Minimum Coancestry Selection I. A Pinus taeda Population and its Simulation

By G. R. Askew[1]) and P. M. Burrows[2])

Summary

Variations in inbreeding effective size as influenced by mating design, population parameters and style of selection, for a single cycle of testing and selection, can be quantified by a combination of analytical and simulation methods. Inbreeding effective sizes are contrasted for extremes of coancestry control, unrestricted phenotypic selection versus minimum coancestry selection, and for extremes of selection efficiency, phenotypic selection versus optimum index selection. Simulation results are in close agreement with those from a field test of *Pinus taeda* L. with hierarchical mating design.

Key words: breeding plans, inbreeding depression, effective population size.

Zusammenfassung

Variationen in der inzuchteffektiven Größe, wie sie durch das Kreuzungsschema, die Populationsparameter und die Art der Selektion für einen einzigen Zyklus des Testens und Selektierens beeinflußt werden, können eine Kombination von analytischen und Simulationsmethoden quantifiziert werden. Die inzuchteffektiven Größen werden den Extremen der Abstammungskontrolle gegenübergestellt, und zwar nicht eingeschränkte phänotypische Selektion gegen die Selektion auf minimale Abstammung, und die Extreme der Selektionseffizienz und phänotypischen Selektion gegen optimale Indexselektion. Simulationsergebnisse stimmen gut mit Ergebnissen aus einem Feldversuch mit *Pinus taeda,* dessen Material in hierarchischer Weise gekreuzt wurde, überein.

1. Introduction

Early generations of some tree breeding plans require that selections be made from test plantings with considerable family structure. Some of these may be progeny tests of previous selections. Others may be plantings designed specifically for the purpose of further selection. In either case there is the possibility of combining individual and family performance in a selection index. It is almost inevitable that some of these selections will be related to one another whether or not such an index is employed. For example, if more than n individuals are selected from progenies generated by matings among 2n parents, without selfing, then some coancestry among selections is guaranteed.

In breeding programs based on recurrent cycles of testing and selection, it is possible to impose more control over coancestries among selected individuals in earlier rather than later generations. In each generation there are two dominant motives for considering such control, corresponding to the two main purposes of selection: (1) indi-

viduals chosen to serve as parents of the next generation of the breeding population, and (2) individuals chosen to serve as parents of future forests. Effective population sizes are convenient summary measures of aggregate coancestry status in a set of selected individuals.

The second motive is more immediate and more tangible in its concerns because it refers to coancestry control over matings between related selections placed into routine seed production with the consequence of inbred forests; inbreeding effective size is an appropriate measure for this purpose. We have discussed elsewhere (Burrows and Askew, 1982) the scarcity of experimental evidence with respect to depression of forest performance in this context. The necessity for avoidance of potential inbreeding depression is unknown without such information. Some tree breeders may consider it prudent to control coancestry by avoiding matings between close relatives in routine seed production from controlled pollinations, or to minimize average pairwise coancestry in seed production units with uncontrolled pollination.

The first motive refers to coancestry control over parental selections for successive generations of the breeding population and its consequences with respect to drift effects; variance effective size is a more appropriate measure for this purpose (the connection between variance effective size and inbreeding effective size is noted later). In this context it is usual to discuss selection strategies relative to long term selection limits imposed by drift in finite populations (Robertson, 1960, 1970; Cockerham and Burrows, 1980), though conservation of genetic diversity in the breeding population is also a short term concern. The pressure to produce rapid gain in early cycles of selection is not in harmony with the need to maintain adequate effective population size.

When designing a test planting for one cycle of selection, we know of no simple and precise method to project effective population sizes as influenced by numbers of parents, mating designs, family sizes, numbers selected, and partitions of phenotypic variances into their genotypic and environmental components. Apart from Robertson (1961) and Rawlings (1970), both of whom considered selection from samples of full sib families generated by simple random pair matings, we know of no attempts at such projection. Here we shall contrast some consequences, especially inbreeding effective sizes, at two extremes of coancestry control in a single cycle of directional selection. At one extreme is selection without regard to pedigree. At the other is a style of selection that we have termed 'minimum coancestry selection.'

The purpose of this first report is to develop these and other concepts, to describe the combination of analytical and simulation methods employed in our investigations, and to present detailed results for a hierarchical mating design. Although it is not widely used in forest tree breeding we selected this design as an introductory example for two reasons. First, because it provides the simplest exposi-

[1]) Assistant Professor of Forestry, Belle W. Baruch Forest Science Institute, Clemson University, P. O. Box 596, Georgetown, S. C. 29440, USA.

[2]) Professor of Experimental Statistics, Clemson University, Clemson, S. C. 29631, USA.

tion of consequences of minimum coancestry selection. Second, because measurements of ten-year height and diameter growth of *Pinus taeda* L. in a planting with hierarchical mating design were made available to us and have been used to validate theoretical projections. Contrasts of inbreeding effective size with and without the most efficient selection index, for this same hierarchical design, are presented also.

