cen einer Selektion von Kreuzungseltern auf hohe Kombinationseignung aufgrund der Leistungen der durch freies Abblühen der Kreuzungspartner erhaltenen Einzelbaumnachkommenschaften.

Schlagworte: Konkurrenz; Konkurrenzabhängigkeit der Korrelation zwischen Nachkommenschaften kontrollierter Kreuzungen und den Nachkommenschaften ihrer frei abgeblühten Eltern; Selektion auf hohe Kombinationseignung aufgrund der Leistungen der frei abgeblühten Einzelbaumnachkommenschaften.

Summary

Some experimental results about the dependence on competition of the correlation between progenies from controlled crosses and the progenies obtained by open pollination of the parents in the character 'tree height'.

To get — using field experiments arranged in plots — quantitative results about the magnitude of the competitive effects at the borders of neighbouring plots and to get results about the biasing effects caused by these competition phenomena a series of field experiments had been performed, where the treatments are different progenies of spruce (obtained after controlled and open pollination of certain selected individuals). We used 6 different locations each with the same 20 treatments, which have to be tested. The design was: A rectangular lattice with 3 replications with 5 blocks, each block with 4 treatments in each replication and 6 X 6 = 36 plants per plot. We have performed two different ways of analysis of the character 'tree height' in the years 1959, 1963, 1966, 1969 and 1971. At first an analysis, where all trees of each plot are used, e.g. all 6 X 6 = 36 single trees of each plot. Secondly, we performed an analysis, where all plants at the borders of the plots are omitted from the analysis. In this case only the remaining interior of the plot, e.g. the 4 X 4 = 16 single trees in the plots interior, are used in this second analysis. From different results of these two procedures of analysis it is possible to draw conclusions about the quantitative relations of these competitive effects at the borders of the plots. The treatments are progenies from controlled crosses and progenies obtained after open pollination of the parents. To investigate the problem of the dependence on competition of the correlation between progenies from controlled crosses and the progenies obtained after open pollination of the parents in the present publication different correlation-coefficients were computed and studied in detail for both different procedures of analysis mentioned above. We, partly, get considerable differences as well as characteristic results and similarities for the temporal variation of these correlation-coefficients between both procedures of analysis. These results as well as the derivation of interesting conclusions for breeding are discussed in detail; for example, the possibility of selecting parents for crosses with high combining ability only using the yield of the open pollinated single tree progenies.

Key words: competition; dependence on competition of the correlation between progenies of controlled crosses and progenies obtained after open pollination of the parents; selection for high combining ability only using the yield of the single tree progenies obtained after open pollination of the parents.

Literatur

COCHRAN, W. G. und COX, G. M.: Experimental Designs. Second Edition. John Wiley + Sons, New York — London — Sydney (1957). — HUHN, M.: Über den Einfluß der Konkurrenz auf die Aussagefähigkeit forstlicher und landwirtschaftlicher Versuche: Experimentelle Ergebnisse aus einer Feldversuchsserie mit Fichtenkreuzungen. Silvae Genetica 23 (1—3), 77—94, 1974.

A Multiple-Index Selection Strategy[1]

By G. NAMKOONG[2]

(Received October 1976)

Introduction

When tree breeders must improve many traits simultaneously, selecting efficiently for these traits is extraordinarily difficult. The economic value of multiple products at various ages requires that several traits be improved, and long breeding cycles mitigate against tandem improvement of one trait at a time. Long rotations make prediction of the economic values of several traits imprecise, and estimation of biological parameters is also often imprecise. Breeders, therefore, are often forced to increase their precision by following conservative strategies, such as reducing the number of traits selected, selecting for broadly adaptable but less extreme types, or using minimax or other loss function criteria (NAMKOONG, 1970). I propose a breeding stratagem which would overcome some of these difficulties.

Single Index Selection

Traditionally, breeders have selected a single, intermating, breeding population with genetic variances and covariances among the traits of concern. From this base population, the breed parents for the next generation are chosen with some constraints on minimal effective population sizes. These constraints are usually formulated to maintain certain levels of genetic variance in subsequent generations and to avoid any of the immediate dangers of monoculture or of inbreeding depression. The particular set of parents chosen for multiple trait improvement depends on the selection and mating system used. If generations can be rapidly cycled, the sequential, tandem improvement of one trait per generation can ultimately improve all traits. When earlier generation pay-offs for all traits are desired, a simple system called "independent culling levels" requires that acceptance levels for each trait be established and that the population be simultaneously culled for all traits. Since neither of these systems uses in-

---

[1] Joint contribution of the Southeastern Forest Experiment Station, U. S. Forest Service, and the Genetics Department, North Carolina State University. Published as Paper No. 5090 in the Journal Series of the North Carclina Agricultural Experiment Station, Raleigh, N.C.

