



S

A * BREEDING FOR VARIABLE ENVIRONMENTS



GENE NAMKOONG Forest Industry Lecturer

*Forestry Program
The University of Alberta
14 August, 1980*

FOREST INDUSTRY LECTURE SERIES NO. 6

THE FOREST INDUSTRY LECTURES

Forest industry in northwestern Canada is cooperating with Alberta Energy and Natural Resources to provide funds to enrich the Forestry Program of the Faculty of Agriculture and Forestry at the University of Alberta through sponsorship of noteworthy speakers.

The Forest Industry Lecture Series was started during the 1976-77 term as a seminar course. Desmond I. Crossley and Maxwell T. MacLaggan presented the first series of lectures. The contribution of these two noted Canadian foresters is greatly appreciated.

Subsequent speakers in the series have visited for periods of up to a week, with all visits highlighted by a major public address. It has indeed been a pleasure to host such individuals as C. Ross Silversides, W. Gerald Burch, Gustaf Siren, Kenneth F.S. King, and F.L.C. Reed. The subjects of their talks are listed on the last page.

Dr. Gene Namkoong was here 11-13 August 1980. He visited with staff and many of the other research scientists who were at the University of Alberta for the Sixth North American Forest Biology Workshop. This paper is the text of his Forest Industry Lecture given on 14 August 1980.

We would like to take this opportunity to express our thanks again to the sponsors of this program — we appreciate very much their willing and sustained support:

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GENE NAMKOONG



Gene's current interests are in the areas of quantitative genetics and tree breeding strategies, population genetics of forest trees and the evolution of growth strategies, the genetics of forest pest species, and systems analysis.

Dr. Gene Namkoong is Pioneer Research Scientist in population and quantitative genetics with the U.S. Forest Service's Southeastern Forest Experiment Station at Raleigh, North Carolina.

Dr. Namkoong received the B.S. and M.S. from the State University of New York College of Forestry at Syracuse. He received his Ph.D. in genetics from North Carolina State University in Raleigh. Dr. Namkoong's professional forestry career has ranged from timber marketing to research. In addition to his position with the Forest Service, Dr. Namkoong has a joint appointment as Professor of Genetics and Professor of Forestry at North Carolina State University. He also is an internationally known statistical and research consultant.

Dr. Namkoong is the author of numerous papers in quantitative and population genetics, tree breeding, and forest genetics. He is the author of the recent book "Introduction to quantitative genetics in forestry", published as a technical bulletin by the U.S. Department of Agriculture in 1979.

I.

INTRODUCTION

Foresters are not strangers to highly variable environments. We deal with variation in all of our professional lives and learn to accommodate differences in stocking, growth rates, harvest yields, etc. More than most professionals, we can learn to appreciate the temporal fluxes of tree life and the environmental variations which are encountered over periods of human' generations. In most of our professional lives, we deal with this variation by either trying to make the environment more uniform in some optimum state, or we accept uncontrollable variation and optimize treatment prescriptions for environmental groups.

Relative to agricultural systems, forestry operates with a lower degree of environmental control, since its return on investment generally justifies lower investments per hectare than in agronomic crop management. Not only does this force us to manage forests on poorer sites, it also forces us to work with sites which are poor in many different ways and dimensions. As site quality declines, variations increase in soil moisture, soil depth, aspect, nutrients, and climatic interactions with all of these effects. Thus, optimum breeding varieties of forest trees commonly will have to be grown on wide variations in site requirements. Furthermore, site averages and the extent of variations in the future will likely be different from the present, and to breed for the future requires an ability to accommodate wider site variations than presently exist. The genetic question for us is: how to best design breeding strategy to accommodate such variations, with the available genetic materials.

In this seminar, I will describe what we know about the mechanics of the genetic system and how we might design breeding programs to accommodate present and future needs. However, in doing so, we will find that a deeper problem exists in managing variability, which requires us to be more complete forest managers and to simultaneously manage both the environment and the genes of forest trees. Silvicultural management systems cannot be optimally designed in ignorance of the genetic capacities of the trees; and, conversely, genetical breeding systems cannot be optimally designed in ignorance of the environments in which the trees will grow. Since breeding programs can affect silvicultural programs, the choice of genetic design for forest trees is too important to be left to geneticists alone. We require extensive dialogue, and I .hope that the opportunity afforded by this Forest Industry Lecture Series to discuss these questions serves to open such communications.

