A MULTIPLE-OBJECTIVE FOREST TREE BREEDING STRATEGY

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Abstract.--A unique concept is proposed for application of multiple-objective linear programming techniques to tree breeding programs. The concept would retain genetic diversity in the breeding population, permit changes in breeding objectives without returning to earlier generations of selection, and still provide for genetic improvement in any selected direction. Problems with inbreeding are considered, and application of the concept to current tree improvement programs is discussed.

Additional keywords: Multiple-objective linear programming, selection method, selective breeding, tree improvement.

Plant breeders working to increase food and fiber productivity are constantly faced with the problem of how to selectively breed for improvement of many traits simultaneously and yet retain the flexibility to change breeding objectives (directions of improvement). Flexibility in objectives comes from maintaining or incorporating genetic diversity in the breeding population, but this diverts resources away from the short-term maximization of genetic improvement for a single objective.

Present multiple-trait improvement procedures in plant and animal breeding include tandem selection, independent culling levels, and selection indices (Hazel and Lush 1942). All of these procedures are directed toward a single breeding objective. When objectives are initially poorly defined or change in future generations, the breeder often must go back to ancestor populations (if they still exist) to obtain the needed germplasm. This is both inefficient over the long run and impractical for plants that have long generation intervals. Furthermore, the gradual Loss of genetic diversity from selection for the same objective over many generations can have disastrous consequences in crop vulnerability.

More conservative, but less efficient, breeding strategies have been followed for forest trees than for annual crops (Namkoong 1970). Recently, multiple breeding populations, or sublining, have been proposed to increase the efficiency of selection indices for trees (Namkoong 1976) and to solve inbreeding problems (Talbert 1979). However, these procedures still are directed toward trait improvement for a single objective.

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Recent advances in mathematical programming techniques suggest that multiple-objective linear programming (MOLP) can be effectively used in directing multi-trait, multiple-objective genetic improvement programs. Kung et al. (1975) noted this potential for forestry seed orchards. The approach represents a new option for breeders, and much work must be done on genetic theory and computer programs before it can be implemented.

This paper describes how the MOLP techniques might be used in forest genetic improvement programs. These new techniques can help tree breeders establish and maintain genetically diverse, flexible breeding populations in an efficient manner while continuing to accomplish genetic improvements for specific objectives.

THE PROPOSED CONCEPT

Schematic Representation of the Breeding Strategy

The breeding population is kept separate from the production (seed orchard) population, as shown in Figure 1 and discussed by Franklin (1975). Up to 15 traits may be considered simultaneously for recurrent selective breeding. These traits can include different variables, such as growth and disease resistance, and different extremes of the same variable, such as high and low wood specific gravity. Potential breeding trees are measured for each trait, either phenotypically or genotypically, and indexed in the multiple-trait space (Figure 2a). The convex hull of the candidates is found and MOLP applied to find the efficient frontier of all trees in that trait space (Figure 2b). Adjacent candidate trees on the frontier (trees 2 and 4, 4 and 9, and 9 and 10 in Figure 2a) are designated for controlled crosses with each other. Note that crosses are not made among breeding trees whose trait combinations fall interior to the convex hull. Furthermore, any "enrichment" of the breeding population by introduction of new genetic material during advanced generations (Franklin 1975) will require that the new material first be progeny tested in a new breeding population, or subline. Candidates on the frontier of this subline population will then be crossed with corresponding candidates of the original breeding population.

The offspring from the controlled crosses will provide the potential breeding trees for the next generation. These trees will again be mapped in the multitrait space, and another MOLP will be solved to identify candidate trees and crosses for the next successive generation (Figure 2c). The candidate crosses may he screened by filter programs to reduce crosses among related individuals and thereby minimize inbreeding buildup. Additional filter programs can be utilized to avoid expanding numbers of candidates and crosses over successive generations.

