or more other test sites along the hazard level continuum probably would have given a more clear definition of the progeny x site interaction for rust infection rate. Progeny testing procedures should include extreme and intermediate sites over the area in which seed orchard stock is to be used, so important interactions can be measured. Accurate quantification of interaction effects is essential for the precise genotype/site matching expected in future forestry practices.

The seedling seed orchard approach was effective in improving fusiform rust resistance and height growth in these slash pine selections. Effectiveness and ease of establishment favor the inclusions of seedling seed orchards in tree improvement programs.

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Mating System and Effective Pollen Immigration in a Norway Spruce (Picea abies (L.) Karst) Plantation

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Summary

Mating system and effective pollen immigration in a Norway spruce (*Picea abies* (L.) Karst) plantation were studied using multilocus allozyme markers. The estimated proportions of ovules fertilized by pollen from maternal trees themselves (selfing), from other trees within the plantation (local outcrossing), and from trees outside the plantation (immigration) were 0.09, 0.75, and 0.16, respectively. These estimates varied significantly among trees within the plantation. The majority of selfs (85%) and pollen immigrants (84%) could be attributed to a small proportion of trees (25%). Fifty percent of pollen haplotypes observed in the plantation were due to immigration and most of them likely were contributed by an extraneous population located about 4 km away. These results advance our knowledge about gene flow in conifers and have implications for seed orchard management.

Key words: Allozymes mating system, gene flow, Norway spruce, EM algorithm.

Introduction

Mating system and gene flow are critical components to theoretical population genetics. They are crucial in determining the spatial genetic structure and evolutionary potential of natural populations (Loveless and Hamrick, 1984). Information on mating system and gene flow is also of great value in forest tree improvement programs. Inbreeding, particularly selfing, and pollen contamination are the most important factors reducing genetic efficiency of wind-pollinated seed orchards. Therefore, minimizing the degree of inbreeding and pollen contamination is paramount for developing orchard designs and management regimes (Adams, 1983; Friedman and Adams, 1982, 1985; Shen et al., 1981). While substantial effort has been expended in examining mating systems during the past 2 decades (Brown, 1990; Brown *et al.*, 1984), there are only a few studies that quantify the level of realized gene flow in forest tree populations (Adams and Birkes, 1990; Fast et al., 1985). Recently, an EM-algorithm procedure has been proposed for joint estimation of mating system and effective pollen immigration parameters in gymnosperm populations (Xie *et al.*, 1991a), enabling the simultaneous investigation of mating system and gene flow.

Norway spruce (*Picea abies* (L.) Karst) is a prominent canopy tree of both boreal and montane conifer-dominated forests in Europe and Asia, and it is one of the most valuable timber tree species in central Europe (Schmidt-Vogt, 1977). Despite its commercial importance, information on the level of realized gene flow in Norway spruce populations is not available and knowledge of the mating

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system of this species is preliminary (Lundkvist, 1979; Müller, 1977). In this study, we examine the mating system and effective pollen immigration in a plantation of Norway spruce.

Materials and Methods

An experimental plantation of Norway spruce named 'Hudson's Place Norway Spruce' located in Petawawa National Forestry Institute, Chalk River, Ontario, Canada was chosen for this study (*Figure 1*). This plantation was established in 1924 with 27 individuals at present. Surrounding the plantation on 3 sides are experimental stands of white and red spruce and on the fourth side by a road. Southwesterly on the road, 0.12 km away, there are 7 mature Norway spruce trees, and about 4 km farther, there is a large and highly productive Norway spruce plantation (Copins, P., personal communication). Cones were collected from all 27 trees in the 'Hudson's Place Norway Spruce' plantation and from 6 of the 7 roadway trees (no cones available on the other tree) in 1989. In most cases, collections were made from the upper crown (generally the upper $^1/_3$ of the crown) and when present, from different locations around the tree. When cones were not available from the upper crown, collections were made from the middle to lower crown. The individuality of the cone lots and, subsequently, seedlots was retained throughout analysis.

