ABSTRACT

A CLINAL MODEL OF TREE IMPROVEMENT PROPOSED FOR DOUGLAS FIR

by Roy R. Silen

The words UNIFORM and CLINAL are used to describe contrasting tree improvement models. For both models improved seed should genetically match the environment. Growing season length is the most important matchup because, as in agriculture, each day of mean genetic mismatch linearly reduces biomass productivity, hence yield. A mismatch of 10 days or less is proposed to prevent significant lost productivity.

The present model of tree improvement used worldwide is termed UNIFORM because it delineates a zone considered to be genetically uniform from which parent trees are selected. Cuttings or seedling families from selected trees are arranged randomly in seed orchards to produce a single uniform seed mixture adapted for planting anywhere in the zone. This model appears appropriate for the gentle topography and summer rainfall climate of eastern United States or western Europe where growing-season lengths may change by only about 10 days per degree of latitude; hence, a million or more acres that differ by less than 10 days can be found in a one-degree latitudinal band.

Unfortunately it is the only tree-improvement model, and severe problems arise in the climatic complexity associated with forests in mountains. In the complex mountainous Pacific Northwest, where valley and ridgetops often differ in elevation 3000 feet or more, a breeding zone having less than a 10-day change in growing season length is difficult to delineate. Each 400-foot rise in elevation is approximately equivalent to one degree of latitude movement northward (from Hopkins' Law). Either movement shortens the freeze-free period about 10 days. Growth within the freeze-free period is regularly reduced as summer drought halts tree growth. Soils commonly reach wilting point by mid-July, but this can occur as early as mid-June in rain shadows of mountains. Frosts can occur any month in valleys that drain cold air from mountains. Snow packs on north exposures delay onset of spring growth. Thus, uniform zones meeting the 10-day criterion become ridiculously small in such variable environments. Using the UNIFORM model, Douglas-fir tree improvement programs have had to accept much larger growing-season variation than 10 days in most commercial breeding zones, hence risk corresponding lost biomass productivity with genetic mismatch of growing season patterns. The problem has long been recognized, but all past tree improvement programs have aimed at defining how high a risk level is acceptable so that economic-sized zones could be defined.

Growing season maps are inadequate in the Pacific Northwest due to sparse weather station coverage. Fortunately, local forest populations are already genetically structured to match growing-season patterns with high, suggestively templatelike, precision.

A CLINAL model is proposed specifically for the Douglas-fir Region of western United States to avoid loss of biomass productivity by reducing need for seed movements. As with the UNIFORM model its goal is to provide a simple way to better meet the 10-day matchup of seed with growing season of the planting site. Conceptually, the UNIFORM model treats genetic clines as a series of uniform stairsteps. In contrast, the CLINAL model tilts the UNIFORM model as an inclined plane to conform with genetic clines, eliminating need for
stairsteps, i.e. zones or boundaries. The key to the model is a seed-orchard concept that avoids mismatching seed movements by producing many overlapping seed mixes, each as specific to a planting site as economically practical. The simplest example is a single aspect on a uniformly sloping mountainside. Cuttings or families of proven parents are placed in an orchard in bands corresponding to the parent tree elevation. Seed is collected from a band that matches the planting-site elevation. For the more typical complex mountainous topography of the Region, placing orchard clones or families in a maplike arrangement according to their relative coordinate arrangement in the forest can provide a close match similar to the UNIFORM model in gentle topography. With abundant tested parents, essentially local seed of correct growing season length and desired gains can be provided for each planting site. But even with inadequate parent numbers placed in a maplike arrangement of orchard, seed collection can start with most local of selected parentage. Additional seed needs would come from the band of adjacent parents in the orchard having growing season patterns as similar as the orchard parentage permits. For existing orchard programs, the concept can be immediately used by combining female parentage into mixes more local than from the entire orchard. Bringing male parentage under the concept may require supplemental mass pollination, future design changes of orchards, larger parental base, and future breeding within local populations.

The model has been under trial for nearly a decade at the J. E. Schroeder orchard complex in the Willamette Valley owned by the State of Oregon. Of the anticipated problems—complexity, inbreeding, higher costs, genetic gains, and inadequate parent numbers—none appear as crucial obstacles. However, only a gradual adoption over several decades appears possible because present programs, based on the UNIFORM model, cannot be quickly changed.
A CLINAL MODEL OF TREE IMPROVEMENT FOR DOUGLAS-FIR

by Roy Silen

INTRODUCTION

The vegetative film of forest and field covering North America has parallels with our own skin. Patches of skin on our unexposed torso can be grafted from a source often many inches away and still be biologically and cosmetically functional. But skin of the face is another story. Surgeons go to great lengths to avoid skin movements of the face. Exposed at all times to dessication, cold, sunburn and abrasion, and with heightened sensory function, it's structure varies greatly as it grades from one inch to the next. For example, grafts that exchange skin from inner and outer lip, less than an inch apart, would leave long term problems. Inner-lip skin would need continual moistening, and sunburn protection; outer-lip skin grafted inside the mouth would create shaving problems. The forest film covering the gentle topography of eastern North America, like the homogenous torso skin, has evolved with much more uniformity, and presents the forest geneticist with far simpler problems than the heterogeneous forest film on the exposed mountains of droughty western North America.

Contrasting Models

The words "UNIFORM" and "CLINAL" are used in this paper to contrast two tree improvement models (FIGURE 1). "UNIFORM", is used to describe a model of tree improvement that evolved nearly a half century ago in western Europe and eastern United States and is still the only model used worldwide. A "CLINAL" model is proposed specifically for the Douglas-fir Region. Both models have the same three goals. The first goal is to select or breed for improved growth rates and a few other economic traits from a species' vast array of traits. The second is to produce adapted tree populations so that they are relatively trouble-free (FT 1). The third is to maximize productivity by using the entire growing season since biomass productivity is linearly related to growing season length. Breeding is not needed for the latter two goals if adapted natural populations are used since their phenology already matches the growing season, and they are relatively resistant to native pests.

Footnote 1: Tree improvement uses a basically different approach than breeding agricultural crops. In agricultural crops, total genetic variability is exploited and adaptation is lost. Highly-improved crops survive only with man's culture, using fertilization, irrigation, total weed or pest control, and even inside environments as values warrant. Forestry, affording only limited culture, and relegated to poor, harsh sites unsuited for agriculture, exercises much less control over environmental constraints. With less controls, forestry must place reliance on using adapted plants, which also limits the immediate genetic variability available for breeding. Forest tree improvement models reflect these two important differences from farm crop breeding. Valuable specialty crops, like Christmas trees, use agronomic and breeding approaches of agricultural crops.
The present UNIFORM model of tree improvement is characterized by delineating a genetically uniform zone from which parents are selected and their clones or families placed at random in a seed orchard for panmixis, so that seed produced would be adapted for anywhere in the uniform zone. The model was conceived by early-day European foresters whose generation had experienced severe losses from off-site seed and were well aware of the need to match seed with local growing season. The phrase "local seed is best" originated from this experience. Their basic tenant in choosing a breeding zone was that it be so uniform genetically that parent trees chosen from it would provide progeny unquestionably adapted to the local growing season pattern.

There was little need to do otherwise. Both western Europe and eastern United States have summertime rainfall and high humidities, hence the entire freeze-free period is usually available for growth. Both have large areas of gentle topography in which growing seasons gradually shorten about 10 days per degree of latitude northward. Thus, a band within a single degree of latitude will often provide a breeding zone of a million or more acres that differ by less than 10 days in growing season. For the gentle topographies of western Europe and eastern United States, the UNIFORM model has raised few growing-season or adaptation questions wherever it has been conservatively applied. Because no alternative model has been proposed since, it has been extended to all other forest regions despite obvious problems with the model where applied in mountainous topography.

As detailed later, such problems are troublesome in the Douglas-fir Region west of the Cascades and south of about 49 degrees latitude in western North America. This Region's mild climate, long days and assured springtime moisture, plus a specific mean adaptation of each stand to match its local growing season (Campbell, R., 1975, 1978, 1986; Hermann and Lavender, 1968; Sorensen, 1967 Silen, 1962, 1963, 1978, 1983; Silen and Mandel, 1983), have evolved one of the world's most productive forests, with tallest species in many coniferous genera. But as in all young mountainous topography, this Region's growing season is very complex, as adiabatic cooling, aspect differences, and rain-shadow drought effects interact. Vastly more climatic complexity is added to each growing season by droughty summers. Only part of the freeze-free period is available, because growth is often truncated just when summer temperatures peak. Thus, in this particular Region, areas of uniform environment are usually small. Yet local tree races have evolved to exactly match needs as the local climate grades from one such environment to the next. Where the UNIFORM model is applied to even county-sized portions of this complex Region there is an unintended, but potentially serious risk of growth losses from genetic mismatches of the seed to these large localized growing-season variations. Attempts to pool similar environments into large zones is error-prone because weather and genetic data are sparse, resulting in undeterminable amounts of mismatching seed movements. The first half of this paper details the Region's unusual climatic complexities and evidence of the close genetic fit of its trees to each stands environment as justification for proposing a new tree improvement model for this Region.

The proposed CLINAL model seeks to avoid lost production by making such potential seasonal mismatches in mountains virtually unnecessary, just as the UNIFORM model does on flat areas. Its name arises from its seed orchard and breeding designs which attempt to match these complex genetic clines by supplying improved seed from parentage essentially local to each planting site. The last half of this paper is devoted to details and questions arising from such a proposal.
Experience with trying the CLINAL model suggest that adoption should be gradual because the Region's present tree improvement programs were all based on the UNIFORM model and cannot be easily or quickly altered. However, some features of the model, like making seed-orchard mixes of seed from local female parents, can be adopted immediately. More importantly, risk-free concepts of the CLINAL model should be seriously considered for future breeding phases of all the Region's programs to assure maximum productivity.

Although this paper is written for a general forestry audience, use of the model's concepts lies with tree improvement personnel. Details too technical for general audience are footnoted for this audience.

THE NEED TO MATCH GROWING SEASON

Biological Perspectives

Biology, considered a descriptive discipline in my college years, has emerged as one of the most exacting of sciences. At all levels from molecular to ecosystems one finds evidence of incredibly complex systems along with surprising precision (PT 2). In nature, mean genetic response of a species to seasonal timing is usually precise, often phenomenally so. Our media remind us of this yearly as swallows return to Capistrano, or on public television in countless wildlife documentaries of complex ecosystems where survival of one species is dependent upon seemingly-incredible inherent precise seasonal timing of another species. Plants and animals appear to have equal sensitivity. This timing involves ancient genetic mechanisms like biological clocks or the sensing of daylength or heat sums that evolved so long ago as to become common to all living things (FT 3), including commercial crops and forest trees.

Although plant communities may sustain one damaging or lethal environmental insult after another, and abberent individuals episodically die from them, still predominantly healthy populations are omnipresent. Plant species in each energy niche of every natural forest ecosystem must begin and end seasonal growth on time if they are to survive and reproduce. Like a great tide in each hemisphere the spring flush of growth moves poleward rapidly across flatlands, and more slowly up mountainsides, following tightly on the heels of the last frost. As autumn cold approaches, an equally precise tidelike progression reverses as leaves fall and plants harden off. It is easy to assume this phenomenon is a simple growth response to warming and cooling. But even the earliest common-garden studies of racial variation showed a far more complex xxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxx

Footnote 2: Such complex systems and high precision are exhaustively documented at molecular and ecosystems levels. Yet, at the species level in forestry the evidence for similar complexity and precision of racial variation between stands along environmental gradients are poorly accepted. Present documentation does suggest the same order of complexity and precision (Campbell, 1978; Silen and Mandel, 1983). One problem is the crudeness of statistics that base acceptance only if differences are greater than two standard deviations from mean values. The huge data bases needed to statistically prove such adaptive precision when true differences are small, have seldom been compiled. This paper adds significant unpublished data to this earlier documentation.

Footnote 3: Even though modern man does not consciously sense seasons and biological rhythms, he occasionally becomes aware of these mechanisms in the form of jet lag. The menstrual cycle is the human's most familiar experience with precise longer biological cycles.
response involving many related traits. Instead of all tree races bursting and setting buds in unison in a common environment, there were large timing differences between races that graded from southern-to-northern, from low-to-high elevation, from droughty-to-moist, or other contrasting environments to demonstrate a strong genetic control over phenologies (FT 4). There were other notable observations. Each species had characteristic patterns that reflect the limitations of its particular niche in the ecosystem. For wide-ranging species, races from warm, mesic, long-growing-season sites were inherently faster growing, but correspondingly less hardy, than those from cool or xeric, short-season sites. Obviously, phenologies, hardiness, and growth were all genetically interdependent. Eventually came the realization that the biological and genetic mechanisms involved with these related phenomenon are incredibly complex and precise.

