SELECTION FROM NATURAL POPULATIONS OF FOREST TREES: VARIATION IN RELATIONSHIP COEFFICIENTS AND SPECIES RESPONSE TO INDIVIDUAL VS. FAMILY SELECTION

Diddahally R. Govindaraju [1]

Abstract.--A knowledge of relationship coefficients has been suggested to be of critical importance in making a decision on choice of selection method from natural populations of forest trees. Data on population structure of several coniferous and angiosperm forest trees were utilized to obtain relationship coefficients. The results suggested that relationship coefficients were low among wind pollinated species; but varied from low to high among insect pollinated species. The choice of individual or family selection may depend on the levels of gene flow characteristic to each species. Species that experience high ($Nm > 1.0$) and low to intermediate ($Nm < 1.0$) gene flow may respond to individual and family selection, respectively.

Additional keywords: Population structure, gene flow, coefficient of relationship, mating system, group selection.

Identification and utilization of genetic variation present in natural populations are fundamental objectives in many tree improvement programs. Genetic gains obtained in selection programs often depend upon the method of selection from base populations. Lush (1947) identified three methods of selection: a) selection based on individual performance or mass selection, b) selection based on the average merit of families or family selection, and c) a combination of individual and family selection. Ledig (19724) evaluated the two most commonly used methods of selection from wild stands of forest trees: individual selection and comparison tree method of selection. He identified the following three parameters that may be critical in making a choice between the two methods: additive genetic variance measured in terms of heritability (h^2), variance due to common environment (c^2), and the coefficient of relationship (r). He speculated that while estimates of heritabilities and variance due to common environment may be obtained for most traits, "it is nearly impossible to quantify the relationship, r, within natural groups of trees...but evidence suggests that such relationships...should vary substantially among species depending upon their population structure", and "a logical choice between comparison-tree selection and individual-tree selection is not possible unless. ..the relationship among trees in groups are known to favor one or the other approach."

The relationship coefficient is defined as the probability of individuals sharing identical genes in common (Wright 1922), and is generally estimated using parent-offspring regressions or complex pedigree analysis on plants grown in common garden experiments. Because of long generation cycles in forest trees, it is formidable to obtain sufficient information on

[1] Research Associate, University of Kentucky, Lexington, KY 40546.

Table 1.--Number of populatons (N), extent of population differentiation (G_{st}), gene flow parameter (Nm), coefficient of relationship (r) and mode of pollination (MP) in forest trees.

Species	N	G_{st}	Nm	r	MP	REF*
GYMNOSPERMS						
Abies lasiocarpa	3	0.015	7.300	0.030	W	1,2
Larix laricina	10	0.032	6.810	0.062	W	1,2
Picea abies	10	0.061	1.967	0.115	W	1,2
P. mariana	21	0.059	3.620	0.111	W	1,2
P. sitchensis	10	0.079	2.370	0.146	W	1,2
P. banksiana	32	0.052	4.270	0.100	W	1,2
Pinus contorta ssp. *latifolia*	9	0.041	4.620	0.079	W	1,2
P. jeffreyii	14	0.138	1.350	0.243	W	1,2
P. monticola	28	0.148	1.340	0.256	W	1,2
P. rigida	11	0.023	8.776	0.045	W	1,2
P. sylvestris	14	0.028	7.483	0.054	W	1,2
Pseudotsuga menziesii	6	0.054	3.041	0.102	W	1,2
Sequoiadendron giganteum	34	0.097	2.190	0.177	W	1,2
ANGIOSPERMS						
Eucalyptus caesia ssp. *caesia*	7	0.994	0.001	0.997	A	1,2
E. caesia ssp. *magna*	6	0.424	0.174	0.596	A	1,2
E. cloesiana	17	0.170	1.081	0.291	A	1,2
E. deligatensis	8	0.240	0.606	0.387	A	1,2
E. obliqua	4	0.243	0.438	0.391	A	1,2
E. pauciflora	3	0.020	5.444	0.040	A	1,2
Quercus ilicifolia	3	0.043	2.470	0.082	W	1,2
Q. marilandica	3	0.161	0.579	0.277	W	1,2
Q. palustris	2	0.017	3.614	0.033	W	1,2
Q. rubra	2	0.072	0.805	0.134	W	1,2
Q. velutina	3	0.171	0.540	0.290	W	1,2

W = prerdominantly wind pollinated, A = predominantly animal pollinated.
*References: 1) Govindaraju (1988a), 2) Govindaraju (1988c).

the relationship among trees within natural populations. Alternatively, several population biologists, particularly sociobiologists, have suggested that allozyme data could be used to estimate both relationship coefficients and make a qualitative decision on the relative opportunities that may exist for individual or group selection in natural populations of animals (Crow and Aoki 1984). This approach has been extended to plants elsewhere (Govindaraju 1988c). This study examines the variation of relationship coefficients among several species of coniferous and angiosperm forest tree species using allozyme data. Data on allozyme variation has been used to describe population structure (Hamrick 1983), gene flow (Govindaraju 1988a,b) and relationship coefficients (Govindaraju 1988c) in various plant populations. Following Slatkin (1981b), I define group and group selection as biologically equivalent of family and family selection.

