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Mating System Variation in a Scots Pine Clonal Seed Orchard

By J. BURCZYK¹⁾

Pedagogical University, Department of Biology and Environment Protection, ul. Chodkiewicza 30, 85-064 Bydgoszcz 1, Poland

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Summary

The mating system was investigated in a Scots pine (*Pinus sylvestris* L.) seed orchard consisting of 32 clones, using 10 isozyme loci as genetic markers. The multilocus outcrossing rate calculated for the data pooled over three years of observations was estimated to be 0.987 (0.005). The population multilocus estimates of three consecutive years exhibited a decreasing trend (0.976, 0.966 and 0.962 for the years 1988 to 1990, respectively), but this variation was not significant. Individual outcrossing rates were homogeneous across years for most sampled ramets. Individual tree estimates were heterogeneous across sampled ramets for the pooled data in the years 1988 and 1990 but not for 1989. Individual outcrossing rates were not significantly related to individual pollen production. Although no significant variation of outcrossing rates in time could be detected, estimates of variance effective population size in the three years suggest temporal variation in outcross mating patterns.

Key words: *Pinus sylvestris*, mating system, outcrossing, inbreeding, flowering, seed orchard.

FDC: 165.3; 165.41; 181.521; 232.311.3; 174.7 *Pinus sylvestris*.

Introduction

Mating systems in conifers were generally found to be variable (MITTON, 1992). Estimates of outcrossing rate vary among species, among populations within species, among

individuals within populations, among different parts of the crown within individuals and among loci (see for reviews: ADAMS and BIRKES, 1991; MUONA, 1990; MITTON, 1992). These variations are due to both genetical and ecological influences, such as stand density and age and the availability of local or foreign pollen (FARRIS and MITTON, 1984; KNOWLES et al., 1987; BURCZYK et al., 1991).

Temporal variation of outcrossing rate resulting either from different pollination patterns or from the time elapsed since fertilization, despite its great practical and theoretical importance, arrested only limited attention in mating system studies (MITTON, 1992). While PERRY and DANCİK (1986) did not find significant variation, several authors found an increase in outcrossing rates with the time elapsed since fertilization (CHELIAK et al., 1985; SNYDER et al., 1985; HAMRICK, 1989). They suggested that selection acting against inbred progeny during the retention of seed in serotinous cones could be responsible for the observed increase, but this has never been proven.

Outcrossing rates estimated at the population level were found to be high in conifers, but individual tree estimates may vary widely from 0.5 to 1.0 (SHAW and ALLARD, 1982; EL-KASSABY et al., 1987; ERICKSON and ADAMS, 1990; BURCZYK et al., 1991). In Scots pine (*Pinus sylvestris* L.), the most important conifer species in Central and Northern Europe, the range of estimates seems to be narrower (KOSKI and MUONA, 1986; BURCZYK, 1991; KÄRKÄINEN and SAVOLAINEN, 1993). Although selfing was generally found to be low, inbreeding depression is still considered an important factor in many genetic programs. It is still unclear, if there are any specific situations when selfing could

¹⁾ phone: (52) 340-07-44 (office), (52) 363-35-72 (home); fax: (52) 340-07-34, (52) 341-35-33; e-mail: burczyk@wsp.bydgoszcz.pl

be considerable. The objective of this paper is to study the extent of temporal variation in the mating system of a Scots pine clonal seed orchard both at the population and at the individual levels.

