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 *a*). 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.

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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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cal inheritance study includes the offspring of many selected or average trees located over a wide area, with the empahsis on testing individual trees and little or no attention to stand of origin.

Wells and Switzer (1971) combined the two types of experiment. Working with loblolly pine, they collected open-pollinated seed from 5 parents in each of 115 stands, and maintained the identity of all 575 half-sib families. They established three plantations, each with several replications and with multi-tree plots. Similar but smaller experiments have been started in several other pine, fir and birch species.

Such combined provenance-progeny tests have obvious advantages, as they can simultaneously provide information about geographic trends and about genetic differences among individual trees. However, they are apt to be large and expensive. The present paper describes an experimental design by which overall size and complexity can be reduced 50—75% without serious sacrifice in the amount of data or in the usefulness of the experiment for breeding purposes.

Essential features and detailed procedures of the proposed design

The proposed design has four essential features, as follows. (1) The design, which is a variation of the split-plot, may be called the compact-family design. Unlike the situation in a randomized complete block design, the sub-plots representing individual families-within-stands are planted together within plots representing stands. (2) Plots are randomized within blocks but sub-plots are planted in a systematic order within plots. This order remains the same in every block. (3) Sub-plots representing families are small, consisting of a few trees each. (4) Each stand should be represented by the same number of families but this may vary occasionally. The detailed procedures are outlined below. In describing these, I assume an experiment involving 100 stands (numbered 1 to 100), five parents per stand (designated A, B, C, D and E), 1-tree sub-plots, 10 replications per plantation and six plantations.

Parental selection. If parental selection is practiced, designate parents in a random manner so that A is not always the best or poorest in its stand. This will insure that the first position in every plot is not occupied by a tree which is expected to be outstanding in some respect. If that were true, measurement bias might occur.

Parental records. Compile a master list giving necessary information about stands 1—100 and parents A—E within each stand. A duplicate of this list should be appended to each plantation map to provide necessary information about the parentage of every tree in the test.

Nursery sowing. Repication is desirable but not mandatory in the nursery. Consider a plot representing a stand to be five adjacent rows, and randomize plots within replications. Do not randomized rows within plots, however. Instead, sow seeds of families A—E in the same order 1—5 within each plot.

Labelling, lifting and packing. To pack stock for a single plantation, first attach labels giving the stand number to 10 trees of family A in every stand. In other words, attach numbered labels to 10 trees in the first row in every plot. Using an easily remembered color code such as Blue-Green-Red-Yellow, attach a colored label to or mark with paint 10 trees in each of the other families, using Blue for family B, Green for family C, Red for family D and Yellow for family E.

Loosen the seedlings, then proceed to the first five rows in Replication 1 and pull one seedling from each row. Check to be sure that each seedling has a number or a color. Tie the five trees in a bundle. Proceed to the second plot (= second five rows), the third plot, etc. When the 5-tree bundles for all 100 stands are lifted and tied, pack them in one 500-tree bundle destined for Block 1 of Plantation 1. Repeat the process for Blocks 2, 3, etc., then for Plantations 2, 3, etc.

Planting. Proceed to the plantation site and mark it in such a way that the trees can be planted in straight lines in both directions. Use 5-tree row plots. Select at random a 5-tree bundle representing a stand and plant the trees in the sequence Number-Blue-Green-Red-Yellow. Repeat with the second, third, etc. 5-tree bundles. When Block 1 is planted proceed to Blocks 2, 3, etc. When planting is completed and one looks perpendicular to the direction of the plots, one should see rows of numbered, blue, green, red and yellow trees in that sequence.

Mapping. Walk along the numbered rows perpendicular to the direction of the plots and record the stand number for each plot. The completed map for a plantation should have 1,000 entries (100 stands × 10 blocks). Add enough description to show that the sequence of families is A, B, C, D and E in every plot. Append the set of parental records giving information about stands 1—100 and parents A—E within each stand.

Data recording and measurement. Prepare a record folder in which the plots are listed in sequence and identified as to stand number. Devote one line to each plot.

The real time saving comes during measurement, which might be done in three different ways: (1) Measure and record data for all 5,000 sub-plots, (2) measure all trees but record data for the 1,000 plots only, or (3) record data for the 1,000 plots only but then remeasure and record data by sub-plots for the 5—10% best families. Obviously, much time can be saved by the partial measurements. In most combined provenance-progeny tests, between-stand difference have been so large that use of the second or third methods would provide 90—95% or 100% as much information, respectively, as could be obtained by measuring and recording individually for all 5,000 sub-plots.