Multilocus allozyme genotypes of all sampled trees were inferred at six allozyme loci (*Aat-3, Pgi-2, 6Pg-1, Idh, Fum*, and *Gdh*) from a sample of at least 8 megagametophytes per tree. Twenty-four trees in the plantation were used as maternal parents due to the availability of sufficient seeds, and 80 megagametophyte-embryo pairs were analyzed for each of them. The electrophoretic methods have been previously described (Xie and Knowles, 1991), and Mendelian segregation and independent assortment of the 6 loci have been confirmed using our progeny array data.

The Expectation-Maximization (EM) algorithm procedure proposed by Xie *et al.* (1991a) was employed for the joint maximum likelihood estimation of mating system and effective pollen immigration parameters. In this procedure, the sources of pollen that could contribute to the pollen pool of a given population are divided into pollen from maternal plants themselves (selfing), from other plants in the same population (local outcrossing), and from plants in the foreign populations (outcrossing due to immigration). An embryo that carries a non-maternal pollen is categorized as discernibly outcrossed, otherwise as ambiguous. Given the assumption described by Brown et al. (1984) and independent assortment among loci, the probability of observing the j^{th} multilocus pollen haplotype in offspring of a maternal plant in the local population, pr[j], can be given as a function of the frequencies of the multilocus pollen haplotype in the local (p_j) and foreign (i_j) populations, along with the rates of selfing (S), outcrossing (O), and immigration (I). If the j^{th} multilocus pollen haplotype could not be produced by the maternal plant (i.e. discernible outcross), the function is given as

$$pr[j] = Ii_j + Op_j,$$

otherwise (i.e. ambiguous),

$$pr[j] = S\varnothing(k) + Ii_j + Op_j$$

where, $\varnothing(k)$ is the probability of the maternal tree producing pollen haplotype j. Starting with arbitrary values of the unknowns (i.e. p_j, i_j, S, O, and I), the E step derives the expected number of pollen from the selfed and outcrossed events (local outcrossing and immigration) based on the above functions and the observed numbers of pollen in the "discernible outcross" and "ambiguous" categories, and the M step provides the maximum likelihood estimates for these mating system and immigration parameters. These estimates are used in another E and M step, and the EM algorithm continues until successive estimates converge to a specified criterion. One of the advantages of the this procedure is its insensitivity to the accuracy of gene frequency estimates in the foreign populations (Xie *et al.*, 1991a).

Due to the lack of sufficient degrees of freedom, individual tree estimates of S, O, and I were obtained by setting p_j's and i_j's equal to the corresponding population estimates. The maximum-likelihood ratio test statistics, G_h and G, (Xie et al., 1991b) were calculated to examine the heterogeneity of S, O and I among trees within the plantation and to test the null hypotheses of $S=0.0$, respectively.

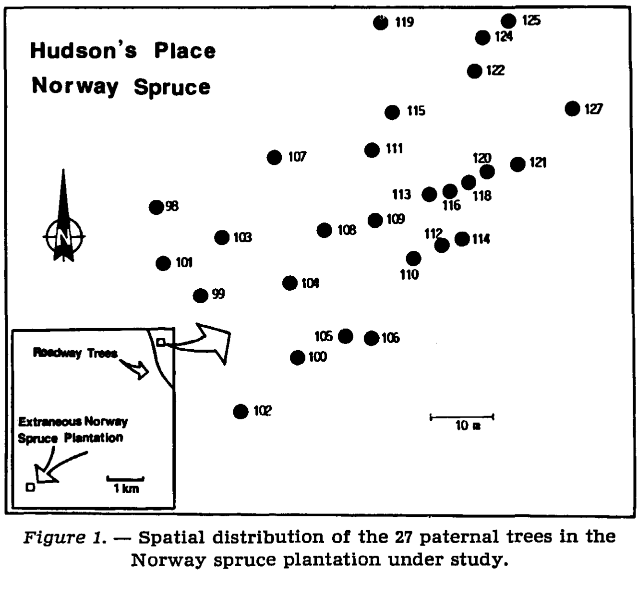

Figure 1. — Spatial distribution of the 27 paternal trees in the Norway spruce plantation under study.