Materials and Methods

The Gniewkowo clonal seed orchard was established in 1972 and consists of 32 clones derived from selected Scots pine plus trees growing in the Tuchola Forests in Poland. The orchard is 3.30 ha in size and is surrounded by farmlands the nearest Scots pine stands being located about 1.0 km away. The orchard consists of three blocks, each containing all 32 clones, but with different numbers of ramets per clone. During investigations there were still 1056 ramets growing in the orchard (BURCZYK, 1990). It was intended to collect cones from the same single ramet of each clone in the middle block during autumn in three consecutive years 1988, 1989 and 1990. Later analysis revealed that the clonal identity of five of the sampled ramets had been mislabeled. Therefore, only 27 clones were sampled but a few clones were represented by multiple ramets (see Table 2). Twenty seeds per ramet per year (embryo and megagametophyte tissues) were assayed electrophoretically in 1991, using methods similar to those presented by CONKLE et al. (1982). Ten unlinked isozyme loci (*Gdh*, *Got-1*, *Got-2*, *Got-3*, *Fest*, *Mdh-3*, *Mdh-4*, *6Pgd-1*, *6Pgd-2* and *Skdh-1*) were scored (NIEBLING et al., 1987; SZMIDT and MUONA, 1989). Allele frequencies in the parental population were calculated from the known genotypes of the 32 clones (BURCZYK, 1992).

Expected heterozygosities and WRIGHT's fixation index *F* were calculated according to NEI (1975) in both the parental and offspring populations. Departure from HARDY-WEINBERG equilibrium was investigated by a standard G-test and genetic similarity of allele frequencies between the parental and the offspring generations were studied using a G-test for heterogeneity (SOKAL and ROHLF, 1981). The population and individual outcrossing rates were estimated using the maximum-likelihood procedures of RITLAND and EL-KASSABY (1985) (MLTF computer program), which is based on a mixed-mating model and was developed for conifers. Heterogeneity of outcrossing rates was investigated by FISHER's heterogeneity χ^2_{HET} test (RAO, 1973). The variance effective population size attributed to paternal contribution was estimated based on allele frequencies estimated in the mature generation (entire orchard) and in the pollen pool of effectively fertilized viable embryos (BURCZYK, 1996).

Results

The mean number of alleles per locus was 2.8 and 3.7 for parental and progeny populations, respectively. The parameters of genetic structure of progeny populations were generally homogeneous across the three studied years. While the expected heterozygosity for the parental population was estimated to be 0.400, the estimates for offspring populations were slightly lower and rather constant in the three consecutive years (0.393, 0.390 and 0.395 for 1988, 1989 and 1990 respectively). WRIGHT's *F* index showed, that the parental population exhibited an excess of heterozygotes (*F* = -0.116), but a slight deficiency of heterozygotes was observed in all offspring populations (+0.016, +0.029, +0.024). However, departure from the Hardy-Weinberg equilibrium for data pooled over years was significant only in the offspring populations at four loci: *Got-3*, *Mdh-3*, *Mdh-4* and *6pg-1*, mainly due to the effect of the year 1990. Allele frequencies were significantly different between parents and offspring for loci *Mdh-4* and *6Pgd-2* in all 3 years, while for *6Pgd-1* only in 1989.

Population outcrossing rates were generally high, but several estimates appeared significantly different from 1 (Table 1). Single-locus estimates were heterogeneous across loci for 1990 and for pooled data. This was mainly due to the *6Pgd-2* locus, which was the only locus for which the outcrossing rate was heterogeneous across the three years. The minimum variance

Table 1. – Single-locus (t_s) and multilocus (t_m) estimates of outcrossing rates for 3 consecutive years of seed collection (standard deviation in parentheses).

Locus	1988	1989	1990 ^a	Pooled ^a
<i>Gdh</i>	1.012 (0.074)	0.867 (0.071)	0.919 (0.073)	0.935 (0.042)
<i>Got-2</i>	1.036 (0.072)	1.044 (0.071)	0.911 (0.056)	0.975 (0.034)
<i>Got-3</i>	0.976 (0.066)	0.985 (0.065)	0.878 (0.068)	0.948 (0.039)
<i>Fest</i>	0.940 (0.044)	0.962 (0.041)	1.061 (0.040)	0.989 (0.024)
<i>Mdh-3</i>	0.940 (0.056)	0.933 (0.055)	0.914 (0.050)	0.929 (0.027) ^c
<i>Mdh-4</i>	0.981 (0.042)	0.903 (0.046) ^c	0.987 (0.039)	0.960 (0.025)
<i>6Pgd-1</i>	1.039 (0.061)	0.959 (0.060)	0.921 (0.059)	0.971 (0.034)
<i>6Pgd-2</i> ^b	1.039 (0.052)	1.039 (0.048)	1.181 (0.041) ^c	1.087 (0.028) ^d
<i>Shd-1</i>	1.018 (0.035)	0.958 (0.048)	0.981 (0.043)	0.986 (0.025)
\bar{t}_s	0.996	0.961	0.987	0.978
t_m	0.976 (0.014)	0.966 (0.016) ^c	0.962 (0.014) ^d	0.987 (0.005) ^d

