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# Nitrogen, Corn, and Forest Genetics

## The Agricultural Yield Strategy-Implications for Douglas-fir Management

Roy R. Silen

EDITOR'S
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## Author

ROY R. SILEN is a geneticist
Forestry Sciences Laboratory,
3200 Jefferson Way,
Corvallis, Oregon 97331.

## Abstract

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Agricultural yield strategy simply aims to increase number of grain bearing stalks per acre. Forestry strategies look to thinning, fertilizer, and genetics, each to provide gains. The agricultural strategies applied to Douglas-fir appear to be impractical for long rotations. Concern is expressed for commitments to perpetual inputs of materials and energy to keep a yield above the land's carrying capacity. Adapted natural populations are the major resource in keeping a yield improvement strategy trouble-free.

Keywords: Yield strategy, tree improvement, agriculture, Douglas-fir, ***Pseudotsuga menziesii.***

## Summary

An agricultural yield strategy aimed simply at increasing number of grain-bearing stalks per unit area has amplified grain yields up to fivefold. Correspondingly large increases in Douglas-fir appear to be impractical. In agriculture, biomass yield increases have come mainly from upgrading site quality by relieving growth constraints of cold, drought, infertility, and pests with irrigation, fertilizer, and chemical control of pests. A similar level of relief from constraints on growth is improbable in the Douglas-fir region. Other factors contributing to agricultural yield improvement such as better harvest index, reducing lodging, earlier maturity, improved harvestability, and better resistance to pests appear less applicable to Douglas-fir. A major shortcoming of the agricultural strategy is that genecological problems of a long-rotation crop like Douglas-fir are minimally considered. The main feature of agricultural crop land races is crop reliability arising from precise adaptation to a locality. An even more precise templatelike adaptation to landforms is now postulated for Douglas-fir. Long rotation crops need assurance of reliable yield, hence precise adaptation is of high priority in a Douglas-fir yield strategy.

A Douglas-fir yield strategy should use the crop reliability of native populations improved in growth rate only to the level that site productivity can be enhanced with better fertility and more moisture from weed control. Thinning, spacing, and genetics — all essentially non-site-enhancing — would play the same crucial supportive role of increasing the harvestable crop as they do in the agricultural strategy. Concern is expressed for commitments to perpetual inputs of materials and energy to keep such a strategy yielding above the land's carrying capacity. Adapted natural populations are the major resource in keeping such a yield improvement strategy trouble-free.

# Introduction

An elegantly simple and certain strategy to amplify the yield of agricultural grain crops up to fivefold has emerged from the "Green Revolution." Unlike forestry strategies which look to thinning, fertilizer, and genetic gains, the agricultural strategy simply aims to increase the number of grain-bearing stalks per hectare. For wheat, rice, and corn, very high plant density can be maintained with such agronomic techniques as irrigation, fertilizer applications, and control of weeds and pests. Genetics plays a supporting, though crucial, role in restructuring the plant for denser planting, efficient use of fertilizer, and more efficient mechanization. Variations of these basic principles are used in non-grain crops. This article attempts to put into perspective considertions that arise if this agricultural strategy were applied to coastal Douglas-fir *(Pseudotsuga menziesii* [Mirb.] Franco).

Why, in contrast, do Douglas-fir strategies stress ample spacing when the successful agricultural strategy aims for high plant densities? Why do we breed for rapid tree growth and larger plants when the key to amplified grain yields is breeding smaller plants? Why do we assume independent yield increases from genetics and fertilizer applications when agricultural breeding stresses the interaction of genetics with agronomy? Would the coordinated agricultural yield strategy be an improvement over presently fragmented, often ill-defined, forest yield strategies? Or is either really appropriate for long-rotation Douglas-fir forestry? It would seem prudent for foresters to examine closely the agricultural experience of the "Green Revolution" for insights on such questions as we enter the age of high yield forestry.

As a forest geneticist most familiar with timber species and conditions of Western North America, my examination is purposely confined to Douglas-fir. The observations may apply to other forest regions, but any generalizations beyond a single species in its native habitat had best be left to the reader. Considering the ranges of forest species, environments, practices, age distributions, rotation lengths, pathological rotations, products, specializations, and philosophies in even a single forest region, an article comparing strategies worldwide is probably beyond the capability of anyone either in agriculture or forestry. Moreover, yield will usually be conceptually considered as gross (biomass or even photosynthate), rather than net, to minimize mortality and thinning complications.

The natural forest stands in mountainous, droughty, and cool climates of the Douglas-fir region contrast sharply with the domesticated field crops in the tropical climate where the agricultural strategy of the "Green Revolution" evolved out of the intensive agriculture in temperate zone countries. Direct comparisons are difficult between production of bolewood of long-lived forest trees growing in a generally wild state, on poor, cool sites, with little culture; and production of grain crops after centuries of selection, grown on cultivated, irrigated bottomland farms. Still, the basic element of the agricultural strategy is not dependent upon the crop. The key to their strategy, and perhaps to ours, is upgrading the site itself.

## The Agricultural Yield Strategy

The "Green Revolution" is a term associated with successes in recent years with intensive agriculture of wheat, maize, rice, and sorghum in developing, mainly tropical countries. Foresters generally have had little contact with or impact from this vast new body of organized agricultural experience. Few publications from the effort have appeared in journals that are widely accessible to foresters, although technical implications have been the subject of forest genetic workshops (1). *Scientific American* published a 220-page issue on food and agriculture in September 1976 which synthesized much of this valuable experience into a few well-written articles by worldwide authorities.

Much of the background needed here is covered in a single article entitled, "Amplification of Agricultural Production" by Dr. Peter R. Jennings (2), Associate Director for Agricultural Sciences for the Rockefeller Foundation, who has directed rice breeding programs in Colombia and the Philippines. A concise presentation of the agricultural yield strategy, which has led to fivefold yield amplification in maize, wheat, and rice, is covered in only six paragraphs.

> The native, unimproved varieties of crops such as wheat, rice and maize are not inferior per se. Given the conditions under which they have been grown, they may represent the optimum choice from among the available varieties. Moreover, the farmers who have grown them for generations are neither backward nor incompetent; on the contrary, their practices reflect a sound agricultural and economic strategy.
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> In traditional agriculture the fertility of the soil is often the factor that limits growth. Nitrogen in particular is commonly in short supply, and the shortage is severer in tropical soils than elsewhere. The native crop varieties extract nitrogen and other nutrients from the soil with great efficiency. They develop extensive root systems, drawing on a large area of soil, and they exhibit vigorous growth, which suppresses weeds that compete for the available nutrients. Having been bred by traditional methods of selection for thousands of years, they have acquired a precise, although narrow, adaptation to the local conditions, including peculiarities of the soil, the water supply, the length of the growing season, average and extreme temperatures and the photoperiod, or number of daylight hours, which is a function of latitude.
>
> A native variety of a crop is rarely a purebred line; instead it is a population in which all the members may have similar outward characteristics but have varied genotypes. Populations of this kind are called land races.

> The genetic diversity of the land race can be of great value to the traditional farmer, since it confers at least partial resistance to insect predation and disease, and partial tolerance of environmental stresses such as drought. If a crop becomes infected with a particular disease, for example, some of the strains in the land race are likely to be susceptible, but others may well be resistant and will survive. Moreover, the nonuniformity of the plant population tends to limit the maximum numbers of pests and disease organisms and thereby to prevent disastrous crop failures. The net effect of this agricultural system is to give the farmer a measure of security. The strategy of the subsistence farmer in particular is not to obtain the greatest yield in the best of years; instead he must ensure some yield even in the worst years.
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> The main failing of the traditional agricultural system is that yields cannot be significantly increased. The one reliable way to obtain more crop per hectare is to grow more plants per hectare, which obviously requires that the plants be placed closer together. With the unimproved types that is not possible because of their characteristic large size and because they compete strongly for light and nutrients. Moreover, the land could not sustain the additional population of a denser planting. The nutrient pool of the soil would quickly be exhausted and the plants would not receive enough sunlight; as a result they would not develop properly.
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> The solution to the problem of nutrient depletion is chemical fertilization, including a generous nitrogen supplement; that is the only way to sustain the higher plant density required for higher yield. When a native variety is grown with a large dose of fertilizer, however, several new problems emerge. First, most of the newly available nutrients are employed not for increasing the edible portion of the plant but for vegetative growth. Leaf area increases greatly, and because the plants are closely spaced each one shades its neighbors; as a result the overall photosynthetic efficiency of the crop is reduced. With cereal crops an even more serious problem arises. Because fertilization increases the size of the plants in traditional varieties, the grain is borne on a much-elongated stalk. Long before the grain is ripe it has become too heavy for the straw, and in wind or rain it "lodges"; the straw bends or breaks and the grain falls to the ground, where much of it is lost.
>
> The problem of lodging and of excessive vegetative growth has been solved by breeding dwarf and semidwarf varieties of the major grains. Indeed, the development of these varieties is the very heart of the green revolution. The dwarf plants have short, upright leaves, so that in dense populations the plants do not shade one another. Their straw is also short and stiff, and capable of supporting a full head of grain to maturity. The root systems are relatively small, but extensive root systems are not required because fertilization ensures an adequate supply cf nutrients. Fertilizer is an essential in the cultivation of the new varieties; without it they do no better than the traditional types, and they may do worse. Although some of the varieties have a broad resistance to diseases and pests, chemical pesticides are frequently applied, and management of weeds and the water supply is also necessary. These requirements add to the cost of growing a crop, but the investment is amply repaid by the increase in productivity.
>
> —Jennings, *Sci. Amer.*,
> p. 182-184

Foresters may find this treatment of yield strategy refreshingly mature. It simplifies agricultural knowledge into an orderly synthesis, distinguishing the primary components of yield from those that merely fine-tune them. The agricultural strategy is a tradeoff. The traditional farmer is asked to exchange the objective of a reliable sustained yield at the land's carrying capacity for an objective of amplified yield. The price, willingly borne, is continuous future inputs of energy, fertilizer, water, and pest control plus a restructured, problem-prone plant. For the Douglas-fir forester, however, conditions are different enough that the total price and payoff are not so clearly favorable. Foresters may find other surprises too. These become more obvious if Jennings' theme is paraphrased in forestry terms:

> Local tree races are precisely adapted to the local site by being well buffered against environmental change such as from pests or climate. Thus they may represent the optimum choice for traditional silviculture. The main failing of traditional silviculture is that yields cannot be significantly increased. The only way to grow more wood annually per hectare is to grow more trees per hectare. The only way to do this is to relieve infertility, drought, and other constraints to growth. Overstocking, by itself, quickly exhausts the soil's nutrient pool. Generous applications of fertilizer, however, may produce too much foliage, and the native trees may become prone to windfall. Genetic restructuring of the stem and roots may be necessary for the tree crop to respond efficiently as infertility and other constraints are relieved. Without fertilizer, cultural, and other site enhancement, genetically improved varieties of trees do no better and may do worse.

