A Model for Reforestation with Optimal and Suboptimal Tree Populations

By R. D. MANGOLD and W. J. LIBBY[1])

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Summary

A hypothetical reforestation model is presented which postulates growth rates by "optimal" and "suboptimal" tree populations. Populations of trees from the central zone of a species' ecological tolerance rnay possess inherently greater capacities for rapid growth due to a "non-conservative" developmental growth strategy. Such a strategy probably evolves where environmental conditions are rarely limiting for growth, but biotic (competitive) interactions between neighboring trees are intense. When these populations are planted in less favorable sites, they rnay outgrow native populations. A method for determining the extent of planting zones for such populations is also presented.

Key words: reforestation model, developmental growth strategy, optimal and suboptimai populations, nonlocal seed.

Zusammenfassung

Aufbauend auf der These von NAMKOONG (1969), daß lokale Baumrassen oft nicht die für einen gegebenen Standort optimale Leistung aufweisen, werden mögliche Gründe für das bessere Wachstum nicht bodenständiger Rassen aufgezeigt.

Recently a theory of nonoptimality of local races has been proposed by NAMKOONG (1969). Prior to this, the old maxim "Local seed is best" (or the somewhat revised "Local seed is safest") had usually been thought to be the most applicable postulate to follow in reforestation projects. This paper attempts to explain briefly how nonoptirnality of local races might occur, and presents a (no doubt oversimple) prototype model based on that explanation. The model rnay serve as a conceptual guide for reforestation using wild seed from optimal or suboptimal tree populations. Much more research is needed to determine the validity and generality of the model, and to refine some of its details. Some of the evidence for such an explanation and model is reported and summarized by MERGEN, BURLEY, and FURNIVAL (1974).

With respect to physical environmental factors, for example temperature, tree growth is near maximum over a moderate range of temperature, but significantly less at temperatures above and below that range. On sites where most or all such physical environmental variables are generally within their favorable ranges for a species, the growth of that species will be relatively rapid. Other populations of that species, on sites where physical factors of the environment are frequently outside of their favorable ranges, grow mare slowly. Furthermore, native seed from such zones rnay have lower intrinsic (*i.e.*, genetic) vegetative vigor than that of populations from favorable sites. It is expected that, over many generations, a native population will have higher reproductive fitness than imported populations, and that it is thus better suited to occupy the site under natural regeneration conditions. However, in the span of one generation, it is possible that some nonlocal populations can grow larger and more rapidly than the native population.

Although magnitudes of the ranges of such physical factors as temperature and moisture rnay be similar in optimal and marginal populations, the periodic extremes of temperature and moisture will generally be more severe in the marginal zones, and more often approach or exceed the physiological limits of the species. In such a situation, a more cautious developmental strategy will probably have evolved. This strategy, which manifests itself in phenological responses and growth rates, maintains genotypes that are better prepared for the more marginal environments, including occasional climatic catastrophies.

The variations in the physical environment that occur in the more optimal zones are usually within the central range of the species' physiological capacity, and only occasionally produce limiting conditions for growth and subsequent reproduction. In such areas, biotic factors are more likely to limit growth and reproduction than are physical factors. Water and warm sunlight rnay be in abundant supply, but neighboring brush and trees vigorously compete for that light and moisture. An advantageous response by the individual tree to such competition is to grow fast as a juvenile. This will have led to the evolution of a nonconservative developmental strategy on such sites. The trees that grew faster (and thus received more light, moisture, and nutrients than neighboring trees) are the trees that were more likely to contribute genes to subsequent generations.

When a population from such a favorable environment is planted in a more restrictive environment, it rnay be capable of better vegetative growth than the native population, particularly if early establishment is aided by such human intervention as nursery practice and site preparation. As rotation age is approached, reproductive maladaptations of the planted population are unimportant because humans will again intervene with artificial regeneration. Only the growth and survival of these introduced populations through rotation age are important.

Figure 1 is an idealized representation of the average annual growth for a single population planted at various elevations on a mountain range. Maximum reproductive fitness probably occurs at 1000 m, where the population evolved. Its maximum growth rate rnay occur there, or perhaps lower, where, however, the native populations rnay grow even faster. At elevations above 1600 m, plantations of this population generally fail. At somewhat lower elevations (1300—1600 m) its growth rate is poor. There is a shoulder-like region, however (in this example from about 1000—1300 m), where it grows nearly as well as where it evolved.

If in fact the growth-response curve in ***Figure*** 1 is representative of how tree populations behave when planted in different environments, four points logically follow:[2])

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[2]) MERGEN, BURLEY, and FURNIVAL (1974) presented evidence that provenances differ significantly in their stabilities, with the centrai provenances generally being the more stable. However, if the shapes of the population curves are similar, even though not exactly the same, these points are still valid.