Subsequent reports will offer detailed results for selection from test plantings with factorial mating and simple pair mating designs, and for selection from polycross tests.

2. Minimum Coancestry Selection

Consider first the selection of n from N individuals in a test planting with specified family structure. The average inbreeding coefficient in progeny obtained by random mating among these selections, without selfing, is identical to the average pairwise coancestry coefficient, $\overline{\Theta}$, in the selected group. Inbreeding, coancestry and unrelatedness are being measured here relative to that among parents of the planting , and so $\overline{\Theta}$ can be formulated from sibship composition of the selected group. We restrict attention to test plantings containing full sibs, half sibs and unrelated individuals, which includes various diallel, factorial and hierarchical mating designs, and simple polycross tests.

Of the $p = n(n-1)$ possible pairings among selections, suppose that p_s are full sib pairings and p_h are half sib pairings. Then

$$\overline{\theta} = (p_h + 2p_s)/8p = 1/2N_e \qquad (1)$$

where N_e is an inbreeding effective size in the sense of WRIGHT (1931). In practice it is not necessary to enumerate all possible pairings in a group of selections when determining $\overline{\Theta}$ or N_e, because given the structure specified by the mating design (excluding polycross tests) it is possible to obtain these quantities from counts of contributions to the selected group from each family.

As a reference base, from which to measure the effects of different selection styles, we use random selection (RS) without regard to phenotype or pedigree. The corresponding inbreeding effective size, denoted by N_{er}, is obtained by replacing p_h and p_s by their expected values determined from the relevant hypergeometric sampling moments, or by replacing ratios p_h/p and p_s/p by their expectations derived from direct probability arguments.

Let N_{es} denote the inbreeding effective size obtained as a consequence of unrestricted phenotypic selection (UPS) defined as selection on the basis of phenotypic ranking without regard to pedigree. For field studies we obtain p_h and p_s directly from observed family contributions and report the corresponding N_{es}. For simulation studies we obtain average values of p_h and p_s over all simulated replicates and use these as estimates of their unknown expectations when calculating N_{es}.

A 'minimum coancestry sample' is defined here as any sample of size n that attains the minimum possible $\overline{\Theta}$ given the family structure in the test planting. After the minimum possible $\overline{\Theta}$ has been determined, let N_{ec} denote the corresponding inbreeding effective size (maximum possible). There will be many such samples in any particular case, similar (but not necessarily identical) in their composition with respect to relationships among individuals included. With each such sample there is an associated

reach statistic defined, in the usual manner, as the deviation of average performance in the sample from that in the test planting. By minimum coancestry selection (MCS) we mean selection of that minimum coancestry sample with the largest reach statistic among all such samples. It should be emphasized that this concept of minimizing average pairwise coancestry among selected individuals is conditioned by n, the size of the selected group. If n is small enough, it may be possible to approach $\overline{\Theta} = 0$ as the minimum, but this is not usually the case in practical applications where n is greater than or equal to at least half of the number of parents of the test planting. On the other hand, if n is not subject to prior restriction then it is possible to define 'zero coancestry samples', including the maximum permissable n as part of the definition and to select among these on the basis of their reach statistics.

3. Hierarchical Mating Designs

Hierarchical mating designs provide simple examples of formulations in the previous section. In general, with m pollen parents (males) and f seed parents (females) per male group, N_e can be evaluated as follows. Let n_{ij} be the count of individuals selected from that full sib family identified to seed parent j in the ith male group. Also, let

$$n_i = \sum_j n_{ij} \quad , \qquad n = \sum_i n_i \qquad (2)$$
$$S_f = \sum_i \sum_j n_{ij}^2 \quad , \qquad S_m = \sum_i n_i^2 \quad .$$

Then

$$P_s = \sum_i \sum_j n_{ij}(n_{ij}-1) = (S_f - n) \qquad (3)$$
$$P_h = \sum_i n_i(n_i-1) - P_s = (S_m - S_f)$$

and

$$N_e = 4n(n-1)/(S_m + S_f - 2n) \quad . \qquad (4)$$

Thus $\overline{\Theta}$ is minimized when $(S_m + S_f)$ is minimized. This can be achieved by an argument due to ANDERSON and CRUMP (1967) in a very different context. The solution requires that contributions from different male groups, n_i's, be as uniform as possible, and within each male group the contributions from different full sib families, n_{ij}'s, should be as uniform as possible. Thus, for hierarchical mating designs, MCS forces most of the selection pressure within full sib families. Indeed, if n is a perfect multiple of mf then MCS is identical to within family selection uniformly. Le $q = [n/m]$ and set $m' = (n-qm)$, where [x] denotes the largest integer less than or equal to x. Then m' male groups contribute $(q + 1)$ selections each, and $(m-m')$ contribute q selections each. Let $r = [q/f]$ and set $f' = (q-rf)$. In a male group contributing q selections, f' females contribute $(r + 1)$ each and $(f - f')$ contribute r selections each. In a male group contributing $(q + 1)$ selections, $(f' + 1)$ females contribute $(r + 1)$ each and $(f - f' - 1)$ contribute r selections each. Substitution of these n_i's and n_{ij}'s into S_m and S_f provides the minimum possible $\overline{\Theta}$ in the form

