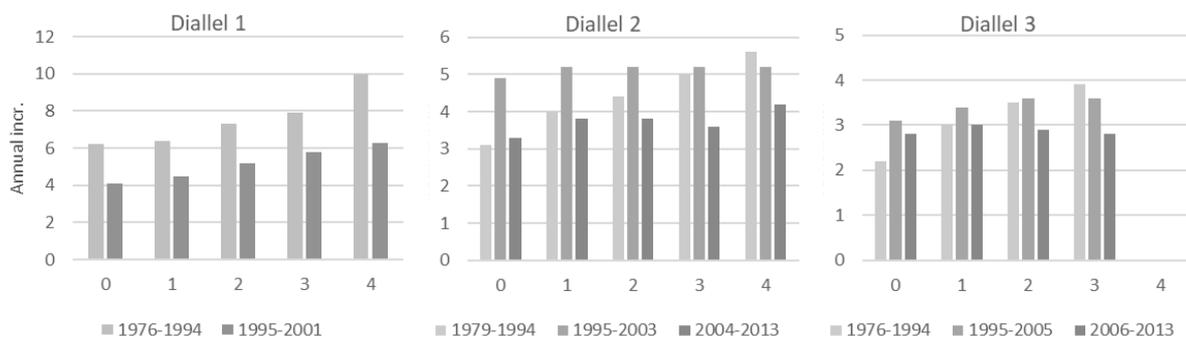


Figure 2
Mean annual diameter increment (mm) in the periods between measurements for Diallels 1, 2 and 3.

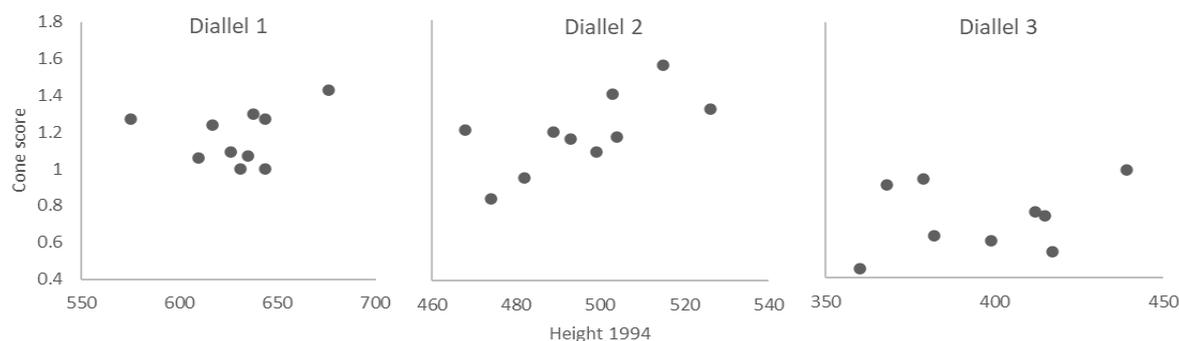


Figure 3

Plot of mean cone score against mean tree height 1994 of parental half-sib family means in each of the three half diallels. The estimated correlation coefficients in these plots are 0.21, 0.65 and 0.26, respectively.

Genetic correlations were estimated in bivariate analyses of pairs of traits between transformed cone score values and height 1994 with values 0.40, 0.50 and 0.35 in the three diallels, respectively (Table 4). The estimated genetic correlations between cone scores and the phenology traits characterizing start and cessation of shoot growth had low and not significant values.

Table 3

Estimates of variance components and narrow sense heritabilities for the transformed cone scores, with standard error of estimates in parentheses.

	Diallel 1	Diallel 2	Diallel 3
GCA	0.020 (0.013)	0.031 (0.018)	0.040 (0.023)
SCA	0.021 (0.013)	0.014 (0.014)	0.019 (0.012)
Plot	0.046 (0.022)	0.120 (0.027)	0.118 (0.023)
Error	0.708	0.667	0.571
h^2	0.10 (0.06)	0.14 (0.08)	0.20 (0.11)

Table 4

Estimated genetic correlations between transformed cone scores, height 1994 and growth start (start) and cessation (end), with standard error of estimates in parentheses.