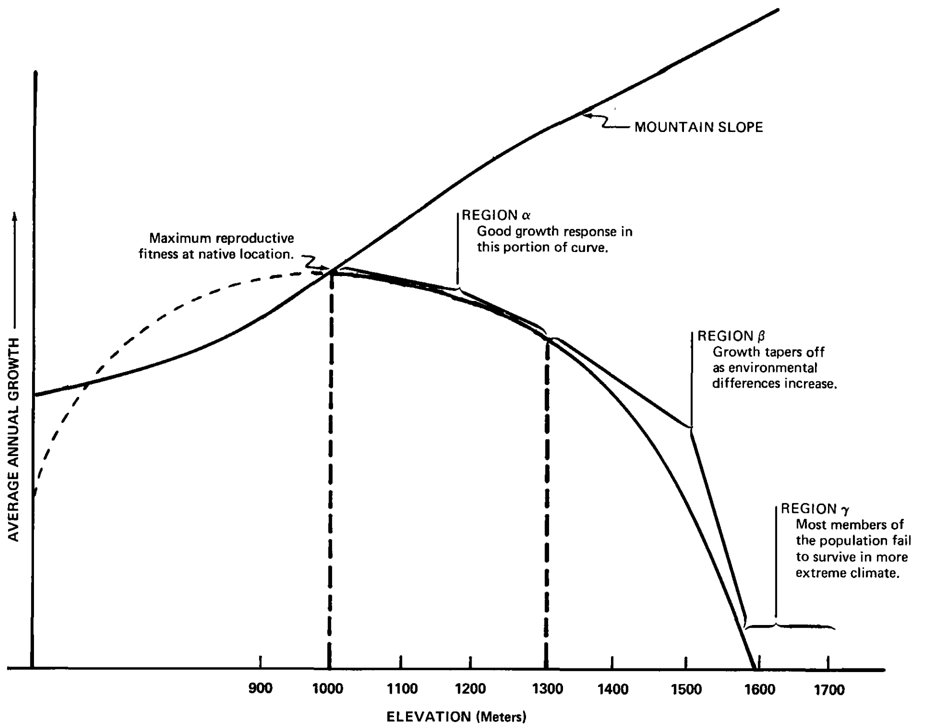

Fig. 1. — Idealized average annual growth for a population planted on its native site and on a gradient of less favorable sites.

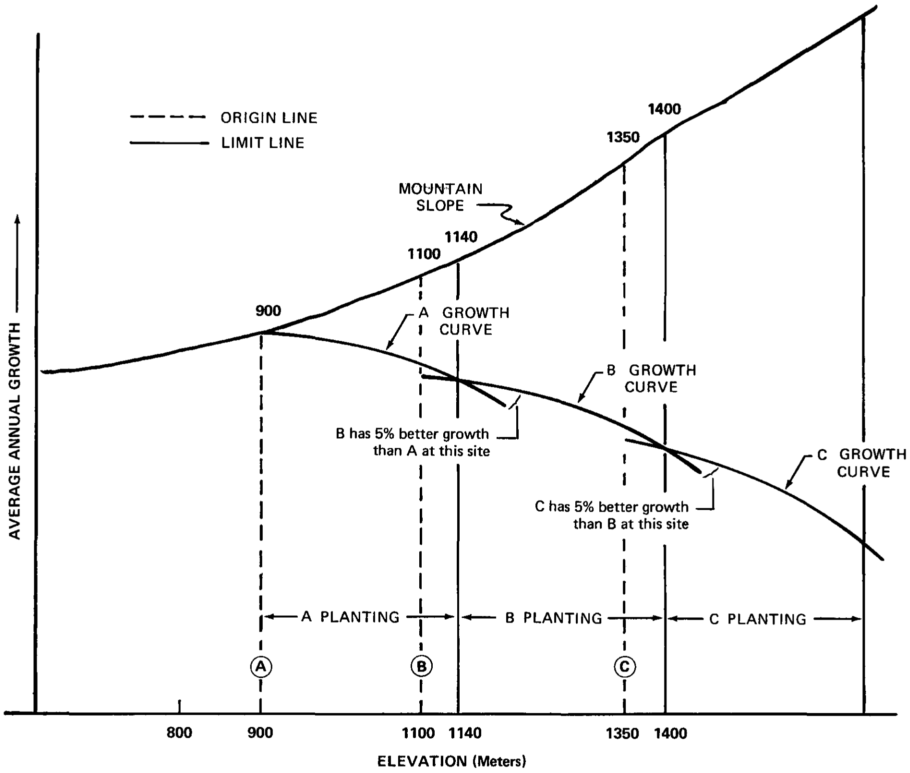

Fig. 2. — Hypothetical reforestation model for several populations on a mountain slope.