Despite the many contradictions to conventional forestry wisdom in the paraphrase, I have come to believe that the principles behind most of those statements apply to a long rotation, biomass crop like Douglas-fir. Adaptation may be even more precise, yield improvement just as dependent upon site improvement, genetic and spacing gains just as indirect, and risks from genetic and habitat modification even greater. This belief arises from a background of both agriculture and forestry information that is gradually conveyed to the reader through the answers to 11 questions.

# Questions of Applicability

## 1. Is there a forestry-like example from the Green Revolution?

The answer is, partially. The large irrigated United States farm growing highly specialized pure lines of grain provides no meaningful parallel to Douglas-fir forestry — nor does the upland wheat farm, despite more topographic and climatic similarity. The wheat crop usually matures before available moisture is depleted, whereas some of the main forestry problems arise from the need to carry a living organism year after year through severe climates between growing seasons. But an example of a wind-pollinated species from the Green Revolution that does have some strong parallels to forestry is maize breeding done for subsistence farmers on poor, hilly, unirrigated lands of the tropics. Jennings' (2) description of this program follows:

> When the Mexican wheat-improvement program was established, a parallel program to increase yields of maize was also begun. Maize is grown widely by subsistence farmers in Latin America, and also in Africa and in some parts of Asia. Yields have traditionally been low.
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> It was in maize that the methods of 20th-century plant breeding were first successful in the developed countries, and particularly in the U.S. The important contribution was a method for the commercial production of hybrid maize, which was devised in the 1920's and 1930's; by 1950 hybrids had been almost universally adopted in the U.S. corn belt. Yields increased roughly fivefold in less than 20 years.
>
> For farmers in the developing nations the cultivation of hybrid maize does not appear to be practical. The hybrids grown are of the $F_1$ generation, and all the plants in a given population are genetically uniform. Such uniformity increases the vulnerability of the crop to diseases and insects, and in the Tropics those stresses are particularly severe. Hybrid maize has another disadvantage: for $F_1$ hybrids new seed must be produced each year by the deliberate crossing of carefully maintained purebred lines. The developing countries lack the facilities for producing the seed or for distributing it, and subsistence farmers may not be able to afford the recurrent cost of seed. The traditional practice since Neolithic times has been to save a portion of the harvest as seed for the next crop.
>
> Methods for breeding maize are different from those for wheat or rice. Maize bears separate male and female flowers, as opposed to the perfect flowers of most cereal crops, and under natural conditions it is almost always cross-pollinated. Lines that are deliberately inbred soon become weak and stunted. The hybrid varieties grown in the U.S. were developed explicitly to counteract this tendency, but the maize-development program in Mexico has placed little emphasis on the creation of hybrids. Instead populations of plants have been developed that are in effect land races composed of much-improved individuals. The plants in a given population are similar in appearance and are uniform in properties such as length of growing season, but they are genetically diverse. The plants are grown and pollinated by natural methods for several generations with only the seed of the favored individuals saved at each harvest. In this way the frequency of desirable genes in the population gradually increases, although a given gene is not likely to be present in every plant. Deliberate crossbreeding is still a basic element in the improvement program, but the object is merely to incorporate new traits into the heterogeneous population, not to create a purebred variety.
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> As in the breeding of wheat and rice, a first objective in the maize-improvement program was the breeding of plants that could be grown in dense plantings and that could be fertilized without danger of lodging. This was accomplished by literally shifting the center of gravity of the plant: crossbreeding tall, tropical plants with dwarf varieties has produced a shorter plant that bears the ear of grain lower on the stalk. The improved populations also have shorter leaves, and the leaves remain upright. Genes that confer resistance to disease and insects have been bred into some of the better populations. As a result of these changes it has been possible to increase the crop density from 50,000 plants per hectare to more than 100,000.
>
> For many years it appeared that broadly adapted varieties of maize could not be created. Instead separate populations were developed for various altitudes, latitudes and growing seasons. Since about 1970, however, some populations with a fairly wide range of adaptation have been created. Sensitivity to photoperiod, for example, has been reduced by crossbreeding selected varieties from different latitudes. In some cases broad-spectrum disease resistance has also been achieved.
>
> Progress in maize improvement has not been as rapid as that in wheat and rice, but it has not been negligible. In Mexico productivity has doubled, and the technology has been exported to Africa and Asia.
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> —Jennings, *Sci. Amer.*, p. 186-187

Note the useful forestry parallels in abandonment of purebred varieties in favor of starting with an adapted heterogenous land race (see paragraph 2 of Jennings' (2) first quotation) to handle disease and insect as well as inbreeding problems. **Also** new traits were bred into the population using population genetic methods, aiming toward a new land race adapted to better fertility. Up to this point the parallel to forestry is strong. But the strategy departs from forestry in use of high plant densities, dwarfing genes, and daylength-insensitive plants. Some very important considerations like the genecological needs of a long-rotation crop are not addressed.

**Also** note that in such less controlled agricultural environments, yields were scarcely doubled after many generations of breeding. Foresters may be optimistic to expect greater gains in Douglas-fir with even less opportunity to cultivate, or to control pests, and, moreover, with a crop that uses so much of the biomass in structural rather than reproductive parts.

## 2. Is agronomy the main factor in amplifying yields in agriculture?

Jennings' brief discussion of components of crop yield may perhaps need elaboration for a forestry audience. He implies that the major source of upgrading yield per hectare is improved agronomy (fertilization, irrigation, cultivation, and control of weed and pest), whether the criterion is grain yield or biomass yield. Apparently changes in agronomy bring on the need for spacing and genetic adjustments, not the reverse. The most dramatic agronomic example of yield changes is with irrigation of desert land, which can change grain yields from zero to many tons per hectare. Yield of a certain crop on a particular field is often known within close limits under each agronomic practice. For grain, forage, or root crops, these limits tie most closely to some elevated crop density that can be maintained on a particular field by means of a particular application of agronomy. In the same sense, the Douglas-fir forester knows fairly closely what the growth and yield will be under natural conditions on lands of a particular site quality. The implication here is that higher yields will come from silvicultural versions of analogous agronomic practices. Some confusion in forestry arises from expectations that the thinning regime, by itself, can produce more gross fiber yield, or that genetics can upgrade yield quite independent of agronomy. These subjects are discussed later.

The whole subject of site-limited yields has been clarified over the last two decades in a theoretical sense by studies of the "law of constant final yield." This "law," developed by Japanese scientists Hozumi, Asahara, Shinozaka, and Kira in 1956 (**3**), deals with yield per unit area of field or forest and with suppression-driven mortality. It states that final yield per unit area is constant and independent of plant density. At any initial spacing, plants grow rapidly at first to fill out a complete canopy, then individual plant growth slows as competition between plants increases. Finally, competition is **so** severe that the only additions to yield are from space made available as a plant dies from suppression. The law proposes that this final gross yield is equal or constant at any spacing, and that the difference in spacing influences only the time required to reach the constant final yield. Final yield is approached most quickly at densest spacing. Actual yields at other spacings approach being asymptotic but do not exceed the constant final yield. Scores of species as diverse as soybeans and loblolly pine have been shown to follow this law. See also reference (1) for technological implications and **(4)** for indicated applicability to cottonwood in the southeastern United States.

The pertinence of the "law of constant final yield" is threefold. First, under any given soil and agronomic or silvicultural practices, neither the spacing nor genotypes used should have much effect on the final yield provided genotypes are adapted and genetically capable of fully utilizing the site. Both may, however, have great effect on time required to reach the stage of severe competition at which unit area yield is at maximum. Second, environmental constraints determine the final constant yield. Third, the original concepts were developed for annual plants but appear to apply to forest trees over the longer time span needed to reach the stage of self thinning. After that, annual increments are probably constant at all spacings. These concepts assume all mortality is recoverable.

The observation that yield of a forest site improves with better fertility, moisture, and length of growing season fits general agricultural experience. That biomass yield may be constant once a forest closes its canopy is not **so** directly observable. Both ideas are clearly incorporated in Jennings' strategy discussion, and both have silvicultural and forest genetic implications.

## 3. What other factors contribute to amplifying yields in agriculture?

Once the basic productivity of a farm has been enhanced with better agronomy, other factors can contribute to even greater yields. Most of these other factors, it turns out, are presently of questionable pertinence to Douglas-fir forestry. The discussion is limited to yield rather than quality or dollar return. In both agriculture and forestry, maximum dollar return often requires some yield **loss** for better quality, uniformity, or mechanization.

The principles underlying other components of grain yield — harvest index (the proportion of grain to total plant), plant density, lodging (beating down by wind, rain, etc.), and early maturity — can be illustrated in a single example. This is a particularly good example for several reasons. **It** deals with maize, the best known genetic plant material. Like Douglas-fir, it uses a wind-pollinated plant genetically improved by a population genetic approach, and with an adapted local land race capable of utilizing the site fully. **It** demonstrates the outcome of many generations of breeding the same population. The study involved was conducted by Dr. Elmer Johnson (5) at the International Center for Improvement of Maize and Wheat (CIMMYT) near Mexico City. The primary objective of this study was to reduce plant size of a heterogeneous native Mexican maize population through **17** successive cycles of selection. Secondary objectives were to reduce lodging and upgrade harvest index.

On the irrigated, fertilized, and pest-controlled site, native maize initially averaged about 3.6 meters (12 feet) tall, but after 17 cycles of selection by a population genetic breeding approach, plant height was steadily reduced to slightly over **1.8** meters **(6** feet). Ear size remained adequate or improved. Gains in maize yield from generation 1 to 6 were mainly from reduced lodging, which by generation 17 was no longer a problem. Harvest index was steadily improved from 35 percent in native maize to 48 percent by cycle 17. Optimum plant density rose from about 30,000 plants per hectare initially to about 65,000 at cycle 17. Grain yields from combining the yield components of better density, better harvest index, and reducing lodging were improved 3 percent per cycle, or more than doubled at cycle 17. The above-ground **total** plant yield per hectare at each cycle, however, was so similar at optimum spacing that no upward or downward trends were detected. This general experience is common to studies of these yield components for wheat, rice, sorghum, and probably to crops in general.

