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Sexual asymmetry in Scots pine seed orchards

Abstract: In seed orchards of Scots pine *Pinus sylvestris* L., the reproductive process is affected by the variation among the clones in fertility and abundance of male and female flowering. There were significant differences between the clones in relative proportion of male and female strobili as well as in seed yield. Thus, clones in Scots pine seed orchards may differentiate into "seed" and "pollen" clones. The least fertile clone produce 4.6 times less pollen than the most fertile clone, while cone yield of the least yielding clones was 5.5 times smaller than that of the most yielding clones.
Amount of the pollen dispersed at the upper part of the crowns was two times greater than at the base of the crowns. The minimum amount of pollen needed for successful fertilization of an ovule was 1500 grains per cm^2. There was no significant relationship between sexual asymmetry of the parental clones and height growth of their progeny.

Additional key words: reproductive process, sexual asymmetry, strobili, pollen, seeds

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Introduction

Flowering process in seed orchards affects the genetic composition of the seed crops (e.g. Eriksson et al. 1973, Matzgiris 1994, Burczyk and Chalupka 1997). The reproductive process in seed orchards is, in turn, affected by abundance of male and female flowering and fertility variation, which are dependent on the interaction between genetic, physiological and environmental factors (El Kassaby and Askew 1991). In a population of monoecious species, such as pine, sexual asymmetry, i.e. unequal proportion of male and female flowers may occur. In seed orchards, sexual asymmetry causes a deviation from the random mating which may (1) reduce genetic variation in the crop of a well-isolated orchard or (2) reduce the gain from seed orchard crop due to increased self-fertilization or background pollination in a less isolated seed orchard (Gregorius 1981; Ziehe 1982; Muller-Stark and Ziehe 1984; Adams and Kunze 1996; Kang and Lindgren 1998; Shoen and Stewart 1987). Therefore, studies on reproductive processes in forest tree populations may contribute to sustainability of the future forests. If sexually asymmetry is an inherited property in Scots pine, it would be possible to control the number of female-type and male-type clones in seed orchards (Efimov et al. 1982; Kang 2000).

A number of studies attempted to describe the possible types of sexual dominance in pine (Pravdin 1950; Wareing 1958; Nekrasova 1960; Efimov 1982; Burczuk and Chalupka 1997). Wareing (1958) defined the following types of sexual dominance in pine trees: (1) male strobili prevail, (2) female strobili prevail, (3) with female and male strobili on separate branches and (4) with female and male strobili on the same branch. If open pollination is assumed, the reproductive process in a population of trees may be controlled through the female parents only. In seed orchards, the relative proportion of male or female flowers may be affected by environment, root stock, age and spacing between the clones, which may bias the identification of the sexual type of a clone (Chaisurisri and El Kassaby 1993; Adams and Kunze 1996). To obtain a desirable pattern of pollination,

the orchard shall be designed to maximise the probability that the clones of the "female" type will be pollinated by the orchard clones of the "male" type, rather than by background pollen. Studies on patterns of pollen dispersal in seed orchards may facilitate the development of seed orchard designs, which minimise the impact of background pollen.

Objectives of this study on flowering of Scots pine clones were to assess (1) broad-sense heritability for production of strobili and variation in sexual type among clones in a seed orchard over 10 year period, (2) amount of pollen received at certain crown height and yield of filled seeds per female cone depending on the daily amount of pollen received in a seed orchard, (3) reproductive capacity of clones (number of strobili and pollen yield) in a clonal archive.

Material and methods

Flowering of Scots pine clones of Lithuanian origin was studied in clonal seed orchard (age 21 to 30) and clonal archive (age 18 to 20) established close to each other in Slenava forest district in Lithuania (54°50', 23°55', 60 m a.s.l).

