EFFECT OF TREE COVER ON SCOTS PINE POLLINATION AND SEEDS

Dag Lindgren
Department of Forest Genetics and Plant Physiology, Swedish University of Agricultural Sciences, S – 901 83 UMEÅ, Sweden

Received June 20, 1994; accepted September 7, 1994

ABSTRACT

The upper half of some Scots pine grafts growing in a seed orchard were covered to prevent pollen to reach the grafts from above. Seeds were harvested from covered and uncovered control grafts.

Frequency of selfing and frequency of non-orchard (alien) fathers were estimated using the embryo-macrogametophyte assay with allozymes. A group of clones with high pollen production and discriminating genotypes was identified. The frequency of aliens was estimated based on the frequency of seeds which could not have any of these clones as father. It is suggested that some errors are avoided by this estimation technique. The frequency of alien fathers was estimated to 53 – 58 % and the selfing rate was 4 %.

The covers increased the fraction of empty seeds and reduced the number of filled seeds per cone. There was no systematic effects of cover on selfing or fertilization with alien pollen. This is interpreted that alien pollen enter the orchard under conditions of hard and turbulent winds, able to raise pollen under the covers.

Key words: Allozymes, *Pinus sylvestris*, seed orchard, pollen, contamination, selfing

INTRODUCTION

Surprisingly high levels of alien (non-orchard) pollen have been found in seed orchards of Scots pine (*Pinus sylvestris* L.). Recent estimates of pollination with alien pollen ranges from 17 to 78 % (HARJU & MUONA 1989, PAKKANEN & PULKINNEN 1991, PAKKANEN *et al.* 1991, PAULE 1991, WANG *et al.* 1991, YAZDANI & LINDGREN 1991). It seems justified to speculate that an alien pollen grain for some reasons, which are not well understood, has a higher likelihood to fertilize than a seed orchard pollen grain. I have formulated a hypothesis for such a mechanism and tried to test it in this study. The alien pollen may arrive from the space above the orchard. The female strobili are mostly situated in the upper part of the crown. The alien pollen may come into the seed orchard as some type of rather continuous slow "rain", and may thus be more successful in reaching female strobili under many meteorological circumstances. The anatomy (opening upwards) and position (in the upper part of the crown) of female strobili indicates adaptation to pollination from above. Thus a hypothesis can be formulated that alien pollen is more successful as it comes from above. The main aim of this study was to test this hypothesis. If the hypothesis is correct, it might be possible to reduce the efficiency of alien pollen by placing "shields" on trees, reducing the possibility for pollen to approach female strobili from above. A preliminary study on this issue was reported by LINDGREN (1991).

The detection of alien pollen by allozyme analysis could be subject to systematic errors. The standard method (cf. e.g. WANG *et al.* 1991) assumes the following:

- each paternal gamete can be determined without error,
- the gene frequencies of the alien pollen cloud are known,
- the genotypes of all orchard clones are known without error.

It is known that mislabelling of grafts is common in Scots pine seed orchards (PAULE 1991, PAKKANEN & PULKINNEN 1993, unpublished report).

An modified way of using allozyme data for estimating frequency of alien pollen when pollen production data are available has been applied in this study. The suggested method may be expected to be more robust to violations against the assumptions of the allozyme method.

MATERIALS AND METHODS

The seed orchard

The study was performed in a Scots pine seed orchard "Skaholma". The orchard is described by WANG *et al.* (1991). The orchard was situated close to Umeå (latitude 63°50, longitude 20°15', elevation 10 m a. s. l.) and had an area of 16 ha. It was regarded as a mature seed orchard and in full production. The pollen production was estimated to be around 30 $kg.ha^{-1}$ (YAZDANI *et al.* 1994). There were 34 "older clones" in the orchard, and eight young ones, which do not contribute much to the pollen-cloud (although they are considered in this study).