In the 17-cycle maize study, another breeding objective was achieved without deliberate positive selection. The crop matured progressively earlier because smaller plants grew fewer leaves. Early maturity is an important trait for grains where the range is being extended to higher elevations, higher latitudes, or where two or three crops are grown in a season. In contrast, where a single crop is grown in temperate climates, a stower-maturing variety is more productive. A major yield variable that responds to genetic selection is how precisely crop maturity matches length of growing season. A crop variety bred to ripen too early generally yields proportionately less than one which uses the entire growing season. But grain crops still immature or maturing at first frost will yield correspondingly lighter — even worthless — grain. Some of the crop reliability of the land race arises from the attunement to average length of growing season by the average plant, in company with a range of maturities distributed normally around the mean represented in a heterogeneous population. Even early frosts find some plants mature. These early plants, however, are likewise at a yield disadvantage over normal or late plants in a long growing season.

But let us extrapolate to annual growth of native Douglas-fir populations —late-starting and early-maturing individuals have a growth advantage in a short season, and early-starting, late-maturing plants in a long season. Together in the same population, they probably provide a capability to maximize stand yields by jockeying for dominance as each season varies in length around the climatic norm — the early ones growing best some years, the late ones best other years, but normal ones best most years. Over a forestry rotation such ability of a Douglas-fir stand to utilize all of each growing season could be a major genetic component of final yield.

In the CIMMYT special study (5), the large leaves of the native maize population of cycle 1 permitted much rust and insect attack, which reduced yield somewhat without threatening the plant. Generalizing from Jennings' paper, by cycle 17 the upright smaller leaves and somewhat narrower genetic base had probably made the plants relatively more vulnerable to pests. However, plants in the study as well as worldwide plantings of this study material were adequately protected by chemical control of such pests. Jennings' (2) point is simply that the improved material would probably be quite vulnerable if returned to the environment of traditional agriculture instead of the controlled environment of amplified yields.

Thus, a single plant breeding study highlights the major and contributing factors of yield amplification. First was the substantial increase in biomass arising from irrigation, fertilizer application, and control of weeds and pests. Additional contributions to yield arose from control of lodging, improved harvest index, denser spacing, and appropriate maturation. From a forestry standpoint the analogous traits (windfall control, better form class, phenological control and pest resistance) are peripheral objectives because Douglas-fir is already adequate in these traits (1). Direct increase in above-ground total yield is considered a primary goal for genetic improvement in this species. Agricultural experience suggests that such improvement should, instead, arise primarily from upgrading site quality and keeping stand closure, followed by genetic adjustments to solve problems. As Jennings (2) suggested, local races proved advantageous as starting material. The end product would be a new heterogeneous land race. Genetics is the crucial component that permits utilizing the benefits of agronomy. Substantial contributions to forest yield may arise from strategies that have few parallels in agriculture.

### 4. Are local races of forest trees as precisely adapted as land races of agricultural plants?

This seemingly innocuous question turns out to be of pivotal importance in the quest for higher Douglas-fir yields. It deals indirectly with growth through another trait — adaptation. It introduces what, for want of a better name, we will call the genecological problem, which grows in importance as rotations lengthen. It involves Jennings' (2) concept that precisely adapted local stands maximize crop reliability.

His discussion of agricultural land races uses the words "precisely adapted" without clarifying how precise. For maize, precision must be very high. Distinct maize land races in different parts of the same valleys were a common occurrence in Mesoamerica. The double selection — human, for better maize, and natural, for survival — tended to optimize each land race both for crop reliability and for adaptation to the local environment. More than 15,000 distinct land races of maize are recognized and maintained in the International Maize Germ Plasm Bank at CIMMYT (5).

In forestry, and particularly for Douglas-fir, a growing number of studies indicates equally precise adaptation and crop reliability of local tree races (6). The study suggesting the most precise adaptation is one in which Dr. Robert K. Campbell (7) of our laboratory has recently sampled heavily and uniformly among 450-year-old parent Douglas-fir trees in a Cascade Range drainage of only 15,000 acres

(6 000 hectares). Progeny seedlings from 193 parent trees grown in our experimental nursery, displayed a distinct pattern of height differences according to parent location. A contour map of this genetic pattern is quite recognizable as mimicking a topographic contour map of this 23-square-mile mountainous drainage. Genetic variation apparently formed a templatelike continuum of local populations that varied their gene or allelic frequencies for adaptive traits in three dimensions (latitude, longitude, and elevation) to fit environmental changes associated with landforms in the drainage.

Support for this concept has come even more recently as 10- and 12-year-old progeny test data have been summarized from three commercial tree improvement programs near Vernonia, Molalla, and Burnt Woods in northwest Oregon ***(8)***. A decade ago, seed was collected from 900, 375, and 160 parent trees, respectively, in the three programs at a lighter sampling density of about two parent trees per square mile (260 ha). Data from these programs clearly indicate genetic variation in progeny height growth that relates to local topographic land forms of the respective 330,000 (134 000 ha), 125,000 (51 000 ha) and 60,000 (24 000 ha) acres of the three programs. Again, genetic variation is related to topographic features such as valleys and ridges of local drainages. For these four areas, variation in Douglas-fir appears to reflect adaptation of the local population to differences in growing season length. Best inherent growth is from local parents occupying mild and moist locales with long growing seasons; the poorest inherent growth, in cold or droughty locales with shorter growing seasons. In some instances nearly the entire range of inherent growth differences occurred on the same mountain slope.

The concept should cause the reader no greater stretch of credibility than templatelike matches between chromosomes and their products, between antigens and antibodies, or at macrolevel, the precision with which all energy niches are occupied in an ecosystem. Precision is turning out to be more the rule than the exception at every level of life's organization. The whole subject of precise genetic adaptation has long been one of the more neglected research areas of both forestry and agriculture.

Jennings' (2) statement provides clues as to what may be required for precise adaptation in a continuum. He views genetic diversity as being needed to provide pest resistance and to limit maximum numbers of pest and disease organisms. In my view, at any point on the continuum, the tree population must be different than elsewhere because the timing and expression of the climate and biology is a bit different. Precise adaptation for each locality along an environmental gradient implies continuously differing gene or allelic frequencies in every pertinent adaptive trait. Nature's most important genetic innovation may well have been this ability to vary a trait through control by many genes. Something as simple as the Aa and Bb dominant-recessive genetic control of a trait described in high school textbooks provides up to nine gradations of variation in genetic expression. Multiallelic or multigene traits permit a potential for fine-grain gene frequency changes to any degree necessary for a genetic match anywhere along an environmental gradient. Actually, there are an array of genetic mechanisms that permit such continuous variation in a trait. A great amount of genetic diversity itself may not necessarily be helpful for precise effective adaptation. Rather, what appears needed is a highly selected, precise genetic architecture of the whole local population in terms of matching gene frequencies of each pertinent trait to fit each local climatic and biotic environment.

There is a theoretical dilemma of a genecological kind in handling the needs of three-dimensional genetic clines. In nature most plant genetic traits are found to vary clinally along environmental gradients such as occur with elevational or horizontal changes in the cited examples. An improved variety, however, fits only a single spot along such a cline. When clinal variation occurs as a continuum in three dimensions over the landscape, as now seems the more general case, a variety can precisely fit only a limited portion. Thus, even when local seed from a single locale of the native species is used to plant a large parcel of cleared land, as is often the case in regenerating a clearcut Douglas-fir forest, the seed can theoretically be precisely adapted only to some single locale of the continuum. Conversely, if a planted variety is made up of a seed mixture from parentage that lightly samples the large parcel or beyond, the variety cannot exactly match the continuum anywhere — it being an approximation of each local native population to some degree but not a precise fit anywhere. The more precise the adaptation turns out to be, the more pertinent becomes the dilemma. There is no simple practical answer to the Douglas-fir foresters' problem of matching seed to fit a genetic gradient, let alone the more common case, a three-dimensional continuum. Nature, however, has apparently long since successfully solved the dilemma of matching the species to the three-dimensional environmental continuum. At present there is little information on which to reject the hypothesis that adaptation to a locale is precise for Douglas-fir.

Problems of reliability with unadapted populations tend to arise gradually as the surrounding natural environment adjusts to the presence of a new “variety.” Gene frequencies probably change for every animal, disease, insect, and weed pest in a locality as they use the new variety for sustenance. Those pests or strains formerly in high frequency may exchange predominance with those formerly in low frequency. In forestry, this change is sometimes expressed in the gradual dominance of pests formerly of such low frequency as to be biological curiosities or even species still without scientific names. For example, Bynum’s blight *(Lophodermella morbida* Staley and Bynum), a rare, previously unnamed defoliator of ponderosa pine, became epidemic in 10- to 20-year-old plantations originating from unadapted seed of eastern Oregon planted in southern Oregon. In like manner, the introduction of Douglas-fir to other temperate zone countries has been characteristically followed by high losses from rhabdocline disease *(Rhabdocline pseudotsugae* Syd.) and Swiss needle cast *(Phaeocryptopus gaumanni* Rohde), both of which are present throughout the natural range of Douglas-fir, but are normally innocuous. Examples are not limited to such large seed movements. More locally, the Douglas-fir Christmas tree industry, mostly planting somewhat off-site seedlings, is presently experiencing increasing losses or degrade each year from native pests. Loss of tree vigor may also contribute to such pest problems. The life of a Douglas-fir stand is so long that any biotic problem can eventually become severe. Plantations of Douglas-fir planted within its natural range prior to 1920, but using seed of unknown western Oregon and Washington origin, are by now universally debilitated to greater or lesser degree compared with surrounding natural stands. Precise adaptation seems to be a prerequisite for maintaining stand health. Even though it is common in a cool climate like the Pacific Northwest for forest geneticists to consider climatic adaptation as the main problem, adaptation to biotic agents becomes just as crucial for long rotations.