Trait	Diallel 1	Diallel 2	Diallel 3
H94	0.42 (0.34)	0.51 (0.31)	0.39 (0.34)
Start	-0.12 (0.41)	-0.18 (0.37)	-0.02 (0.40)
End	-0.04 (0.42)	-0.37 (0.62)	0.31 (0.44)

A selection of the three tallest families in Diallel 2 showed an increase in the percentage of tree that set cones from 65.8 to 70.6 % and in mean cone score from 1.19 to 1.35. In the two other diallels selection for tree height resulted in small responses in the cone production traits. Similarly, a selection for early

and abundant cone production resulted in a positive correlated response only in Diallel 2.

Discussion

This study provides information about precocity and fruitfulness at a young age of Norway spruce families originating from three diallel crosses, each made within a natural population. In addition, estimates of genetic parameters characterizing inheritance patterns of cone production are presented. An important factor is the relationship between tree height and diameter and the number of cones produced.

More than 50 % of the trees in these trials produced cones at this early age, but with a quite large variation among half-sib families in each diallel. This indicates genetic control over precocious flowering which could be due to family differences in the length of the juvenile period. However, it could also be related to genetic differences in tree growth as both the tallest families and the tallest individuals in each family produced cones. The tallest trees have the greatest exposure to sunshine and temperatures during the part of the growth season when female flowering is induced. The tall trees may also be more exposed to draught stress during this period, normally in late June and early July in the boreal forest.

The two traits precocity and fruitfulness seem to be strongly related at this age, as they were strongly correlated for half-sib families in all three half diallels. Families with a high percentage of trees with cones therefore had a high mean cone score. The same was found at a very early age in loblolly pine (Schmidtling 1981).

Additive genetic variation was found for the cone score (fruitfulness) in two of the diallels with GCA variance components more than twice the size of the SCA components. In Diallel 1, these two variance components were of similar size and the estimate of heritability had the lowest values. These families had the largest transfer in climatic conditions from the origin of the parents to the progeny test site where cone

production occurred. Such changes in environmental conditions most likely influenced the flowering ability of the trees (Chalupka and Cecich (1997). The estimates of heritability found here are lower than those found for loblolly pine by Schmidting (1981) who estimated high GCA variance components and additive inheritance for both flowering traits.

Positive genetic correlations were estimated between cone scores and height, but with quite high standard errors. Most families with a high cone score were among those with the highest height means. However, in all three progeny tests there were families with low mean height that had a high mean cone score. This indicates genetic control of female flowering in addition to those related to tree heights. Discussing the relationship between flowering and growth traits, Chalupka and Giertych (1975) state that poorly growing trees with defects may flower abundantly since most metabolic effects are directed into flowering. This cannot be the reason for the performance of these families as all trees scored had normal tree growth without any specific defects.

The inheritance patterns of cone production differed from those found for tree height and diameter in the same trials (Solvin et al 2024). For height, Diallel 2 had the highest value of the SCA variance component and with low heritability estimates. In two other diallels these estimates were of similar size as those found here for cone production.

The relationship between cone production and tree size have been studied in natural populations and in few provenance and progeny tests. Positive relationships have been found in natural stands between the size of the cone crop and tree height and diameter for Norway spruce (Chalupka and Cecich 1997), silver fir (Davy et al 2016) and white spruce (Bronson 2020). In a provenance trial with Maritime pine negative relationships were found between mean cone production and height due to differences in provenance transfer (Santos-del-Blanco et al 2012). Negative relationships between flowering traits and tree heights of families were found in very young trials with families of loblolly pine (Schmidting 1981) and eucalyptus (Chambers et al 1997). In our trials, the opposite relationship was found, but with some families deviating from the positive relationship between cone score and tree height (Figure 3).

Assessments made in a 20-year-old provenance trial with Norway spruce demonstrated provenance variation in cone production and showed that trees with an early bud flush produced the highest number of cones (Öhrn 2023). This may depend on relationships between the timing of shoot growth development and the temperature conditions the previous summer when female flowers were induced. In our trials there were no relationships between the timing of shoot growth and cone production.