Precise timing is not accidental, but results from a well-understood combination of causes. Within species like Douglas-fir there is ample genetic variation in phenological traits for even its westwide fire-related ecological niche. Phenological traits typically are multigenic to achieve infinitely fine clinal variation so that it can match climates of each locale along an environmental gradient. The traits are highly heritable, hence can change markedly and precisely each generation where natural selection pressure is strong. Gene flow is seldom restricted, and selection has used virtually infinite numbers over almost infinite time to attain or maintain precision. For the same reasons, most multigenic growth, form, and resistance traits become similarly precise. In perspective, evolution of multigenic inheritance that permits precise local adaptation of each trait to a wide range of environments, was probably crucial to the spread of life over most of the planets varying surface.

Genetic Structure

For wide-ranging tree species like Douglas-fir and its associates, genetic variation among racial mean values is large (FT 5 and FT 6). In each locale the mean genetic match between growing season, phenology and such related traits is precise enough to produce a highly structured, yet genetically heterogeneous population I referred to above as a race. Even though local stands are genetically quite heterogeneous, such genetic structure arises because most individuals respond near mean values. Considerable heterogeneity appears needed to adapt to changing environments. On extensive flatlands the genetic structure is observed as a gradual change northward in local phenologies, hardiness, growth rates and other traits as growing seasons shorten. The same precision and range of change occurs over short distances on steep mountain slopes as seasons shorten with increasing elevation. And where seasonal drought ensues within the frost-free period, plants become

Footnote 4. The word phenology is used in this paper in its broad sense as of natural phenomenon that recur periodically. Most forest phenological studies observe budburst, elongation and bud set, which involve only a portion of the yearly cycle of phenologies. Yet, most of the tree's phenological phenomenon, like hardiness, various cambial or tissue development, bud formation, or root growth involve recurring physiological or development cycles over many months of the year, and are often poorly related to shoot development data.
quiescent or dormant on time. Thus in each locality, there appears to be a
virtually template-like mean matchup of genetics and environment. Evidence for
such local stand genetic structure is presented in this section. How precise is it?

Footnote 5: On preliminary pages of this paper, the complexities of
variation around the mean of phenological and other traits are ignored to
present concepts in simple statements. The complexities are acknowledged, and
covered in later pages as needed.

Footnote 6: My concept of racial variation of a tree species follows that
related by W. I. Righter, Institute of Forest Genetics, Placerville,
California. It came as a response to my question, "How would you characterize
races of two species occupying separate ranges, like ponderosa pine and Douglas
fir, in the areas their ranges overlap." His response was "They are as alike
as their genetic variation allows; otherwise their ranges would have shifted to
a different area of overlap." Species survive by dominating environmental
niches. Ponderosa pine predominates in western forest areas below 30 inches of
annual rainfall; Douglas fir dominates most of its range of 25 or more inches
of rainfall. In the overlap zones are fast-growing ponderosa races and
slow-growing Douglas-fir races that respond similarly in many ways. A
wide-ranging species like Douglas fir has enough genetic variability to evolve
races that almost fit the niches of many of its diverse associates, like Sitka
and Engelmann spruce, grand and noble fir, shore and lodgepole pine, western
and mountain hemlock.

The east slope of the mile-high Cascade range in central Oregon provides a
dramatic example of species similarity in overlapping ranges. A strong
moisture and temperature gradient begins with mesic alpine species at the
Cascade summit and ends with desert shrubs less than 20 miles eastward about
2000 feet lower. At the desert edge are shrublike western junipers. As one
travels westward from this desert edge, junipers slowly change in stature from
shrub to trees with increasing annual rainfall. Still further west one begins
to encounter ponderosa pine trees no taller than junipers. Juniper reaches its
largest size further west as its range is terminated by small but dominating
ponderosa pine of the same stature as the tallest junipers. The same pattern
is repeated for ponderosa pine. Its stature grows westward as moisture
increases, until its range merges with Douglas fir. In the region of overlap,
the two species are of equal stature. The tallest ponderosa pines again are on
the western edge of its local range. Westward, Douglas fir ranges to high
elevation where slower-growing, cold hardy races compete, but finally give way
to alpine species of similar stature. Inherent growth rates of these species
also mimics the dominant tree height at points along this cline. Analogous
banding of species is consistent north-to-south for nearly a hundred miles east
of the Cascade summit.

While any one race of a wide-ranging species may grow reasonably well
planted over a considerable range of environments, the local race has a
fine-tuned genetic structure for a balance of needs for the local environment.
Growth rate is only one of these needs. Hence, for wide-ranging species,
 faster growing races from more favorable environments than the local race are
almost always available, or can be bred. As will be brought out, however, the
adapted local race will likely produce the maximum biomass because it can more
precisely fit (gen.)
The 10-day Criterion

Crop breeders manipulate the same ancient genetic mechanisms as natural selection manipulates natural populations to assure accurate timing of maturation—one of the four major components of improved agricultural yield (FT 7). A genetic resolution of about 5 days is attainable with maturation of most intensively-bred crops. A familiar example is the springtime seed display in garden stores where corn seed packages are labelled to ripen in 70, 75 or 80 days, and so on. Crop breeders strive for a uniform genetic precision with each variety; natural populations instead need a precise mean within a limited range of individual plant variation.

In agriculture, it is economically crucial to accurately match the average or typical growing season as closely as practical constraints allow. For crops like corn or wheat that can use all of the growing season (FT 8), each additional day of growth (Degree day) adds a linear increment to crop tonnages or more fundamentally, to total annual biomass (FT 9). But there is a dilemma. Prudence is needed because a crop beginning growth too early or still maturing at first autumn frost can be ruined, or have much lightened yields. To illustrate, if a farmer sowed three fields with 75-, 100-, and 125-day maturing varieties respectively, and a killing frost occurred after 100 days, he would expect only 3/4 of the 100-day variety yield from the 75-day variety that matured too early. The 125-day variety probably would be worthless, killed at its immature stage, even though its above-ground biomass would probably equal the 100-day variety. Seeking a variety that ripens with a growing-season cushion of 10 days or less is common practice. Even so, reduce yield both from frost or from too early maturation still can occur from year-to-year seasonal variations. Since the forester has the same opportunity to use all the growing season, and runs the same risks as the farmer if he tries to use too much or too little, the same mean matchup of 10 days or less should be adopted for genetically improved forest populations. As with the farmer (FT 10), a greater mismatch risks loss of biomass productivity and wood yield.

Footnote 6 continued: the growing season both in length and in timing pattern, and faster-growing genotypes are selected against.

Footnote 7: Many of my basic assumptions are covered in this footnote. Agricultural concepts cited have been thoroughly reviewed. The four major components of improved farm-crop yields, as described by Jennings (1976), are (1) timing of maturation, (2) improved harvest index, (3) adjustment of growth rate, and (4) agronomy. All four together are aimed at a strategy of simply packing more crop-bearing stems per unit area. Of the four, three involve genetics. Genetic timing of maturation to use all of the growing season assures full biomass productivity. Improvement of harvest index involves a genetic restructuring to increase the portion of the plant that is crop. Genetic adjustment of inherent growth rate, such as by use of dwarfing genes, is used to reduce size for closer packing and to stiffen stems to reduce lodging. The non-genetic fourth component is agronomy, which uses fertilizer, irrigation, weed and pest control as agronomic techniques to alleviate environmental constraints to free growth. Of the four, only timing and agronomy straightforwardly increase crop biomass.

Throughout this paper two distinctions are emphasized. One is between total biomass and the crop yield, which is only a part of total biomass. The other distinction is between biomass productivity and growth rate. In the agricultural strategy, growth rate has been primarily used to slow rather than
Feedback mechanisms

The farmers dilemma with annual crops illustrates the biological negative feedback mechanism that also fine-tunes forest phenologies, and their related traits to use all of the growing season to maximize yields in the biomass sense (FT 11). Perennial plants that are ready to flush can use the growing season even more completely than annuals beginning from seed. With natural Douglas-fir forests, analogous but more complex negative feedback mechanisms are involved in a population genetic sense for a spectrum of interrelated, multi-gene traits. These mechanisms produce natural populations that indeed tend to maximize biomass production.

Footnote 7/continued: speed height growth. Genetic improvement has had almost no effect on annual biomass productivity (Gifford, et al. 1984, Johnson, et al. 1986. See also FT 9 and Figure 9). In contrast, agronomic techniques have often doubled or quadrupled biomass production. The relative contribution of each component to an amplified crop yield depends on circumstances. With ample summer rainfall and fertile soils, the three genetic components are primary. Of these three, improved harvest index has contributed most to crop yields. In locales typified by summer drought or infertile soils, agronomy is primary by relieving these growth constraints.

Biomass productivity is of major interest to foresters. As stands age, up to three-quarters of annual above-ground biomass production goes into tree stems. Applying the concepts above to Douglas-fir improvement of stemwood, there is much less opportunity than with farm crops to improve harvest index, maturation timing, or to relieve drought. Best opportunities to enhance yield are to control pests and weeds, improve soil fertility, then adjust inherent growth rates to match an improved level of biomass productivity.

A further assumption of this paper is that forest biomass productivity is maximized when growth is unconstrained, when genotypes are capable of full utilization of the site, and when a full canopy is present all of the time. This full productivity is approached as stands attain self-thinning densities. Reduced canopy densities, such as occur on poor sites, and after thinning or during stand regeneration, are assumed to produce biomass at lower rates, as they would with agricultural crops. Canopy densities are not age-dependent. Dense canopies of one-year Douglas-fir seedlings grown in containerized greenhouses produced 17 metric tons of biomass per hectare in about 6 months (Personal communication from Phillip Hahn, Georgia Pacific Nursery). In perspective, both aquatic and terrestrial ecosystems of the world peak around 40 metric tons of annual biomass production (Whittaker, 1975). Maximum annual biomass productivity also approaches such high levels in spruce-hemlock and redwood forests, but is only about 15 tons on Site I Douglas-fir forests, about 10 tons on average Site III, and less than 5 tons on Site V lands. Since full-canopied stands are common, it is assumed that these large variations are due primarily to variation in number of days of unconstrained growth per season as microclimates and soils vary over the Douglas-fir Region. Genetic improvement of growth rate is assumed to affect biomass production primarily by speeding canopy closure after regeneration or thinning, but to have little effect at self thinning stages, as with corn (Johnson, et al. 1986).

Footnote 8: In the temperate zone corn or wheat is usually bred for one late-maturing annual crop; in the tropics for two or three, often shorter-maturing annual crops, in order to use the entire growing season.

Footnote 9: A classic 15-generation genetic study of maize (Johnson, et al. 1985) is clear in showing that while breeding nearly doubled corn yield,
A simple forestry illustration of a negative feedback (FIGURE 4) concerns the growth period between spring and fall frosts (FIG 12). Populations with too long an inherent growth pattern can produce more biomass than can adapted populations during years with longer than average growing seasons. But most trees of such long growing-season populations flush too early or become dormant too late, and will eventually be damaged or killed at some vulnerable stage of growth by early or late frosts. In contrast, populations with too short a growth pattern avoid risk of frost damage. But in such short growing-season populations, the trees which inherently initiate growth too late or harden off too early will fall behind and be overtopped by adapted trees that are XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
FT 9 cont.: biomass production per hectare was very nearly the same per day in generations 0, 6, 9, 12, and 15 when tested together on the same plot. Starting with unimproved Mexican maize, the study provides detailed data on how, under selection for small size, uniformity, stem stiffness and yield, the proportion of biomass switched from stalk to corn in almost linear increments each generation while total and leaf area biomass remained nearly constant (FIGURE 3). The study is remarkable for its completeness of the crop record, meticulous attention to details, and consistency of the data through 15 generations of selection by population genetic methods. Its results appear broadly applicable, even to forest trees. It suggests that the "law of constant final yield" must apply in a genetic as well as a mensurational sense.

Footnote 10: Forest genetics has been modeled from its beginning from agricultural sciences. In forestry, lost productivity from mismatched seed sources is well established from provenance and individual parent genetic studies in the Region's tree species. This evidence is consistent in showing lower biomass productivity than local populations with seed from sources having shorter growing seasons. It is only races adapted for longer growing seasons and accompanying faster growth rates than local sources that show greater biomass productivity initially on uncrowded plots. Numerous instances are reported of such sources being gradually depauperized, or wiped out by extreme drought, cold or pests. But direct evidence of general biomass deficiencies from a 10-day mismatch with mean or extreme growing season cannot yet be shown with forestry data. Such data is still simply too scarce or too short term or statistically inadequate. However, the fact that agricultural crops are bred toward even closer matchups, that multi-genic traits permit infinitely fine gradations of phenological and growth traits, and, as discussed later, that natural Douglas-fir populations have evolved a close mean matchup that maximizes biomass productivity, leaves a risk of unknown size when a more liberal criterion is accepted.

Footnote 11: The forestry goal to maximize biomass productivity is straightforward with crops like pulp and energy which use the entire above-ground wood component. Tree boles constitute the major portion of this component, particularly in maturing stands. If the goal of intensive forestry is to produce large stems quickly in thinned stands, there is some sacrifice of maximum biomass productivity. However, a genetic match to the growing season also maximized production with this goal, since all of the growing season is utilized.