$$8n(n-1)\overline{\theta} = 2n(q+r) - mq(q+1) - mfr(r+1) \qquad (5)$$

for hierarchical mating designs. If n is a perfect multiple (r) of mf this reduces to

$$8(n-1)\overline{\theta} = r(f+1) - 2 \qquad (6)$$

and then

$$N_{ec} = 4(mf - 1/r)/(f+1 - 2/r). \qquad (7)$$

In these manipulations it has been assumed that the minimum family size available for selection is at least $(r + 1)$.

Evaluation of N_{er}, for RS, requires specification of family sizes. Let t_{ij} be the number of individuals available in family j of male group i, and let

$$t_i = \sum_j t_{ij} \quad , \quad N = \sum_i t_i \qquad (8)$$

with

$$T_f = \sum_{ij} \sum t_{ij}^2 \quad , \quad T_m = \sum_i t_i^2 \; . \qquad (9)$$

Then

$$E(P_s) = p \sum_{ij} \sum t_{ij}(t_{ij}-1)/N(N-1) = p(T_f - N)/N(N-1) \qquad (10)$$

and

$$E(P_h + P_s) = p \sum_i t_i(t_i-1)/N(N-1) = p(T_m - N)/N(N-1) \qquad (11)$$

so that

$$N_{er} = 4N(N-1)/(T_m + T_f - 2N) \qquad (12)$$

and is not a function of n. If $t_{ij} = t$ all i, j then $N = mft$ and

$$N_{er} = 4(mf - 1/t)/(f + 1 - 2/t) \; . \qquad (13)$$

Minimum coancestry selection from a test planting with hierarchical mating design is simple to practice. First, each full sib family contributes its r best performing individuals. If this is insufficient (mfr < n), only top ranking individuals remaining within each full sib family are eligible for further selection. These mf eligible individuals are ranked within their male groups. Selection proceeds sequentially, first among those ranked best in their male groups, then among those ranked second best in their male groups, then third best, etc., as necessary until the required number n has been selected.

4. A Field Study

The test planting investigated here was taken from *The Loblolly Pine Heritability Study* at Bainbridge, Georgia; full details are given by STONECYHPER (1966) and are not repeated here. The 1963 planting of that study includes three sets of progenies each in the same hierarchical mating design, with m = 5 and f = 4, arranged in three replicate blocks at each of two locations, with 12 trees planted per family plot. Dr. JAMES A. BARKER of the International Paper Company supplied us with measurements of stem height and diameter at breast height made after the 1972 growing season, and before the 1973 thinning, for one of these sets (Set 42—63 of STONECYPHER, 1966). With previous losses and our discarding of dead, damaged and otherwise unmeasurable stems, the original planting of 72 trees per full sib family was reduced by approximately 30% overall.

Location and block effects were removed from all measurements by least squares analysis assuming additive effects of families, blocks and locations. Then each full sib family was standardized to t = 40 stems, the maximum possible, by randomly discarding surplus stems with the restriction that representation of the original blocks was as uniform as possible in each family. Standardization to a uniform family size is not a necessity for application of selection styles, and N_e calculations, formulated in the previous section. It was performed in order to provide a test planting with standard design for comparison with results from simulation studies.

5. Simulation Studies

Results from this *P. taeda* field study are illustrative but restricted by specifics of that mating design, and that population of that species in those conditions of growth. We are interested in developing the capability to project consequences of a single cycle of selection for more general combinations of mating designs and poulation parameters.

Evaluation of N_{ec} is straightforward once the composition of a minimum coancestry sample has been determined. Selection differentials for within family selection (BURROWS, 1975; RAWLINGS, 1976) are appropriate for projection of expected reach under MCS from a test planting with hierarchical mating design when n is a perfect multiple of mf, but not otherwise and not for some other mating designs.

Analytical formulations of selection differentials under UPS, from test plantings with specified family structure, might be possible using the methods of RAWLINGS (1976) and HILL (1976); but complexities invoked by the structure they consider (simple random pair matings in the present context) are discouraging when extensions to factorial and hierarchical mating designs are contemplated. Projection of N_{es} for UPS from any of these structures, by similar methods, adds yet another layer of complexity. In this circumstance we resort to simulation studies based on a model of combining abilities that is general with respect to mating design and style of selection.

Let P_{ijk} denote phenotypic performance of the kth individual in the full sib family obtained by mating parents i and j. It is assumed that

$$P_{ijk} = \mu + g_i + g_j + s_{ij} + u_{ijk} + e_{ijk} \qquad (14)$$

where μ is population mean performance,
g_i is the general combining ability of parent i,
s_{ij} is the specific combining ability of parental pair i, j
u_{ijk} is the genotypic deviation of the kth individual from its full sib family mean,
e_{ijk} is the environmental effect unique to the kth individual.