Flowering and cone production demand resources that could be invested in vegetative growth. Different results have been published whether abundant cone production results in reduced (Holmsgaard and Bang 1990, Hacket-Pain et al. 2019) or in no change in biomass production (Seiffert and Müller-Starck 2009, Avanzi et al. 2019). The most likely effect could take place the first couple of years after flowering. Such

information is not available from our trials. Height and diameter growth are available for the next period which lasts for six to eight years. Reduced growth in this period was found for the class of trees which did not produce cones compared with the tree in the other cone classes. The trees that produced abundant numbers of cones at the early age were still the tallest at ages 28, 26 and 32 years, respectively, and had also the largest diameters and were the dominant trees in the stands at ages 36 and 40 years in Diallel 2 and 3. They will also most likely produce the largest number of cones in later years with abundant cone production. At this age, and most likely at later ages, the natural reproduction in a stand will thus be in favour of families with superior height growth and the tallest trees within these families. However, our results are obtained in plantations at a very young age, and it has not yet been shown that precocious flowering is correlated with prolific flowering (Chalupka and Cecich 1997).

In tree breeding, strategies and breeding plans must be based on knowledge of genetic variability and genetic correlations. The positive genetic correlations between height growth and early flowering observed indicates that selection for growth might have positive effect on reproductivity and fitness. No adverse effects of selection for growth rhythm traits, often important for adaptation, seems profound.

In operational breeding, materials for the second and advanced generations are selected from progeny trials and grafted into breeding arboretums and seed orchards as early as 10-15 years after seed (Jansson, Li and Hannrup 2003). In Norway spruce breeding arboretums, the first attempts to promote flowering by heat and hormonal treatments (Johnsen et al. 1994) are often made 5 – 10 years later, at a total age of 20 - 25 years, to facilitate controlled crossings for new progeny trials. In seed orchards, flowering is expected to occur more according to the natural sexual maturation of the trees. In both situations, individuals prone to reproduce earlier will start contributing to the breeding population earlier. In the breeding arboretums, containing the selections that comprise the breeding population, variable age of first flowering potentially causes unbalance of the genetic representation in subsequent generations. Particularly trees with late sexual maturity might be difficult to include and genetic diversity might be unintentionally lost. A solution might be to increase the size of the breeding populations to allow some decay of the latest flowering individuals in each generation.

Acknowledgements

The diallel crosses were financed by the former Agricultural Research Council of Norway. Statistical analyses and the writing of the manuscript were done as part of the project OptFOREST (Horizon-CL6-2022_BIODIV-01).