How it is possible to decide which measurement method to use? One can proceed on the assumption that between-stand differences are considerable and use the second or shortest method. If the F value for stand is significant at the 1% level, the use of that or the third method is vindicated. Within-stand differences can almost be ignored if the F value for stand is very high, say 6 or 7.

Thinning. Many provenance-progeny tests are meant to serve as breeding arboreta or seed orchards as well as to provide data on inheritance. They will be thinned by family, removing all trees of the poorest families and poor trees in the better families. If there are pronounced between-stand differences, some stands will contribute two or three superior families whereas others will contribute none. Furthermore, with the systematic arrangement of sub-plots within plots, there will be many cases where good families occupy adjacent positions in each block. Thus, spacing will be irregular after thinning unless some concessions in genetic quality are made to insure even spacing.

This problem is the most serious defect in the proposed new design. It would be present to some extent in any experiment involving multi-tree plots but could be avoided by the use of 1-tree plots in a randomized complete block design.

Effects of non-randomization within plots

The unique feature of the proposed design is the systematic arrangement of sub-plots within plots. That feature permits much labeling time to be saved prior to field planting. It also causes the plantation to become less complex to map, measure and analyze. In the example given previously, a 1,000-entry map is sufficient whereas 5,000 entries would be needed if every sub-plot were mapped.

Randomization of plots within blocks is usually stipulated in order to prevent bias, which may originate in one of three ways. First, site gradients common to all blocks may cause plots located in a certain portion of each block to encounter unusually favorable conditions. Second, if one slow and one fast growing seedlot are always planted adjacent to each other, the former may have a constant adverse affect on the growth of the latter. Third, a person evaluating a plantation may notice on exceptional plot, remember its relative location and let his memory influence his observation the next time he encounters that seedlot.

Such biases are not apt to occur, however, for systematically arranged 1- or 2-tree sub-plots within plots. Environmental gradients are not apt to be so constant as to result in exceptional growth of a certain tree in every plot. Unless within-stand differences are exceptionally large, there is not likely to be a constant growth effect of one fast on one adjacent slow growing family. One is unlikely to remember the location of exceptional families within hundreds of plots.

Permitted variations in design

In the example previously quoted, the experiment consisted of 100 stands and 5 parents per stand, with 1-tree sub-plots representing parents within stands. The proposed design can be used with any number of stands. There is a practical limit to the number of colors one can work with, and 8—10 families per stand is probably the maximum.

Small plots or sub-plots yield the most information per tree planted (Wright and Freeland, 1960; Conkle, 1963), and statistical efficiency falls off rapidly with plot sizes greater than 20. With 1- or 2-tree sub-plots and 4—5 families per stand, statistical efficiency is relatively high. With larger sub-plots, statistical efficiency may become low as regards measuring differences among stands.

With 1- or 2-tree sub-plots, mortality results in missing sub-plots. This is unimportant if mortality is less than 5% or if one measures plot measn only. It may be a serious problem statistically if mortality exceeds 25%.

Either linear or rectangular plots can be used. Within a given plantation, of course, all plots must be of the same size and shape.

For this or any compact-family design to work, all plots must contain the same number of sub-plots. That is, all stands must be represented by the same number of families. Suppose, however, that one plans on five families per stand but finds that there are 15 good parents worth progeny testing in some. The 15 parents can be treated as three groups of five and one stand can be treated as three stands for the purposes of design. Or, assume that one or two families are deficient in some stands. "Dummy,, or "standard" families, not to be measured, may be substituted for them.

Advantages and disadvantages of the proposed design

When listing advantages, it is necessary to state the alternative procedures. One possible comparison is with an ordinary provenance test. For experiments of the same size, the proposed new design will require sightly longer sowing time in the nursery and some extra time to color code the trees prior to lifting. Time required to plant and map will be virtually the same for the two methods. If only provenance data are required, measurement and analysis time will be the same but the proposed new design will yield silghtly better information because it insures that all families in a stand are represented equally in all plots. The proposed design has one big advantage in that it can yield data on family differences whereas an orthodox provenance test can not.

A second possible comparison is with an ordinary progeny test using a randomized complete block design. The proposed new design would be simpler to install. It could be much simpler to measure and analyze if one desires only information about stand differences or about families from the best stands. As compared with the randomized complete block design, the compact family design can yield more reliable information about between-family-within-stand differences and less reliable information about between-stand differences. That could be a real problem if plot sizes greater than 20 trees were used. Another disadvantage of the compact-family design is the uneven spacing which will result if a plantation is thinned to leave the best families in the best stands.

A third possible comparison is with a combination provenance-progeny test using the compact-family design and random arrangement of sub-plots within plots. The proposed new design is much easier to install and map. The two designs would be approximately equal as regards ease of measurement and analysis, and quality of data.

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