Footnote 12: The problem of providing a simple example, such as Figure 4, is recognized. Every statement could probably be challenged with detailed exceptions, and the discussion could be extended to incredible levels of complexity. Relationship of phenology with freeze-free period involves an XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
genetically programmed to use the entire average growing season. Adapted populations have a smaller portion of such aberrant individuals. Slow attrition of individuals from each tail of the distribution tends to center adapted populations ever more closely near the optimum onset and cessation of growth for maximum biomass productivity. Some within-population spread around the mean dates is efficient in capturing extra days of growth because growing seasons vary in length (PT 13).

With Douglas-fir the actual situation is vastly more complex. First, in contrast to frost-damaged annual crops, conifers can survive loss of a year's succulent new foliage since hardened, older leaves photosynthesize. Also, stored reserves are appreciable. However, any such injury weakens the plant, and under competitive stress, injuries cannot be sustained repeatedly without growth loss. Without competitive stress, as in a garden or a widely spaced plantation with weed control, almost any Douglas-fir will try to grow at its relative inherent growth rate until severe cold, drought, competitive stress, or biotic damage occurs. Frost or severe cold can injure unhardened cambium tissue on twigs or stems, weakening the tree and reducing tree growth sometimes for decades before recovery or death. As trees age, the genetic response to unfavorable elements in its environment often override inherent growth rates in its eventual performance. Secondly, the range in phenological expression of individual trees in natural stands is large, and the tree's ability to adjust to seasonal change is also appreciable, both of which slow expression of genetic mismatch. Thirdly, compared with climatic factors, biotic factors have an even larger influence on productivity. Natural populations have come to some dynamic balance with hundreds of insects, diseases, viruses, and vertebrates that feed on them, but do not consume them completely. Weakened trees are first to be challenged. Combined with climatic factors, biotic factors often override inherent growth rates in determining a stand's productivity as it matures and ages. Fourthly, when considering similar adaptation for all potentially damaging or lethal environmental factors, attrition of mismatched genotypes gradually shifts normal distributions of forest populations to express an inverse relationship between growth rate and hardiness. A time frame of decades, or in some cases centuries, is appropriate before reaching the outcome of a growing-season mismatch (Squillace and Silen, 1962; Silen, 1968; Silen and Olson, in press, FT 14). Given this complexity and difference in time frame for Douglas-fir, essential features of many similar feedbacks and final outcome are the same -- a local population precisely adapted with a balanced array of phenological, growth and hardiness traits, that tend to maximize productivity at each site.

FT 12 cont: array of traits, some of which alone are poorly related to the free-free period. Bud burst, for example, adjusts toward each year's heat sums in some populations and toward day length in others, and overall may relate poorly to growth rate. Bud set, which adjusts toward onset of drought, is usually better correlated with growth traits in summer drought climates. Related traits, such as differential frost tolerance of new shoot tissue, permit a wider range of bud burst without injury. Unseasonably late or early frosts can damage high portions of even adapted populations, and rapidity of recovery may be associated with portion of latent buds that sprout. Hardening in fall involves a similar array of avoidance and resistant traits. But the generalization holds that local populations are adapted to use the growing season more efficiently over the long run than any other population.
Phenology-Growth-Hardiness Interrelationships

Although potential for lost yield from phenological mismatch is the reason to propose a new tree improvement model for the Douglas-fir Region, the strong genetic interrelation of phenology with growth rate and hardiness means that any genetic manipulation of one is almost certain to effect the other (Silen, 1978). Growth rate and hardiness are inversely related. Hardy plants tend to be slow-growing; fast-growing plants tend to be non-hardy. For over a half century crop breeders have tried to combine fast growth with hardiness against cold or drought without any instances of major success. It is as if the hardiness genes were competing with growth-rate genes for the plant's common energy source (FT 14). All racial variation studies of western conifers show this inverse relationship. Fast inherent growth rates have evolved in warm mesic environments that also have long growing seasons. Conversely, slow inherent growth rates have evolved in cool or xeric environments that have short growing seasons. A full gradient of races can be assumed to exist between, but it is difficult to show more than points along the gradient to adequate statistical accuracy.

Footnote 13: In Figure 2, one might expect a relatively faster growth rate for the long-season pattern, a slower one for the short-season pattern, and a dynamic balance between phenology and growth rate in the local population. The figure, however, which deals with annual biomass production rather than growth rate, shows the same rate of biomass production per day for all the patterns, as would be expected from the "law of constant final yield." discussed later under "Yield".

Footnote 14: Since most readers will not be able to easily access these references, the gist of the time-frame information is presented. Each provide examples of the extended periods involved before even lethal trends first become observable. The Wind River Arboretum, where hundreds of exotic species or varieties were tested, each now with over a half century record, eventually showed that none rivaled the performance of native species, yet many had superior early growth rates that appeared promising for up to 40 years. Even species that have died out completely often had survivors for decades under Arboretum care. For example, among the Pseudotsugas, bigcone fir from California survived 30 years. A Colorado variety of Douglas fir required over 40 years for its demise. All the other races of interior Douglas fir have reasonably good survival for nearly 50 years despite eventually fading in performance. Several species of southerly origins had grown vigorously for 20 to 40 years before the first extreme cold, the "1955 Deep freeze" decimated them.

The Douglas Fir Heredity Study, started in 1912, is both a racial and family-within-race study. All races and families were growing well when reported initially at age 17. By age 40, serious decimation had begun to low elevation races at the 4600-foot site, but even there almost every family had healthy survivors. By age 70, only two races from high elevation were forming closed stands at 4600' elevation, but several middle-or low-elevation races had appreciable numbers surviving in some families. At the middle and low elevation plots of the study most races are becoming understocked to differing degrees despite the original 7' x 7' spacing, and many instances of serious understocking are seen in unadapted races, a trend that could not be observed in the first half century.

The Ponderosa Pine Regional Races study, installed in 1928, required 60
All these traits are multigenic, so it is not difficult to imagine why some balanced interrelationships developed to conserve energy. The growth and hardiness relationships, while not as obvious or precise as with phenologies, nonetheless means that an average growing season mismatch of over 10 days for a population would probably have consequences for both productivity and hardiness, as in field crops. Tree breeders selecting for fast growth can expect to encounter this constraint.

**Templatelike matchup**

With phenology, growth and hardiness traits capable of quite exact adjustment to effective growing season length, a precise, perhaps templatelike, adaptation of natural tree populations to the local environment should come as no surprise. Even land races of agricultural crops, which were grown on individual farms through many cycles from seed of the previous crop, also became "precisely" adapted to each farm's environment for a balanced array of traits. Jennings (1976) description bears a strong resemblance to tree races: "Having been bred by natural methods of selection for thousands of years, (agricultural land races) have acquired a precise, although narrow, adaptation to land conditions of growing season, average and extreme temperatures, and photoperiod (along with) at least partial resistance to insect predation and disease, and partial tolerance of environmental stresses such as drought."

In summarizing the need to match growing season, natural plant populations and crop land races have used ancient genetic mechanisms to accurately match environmental gradients with clinal genetic variation. Crop breeders strive for a comparable match because yield is closely related to growing season length. The breeders additional desire to incorporate genes for faster growth that evolve in milder, longer-growing-season environments than the planting site, have met with little success because growth and hardiness are inversely related. In tree improvement, the UNIFORM model sidesteps this problem by delineating an appropriate uniform breeding zone. This is practical in gentle topography, of eastern U. S. or western Europe. But the Douglas-fir Region presents a far more complex, fine-grained pattern of environmental variation. Can uniform breeding zones of economic size be confidently delineated in complex environments? Is the matchup of genetics and environment essentially templatelike (FT 16) on so fine-grained a scale? Can use be made of this matchup to design a better tree improvement model? Before considering these questions, one needs to understand the underlying reasons for the Region's complex climate.

Footnote 14 cont.: years before even the most off-site race from South Dakota died completely on even one of the five plots. Survivors of most races were reasonably healthy when reported in 1962 at age 40, but those from the eastern part of the species range were becoming understocked. By age 60, only a few of the ten tested races are still forming stands on any of the plots. Most races range from open stands to virtually barren plots on all five sites.

With forestry careers spanning only 20-30 years, it is difficult to experience how slowly maladaptation trends proceed to reduce productivity. Footnote 15: The extremely high demand in ATP to synthesize macromolecules (Alberts, et al., 1983) involved with genetic controls and resistances suggests such a competition.

Footnote 16. The word "templatelike" is used conceptually in this paper to suggest a fitting of the phenology of the local race to its mean growing season within perhaps 5 days, a realistic day-length sensitivity. Variation in other
CLIMATIC COMPLEXITY OF THE DOUGLAS-FIR REGION

For mountainous western North America in general, and the Douglas-fir Region in particular, applying the 10-day criterion encounters seemingly hopeless environmental complexities. The first complexity is a magnifying effect of elevation in shortening the freeze-free period, which is further complicated by aspect, exposure, and air drainage. A second complexity is summer-drought modified by rain shadows that truncates growth for differing portions of the freeze-free period. Together, these complexities greatly alter the effective period of annual growth over short distances to form a complex regional environmental mosaic which grades imperceptibly from one locale to the next. Moreover, weather stations are so sparse outside the settled lowlands that growing season maps which might show such complex seasonal patterns on commercial forest areas are too data-poor and unreliable for most of the forested mountains of the West. Fortunately there is a simple way.

Freeze-free period

Freeze-free period, usually a good measure of the growing season, is not so good a measure for the West. A dramatic illustration of the contrast in growing season between eastern and western North America is shown in FIGURE 4, a map of 30-day intervals of freeze-free periods for continental United States and its territories. The gentle gradients in 30-day isolines across eastern North America give way to a riotous complexity west of the 100th meridian. Freeze-free period isolines that typically separate by 50 miles or more in many parts of the East are packed so close in the figure for parts of the West that they can scarcely be seen separately. The complex patterns of western North America reflect mainly projections of simple adiabatic cooling into western mountain zones, rather than actual weather records, because of the sparseness of weather stations.

Still, much can be observed about the Regions climate from FIGURE 4. The 300-day freeze-free isoline that goes through New Orleans also follows the coastline of western Washington. The same 90-day isoline that parallels the northern U. S. border also circles the summit of the Olympic Mountains less than 40 miles inland from the Washington coast. Across this elevational gradient the freeze-free period shortens about 10 days every 2 miles! There are as many "life zones" in this 40-mile span as in all of eastern United States. Even steeper gradients occur in numerous western localities. Most western counties have more change in freeze-free period than most eastern States.

The West's coastal climate is odd. A most noteworthy feature is the 300-day isoline which parallels the Pacific coastline from San Francisco through northern Washington. This line of unusually long freeze-free period, caused by the northward warming of the Japan current, creates a coastal band of equable climate that unfortunately is mostly only a few miles wide even if over a thousand miles long. And because summer days become longer at high latitudes, the longest effective growing seasons are at the north end of this strip. Though cooler, coastal Washington thus enjoys a growing season with many more daylight hours than New Orleans, a fact not commonly realized. Thus it is not entirely accidental that the world's tallest firs, redwoods, spruces, FT 16 cont: traits, like growth rate, hardiness, form and resistances to stress and pests would be of a related precision. In practice, the concept should not be construed as being more rigorously precise.
hemlocks, and cedars developed in this strip. Unlike most forest regions with predominantly south-to-north oriented growing season gradients, this Region's gradients are mainly west-to-east. Between this narrow, mild, coastal strip and the summit of the Cascades (150-miles inland)--the so-called Douglas-fir Region--freeze-free periods sometimes are shortened to a mere 90 days because elevations of a mile or more are common. And while the narrow coastal strip with its long growing season has produced the world's tallest conifer species, the shortened growing season inland has produced some of the hardiest species of this latitude in some of the same genera.

Elevation

A major climatic complexity for the West in general is the magnifying effect of elevational change on growing-season length. FIGURE 5, a graph conceptualizing various interrelated factors, has five approximately matching scales on its horizontal axis. At sea level or other common elevation, three related scales show that a northward movement of 3+ degrees or about 210 miles shortens the freeze-free period nearly a month. The fourth related scale shows the same 30-day shortening to occur at any point with a rise in elevation of only 1,200 feet. The elevational scale is from "Hopkins Law"; for each degree of latitude northward, the same life zone occurs about 400-feet lower. A verification of the phenological matchup for the springtime half of the seasonal change is Campbell's (1974) and Silen's (1963) estimate of 5 days delay of Douglas-fir bud burst or flowering per 400-foot rise in elevation. And, as observed earlier, the fifth scale shows a 3+ degrees northward movement matched genetically by corn breeders with six corn varieties, each differing by 5 days in ripening period. Estimated inherent change in volume growth rate is the vertical axis. The graph's regression line shows a clinal relationship between growing season and inherent volume growth rate, an example of the inverse relationship between growth rate and hardiness. Douglas-fir data from Campbell (1978) suggests roughly 10-percent less volume growth rate per 1000' rise in elevation. I use approximations deliberately for these environmental/genetic change relationships--movement of 3+ degrees north equals about 200 miles, equals about 1200' rise, equals about 1-month delay, equals about 10% less volume growth-rate, equals about six potential corn varieties. They are not exact, particularly for complex topography, but they are rules of thumb that are reasonably close and serve to dramatize how mountains magnify the Region's environmental/genetic complexities.