Results

A total of 50 haplotypes were observed in the sample of 1920 pollen, of which 25 could be produced by the trees within the plantation (Xie and Knowles, 1991). Among the other 25 pollen haplotypes, only 2 of them could be the products of the 6 roadway trees (*Table 1*). The remaining 23 haplotypes cannot be produced by the single unexamined tree on the roadway, indicating that the extraneous Norway spruce population may have contributed majority of pollen immigrants to the plantation under study.

Seventy-nine pollen immigrants were identified by their distinguishable multilocus allozyme genotypes. The proportion of viable embryos resulting from outcrossing due to immigration (I) was estimated at 16 %. Among the remaining embryos analyzed, 75% of them resulted from local outcrossing (i.e. $O=0.75$) and 9% from selfing (i.e. $S=0.09$). Rejection of the null hypothesis of $S=0.0$ ($G=10.288$, $p<0.01$) indicates the amount of selfing in the plantation was significant. Individual tree estimates of selfing, local outcrossing, and immigration ranged from 0.00 to 0.58, 0.00 to 1.00, and 0.00 to 0.78, respectively, and showed significant heterogeneity for all 3 parameters (*Table 2*). While a large proportion of immigration was estimated, the distribution of immigrants was highly skewed, with 25% of trees (trees 98, 99, 114, 118, 121 and 124) lodging 85% of the total pollen immigrants (*Table 2*). Similarly, 25% of trees (trees 98, 99, 108, 112, 114, 116) produced 84% of the selfs sampled from the plantation. In addition, the three trees with the highest immigration rates (trees 98, 99 and 114) had extremely low levels of outcrossing (*Table 2*).

Discussion

Results from the present study provide important evidence indicating that gene flow in conifers is substantial rather than restricted as in many other plants (EHRLICH and RAVEN, 1969; LEVIN and KERSTER, 1974; LEVIN, 1981). The observation of effective pollen immigration over a distance as long as 4 km is of particular value. Although indirect methods have inferred significant gene flow between populations many kilometers apart (e.g. MILLAR, 1983; YEH, 1988) and pollen dispersal studies have shown massive movement of pollen over 10s of kilometers (examples cited in LANNER, 1966), the documentation of direct gene transport over a distance of a few kilometers, if any, is rare. In addition, these results add to the documentation that conifers are predominant outcrossers with outcrossing rates usually higher than 90% (ADAMS and BIRKES, 1990) and with significant variation in the level of outcrossing among individual trees (NEALE and ADAMS, 1985; SHAW and ALLARD, 1982; XIE *et al.*, 1991a).

Table 1. — The genotypes and frequencies of pollen that cannot be produced by the trees within the plantation.

Genotype[a]	Frequency
111122	0.006
111211	0.002
111221	0.005
121112	0.006
122111	0.005
122112	0.001
131112	0.001
131221	0.001
211112	0.002
211131	0.022
211132	0.022
211211	0.001
211221	0.003
212111	0.002
212121	0.003
221112	0.004
221132	0.005
311111	0.007
311121[b]	0.015
312121	0.001
321111	0.014
321121[b]	0.031
321122	0.003
322121	0.003
322122	0.001

[a] Loci in the order: *Aat-3, Pgi-2, 6Pg-1, Idh, Fum, Gdh.*

[b] Pollen haplotypes that could be produced by the 6 roadway trees with genotypes: 221121/321121, 121211/221211, 111121/321121, 211121/221121, 121121/231121, 111121/221121.

Table 2. — Individual tree estimates of selfing (S), outcrossing (O), and effective immigration (I) rates.