Treatment

A cover (similar to an umbrella, a roof or a shield) was built around the top of some trees. The device covered the horizontal projection of the tree crown on the ground. The cover was not transparent, but neither completely opaque, the shading was similar to a dense forest canopy. For each treatment tree, a control tree of the same clone was identified. Some details about the treatments and the size of the material behind measurements are presented in Table 1.

Grafts of three different clones were studied (variable *CLONE*). In 1989/90 there was one covered tree (tree 1) and one control tree (tree 4) for each clone. In 1990/91 the same trees were used again, but are now called tree 2 and tree 5, respectively. An additional tree was covered (tree 3) and a control identified (tree 6) for each clone.

The tree crowns were stratified into three levels (variable *LEVEL*, compartments) and the cones from these different compartments were kept separate:

* **Top.** Within 1.5 m of the top. The cones have been exposed only from below.
* **Middle.** 2 – 3 m from the top. In the same level as the lower fringe of the cover. Cones have been well protected upward, but may be exposed horizontally
* **Bottom.** Two lowest healthy branch whorls. Below the cover.

Equal amounts of cones were harvested from each of four directions in the crown and later pooled.

Phenological development

Female bud development phenology was followed during the spring of 1990 on one covered and one uncovered graft of three clones. For each graft three buds representing three aspects (south, east and west) at the fourth branch whorl were observed using the classifications used by YAZDANI *et al.* (1994).

Seed characters

A known number of cones were harvested (Table 1). Cones collected at branches facing different directions were pooled. Records were based on around 20 cones each. For the experiment 1990/91 aborted ovules were estimated for some cones. Seeds were extracted. Empty seeds and filled seeds were separated. Statistics was produced for the following characters:

- Aborted ovules (variable *ABORT*). Fraction of potential seeds which did not develop into seeds. A common cause of aborted ovules in Scots pine is lack of pollination.
- Seed per cone (variable *SPERC*). Total number of seeds extracted divided by number of cones.
- Empty seeds (variable *EMPTY*). Number of empty seeds divided by total number of seeds. An important cause of empty seeds in Scots pine is an expression of genetic load following selfing.

Estimate of alien pollen

Allozyme polymorphism was assessed at 18 allozyme loci in haploid macrogametophytes and diploid embryos of the same seeds using the electrophoretic methods and the 18 loci used by WANG *et al.* (1991).

For estimating the frequency of alien fathers it is necessary to estimate the frequency of alien father gametes which match a seed orchard clone by chance. For this estimation the gene frequency in the alien pollen cloud must be estimated. In this study a reference population was constructed by pooling the genotypes of all clones in the following seven Swedish Scots pine seed orchards: Robertsfors, Brån, Östteg, Klocke, Bogrundet, Askerud and Skaholma. The compilation has not been published, although some of the individual data-sets are published. The gene frequencies of the alien pollen is assumed to be the same as that of the reference population.

A modified method of relating allozyme data to the presence of alien fathers was developed. The orchard clones were characterized for two criteria:

1. The probability that a gamete drawn from a panmictic population with the same gene frequencies as the reference population could originate from the clone.

2. The amount of pollen spread by the particular clone. The pollen production per graft was registered for each clone (based on five grafts/clone and inlcuding also the clones which were planted later), the figures were published by YAZDANI *et* al . (1994).

Ten clones (BD1010, BD1015, BD1174, BD1176, BD1177, BD2039, BD2058, BD2066, BD2068, BD2074) were selected based on the two criteria mentioned above, thus low probability that random alien gametes will match and high pollen production. These ten clones were expected to contribute 48.1%