All of g_i, s_{ij}, u_{ijk} and e_{ijk} are assumed to be independent Normally distributed random variables with zero means and variances σ^2_g, σ^2_s, σ^2_u and σ^2_e respectively. Thus phenotypic variance is $\sigma^2_p = (2\sigma^2_g + \sigma^2_s + \sigma^2_u + \sigma^2_e)$. Parameter μ is arbitrary, as is σ^2_p; we set $\sigma^2_p = 100$. Normal random deviates are obtained by the transformation of Box and MULLER (1958) applied to pairs of uniform random variates produced by the method of CHEN (1971). In practice it is convenient to set $w_{ijk} = (u_{ijk} + e_{ijk})$ with variance $\sigma^2_w = (\sigma^2_u + \sigma^2_e)$.

Individual performances, for one simulated replicate of a test planting with specified family structure, are generated sequentially. All of g_i, g_j, s_{ij} and w_{ijk} are produced by scaling Normal random deviates by the corresponding standard deviations (σ_g, σ_s, and σ_w). In the case of a hierarchical mating design, for example, g_i is common to all offspring in the ith male group, and then $(g_j + s_{ij})$ is common to all full sibs from the jth female in the ith male group, and then w_{ijk} is unique to the kth individual in that full sib family. The corresponding sequence for factorial mating designs is obvious but that for polycross tests requires an assumed specification for the distribution of full sib family sizes within each seed parent family.

Table 1. — Inbreeding effective sizes for selection from a *P. taeda* test planting with hierarchical mating design (m = 5, f = 4, t = 40).

Percentage Selected	MCS (N_{ec})	RS (N_{er})	UPS(N_{es}) Diameter	UPS(N_{es}) Height
2	26.67	16.14	9.73	10.43
4	20.04	16.14	11.27	11.74
6	18.57	16.14	12.59	11.66
8	17.92	16.14	12.83	12.02
10	17.56	16.14	13.92	12.69
12	17.24	16.14	13.73	13.49

Table 2. — Reachstatistics for selection from a *P. taeda* test planting with hierarchical mating design (m = 5, f = 4, t = 40).

Percentage selected	Diameter (cm) MCS	Diameter (cm) UPS	Diameter (cm) ratio†	Height (m) MCS	Height (m) UPS	Height (m) ratio†
2	5.32	6.00	0.89	1.91	2.25	0.85
4	4.76	5.26	0.90	1.81	2.03	0.89
6	4.37	4.83	0.90	1.68	1.86	0.90
8	4.16	4.52	0.92	1.61	1.77	0.91
10	3.98	4.27	0.93	1.58	1.70	0.93
12	3.77	4.06	0.93	1.48	1.63	0.91

†: ratio = (MCS reach)/(UPS reach)

For each selection style of interest, reach statistics are compiled and contributions n_{ij} are converted to p_s and p_h at the required selection intensities (specified by values of n) in each simulated replicate and are then averaged over all replicates as substitutes for their expectations. We assure the quality of simulation results by two methods: first by sequential monitoring of the variance components σ^2_g, σ^2_s and σ^2_w accumulated over replicates, and second by setting $\sigma^2_e = \sigma^2_p$ for which N_{es} should be identical to the known N_{er}.

6. Results

Results of selection from the *P. taeda* test, employing UPS or MCS, were compiled at six equally spaced selection intensities, defined by n = 16, 32, 48, ... , 96 out of N = 800, for stem height and diameter independently. Inbreeding effective sizes (N_{er}, N_{ec} and N_{es}) are given in *Table 1* and reach statistics in *Table 2*. Average stem height of the 800 trees was 9.81 m and average diameter was 14.2 cm.

Projections of N_{es} and reach for the same test structure (m = 5, f = 4, t= 40) were obtained by simulation, as described in the previous section, with $\sigma^2_s = 0$ and $\sigma^2_u = 2\sigma^2_g$ as would be the case for an equilibrium population with only additive genetic variance in performance. Selection intensities were set at 1%, 2%, 3%, ... , 12% at each of σ^2_g = 5, 7.5 and 10. These results, based on 100 replications, are compared with those from the *P. taeda* field study in *Figure 1* (inbreeding effective sizes) and *Figure 2* (reach ratios); simulated reach statistics are obtained in arbitrary units, σ_p = 10, and are converted to the ratio (MCS reach)/(UPS reach) for comparison with the field results.

Also shown in *Figure 1* are N_{er} and N_{ec}. The irregular nature of N_{ec} in relation to proportion selected is due to the diophantine nature of the arithmetic; all of n, m, f, q and r are integers.

7. Index Selection

As noted at the outset, the existence of a regular family structure in the test planting provides an opportunity to employ a selection index. In this section we contrast unrestricted index selection (UIS) using the best possible index, with UPS, in absence of environmental correlations within families. Formulation of the efficiency of UIS relative to UPS is well known. Here we examine the effect on N_{es} of UIS in the simulated replicates described in the previous section.

