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GENETICS

of DOUGLAS-FIR



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This publication is one in a series on the genetics of important forest trees of North America being published by the Forest Service, U.S. Department of Agriculture, in cooperation with the Society of American Foresters. Development of this series is in accord with the resolutions of the World Consultation on Forest Genetics and Tree Improvement at Stockholm in 1963 and the Second World Consultation on Forest Tree Breeding at Washington, D.C., in 1969. The Committee on Forest Tree Improvement of the Society of American Foresters undertook the preparation of manuscripts for North American species.

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RESEARCH SUMMARY

Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) dominates the most productive forest lands of Western North America. More genetics research is being done on this species than on any of its associates. Tree improvement, however, has lagged because of technical problems for which solutions were only recently found.

Evolution of the genus is relatively recent, possibly originating from *Larix* which it closely resembles in morphology and floral mechanisms. The species existed north of its present range in recent geological times. Present distribution of the six species of *Pseudotsuga* around the north Pacific Rim places four species in Asia and two in North America. Only *P. menziesii* has a chromosome complement of $N = 13$ instead of $N = 12$. Only crosses between *P. menziesii* and *P. macrocarpa* have succeeded. *P. menziesii*'s latitudinal distribution from 19° to 55° N. is the most extensive of commercial western conifers. Most of its traits display clinal variation along its range, which resembles an inverted V. A variety, *glauca*, is recognized as applying to more continental races of the interior arm. Maximum development occurs along its coastal arm west of the Cascade Range and the Coast Ranges. The species occurs on almost any moist, well-drained forest habitat in its range below midalpine zones, yet it withstands droughts of several months. Its evolutionary niche as a fire species arises from its rapid growth, tallness, durable wood, thick bark, and long life, the last two traits being of minor breeding interest. Its rapid growth period is preceded by a decade of slow seedling growth. The older growth, soft, fine-grained wood production, is preceded by a long period of producing coarse-grained wood.

Douglas-fir is monoecious. It rarely flowers as early as 2 years and produces only small quantities of seed the first decade. Cone crops are usually cyclic, causing occasional severe local seed shortages. Nitrate fertilizers and gibberellins have been successfully used to enhance crops. Naturally harvested cones average about 16 filled seed but can range up to 54 filled seed on some trees. Only about 7-percent average selfing occurs despite the majority of pollen being received from the tree itself. Inbreeding coefficient is estimated at 0.025, leading to estimates of 1 to 1.5 percent inbreeding depression in seedling height.

Details of the life cycle of Douglas-fir have only recently become complete enough that the germinal line can be followed through pollen and seed development. Pollen is captured by a sea-anemone-like growth of the developing seed. The species is characterized by very large, round, featureless pollen grains with a mechanically strong intine layer permitting expansion longitudinally to the 500 micrometers needed to grow across a liquidless micropylar canal. No physiological or physical barriers to pollination are known, but embryo collapse following fertilization is common. One embryo per seed is normally produced, the competitive outcome of up to nine pollen grains per micropylar canal, four to six archegonia, and up to four cells that can contribute their chromosomes to the resulting embryo. Seedlings with chlorophyll-deficient recessive marker genes and yewlike mutations are reported. Polyploidy has been induced with colchicine.

The species grafts well initially, but about 35-percent rejection of grafts is normal. Early recognition of anatomical symptoms permits two kinds of evasion techniques so seed orchards may now be established virtually free of incompatible grafts. A high percentage of cuttings from year-old seedlings root, but success falls off to about 20 percent for 10- to 50-year-old trees. Cuttings of mature trees are usually rooted with great difficulty.

Genetic variation is documented for many traits. Exact adaptation to local environments is suggested from many studies showing growth, phenological, and terpene differences between nearby populations despite pollen exchange. Inherent growth differences appear to follow a westwide pattern of relative assurance of adequate springtime moisture. The best inherent growth has evolved in the western and northern parts of Douglas-fir's range and the poorest in the eastern and southern parts. Growth ratios between families within local populations can exceed 2:1, providing impetus for practical improvement of already adapted genotypes. Growth traits require one or more decades for adequate expression. Heritabilities of growth and form have been generally moderate and heritabilities of phenology, resistances, and wood traits generally strong.