Table 1 Treatments and size of materials

Treatment, year Covered trees Covers raised Covers removed Cone harvest	1989/90 3 May 23, 1989 June 27, 1989 September 28, 1990		1990/91 6 May 15 – 16, 1990 June 25 – 26, 1990 September, 1991	
Treatment	Covered	Control	Covered	Control
Trees	3	3	6	6
All cones harvested	167	228	337	409
All seeds harvested	3005	4609	5611	10982
All paternal genotypes successfully derived	468	197	855	441

of all orchard pollen. All gamete genotypes which could be produced from these ten clones were listed. Based on the frequency of the observed pollen genotypes, which were found on the list, the total contribution of orchard pollen to fertilizations was estimated (see below). This assumes that the pollen contributions registered by YAZDANI *et al.* 1994 also reflects actual fertilization, or if there are deviations, that the ten clones selected can be regarded as a random sample as far as deviations are concerned. Deviations can occur for several reasons. It was assumed that all clones were equally represented in the orchard. They were in the initial design, but unequal mortality has caused deviations. Phenological differences may cause deviations. Differences between years may cause variations. Different pollen may experience different reproductive success.

Estimation procedure – mathematical

The paternal gamete may come from the orchard or from outside the orchard (alien). The fraction with origin from outside the orchard is c and the fraction from within the orchard is $(1 - c)$. Of the orchard gametes, the fraction g originates from a defined group of clones (or a single clone), which will be denoted G. Some alien gametes may by chance have genotypes which can also occur among the gametes from the defined group of clones. The probability for such a coincidence is g'. The fraction of paternal orchard gametes from other clones than G is $(1 - g)$. Even members of this group may be indistinguishable from G. It is assumed that the probability for that is also g'. Y_G is the expected fraction of gametes matching G. Y_G is a sum of contributions from three sources:

1. Gametes from G,
2. orchard gametes from other orchard clones which incidently match G, and
3. alien gametes, which incidently match G.

The sum of these three terms is formulated as

$$Y_G = g(1 - c) + g'(1 - g)(1 - c) + g'c$$
$$= g - gc + g'(1 - g + gc).$$

From this expression the fraction of alien gametes, c, can be evaluated as

$$c = (Y_G - g - g' + g'g) / (g'g - g). \quad [1]$$

Selfing can be treated analogously. The true fraction of selfing gametes is s, Y_s is the expected fraction of the gametes which could originate from selfing, s' is the fraction of the outcrossing gametes which match the mother. Observed matches is the sum of selfing and incidently occurring matches,

$$Y_s = s + s'(1 - s).$$

From this follows that

$$s = (Y_s - s')/(1 - s'). \quad [2]$$

Estimation procedure – numerical

The likelihood that an alien gamete will match G, g', can be calculated by adding the probabilities that each gamete genotype which can be produced by G is produced by chance. The value obtained was $g' = 0.1077$. Based on expected contributions (see above), the estimate $g = 0.481$ was used. For numerical calculations the observed values of Y_G and Y_s will replace the expectations.

Using these values, expression [1] will become

$c = (0.536 - Y_G) / 0.429.$ [3]

By adding probabilities for the gametes the mother clone is able to produce occur by chance, s' can be estimated. The following values were found: 0.0964, 0.0017, 0.0532; for BD1032, BD1033 and BD1240, respectively.

Statistical procedures

For statistical evaluation the SAS procedures GLM and VARCOMP were used. The model used was:

$$Y_{ijkl} = \mu + COVER_k + CLONE_{i(k)} + LEVEL_{il(k)} + e_{ijkl} \quad [4]$$

where: μ – experimental mean, *COVER* – fixed effect of the presence of a cover, *CLONE* – fixed effect of clone i within a treatment, *LEVEL* – fixed effect of level l within a treatment, e_{ijkl} – residual for the k-th tree.

Years were not included in the model, but trees from different years were considered as different replications. Thus statements concerning differences between years cannot be supported by significance levels.

RESULTS

Phenologic development

The covers forced the female buds to develop faster ("greenhouse effect"). The female strobili entered the receptive stage 2 – 5 days earlier. Around half of the female strobili under cover become receptive before the orchard grafts started pollen production. The implications are discussed below.

Seeds per cone

The total number of seeds per cone was reduced under the cover (Table 2). The level had no effect. There were variations between clones, BD 1248 had most seeds per cone.