Seed orchard study 1. Objectives were to assess (1) broad-sense heritability for production of strobili and (2) variation in production of male and female strobili among the clones over 10 year period. Number of male and female flowers was scored annually on 15 ramets from each of 18 clones according to the 5 score scale of Korchagin (1960) (score 0 – no flowers, score 5 – abundant flowering) since age 21 to 30. Sexual type of the clones was expressed as ratio of mean score for male strobili over mean score of female strobili. The estimates of individual and clonal mean broad-sense heritability for production of male and female strobili were calculated for each year by using mean ramet number of male or female strobili as the unit of observation:

$H^2_{individual} = {}^2_c/({}^2_c + {}^2_e)$

$H^2_{clone\ mean} = {}^2_c/({}^2_c + {}^2_e/n)$, where

^2_c – is variance between clones, estimated as sum of squared deviations of clonal means from the total mean divided by degrees of freedom for clones;

^2_e – is variance within clones, estimated by subtracting the variance between clones from the total phenotypic variance (calculated as sum of squared deviations of each individual observation from the total mean and divided by the total degrees of freedom);

n – is harmonic mean of number of ramets per clone.

Seed orchard study 2. Objective was to assess the amount of pollen received at certain crown height and yield of filled seeds per female cone depending on the daily amount of pollen received during a 14-day-period in May 1984. 5 ramets from each of 3 randomly selected clones at age 21 were used. In early spring, male strobili were removed and pollen traps of type Hoekstra (1965) were attached on 14 terminal shoots of whorl branches at each of 5 whorls of each ramet (on each fourth whorl from the ground). The annual shoots were isolated with paper bags. Daily amount of pollen received per trap on a given height was estimated by removing the bags from one shoot at each of 5 whorls on each ramet in the morning and leaving the traps open until evening, followed by removal of the traps and counting of pollen in the evening. This procedure was repeated daily during a 14 day period starting on 18th of May. After maturation, the cones on the terminal shoots studied were collected and seed properties were assessed separately for each original terminal shoot.

Clonal archive study. Objective was to assess reproductive capacity of the clones (number of strobili and pollen yield). During a 3 year period since 1988, number of male and female flowers was assessed annually on 5 ramets from each of 3 randomly selected clones by counting male and female strobili on one whorl branch of average thickness on every whorl in each ramet. Prior to opening of the strobili, the branches, on which the strobili were counted, were removed to estimate pollen weight indoors. Number of main order branches were counted on each ramet to estimate mean ramet number of strobili and weight of pollen by multiplying number of strobili and pollen weight on the "sample" branches from the total number of branches on a ramet. This procedure was repeated in each of 3 years.

Results and discussion

Seed orchard study 1. There were pronounced differences between the clones in relative proportion of male and female strobili as well as in total strobili production for all years examined. 3 of 15 clones produced significantly higher proportion of male strobili every year (male-type clones) and 2 of 15 clones produced significantly higher proportion of female strobili every year (female-type clones) (Fig. 1). On the remaining 10 clones, the relative proportion of male or female strobili varied between years, most probably, in response to the variation in climatic conditions. Broad sense heritability for abundance of male strobili and female strobili are given in Table 1. The coeffients indicate that the orchard population is not panmictic which will influence genetic composition and estimates of gain from the orchard crops (Griffin 1982). Presence of male or female type clones may reduce gene diversity in orchard crops and increase the rates of self-fertilization. 1985, 1988, 1990 may be considered as the years with increased male flowering. 1986, 1987 and partially 1989- as the years with increased female flowering.

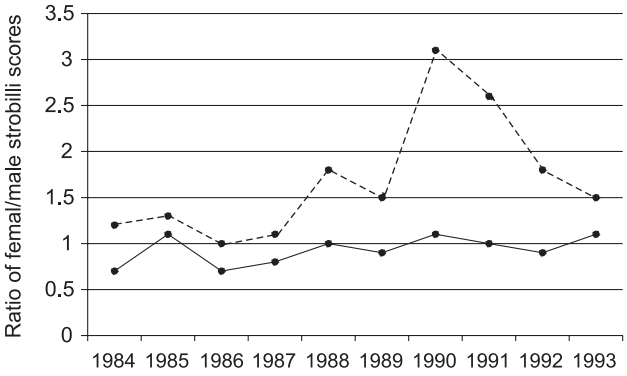

Fig. 1. Variation in ratio of the scores for male over female strobili averaged over 3 clones of female-type (solid line) and averaged over 2 clones of male type (dashed line) during 10 year period (age 21–30) in Slenava seed orchard (low ratio means prevalence of male strobili)