No economic or heritability weights will be used in the MOLP breeding strategy, since the procedure involves only the breeding population and aims at maximizing gains for all breeding objectives

MODEL OF RECURRENT SELECTION PROGRAM

Wild
Stands

Breeding Populations

Production Populations
(Seed Orchards)

Mild selection
of frontier trees

◄ − −(MOLP)

1st Generation   Strong selection for   1st Generation
Breeding Pop'n   specific objectives   Seed Orchards

◄ − −(MOLP filter
        of matings)

Rogue on
progeny info

Control-Pollinated
Progeny Test

Mild select. of frontier trees

◄ − −(MOLP)

2nd Generation   Strong selection for   2nd Generation
Breeding Pop'n   specific objectives   Seed Orchards

◄ − −(MOLP filter
        of matings)

Rogue on
progeny info

Control-Pollinated
Progeny Test

Mild select. of frontier trees

◄ − −(MOLP)

3rd Generation   Strong selection for   3rd Generation
Breeding Pop'n   specific objectives   Seed Orchards
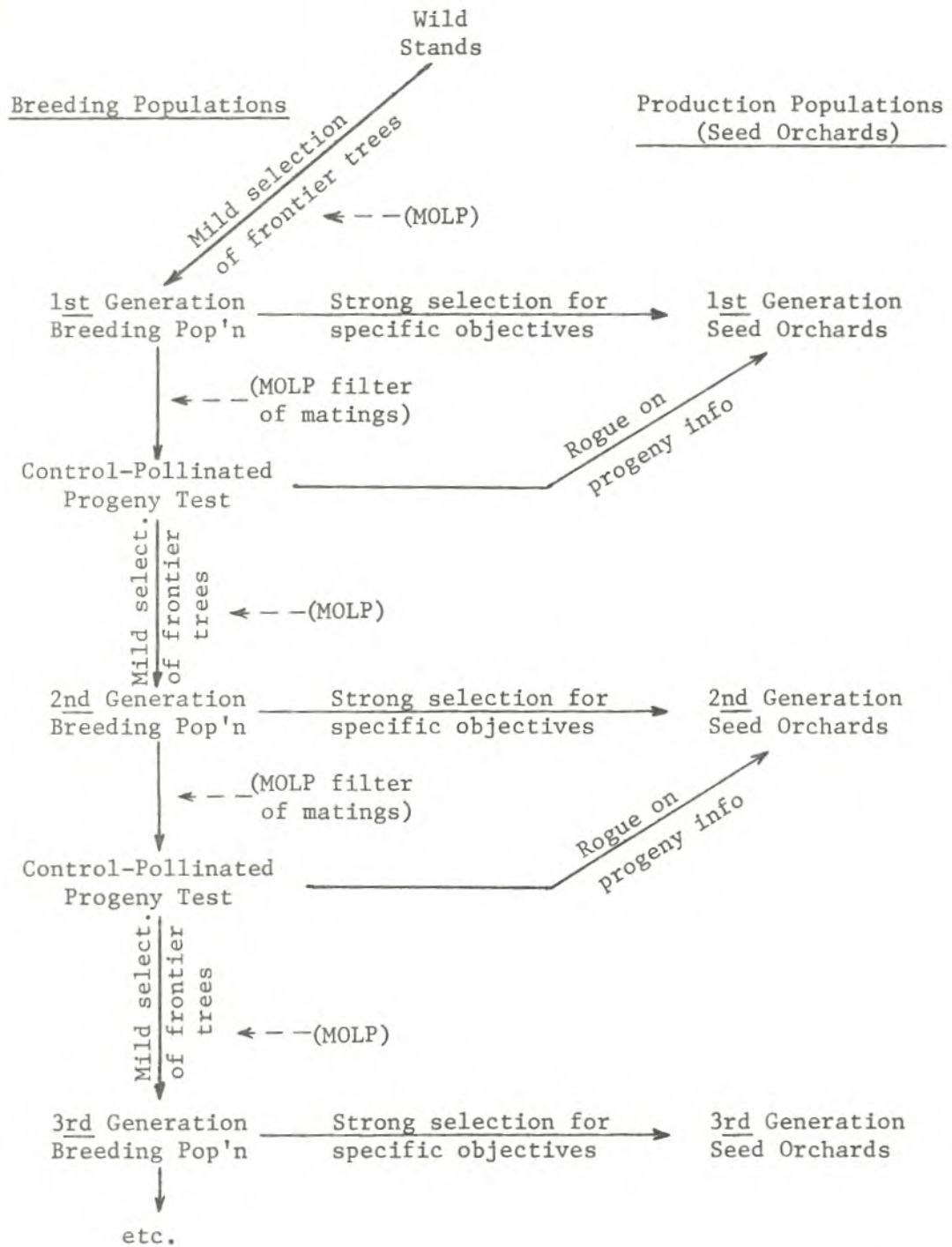
etc.