Aborted ovules

The incidence of aborted ovules (Table 3) was approximately doubled under the cover. There were clonal differences. There was a not significant tendency that aborted ovules were less frequent in the bottom of the crowns.

Empty seeds

The proportion of empty seeds per cone was higher under the covers (Table 4). The changes did not seem to be associated with the level of the cones. There were clonal differences, BD1032 got the highest incidence of empty seeds and BD1248 the lowest.

Selfing

None of the factors studied had a significant effect on selfing (Table 5).

Alien fathers

The frequency of alien fathers was not affected by any of the factors studied (Table 6). There was an indication that aliens were more common in the top of the covered grafts but in the bottom of the controls.

Statistical considerations

The number of cones, seeds and genotyped gametes are listed in Table 1. An entry in the statistical sense refers to a level within a tree. Aborted ovules (*ABORT*) were based on 72 or more potential seeds per entry. Number of seeds per cone (*SPERC*) and empty seeds (*EMPTY*) were based on 51 or more seeds per entry. Selfing (*SELF*) and alien (*ALIEN*) were based on more than 6 paternal genotypes per entry. Entry values on less than 16 genotypes are indicated in Table 5 and 6, and are to be regarded as non accurate.

Analyses of variance is summarized in Table 7.

DISCUSSION

Tree cover had affected the three seed characters studied significantly. There were fewer seeds per cone, more aborted ovules and higher frequency of empty seeds. The effects of the cover seems as strong in the top as in the bottom of the crown, which is surprising considering that only the tops were well-covered. If the reason for the effect is the shading or heat or poor mobility of pollen in the covered region, it would be expected that the top was most affected and the bottom unaffected. It does not seem likely the covers reduced the water uptake of trees much, the tree ought to be able to use most of the precipitation even if the covers moves the falling rain some meters

Table 2 Total number of seeds per cone (*SPERC*)

Clone	Level	Cover			No cover		
	Tree	1	3	4	2	5	6
BD 1032	Top	11.4	16.9	6.2	15.8	24.9	27.0
	Middle	11.0	22.3	19.3	19.1	20.1	22.7
	Bottom	11.0	20.7	15.4	17.0	14.6	25.6
BD 1033	Top	14.9	7.1	23.4	7.4	27.4	15.6
	Middle	10.0	17.1	25.0	7.1	25.3	12.6
	Bottom	9.1	21.5	23.7	12.1	20.6	24.3
BD 1248	Top	14.7	7.3	13.4	26.7	37.6	43.9
	Middle	15.8	11.2	14.6	26.7	33.0	36.1
	Bottom	15.7	17.0	no cone	19.6	31.2	36.2

In this and the following tables significances are indicated as follows: *** $p<.001$; ** $p<0.01$; * $0.05>p>.01$; ns $p>0.05$

Means: 1990(1+4): 14.7; 1991: 21.6; total: 19.4

	Cover	No cover	Effects:
			Cover, ***, decrease
Top	12.8	25.1	Level, ns, no effect
Middle	16.3	22.5	Clone, ***, BD 1248 high
Bottom	16.8	22.4	Year, 1990 low

Table 3 Aborted ovules (*ABOV*, fraction of potential seeds)

Clone	Level	Cover		No cover	
	Tree	3	4	5	6
BD 1032	Top	0.40	0.49	0.26	0.08
	Middle	0.34	0.38	0.30	0.27
	Bottom	0.36	0.36	0.32	0.24
BD 1033	Top	0.71	0.38	0.32	0.65
	Middle	0.48	0.38	0.19	0.53
	Bottom	0.31	0.29	0.29	0.12
BD 1248	Top	0.58	0.34	0.06	0.02
	Middle	0.57	0.54	0.03	0.02
	Bottom	0.29	no cone	0.04	0.03