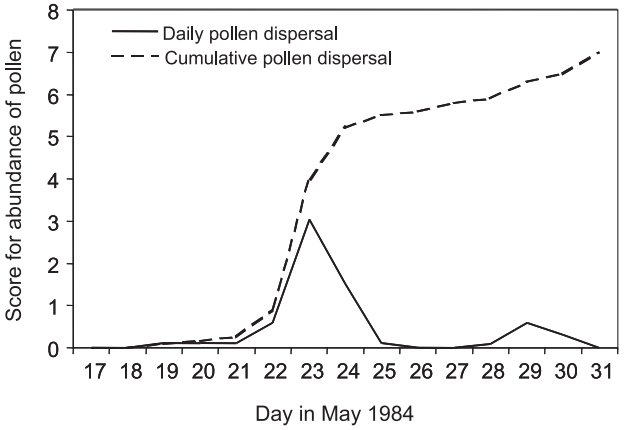

Fig. 2. Pattern of Scots pine pollen dispersal assessed in Slenava seed orchard during May 1984

Table 1. Individual and clonal mean broad-sense heritability coefficients for flowering traits estimated during 10 year period (age 21 to 30) in Slenava seed orchard. Mean heritability is mean of heritability coefficients estimated in each of 10 years. Minimum and maximum heritability are the lowest and highest coefficients during 10 years

Trait	Individual tree H^2			Clonal mean H^2		
	Mean	Minimum	Maximum	Mean	Minimum	Maximum
No. of female strobili	0.20	0.03	0.40	0.63	0.21	0.85
No. of male strobili	0.16	0.06	0.27	0.59	0.38	0.76
Total number of strobili	0.18	0.04	0.31	0.58	0.23	0.80
Ratio male/female	0.08	–0.002	0.19	0.34	–0.02	0.67

Seed orchard study 2. Abundance of pollen had a marked effect on development of sound seeds. The period of abundant pollen dispersal lasted for three days (Fig. 2). Patterns of pollen dispersal in an orchard are important not only for successful fertilisation but also for dispersal of genes, i.e. maintenance of gene diversity. Study on vertical patterns of pollen dispersal over time showed that amount of pollen at the top of the crowns was for 50% greater than at the base of the crowns. Thus, gene diversity in the pollen available at the top of the crowns may be greater than at the base of the crowns. Study on the amount of pollen landing at female strobili over time revealed strong relationship between the number of filled seeds per cone and the amount of pollen available per strobili (r=0.92) (Fig. 3). The highest number of filled seeds was found in the cones which obtained more than 2000 pollen grains per cm^2. After amount of pollen which landed at female strobili dropped below 1500 grains per 1 cm^2, the number of filled seeds per cone has markedly decreased.

If the number of male strobili per tree and amount of pollen per strobili are known, it is possible to estimate the amount of pollen produced per 1 ha and pollen density in the air. According to our calculations, to reach pollen density of 1500 grains per cm^2, 200 thous. of male strobili per ha are needed. Though ac-