Maternal Tree	S	O	I
98	0.38	0.00	0.62
99	0.22	0.00	0.78
100	0.00	0.94	0.06
101	0.00	0.97	0.03
102	0.00	1.00	0.00
104	0.00	1.00	0.00
105	0.00	0.95	0.05
106	0.00	1.00	0.00
107	0.00	0.97	0.03
108	0.26	0.61	0.13
110	0.15	0.83	0.03
111	0.05	0.95	0.00
112	0.58	0.40	0.03
113	0.00	1.00	0.00
114	0.19	0.03	0.78
115	0.02	0.98	0.00
116	0.23	0.77	0.00
118	0.00	0.73	0.28
120	0.02	0.90	0.07
121	0.00	0.55	0.46
122	0.04	0.96	0.00
124	0.00	0.73	0.27
125	0.00	0.96	0.05
127	0.08	0.86	0.07
Heterogeneity			
G_h (df=23)	110.078	169.404	273.818
$\underline{p}$	<0.001	<0.001	<0.001

Based on our results, 16% of the pollen effective in fertilizing ovules in the plantation came from trees at least 120 m away, and these immigrants brought in 50% of the total pollen haplotypes observed in the plantation. Since all foreign pollen contributors are located on one side of the plantation (southwest), the estimated rate of effective pollen immigration might be much higher if the plantation was surrounded by trees of the same species.

In this study, it is not clear what proportion of pollen immigration was contributed by the roadway trees versus the more distant extraneous Norway spruce population. However, the fact that 6 of the 7 roadway trees donated only two pollen haplotypes made it reasonable to infer that most of the novel pollen haplotypes observed in the plantation under study were from the extraneous population. Long-distance and mass movement of pollen has been recorded in Norway spruce. For example, ANDERSSON (1955) collected pollen along a series of transects for Norway spruce in Sweden. At Yfre he collected 47% as much as pollen at 1.5 miles (2.4 km) as at the edge of the forest. More strikingly, in a heavy pollen crop year in Sweden, ANDERSSON (1963) observed that some high rocky islands in Lake Vänern (Lurö Archipelago) which were 2.5 miles to 5 miles (4 km to 8 km) from the nearest forest were covered with a layer of Norway spruce pollen almost 1 cm thick. It has been demonstrated that pollen of conifer trees not only can travel long distances but also can maintain viability over those distances (ANDERSSON, 1963). Since the large extraneous Norway spruce population near the plantation produces heavy pollen crops (COPIS, P., personal communication), substantial effective pollen immigration into the plantation over a distance of 4 km is not unexpected.

Variation in the rate of effective immigration among individual trees could be attributed to many factors such as geographical distance to the foreign pollen sources and floral phenology. From *figure 1* we can see that distance to the foreign pollen sources may not be important. For instance, the nearest tree to the foreign pollen sources, 102, had no immigration at all while tree 124 located on the other side of the plantation had an immigration rate as high as 27%. In contrast, differences in floral phenology among trees likely played a significant role. It is important to note that the 3 trees with the highest immigration rates (i.e. trees 98, 99, 114) had extremely low levels of local outcrossing (0.00, 0.00 and 0.03, respectively) (*Table 2*). In other words, these 3 trees were fertilized almost exclusively by pollen produced by themselves and by the background trees. Lack of floral overlap between these and the rest of trees within the plantation is very likely the explanation for this observation.

The estimated proportion of viable embryos resulting from cross-fertilization (i.e. O + I) in Norway spruce is similar to those reported for most other conifers (ADAMS and BIRKES, 1990). The outcrossing rates in natural populations of Norway spruce were estimated at 0.89 (LUNDKVIST, 1979) and 0.88 (MÜLLER, 1977) based on single-locus estimation. The slightly higher level of outcrossing (0.91) derived in this study might result from the lack of genetic substructuring within the plantation, or simply due to chance.

Variation in the level of outcrossing among trees within natural and artificial populations has been documented in many other conifers (EL-KASSABY et al., 1987; NEALE and ADAMS, 1985; PERRY and DANCIK, 1986; PERRY and KNOWLES, 1990; SHAW and ALLARD, 1982; XIE *et al.*, 1991b) and the potential causes underlying this variation can be numerous. Inbreeding loads among trees have been found to be highly variable in many conifer species (BINGHAM and SQUILLACE, 1955; PARK and FLOWLER, 1984; SORENSEN, 1969); thus trees with more embryonic lethals are expected to have higher apparent outcrossing estimates. Floral phenology and pollen productivity are also important factors influencing the outcrossing rates of individual trees. Floral overlap is a significant determinant to the success of intermating (ERICKSON and ADAMS, 1989; SHEN et al., 1981), and therefore trees with very early or very late flowering may have lower rates of outcrossing. Trees producing greater amounts of pollen are expected to have lower rates of outcrossing owing to higher proportions of self pollen in their pollen pools. Indeed, a negative correlation between pollen yield and outcrossing rate has been observed in a number of conifer species (DENTI and SCHOEN, 1988; SHEA, 1987). Substantial variation in floral phenology and pollen productivity has been observed in Norway spruce (SKROPPA and TUTTUREN, 1984) and such variation may have partially contributed to the detected heterogeneity of outcrossing rates among trees in this plantation.