Practical programs include seed orchards, wide crossings, wind-pollinated seed, and clonal

emphasis. Practically all programs in the Douglas-fir region use locally adapted parentage. Programs in other temperate forest regions involve search for adapted races. Earlier seed orchard problems are now largely alleviated. A graftless concept, based on tests of large numbers of parents with wind-pollinated seed, is widely used in the Douglas-fir region. Second-

generation programs for full-sib crosses are established at several seedling orchards. Variations of the commonly used technologies have developed especially for Douglas-fir. Special strategies have also been developed to maximize efficiencies, to utilize within-stand or racial variation, and to minimize losses from maladaptation.

GENETICS OF DOUGLAS-FIR

Roy R. Silen¹

INTRODUCTION

In the natural forest, Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) is a remarkably successful species. It vies with coastal redwood for height supremacy among the world's conifers. In the droughty, fire-prone natural environment of Western North America, it has dominated the better sites, often relegating its associates, most of which are the best in their genus, to ecological niches too wet, dry, cold, hot, exposed, or shaded for Douglas-fir. Douglas-fir's latitudinal range is the greatest of any commercial conifer of Western North America. The success of this species suggests an ample, complex gene pool from which natural selection has produced populations competitive and adapted for each locality in its vast range.

In the managed forest, Douglas-fir is preferred for its good growth and relative freedom from major pests (fig. 1). Its nearly pure continuous stands on the moist Pacific slopes from British Columbia to California—the so-called Douglas-fir region—dominate the forestry of Western North America. In its drier interior range it is rapidly gaining in commercial importance. Its use is expanding as an introduced tree for temperate zones of both hemispheres, where appropriate races typically outgrow the native conifers (Silen 1962a). Yet, it is sometimes difficult to regenerate after harvest on the best sites it once held. Wood of fast-growing young Douglas-fir trees is strong and durable but dense and coarse grained and less workable than the soft, fine-grained old growth for which people have found more uses than any other tree.

Genetically, its haploid chromosome complement of 13 instead of the basic 12 of the

Pinaceae is interesting. The problems of grafting incompatibility, pollen contamination, difficult rooting, and inadequate cone production of Douglas-fir delayed large scale improvement programs until recent research found ways to avoid them.

Geneticists must be knowledgeable of the natural role of the genetic variability they discard as well as that small portion of variability they now select to fulfill immediate needs. Thus, their general understanding of the species in nature is fully as important as a knowledge of its genetics.



Figure 1.—An old-growth Douglas-fir tree. This record tree found near Coos Bay, Oreg., was 13 feet in diameter and 302 feet tall. It blew down in 1975 (photo courtesy Bureau of Land Management, Coos Bay District).

¹ Principal plant geneticist, Forest Service, U.S. Department of Agriculture, Pacific Northwest Forest and Range Experiment Station, Forestry Sciences Laboratory, Corvallis, Oreg.

THE GENUS

TAXONOMY

The genus includes two North American species (*Pseudotsuga menziesii* and *P. macrocarpa*) (Little 1953), and three to five (Peoples Republic of China 1972) Asiatic species (*P. japonica*, *P. wilsoniana*, *P. sinensis*, *P. forestii*, and *P. gaussenii*—the last three sometimes considered a single species). Nine additional species proposed for the *Pseudotsuga* of interior North America (Flous 1935, Martinez 1963) have had little support from other taxonomists (Little 1952, Tusko 1963).

The genus is distinguished by woody cones with persistent scales and protruding, trident-like bracts; by spindle-shaped, pointed buds resembling those of beech; by firlike or yewlike narrow leaves soft to the touch; by larchlike winged seed; and by resin blisters on smooth bark that becomes furrowed and marbled with cork layers as it develops. The pollination mechanism and round pollen grains closely resemble *Larix* (Christiansen 1972). Its intolerance to shade, fire-resistant marbled bark, wood anatomy, and the appearance of its seedlings, seeds, and cones are also strikingly similar to larch—enough to suggest that the genus *Larix* has contributed most to its origin, if not its direct ancestry.