- a) estimates significantly heterogeneous across loci: $P < 0.01$
b) estimates significantly heterogeneous across years: $P < 0.05$
c) estimate significantly different from $t = 1$: $P < 0.05$
d) estimate significantly different from $t = 1$: $P < 0.01$

Table 2. – Multilocus estimates of outcrossing rates for individual ramets (t_{mi}) in 3 consecutive years. Dashes (–) indicate lack of the estimate convergence (estimates for ramets 213, 215a, 237 and 238 did not converge in any studied period).

(a) mating model approach:

Sampled Females	Clonal paternal contribution						log-likelihood
	1037	1127	1138	1139	1149	1150	
E1037	0.8950 (0.0457)	0.0000 (0.0000)	0.0835 (0.0492)	0.0029 (0.0078)	0.0000 (0.0000)	0.0186 (0.0177)	-159.5079
E1127	0.9538 (0.0295)	0.0053 (0.0058)	0.0332 (0.0290)	0.0024 (0.0062)	0.0053 (0.0058)	0.0000 (0.0000)	-160.7509
E1138	0.9638 (0.0262)	0.0000 (0.0000)	0.0323 (0.0277)	0.0039 (0.0081)	0.0000 (0.0000)	0.0000 (0.0000)	-147.0990
E1139	0.8521 (0.0480)	0.0000 (0.0000)	0.1177 (0.0549)	0.0099 (0.0151)	0.0000 (0.0000)	0.0203 (0.0200)	-167.1326
E1150	0.9854 (0.0131)	0.0000 (0.0000)	0.0038 (0.0072)	0.0108 (0.0118)	0.0000 (0.0000)	0.0000 (0.0000)	-114.9691
Pooled	0.9258 (0.0155)	0.0012 (0.0012)	0.0628 (0.0168)	0.0015 (0.0037)	0.0012 (0.0012)	0.0075 (0.0052)	-786.3069

(b) fractional paternity approach:

Sampled females	Clonal paternal contribution					
	1037	1127	1138	1139	1149	1150
E1037	0.6764 (0.0284)	0.0026 (0.0018)	0.2813 (0.0243)	0.0102 (0.0072)	0.0026 (0.0018)	0.0270 (0.0122)
E1127	0.7042 (0.0276)	0.0059 (0.0053)	0.2738 (0.0250)	0.0047 (0.0045)	0.0059 (0.0053)	0.0055 (0.0047)
E1138	0.7350 (0.0273)	0.0012 (0.0012)	0.2512 (0.0245)	0.0050 (0.0050)	0.0012 (0.0012)	0.0063 (0.0053)
E1139	0.6680 (0.0313)	0.0050 (0.0025)	0.2670 (0.0248)	0.0200 (0.0099)	0.0050 (0.0025)	0.0350 (0.0143)
E1150	0.7390 (0.0278)	0.0015 (0.0015)	0.2507 (0.0262)	0.0059 (0.0062)	0.0015 (0.0015)	0.0015 (0.0015)
Pooled	0.7090 (0.0127)	0.0032 (0.0013)	0.2605 (0.0110)	0.0088 (0.0030)	0.0032 (0.0013)	0.0153 (0.0039)

- a) estimates significantly heterogeneous across sampled ramets: $P < 0.001$
b) estimate significantly different from $t = 1$: $P < 0.05$
c) estimates significantly heterogeneous across years: $P < 0.001$
d) estimates significantly heterogeneous across years: $P < 0.05$

means of single-locus outcrossing estimates (\bar{t}_s) rates were similar to the respective multilocus estimates (t_m). Among multilocus estimates, only that for 1988 was not significantly different from 1. The population multilocus estimates of three consecutive years exhibited a decreasing trend (0.976, 0.966 and 0.962 for the years 1988 to 1990, respectively), but this variation was not significant. However, neither t_m nor \bar{t}_s were significantly heterogeneous across the three years of observations.