METHODS

The study involved 13 coniferous and 11 angiosperm forest tree species. Data on the degree of population differentiation, G_{st}, and mode of pollination for these species were obtained from published and unpublished sources (Table 1). The gene flow parameter, Nm, and the coefficient of relationship, r, were caculated from G_{st} values according to Crow and Aoki (1984) as follows: $_{st}\ [4 \alpha Nm + 1]^{-1}$ where $a = (n/n-1)^2$ and G_{st} is equivalent to a weighted average of Wright's F_{st} over all alleles (Nei 1973), and n is the number of populations; the coefficient of relationship, $r = 2 G_{st}/(1 + G_{st})$. The Nm values were grouped into high (> 1 .0), intermediate (0.250 - 0.99) and low (0.0 - 0.249) categories following Slatkin (1981a, 1985) and Govindaraju (1988a). Similarly, the r values were grouped into three categories: low (0.0 - 0.33), intermediate (0.34 - 0.66) and high (0.67 - 1.0). The classification of r values was arbitrary. The rationale for the choosing the above model is provided elsewhere (Govindaraju 1988a,b).

RESULTS AND DISCUSSION

Gene flow (Nm) values varied from 1.340 to 8.776 and 0.001 to 5.444 in gymnosperms and angiosperms respectively. The relationship coefficients for gymnosperms and angiosperms varied respectively from 0.030 to 0.256 and 0.033 to 0.997 (Table 1). Note that the relationship coefficients among half sibs, full sibs and clones are 0.25, 0.50 and 1.0 respectively. Accordingly, the relationship coefficients in wind pollinated species approached zero (0.03) in *Abies lasiocarpa* to 0.290 in *Quercus velutina*, which is comparable to the coefficient of relationship among half-sib families. These results agree with the relationship coefficients reported on other conifers using conventional breeding techniques. For example, Coles and Fowler (1976) obtained r values of 0.23 and 0.30 in two white spruce stands; but these values were only 0.06 and 0.16 in two black spruce stands (Morganstern 1972). Similarly, using Sittman and Tyson's (1971) data, Ledig (1974) reported that relationship coefficients may be at least 0.1 for *Pinus banksiana*. The r values in insect pollinated eucalypts, on the other hand, varied from 0.04 in *Eucalyptus pauciflora* to 0.997 in *Eucalyptus caesia* ssp. *caesia*, indicating that relationship coefficents in insect pollinated species are comparable to the levels of relationship that may exist among clones (also indicate substantial inbreeding) to almost zero; which is characteristic of many predominantly wind pollinated species. Clearly, these results corroborate Ledig's (1974) intuitive conclusions that forest tree species may show different relationship coefficients depending upon population structure.

Although the magnitude of relationship coefficients indicate relative opportunities for group selection (Crow 1986, P.206; Govindaraju 1988c), they do not indicate a threshold limit at which individual selection may override group selection. Leigh (1984) analyzed various constraints that may encourage either individual or group selection, and found that individual selection would operate if the interpopulation gene flow parameter Nm or simply M exceeds 1.0, and family selection would be important if Nm is less than 1.0, but preferably close to zero, per generation. Accordingly, virtually almost all conifers, and a few wind/animal pollinated angiosperm species may respond to individual selection. On the other hand, some eucalypts (particularly *Eucalyptus caesia*), examined in this study may respond to group (family) selection. It is important to stress that the results of the present study represent broad generalizations based on average G_{st} values for any given species. The G_{st} values and hence the relationship coefficients tend to vary among populations, in relation to their geometrical proximities in the distribution range of a given species; suggesting that opportunities for both individual and group selection may exist simultaneously within a species (Govindaraju 1988c). Such a scenario would also influence the choice of selection within the same species. Experimental data are needed to test the validity of the predictions made in the present study.

LITERATURE CITED

Coles, J. F., and Fowler, D. P. 1976. Inbreeding in neighboring trees in two white spruce populations. Silvae Genet., 25: 29-34.

Crow, J. F. 1986. Basic concepts in population, quantitative and evolutionary genetics. 246 p. N.Y.: W. H. Freeman.

Crow, J. F., and Aoki, K. 1984. Group selection for a polygenic behavioral trait: Estimating the degree of population subdivision. Proc. Natl. Acad. Sci. USA., 81: 6073-6077.

Govindaraju, D. R. 1988a. Relationship between dispersal ability and gene flow in plants. Oikos 52: 31-35.

Govindaraju, D. R. 1988b. A note on the relationship between outcrossing rate and gene flow in plants. Heredity (In press).

Govindaraju, D. R. 1988c. Mating systems and the opportunity for group selection in plants. Evol. Trends in Plants (submitted).

Hamrick, J. L. 1983. The distribution of genetic variation within and among natural populations: *In* C.M. Schoewold-Cox rt al. (eds.) Genetics and Conservation, P. 335-348. Menlopark: Benjamin Cummings.

Ledig, F. T. 1974. An analysis of methods for the selection of trees from wild stands. For. Sci., 20: 2-16.

Leigh, E. G. 1983. When does the good of the group override the advantage of the individual? Proc. Natl. Acad. Sci., USA., 80: 2985-2989.

Lush, J. L. 1947. Family merit and individual merit as basis for selection. Part I. Amer. Natur., 81: 241-261.

Morgenstern, E. K. 1972. Preliminary studies of inbreeding in natural populations of black spruce, Picea mariana. Can. J. Genet. Cytol., 14: 443-446.

Nei, M. 1973. Analysis of gene diversity in subdivided populations. Proc. Natl. Acad. Sci. USA., 70: 3321-3323.

Sittman, K., and Tyson, H. 1971. Estimates of inbreeding in Pinus banksiana. Can. J. Bot., 49: 1241-1245.

Slatkin, M. 1981a. Estimating levels of gene flow in natural populations. Genetics 99: 323-335.

Slatkin, M. 1981b. Population heritability. Evolution 35: 859-871.

Slatkin, M. 1985. Rare alleles as indicators of gene flow. Evolution 39: 53-65.

Wright, S. 1922. Coefficients of inbreeding and relationship. Amer. Natur., 56: 330-338.