[2] Geneticist, U. S. Forest Service and Professor of Genetics and Forestry, North Carolina State University, Raleigh, N.C.

formation on genetic or phenotypic correlations among traits, simultaneous trait improvement can be hampered by opposing or poorly directed selective efforts. The index system of simultaneous selection was developed by Hazel and Lush (1942) to use data on genetic and phenotypic variances and covariances, and economic weights. It has many optimal properties (Henderson, 1961) and has been adapted for use even when a trait has no direct economic value (Kempthorne and Nordskog, 1959).

However, in spite of its theoretically optimal properties, two persistent problems have inhibited the utility of trait index selection. One problem is that the economic value of the component traits is rarely reducible to a linear function and, even if it is, the relative economic weights are estimated with some error (Namkoong *et al.*, 1969). The other problem is that the optimum index weights involve errors in estimating the genotypic and phenotypic covariance matrices (Williams, 1962a), and these errors can often be so large as to yield poor breeding gains (Namkoong and Matzinger, 1975). In the latter case, one may resort to a "base" index which gives weights according to a linear economic function (Williams, 1962b) or one may improve weight estimates by approximating the moments of the error distribution (Williams, 1962b). The approach described below is applicable where these approximate solutions are viable and also where only economic estimation errors exist.

If several traits are measured on each entry tree, the trees can be mapped by their coordinates $x_1, x_2, \ldots. x_n$ into an n-dimensional space. The $\mathbf{x}$ vectors for each tree then form an n-dimensional multivariate centroid for the population with mean $\mathbf{m}$ and dispersion matrix (Σ). The index is a line in this space onto which each tree's $\mathbf{x}$ is projected to produce a single scalar value on which selection is based. The projection is perpendicular to the index line and is made by assigning coefficients $\mathbf{b}$ to each trait, and summing the products, $b_1x_1 + b_2x_2 + \ldots. + b_nx_n = \mathbf{b'x} = \mathrm{I}$. The weighting coefficients b_i are the direction cosines of the index line.

The $\mathbf{b}$ vector may be estimated by a vector $\mathbf{B}$ of relative economic weights ($\mathbf{a}$) for each trait for a "base" index, or by the product $\mathbf{P}^{-1}\mathbf{G}\ \mathbf{a}$, where $\mathbf{P}$ and $\mathbf{G}$ are the covariance matrices of phenotypic and genotypic values respectively. However it is derived, $\mathbf{B}$ can only estimate the true optimum weights $\mathbf{o}$ with some error, and hence an error distribution f($\mathbf{B}$) exists. If $\mathbf{P}^{-1}\mathbf{G}$ is estimated with negligible error, but $\mathbf{a}$ is estimated by $\mathbf{A}$ with some error, then the error in $\mathbf{B}$ is a linear function of the errors in $\mathbf{A}$. If $\mathbf{A}$ has a multivariate normal distribution (MVN), then f($\mathbf{B}$) is also MVN. This can be expected to be only approximately true for small steps in genetic gain if the value relationships among traits is actually non-linear.

If $\mathbf{P}^{-1}\mathbf{G}$ is subject to substantial estimation error, and the index is estimated by $\mathbf{P}^{-1}\mathbf{G}\ \mathbf{a}$, then f($\mathbf{B}$) is unknown. However, the lower moments can often be approximated and the variance properties of $\mathbf{B}$ thereby also approximated. These errors can only increase the variance in $\mathbf{B}$ over the case when only error in $\mathbf{A}$ is involved.