Individual outcrossing rates were significantly heterogeneous among sampled ramets for pooled data and for 1988 and 1990 (Table 2). For these two years the largest number of departures from $t=1$ was observed. Significant heterogeneity across years was found only for two ramets (233 and 241).

Allele frequencies in the outcrossed pollen pool were always homogeneous across sampled females, except for *Got-3* in 1989, and *Mdh-3* and *6Pgd-2* for pooled data. The variance effective population size attributed to paternal contribution was estimated to be 55 (95% Confidence Interval: 23-112), 63 (C.I.: 26-130) and 70 (C.I.: 29-147) in the three consecutive years.

Discussion

Population outcrossing rates estimated in this study were very high (0.987 for data pooled over the 3 years), which is typical for Scots pine seed orchards (EL-KASSABY et al., 1989; MUONA and HARJU, 1989; BURCZYK, 1991). However, the proportion of seeds resulting from self-fertilization is still a significant component of the mating system in this seed orchard. The estimate of outcrossing rate obtained here was very similar to a previous estimate based on flowering observations ($t=0.977$) (BURCZYK and CHALUPKA, 1997). The similarity between mean single-locus and multilocus estimates at the population level, suggests that selfing is the main factor affecting the level of inbreeding (SHAW and ALLARD, 1982).

In this study no significant temporal variation was observed but there was a trend for outcrossing rate to increase with storage time since fertilization. A similar pattern was observed for a few other conifers which retain seeds in serotinous cones (CHELIAK et al., 1985; SNYDER et al., 1985; HAMRICK, 1989). This suggests, that selection may eliminate a proportion of selfed

seeds during long time storage. However, vitality of seeds was not investigated in this study.

The estimates of outcrossing rate calculated for individual trees of various conifers indicated that they may vary considerably, from 0.5 to 1.0 (SHAW and ALLARD, 1982; EL-KASSABY et al., 1987; ERICKSON and ADAMS, 1990; BURCZYK et al., 1991). The range of estimates observed in this study was narrower (0.715 to over 1.0), which confirms previous findings for Scots pine (KOSKI and MUONA, 1986; BURCZYK, 1991; KÄRKKÄINEN and SAVOLAINEN, 1993). Thus, for this species, individual estimates lower than 0.7 are not seen likely to occur.

The two main factors responsible for the level of individual outcrossing rate determined at the seed stage are the rate of self-fertilization and the rate of survival of selfed offspring compared to outcrossed offspring (self-fertility). It could be expected, that individuals with high pollen production have lower outcrossing rates than those that produce less pollen. In this paper the individual outcrossing rates calculated for the pooled data over three-years period could be related to the pollen production estimates presented in previous studies of the same seed orchard (BURCZYK, 1992; BURCZYK and CHALUPKA, 1997). Although outcrossing rates were decreasing with an increase of the average amount of pollen produced by individual ramets of respective clones (Figure 1), the relationship was not significant (PEARSON product-moment correlation: $r=-0.31$; $P=0.124$). This shows that the mean level of pollen production of individual trees is not a good predictor of the mean expected individual selfing rate observed at the seed stage. Rather other factors, including floral phenology differences, pollen production of neighbouring trees and self-incompatibility mechanisms due to embryonic recessive lethals seem to be more important (ERICKSON and ADAMS, 1990; KÄRKKÄINEN and SAVOLAINEN, 1993; BURCZYK and PRAT, 1997).