For a hierarchical structure the index is formed as follows (Osborne, 1957). Let P_{ij}, P_i and P denote averages of phenotypic performance in the i, j full sib family, in the ith male group, and in the whole test respectively; and let $X_1 = (P_{ijk}-P_{ij})$, $X_2 = (P_{ij}-P_i)$ and $X_3 = (P_i-P)$. Then index value I_{ijk} is defined as

$$I_{ijk} = b_1 X_1 + b_2 X_2 + b_3 X_3 \tag{15}$$

with optimum choice of weights, maximizing the correlation between I_{ijk} and $G_{ijk} = (g_i + g_j + s_{ij} + u_{ijk})$, given by

$$b_1 = \sigma^2_u/\sigma^2_w \,,$$
$$b_2 = [t(\sigma^2_g+\sigma^2_s) + \sigma^2_u]/[t(\sigma^2_g+\sigma^2_s) + \sigma^2_w] \,, \tag{16}$$
$$b_3 = [ft\sigma^2_g + t(\sigma^2_g+\sigma^2_s) + \sigma^2_u]/[ft\sigma^2_g + t(\sigma^2_g+\sigma^2_s) + \sigma^2_w] \,.$$

Simulation results for the same configurations as before (m = 5, f = 4, t = 40, $\sigma^2_s = 0$, $\sigma^2_u = 2\sigma^2_g = 10, 15$ and 20) are shown in *Figure 3* together with those from UPS for comparison. Calculation of N_{es} for UIS was exactly as
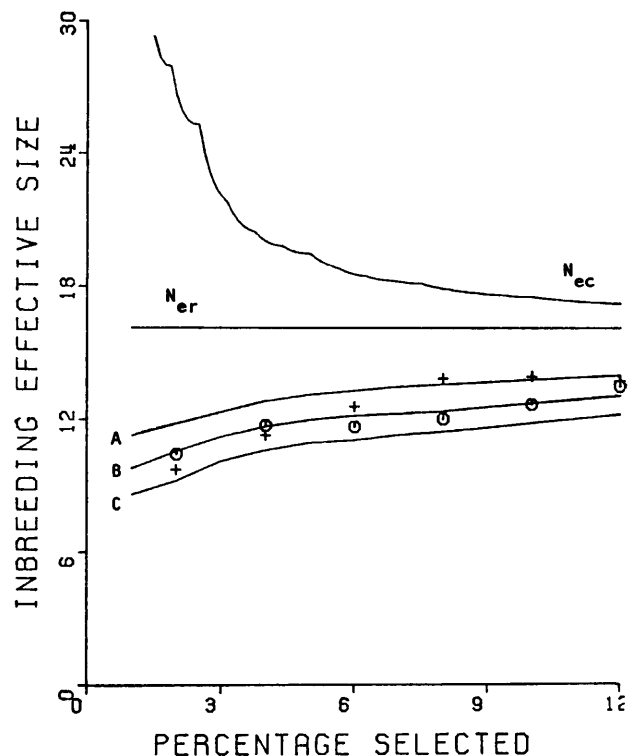

Figure 1. — Inbreeding effective sizes N_{ec}, N_{er} and N_{es} for a planting with hierarchical mating design. Observed N_{es} under UPS for stem height (0) and diameter (+) from the *P. taeda* planting. Simulated N_{es} under UPS for σ^2_e = 80 (A), 70 (B) and 60 (C).
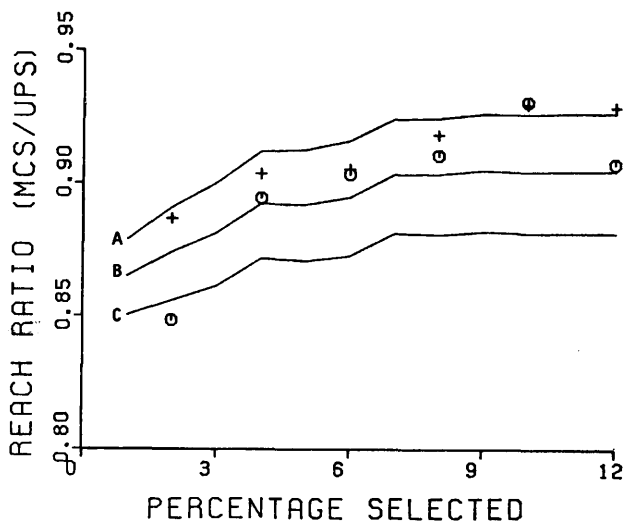
Figure 2. — Ratio (MCS reach/UPS reach) for a test planting with hierarchical mating design. Observed ratios for stem height (0) and diameter (+) from the *P. taeda* planting. Simulated ratios for $\sigma^2_e = 80$ (A), 70 (B) und 60 (C).

described formerly for UPS, but with I_{ijk} replacing P_{ijk} everywhere; weights b_1, b_2 and b_3 were calculated from the assigned parameter values (not from estimates of these parameters in each simulated replicate).