This fundamental problem of replacing native plants in a natural continuum with a variety has its counterpart in agricultural breeding. Rarely has a variety of wheat or corn been widely planted for even a decade. All eventually suffer reduced yield or lack resistance to a strain of pest that finds sustenance from it. Only a few cycles of breeding are usually required to reach such breeding objectives as desired plant size, phenotype, and resistance to expected pests. Plant breeding would be a highly efficient enterprise if breeding could stop there. But breeding usually continues indefinitely for adaptation to changing pest problems. The present trend in agricultural breeding is to produce varieties with greater genetic diversity. Varieties are made from multiple pure lines in self-pollinated crops, or from crosses of large numbers of parents in outcrossing species. Such varieties are scarcely distinguishable phenotypically from the pure lines. A trend appears started in agriculture toward returning to the precise adaptation and reliability of the land race, just as trends have started toward greater use of biological control of pests.

The genecological problem is quite tolerable in agriculture, where crops can be replaced annually and cultural or chemical pest control is practical. In long-rotation forestry, the crop reliabilty problem is magnified until it becomes pivotal. It is as though one said to the agricultural plant breeder, “Produce a perennial agricultural variety that will guarantee a healthy, good-yielding stand on this acre with little attention for 80 years.” Yet foresters are so accustomed to just such phenomenal genetic material everywhere that they have little appreciation for it. Why should they worry about the health of an 80-year-old Douglas-fir stand when the species lives over 10 times that long? Yet the real world of forestry shows case after case where problems arise within a few decades when forests are maladapted. Douglas-fir foresters have long accepted the admonition that “local seed is best,” and many landowners have made major investments to assure that seed movements are within seed or breeding zones. The concept of precise templatelike adaptation to match the concept of variation in a three-dimensional continuum is reasonably new to foresters. If a trouble-free forest should require such precise adaptation, present silvicultural and genetic concepts would need to be altered. Even with the sketchy data available now, adaptation appears far too precise for economic convenience. Fortunately the precise adaptation and reliability, already genetically incorporated in the local tree race, does not need to be foregone in the quest for better yields. It does need to be given priority.

### 5. Can the agricultural strategy be applied to Douglas-fir”

The vast differences between farm and forest would have to be rationalized somehow to conceive a forestry version of the agricultural strategy for Douglas-fir. One approach is to examine the basis of these differences.

The area of the Pacific Northwest where agriculture is successful has a narrower and more controllable environment than that of the commercial forest. Constraints to growth in agriculture are easier to relieve. For example, the constraint of cold, expressed as a short growing season between killing spring and fall frosts, is mitigated by either selecting the warmer climates of valley locations or selecting crops that mature quickly. The constraint of summer drought is avoided by choosing moist micro-climates or by irrigation. Drought is also relieved by fallowing, by complete weed control, or by using plants that mature before available soil moisture is depleted. Pest constraints are controlled in a variety of economically practical ways. Thus, the key item of Jennings’ (2) agricultural strategy, a generous fertilizer supplement to relieve the constraint of soil infertility, is simple and certain only because agricultural field crops are ordinarily much less constrained by cold, drought, or pests than Douglas-fir forests.

In contrast, Douglas-fir forestry is practiced on lands usually too poor, rough, droughty, or cold to be farmed. They typically have some or all of the above growth constraints and poorer prospects of relief. There is little prospect that scarce water resources will be available for widespread forest irrigation, particularly during the droughty summers of the Northwest. Relief from cold constraints is an unlikely prospect. Relief from pests, weeds, and infertility is at best periodic over the long life of a Douglas-fir stand, and generally less controllable or profitable. Thus, generous application of fertilizer can only be a partial answer, at best. As one would expect from the "law of the minimum,"[1] its main relief applies only up to the level of growth at which drought, cold, and pests become constraining (9).

A forestry version of the agricultural strategy for Douglas-fir is not less simple to conceive: It is only more difficult to apply. The agricultural strategy would need to be expanded to artificially lessen all of the above growth constraints — cold, drought, pests, and infertility — to maintain an enhanced site quality. Such an expanded expression of the agricultural yield strategy (i.e., enhancement of site quality) would seem to apply to both forestry and agriculture.

Suppose foresters could successfully enhance site quality by mitigating growth constraints. Would the expanded strategy work? Douglas-fir Christmas tree growers routinely employ agricultural techniques of fertilization, cultivation, and control of weeds and pests to successfully shorten rotations. Containerized nurseries now routinely grow millions of Douglas-fir seedlings to heights of 12 to 20 inches (30 to 50 cm) in a single season when growth constraints are artificially lessened. We once grew ordinary coastal Douglas-fir seedlings 8 feet (2.4 m) tall in our laboratory in two growing seasons by artificially relieving all constraints to growth within our capabilities — a fivefold height increase over prevailing field nursery practice (10).

With mature Douglas-fir forests such an expanded strategy is far more difficult to apply. In the typical summer drought of the Douglas-fir region, the main constraint to growth is moisture deficiency. At higher elevations the constraint is a cold-shortened growing season. Though seemingly workable in farmlike situations, heroic efforts and expense might be encountered in applying the expanded strategy generally over the Douglas-fir region.

## 6. Is forest thinning at odds with plant density concepts of the strategy?

The close-planting strategy Jennings (2) describes might be seen by foresters as obviously at odds with spacing concepts of intensive forestry. Doubling or tripling trees per acre for greater volume production would usually lead to undesirable results on most Douglas-fir properties. Foresters usually desire ample spacing to forestall suppression and promote good diameter growth. Larger stems meet most economic goals better. The strategy might apply if small stem sizes and short rotations were the only goals.

On moist sites all crops develop through successive stages of understocking, optimum stocking, and overstocking of the sites' potential for yield. In the period from germination to canopy closure, growing space is underutilized. Beyond canopy closure, further plant growth leads to overstocking, suppression, and self thinning. Agricultural field crops using smaller mature plants can develop through the underutilization period quickly if kept at close spacing and without competition of weeds. If original spacing is optimum for the final plant size, the overstocking stage is also avoided with agricultural crops. In contrast, Douglas-fir crops may underutilize the sites' potential for decades. The understocking stage is further prolonged by severe weed or brush competition. The stage of optimum stocking is brief. With continued tree growth and with mortality from suppression, the overstocking stage can continue in natural stands for centuries. One aim of thinning is utilization of a substantial loss of fiber on trees that would die from suppression. Any additional thinning that opens the canopy may temporarily renew the underutilization stage. Viewed from an oversimplified perspective of maximizing biomass yields, it is difficult to rationalize the forestry goal of always providing ample growing space with the dense stocking strategy of amplifying yield. An intensive thinning schedule would appear to keep growth levels somewhat below constant final yield until just before harvest. On droughty sites mortality may begin at stocking levels **below** canopy closure.

Stocking control of tree species, however, has a unique facet. For Douglas-fir, my recent inquiry among scientists[2] in this discipline suggests that gross fiber gains from stocking control alone may, indeed, be difficult to demonstrate on best sites. On high site quality lands, thinned stands usually produce somewhat less wood fiber per unit area than dense, but not over dense ones. Lower site quality Douglas-fir stands may be an exception. They commonly grow substantially taller trees when provided adequate spacing and thus carry more volume on a longer and larger bole than at normal or tight spacing. In this three dimensional view for a tall species like Douglas-fir, well distributed stems could carry additional volume. As a cautionary note, however,

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[1] Liebig originally proposed a "law of the minimum" in **1843.** Mitscherlish, in **1909,** improved the concept which he stated as follows: "The increase in any crop produced by a unit increment of a deficient factor is proportional to the decrement of that factor from the maximum."

[2] The subject was discussed with Richard Williamson, Dave Bruce, Don Reukema and Robert Curtis, Pacific Northwest Forest and Range Experiment Station, who have devoted their careers to study of conifer yields. The subject of this paragraph was first suggested by Reukema. See also discussion of light interception by Cannell **(1).**

Jennings' (2) inference that overstocking leads to exhausting the soil's nutrient pool implies that such gains could also be temporary over a longer time frame without replacing deficiencies with nutrient supplements.

But thinning schedules have more sophisticated goals than simply maximizing fiber yield or forestalling mortality losses. All thinning schedules aim to improve harvest index, but not quite in the same sense as with a crop of wheat. Neither the farmer nor the forester can ordinarily sell all the fiber produced. On most Douglas-fir properties, trees below a certain size are as uneconomic as the stubble in a wheat field. Thinning schedules improve harvest index to maximize dollar returns of that portion of the total biomass composed of marketable logs. Even if fiber yields were amplified, this incentive would remain as long as larger sizes meet economic goals better.

Thinning aside, a recurring question with amplified yield is whether to grow more wood per hectare in a given rotation or alternatively, to shorten the rotation for a given amount of wood. The latter option appears preferable for Douglas-fir even though the agricultural strategy uses the first option. Either more slender trees (the "crop" ideotype (1)) or the same numbers of stocky trees (the "competitive" or "isolation" ideotypes) would seem to be needed for the first option. Despite inheritance of taper being quite strongly additive (6), breeding such populations, though possible, seems needless and may create more problems than it solves. There must be some sensitive biological relationship involved between stand density and taper. Yield tables of Douglas-fir embrace the range of site qualities beyond any expected outcome of artificial site enhancement. Yet, an inspection of tree tapers over this range shows surprisingly consistent patterns. For example, when stands self-thin to a density of 200 trees per acre, the average height is about 130 feet and diameter about 16 inches. This happens whether this height is reached at 40 years on high site I land or 140 years on low site IV land (11). This suggests that some principle operates at the stand level like the proposal of early-day foresters that a tree stem becomes a "beam of uniform resistance" (12). There may be rather narrow limits around which average tree tapers can vary successfully for a given size and spacing. Thinning under the second option might aim to remove the accelerated growth. Under the first option more than normal volumes might be carried between thinnings.

What emerges from this array of considerations is a reasonably consistent spacing rationale. With or without site enhancement, foresters successfully use spacing to improve the dollar yields. As in agriculture, some underutilization of the site is tolerated during stand regeneration and temporarily after thinning. On low sites, spacing alone may actually produce more total wood on longer stems. Site enhancement may require different ideotypes as in agriculture, but more plausibly, only shorter rotations with normal ideotypes. Some genetic implications of spacing as related to the genecological problem will be considered later.

Before leaving this question, it may be well to point out that no greater opportunity exists in upgrading Douglas-fir yields than the traditional forestry role of bringing understocked and nonstocked lands to full stocking. Nearly one-third of the cutover lands of the region are understocked.

## 7. How does weed control fit into the strategy?

The regularity of summer drought in the Pacific Northwest elevates this subject to special importance. Growth is constrained by drought most years just when maximum heat sums of the growing season accumulate. Thus, loss of growing season moisture to competing plants shows up in reduced seedling survival and in lost annual growth throughout the rotation. For many years the Christmas tree industry in the Pacific Northwest has recognized control of competing vegetation, particularly grasses, as the major factor in assuring high seedling survival, as well as producing better growth and shortened rotations. The same experience is gradually accumulating on commercial Douglas-fir forest land.