GENETIC THEORY

The adaptability of plants to particular environments is governed by many physiological functions, which are in turn governed by environmentally affected substrates and by enzymes, which are governed by structural genes and by genes which affect the rate or timing of structural gene actions. Thus, the collective effect of several genes affects adaptability through complicated pathways and is expressed in various organs and tissues, rates of growth, and episodes of activity and inactivity. Different adaptations evolve when allelic variations exist such that some alleles are better adapted to certain environments while other environments favor alternate alleles. Any alleles which are superior in all environments will clearly predominate in all populations and any which are deficient in very many environments will gradually be displaced. However, alleles which are beneficial in some and deficient in other environments, such as temperature or pH sensitive alleles, may coexist in populations. The persistence of multiple response types is more likely if there is any restriction on mating, such as occurs if neighborhood sizes are small or isolation among populations exists.

Natural systems have evolved which take advantage of different environmental adaptabilities. These are most readily observed when environmental extremes exert strong selective pressures. In nature, there is a balance of forces which tend to diversify populations and those which homogenize them. In artificial breeding systems, we can control the extent to which heterogeneity is maintained among as well as within populations. The question we must answer is whether natural evolution of trees over the variable environments of the past has produced broadly adapted "super" trees with little variation in response, or if some level of variation exists such that some genotypes are best in some environments and others are better elsewhere. We can then answer the questions of whether we can produce a more optimal management system by breeding for specific adaptabilities and whether we want every tree or population to be maximally productive everywhere, or if we want to build in heterogeneity at the population level and create more specific adaptabilities.

During the 20th Century, agronomic crop breeders have tended to answer this question by eliminating genotype x environment interaction and by

homogenizing farm environments and the varieties planted on them. However, the opportunity to have answered otherwise often existed. In fact, most natural plant populations exhibit considerable variation in adaptabilities, and it is likely that the special adaptation exhibited as genotype x environment interactions could have been profitably used.

In transplant experiments with *Agrostis tenuifolia*, Antonovics *et al.* (1967) found that even in continuous populations, genetic differences in adaptation to soil metals existed. The growth response of plants originating from contaminated soils show less deleterious effects when planted in contaminated soils than of plants originating from adjacent "clean" soils. In fact, the plants originating from metal contaminated soils grew better on soils slightly contaminated with copper than on "clean" soils, thus showing a peaked response function instead of the usual monotonically declining response. Similarly, Knight (1970) showed that when several grass varieties are planted over a temperature gradient, the response functions peaked at different points of the temperature scale and the degrees of curvature of the response functions were different. He also found that the genetic variance changed when measured at different points on the environmental scale and speculated that the underlying gene effects may be quite simple shifts in environmental optima but the response functions may cause the genetics of growth to be quite complicated.

OBSERVATIONS ON FOREST TREES

These observations should be no surprise to forest geneticists who have observed similar phenomena in most provenance analyses. Extensive European and North American experiments with transplant and common garden experiments show a specificity of optimum environments for different provenances (Wright, 1976; Namkoong, 1969). More recently, adaptational differences along environmental gradients have been observed on finer populational subdivisions in ponderosa pine (Namkoong and Conkle, 1976), pitch pine (Fryer and Ledig, 1972), and Douglas-fir (Campbell, 1979; Rehfeldt, 1978).

In a previously reported study (Namkoong, Roberds and Davey, 1976) loblolly pine families were tested on five nitrogen fertilizer levels and their response curves were measured. In spite of the fact that all families originated from good sites, there was substantial variation in the form of the response curves. Some curves were distinctly peaked, others flat and still others were sloped, and the genetic variance measured at each point along the environmental gradient consequently changed.

It seems evident for plants in general and forest trees in particular that natural evolution has presented us with mixed strategies for response to variable environments. For any given level of effective pollen and seed migration over a range of environments, the severity of natural selection on adaptively important traits has been sufficient to discriminate clinal variation but generally not so severe as to eliminate genetic variation within environmentally similar areas. In fact, for most temperate zone tree species, at least as much, and often more genetic variation exists within populations as among provenances. Regardless of where these variations in response form may lie, it behooves us to understand that variations in response to planting sites do exist and, for breeding purposes, to consider how we can best design response • functions.