8. Discussion

In this analysis of consequences of a single cycle of testing and selection we have concentrated on variations in inbreeding effective size as influenced by mating design and population parameters, and as manipulated by intensity and style of selection. Calculation and reporting of observed N_{es}, as for the *P. taeda* field study, is retrospective in the sense of CROW and MORTON (1955); averaging over simulated replicates, for a particular model of the test population, is prospective (estimates of expectations serve as projections).
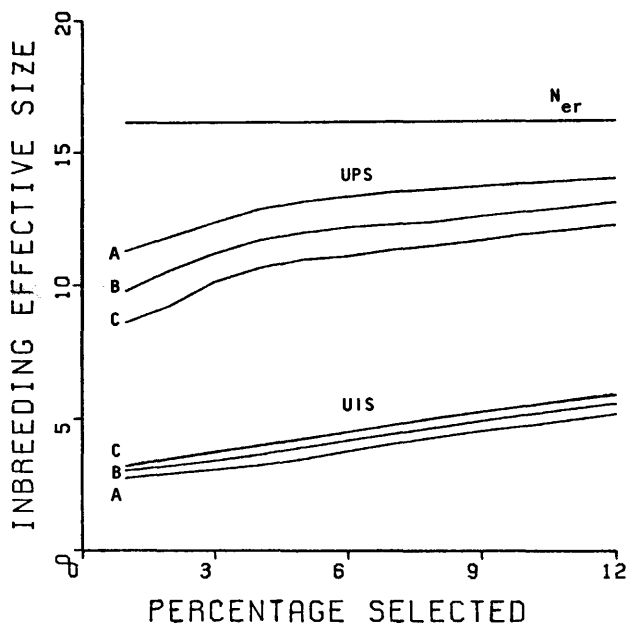

Figure 3. — Inbreeding effective sizes N_{er} and N_{es} for a test planting with hierarchical mating design. Simulated N_{es} under UPS and UIS for $\sigma^2_e = 80$ (A), 70 (B) and 60 (C).

In the adopted definition of $\overline{\Theta}$, based on sibship pairings in the selected group, we have omitted self pairings. If these are included the amended average pairwise coancestry, $\overline{\Theta}_*$, is given by

$$\overline{\theta}_* = \left(\tfrac{n-1}{n}\right)\overline{\theta} + \tfrac{1}{2n} \quad . \tag{17}$$

Then the corresponding effective size, $N_{e_*} = 1/2\overline{\Theta}_*$, is equivalent to the variance effective size (COCKERHAM, 1969) obtained by calibrating against variance of change in gene frequency for neutral alleles.

If selections are pooled from unrelated sources, the inbreeding effective size applicable to their random recombination is simple to obtain. For example, if n_1 selections (with N_{e1}) are obtained from one source and n_2 (with N_{e2}) from an unrelated source, then their combined inbreeding effective size, N_{e12}, is given by

$$\frac{(n_1+n_2)(n_1+n_2-1)}{N_{e12}} = \frac{n_1(n_1-1)}{N_{e1}} + \frac{n_2(n_2-1)}{N_{e2}} \tag{18}$$

If n individuals are to be selected from each of d disconnected repetitions of the same design, for which the projected effective size is N_e, then the projected effective size for the pool of dn selections is larger than dN_e:

$$N_{ed} = dN_e[1 + (d-1)/d(n-1)] \quad . \tag{19}$$

The ordering $N_{ec} > N_{er} > N_{es}$ can be argued generally in terms of variances in family and parental contributions to the group of selected individuals. These variances are smaller under coancestry control than under RS (COCKERHAM, 1967), hence $N_{ec} > N_{er}$, and are larger under phenotypic or index selection than under RS (ROBERTSON, 1961), hence $N_{es} < N_{er}$. Our purpose is to quantify this qualitative ordering, in specified contexts, using a combination of analytical and simulation methods. Though various degrees of avoiding selection of relatives are possible, we have considered only the extreme style 'minimum coancestry selection' for which N_{ec} is analytical, being then a function of mating design and pedigrees, and not of test population parameters. Similar formulation of N_e are possible for lesser degrees of avoidance. For selection unrestricted by coancestry we have considered only the extremes of UPS and UIS, and have resorted to simulation methods.