Figure 1.   Schematic model of the proposed recurrent selection breeding
            strategy utilizing multiple objective linear programming (MOLP).

$$y_{ij} = (X_{ij} - \bar{X}_j)/\sigma_j \quad , \quad i = 1, \ldots, I.$$
$$j = 1, \ldots, J.$$

Consider the following system defining P.

$$P = \{ p \mid \sum_j^J y_{ij} \, p_j \leq 1, \, i=1, \ldots, I\}$$

P is a polytope whose interior contains the origin. Therefore, an inclusion reversing map is established between P and its polar dual P* (Grunbaum 1967).

$$P* = \{ P* \mid \sum_{j=1}^J v_{mj} \, p*_j \leq 1, \, m=1, \ldots, M \},$$

where v_{mj} are the components of the M vertices of P. A survey of algorithms for finding all vertices of a polytope may be found in Mattheiss and Rubin (1980).

Now let P* = T(x) to obtain the inequalities defining X.

$$P* = T(x) = \{ T(x) \mid \sum_{j=1}^J v_{mj} T(X)_j) \leq 1, \, m=1, \ldots, M\}$$

So,

$$\sum_{j=1}^J \frac{v_{mj}}{\sigma_j} X \leq 1 + \sum_{j=1}^J \frac{v_{mj} \bar{X}_j}{\sigma_j}, \quad m=1, \ldots, M$$

or simply

$$Ax \leq b.$$

Now that X is defined by a system of linear inequalities whose extreme points correspond to certain individuals who are candidates for the breeding program, X may serve as the feasible region for the following multiple objective linear program (MOLP).

Maximize Cx
x ∈ X

where: $X = \{x \mid Ax \leq b\}$, as obtained above, C is a K x J real matrix.

Cx is a set of K linear functionals which are to be maximized. The solution to the MOLP is a set of nondominated extreme points or efficient points E, corresponding to candidates who should be selected to participate in the breeding program. Techniques for the solution of the MOLP are given in Zeleny (1982), which contains an excellent 36 page list of references.

There are two primary constructs which may be used to specify a row of C. The first is the notion of the selection index. Each of the J traits of interest may he given a weight based on economic, heritability, genetic correlations or other arbitrary considerations. Several different selection indices may be constructed and considered simultaneously. The second notion is based on the idea of breeding all individuals who are undominated on one or more, or a combination of traits. In this case the matrix C would be a J dimensional identity matrix, since all traits are positively oriented.

Given X, a specific C will yield a set of individuals E which should participate in the breeding program. For every choice C, some set E results.

Let candidates i and ^{2} he members of E. The breeding program should comprise all pairs of candidates lying on a maximally efficient face of E, for every maximally efficient face of E. Let this set of candidate crosses be called S.

$$S = \{(X_1, X_\ell) \mid X_1, X_\ell \in F_{ME}\}, \text{ for all } F_{ME},$$

where F_{ME} is a maximally efficient face of X. It may be desirable to filter S on the basis of inbreeding coefficient, breeding population size, ancestor, distance, managerial considerations, or other criteria. That is, some subset of S may be obtained for the implementation of the actual breeding program, based on several heuristics (Steuer 1980).

DISCUSSION

The MOLP procedure can be applied to either phenotypic or genotypic selection. Because of the long generation interval for most forest trees, however, we feel that phenotypic (mass) selection in the first generation and combined selection (family selection plus phenotypic selection within families) in progeny tests for later generations will continue to be used. Therefore, phenotypic values (or phenotypic scores on a comparison-tree basis) for each of 10 to 15 traits would be mapped for each tree (Figure 2a) in the first generation. A score based on family performance and individual phenotype, and weighted by family and individual heritahilities, would be used for each trait of each tree in the advanced-generation progeny tests. Genetic gains for single objectives could be calculated by standard methods, where the direction of gain is specified. Measurement of multiple-objective gain is a difficult and unresolved question, since there are an infinite number of starting points and directions which may be chosen. The distance between the frontiers of two successive generations might he used as an omnibus measure of genetic change in the total breeding program.

Inbreeding may or may not be allowed in the breeding program, depending on decision criteria made at any time and programmed into filter software. A necessary requisite will be the maintenance of pedigrees on all individuals in the breeding population and calculation

of inbreeding coefficients that would occur for each candidate cro
Those crosses which would provide inbreeding coefficients about
designated cutoff level would not be made. If inbreeding rea
unacceptable levels and can no longer be constrained by this fil
process, alternative methods for alleviating the problem include
enrichment with new selections or (ii) maintenance and crossing a
subline populations.