If a population is selected in a particular direction that does not coincide with the optimum direction $\mathbf{o}$, the value of the population is expected to be less than if $\mathbf{p} = \mathbf{o}$. It may be reasonably modeled, that the population value declines symmetrically as $|\mathbf{p} - \mathbf{o}|$ increases. A convenient value function, g($\mathbf{b}$), to consider has the form of a scalar multiple of a probability density function with a maximum at $\mathbf{p}$ and dispersion (τ). The expected population value, v, is then the product of the value it has at a point g($\mathbf{b}$) and the probability f($\mathbf{b}$) that $\mathbf{b}$ is the optimum vector $\mathbf{o}$ integrated over all possible $\mathbf{b}$ points. Hence:

$$v = \int_{b_n} \ldots \int_{b_1} g(\mathbf{b})\, dF(\mathbf{b}).$$

Multiple Index Selection

In many breeding operations, it may be possible to develop several breeding populations and to use the seed from the one that turns out to be best when the optimum direction is better defined. Instead of a single, large population selected for a single direction of trait improvement, a breeder may choose which one(s) among the several populations developed more nearly approximates the optimum trait combination. Lead time is still required for the chosen seed to mature, but the final direction need not be chosen an entire generation in advance. As an example, consider a two-trait case where the economic predictions are such that the relative weights are normally distributed. Then, f($\mathbf{b}$) can be reduced to a univariate normal probability density function. Assume also that the form of the population g($\mathbf{b}$) is univariate normal. Then,

$$v_i = k \int_{\mathbf{b}} \exp \left[-\frac{(\mathbf{b} - \mathbf{o})^2}{2\sigma^2_f} - \frac{(\mathbf{b} - \mathbf{p}_i)^2}{2\sigma^2_{g_i}} \right] d\mathbf{x},$$

where k is a scalar constant dependent on $\sigma^2_{g_i}$ and σ^2_f, $\sigma^2_{g_i}$ is the second moment of the i-th population's value function, σ^2_f is the variance of the probability function f($\mathbf{b}$), $\mathbf{o}$ is the expected value of the weights, and $\mathbf{p}_i$ is the set of weigths for which the i-th population is optimum. If multiple populations are carried and a decision rule for choice of one or the other is made, the total value of the set of populations is the sum of single population values within the bounds of the decision function. The errors in this choice are assumed here to be small.

In the simplest case of two-variate, two = population breeding, it can easily be derived that if the σ^2_f is large relative to the $\sigma^2_{g_i}$, the benefits of splitting the breeding population into sub-units can be considerable. Even if $\sigma^2_{g_i} = \sigma^2_f$, the strategem of aiming two populations not at the expected optimum weights $\mathbf{o}$ but at $\pm 0.7\ \sigma_f$ units from the expected optimum weights can give a sum of v values 17% greater than a single population.

Actual gain in such cases is reduced by a loss in selection differential as well as by additional cost of maintaining two populations, but an examination of the population sizes used in forestry indicates the loss in selection differential can be relatively modest. Consider that 100,000 trees may constitute an initial candidate population. It is now common to select 50 parents. The standardized selection differential (i) is 3.554. Alternatively, two populations of 25 each would have the same aggregate i = 3.554, while two populations of 50 each would have an aggregate i = 3.367, a 5% loss in i for a net gain of 11%. Even 250 parents grouped into 5 subpopulations of 50 each have an aggregate i = 3.104. The 13% loss in i however is offset by enriched opportunities for larger gains than the 17% for two = population deployment. Since 50 parents have often been chosen as a hedge against errors in selection and since gains can be insured better by splitting populations, small subpopulations seem feasible. Perhaps 10 populations of 15 parents each can be considered for multidimensional selection. These would provide a widely secure and higher gain opportunity for directed selection at a moderate 8.5% loss in aggregate selection differential.

Small populations carry high risks of losing useful alleles by accident and of inducing inbreeding depression in yield. While intercrossing among unrelated individuals for seed production would avoid inbreeding depression, a loss of alleles is difficult to compensate for. Hence, multiple replicates of small populations would eventually require intercrossing among some of them to regenerate genetic variances. Alternatively, the replicates could be selected in a reciprocal recurrent selection system for hybrid performance, but this would still require larger populations to maintain genetic variances.