Do such relationships apply more generally? I have reviewed recent papers or manuscripts of Wells for loblolly pine, Kraus for longleaf pine, Riemenschneider for Jack pine, and Funk, Allen, and Williams for eastern white pine. As one might expect from such ancient genetic mechanisms, all these eastern U.S. species show about the same inherent growth rate changes with latitudinal change as we expect in the West with Douglas-fir. Rehfelt's (1988) data for lodgepole pine suggests similar relationships in other parts of the West with elevational change.

Summer Drought

If summer rains were ample, the UNIFORM model might still apply to many parts of the Douglas-fir region despite the elevational complexity. For example, a 400-foot elevational band might be proposed as a breeding zone to meet the 10-day criterion. However, locally contrasting aspects, cold air drainages, toposhade, and persistent snow packs seriously complicate so simple an elevational delineation of growing season lengths. But a far more serious climatic complication interferes to make such simple delineation highly
error-prone. This is the truncation of growth for varying portions of the freeze-free period by summertime drought modified by rain shadows.

Most of the world's major forest zones, including eastern North America and western Europe, normally have reliable summer rains. In contrast, the west coast of North America south of about 49 degrees latitude typically has summer drought during July and August. In some areas, drought may regularly ensue as early as June and extend into September or October. Douglas-fir and its associate conifer species usually become quiescent or dormant to halt growth during this midsummer period. About one year per decade, drought occurs so early that there is no recharge of springtime soil moisture, and every surviving plant must be genetically equipped to somehow survive an entire summer with only the available springtime moisture around its roots (FT 17).

**Topographic Interactions with cold and drought**

Growing-season pattern is modified greatly in mountains by a host of local environmental factors. In FIGURE 6, I attempt to illustrate how the region's free-growth period at a site is compressed by local factors that intensify drought and cold. Using a convention of displaying annual potential photosynthesis as a bell-shaped curve (Emmingham and Waring, 1977), the seasonal truncations and shortenings of the potential growth period are shown for a typical freeze-free period from April to October. At sites in rain shadows of north-south-oriented ridges, growth cessation from summer drought is advanced up to six weeks. For example, the rain shadow of the low-elevation coastal hills west of Corvallis, Oregon, depletes rainfall from the Pacific so that soil wilting point of valley lands is typically reached by June 15. At the summit of the Coast Range 15 miles westward and only 700 to 1500 feet in elevation, wilting points are reached a full month later. Major ranges of the Olympic, Siskiyou, and Cascade mountains cast even more formidable rain shadows. For example, annual rainfall at sea level on the west side of the Olympic Mountains is over 100 inches, but is as little as 12 inches on the east side.

Typically, rain-shadow drought is most severe in valley bottoms and decreases with increasing elevation. This is the opposite in direction to the trend of decreasing growing-season length with elevation caused by adiabatic cooling. A typical situation in the mountains at the southern part of the Region is for best growth of Douglas-fir to occur at middle elevations, with growth restricted by increased cold upward and by more intensive drought downward. Along the west slope of the Cascades, the corresponding elevation of maximal growth descends northward from mid-elevation in southern Oregon to about sea level in northern Washington, with a gradually narrowing band of droughtiness below, and colder temperatures upward toward timberline. These opposing effects of drought and cold on the free-growth period often seemingly upset expected elevational trends of racial variation and complicate growth predictions in complex valley systems.

Footnote 17: Variation in the reliability of springtime moisture has provided a useful index of inherent growth rate for western conifer races. The Pacific Northwest has highly reliable springtime moisture and droughty summers. Springtime soil moisture becomes increasingly less reliable southward and eastward. Arizona and New Mexico have springtime drought and summer rainfall. For ponderosa pine, the percent of total annual rainfall that falls in July and August correlated strongly, but inversely, with growth rate of 32 races in long-term racial variation studies (Squillace and Silen, 1962).
Other factors shown in FIGURE 6 shorten the growing season more locally. Lower humidity, clearer skies, and correspondingly sunnier conditions behind each successive ridge eastward from the Pacific Ocean (termed "Continentalness" in the figure) hastens droughtiness from increased evaporation by day, and increases frostiness by radiative cooling at night. Where coupled with flat areas, particularly at higher elevations, frost can occur every month of the year. Cold air draining from mountains into narrow valleys can cause frost every month as well. Shade of steep northerly aspects perpetually reduces light and temperatures, and snow packs from heavy snow accumulations can delay springtime growth for weeks on these northerly aspects. Thin soils on south aspects speed or intensify drought effects. Cold fogs and cloudiness appreciably lower temperatures and increase humidity along the entire Pacific coastal strip. Fog drip on ocean-facing ridges, particularly near the ocean, can provide substantial relief from summer drought. All these elements can effectively reduce the growing season, or even lengthen it, in complex patterns that grade clinally from one locale to the next across the variable mountainous landscape of the Douglas-fir Region.

Whether spring comes early or late at a locale, there is one growth commonality with all sites west of the Cascade Mountains. Springtime soil moisture is usually ample, and by flushing date temperatures are usually mild enough for rapid daytime growth and low nighttime respiration. Dense canopies form and intense stand competition for light ensues. Self thinning is normal and selection for dominance is intense. Competition in tight Douglas-fir stands often prevails into the fourth and fifth century, so that trees with even slight inferiority in leader elongation are overtopped. This assured springtime soil moisture may well account for selection of unusual inherent growth rates and exceedingly tall trees in so many of the region's species, despite a short summer growth period and nutrient-poor soils from severe annual leaching.

**Within-season patterns**

A generally unrecognized need has evolved another kind of genetic complexity of the Region's forest population. This is the variation in timing of growth within the growing season. A record of within-season complexity of local environments is presented by Fujimori and Waring (1977) who sampled four Oregon sites with detailed measurements of incoming radiation, temperatures, rainfall, and soil moisture (FIGURE 7). They computed total potential photosynthesis as the upper curve in each of the four graphs, and the drawdown of this potential by frost and drought periods, the lower curves. The coastal site with 300 freeze-free days attained near-potential biomass productivity from February to December, the main exception being a drawdown during the summertime drought period. The site of this plot is the same experimental forest where Fujimori (1971, 1972) recorded a world record forest biomass productivity of 36 metric tons for temperate forests. In contrast, the Cascade Mountain site is characterized by little potential photosynthesis until snow packs melt in May, then near-potential productivity through June, low potential through the droughty July-September period, a brief spurt in early fall, followed by onset of winter. Between these two growing-season extremes, the Coast Range and Willamette Valley plots had very complex patterns, with bursts of photosynthesis alternating with numerous drawdowns by both spring and fall frosts, and a major drawdown during summer drought. The authors reported a fortuitous near-perfect relationship between estimated carbon fixation and measured site quality.

Their record illustrates several points about within-season patterns. One is that, except for the coastal site, growth opportunities occur in spurts,
sandwiched between frosts or droughts that can kill succulent tissue. Phenology of bud flushing must be accurate; the risk-free period for free growth between last frost and summer drought is often brief. Another point is that with more within-season complexity, more complex genetic control over phenology would be needed by the plant. For example, the quick switch from succulent springtime growth to early summer quiescence or dormancy, would involve quite different genetic systems. Slow-growing hardy plants may well be more genetically sophisticated than fast-growing ones. A third is that substantial potential for biomass productivity is outside the freeze-free period, and indeed there is much growth of partially cold-hardy meristems and those protected under bark or soil in spring, fall, and during mild winter periods. And fourthly, selection would have to produce a distinctive population phenology/hardiness for the tree population at each of the study sites to match such complex within-growing-season differences (FT 18). The true growing season would be hard to even measure accurately at three of the four sites. In the complex environmental gradients of the region, delineating an area meeting the same 10-day criterion would become very error prone. Fortunately, appropriately attuned natural populations probably evolved on every site.

Biotic Factors

Interaction of cold and drought variables with biotic factors, though relatively unstudied, add further environmental complexity. The impact of disease, insect, and vertebrates is continual for every forest-tree population, but they are far from uniform geographically, or over time. Leaf diseases like rhabdocline and Swiss needle cast increase in severity toward mild, mesic parts of the region, and resistance follows the same environmental trend. Phomopsis attacks are just the opposite, increasing in severity with drought stress. Mountain beavers prefer mesic, but pocket gophers prefer xeric habitats. Spruce budworm, tussock moth, shoot moth and bark beetle attacks increase as environments become more xeric. Ambrosia beetles prefer colder than warmer environments. Most pest distributions grade toward some environmental preference, matched by whatever resistance or tolerance mechanisms are displayed in the tree population. Cyclical environmental stresses that weaken xxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxx

Footnote 18: The graphs open myriad questions about seasonal growth that have genetic implications. Obviously, there must be a longer, hard-to-define period than freeze-free period that could produce biomass, probably under tight genetic controls. The winter-spring portion of the period is probably less efficient than the fall-winter portion because photosynthesis depends on old leaves and how gradually cold hardiness is lost. A surprisingly large portion of seasonal biomass in Douglas-fir is synthesized during fall, but active tissues of the plant are exposed to much risk from freezing until cold hardiness develops. The graphs suggest that the biomass production period may be hard to accurately characterize during these periods except with direct dry-weight measurement. The free-growth period when springtime growth is unconstrained by moisture, nutrients, cold or drought is the showy period when shoots elongate, and springwood is added. The shoot's contribution to biomass, however, must be a mixed one. A shoot's elongation is well related to last year's bud size, and during part of the spring period there is no contribution, or even a negative contribution to biomass. But this period of unconstrained xxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxx
the tree often trigger cyclic variation in the impact of biotic factors, adding a time component to the complexity. Long-lived species adjust to worst-case biotic impacts on a time scale measured in centuries.

Effective Growing Season (EGS)

In the Douglas-fir Region the result of this environmental complexity is that the period of unconstrained growth, the effective growing season (EGS) which relates to biomass productivity, bears an uncertain relationship to the freeze-free period. The environment is far more locally complex than shown on the 30-day freeze-free map in FIGURE 4. At the same elevation, different topographies can exhibit quite different EGS within the span of a few miles. On north slopes, for example, toposhade, deep soils, and snow packs can provide large contrasts in EGS with south slopes where extreme exposure and shallow soils are common. At the same elevation, rain-shadow effects of steep ridges can cause as large EGS contrasts between east and west slopes. Cold air drainages cause large EGS differences between valleys and adjacent slopes. Wide and narrow valleys can contrast in EGS because of differences in air drainage, toposhade and radiative cooling. Foggy, cool, coastal aspects and valleys contrast sharply in EGS with similar, but warmer, topographies a few miles inland. Extensive thin or poorly drained soils can markedly reduce the period of free growth. Fog drip can add weeks of relief from summer drought for ocean-facing slopes. And "continental" of valleys behind high coastal hills cause abrupt differences in EGS over short distances (Sorensen, 1983). The interactive effects of cold, drought, soils, fog, and mountain orientation complicate EGS gradients along otherwise topographically similar mountain slopes. The contrasts are often reflected as obviously different plant associations at the same elevation. Outside of settled lowlands a contiguous area larger than half a township that meets the 10-day EGS criterion would be difficult to delineate (FT 19).

MATCHUP OF LOCAL STAND GENETIC STRUCTURE WITH EFFECTIVE GROWING SEASON

The Region's EGS complexity severely strains the concept of a close, if not templatelike, match of genetics and environment. Can populations change in genetic composition with every few hundred feet of elevational change or horizontally in just a few miles? There are four kinds of evidence to suggest that the match is indeed precise. Some of the evidence is obvious, some old, some recent, and some unpublished.

Precise Phenology

The first such evidence of precise phenological fit to EGS is omnipresent; natural stands begin and end growth on time with surprising accuracy.

Footnote 18 continued: elongation must be genetically limited by control over flushing and bud set in order to avoid frost and drought injury. The implications for this paper is that all this intricate genetic selection comes at low cost with adapted local populations, but would be unaffordable if geneticists had to breed for such traits in a synthetic population.

Footnote 19: Some notion of how fine-grained the environmental pattern can be in the Region's most gentle topography, the Willamette Valley, is provided by
considering seasonal differences and the genetic adjustments necessitated by all the steep and complex environmental gradients throughout the Region.

The genetic evidence is also persuasive that phenology, hardiness, and inherent growth rate are delicately integrated. In local populations, genetic adjustments in phenology and growth rate to match EGS have favored as tall, productive, and genetically structured a local population as the complex, often interrupted, EGS would support over time. Where free-growth conditions persist over a long season, such as in the coastal strip, species have responded with record growth rates, but with early flushing and frost-tender genotypes. It has always been alluring to select fast-growing parentage for tree improvement programs from such favorable places, but such parentage is not hardy enough for most of the Region. Where a mountainous and droughty local environment has permitted only a few brief bursts of free growth per season interspersed with perilous conditions for succulent tissue, slow-growing, hardy populations are found in genetic tests of Douglas-fir and its associates. Every gradation between these extremes has a race with an appropriate balance of traits.