As the number of traits and the number of trees in the breed
population increase, the number of crosses in the breeding prog
becomes combinatorially explosive. However, many trees that would
included in crosses in present breeding programs will not be used, si
they are interior to the convex hull. Thus, the numbers of required
crosses could still be less for the MOLP process than for of
programs. Furthermore, filtering procedures based on heuristics such
inbreeding coefficients, mathematical "distance" between individuals
the convex hull, and number of crosses allowed per individual can
used to reduce the number of crosses to manageable proportions.

An added benefit of the MOLP-directed breeding program will be
better   conservation   of   gene   resources   than would occur in
single-objective programs.   Schoenike   (1975) has listed breeding
programs and their associated progeny tests as one method of gene
conservation for forest gene pools. The increased number of trait
combinations maintained in the MOLP program will greatly enhance the
probability of conserving a broad-based sample of the natural gene pool.

APPLICATION

Current tree breeding programs can be quickly converted to the MOLP
strategy by (i) combining the separate company, state, and federal
programs for a particular breeding region (a provenance, or geographic
race where all the trees are compatible in flower timing) into one
multiple-objective program, (ii) mapping the many existing selections
from this breeding region into the multiple-trait space for an expanded
number of traits, (iii) identifying candidate trees on the efficient
frontier to include in the MOLP breeding population, and (iv) starting
the MOLP-identified controlled crosses. The university-industrial
cooperatives in the southern U.S. would be logical first choices for
such a strategy, since the university in each cooperative is already set
up to provide the centralized administration of the breeding program.
The breeding population would be maintained and managed by the
university at a centralized location(s).

One advantage of a centralized multiple-objective tree breeding
program for a given species in a particular breeding region would be
greater efficiency in administration and costs than for many small
programs. The various organizations contributing to the breeding-region
MOLP program could specify their particular objectives for each
generation, and the breeders would be able to identify and release to
them the most genetically-advanced candidate trees for the specific

objective. Vegetative propagules from these candidates can then be propagated in clonal production seed orchards at each organization's site. This procedure would allow flexibility for producers to change objectives at any time in the history of the breeding program.

CONCLUSION

MOLP procedures have been employed in water resource management and in multiple-use forestry applications. The concept represents a developed technique for addressing multiple criteria decision problems. Genetic selection is essentially a multiple criteria decision problem calling for the best available management approach. To use single objective techniques on a multiple criteria problem is to sacrifice potential gain in several traits to the attainment of one objective, which often will not withstand the test of time.

LITERATURE CITED

Franklin, E. Carlyle. 1975. Strategies for genetic gains in advanced generations of forest tree breeding. In: Forest Tree Improvement --The Third Decade. Bart A. Thielges (ed.). Division of Cont. Ed., Louisiana State Univ., Baton Rouge. pp. 147-160.

Grunbaum, B. 1967. Convex Polytopes. John Wiley & Sons, New York. 550 p.

Hazel, L. N., and J. L. Lush. 1942. The efficiency of three methods of selection. Jour. of Heredity 33:393-399.

Kung, Fan H., Calvin F. Bey, and T. H. Mattheiss. 1975. From progeny testing to seed orchard through mathematical programming. In: 13th Southern Forest Tree Improvement Conference. Sponsored Pub. No. 35, Southern Forest Tree Improvement Comm., Raleigh, NC. pp. 242-249.

Mattheiss, T. H., and D. S. Rubin. 1980. A survey and comparison of methods for finding all vertices of convex polyhedral sets. Mathematics of Operations Research 5(2).

Namkoong, G. 1970. The problem of optimality in multiple trait breeding. FAO Second World Consultation on Forest Tree Breeding. FAO. Rome. Vol. 2:775-781.

Namkoong, C. 1976. A multiple-index selection strategy. Silvae Cenetica 25(5-6):199-201.

Schoenike, Roland E.   1975.   Tree improvement and the conservation of gene resources.   In: Forest Tree Improvement--The Third Decade, Bart A. Thielges (ed.).   Division of Cont. Ed., Louisiana State Univ., Baton Rouge. pp. 119-140.

Steuer, R. E. 1980. Operating manual for the ADBASE package for solving multiple objective linear programming problems: Release 8/80. College of Business and Economics, Univ. of Kentucky, No. BA 7. 66 p.

Talbert, J. T. 1979. An advanced—generation breeding plan for the N.C. State University—industry pine tree improvement cooperative. Silvae Cenetica 28(2-3):72-75.

Zeleny, M.   1982. Multiple Criteria Decision Making. McCraw—Hill Book Co., New York. 563 p.