1. The optimal population will outperform local populations in many environments which are similar to that of the optimal population's place of evolution (region α, *Figure 1).*

2. In environments where the optimal population's performance drops off sharply (region β, *Figure 1),* or where it fails (region γ, *Figure 1),* some nonlocal suboptimal population should outperform it and the local populations *(Figure 2).*

3. Suboptimal populations are likely to be better than local populations in environments somewhat less favorable than the environment in which the suboptimal populations evolved *(Figure 2,* and discussion below).

4. Some nonlocal populations should outperform local populations in all cases (except at the native site of the optimal population), even though the local population proves best at some other sites.

In *Figure 2,* average annual growth is plotted with elevation for three populations. Note the maximum growth for population *A* is greater than the maxima for *B* or C. Seedlings or rooted cuttings from the *A* population, which evolved at 900 m, can be reasonably planted up the mountain slope to about 1200 m. This region corresponds to the shoulder portion of the curve in *Figure 1* (region α). The limit to planting *A* occurs where its performance curve drops more sharply, due to its poorer adaptation (region β, *Figure 1).* The replacement of *A* with another population might be determined by the point where its annual growth is (say) 5% below that of the best alternative population for that site, which is designated *B* in *Figure 2.* Once that point and alternative population are determined, the *B* population can be used instead of the *A* population at 1140 m and above *(Figure 2).* This suboptimal source *B* evolved at 1100 m. According to the model, some other populations would outperform both *A* and *B* at some sites between 900 m and 1200 m, but the difference would be less than 5%, and thus not likely to warrant a separate domestication program. The *B* population will be planted between 1140 m and 1400 m, and the *C* population, which evolved at 1350 m, can be planted over the rest of the upper region starting at 1400 m. Thus three populations suffice for all planting sites on this idealized mountain slope. Such plantations should have a greater genetic capacity for growth than plantations using local populations or natural regeneration, assuming that the nonlocal trees are suffficiently adapted to survive to rotation age.

The example assumes that elevation is highly correlated with the causes of growth-rate variation. This will not be the case in all areas or for all species (see contrasting examples by CAMPBELL 1974; TEICH, SKEATES, and MORGENSTERN, 1975). Certain environments may change in erratic patterns, which will make delimitation of a population's potential planting zone complicated. In such cases, it will be important to assess each planting site's environment in order to predict how much and what kinds of stress the planted trees will encounter. Experiments should be conducted in order to elicit the actual shapes of the growth responses (which we have idealized in the model), and to discern the degree of mobility of nonlocal provenances. The amount and organization of the genetic variation in a species, and plasticity of responses of typical genotypes to environmental variation, will affect the shapes of curves. These in turn will influence decisions concerning the number of populations to be selected in order to cover a set of environments.

The model we have presented is crude. We have used as an example a mountain slope, but it can also be applied to broad-ranging species which occupy non-mountainous physical environments which vary from favorable to less favorable. The model can be tested and modified by further experimental and theoretical research, and we hope it serves as an early conceptual framework for such research. Meanwhile, we offer it as a consideration in practical reforestation decisions.

Literature Cited

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A simplified design for combined provenance and progeny testing[1])

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Summary

It is often desirable to combine the functions of provenance and progeny tests into one experiment testing the offspring of several different trees from each of many stands. A design is proposed whereby such an experiment may be simplified. The proposal is a variation of the compact-family design, with plots representing stands randomized within blocks, small sub-plots representing families within stands, and sub-plots systematically arranged within plots. The systematic arrangement is obtained by color coding when planting. That feature permits simplifications in the labeling, mapping and record keeping procedures without a sacrifice in quality of data. With the proposed design, a combined provenance-progeny test can be conducted almost as simply as an ordinary provenance test.

Key words: Provenance-test, design.

Zusammenfassung

Es ist oft notwendig, Provenienz- und Nachkommenschaftsteste zu kombinieren. Hierzu wird ein vereinfachtes Design vorgeschlagen, welches die Prüfung der Nachkommenschaften verschiedener Bäume aus vielen Beständen in einem Versuch zuläßt. Gleichzeitig werden Vorschläge für eine vereinfachte Kennzeichnung auf der Versuchsfläche durch farbliche Abstimmung gemacht.

Introduction

For a typical provenance test, seeds are collected from a number of trees in different stands and are then bulked by stand. No effort is made to maintain separate identity for the offspring of individual trees within a stand. A typi-

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