A GENETIC MODEL

Let us consider that we can successfully select and breed for improved yield over a range of environments. Obviously, any trees that perform uniformly well for all conditions will be chosen, and if one choice simply involves choosing among higher or lower yields and every tree maintains its rank over all environments, then we have no breeding problem with regard to response function selection. In this case, all genotypes have a similar response function with some functions simply being higher than others, but otherwise identical in shape and hence having the same homeostasis. Then, we can pick the best in any and all environments (since performance rank doesn't change) and breed among the selected trees. It would also be expected that silvicultural treatment variations or any other environmental variations have no effect on the correct genetic choice. However, if variations among these generally better genotypes exist, such that they do change rank in some environments, then the choice depends on which environments are more frequent or probable. Consider Figure 1 where a normal curve of frequency is drawn for a range in an environmental scale and below that is a yield function for a genotype which represents its expected performance if grown in that environmental range. If the choice among genotypic variations is merely that some have yield functions which are generally elevated or depressed, (type A) then we have the simple selection situation described above, and environmental and genetic management decisions can be independently taken. However, if the yield functional variations are such that they can shift in form or in location of the optimum environment (type B), then genotypic value is dependent on the environmental distribution. If we designate the environmental frequency distribution as $f(x)$ on the environmental variable (x), and the *ith* genotypic response function as $Y_i = g_i(x)$, and the value of the *ith* genotype as $v_i(x)$, then

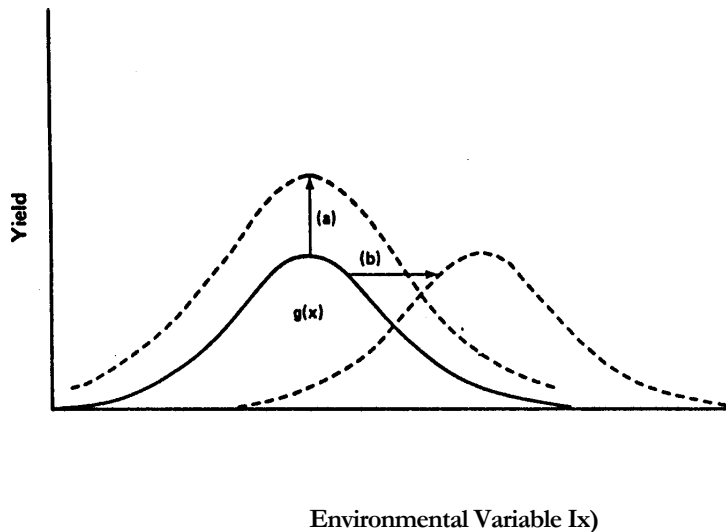
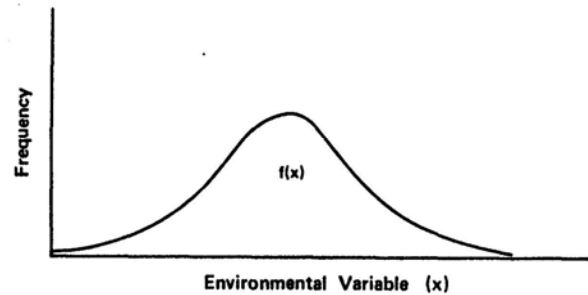


Figure 1: Environmental frequency distribution and genotypic yield function variations when both are functions of an environmental variable.

The population genetics dynamics of such genotypic value systems are quite similar to the quadratic fitness function analysis of Wright (1935) and Kojima (1959) and display similar stability properties. It is indeed feasible to expect that genetic variations in response forms can be maintained in populations of forest trees and that multiple adaptive peaks for multiple loci can create stable equilibria.

Perhaps of greater interest for tree breeders is an application of this model and analysis to breeding populations or varieties. Consider for example that we can generate two varieties at slightly greater cost than working with just one variety. Since the selected genotypes which compose any one variety have limited ranges of adaptability and such variety's yield is the sum of its component genotypes in simple recurrent selection systems, all genotypes in a variety should be selected for maximizing yield for the same range of environments. The problem we have is to determine the environmental range to which we should direct each variety.