Mean: 0.31

	Cover	No cover		Effects:
				Cover, ***, Increase
Top	0.48	0.23	ns	Level, ns, Bottom low
Middle	0.45	0.22	ns	Clone, *, BD 1248 low
Bottom	0.32	0.17	ns	

out from the stem. Perhaps the increased heat caused increased evaporation and water stress on trees, and this stress may have affected the cones and seeds. The formation of a pollination drop may be important in pollination (OWENS *et al.* 1981). The covers may prevent formation of such droplets, and thus greatly reduce pollen intake. The strong negative effects of the covers, which were applied only on part of the tree and in a limited time, can be considered as a warning that big scaled seed production (controlled crosses) in pollen isolated environments may under some circumstances result in reduced yield of good seeds.

Phenology is forced some days by the covers, but there is a considerable overlap between covered and not covered trees. For BD1032 and BD1033, the receptive phase was initiated almost a week later than for the earliest clones (YAZDANI 1989, YAZDANI *et al.*

Table 4 Occurrence of empty seeds related to all seeds (*EMPTY*)

Clone	Level	Cover			No cover		
	Tree	1	3	4	2	5	6
BD 1032	Top	0.39	0.55	0.53	0.20	0.24	0.24
	Middle	0.42	0.60	0.76	0.17	0.18	0.31
	Bottom	0.38	0.36	0.49	0.19	0.31	0.25
BD 1033	Top	0.16	0.41	0.39	0.19	0.19	0.18
	Middle	0.24	0.37	0.37	0.17	0.12	0.23
	Bottom	0.33	0.17	0.19	0.16	0.28	0.29
BD 1248	Top	0.18	0.26	0.23	0.10	0.07	0.07
	Middle	0.16	0.30	0.30	0.07	0.06	0.09
	Bottom	0.16	0.53	no cone	0.13	0.09	0.12

Means: 1990(1+4): 0.21; 1991: 0.29; Tot: 0.26

	Cover	No cover		Effects:
Top	0.34	0.16	ns	Cover, ***, Increase
Middle	0.39	0.16	**	Level, ns, No effect
Bottom	0.33	0.20	ns	Clone, ***, BD 1032 high, 1248 low

Table 5 Estimated proportion of selfed seeds related to all germinating seeds (*SELF*)

Clone		Cover			No cover		
	Tree	1	3	4	2	5	6
BD 1032	Top	0.027	0.111	0.101	0.631[c]	0.044	–0.107
	Middle	0.006	0.058	0.123	–0.107[c]	–0.107	0.004
	Bottom	0.156	0.025	0.042	–0.107[c]	–0.070	0.051
BD 1033	Top	0.054	–0.002	0.018	0.098	–0.002	–0.002
	Middle	0.018	–0.002	–0.002	–0.002	–0.002[c]	–0.002
	Bottom	0.068	0.017	–0.002	–0.002	–0.002	–0.002
BD 1248	Top	0.027	–0.018	0.105	0.120	0.089	–0.056
	Middle	–0.038	–0.056	–0.020	–0.021	0.095[c]	0.025
	Bottom	0.040	0.173	no cone	0.017	0.170	0.085

Means: 1990(1+4): 0.055; 1991: 0.026; Tot: 0.036

	Covered	Uncovered		Effects:
Top	0.047	0.091	ns	Cover, ns, No effect
Middle	0.010	–0.013	ns	Level, ns
Bottom	0.065	0.016	ns	Clone, ns, BD 1033 low
				Year, 1990 high

[c] indicates that value is based on 15 or less paternal genotypes, and thus unreliable.

1994). The pollen contamination in this orchard was not closely associated with the earliness of the clones (YAZDANI *et al.* 1994). Thus it does not seem likely that the forced development is a major reason for observed effects of the cover.

The incidence of selfing (Table 5) was influenced by an extreme observation (63 %), which was based on only six gametes. This probably reflected an atypical incidence of high selfing in a single cone. The overall average value of selfing, 3.6 %, is agreement with what often has been found in Scots pine seed orchards (LESTANDER & LINDGREN 1985). The cover does not seem to prevent outcrossing pollen, thus pollen seem movable.