Yield Tables

An unusual Regionwide indication for Douglas fir that "feedback mechanisms" are precise, probably template-like, in matching genetics to environment is seen in Douglas-fir yield tables produced by McArdle and Meyer in 1930 when the Douglas-fir Region was mainly in natural forests. The tables give total yield by decade for stands indexed into 10-foot height classes attained at 100 years. For example, dominant trees on best, average and poorest sites (Classes I, III, and V) attain 200, 140 and 80 feet in height, respectively, at age 100 years. They sampled over 1900 plots throughout the Region, confining plots to pure stands of "normal" stocking, which were dense-canopied stands in the self-thinning stage and generally almost barren of other vegetation. This sampling bias has often been criticized by mensurationists, because less dense stands are more common, as initial low stocking or ice, snow, wind, disease and insects open many holes in the canopy. However, the authors easily found such fully-stocked conditions in all ages of stands since Douglas fir cycles through overstocked and understocked stages repeatedly in its long life. When analyzed decades later in terms of the "-3/2 power law of self thinning," the data produced slopes with an exponent value of -1.5, the theoretical limiting value (Reukema, pers. comm. 1988, also Drew and Llewelling, 1977). Although the "-3/2 power law" itself is controversial applied to trees (Zeide, 1987), the

Footnote 19 continued: a weather map for Portland, Oregon, and vicinity (FIGURE 8). The map is unusual, being a compilation of rainfall observations by amateur meteorologists during 1976 by the Bonneville Power Administration. Within the Portland metropolitan area itself, rainfall varied 12 inches. The map shows the severe rain shadow of coastal hills at the western edge of the Willamette valley where rainfall amounts dropped from 44 to 30 inches in about 4 miles. In contrast there was an even steeper gradient of increasing rainfall with elevation eastward toward the Cascade foothills. A township-sized area of similar seasonal climate would be difficult to delineate in the foothills. Even on the Willamette valley floor rainfall varied 14 inches over a 6-mile span in the rain shadow of 300-foot hills between Newberg and Beaverton. Although the map does not directly show growing-season differences, drought occurs substantially earlier in the drier areas over the short distances cited. Mountainous forested areas would have much greater variability, but maps from such detailed sampling are rare, if they exist.
debatabile factors mainly hinge around incomplete, rather than complete canopy closure, the only stage the authors sampled.

A frequently overlooked, but important point is that the "-3/2 power law," which expresses average tree size over the range of spacings, has an interchangeable alternate form, the "law of constant final yield." This version uses the same data to expresses volume per unit area over spacing, instead of average tree size over spacing. If this data from fully-stocked stands fits the theoretical -1.5 slope, it follows that a given site will also attain a constant final yield over a great range of initial densities. It is important to stress that annual biomass productivity is the constant, not some final stand volume at rotation age. This provides a common denominator with numerous field crop biomass annual yields for which the "law" has been shown to apply. It is also important to grasp that most fully stocked stands in the sample must have approached theoretical maximum yields which occur at the theoretical -1.5 slope.

This precision seen in so rigorous a modern analysis of this vast early sampling of the regions natural forests makes quite a statement. To have such sampling accurately approximate theoretical yield maxima suggests, among other things, that natural populations at each locale must be attuned phenologically to use the entire growing season. Otherwise agricultural data (FT 7 & 9) suggests such maximum annual biomass production would not have been so generally attained on the plots. The average precision of growing-season matchup appears to be 10 days or less, since stands differing only a few hundred feet in elevation on sampled mountain slopes have measurably different phenologies of less than 10 days (Silen and Krueger, 1962; Silen, 1963). Also, despite plenty of genetic variation in growth rates available to do otherwise, the analysis certainly suggests that selection of the appropriate rate of growth in each stand tends to balance growth and hardiness needs.

But regardless of the underlying biology, the finding that natural stands in the 1900 spots in the Region tended to attain an annualized maximized "constant final yield" at each site suggests a templatelike fit between genetics and environment for the species at a rather fine-grained resolution. Although genetics research now provides numerous examples that show a reasonably precise matchup in terms of statistical correlations between inherent growth rates and site-quality variability even in steep local environmental gradients, this regionwide example that directly involves yields is an even more general indicator of matchup.

Three-dimensional maps of geographic genetic variation

Scarcity of examples showing close genetic/environments matchups is largely due to inadequate sampling density of parent trees in geographic variation studies. In one early example, however, large differences in inherent growth rates of populations were found on contrasting north and south slopes of the same ridge in southwest Oregon (Hermann and Lavender, 1968). Campbell's (1978) study of variation in a small watershed in the Oregon Cascades illustrated the sampling density necessary to show a three-dimensional templatelike matchup. He sampled 187 parents in a drainage embracing only 15,000 acres or about half a township. This 9-tree-per-square-mile sampling readily revealed strong genetic differences in phenology and growth over short distances because environmental gradients were very steep, particularly between the 1500-foot valley bottom and the 5200-foot ridgetop within a span of less than 5 miles. Because the nearly 100-day shortening of growing season with elevational change is by far the strongest environmental gradient in this drainage, the families from his common-garden experiment displayed 3-year
height isolines that virtually followed elevation contour lines for a templaten-like match (FIGURE 9). There were major influences of aspect, however, that complicated the patterns for his maps of principal components. He has recently completed a fairly dense sampling of Sitka spruce on Mitkof Island, in southeast Alaska, that shows a correspondingly complex three-dimensional genetic/topographic variation pattern for stands on this small island.

Data from commercial testing of Douglas-fir families in the Region's cooperative programs (Silen, 1983, 1984) has become so voluminous as to leave little doubt that Campbell's results are the rule. Additional maps of geographic genetic variation in two dimensions have been published based on such data (Silen and Mandel, 1983; Silen, 1983; Silen, 1984). For those unfamiliar with tree improvement in Oregon and Washington, the program is one begun in 1966 by Industrial Forestry Association and USDA Forest Service, PNW Experiment Station (Silen and Wheat, 1979). This so-called "Progressive Program" is now carried out by 23 local tree improvement cooperatives that involved 44 landowners large and small, public and private, and cover over 8-1/2 million acres. It began by testing two selected parent trees per square mile. The present data base involves over 20,000 parent trees, tested by over two million tagged progeny on over 600 test sites in the Region. With this volume of genetic data we have ample statistics on selection differentials and heritabilities for reliable estimates of genetic gains (Silen, 1985). From this moderately intensive sampling over many parts of western Oregon and Washington, 20 three-dimensional maps of geographic genetic variation have been drawn. Where sampling is uniform and test data excellent, the conformation of inherent growth rates with local topographic features is clear, and often striking. Clinal match-up of growth rate with environmental gradients is the rule. Among the breeding zones now mapped are some that have simple environmental gradients. One shows a genetic match-up with a simple gradient in adiabatic cooling with elevation, four show match-ups with simple drought gradients in the rain shadow of the Coast Range, and two show depressed inherent growth rates of parents from large, frosty flat valleys. Along the Pacific shoreline, four maps display a pattern of depressed inherent growth rate in the cool fog zone, with a band of average growth immediately inland. Patches of fast inherent growth within the average zone occur a few miles inland in sunnier locales. Most maps, particularly those from the Cascade Range, display a complex inherent growth pattern reflecting environments of a dissected, complex topography. These match-ups are apparent despite only medium-to-low correlations between inherent growth rate and the latitude, longitude, and elevation of parentage. FIGURES 10-13) show maps with examples of these match-ups.

Local stand genetic structure

Besides its use in three-dimensional mapping of geographic genetic variation, the vast data base of these commercial Douglas-fir tests has shown that local native populations have a distinctive genetic structure. In many breeding zones the tests deliberately grouped parents from the same stands into sets of 25 to 50 parents tested alike. These sets show normal frequency distributions of heights or volumes that are clustered around the stand average. These stand mean heights or volumes vary appreciably, even at the same elevation, within any township-sized forest area. These normal distributions of stand growth parameters are clearly different when stands are located at various points along environmental clines. In other words, each stand has adjusted its growth rate to cluster most of its population around an appropriate value, yet carry a smaller portion of variants, normally
distributed, that are faster or slower growing. Not surprisingly, stand means are highest at the most favorable ends of such gradients. There are also clear instances at corresponding elevations of substantial inherent population differences in growth over a span of 10 miles or less (FIGURE 14), probably reflecting some difference in effective growing season. All these commercial tests were designed primarily to test family differences, and not to map geographic genetic variation. Still, the large numbers of progeny per family, plus the general consistency with which genetic variation reflects landforms, often in fine detail, is persuasive in suggesting that the precise matchup seen in Campbell's (1978) study is a general phenomenon.

Thus, the evidence is growing to suggest that the same biological precision seen at the molecular and ecosystem levels probably applies for variation within species for a templatelike match of genetics to local environments. Faced with such a complexity of EGS and matching genetic response, the forest geneticist of the Douglas-fir Region has severe problems in delineating a commercially ample breeding zone for the UNIFORM model.

PREVIOUS APPROACHES

Concerns about genetic adaptation to the Northwest's climatic variability were expressed early (Isaac, 1949). Without alternatives, the UNIFORM model has had to be used ever since tree improvement began in the region over 30 years ago. Programs based on the model now extend to every corner of the Region. Typically, breeding zones of over a hundred square miles were delineated that were judged on various climatic criteria to be environmentally similar. Even this restricted zone size were viewed as needlessly small by geneticists in other parts of the world. Meanwhile, assumptions expressing need to match genetics and environment have become accepted to varying degrees by all western forest geneticists who study geographic genetic variation. Campbell (1986) expresses it best in an assumption used in a recent paper--"a population of a given species is better adapted to its place of origin than is any other population." But there was a range of viewpoints regarding how fine-grained the matchup really needed to be, and how to handle a mismatch as breeding zones were expanded in size within the UNIFORM model to achieve economies of scale. Thus, the question until now has been--"how much seed movement (mismatch?) is acceptable?" (PT 20). Because the UNIFORM model was unquestioned the quest of research was to find a basis to define larger zones. Despite growing evidence for seed movement concerns, no one was prepared to suggest that seed zones should be restricted to a 10-day criterion to avoid lost productivity, or to propose a way to avoid most seed movements.

Footnote 20: Seed movement accepted by forest geneticists varies greatly. USFS locally specify 500-foot elevational bands. Most breeding zones and the standard seed-zone maps are based on 1000-foot elevation and one-degree latitude limits. But movements of over 100 miles have also been used. Studies are also underway or proposed to investigate gain expectations from wide seed movements.

Footnote 21: Published seed zone maps for Oregon and Washington dating from the 1960's were initially the most widely used approach. The Region was divided into zones along major north-south ridges of the Coast and Cascade Ranges, and east-to-west at about one-degree latitudinal intervals. Bands at
Among the most widely-used seed movement approaches were seed zones maps, breeding zones, seed movement rules, geographic genetic maps, risk limits, and one not so well known but widely used--encouraging natural regeneration on planted clearcuts (FT 21). All past approaches to seed movement expressed the state of the art for its time. All were attempts to define forest areas of ecological or genetic similarity, (and as large as possible), to approximately meet the intent of the UNIFORM model's uniform breeding zone. Possibly any or all of the approaches might be workable in the most uniform parts of the region. The problem is the unquantified and unpredictable complexity arising from the mountainous topography and droughty climate of most of this particular Region. The potential for an unforgiving error in matching EGS is very large, often embracing growing seasons that differ 20 to 40 or more days over short distances in the same zone. For example, a 1000-foot elevational band, commonly accepted in many approaches, embraces nearly a month of growing-season variation. As previously mentioned, seed-zone maps based on 400-foot elevational bands might meet the 10-day criterion in a summer rainfall climate. But without data, one can only guess how much they depart from the criterion at any planting site. Maps of geographic genetic variation in growth, as detailed as they are, do not have a certain enough informational base to assure breeding zones that meet the 10-day criterion. The Region's complexity also leaves the application of the risk limit approaches with very large uncertainties for a particular planting site (FT 22).