It is interesting, that the estimated variance effective paternal population size was increasing in the three years (55, 63, 70), indicating that the genetic similarity between parents and offspring in subsequent generations was increasing (BURCZYK, 1996). Also, the proportion of detected contaminant pollen gametes, that could not be produced by any of the orchard clones, was decreasing (17.7%, 14.8% and 13.3%;

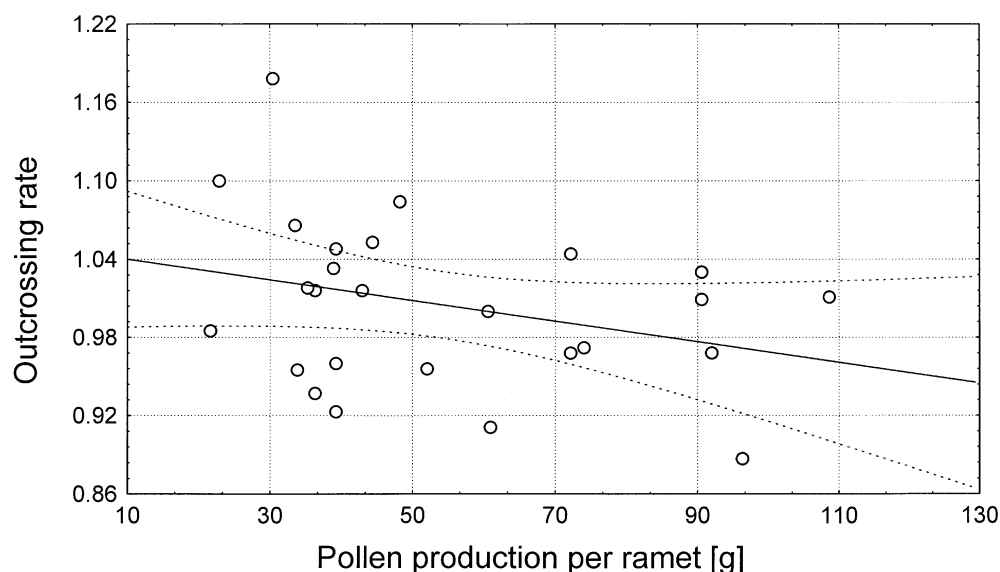


Figure 1. – Relationship between mean pollen production and outcrossing rate estimates (data pooled over three-years period) for individual ramets of Scots pine (PEARSON product-moment correlation: $r=-0.31$; $P=0.124$).

BURCZYK, 1992). These two trends suggest that the genetic efficiency of the seed orchard considered as a mating unit was increasing. However, significant temporal variation in male strobili production was observed for the studied orchard (BURCZYK and CHALUPKA, 1997). Those findings suggest, that despite little temporal changes in outcrossing rates, the outcross mating patterns (contamination, parental contribution, pollen dispersal) may vary in time, resulting in a variable genetic composition of the progeny produced in different years. Since selfing in conifers seems relatively constant, and usually accounts for less than 10% of effective fertilizations, it might be more interesting for future studies to focus on the temporal variation of outcross mating patterns both in natural and seed orchard populations.

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Genetic Control of Growth Traits of *Eucalyptus urophylla* S. T. BLAKE in South East China

By X. WEI and N. M. G. BORRALHO¹

Cooperative Research Centre for Sustainable Production Forestry and School of Plant Science, University of Tasmania,
GPO Box 252-55, Hobart 7001, Tasmania, Australia

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Abstract

Data from five thinned *E. urophylla* progeny trials in south east China were used to estimate the genetic parameters

heritability, age-age correlations and Type B correlations for DBH and height from age 1 to 5 years. Heritabilities ranged between 0.11 and 0.41 for DBH, and between 0.12 and 0.49 for HT. Heritability increased with age. Age-age correlations for DBH and height were generally very high; effective early selection could be made as early as 12 months. High Type B correlations and low family-by-fertiliser interaction for both DBH and height suggested that genotype-by-environment interaction should not be important for this species in the

¹ Address: School of Plant Science, University of Tasmania,
GPO Box 252-55, Hobart 7001, Tasmania, Australia
Phone: +61 3 62267615
Fax: +61 3 62262698
Email: x.wei@utas.edu.au
n.borralho@utas.edu.au