The high outcrossing rate and substantial, long-distance gene flow observed in the present study is of importance for our understanding of the genetic structure of this species. Since outcrossing promotes the maintenance of genetic variability and gene flow prevents differentiation among populations, Norway spruce, like most other coniferous trees, is expected to retain large amounts of genetic variation but little population differentiation. This expectation is consistent with the recently reported empirical results (LAGERCRANTZ and RYMAN, 1990). The results presented here also may be of significant value to seed orchard managers. Although Norway spruce is a predominantly outcrossing species, it showed a significant level of self-fertility. Therefore, minimizing self-fertilization is still a top priority in designing and managing Norway spruce seed orchards. Since the majority of the selfs appeared to be produced by a small number of individuals, avoiding the use of clones with exceptionally high selfing rates may be an effective way to reduce self-fertilization in the seed orchards. The observed massive, long-distance effective pollen flow suggests that a meaningful reduction in pollen contamination may not be achieved by the establishment of a dilution zone with conventional size (122 m to 152 m; ZOBEL and TALBERT, 1984), particularly when a small seed orchard is surrounded by a large number of trees of the same species. The fact that a large proportion of pollen immigration was attributable to a few trees lacking floral overlap with others in the plantation suggests that removing those clones with unusually early or late flowering from the seed orchards may be effective in reducing pollen contamination. When both their male and female flowers are late or early, not only pollen contamination but also selfing could be minimized by roguing those clones.

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Stand Features and Height Growth in a 36-Year-Old Maritime Pine (Pinus Pinaster Ait.) Provenance Test

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Summary

A trial comparing 10 maritime pine provenances was measured at age 36 years. Ranking for vigour remained stable throughout the test period. Two major groups were obvious, Atlantic lowland seed sources with high vigour and frost resistance and southern seed sources with low vigour and low frost resistance. Three provenances had intermediate features. Height growth curves were fitted with a non-linear growth model and the shape of the curves (relative height of the inflexion point) was almost the same for all provenances. The asymptote and the maximum growth rate were correlated at the provenance level but not at the individual phenotypic level. This indicates a good juvenile-mature correlation for seed source vigour. The results for growth characteristics were compared to previous findings concerning the structure of genetic variability and the physiological features of provenances. The growth potential of Maritime pine seed sources appeared to be mostly a result of natural selection for drought resistance.

Key words: provenance test, *Pinus pinaster*, height growth curves, non-linear regression.

Résumé

Un test de comparison de 10 provenances de Pin maritime situé à Mimizan (Landes) a été mesuré à l'âge de 36 ans. Le classement pour la vigueur est resté stable pendant la période de test. Les provenances peuvent être classées dans 2 groupes principaux : d'une part les provenances atlantiques de plaine qui sont vigoureuses et résistantes au froid et d'autre part des provenances méridionales qui sont peu vigoureuses et sensibles au froid. Trois provenances ont des caractéristiques intermédiaires. L'ajustement des courbes de croissance en hauteur d'arbres dominants avec un modèle non linéaire montre que les courbes des différentes provenances ont pratiquement la même forme (paramètre de forme = hauteur relative du point d'inflexion). L'asymptote et la vitesse de croissance maximale sont corrélées au niveau des moyennes de provenances, mais pas au niveau phénotypique individuel. Ceci indique une bonne corrélation juvénile-adulte de la vigueur des provenances. Les résultats sont comparés à ceux obtenus précédemment concernant la structuration de la variabilité génétique dans l'ère de répartition et certaines caracteristiques physiologiques des provenances. Le poten-