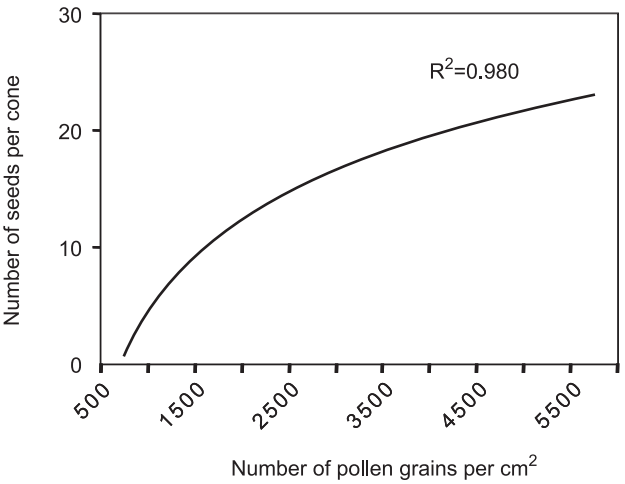

Fig. 3. Relationship between number of filled seeds per cone with number of pollen grain in the air in Slenava Scots pine clonal archive

cording to Abaturova (1988) this number can be less. Under the local environment, a grafted clone of Scots pine of age 21 is capable to produce 4.5 thous. of male strobili or 386 g of pollen grains. Therefore, a seed orchard should contain not less than 30–35 trees of male sexual type as the pollinators per ha or 50 trees-pollinators of neutral sexual type per ha. The variation coefficient for pollen dispersal over the hori-

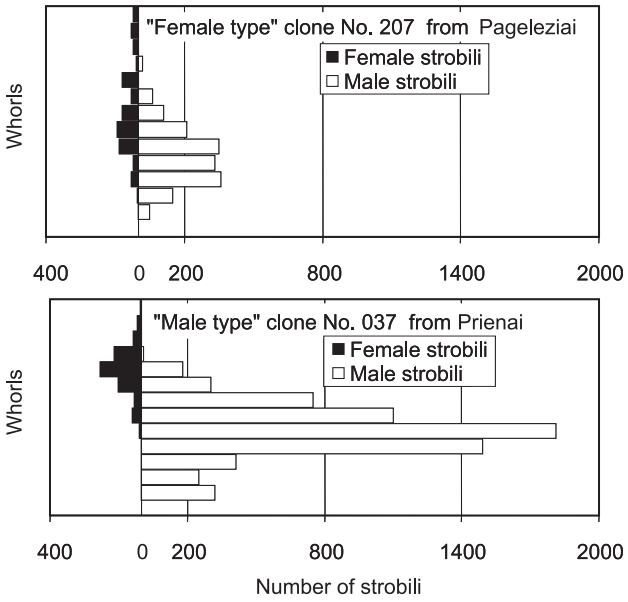

Fig. 4. Difference in proportion of male and female strobili between a Scots pine clone of "female type" (the upper plot) and a Scots pine clone of "male type" (the lower plot). The measurements were made in Slenava clonal archive

zontal direction was 127% (72–212%) and over vertical direction – 145%. Amount of pollen at the base of the crowns was for 18% lower than at the middle section of the crowns and for 50% lower than at the top of the crowns.

Clonal archive study. On the average over 3 years, clone No. 037 produced 3.4 times more male and 2.6 times more female strobili than clone No. 207 (Table 2). Pollen of clones of similar reproductive capacity as of clone No. 037 may dominate in the seed orchard.

Abundance of male flowering was strongly positively correlated with mean air temperature in the third decade of June and the first decade of July in the previous year (r=0.92 and r=0.95, respectively). Abundance of female flowering was strongly positively correlated with mean air temperature in the second and the third decade of July in the previous year (r=0.93 and r=0.97, respectively) (Table 3). Probably, a lower temperature in June caused reduction of male flowering and a lower temperature in July caused reduction in female flowering. Less favorable climatic conditions lead to a more pronounced expression of sexual asymmetry. The female flowers were receptive during a 3-day-period and there were up to 5 day difference between the clones from different populations in timing of the receptive phase.