While the formulations and methods presented are quite general, we have concentrated here on hierarchical mating designs and detailed results are given only for the specific design provided by the *P. taeda* field test. We have used these same methods to investigate a variety of hierarchical structures (ASKEW, 1981), including f = 1 (random pair matings), with parental resources ranging from m (f + 1) = 30 to 90, and either a fixed testing resource (variable family size) or a fixed family size (variable test resource). The pattern of results reported here is typical in all respects: only the quantitative details differ. Thus N_{er}, which serves as the limiting value for both N_{ec} and N_{es} as n increases and therefore determines the vertical location of graphs of N_{ec} and N_{es} as in *Figure 1*, is less than the parental census unless f = 1. The marked contrast in behavior of N_{ec} and N_{es} as selection intensity increases over its practical range is a general feature throughout. Also typical are the magnitudes of proportionate reduction in effective size under UPS and UIS relative to RS, especially at high selection intensities; the effect of UIS on N_{es} is particularly drastic when the efficiency of UIS to UPS is high. The reversal of pattern in N_{es} with change in σ^2_g, from UPS to

UIS (see A, B, C in *Figure 3)*, is a constant feature in all these results and follows from the tendency of UIS to concentrate less and less on particular families, and to produce selected groups with more and more individuals in common with those produced by UPS, as σ^2_g increases.

Changes in family size t have negligible effect on N_{es} unless n is large relative to both t and the number of families included. In preliminary simulations we observed occasional abrupt changes at n = t in graphs of N_{es} against n when working with small family sizes (t = 10 for example). As efficiency of selection increases, while both t and the number of families decrease relative to n, there is a higher incidence of cases where whole families are included in the selected group. When developing projections for a particular test design with a specified family size anticipated at age of selection, that family size is employed in the simulations of course. But for more general studies, including comparative evaluation of different test structures, it is convenient to keep family sizes fixed at some realistic value. In simulations of designs with practical numbers of families (40 to 180), with $\sigma^2_e \geqslant 50$ and n $\leqslant$ 100, decreasing t from 60 to 30 had negligible effect on N_{es} under both UPS and UIS.

The simulation results are based on a simplistic model, especially with $\sigma^2_s = 0$, but one that is apparently adequate for projection of field results. Comparisons of both N_{es} and reach ratios, *Figures 1* and *2*, indicate close agreement between projections and observations in the *P. taeda* field test. Results for both diameter and height are consistent with $0.05 \leqslant (\sigma^2_g/\sigma^2_p) \leqslant 0.10$; that the results for both traits are so similar is attributed to a similar partition of phenotypic variance and to their positive phenotypic correlation. Similar comparisons, for other mating designs and other species in other conditions, are required for further validation of the method. In the present comparisons it should be remembered that field observations are from one replicate experience only, whereas the projections are from averages of 100 simulated replicates. Analysis of variation among replicates of this particular design, for levels of σ^2_g included in *Figures 1* and *3*, indicates maximum standard errors per average of 100 replicates, of $\pm$ 0.35 and $\pm$ 0.19 in N_{es} projections for UPS and UIS respectively. These occur at $\sigma^2_g = 10$ and at the highest selection intensity only; as selection intensity is reduced, the standard errors decrease and eventually stabilize at approximately one half of these maximum values. This analysis and similar results from other simulations suggest that 100 simulated replicates is ample for most purposes. This simulation method was devised specifically to provide projections of inbreeding effective size for one cycle of selection. A model of general and specific combining abilities is sufficient for that purpose. One limitation is that with a special exception, this does not provide for projection of gain. That would require a gene or chromosome model in order to account for recombination after matings among selected individuals. The exception is selection of genotypes for clonal forests with gain based on vegetative replication of G_{ijk}.

If it is believed that $\sigma^2_s = 0$ is inadequate for a particular population, then $\sigma^2_s > 0$ can be incorporated, perhaps with $\sigma^2_u = (2\sigma^2_g + 3\sigma^2_s)$ as would be the case in an equilibrium population with no epistasis in performance. If appreciable quantities of σ^2_s are believed necessary, then attention should be directed to alternative breeding plans specifically designed to exploit specific combining abilities.

As noted previously, MCS from hierarchical structures forces almost all of the selection pressure within full sib families. This has two implications in need of further elaboration. First, there is the obvious consequence for projected gain when compared to that for UPS. This is the simplest demonstration of the penalties of practicing coancestry control among selections. Second, combining the minimum coancestry criterion and index selection produces selections very similar to MCS on phenotypic performance (indeed they are identical if n is a perfect multiple of mf). This is because individuals are ranked exactly the same *within families* whether ranking is by phenotypic values or index values. Thus under MCS there is little or no advantage in using a selection index. This is not the case for some other mating designs, especially factorial structures, where MCS has different consequences. Even for hierarchical designs the penalties of coancestry control can be alleviated to some extent by manipulating selection intensities. As selection intensity increases under UPS, reach increases of course, but N_{es} decreases; whereas under MCS, both N_{ec} and reach increase as selection intensity increases over the range producing practical numbers of selections. Thus the same high selection intensity producing an intolerably small N_{es} under UPS may produce a very desirable N_{ec} under MCS. Large family sizes (t) are therefore valuable when practicing MCS. More generally, this and other manipulations aimed at balancing projected gains against inbreeding effective size are in need of criteria based on more immediate consequences rather than consideration of long term selection limits.