FT 21 cont: 1000-foot or lesser intervals further divide each of the zones elevationally. More recent programs use breeding zones developed locally as needed for each one. Some breeding zone boundary segments corresponded with seed zone boundaries, but breeding zones are generally more confined than seed zones, and often follow ownership boundaries. In common with seed zones maps, boundaries were based primarily on the best understanding of the local ecology. The seed movement rules, geographic genetic maps, and risk limits were developed by geneticists. All are based on the reasonable assumption that the stand has evolved an average inherent growth rate, plus associated traits, which correlate reasonably well with adaptive needs. All involved interpretations of common-garden studies of progeny from parents sampled at low densities over the region or parts of it. Seed movement rules and risk limits attempt to set breeding zone boundaries at some accepted limit of nonadaptation; the limit is defined statistically in terms of standard deviations from growth means of local populations, and the proportion of overlap of population frequency distributions. An interesting development was the idea of planting at higher densities to assure adequate stocking where seed-movement risks were larger. The direct mapping of geographic genetic variation for each breeding zone uses family test data from the high density sampling of parent trees in the regional tree improvement program (Silen and Wheat, 1979; Silen and Mandel, 1983). Encouraging natural regeneration on clearcuts, whether planted or not, and picking the winners is practiced by USFS in the Region. The main drawback is the unequal start between planted and natural seedlings that initially strongly favors the planted ones.

Footnote 22: With only the UNIFORM model available, a case for using large seed zones in the Douglas-fir Region has developed around one or more of the following rationales:

(1) Family and provenance tests of widely differing seed sources have been observed with acceptable survival and good growth for 15 years and longer.
Erasing these uncertainties with highly refined local weather data or with genetic information would be far too expensive for the gains involved. There is no serious prospect of actually mapping our region for effective growing season from weather station data. To sense effective growing season, soil moisture data at various depths needs to be taken as well as air temperature. A system of weather stations that took detailed enough data, installed at the high densities needed in our complex mountainous topography, and for enough years, is financially out of the question. And no one can say how long a record period is adequate. The genetic testing effort needed to assure that genotypes then matched these data would be enormous.

Genetic improvement of Douglas-fir to date is quite effective in selecting or breeding populations with faster inherent growth rates and better form. Few data are kept on matching EGS. Such data would be unnecessary if the Region were flat. But unless the new population matches EGS locale by locale in our droughty mountainous region, a reduced biomass productivity is a long-term prospect, as it would be with any improved agricultural crop.

In recent years I have been led to suspect that the problem lay in the tree improvement model itself. We were trying to apply a model that fits regions of gentle topography and summer rains having extensive zones of similar growing seasons to a summer-drought mountainous region having locally steep and complex environmental gradients. The better opportunity is to somehow use the EGS matchup evolved in each forest stand in the Douglas-fir Region to assure the same full productivity so easily achieved in flatland regions. An alternate model of tree improvement is proposed to accomplish the matchup without appreciable seed movement, thus using one of the regions finest resources - - precise genetic adaptation of native populations. This paper proposes an alternative tree improvement model I term CLINAL to stress its main feature - - matchup of parentage with planting site at each spot along environmental gradients.

FT 22 cont:  (2) Every local race has large genetic variability, so varying portions are presumed to be reasonably adapted to a wide variety of sites.

(3) Much of the genetic variability of the local race is thought to be needed to survive as seedlings, which would not be needed in plantation forestry.

(4) Cultural measures, such as spacing, fertilizer, and weed control will permit quite off-site races, particularly faster-growing ones than the native population, to meet forestry needs.

The major problems with such rationales are simply that none assure a close enough match to the growing-season pattern to avoid potential loss of biomass productivity. All involve risk for which no studies have been run sufficiently long duration to assess. It becomes difficult to justify a need for larger improvements in growth rates than provided by the large genetic variation in risk-free local populations. Hence, improvement using local populations should be the preferred direction of program design.
A CLINAL MODEL PROPOSAL

Conceptually, the proposed CLINAL model simply tilts the UNIFORM model to conform to genetic clines. In comparing models, the UNIFORM model fits clines like a staircase, with each step or breeding zone served by an orchard. For gentle clines the treads are very wide and the risers small. For steep clines, however, a wide tread would require tall risers. Either the mismatch at each side of a boundary area becomes large, or breeding zones become physically narrow and numerous. In contrast, the CLINAL model can be thought of as an inclined plane instead of a staircase. Conceptually it has neither steps nor borders. Since a new seed mix can be made for each planting site at any point along the plane, each can be from equally local proven (FT 23) parentage, whether located at center or edge of presently delineated zones. For adjacent points along the inclined plane two seed mix would overlap somewhat to have some parents in common.

The CLINAL model is basically distinct in several regards. Conceptually, it permits planting each harvested site with progeny of improved local parents. It does not define a breeding zone as the initial step, nor limit a seed orchard to produce only one seed mix. A most distinctive feature of the model is that of producing many different seed mixes in the same seed orchard. Tested parent trees are selected from an ownership block as densely and uniformly as practical. Then, clones or progeny from proven parents are arranged in an orchard in the same relative coordinates as the parents in the forest, but locally randomized to reduce inbreeding. Seed collections for a particular planting site are taken first from orchard parentage nearest to the planting site. If more seed is needed, collection is extended to neighboring orchard parentage having the most similar EGS. Two-dimensional maps of geographic genetic variation, produced for many programs, can aid initially in deciding the most similar neighboring parentage. As seed orchard trees increase in seed production, local parentage contribution increases, and uncertainty of matching EGS lessens.

A simple, idealized example would be a single aspect of a uniformly sloping mountainside. Tested clones or families of parents chosen uniformly from over the mountain aspect would be arranged maplike in a seed orchard. Improved seed for a particular planting site on the mountain would be taken from a band in the orchard having the most local parentage, but no wider than needed to meet the 10-day criterion. Bands would overlap as needed for adjacent planting sites. Given adequate numbers of tested parents, each year's seed collection could have different parent mixes as the forest rotation requires matching new sites to be planted on the mountain. Thus local seed mixes from the orchard would match the clinal genetic variation of the mountain slope. Questionable seed movements becomes just as unnecessary as it would be using the UNIFORM model in the gentle topography of eastern North America.

For more complex topography, again given adequate parent numbers, the maplike layout of parentage appears to handle the CLINAL concept as well as for the simple example. A seed mix of parents that meet the 10-day criterion would again be from a band in the orchard centered on parents from nearest the planting site. However, the major axis of the band may not be elevational,

Footnote 23: Inherent growth rate is not different between the two models. Selection would be for parents each with the same growth rate improvement over the local stand mean in either case.
but may be strongly adjusted toward a single environment or aspect. High and low elevations, contrasting major aspects, wet and dry areas, or other environmental contrasts are usually physically separated enough so that parents from areas of environmental extremes are also usually separated in the orchard. Since so little specific information is known about actual genetic clines in our complex topography, safety lies in reducing the band's size to parentage as local as practical.

The CLINAL model has other key features. It also provides for keeping intact the genetic structure or architecture of local stands by first selecting parentage neighborhood by neighborhood that is appropriately superior in growth rate to the local stand mean, and by giving preference in future breeding to crosses between parents within the same stands. The assumption here is that growth rate can be enhanced, but no appreciable genetic improvement can be made in matching EGS and biomass productivity over that already inherent in local stands.

The CLINAL model perpetuates genetic stability. Highly bred agricultural crops need increasingly more help from man to survive as genetic improvements progress. In forest populations destabilization of local genetic structure is the initial step in the same pattern. The CLINAL model has little need to disturb gene frequencies of the hundreds of presently non-economic resistances, phenological or form traits that accurately adapt local populations to the rigors of local environments. Genetic improvement of trees is mainly concerned with growth, and possibly a few other economic traits. However, too severe selection for growth rates, even when confined to local stands, could alter it's genetic structure. Applied conservatively, the vast reservoir of adaptive traits probably can be kept intact and stable over time. The same, of course, can be said for the UNIFORM model applied to flat land. But when the UNIFORM model is applied to mountainous terrain, parent trees selected for growth rate are usually combined from genetically diverse locales to reconstitute a synthetic population unlike the highly structured natural populations for which the effects on non-economic adaptive traits are usually unknown.

Although practical problems and objections immediately arise in one's mind in bridging decades of present practice toward some ideal application of the CLINAL model, my initial goal in proposing the model is mainly to suggest a future direction. This direction avoids the uncertainty of defining a seed zone with little information, removes the questionable logic of trying to make stairsteps out of clines, and assures full productivity from full utilization of the growing season. Such assurance, for decades ahead, lies mainly in using the genetic structure of local tree populations.

Proposal of a new model need not be disruptive. A problem arises because most of the Douglas-fir Region has existing tree improvement programs that cannot be changed quickly. Except for new programs, the changeover would have to be gradual over several decades. Changes are easiest with the female orchard component. Initially, any seed orchard that collects seed by individual parent or clone, as many do to mitigate the "80-20" problem (80% of seed produced by 20% of clones), can initially make numerous seed mixes of parentage that are more local than the general seed orchard mixture for only pennies more per pound. Changes of the male component of an orchard is more complex. Techniques for supplemental mass pollination, and even auxiliary orchards for pollen production have been suggested for the short term to provide more local pollen in the seed mix. Gradually, new or "moving front" additions to orchards can institute design changes to promote pollination from increasingly more local parentage. Where parent numbers are presently inadequate to give a desirable localized genetic base, or intensify inbreeding
concerns, economical steps described later can be gradually taken toward adequacy. Because breeding programs are still largely a future activity in the region, the next generation can more easily be phased into the model. Concerns about reduced gains, higher costs, and inbreeding can be minimized. Such technical problems and solutions that have surfaced as the model developed are discussed later in more detail.

Experience With the CLINAL Model

An orchard of a CLINAL design was established in 1977 in the Willamette Valley at the J. E. Schroeder Orchard complex of the Oregon State Forestry Department (Silen and Wanek, 1986). The orchard was not deliberately planned with a new model of tree improvement in mind. The geneticist, Jack Wanek, wanted seed adapted to State-owned lands that are mainly at higher elevations than lands of the other three landowners of the Molalla Tree Improvement Cooperative. This Cooperative serves 120,000 acres of ownership in the foothills of the Cascades east of Salem, Oregon. Although lower-elevation parentage produced faster growth rates, he wanted improved, but more hardy seedlings from high-elevation parents. The seedling orchard was of full-sibling parentage. He computed the midparent elevation of each cross, placed the 1000-1100-foot group of families in a band at the south side of the orchard block, with the 1100-1200' parentage in the next band northward, and so on. Parentage originating at 2400'-2600' were planted in the final band on the north side of the block (FIGURE 15). When the orchard reaches full production, each landowner can specify seed of a different desired elevation for each year's plantings. Unfortunately, we learned later that the main component of geographic genetic variation for this particular breeding zone was latitude, not elevation (Figure 10).

Once I grasped what Wanek had done, I saw that this was the key to a CLINAL concept. Orchards did not have to be designed to produce just a single seed mix. Had the main component of variation in the orchard been elevational, parentage from one or two bands would be genetically far more closely matched to the growing season of the planting site than a mix of seed from parentage of the entire breeding zone.

We now have considerable experience with the CLINAL model. Since 1979 I have helped Wanek work out the many problems and patterns of a new model. Of the four seed orchards involved with the CLINAL concept, the first two use elevational bands. In the third, the original breeding unit was broken into six smaller segments arranged in maplike order. In the fourth, the chosen families of 96 progeny were first grown at close spacing in a holding area with the intent that fifteen members be moved at age five into permanent orchard locations at 30' x 30' spacing using a maplike design.

Addressing Problems

Handling a simple cline of increasing elevation was one thing; but to handle the complex interlocking clinal variation when numerous climatic elements of a droughty, mountainous region was not initially apparent. We first tried banding or blocking patterns as noted above. It finally occurred to us that a maplike arrangement of the orchard provided an almost elegant solution. Seed for a planting site could be collected in the part of the orchard that matched the geographic coordinates of the planting site. The more proven parents that are available the better the pattern worked, because this reduced the distance from the planting site from which orchard parent trees are chosen for the local seed mix. In our case, one parent per 2 square miles of
ownership was the typical base population of selected parents. Even elevational differences within the ownership did not present much of a problem because high and low elevations, or other contrasting environments, were usually amply separated.

What about inbreeding? True, a small local parental population in an orchard of CLINAL design makes it more difficult to widely separate the same ramets or family members that might interpollinate than in the Uniform model.

Inbreeding depression from orchard seed first needs discussion from a silvicultural perspective. Mature Douglas-fir stands usually have no inbreeding-depression problem. Most self seedlings are removed in nursery culling, or die early in natural regeneration. Virtually all remaining inbreds are overtopped and die in a single cycle of self thinning. Such silvicultural events are far more thorough in eliminating inbreeding problems than tree improvement techniques. However, some inbreds are carried through the nursery processes, and might reduce growth noticeably in the final stand if repeated silvicultural thinnings prevented a cycle of self thinning, but only if genetic gains in growth are small.

The attempt by Douglas-fir seed orchardists to eliminate selfing by seed orchard design can never be more than partially successful. This is because such a high proportion of the pollen any flower receives is from the tree itself. Pollen coming as a pollen plume from even nearby members of the same parentage would be in much smaller amounts. Fortunately, Douglas-fir embryos from self and closely related pollinations usually pair homozygous lethal genes and thus never produce seed. At least half of Douglas-fir parents produce almost no selfed seed, and parents are rare that produce over 10 percent filled seed after controlled self pollination. In addition, Douglas-fir has developed other mechanism to reduce selfing. With a seed's micropylar canal that can hold up to nine pollen grains, and typically with five archegonia, multiple embryos are potentially possible but seldom result. A single outcrossed pollen grain among multiple self pollen grains will usually produce the successful embryo. That grain, however, can carry non-lethal related genes that still can reduce growth.