Study on relative distribution of male and female strobili within the crown of a clone showed that female strobili were set on young shoots, while male strobili were set on older shoots. Therefore, 75% of female strobili were found on the upper part of the crown and 75% of male strobili were found on the lower part of the crown (Fig. 2). Number of strobili on the southern side of the crown was for 3–4% higher than on the northern part of the crown. Most of male and female strobili were set in the middle-part of the crown, where the most intensive exchange of nutrients and energy occurs. In Scots pine,

Table 2. Abundance of flowering and pollen production of three Scots pine clones of Lithuanian origin in Slenava clonal archive

Year	Average No. of strobili per tree				Amount of pollen (g) from 100 strobili	Amount of pollen per tree, g	Weight ratio of pollen/ number of macrostrobili	Amount of pollen (kg/ha 200 trees/ha)
	male	female	male+ female	male/female				
Clone No. 204								
1987	3793	1351	5144	2.81	6.12	232	0.172	46.4
1988	4687	794	5491	5.90	6.72	315	0.397	63.0
1989	5463	862	6325	6.46	8.38	465	0.539	91.6
1990	5824	665	6489	8.75	8.40	489	0.735	97.8
Mean	4942	918	5860	5.38	7.40	375	0.461	84.1
Clone No. 207								
1988	1708	524	2232	3.26	5.42	93	0.177	18.5
1989	2306	494	2800	4.66	7.88	182	0.368	36.3
1990	1845	150	1995	12.30	7.90	146	0.973	28.0
Mean	1953	389	2342	5.02	7.07	140	0.506	27.4
Clone No. 037								
1988	6645	716	7361	9.28	9.54	634	0.885	126.8
1989	6531	1908	8439	3.42	9.91	647	0.339	129.4
1990	6653	429	4082	15.50	9.70	645	1.504	129.1
Mean	6610	1018	7628	6.49	9.72	642	0.909	128.5

Table 3. Pearson correlation coefficients between the number of strobili on three Scots pine clones in Slenava clonal archive and air temperature during the previous growth period averaged over 1988 to 1990

Mean air temerature over 10-day period (decade) for	Sex of strobilli	Correlation coefficient			Mean for all 3 clones
		Clone 204	Cone 207	Clone 037	
June, 1st decade	male	0.51	0.16	0.55	0.42
	female	–0.89	0.99	0.65	–0.27
June, 2nd decade	male	–0.91	0.09	–0.36	–0.78
	female	0.96	0.09	–0.36	0.75
June, 3rd decade	male	0.96	0.99	0.47	0.92
	female	–0.26	–0.66	0.21	–0.28
July, 1st decade	male	–0.99	–0.60	0.35	0.95
	female	–0.82	–0.63	0.25	0.61
July, 2nd decade	male	–0.54	0.99	0.98	–0.30
	female	0.85	0.32	0.96	0.93
July, 3rd decade	male	0.90	0.89	0.73	0.97
	female	–0.66	0.14	0.64	–0.26
June 3rd and July 1st decade	male	0.98	0. 59	0.34	0.99
	female	–0.67	–0.65	0.22	–0.53
July 2nd and July 3rd	male	–0.07	0.99	0.93	0.22
	female	0.48	0.45	0.88	0.77

removal of the three upper-most whorls would not result to a marked decrease in the seed yield.

In seed orchards, seeds and pollen of the clones with a high reproductive capacity may prevail. In case of the orchard studied, the several male-type clones produced 4.6 times more pollen than female-type clones. Consequently, most of the pollen in this orchard may originate from several clones only. The clones were markedly different not only in the number of male strobili but also in amount of pollen produced. Correlation coefficient between the number of male strobili and the amount of pollen produced was 0.84.

Conclusions

1. There are significant differences between the clones of Scots pine in sexual asymmetry, which may influence the genotypic constitution of the future generations.
2. The degree of sexual asymmetry may be affected by climatic conditions, thus, to increase gene diversity in seed orchard seeds used for reforestation, a mixture of seeds harvested over a number of years should be used. Sexual asymmetry is expressed to a higher degree during the years of weak seed yield.
3. When establishing seed orchards, sexual asymmetry of the clones or relative proportion of female-type and male-type clones shall be considered and heritability of sexual asymmetry shall be tested.
4. When establishing a hybrid seed orchard designed to utilise specific combining ability of the parents, sexual asymmetry may be used as a criterion to select for pollen-clones and seed-clones.

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