We can solve this problem theoretically if we can specify the environmental frequency distribution and the varietal yield functions which may be made available by breeding. If the $f(x)$ of equation (1) describes the environmental distributions and the $g_i(x)$ is the i th possible varietal yield function, then we simply maximize (1) with respect to the i varietal variations. For example, if $f(x)$ is normal density function with mean μ and variance σ^2 ; and $g_i(x)$ are symmetrical functions with one peak, then the single best population to breed is one with mode at μ . This is intuitively obvious, but what may be more interesting is when two varieties may be bred and planted in two subdivisions of the environmental distribution. For then, if we split the environment into those sites which are above μ and below μ , it turns out that we can obtain a greater value gain by breeding two varieties. One variety should be bred with its mode close to, but below μ and the other should be bred with its mode close to, but symmetrically above μ (Namkoong, 1976). The particular modalities are not important to detail here, but suffice it to say that their locations are a function of the genetic homeostasis within varieties and the environmental variance. The significant point is that we can almost always obtain greater gains of breeding multiple varieties even if the genetic homeostasis is high. The more varietal populations we can breed, and the finer subdivisions of the environment we can manage, the greater the gain.

A reasonable multiple population breeding strategy to follow would involve breeding as many populational varieties as possible, with several lying close to the expected environments and others dispersed among less frequent or less probable environmental ranges. Then, as our knowledge and control of environmental variations increases, we can re-deploy the populations as the distribution of environments changes. The cost of breeding multiple varieties must be balanced by the benefits expected, but preliminary analyses indicate that some level of subdivisions will often be desirable.

A FOREST-GENE-MANAGEMENT MODEL

An assumption made in the above analysis is that the environmental distribution is known, and while this is often closely approximated and can be predicted for the future with some probability weightings, the act of breeding will itself have an effect on the distribution. Management will intensify on some sites, and may extend to previously unmanaged areas as breeding influences survival and economic return values. Management may thus increase site homogeneity in some areas and increase site heterogeneity in others at the same time as a result of genetic as well as other influences. Thus, the environmental distribution is not independent of the genetic management decisions made. It is also obvious that the varieties we breed will depend on the environmental distribution, and hence the genetic and general forest management decisions are mutually interacting.

We might also note that the development of multiple varieties for multiple present or future environments is not qualitatively new to foresters. In a sense, the old species-site types of studies are a primitive form of population selection for specified site types. We are advancing that concept to include genotypic level variations and also providing the new breeding capacity to continually evolve better adapted and more productive genotypes. The concept of forest management for multiple species remains valid for this level of sub-specific differentiation. We might add at this point that the environment we refer to need not be limited to physical site factors, but all previous discussions can just as easily refer to social or economic elements of the environment which can also be variable and may also have to be satisfied by developing multiple species or varieties.

As in the use of optimum species-site management, varietal-environmental joint designs involve different levels of management intensity among the management units. Thus, different units will generally require different levels of genetic or environmental management at any one time and the management plan will have to include an investment profile for all those elements over long periods of time. This is not qualitatively different from traditional forest managers' duties though it may require a quantum leap in the foresters' vision that managers should be managing the genes as well as the sites.

The immediate problem exists of how we might most efficiently coordinate plans among silviculturists, economists, and geneticists for timely action and for developing varieties for changing arrays of sites. A longer range problem exists in developing a strategy so that the results of the short-term variety-site combined decisions lead us to the kinds of forests we want. It is possible that a series of short-term development decisions could lead to undesired results. We could for example invest in very strong environmental controls and breed for adaptability to those uniform environments and hence become susceptible to some unavoidable future environmental variations as have some agronomic crop species.

If we take a long view of forest management with a genetic element included as one of the management variables, it is clear that we must control and use both the environmental and genetic variability to maximize forest productivity. If we foresters are not strangers to huge and uncertain variations, then we can appreciate the necessities of such variations and perhaps guide a co-evolution of genes and environments into productive patterns. It seems to me that the Province of Alberta is in the unique position of being able to initiate a total management system and to take advantage of a rich natural heritage in building an optimal evolutionary path for its forests.

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