The covers had no evident effect on alien pollination (Table 6), although there is an indication that frequency of aliens increases towards the top in the covered trees and decreases in the controls. The hypo-

Table 6 Estimated proportion of germinating seeds with alien fathers (*ALIEN*)

Clone	Tree	Cover			No cover		
		1	3	4	2	5	6
BD 1032	Top	0.77	0.79	0.67	–0.30[c]	0.72	0.50
	Middle	0.62	0.71	0.64	0.78[c]	0.67	0.47
	Bottom	0.58	0.30	0.67	0.47[c]	0.09	0.67
BD 1033	Top	1.06	0.64	0.71	0.94	0.52	0.23
	Middle	0.60	0.81	0.42	0.55	0.55[c]	0.32
	Bottom	0.66	0.72	0.49	1.05	0.78	0.67
BD 1248	Top	0.56	0.66	0.42	0.24	0.05	0.86
	Middle	0.07	0.50	0.38	0.40	0.58[c]	0.80
	Bottom	0.11	0.44	a	0.45	0.75	0.78

Means: 1990(1+4): 0.533; 1991: 0.570; Tot: 0.557

	Covered	Uncovered		Effects	
					Cover, ns, No effect
Top	0.697	0.417	ns		Level, ns, No effect
Middle	0.526	0.571	ns		Clone, ns, No effect
Bottom	0.496	0.635	ns		Year, No effect

[c] indicates that value is based on 15 or less paternal genotypes, and thus unreliable.

Table 7 Analyses if variance factors are significant

Source	df	*SELF*	*ALIEN*	*EMPTY*	*ABORT*	*SPER*
Treatment	1	0.00084^{ns}	0.0079^{ns}	0.403^{***}	0.403^{***}	1298^{***}
Clone (trt)	4	0.0093^{ns}	0.1201^{ns}	0.075^{***}	0.081^{*}	304^{***}
Level (trt)	4	0.0132^{ns}	0.099^{ns}	0.0128^{ns}	0.010^{ns}	38.5^{ns}
Error	43(25)[d]	0.0089	0.051	0.0075	0.0148	14.21

[d] Degreess of freedom for error is 43 for SELF and ALIEN and 25 for fraction of empty seeds (*EMPTY*), fraction aborted ovules (*ABORT*) and seeds per cone (*SPERC*).

thesis that the alien pollen has an advantage as it comes from above could not be supported. The alien pollen must be transported by rather strong and turbulent winds to reach the reproductive structures under the cover. It seems logical that pollen can move long distances under such conditions, and the orchard pollen may blow away. My interpretation of the results is that the alien pollen reaches the orchard under conditions of rather strong surface winds. It does not seem likely that pollen sedimentation during calm nights or with a light rain is important for alien pollination. A relation may be searched with meteorological data on wind, rain and temperature, but I feel it is to uncertain when the fertilizating pollen enter the seed orchard to make such an approach meaningful.

It has been proposed that one way to reduce alien pollen would be to have high trees as fathers. The experiences obtained from this investigation suggest that this would be inefficient, the pollen is able to move around in eddies.

The modification of the standard method was to study the paternal contribution from a share of the orchard clones which were characterized by high pollen production and production of gametic types which seldom occur in a random mating population. This reduces some problems, like the presence of unknown orchard clones, the hordes of possible gametes clones which actually do not produce much pollen still theoretically can produce, the difficulty to identify aliens which could have arisen within the orchard. On the other hand it raises the question how accurately pollen production will predict actual paternal contribution. This problem is however reduced then the summed effect of several clones is calculated. For comparative studies of alien frequency in different compartments (like the effect of cover) this uncertainty is likely to be less important, but when the actual rate of alien pollen is calculated, the uncertainty is more severe.