The species regenerates poorly in brush or grass. A high level of control over competing plants appears as important to full, prompt restocking following stand harvest as it was in nature. The great wildfires that originated the region's prime virgin forests usually wiped out all competition for Douglas-fir seedlings. Usually these fires burned when the soil was below the wilting point destroying all vegetation and burning much of the soil's humus. After stand closure in the moister portion of the region, the species can be grown dense enough to shade out competing plants, so that virtually all the productivity of the site is converted to fiber growth for much of the rotation. But during the brushy regeneration period, and during understocked periods later in the rotation all yield strategies benefit from weed control. Thinning, which permits growth of competing vegetation, becomes less efficient without weed control. The economics of forest weed control in rough topography, however, and the many associated environmental questions make weed control a far more complex problem for the forester than for the farmer and Christmas tree grower. The special problems of weed control by repeated cultivation will be taken up in discussions of maintaining the nutrient capital of the soil.

But even on gentle topography, a weedless Douglas-fir forest is not a reasonable goal. The role of associated vegetation in nutrient recycling must also be met. A major question in all sustained yield forestry is how much of the biomass production, both from trees and associated plants, must be recycled to maintain productivity.

## 8. Is the role of genetics of Douglas-fir somehow different than its role in agriculture?

In Douglas-fir forestry, genetics is looked upon to independently increase forest yields, whereas in agriculture genetics has a supportive role to site enhancement. Consider again how Jennings (2) develops this role.

His paragraphs on the agricultural strategy begin by pointing out that the precisely adapted, genetically heterogeneous land races of wheat, corn, and rice may represent the optimum choice for traditional agriculture, where the objective is a reliable crop. When agriculture's objective becomes amplified crop yield, the strategy does not depend upon genetic gains. First, site quality is enhanced with fertilizer, ample moisture, and pest control. Then, resulting biological, mechanical and structural problems are solved with genetics. The suggestion for forestry from this is, first, that local races of native trees may be the optimum choice for crop reliability goals of traditional silviculture; and, secondly, that for high yield goals, site enhancement should be primary and genetic manipulation supportive to solve problems that arise. Of all the forestry questions raised by the agricultural strategy, those associated with genetics are the most confusing.

One reason is that, worldwide, forest genetic gains, independent of site enhancement, seem well documented. Without fertilizer or other site enhancement, superior growth has been demonstrated for certain introduced species, for selected races of several species, and selected individual trees within races. Yet, examination of these examples reveals no unequivocal contradiction of Jennings' (2) strategy statement.

The best demonstrated genetic gains involve use of North American tree species on other continents. In a sense, this could be a special case. Where they are adapted, North American tree species, particularly those from Western North America, usually outgrow by wide margins their counterparts in the same tree genera from other lands, whether grown together on other continents or in North America. There is a well-based speculation that great losses of inherently fast-growing tree species and races must have occurred on the Eurasian land mass during ice ages as southward-migrating forests were trapped against east-west oriented mountains and seas. North American forests could successfully migrate southward toward tropical climates on north-south oriented mountain ranges to preserve fast-growing, cold-sensitive genotypes through the ice ages. Thus, higher yields of North American species used as exotics could be interpreted either as a case of demonstrated large genetic gains or, alternatively, of bringing yields up to what may once have been the norm of other temperate zone continents. Similarly large genetic gains from exotic species have not occurred in Western North America because of the relative superior inherent growth of Pacific Northwest species (13). Apparently a forest species must first be genetically capable of using a site completely.

Genetic gains demonstrated for certain races of many North American species are just as real. Most instances of superior racial growth occur with races or stands that developed in localities having more assured moisture and a longer growing season than the test area. For Douglas-fir, there is a general inverse relationship between growth and hardiness to either cold or drought. Increased inherent growth potential is accompanied by less hardiness. Trees genetically improved for faster growth may carry a greater long-term risk of loss when grown in a more severe climate. Interpretation of documented instances of superior racial growth could be either a true genetic gain, or short-term rapid growth of what may prove to be genetically vulnerable, nonadapted plants.

For selected individual parent trees within races, large inherent growth superiority is adequately demonstrated. Typically, in our studies, progeny from best parents in most stands produce about 20 percent more stem volumes than average. The confusion here is whether inherent superior annual growth on a **per-tree** basis will be demonstrated on a **per-area** basis. Virtually all instances in Douglas-fir come from plots of trees with room to grow. Few experiments have yet reached the age or stage to express differences in family volume per unit area. One study of closely spaced loblolly pine seedlings indicated that family differences were large in the underutilization stage but dropped below statistical significance as stands approached the stage of self thinning **(14).** This is also reported for a 60-year-old family study still maintained by our laboratory (15) even though family growth differences at this age are obvious. At present few plots are old enough to adequately demonstrate superior family performance on an annual growth-per-hectare basis. Again, the final word is still to come on whether genetic gains will be substantial without site enhancement.

This discussion emphasizes how difficult it is to seriously challenge the basis of the agricultural strategy with presently inadequate forestry data.

Genetic gains in yield claimed for present tree improvement programs are modest and may develop in suggested ways that do not involve site enhancement (1). Selected genotypes may be appreciably more competitive with brush, resistant to browsing, or efficient in using existing nutrient levels, or in using less photosynthate for respiration (1), or are better crop ideotypes (1), or can better overcome drought or cold constraints. Our wild trees are so unimproved compared with agricultural land races with centuries of domestication that modest gains may be possible before site constraints are even taxed. Gains in other traits besides yield may alone justify genetic programs.

One certain source of potential genetic gain in forestry has little relevance with closely spaced field crops. This is the use of inherently faster-growing trees to more quickly occupy open space or attain canopy closure. As discussed earlier, modern silviculture provides growing room at all periods of the rotation, from initial tree spacing through intermediate thinning schedules. With or without thinnings, more rapid canopy closure should shorten rotations, a genetic gain as real and probably just as large as providing more final volume per unit area. As will be discussed later, this potential for genetic gains also has a theoretical question.

Another related source of potential genetic gain in forestry is the opportunity to improve harvest index. Genetic contributions toward producing larger, straighter, healthier, better-formed, and defect-free trees all increase the proportion of the stand harvested.

In the above forest genetic discussion, the question has centered on yield increases without fertilizer or other site enhancements. The most prevalent assumption, however, is that on sites worth tree improvements, fertility and other constraints will be relieved when possible. Synergistic effects of fertilizer and genetics are also a possibility. As in agriculture, genetics and fertilizer will be used together and studied together. Separating the two contributions seems needless. From both agricultural experience and genecological considerations, each effective site enhancement probably calls upon the geneticist for some commensurate adjustment of the genetic population.

A prediction from agricultural experience following fertilizer supplements or other site enhancement is that trees might over-respond by producing too large and dense a crown before enough stemwood can be added for this added stress. The need to restructure plants to resist lodging following fertilizer use has been a common experience in many non-grain as well as grain crops. The phenomenon is already reported in forest fertilizer studies that resulted in increased blowdown (16) and stem breakage from ice and snow (17, 18). It is not beyond expectation that Douglas-fir might need to be restructured toward greater stem strength, stockiness or root anchorage if large growth increases are obtained with fertilizers and site enhancement. Breeding for greater stockiness appears promising in some species (6), but, as mentioned earlier, raises questions of its own. However, ample early spacing may alone produce adequately strong stems.

Jennings' (2) additional observation that most agricultural land races already efficiently use fertilizer for vegetative growth has special significance. If local Douglas-fir races respond similarly, as they now appear to do, breeding for good fertilizer response may be easy. Local Douglas-fir tree races might already have the response capacity to attain desired constant yield at modest, practical levels of silvicultural site enhancement. All such potential interactions of genetics and fertilizer, however, become meaningless on sites where other growth constraints, for example drought or cold, severely limit increases in productivity.

Is the role of genetics for Douglas-fir yield somehow different than for agriculture? Considering the generally supportive role genetics plays in agriculture, forestry would be different if direct, independent, substantial genetic gains in yield per hectare would materialize; and they may. The emphasis placed on better inherent growth to capture underutilized space or overcome brush competition will surely be different, as will strategies involved with improved uniformity, quality, or harvest index. Otherwise, as forestry intensifies, the potential for the geneticist is to also fill most of the crucial supportive roles as they have in agriculture, possibly over a much extended time frame. These are to find resistances to pests and to restructure the tree for better utilization or to fit the strains of an altered environment. With scarcely half of the forest biomass now harvested, potentials for geneticists' contribution to better harvest index would appear comparable to those in agriculture.

### 9. Can fertilizer use in Douglas-fir forestry parallel its role in the agricultural strategy?

Incentives are strong to follow agriculture's deep-furrowed path to amplified yields via fertilizer and attendant farmlike practices of cultivation and weed control. But environment of the Douglas-fir crop is different enough to need a path more suited to forestry.

The low minimal nutrient requirements of Douglas-fir are met in most soils of the region. Differences in yield over the region are more related to moisture availability than soil fertility. There are no widespread gross nutrient deficiencies like that for phosphorous in the Southeastern United States. Nitrogen and occasionally sulphur are the main deficient elements that provide a yield response. Despite many shortcomings (19), foliar plus soil analysis are prerequisites for efficient use of fertilizer.

As discussed earlier, Douglas-fir yield responses from alleviating infertility with fertilizer has generally followed the "law of the minimum" (9). For well-spaced trees, fertilizer growth response is greatest when trees are free to grow and diminishes progressively with increasing constraints of cold, drought, and pests. For example, laboratory trials (10) and containerized nurseries provide examples of unusual growth response virtually with hydroponic methods. Field nurseries and Christmas tree plantations provide an intermediate growth response when moisture stress is relieved with irrigation or complete weed control. In the typical Douglas-fir forest, however, the response has been generally lower and varies according to natural constraints of cold and drought as well as with spacing (19). Trials on commercial forest land in mild and mesic portions of the Douglas-fir region, with nitrogen fertilizer applied at about 200 kg/ha have usually resulted in positive, sometimes substantial, growth increases lasting over several seasons (9). Such yield increases commonly range around 2 to 6 $m^3$/ha (20). About a quarter of the Northwest trials, however, have resulted in neutral or even negative responses. In higher and more arid parts of the Douglas-fir region, the response has been poorer and even less predictable. Agriculture could probably duplicate such a spectrum of experience where fertilizer has been applied to cover a range that includes equally uncultivated, untended, and unirrigated field crops on poor soils.