References

- Andersson E (1965) Cone and seed studies in Norway spruce (*Picea abies* (L.) Karst.). *Studia Forestalia Suecica* 23. 214 p.
- Avanzi C, K Heer K, Büntgen U, Labriola M, Leonardi S, Opgenoorth L, Piermattei A, Urbinati C, Vendramin GG, Piotti A (2020) Individual reproductive success in Norway spruce natural populations depends on growth rate, age and sensitivity to temperature. *Heredity* 124:685-698. <https://doi.org/10.1038/s41437-020-0305-0>.
- Butler D (2009) ASReml Analysing data with new ASReml-R3; www.vsnl.co.uk.
- Chalupka W (1972) Cone production in 1971 and the age of trees and stands of Norway spruce. *Sylvan* 116:73-77. (In Polish with English summary).
- Chalupka, W, Giertych, M (1975) The effect of growth on cone crops in Norway spruce (L.) Karst.). *Arboretum Kornickie* 20: 201-212.
- Chalupka W, Cecich RA (1997) Control of the first flowering in forest trees. *Scand. J. For. Res.* 12: 102-111. <https://doi.org/10.1080/02827589709355390>
- Chambers PGS, Potts BM, Tilyard PA (1997) The genetic control of flowering precocity in *Eucalyptus globulus* ssp. *globulus*. *Silvae Genetica* 46: 207-214.
- Davi, H, Cailleret M, Restoux G, Amm A, Pichot C, Fady B 2016 Disentangling the factors driving tree reproduction. *Ecosphere* 7(9):e01389. <https://doi.org/10.1002/ecs2.1389>.
- Eriksson G, Jonsson A, Lindgren D (1973) Flowering in a clone trial of *Picea abies* Karst. *Studia Forestalia Suecica* 111. 45 p.
- Hacket-Pain A, Ascoli D, Berretti R, Mencucci M, Motta R, Nola P, Piusi P, Ruffinao F, Vacchiano G (2019) Temperature and masting control Norway spruce growth, but with high individual tree variability. *Forest Ecology and Management* 438:142-140. <https://doi.org/10.1016/j.foreco.2019.02.014>
- Holmsgaard E, Bang C (1990) Loss of volume increment due to cone production in Norway spruce. *Det forstlige forsøksvesen in Danmark* 42: 216-231.
- Jansson G, Li BL and Hannrup B (2003) Time trends in genetic parameters for height and optimal age for parental selection in Scots pine. *For. Sci.* 49 (5): 696-705. <https://doi.org/10.1093/forestscience/49.5.696>
- Johnsen O, Haug G, Dæhlen OG, Grønstad BS and Rognstad AT (1994) Effects of Heat-Treatment, Timing of Heat-Treatment, and Gibberellin a(4/7) on Flowering in Potted *Picea-Abies* Grafts. *Scand. J. For. Res.* 9 (4): 333-340. <https://doi.org/10.1080/02827589409382849>
- Lindgren K, Ekberg, I, Eriksson, G (1977) External factors influencing female flowering in *Picea abies*. *Studia Forestalia Suecica* 142.
- Nikkanen T, Ruotsalainen S (2000) Variation in flowering abundance and its impact on the genetic diversity of the seed crop in a Norway spruce seed orchard. *Silva Fennica* 34:205-222. <https://doi.org/10.14214/sf.626>
- Öhrn P (2023) Granens herkomst viktig för blomningens omfattning. *Kunskapsbanken* nr. 42-2023. Skogforsk. (In Swedish). <https://www.skogforsk.se/kunskap/kunskapsbanken/2023/>
- Owens JN, Blake MD (1985) Forest tree seed production. *Petawawa Natl. Forestry Inst. Info. Rep. PIX-53.* 161 p.
- Santos-del-Blanco L, Client J, Gonzales-Martinez, SC, Pannel JR (2012) Genetic differentiation for size at first reproduction through male versus female functions in the widespread Mediterranean tree *Pinus pinaster*. *Annals of Botany* 110:1449-1460. <https://doi.org/10.1093/aob/mcs210>
- Sarvas R (1968) Investigations on the flowering and seed crop of *Picea abies*. *Com Inst For Fenn* 67.5. 84 p.
- Schmidting RC (1981) The inheritance of precocity and its relationship with growth in Loblolly pines. *Silvae Genetica* 30:188-192.
- Seifert T, Müller-Starck G (2009) Impacts of fructification on biomass production and correlated genetic effects in Norway spruce (L.) Karst.). *Eur. J. For. Res.* 128:155-169. <https://doi.org/10.1007/s10342-008-0219-5>
- Skrøppa T, Tutturen R (1985) Flowering in Norway spruce seed orchards. *Silvae Genetica* 34:90-95.
- Skrøppa T, Tho T (1990) Diallel Crosses in *Picea abies* I. Variation in seed yield and seed weight. *Scandinavian Journal of Forest Research* 5:355-367. <https://doi.org/10.1080/02827589009382619>
- Skrøppa T, Solvin TM, Steffenrem A (2023) Diallel crosses in *Picea abies* IV. Genetic variation and inheritance patterns in short-term trials. *Silvae Genetica* 72: 58-71. <https://doi.org/10.2478/sg-2023-0006>
- Solvin TM, Skrøppa T, Steffenrem A (2024) Diallel crosses in *Picea abies* V. Can early testing predict long-term performance. *Silvae Genetica* 73: 48-59. <https://doi.org/10.2478/sg-2024-0005>
- Wareing, PF (1959) Problems of juvenility and flowering in trees. *J. Linn. Soc. London, Bot.* 56 (366):282-289.