The frequency of alien pollen in this seed orchard has earlier been investigated by WANG *et al.* (1991), and the results were quite similar.

	Wang *et al.* (1991)	Present study	
Seed maturation year	1986	1990	1991
Alien pollen (%)	51–55	53	57

No large variations between years have occured in this orchard and the contamination rate is consistently high. That both estimation methods give similar results increases the creditability of both methods.

ACKNOWLEDGEMENTS

I am indebted to Marja-Leena and Lars-Göran Lejdebro for making the practical arrangements of the experiment and the seed collection, to Roger Granbom and Inga-Britt Carlsson for running the isozyme analyses, to Reza Yazdani for cooperation in the planning phase, to Alfred E Szmidt for discussions about the evaluation, to the participants of the meeting of Nordic Tree Breeders 1991 for comments in the field, to Zeki Kaya for making the statistical analyses on SAS, to anonymous referees for valuable comments, and to the Swedish Council for Forestry and Agricultural Research for funding the study.

LITERATURE

HARJU, A. & MUONA, O., 1989: Background pollination in *Pinus sylvestris* seed orchards. *Scandinavian Journal of Forest Research* **4**:513–520.

LESTANDER, T. & LINDGREN, D., 1985: Fröplantagernas genetiska effektivitet. *Swedish University of Agricultural Sciences. Department of Forest Genetics and Plant Physiology. Report* **4**:111–127.

LINDGREN, D., 1991: Can shields stop aliens from upper space? *Swedish University of Agricultural Sciences. Department of Forest Genetics and Plant Physiology. Report* **10**:34–42.

LINDGREN, D., YAZDANI, R., LEJDEBRO, M.-L. & LEJDEBRO, L.-G., 1991: The spread of conifer pollen from a point source. *Swedish University of Agricultural Sciences. Department of Forest Genetics and Plant Physiology. Report* **10**:86–99.

OWENS, J. N., SIMPSON, S.J. & MOLDER, M., 1981: Sexual reproduction of *Pinus contorta*. I. Pollen development, the pollination mechanism and early development. *Canadian Journal of Botany* **39**:1828–1843.

PAKKANEN, A. & PULKKINEN, P., 1991: Pollen production and background pollination levels in Scots pine seed orchards of northern Finnish origin. *Swedish University of Agricultural Sciences. Department of Forest Genetics and Plant Physiology. Report* **10**:14–21.

PAKKANEN, A., PULKKINEN, P. & VAKKARI, P., 1991: Pollen contamination in the years 1988-1989 in some old Scots pine seed orchards of northern Finnish origin. *Report of the Foundation for Forest Tree Breeding* **3**:1–8.

PAULE, L., 1991: Clone identity and contamination in a Scots pine seed orchard. *Swedish University of Agricultural Sciences. Department of Forest Genetics and Plant Physiology. Report* **10**:22–32.

WANG, X., LINDGREN, D., SZMIDT, A. & YAZDANI, R., 1991: Pollen migration into a seed orchard of *Pinus sylvestris* and the methods of its estimation using allozyme markers. *Scandinavian Journal of Forest Research* **6**:379–386.

YAZDANI, R., 1989: Flowering phenology and male and female flower production in a *Pinus sylvestris* seed orchard. Sveriges Lantbruksuniversitet. *Institutionen för skoglig genetik och växtfysiologi. Arbetsrapport* **32**.

YAZDANI, R. & LINDGREN, D., 1991: Variation of pollen contamination in a Scots pine seed orchard. *Silvae Genetica* **40**:243–246.

YAZDANI, R., LINDGREN, D., SEYEDYAZDANI, F., PASCUAL, L. & ERIKSSON, U., 1994: Flowering, phenology, empty seed and pollen contamination in a clonal seed orchard of *Pinus sylvestris* in northern Sweden, *In*: Proceedings of Szmposium on Population Genetics and Conservation of Forest Trees. Bordeaux 1992 (in press).