Nutrient response in association with spacing appears also to follow the "law of constant final yield" in interesting ways. Apparently the major portion .of a stand's response to applied fertilizer results from rapid expansion of its photosynthetic surface. Greatest response is seen in stands with room to grow, whereas overstocked stands seldom show much net growth response (19). For a given site, the question is whether nutrients, particularly nitrogen, provide extra growth once the canopy closes. If gross nutrient deficiencies cause the understocking, supplements surely should provide more yield. But most soils of the Douglas-fir region can support closed canopies if moisture is adequate. In the summer-drought climate of the Pacific Northwest, is the main effect of fertilization simply to speed up crown closure with constant final yields thereafter? The larger trees in a stand usually respond most at any spacing, and appear to continue to grow at the expense of smaller trees even after stand closure. One potential for greater biomass yield from fertilizer would arise if shoot growth during the moist spring or fall increased enough each season to grow taller trees at canopy closure, thus provide longer boles as was suggested in the discussion on spacing. Constant final yield concepts may suggest that the enlarged trees would need reduced stand density. Agricultural experience on these points is not wholly clear. Where moisture is limiting, such as with upland wheat, stand densities reflect moisture availability more than fertility levels. With irrigated crops, response is mainly quadratic, in that crops benefit up to a point beyond which yields reduce. The point of such questions is to note that stand closure may set an upper limit to fertilizer response and to call attention to the possibility that fertilizer gains, like spacing and genetics, may also have a large element of better harvest index by shifting the harvested portion toward larger, better quality trees.

With such emphasis on importance of moisture to fertilizer response, the question naturally arises as to how much added growth would occur if agricultural practices of cultivation and weed control were vigorously applied to Douglas-fir forests to amplify fertilizer effects. Setting aside for the moment the huge practical problems of such farming of Douglas-fir lands, a rough estimate suggests additional yields over a rotation might not be very large. The main gains from these attendant practices to control competition would be to provide trees more moisture mainly at onset of summer drought. After stand closure, such practices become pointless because Douglas-fir shades out its competition; so major effects would take place during understocked periods, especially during stand regeneration and after thinning. Suppose growth could be extended 25 percent of the growing season for 25 percent of the rotation. This overly liberal computation would suggest only a 6-percent lengthening of the growing period to amplify fertilizer effects. The economics are also unfavorable since returns are considered tenuous when fertilizer is applied to Douglas-fir stands more than a decade before harvest (9).

Attempts to upgrade production by emulating agriculture with farmlike cultivation and fertilizer amendments are sometimes done with little understanding of nutrient cycling. Douglas-fir foresters are usually surprised when they first learn their soils have 1 to 10 metric tons of total nitrogen per hectare mainly bound organically in upper soil layers or in the biomass (9). Such reserves accumulate over centuries from a small positive imbalance between nitrogen-fixing and accumulating processes, and those that release it into the atmosphere or streams. Paradoxically, a mere 200 kg nitrogen supplement per hectare usually causes a growth response. This is because scarcely a percent of this large reserve is released annually for recycling (9). Yet, maintaining a healthy recycling nutrient reserve is like owning a perpetual fertilizer factory. Even so small an annual release from so large a reserve can total far more available nitrogen over a rotation than is normally applied as fertilizer. A rapid release of the bound nitrogen reserve by artificial means might provide a temporary growth increase, but any such diminution of the reserve would probably lead to long-term reduced yields (19).

Many forestry activities degrade the nutrient capital. While Douglas-fir harvesting practices release little nitrogen into streams, an appreciable loss into the air may occur with burning and humus destruction. Over time, however, repeated harvesting can sequentially diminish soil fertility (19, 21, 22). In agriculture, fertilizer application itself appears to have a priming effect in releasing bound nutrients. All practices that result in such soil changes influence insects, browsing animals, and plant populations in intricate ways (23). In perspective, however, loss from any single harvesting, cultivation, slash burning, or fertilizer application pales in comparison to the estimated nutrient capital loss during and after the great wildfires that provided the species its dominant ecological niche over most of the region. Even after such severe losses, usually a large nutrient reserve was rebuilt over a long undisturbed period. Time is the key. If site enhancement is required for amplified yield, the wisest and surest practice is to build up the reserve whenever possible over the rotation.

This buildup might occur by natural or artificial processes. How much of the biomass produced in a forest is needed just to maintain a positive imbalance of nutrient cycling is not known. Good agricultural practice devotes a substantial portion of any crop rotation. A problem for the Douglas-fir foresters is that a competition-free period after harvest is a virtual requirement in each rotation to assure adequate, prompt, uniform restocking, whether in nature or in the managed forest. This is a period when nutrient reserves are likely to be depleted, but substantial buildup may also occur from nitrogen fixers such as alder and ceanothus. The remainder of the rotation provides the opportunity to enhance yield with building of the reserve through recycling. How much net buildup can be accomplished with artificial fertilizers is a question that must be addressed. Since natural nitrogen fixers are uncommon after the brushy regeneration period in closed stands less than a century old, short rotations pose the long-range prospect of degrading the reserve, and with it yields, without some deliberate soil management (19).

The subject of fertility also has a genetic aspect. If better fertility does lead to higher Douglas-fir yields, there is likelihood, if not certainty, of a need for commensurate genetic adjustment in the forest population. Jennings (2) develops this concept simply and clearly in his description of the agricultural strategy. The best evidence that foresters will encounter a similar experience is that Douglas-fir populations have been shown to be inherently different in growth rate on good or poor sites over short distances (7, 8). The genetic adjustment to a higher yielding site will probably occur at some price, whether planned or unplanned.

To summarize, a farmlike role for fertilizer and attendant agricultural practices is questionable for Douglas-fir. Several kinds of constraints limit yield increases from fertilizer. The first kind is environmental, primarily drought and cold constraints. The second kind is associated with under-stocked periods of the stand history which appear to be the main times of benefit, if rapid canopy closure is the main source of biomass yield enhancement. Rather than primarily biomass gains, the forester's role from controlling stand density and fertility may possibly be in upgrading the harvestable part of the biomass through favoring larger stems, as discussed for spacing earlier. The third kind of constraint involves the complexities of nutrient cycling and nutrient reserve. Reserves could well be at maximum in virgin stands, so that lost yield from degrading the reserve may be difficult to avoid — and increases may be difficult to achieve — without successful soil management. The fourth kind involves the concept that changes in the sites' productivity go hand in hand with genetic changes in the population, whether upward or downward. Thus while the goals for Douglas-fir are not very different than with agricultural crops, the pathway appears very different.

### 10. What tradeoffs are involved as forestry is intensified for amplified yield?

Jennings (2) began his discussion of the agricultural strategy by constrasting the crop reliability objective of the traditional farmer with the modern objective of amplified yield. His expression to describe the traditional farmer's objective is "not to obtain the greatest yield in the best years; instead he must ensure some yield even in the worst years." This objective was once of overriding importance in all agriculture. Modern agriculture, however, discards this objective willingly for the obvious economic payoffs of amplified yield. In this paper the emphasis on the substantial differences between forestry and agriculture lead now to the basic question of whether this change of objective is so broadly correct for modern Douglas-fir forestry. Can our forestry ever depart very far from the objective of crop reliability?

The first tradeoff for amplified agricultural yield is departure from ordinary sustained yield concepts. Sustained yield usually implies a yield at the land's carrying capacity—a sustainable yield without constant inputs. The amplified yield objective is based upon constantly exceeding the original carrying capacity of the land via inputs of nutrients, moisture, and energy from elsewhere. Amplified forest yields will probably need similar sustained inputs plus a genetically altered population. If this concept is essentially valid, amplified yield of Douglas-fir constitutes a far more permanent and weighty management decision than is typically made. The reason is that the appropriate genetic population adapted for amplified yield would probably be maladapted if inputs were discontinued, in the same sense that, without modern agronomy, improved agricultural varieties are less adapted than land races.

If we assume the strategy is correct for agricultural crops, it becomes so because amplification of yields is relatively large, financial outlays relatively small, crop rotations short, sites reasonably enhanceable, and genecosystem failures quickly and successfully corrected. If, however, amplified yields are relatively low, financial outlays relatively high, crop rotations long, site enhancement difficult, and ability to rectify genecological failures questionable, then the benefit-to-price becomes too high. Any or all of the less favorable conditions apply to Douglas-fir forestry more than to agriculture. Agricultural experience cited in Jennings' (2) paper suggests that maximum practical amplification under our forest conditions might still be comparatively low, probably substantially less than the doubled yield after several generations of breeding maize for subsistence by tropical farmers. Fertilizer response is less predictable under forestry conditions and is becoming relatively more costly. Regular use is certain to initiate a series of ecological changes on the site that need to be better understood. Additionally, long-term dependence upon the world's dwindling petroleum supply as raw material for fertilizer production is questioned more closely now. Relative ease of site enhancement is less, generally much less, on Douglas-fir lands. Genecological changes, many of which would be irreversible if our local forests were removed over extensive areas, seem an unavoidable product of amplified yield. For the present, the significance of genecological changes for long-rotation Douglas-fir forests is an open question.

If intensified Douglas-fir forestry also requires a new genetic population capable of substantially enhanced yields, what adjustments can be expected? Plant restructuring might be involved. This would be a simple change, however, compared with probable complex genecosystem changes when new weed and pest combinations begin to find sustenance among the altered population. From agricultural experience, constant weed and pest control can be predicted as a much heavier price than any cost of restructuring the tree. Besides the cultural and chemical controls that may be involved as adjustments, constant breeding for resistances is also part of agricultural experience with amplified yield. Despite many successes in agricultural pest control, still the best modern agricultural varieties have nothing comparable to the minimal pest control needs of our present natural Douglas-fir stands, which are usually quite healthy.

The question of tradeoffs becomes the most important of all those involved in our use of the agricultural strategy. Most past financial evaluations have probably left out, or given far too low a value, to crop reliability. It has even been popular to commit forest ownerships to intensified forestry on a vague faith that agricultural successes with a new variety can surely be duplicated. Crop reliability would seem to be the most important requirement of a long, forest rotation. It is the first thing given up in applying the strategy to agricultural crops. 'Some yield even in the worst years" should be the last thing given up in a strategy for Douglas-fir.