Conclusion

Multiple populations would have to promise sufficient improvement over single populations to justify their costs. When uncertainty exists in estimating optimum index weights, splitting populations can provide substantial advantages. It has also been proposed by Baker and Curnow (1969) that, even when directed towards a single objective, multiple small populations can give greater gains than single populations by selecting and intercrossing among replicates. A heuristically optimal strategy is for tree breeders to manage their gene pools in much the same way that experimental designers allocate test units. If replicate populations are deployed, around points of high expectation, and some populations are deployed more distantly from the expected, some sample will be reasonably close to optimum whatever true **o** results. Ordinarily, one would array the sample points to span the major trait variations expected and hence to vary in all n dimensions. Reductions in the dimension of the space the points occupy would also probably reduce the dimensionality of the error surface of **b**. If the base breeding populations can be crossed and foundation breeds quickly developed for subsequent commercial seed production, more extreme sampling points can be used. In such cases, the "corners" of the n-dimensional space might be heavily sampled to help assure a large diversity of alleles among the base populations. In slower breeding as is typical for trees, a tighter contour in n space would seem more likely to be optimal for population sampling. In any case, the breeding design should accommodate both the desirable points specified by the breeder and changes in direction that may occur with time. A failure to specify population directions is an abdication of responsibility and is in fact a choice of a **b** vector made by indirection. While an optimal strategy may not be easily defined, the multiple index selection system provides an opportunity for obtaining immediate genetic gain and for simultaneously accommodating an uncertain future.

Key words: Simultaneous selection, single index selection, multiple index selection, multiple population selection.

Literature Cited

Baker, L. H., and Curnow, R. N.: Choice of population size and use of variation between replicate populations in plant breeding selection programs. Crop Sci. 9: 555—560 (1969). — Hazel, L. N., and Lush. J. L.: The efficiency of three methods of selection. J. Her. 33: 393—399 (1942). — Henderson, C. F.: Selection index and expected genetic advance. In: Statistical Genetics and Plant Breeding. Ed. by Hanson, W. D., and Robinson, H. F. Publ. No. 982: 141—163, NAS-NRC. Washington, D. C. (1967). — Kempthorne, O., and Nordskog, A. W.: Restricted selection indices. Biometrics 15: 10—19 (1959). — Namkoong, G.: The problem of optimality in multiple trait breeding. FAO Second World Consultation on Forest Tree Breeding. FAO. Rome. Vol. 2: 775—781 (1970). — Namkoong, G., Barefoot, A. C., and Hitchings, R. G.: Evaluating control of wood quality through breeding. TAPPI 52: 1935—1938 (1969). — Namkoong, G., and Matzinger, D. F.: Selection for annual growth curves in *Nicotiana tabacum* L. Genetics 81: 377—386 (1975). — Williams, J. S.: Some statistical properties of a genetic selection index. Biometrika 49: 325—337 (1962 a). — Williams, J. S.: The evaluation of a selection index. Biometrics 18: 375—393 (1962 b).

Zur intraspezifischen Variation von Pinus contorta auf Versuchsflächen in der Bundesrepublik Deutschland

I. Ergebnisse aus der Versuchsserie von 1960/61[1])

Von B. R. Stephan[2])

Aus der Bundesforschungsanstalt für Forst- und Holzwirtschaft Hamburg-Reinbek, Institut für Forstgenetik und Forstpflanzenzüchtung

(Eingegangen Oktober 1976)

Einleitung

Pinus contorta Douglas ex Loud. besitzt ein außerordentlich großes natürliches Verbreitungsgebiet im westlichen Nordamerika, das sich in Nord-Süd-Richtung vom 64. (Alaska) bis zum 31. Breitengrad (Nieder-Californien) und in West-Ost-Richtung vom 140. (Pacifik) bis zum 105. Grad westlicher Länge (Ostseite der Rocky Mountains) erstreckt. In vertikaler Ausdehnung kommt die Art von der Meeresküste bis in Gebirgsregionen über 3300 m ü. NN vor. In diesem geographisch, klimatisch und ökologisch uneinheitlichen Gebiet ist *P. contorta* Bestandteil der unterschiedlichsten Waldtypen und Pflanzengesellschaften und stockt auf den verschiedensten Bodentypen. Es ist daher nicht verwunderlich, daß *P. contorta* große kontinuierliche und diskontinuierliche geographische Variation zeigt, was in der Vergangenheit zur Beschreibung zahlreicher Taxa führte. Nach der eingehenden Bearbeitung durch Critchfield (1957) werden innerhalb der Art *P. contorta* 4 Unter-

---

[1]) Herrn Professor Dr. W. Langner zum 70. Geburtstag gewidmet.

[2]) Anschrift des Verfassers: Institut für Forstgenetik und Forstpflanzenzüchtung, Siekerlandstraße 2, D-2070 Großhansdorf-Schmalenbeck.