The problem of inbreeding depression arising from pairing of nearby related parents could become a noticeable problem if gains in growth rate were smaller than the percentages presently anticipated, or if local parentage became too closely packed in the orchard. The best solution with either model is to use large numbers of parents to increase distance between related orchard trees. Inbreeding concerns seemingly vanish if only one representative per parent were needed per orchard. However, a substantial selfing problem still remains from each tree's own pollen. Programs in Oregon and Washington begin with an unusually large genetic base compared to programs in other forest regions. So inbreeding starts with less of a problem than would be the case elsewhere. Just as now, in the future the final reliance to reduce inbreeding as a problem will be nursery culling and natural or silvicultural thinning.

What about matching phenology of orchard trees? Positioning trees phenologically in an orchard so that neighbors interpollinate is a frustrating problem with random designs. Moving orchard trees provides a potential solution, but randomization is usually violated. With large parent numbers the problem is not worsened if the orchard design is maplike. However, when parent numbers are inadequate the matching of phenologies of neighboring trees is more difficult. The best overall solution would lie in efficient mass supplemental pollination by providing trees with desired pollen mixtures as each becomes receptive. A technology with such capability is developing well.
What about costs? As mentioned, the practice of collecting orchard seed separately because of the "80-20" problem encourages every existing orchard program to make multiple seed mixes, a low-cost first application of the concept. Thus, advancing the female component toward the concepts goals is practical, but advancing the male component of the seed mix will pose cost problems if seed orchards are already established. Innovative approaches can minimize such costs, particularly when incorporated with orchard changes already programmed, such as when incorporating new parentage. Starting with new programs as we did, neither costs nor inconveniences were substantially different among the four orchards we established using the UNIFORM model and four on the same site using the CLINAL model, except the normal initial development time spent in planning new procedures (Silen and Wanek, 1986). Orchard layout costs may be slightly higher. But the largest potential new cost for most landowners is the need for a larger parental base.

What about inadequate parent numbers? Most geneticists would become uneasy with less than ten parents represented in any seed mix, and feel good with over a hundred. Any recommended number would be controversial, because what constitutes minimal parent numbers is still conjectural. The notion is widespread that something essential is accomplished from maximizing genetic variation by mixing large numbers of widely differing parent sources in seed orchards. In contrast, mature natural tree populations are highly structured, and, over centuries, genetic variation eventually becomes limited to adapted individuals. As a fire species, virgin Douglas-fir stands often originated from rather few, but adapted, old-growth parents. Deliberately expanding unstructured genetic variation in seed orchards dilutes essential structured variation. Considering the variation arising from windborne orchard plus stray outside pollen, an orchard seed mix from even ten parents could conceivably have a wider range of diluting genetic variation than was typical of natural stands.

At best, present tree improvement programs will rarely be able to advance more than par toward the goal of the 10-day criterion. Steep environmental gradients plus limited parent numbers and non-uniform distribution are initial problems. The suggestion that present orchards might combine seed of most local parentage into a mix for a specific planting site immediately surfaces a numbers problem. Such a mix may presently be forced to start with perhaps as few as 10 adapted parents. This is because the region's most common program usually begins with about two selections per square mile. If, after testing, as many as 1 in 5 are selected, this means one selected parent per 2.5 square miles, which calculates to a 25-square mile area, or 2/3 of a township, or roughly a 2 x 12.5-mile band as the typical minimal area. In other words, present parentage permits a resolution of localness that may be seldom less than half a township. This may be an acceptable resolution in some gentle topography of the region's forests. But, programs in droughty, mountainous topography need a more fine-grained resolution, a higher selection differential, and larger parent-tree bases. Campbell's classic study of precise adaptation in the Oregon Cascades (1978) leaves little doubt that such a mountainous area of about 2/3 of a township would need several seed mixes to meet the 10-day criterion. So the most likely application with presently operational programs is to expand to more than 10-days, despite productivity risks, until more parents are tested. The numbers problem may simply make some portions of present breeding units uneconomic, if genetic clines are too steep and complex.

One sees from such calculations the huge advantage other regions with gentle topography and summer rains have in minimizing this numbers problem.
Still, a doubling of the present parent numbers to improve parent distribution and to permit a resolution to an area of similar growing season embracing less than half a township may well meet the 10-day criterion for much of the region. One feature of the CLINAL model suggests that such a goal seems attainable at reasonable costs.

Expensive, long-term tests may not be needed to produce improved, but relatively local seed. Early testing readily identifies differences of family growth rates. Long term tests, while they also identify slow starters and sprinters, are most useful in identifying adaptation problems. If adaptation concerns approach zero, as they would be with the CLINAL model, a well-planned, low-cost nursery test has the prospect of rapidly expanding the base of local parents with superior growth rates. One kind of evidence already suggests that some form of early test may actually reveal most of the growth rate differences among families. In my experience with diallel or factorial matings the correlation grows successively lower each year between mean growth rates of wind-pollinated families versus means of multiple controlled pollinations of the same parent. The main source of this trend appears to be the increased environmental variation that develops in field plots over time to diffuse the relatively more stable inherent growth differences. Some risk associated with potential long-term inaccuracy for growth rate estimation is much more acceptable than inadequate numbers of parents and a general seed orchard risk of reduced productivity.

What about potential reduction in gain as the original parental population is divided into specific local seed mixes? Here the question boils down to viewpoints and tradeoffs. To illustrate, in calculating gain, a base of 100 proven parents for a breeding zone that embraces a 40-day difference in effective growing season is a typical situation for the region. Alternatively this population could become four local populations of 25 parents, each meeting the 10-day criterion. For either alternative, the parent tree's selection differential, based on the mean of the stand from which it was chosen, does not change. The theoretical selection differential for 100 parents is obviously higher than for 25, and the "genetic base" is obviously larger. But is the 100-tree population a truly "improved" population? Three quarters of the seed will tend toward "too early" or "too late" tails of a normal growing season distribution as they are planted at a particular site in the 40-day zone. Which choice would maximize biomass productivity if this were an agricultural crop? And which raises fewest long-term productivity and adaptation questions? Obviously multiple seed mixes from a parental population in an orchard make the estimation of gains in growth rate more involved. Instead of one gain figure for the whole orchard, the gain for each specific mix would need to be computed based on the parentage of that mix.

The best approach to solve both inbreeding and gain concerns is to avoid the questions by having a larger proven parental population. How much larger depends on the steepness of environmental gradients—probably no larger than now for extensive areas of gentle topography, and possibly uneconomically larger in the steepest gradients of the region. The amount of the gain in growth rate that is appropriate depends, ultimately, as in agriculture, on how much biomass growth improvement is provided by silvicultural enhancement of site productivity.

Future Breeding

The CLINAL model calls for conceptual changes in breeding strategy. Instead of crossing parents from anywhere in the breeding zone, crossings would
be made instead among best proven parents within each neighborhood or stand. This achieves the goal to improve only a few commercial traits like growth rate, while deliberately keeping genetic structure nearly intact for each local population. There is plenty of genetic variation in growth rate in each local population to make lucrative gains per generation. For example, a study of 600 wind-pollinated Douglas-fir families, each tested with 108 progeny and grown for 15 years on 12 sites in northwest Oregon, revealed that the mean tree volume of the selected top 20% of the families averaged 17% superior to the mean tree volume of the local stand from which the parent originated (Figure 16; Silen, 1985). These figures, which are measured gains, not predictions, appear typical of the 23 cooperative programs I have monitored. Thus, progeny of first generation crosses among local parents, at even such a modest selection differential as 1:5, should average well over 17% superiority in volume growth rate compared to the stand mean. Using only local stand variation, any reasonable goal of growth rate enhancement should be achievable in very few generations of breeding while still minimizing risk of lost productivity. I suspect that translating these individual-tree gains in growth rate into stand volume gains much greater than 20% may be difficult to sustain for a full rotation, since maintaining such gains will probably depend upon commensurate steady silvicultural site enhancement (FT 24).

Greater gains may also require acceptance of less hardy parentage and concerns about loss of genetic structure even with local parentage. Together, these constraints may set realistic upper limits on tree improvement in the Douglas-fir Region.

Footnote 24: This footnote covers many silvicultural assumptions of the paper. The concern that more than 20% enhancement of biomass may be difficult to maintain arises from these assumptions:

The basis for estimating gains in biomass yield of Douglas fir should be improvement over that of a natural stand on the same site. Presettlement stands arising from wildfires had average initial stocking levels over 1000 seedlings per acre; hence canopy closure on most sites occurred mainly before age 20, and usually remained almost complete the first century and beyond. Except during the stand regeneration period, competition from weed species was minimal, and productivity at a site approached maximum biomass values.

Silvicultural yield improvement beyond that basis must arise from the same components as in agriculture--irrigation, nutrient supplementation, weed and pest control. As for irrigation, there is little prospect of widespread irrigation of forests in a region where surface and ground water is already overcommitted to higher uses during summer drought. Benefits from nitrogenous fertilizers encounter a practical limitation. If their main effect is to

CONCLUSION

The dominant opportunity of the CLINAL model is the prospect of placing the Douglas-fir Region programs on as firm an adaptational basis for maximizing productivity as programs in other regions of the world. The dominant problem is acceptance in the Pacific Northwest. In mesic flatland forest regions of the world, there is little need to depart from the UNIFORM model. But the fact that one of the major components of increased yield in agriculture is adjusting maturation to growing season suggests that successful foresters everywhere will
want to match growing season ever more closely as our understanding of forest genetics matures.

In the xeric, mountainous western North America and particularly the Douglas-fir Region, the UNIFORM model becomes seriously flawed when we try to delimit breeding zones to a 10-day growing season span. Environmental and genetic variation is too complex. The proposal of the CLINAL model addresses this problem by making questionable seed movements unnecessary. At least one decade-long developmental trial shows the CLINAL model to be practical and cost-effective while addressing the potential of better yields by using more of the effective growing season.

Yet, there is great reluctance among northwest tree improvement personnel to even admit interest in the CLINAL model. The reluctance is understandable. They are being asked to alter long-held ideas like the concept of a uniform breeding zone and randomized single-population orchards, forgo potential gains in growth rate from racial variation, complicate all their calculations of genetic gains for orchards and programs, accept that seed movement beyond the 10-day criterion may be unnecessary to achieve appropriate gains, that local populations have an important genetic structure, that without it maladaptation will slowly become a serious yield problem, that seed orchards should be designed maplike to produce multiple seed mixes, that each seed mix should be specific for a planting site, and that gains can be large from parents in local populations. Acceptance of so many new concepts all at once is perhaps beyond reasonable expectations.

Despite advancing years, I still have the patience to let normal digestive processes take place. I expect to see a gradual replacement of the UNIFORM with the CLINAL model in the Douglas-fir Region.

Footnote 22/continued:
accelerate expansion of photosynthetic surfaces, there may be little benefit in already closed stands. Likewise, weed control is little needed in closed stands. During the regeneration period, however, nitrogenous fertilizers will surely speed canopy closure and shorten the period. Weed control then should provide young trees with more moisture to also shorten the period. But if gains are questionable during stand closure, and the regeneration period occupies only 1/5 to 1/3 of a rotation, even a 20% biomass gain for a rotation might require shortening the regeneration period to near zero.

If, instead, the silvicultural goal is to produce trees of a given size in the shortest time with repeated thinnings, then fertilizer, weed control, and genetically improved growth rate accelerate crown expansion appreciably shorten thinning cycles and the total required time. But with a constant reduced canopy density, biomass productivity would seemingly have to be constantly less than that of fully stocked natural stands. The potential biomass reduction of this goal needs to be assessed in any calculation of financial returns from silviculture and tree improvement.
FIGURES

FIGURE 1: The two models of tree improvement contrast conceptually in approach to clinal genetic variation. Along an environmental gradient with clinal genetic variation such as increasing elevation, the UNIFORM model delineates zones, like stairsteps, narrow enough to minimize genetic variation so that seed from an orchard is adapted within the zone. The CLINAL model tilts the UNIFORM model to an inclined plane conforming to the genetic cline. Seed for each planting site comes from a different band of parent trees that matches the local population. A gradient of increasing elevation is shown that would have clines of shortening phenological period, slowing growth rates, and increasing hardiness.

FIGURE 2 illustrates a simple negative feedback mechanism involving late spring and early fall frosts described in the text. The top line depicts a population (bell-shaped frequency-distribution curves for bud burst or hardening traits) evolved for a short growing season. All trees of the population burst buds sufficiently late and harden off early enough to avoid damage from early or late frosts, but many more trees produce biomass fewer days each season (shaded underutilized component) than for the adapted population shown in the second line. The third line depicts a population evolved for a long growing season. It produces more biomass those years having a long growing season, but virtually all the population is ultimately vulnerable to early or late frosts (cross-hatched frost-vulnerable component). The adapted natural population would also lose some vulnerable individuals to frost, but most would not be affected, and the surviving population would eventually outproduce the survivors in other two. Despite substantial expected differences in growth rate between such populations, the "law of constant final yield" predicts all three would produce biomass at the same rate, as shown. Analogous feedback mechanisms apply to drought and biotic factors.