## 11. Is there an appropriate strategy for Douglas-fir?

Applied to Douglas-fir, the agricultural yield strategy of the Green Revolution is tantalizing. But it provides no free lunch. The tradeoffs are not nearly as attractive as with agricultural field crops. The strategy does not fit Douglas-fir forestry very well. Nor do present Douglas-fir yield strategies fit our needs very well, either. The vast agricultural experience behind their strategy, however, showing outcomes of many generations of intensive management, should help foresters conceive an appropriate model.

Briefly reiterated into forestry terms, agriculture's basic experience has been that biomass yield enhancement comes mainly from site enhancement. Yields appear to follow the "law of constant final yield" for each site quality. Our Douglas-fir clearcuts would have to be artificially and constantly maintained somehow at a higher site quality than present carrying capacity. To do so, ecological constraints to growth would have to be alleviated with more moisture, nutrients, and energy brought in from somewhere else. Genecological changes involving both the tree population and its associated plants and pests would seemingly be inevitable. Forest genetic adjustments may be necessary for mechanical restructuring, for harvesting efficiencies, but surely to resist pests newly adapted to the altered new environment. The altered genecosystem would probably be unstable, requiring frequent need of weed and pest control, as well as plant breeding, to stabilize it. And some, as yet undefined, portion of the biomass would have to be recycled in any sustained cropping regime.

The first consideration in applying the agricultural model to Douglas-fir is a less certain economics than in agriculture. Prospects for yield amplification are much less. A biomass trait like stem growth offers less opportunity for improvement of harvest index than for reproductive structures. Amplification is highest if unconstrained growth is sustained throughout a long growing season. Cold and drought, both essentially unmanageable for Douglas-fir sites, already constrain growth so much that a 50-percent growth enhancement mainly from weed control and fertilizer application, is probably harder to sustain than a 500-percent amplification in agriculture where irrigation and cultivation are practical.

If returns are lower, costs are also higher. The region's rough topography makes much of the forest land inaccessible to cultural machinery, greatly increasing direct costs or limiting site enhancement potentials. Indirect costs are an imponderable. Some indirect costs of agricultural site enhancement have involved depletion of soil fertility, depletion of fertilizer deposits and underground water reserves, erosion, chemical pollution, ecosystem damage, as well as public water development projects, and salt accumulation in soil. Indirect costs in forestry would involve some of these. Of more concern to Douglas-fir forestry, however, is the indirect cost of maintaining genecological stability through the long rotation. In agriculture the cost is partially reflected in supporting the agri-chemical industry and sophisticated breeding programs. A parallel development is already seen in forestry.

Foresters are so accustomed to working in a balanced, self-regulating, natural Douglas-fir genecosystem that they seldom encounter any costs from imbalances. They may not even need to visit a stand for decades. But, Pacific Northwest farmers would expect any untended crop to soon become pest-ridden and overrun with weeds. The farmer must stabilize his genecosystem with constant intervention to bring imbalances under control. For annual crops, the effort of weed and pest control may be acceptable. With perennial crops, the effort becomes magnified. The difficulties of maintaining stability of any single genetically altered crop for most of a century on an enhanced site would probably be as great in forestry as in agriculture.

This genetic side of genecological considerations is likely to be most important of all. To expect to greatly increase yields of Douglas-fir by simply planting clearcuts with a special seed at a special spacing does not fit agricultural experience. Neither practice is site enhancing. But even if successful site-enhancement practices are also applied, alteration of the genetic population should be a concern. All surviving parts of the former genecosystem — competing plants, animals, pathogens, and insects — must adjust to it.

Over a long period, the likelihood that one or another vector will find varying proportions of the improved trees to be a favorable habitat is indicated from agriculture as being an almost universal experience. Foresters are not without similar experience in this area. The problems of growth loss and stand degeneration is well documented for unadapted forest populations in arboreta, in provenance trials, and in plantations planted with off-site seed. If such problems ever developed on a large scale in the Douglas-fir region the economic results would be troublesome. The only question is not whether genecological problems will occur but, as mentioned earlier, how little genetic alteration of the natural population is required before it does. With recent evidence, both from agricultural land races and Douglas-fir studies, that precise, perhaps templatelike, adaptation may be a general phenomenon, there is not much comfort in the former optimism about using a single seed lot over a large area. An unknown portion of every such seed lot presumably would be maladapted. The two alternatives in any forestry model for increased yield are to try to keep the native genecosystem as intact as possible, or to alter the system and intervene with controls each time it destabilizes. The first alternative should be the preferred one.

With smaller returns, higher costs, and greater risks than the farmer, the prospects of general use of the agricultural yield strategy for Douglas-fir seem unlikely. For special situations, however, the strategy works. Containerized nurseries furnish a classic example. With their short rotations, Christmas tree growers also use the strategy effectively. Even so, their weed and pest problems are increasing; and the need is visibly growing to regularly stabilize the genecosystem with human intervention. To blindly carry the agricultural model to long-rotations of Douglas-fir forestry, however, seems unnecessarily risky. Surely a more appropriate model can be conceived.

Unfortunately, agricultural experience furnishes no ready-made alternative. Maize breeding for the subsistence farmer does have useful parallels. It illustrates use of a population genetics approach for needed genetic diversity aimed at producing a new land race, but does not address problems associated with growing a long rotation crop. For this, the needed strategy for Douglas-fir should stress that maintaining a stable, trouble-free ecosystem at low cost is of overriding importance. In addition the strategy should recognize that biomass growth per acre is probably constrained within narrow limits by site quality, that enhancement potentials are limited, that natural stands probably already approach final constant yield for the sites' natural carrying capacities, and that most stands managed at wider spacing for a more desirable product produce somewhat less than maximum biomass yield. And, finally any templatelike genetic fit of the species to the land form should be capitalized upon rather than ignored.

Past Douglas-fir strategies, which replace the natural stand as an initial step, put the "cart before the horse." If one assumes the potential for site enhancement is limited mainly to fertilizer and weed control, then the question is how much genetic improvement in growth rate is appropriate. In other words, there is always an upper limit. For example, there seems little point to producing Douglas-fir genotypes capable of site I growth for a site V forest (11) that can be enhanced only as high as site IV. The first question is how much site enhancement is realistic. For substantial acreages in the region where constraints on growth are severe and cultural methods cannot improve growth much, the natural populations may already have ample inherent growth capacity to reach constant final yield without genetic improvement. I wonder if the situation is greatly different on highest Douglas-fir sites where, conversely, the fastest inherent growth rates appear already located. The best opportunity for combining site enhancement with genetic improvement for growth may be on those sites between these extremes.

If, in contrast, one assumes that considerable site enhancement is achievable, necessitating substantial genetic improvement, how might improvement of growth rate be approached with genecological safety? As in maize breeding, the plan would be to incorporate needed changes into an adapted new land race. The immediate possibility is to breed among faster growing genotypes in the local population and to somehow infuse an appropriate portion of them into the adapted natural population. Present genetic programs in the Douglas-fir region are quite local and possibly could be redirected toward such a model. Most genetic programs are testing large numbers of parent trees well-distributed over their properties. The present policy of the Pacific Northwest Region of the USDA Forest Service to encourage natural regeneration of all clearcuts, whether planted or not, would even more readily fit into such a model. Along with natural seedlings, a wide spaced planting could be done with faster growing genotypes, favoring the improved plants only to the extent needed to capture growth increases from fertilizer and weed control. The second possibility for a genecologically safe improvement would be somewhat harder to do with equal confidence. This would be to use seed from nearby stands growing on somewhat higher site land. The presumption, which could be tested, is that these tree populations have inherently faster growth rates and would be part of a stable genecosystem developed for more fertile, moist, or warmer sites. The third possibility is to try to regenerate cutovers partly with seed orchard seed that fits the three-dimensional genetic clines of the breeding zone, the proportion infused into the local population depending upon the level of site enhancement. Obviously this is a far more complex concept than technically practical for seed orchards now. Yet, recent attempts to map three-dimensional genetic variation in Douglas-fir and recent advances in commercial methods of pollinating the individual orchard tree provide some encouragement that this direction of tree improvement and orchard management will become practical. Some Douglas-fir orchards are already trying such concepts.

How might such an orchard be designed? If a templatelike match of genetics to environment of each landform were the ultimate goal, the Cascade Range watershed in Campbell's study (7) provides a glimpse. Proven clones or seedling families had best be located within the orchard in the same general coordinate relationship as parent trees in the watershed but mixed enough to avoid inbreeding. The genecologist may wish to warp the coordinates somewhat to match three-dimensional environmental clines. The maplike layout handles elevational changes to some extent, but he may also wish to have separate blocks for elevational bands. After supplemental artificial pollination of individual orchard trees, a mix of seed from an appropriate small neighborhood of clones or progeny families in the orchard would be used to regenerate a specific clearcut. Obviously numbers of tested parent trees represented in the orchard from the drainage would have to be quite large to assure adequate genetic heterogeneity of each seed mix. But also, natural regeneration might supply an appropriate portion of the final stand. Such a futuristic concept for ultimate genecological safety is not as financially attractive as present orchards. The problem is that few data exist now to suggest which presently used shortcuts have acceptable risks. Agricultural experience is no more helpful than forestry experience on the subject.

Finally, a case for breeding markedly faster growing Douglas-fir population arises in connection with thinning objectives. Thinning constitutes a forestry dilemma. As discussed previously, to get desired sizes quickly requires wider spacing. Such temporary understocking of the site results in less than maximum fiber yield. The opportunity to enhance growth rates to more quickly recapture open space is considered to be a major opportunity for forest genetics. Yet, thinning is also a genetic dilemma. The more the silviculturist pursues the genetic solution to underutilization of the site, the more he probably alters precise adaptation and increases risks of genecologic problems. Rather than maximizing the genetic solution to the understocking dilemma, it may be better silviculture to adjust the thinning schedule to more closely correspond with the level of genetic improvement required for site enhancement. The point is that, assuming the general correctness of the "law of constant final yield," the genetic solution to understocking corrects only for the amount of fiber the silviculturist programs to lose in the first place. It creates no yields above the constant final biomass yield. As with most other facets of this problem analysis, a potential gain from each cultural technique turns out to have a commensurate potential price. There is no free lunch.

Throughout this discussion the possibility has not been forgotten of breeding a population that permanently produces higher yields independently of site enhancement. Such a fortunate outcome would not need to change the strategy. But the strategy does not depend upon this outcome.