Coancestry control over selections cannot be ignored when assessing relative merits of different designs for selection plantings, because with regard to both effective size and gain it has the potential to dominate the effects of other design variables that can be manipulated. Its benefits must be balanced against its possible detriments. When selection is restricted by coancestry considerations there is an expected reduction of selection differential (reach) in comparison with unrestricted selection *at the same selection intensity*. Whether or not this translates into an eventual sacrifice of genetic gain depends on the magnitude of losses due to drift, or to inbreeding depression, that may have been avoided. Moreover, discussion of relative genetic gain need not be limited to comparisons between selection restricted and unrestricted by coancestry made at the same selection intensity.

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Somatic Cell Differentiation and Rapid Clonal Propagation of Aspen

By M. R. Ahuja

Federal Research Center for Forestry and Forest Products,
Institute of Forest Genetics and Forest Tree Breeding,
Sieker Landstrasse 2, D-2070 Grosshansdorf,
Federal Republic of Germany

Summary

Tissue culture*) techniques were employed for investigating growth and differentiation in relation to rapid clonal propagation of difficult to root aspen *(Populus)* genotypes. Bud stem, leaf and root explants from 48 aspen clones, including *P. tremula, P. tremuloides* and their hybrids, were cultured on modified Woody Plant Medium (WPM), here designated Aspen Culture Medium (ACM). Results of the present study indicate that bud explants can be induced to undergo growth and organogenesis, without much visible callus formation. So far a large number of plants have been regenerated via tissue culture technology from 8 *P. tremula* clones and 6 hybrid aspen *(P. tremula × P. tremuloides)* clones, and from these several hundred plants have been transplanted under field conditions. Plantlet regeneration in 8 more clones is in progress. However, many aspen clones (26 of 48) were largely unresponsive to the *in vitro* conditions provided, indicating that growth and differentiation response is not only controlled by the cultural environment, but is also dependent upon the genotype. The potential of root, leaf, and stem tissues for rapid clonal propagation is being further explored.

Key words: Aspen *(Populus)*, Hybrid aspen, Somatic cell differentiation, Clonal propagation, Clonal variation, Tissue culture.

Zusammenfassung

Gewebekulturtechniken wurden für die Untersuchungen des Wachstums und der Differenzierung im Zusammenhang mit der schnellen klonalen Vermehrung von Genotypen der Aspe, einer bei vegetativer Vermehrung schwer zu bewurzelnden Baumart, angewandt. Explantate, die von der Knospe, dem Stamm, dem Blatt und der Wurzel entnommen wurden, von insgesamt 48 Aspenklonen der beiden reinen Arten *Populus tremula* und *Populus tremuloides sowie* deren Hybriden wurden auf einem modifizierten Woody Plant Medium, das hier als Aspen Culture Medium bezeichnet wird, kultiviert. Die Ergebnisse der vorliegenden Untersuchung zeigen, das Knospenexplantate zu Wachstum und Organogenese angeregt werden können, ohne viel sichtbaren Callus zu bilden. Bislang wurden mehr als 1000 Pflanzen mit Hilfe der Gewebekulturtechnik regeneriert, und zwar von acht Klonen *(Populus tremula)* und sechs Hybridaspen-Klonen *(Populus tremula × Populus tremuloides)*. Hiervon wurden bereits mehrere 100 Pflanzen unter Feldbedingungen aufgezogen. Die Regeneration von kleinen Pflanzen macht bei weiteren acht Klonen Fortschritte. Viele Aspenklone (26 von 48) zeigten jedoch weitgehend keine Reaktion auf die gegebenen in vitro-Bedingungen. Dies zeigt an, daß Wachstum und Differenzierung nicht nur durch die Kulturbedingungen kontrolliert werden, sondern auch von der Reaktion des Genotyps abhängig sind. Das Potential der Wurzel, Blatt- und Stammexplantate, die für eine schnelle klonale Vermehrung verwendet werden, wird weiter erforscht.

Introduction

Tissue explants from tree species are generally difficult to grow and differentiate *in vitro*. This is further compounded by the fact that presence of genetic variation between members of a tree species makes it extemely difficult to design an allpurpose medium for the growth and differentiation of tissues from a given tree species. Nevertheless, slow but gradual progress has been made, in the last few years, towards culture of organs, tissues, and protoplasts from woody plants (see reviews by Karnosky 1981; David 1982; Brown and Sommer 1982; Ahuja 1982). At the present time, a good deal of effort is directed towards vegetative propagation of tree species through tissue culture technology, In many tree species woody cuttings are difficult to root, and in others the rooting frequency may be rather low. In such cases, tissue culture techniques may be exploited as means of accomplishing clonal propagation. Aspen *(Populus* species) are difficult to root from woody cuttings. Previous tissue culture studies based on callus and bud explants of aspen *(P. tremula* and *P. tremuloides)* have revealed that it is possible to induce differentiation of roots, shoots, and plantlets under *in vitro*

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*) The term tissue culture is used in the broadest sense to include culture of meristematic explants from buds, leaf discs, stem segments, and root segments.