FIGURE 3. The allocation of maize biomass among corn, stems, leaves, and floral parts is shown for a 15-generation study of maize (Johnson et al. 1985, and personal communication with senior author). Component figures are kilograms. By generation 15, selection and breeding had shortened stalks from 10 to 6 feet, and improved the proportion of total biomass allocated to corn to nearly double, mainly by reducing stem biomass by half. Leaf and floral biomass remained nearly constant. Genetic improvement in this exhaustive, long-term study also had no measurable effect on total biomass production, which remained at about 14 tons through the 15 generations. These results would appear to extend the "law of constant final yield" to genetic improvement.

FIGURE 3. Freeze-free days for the continental United States and Territories. The map dramatically highlights the contrast between eastern continental United States characterized by gentle growing-season changes and widely spaced 30-day isolines, and the West, characterized by extreme complexity of growing season. In eastern United States, large breeding zones are readily delineated that have less than a 10-day difference in growing season length desired for the UNIFORM model of tree improvement. Such uniformity is rarely found over extensive areas in the Douglas-fir Region west of the Cascade Mountains, necessitating proposal of a CLINAL model which avoids the problem of delineating a uniform zone by eliminating need for most seed movements. Note particularly the 300-day isoline which parallels the Pacific coastline for most of the map as an indicator of the unusual west-to-east orientation of the isolines in the Douglas-fir Region.
FIGURE 4. A graph illustrating the magnifying effect of elevational change on growing-season length. The five scales of the horizontal axis are approximately equivalent. Note that a rise of only 1200 feet in elevation is about equivalent to a 210-mile or 3 degree northward movement. The 1200-foot rise is also about equal to a month's shortening of the growing season, and about a 10% reduction of inherent volume growth rate of young Douglas-fir. Also, corn breeders could produce six varieties or races that could match growing seasons at 5-day intervals along latitudinal or elevational gradients. A maximum growing season mean mismatch of 10 days is proposed as the limit for Douglas-fir to avoid long-term biomass productivity losses.

FIGURE 6. A schematic display of Douglas-fir growing season variation as cold and drought intensify local environments. The annual potential for photosynthesis is shown as the area under a bell-shaped curve peaking at midsummer, with the period of biomass production in the freeze-free period shown increasingly shaded. An average freeze-free period is shown from April to October. Delay of growth initiation by cold can occur locally from persistent snow packs, from radiative cooling with increased "continentalness," and from cold air drainage of mountain masses. Biomass production is reduced or halted by summer drought usually from July until September. Drought period is locally intensified by rain shadows of mountains, by increasingly lower humidities with increased "continentalness" inland from the Pacific, and by thin soils. Areas having all constraints to growth would have free growth mainly in the two black portions. In mountainous terrain the interplay of such intensifying factors at a site makes estimates of growing season from weather data highly error-prone.

FIGURE 7. (From Emmingham and Waring, 1977) The authors display estimated potential carbon fixation (biomass productivity) for four sites in western Oregon they sampled with detailed measurements of incoming radiation (upper curves), air and soil temperature, and soil moisture. The lower curves (shaded for contrast) are estimates of actual photosynthate production at each site after drawdown of potential by cold and drought. Bottom graph samples a coastal site that produces record biomass. Photosynthate is produced there most of a 300-day freeze-free season, the major drawdown being from summer drought. At the Cascade Mountain site biomass is produced mainly in the summer, again greatly reduced by drought. In addition to this summer-drought drawdown, the two other areas sites have numerous and complex drawdowns from spring and fall frosts. Each of the four areas probably require a different complex pattern of within-season genetic controls over phenology and growth.

FIGURE 8. (From THE OREGONIAN, 1976). Precipitation for the Portland, Oregon area, 1976. The highly detailed precipitation map provides a glimpse of how complex and steep are environmental gradients in the Region when weather stations sampling is dense enough to display them. The map was prepared by Bonneville Power meteorologists from data largely provided by numerous amateur weathermen throughout the mapped area. Rainfall varied over 14 inches within the metropolitan area. Note the steep rain-shadow gradient of depressed rainfall west of Portland and along the west edge of the Willamette Valley, and an equally steep increasing rainfall gradient in the Cascade foothills on the east side. Growing-season drought varies in the same pattern. Detailed maps of genetic variation in growth show equally steep clinal gradients in the same areas on each side of the valley (Figures 11 and 12).
FIGURE 9. Dense sampling of parent trees is required to display the precision of fit between genetics and environment. Figures 10-14 are examples of the precision of fit illustrated with family growth data from dense sampling in various areas of the Douglas-fir Region. An almost template-like fit between inherent growth rate and topographic contours is seen in the map of the H. J. Andrews Experimental Forest, a small Cascade Range watershed with a 450-year-old stand. Campbell (1978) sampled about 9 trees per square mile for genetic variation in a common-garden study. His response-surface map, drawn from 3-year family heights, shows the close correspondence between the 71, 65, 60, and 55 cm. isoheight lines and respective 1500', 2600', 4000', and 5000' contours. Here the main environmental gradient is shortening of growing season with increased elevation, matched by inherently slower growth rates. (His figure was redrawn to emphasize four topographic contour lines.)

FIGURE 10. Data from commercial progeny tests (from Silen and Mandel, 1983) were used to produce maps of geographic genetic variation that reflects drought and cold effects on inherent height growth influenced by local topographic features. Shown are maps of two local cooperative areas in northwest Oregon with family isoheights contour lines drawn at intervals of 2 1/2 % differences in family heights at 10 years, which corresponds to about a 6% difference in volume. Parent trees were sampled at about two per square mile, and a response surface was used to smooth the isolines. Note the drought influence extending from the Willamette Valley to Vernornia in the Nehalem Valley and to Gates in the Santiam Valley, with faster growth rates upslope, often at ridgetops.

FIGURE 11 displays the reduction of inherent growth rates as summer drought is intensified in the rain shadow of the Coast Ranges on the northwest edge of the Willamette Valley. Inherent height growth rate decreases clinally eastward from about 1500 feet in the Coast Range toward the grasslands at the valley edge where wilting points are reached by mid-June, and slowest inherent growth rates occur. The map merges data from three separate local Cooperatives (Vernonia, Sunday Creek, and Dallas) after adjusting data to comparable means. Note similarities to the detailed rainfall map in FIGURE 4, particularly where this rain shadow extends northward into the headwaters of the Nehalem River.

FIGURE 12 displays coastal sections of four Cooperatives (Olympic, Tillamook, Mapleton, and Gold Beach). In each, a band of slow inherent growth occurs along the cool foggy coastline, with bands of average, then slower growth rates occurring farther inland. Within the average-growth bands, very rapid inherent growth occur at spots a few miles inland from the ocean probably with warmer environments.

FIGURE 13 is an example of the complex patterns of drought and cold gradients seen in breeding zones of the southern Cascade Range and Siskiyou Mountains. The Butte Falls and Prospect area southeast of Crater Lake has a distinctive conical extinct volcano, Round Mountain, bounded by Rogue River and Butte Creek. From the mountaintop to middle elevations, inherent growth rates increase in concentric bands as growing seasons lengthen; from mid-elevation downward inherent growth rates decrease toward the valley bottoms as droughtiness increases. In response to both drought and cold, slowest growth rates have developed in the frosty flat valley bottom south of Round Mountain and on the 20-mile-long Prospect Flat to the northeast.

FIGURE 14. An example of local stand structure of family mean heights typically seen in commercial progeny tests in the Progressive Tree Improvement
Program. The frequency of means at 0.2-meter intervals is shown for 15 stands of Douglas fir (numbers 1-15), each sampled with families of 25 parents in the Molalla Tree Improvement Cooperative (Silen and Mandel, 1983). The heavy dashed line is the curve appropriately scaled for all 15 stands. In the tests, the 25 family means from each stand are separately displayed as a bell-shaped curves that clusters most values near the stand mean. Stand means are often quite different even at the same elevation. The clearest example is the contrast between sets 14 and 15 (shaded), both of which are at 2200 feet elevation about 14 miles apart. Note the small overlap (crosshatched) representing the portion of each population with similar heights. In this Cooperative the fastest inherent growth rate occurs in low elevation stands in the north (stands 8, 9, and 10). As seen in Figure 11, the slowest inherent growth rate is found in low elevation stands 40 miles to the south, probably reflecting a more droughty environment (stands 1-5). Genetic structure of local stands is made up of hundreds of quantitative growth, form, and resistance traits that are differentially selected by environmental variation from one locale to the next. The small inset graph shows how tightly the entire 375-tree population of the 15 sets clusters near the mean 8-meter height.

FIGURE 15. The initial trial of the CLINAL model was at the J. E. Schroeder Seed Orchard in the Willamette Valley. The block shown was designed to produce a different seed mix for each 100-foot elevational change of planting site. The band of four rows in the foreground has families of parents from 1000-1100 foot elevation in the Cascade foothills seen in the distant background. The second band is from 1100-1200-foot parentage, and so on. The farthest band has 2400-2600-foot parentage. Such an orchard solves adaptation problems only for a large single sloping aspect. Most seed orchards serve breeding zones with complex topography, and a maple-like layout is proposed for them to provide seed for each planting site that is essentially local. The CLINAL concept evolved as three similarly-planned orchards were established at this site, owned by State of Oregon.

Figure 16: That highly heritable traits can change substantially per generation with intensive selection is illustrated with growth data. As parents of slower-growing wind pollinated families are culled from the population, the average volume of remaining trees of their families is increased substantially. The graph of average-tree volume over percent of retained families shows that removing half the poorer-growing parents raises family volumes of remaining average tree by 10%. When families of only the better 20% of the parents remain, the superiority over the population mean is 17%. Data is from 15th-year progeny measurements of 300 Douglas-fir wind-pollinated families allotted among 12 test sites in northwest Oregon, hence only displays genetic contribution of the female parent. Changes would be greater if both parents contributed. Phenological traits usually have higher heritabilities, and would respond even more rapidly per generation, than growth.
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Figure 1

UNIFORM

CLINAL

ELEVATION

PHENOLOGY

GROWTH RATE

HARDINESS
SCHEMATIC FEEDBACK

INITIATION (Bud burst)

“TOO SHORT”

BIOMASS

ADAPTED NATURAL STAND

BIOMASS

“TOO LONG”

BIOMASS

FREEZE-FREE PERIOD

late frost

early frost

CESSION (Hardening)

underproductive component

frost-vulnerable component
Figure 3
GROWING SEASON REDUCTIONS

Figure 6

- EFFECTIVE GROWING SEASON
- DROUGHT
- COLD
- FREEZE-FREE PERIOD
- SUMMER QUICHCENCE

POTENTIAL PHOTOSYNTHESIS

MONTHS: JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC

- EFFECTIVE GROWING SEASON
- DROUGHT
- COLD
- FREEZE-FREE PERIOD
- SUMMER QUICHCENCE
Fig. 5. The yearly pattern of photosynthesis at four sites in western Oregon. Potential values (●) assume no limitation by drought or by extremes in temperature; predicted values (○) include reductions from effects of drought and temperature.
GENETIC VARIATION IN HEIGHT GROWTH
H. J. ANDREWS EXPERIMENTAL FOREST

Fig 9
Figure 10

VERNOMIA COOPERATIVE

\[ \hat{y}_{1} = 4.09 \times 10^{-3} L + 1.91 \times 10^{-2} E^2 - 1882 \]

WHERE, \( \hat{y}_{1} \) = PREDICTED HEIGHT GROWTH BETWEEN 7 AND 10 YEARS IN CM.

\( \hat{y}_{2} \) = PREDICTED TOTAL HEIGHT AT 10 YEARS IN CM.

MOLALLA COOPERATIVE

\[ \hat{y}_{2} = 6.81 \times 10^{-4} L^2 + 5.35 \times 10^{-4} L E + 2.10 \times 10^{-2} E^2 + 4.40 \times 10^{-1} DE - 2.32 \times 10^{-1} D - 586 \]

L = PARENT LATITUDE IN KM (MILITARY GRID)
D = PARENT LONGITUDE IN KM (MILITARY GRID)
E = PARENT ELEVATION IN METERS
Figure 16

![Graph showing the relationship between percent selected and percent superiority in volume growth rate. The graph is a downward sloping curve indicating a negative correlation.]
MEAN LENGTH OF FREEZE-FREE PERIOD (Days) Between Last 32°F Temperature in Spring and First 32°F Temperature in Autumn

Legend:
- 100 days
- 200 days
- 300 days
- 400 days
- 500 days

Map shows the mean length of freeze-free period across the United States.