Is there an appropriate strategy? A flood of questions remain unanswered. But agricultural experience has clarified the needed elements of a holistic strategy.

## Conclusion

The subject of yield strategies is complex. Yet, out of the vast array of crop science and agricultural experience appear five simple requirements or observations. For maximum crop production over a long time span, the soil must be improved, not degraded. The land must be completely occupied all the time by a full canopy of growing plants. The crop, in turn, must be genetically capable of using the site completely. Maximum potentials are seldom attained because final yields are mainly set either by natural environmental constraints on growth, or by those constraints partially relieved by man. And fifth, continuous genetic variation is used by plants to fit populations precisely to clinally varying environments, possibly with template-like precision. Such precision maximizes crop reliability.

In this paper, I have examined a simple agricultural yield strategy for possible future application to Douglas-fir. The strategy maximizes the first four requirements, particularly the fourth by artificially relieving growth constraints. The fifth, precise adaptation, can ordinarily be ignored with annual crops as long as reasonably cheap cultural or breeding options keep crops productive. For the long-rotation Douglas-fir crop grown with little culture, however, crop reliability from precise adaptation is likely to be the most important requirement.

Human beings were not the first to respond to these requirements. Long before survival-driven plants like Douglas-fir fit themselves to all five to a high perfection. Over its vast range, stable, healthy, well-stocked Douglas-fir stands of precise genetic match to each site improved the site while they occupied the land completely for centuries at a time and, fortuitously, concentrated a high proportion of the total biomass production into stem growth. Agricultural experience suggests only a few, mainly modest, ways to achieve better total productivity on unaltered Douglas-fir sites. But substantial improvement in value and useable product may occur as a better harvest index from thoughtfully applied spacing and genetic technologies. Improvement of total fiber yields beyond traditional silviculture, however, may be difficult without some kind of artificial improvement of site quality.

A yield strategy for Douglas-fir could be as elegantly simple as the agricultural strategy. Figure 1 is a conceptual display of the interplay of the main factors. Biomass yield increase of each site would depend upon how much relief of growth constraints is practical. A basic question, however, is whether a permanent commitment to yields above the land's carrying capacity is wise per se. The strategy would require perpetual inputs and a new genecosystem which may never again be as reliable as the present one. The question is avoided where potential to improve the site is only modest, since near-natural populations may well provide superior long-term yields. Assuming a risk-conscious commitment is made, however, the Douglas-fir strategy for a particular site would be to ascertain the new yield levels attainable with site enhancement options, primarily fertilizers and weed control. Then a long-term, hopefully permanent, genecological balance would be struck with an appropriate, stable, new Douglas-fir genetic population.

Although not site-enhancing, improved quality, uniformity, and harvest index are part of any strategy. With perhaps half of the rotation's biomass production presently unharvested, or unharvestable, value gains from better harvest index could well equal yield gains from site enhancement. A major potential genetic goal is more rapid canopy closure. Yet, the strategy should purposely avoid the genecological trap of the thinning-genetics dilemma. There is no limit to the growth improvement wanted to quickly capture underutilized growing space. Without recognizing that the answer to the dilemma is basically silvicultural, foresters could futilely seek ever-faster inherent growth accompanied by ever more doubtful adaptation.

Thus the strategy would involve an upper limit, perhaps a modest one, in the improvement of inherent growth rates. Local stands, or some appreciable fraction of individuals within the local Douglas-fir stand, would probably have the genetic amplitude to provide this appropriate population. The genetic testing programs already underway in Douglas-fir appear to serve this proposed strategy as well as existing strategies. Should the upper limit become so high as to require a synthetic population, the geneticist's role would parallel the agricultural role of handling an unstable genecosystem.

In view of many uncertainties, the best present stance for the Douglas-fir landowner would be to keep options open. The point of this article is not so much to propose a particular strategy, but rather to accent many unanswered questions about intensive forestry raised by agricultural experience that must be considered. The foremost of such questions is: How well do practices meet the five simple requirements involving yield? Do they upgrade soils, relieve growth constraints, and enhance canopy closure, genetic capability, and crop reliability? Fortunately, few intensive practices in Douglas-fir now involve irretrievable commitments. The one possibility of immediate concern is removal of natural populations over large expanses because they probably will be needed for their priceless adaptation. No landowner could afford the genetic program to reconstitute them, if exact reconstitution were even possible. It would be tragic if long-term costs of stabilizing a less-adapted genetic population were so high as to make Douglas-fir forestry unprofitable.

Whether or not involved with intensive management, the Douglas-fir landowner in quest of better yield may also wish to review present forestry habits. The best chance of improving yield is still simply to bring the land up to full stocking with precisely adapted trees. Certainly, the landowner should avoid further retrogression toward human-caused ecological successions to low-yielding, low-value species such as the loss of nearly 3 million acres of the best sites of the Douglas-fir region to hardwoods. Yield reducing practices that magnify constraints to growth should also be avoided. Examples are harvesting methods that permanently remove fertile upper soil horizons, compact them, ruin water tables, or accelerate humus oxidation. Other examples concern practices in areas of summer drought which increase loss of soil moisture to competing plants, such as sowing forest areas to grass **(24)** or opening of the forest canopy without understory vegetation control.

The six paragraphs in Dr. Jennings' article and the vast agricultural experience they signify have served to raise questions that could clarify the future path of forestry through the few decades before the reserves of the earth become depleted. The experience tells foresters that much more silvicultural, soils, and genetic information is needed before making irretrievable commitments to amplify yields. They also suggest that our native tree populations, which we seem to thoughtlessly waste, may be our prime resource when the world of the 21st century must once again return toward truly sustainable yields.

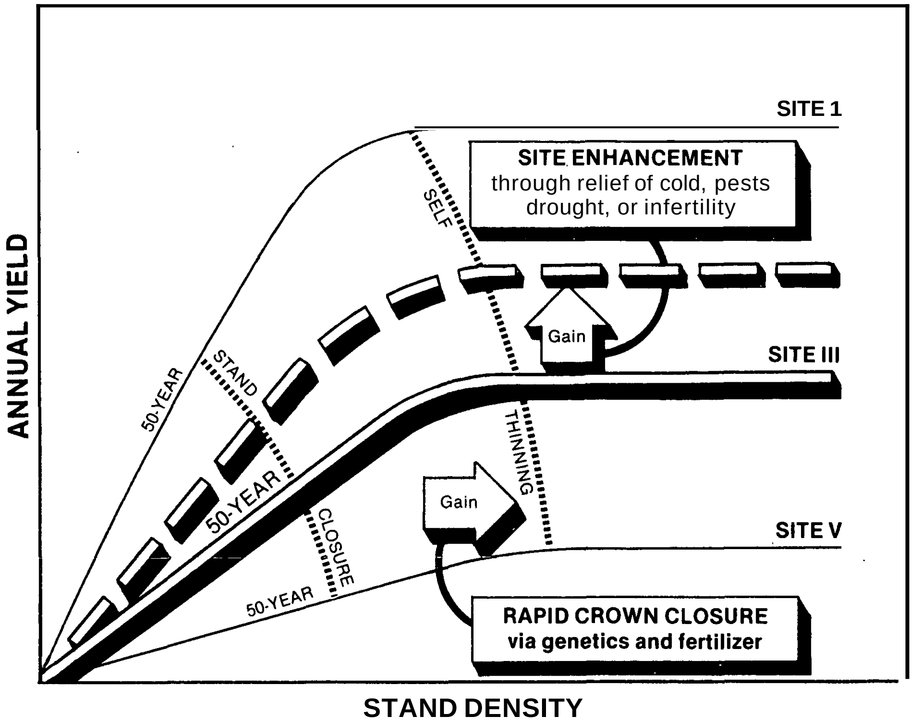

Figure 1. — This conceptual, mensurationally slanted figure shows the interplay of factors of a Douglas-fir yield strategy. The background graph shows assumed stand yield-versus-density relationships for sites I, III, and V (11) at age 50 years. As stands approach self thinning, presumably they approach maximum annual biomass or photosynthate yields per unit area. Stand closure occurs at somewhat lesser densities, or earlier at a given stand density. Managed stands aim at densities between stand closure and self thinning stages. Accuracy of these concepts might be improved if densities are expressed in leaf area and yield in living basal area (25, 26).

The bold lines in the graph depict an example of site III stands at age 50 years. Annual yields of stands beyond about 400 trees per acre (self thinning) are assumed at maximum, as long as maximum leaf area per unit area is maintained. Site enhancement through providing relief of cold, drought, pests, and infertility constraints provides a longer effective growing season. Weed and pest control and correction of soil nutrient deficiencies are primarily involved. This effect is shown by the vertical arrow, changing site III yield to about site II in this example.

The second horizontal arrow depicts the effects of genetics and fertilizer in providing more rapid crown closure. The effect on yield is the same as reducing rotation age or increasing response to thinning, rather than directly increasing productivity per unit area. Effects of genetics on yield are speculated as primarily of this source although direct contribution to yield may occur. Fertilizers may have direct yield effects in relieving deficiency constraints, or indirect effects of overcoming understocking. Pest control also may have direct and indirect effects.

The strategy of relieving growth constraints in Douglas-fir is primarily one of lengthening the effective growing season with more moisture during summer drought periods. Relief of cold is generally impractical. Relief of nutrient deficiencies, primarily nitrogen, may be limited to leaf densities below self thinning. Genetics and fertilizer have major potentials of shortening the underutilization stage, both with rapid crown closure, and favoring larger stem sizes in the stand, thus increasing the proportion of the stand utilized (the "harvest index").

Genetics plays a further role. Since each site is presumed to have evolved a precisely-adapted population, the perpetuation of a site II growth environment on site III lands in this example probably requires a different, precisely-adapted population to perpetuate genetic stability.

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Agricultural yield strategy simply aims to increase number of grain bearing stalks per acre. Forestry strategies look to thinning, fertilizer, and genetics, each to provide gains. The agricultural strategies applied to Douglas-fir appear to be impractical for long rotations. Concern is expressed for commitments to perpetual inputs of materials and energy to keep a yield above the land's carrying capacity. Adapted natural populations are the major resource in keeping a yield improvement strategy trouble-free.

Keywords: Yield strategy, tree improvement, agriculture, Douglas-fir, ***Pseudotsuga menziesii.***

Pacific Northwest Forest and Range
Experiment Station
809 NE Sixth Avenue
Portland, Oregon 97232