Vegetative portions of adult trees of the two American species of *Pseudotsuga* are similar. Douglas-fir cones average 2 to 5 inches (5-13 cm) in length. Botanical distinction of *P. macrocarpa* is based on the 3½- to 6½-inch (9- to 13-cm) cones, the largest in the genus. The germinants of *P. macrocarpa* are likewise much larger and have 10 to 15 cotyledons compared with the 4 to 11 cotyledons typical of *P. menziesii*. Maps of the ranges of the two species show no overlap, nor is there any evidence of gene exchange from studies of terpene composition (Zavarin and Snajberk 1976).

For *P. menziesii* the variety *glauca* (Little 1953), or alternatively, the subspecies *gaussenii* (Tusko 1963), of the interior West is recognized botanically as distinct from *P. menziesii*, the typical coastal Douglas-fir. Little lists all other interior *Pseudotsuga* described for North America as synonyms of variety *P. glauca*. The clinical nature of both morphological and chemical traits over the range of Douglas-fir and the variability of types in a locality (Schober 1963) still raise doubts about the logic of varieties or subspecies within the species. A taxonomic

separation of coastal and interior types will probably be long maintained for botanical convenience, and the status of possible varieties in Mexico is unsettled.

CYTOLOGY

Support for classifying the genus into at least six species was provided when distinctive karyotypes were shown for each species (Doerksen and Ching 1972).

Karyotypic investigations of the genus show Douglas-fir with $2N=26$ chromosomes (Sax and Sax 1933) to be a striking exception in the Pinaceae to the basic $2N=24$ diploid chromosome complement. Both its coastal and Rocky Mountain races have similar karyotype (Livingston 1971, DeVescovi and Sziklai 1975). Other members of the genus, including *P. macrocarpa*, have $2N=24$ complement (Christiansen 1963, Doerksen and Ching 1972). The karyotype of Douglas-fir includes 2 chromosomes strikingly dissimilar to the other 11 in that they appear to have terminal centromeres. Such telocentric chromosomes have not been observed in other species of *Pseudotsuga*; this suggests that the two somehow originated from a 12th metacentric chromosome. The telocentric chromosomes provide a potentially sensitive but still unsuccessful means for verifying putative hybrids with Douglas-fir. Existence of chromosomal aberrations (Owens 1967) and a trisomic ($2N+1$) chimera (Ching and Doerksen 1971) has been shown for Douglas-fir. Polyploid seedlings of slow growth with thick cotyledons were produced with colchicine in our laboratory, but they did not live beyond the first year.

ANCESTRAL DISTRIBUTION

Origin of Douglas-fir appears geologically recent. Even for the genus, the oldest known fossil remains date to the early Tertiary period only 50 million years ago. Morphological characteristics of the genus have changed little. Cones, seeds, and needles of the modern *Pseudotsuga* can hardly be distinguished from those of its ancestors. Thus, we lack a record of most of the evolution of the genus *Pseudotsuga* as well as clues to its geographic center of origin.

All available evidence indicates that ancestral North American *Pseudotsuga* was represented

through much of the present range of Douglas-fir, but the range then extended considerably farther north. *P. sonomensis* Dorf., predecessor of *P. menziesii*, however, seems to have been an insignificant component of Tertiary forests. Two lines of evidence indicate this: Megafossil remains of the genus are noticeably scarce in Tertiary floras, and pollen of the genus is not abundant in any pre-Pleistocene pollen assemblage known so far (Wolfe 1969).

In contrast to its scarcity in the Tertiary period, *Pseudotsuga* is often abundantly represented in Quaternary megafossil and microfossil assemblages, especially in the second half of the Pleistocene Epoch. This contrast would indicate that dominance of Douglas-fir in the present conifer forest of the Northwest was attained during middle or late Pleistocene. It may very well have been the time when the modern *P. menziesii* with a chromosome complement of $N=13$ evolved. The cyclic climatic changes during the Pleistocene and the ensuing migrations may have favored evolution of a new species.

Mid-Pliocene marks the first and only time that *P. premacrocarpa*, the predecessor of modern *P. macrocarpa*, appears in the Tertiary fossil record (Axelrod 1937). The character

of the accompanying flora was as distinct from that of floras containing *P. sonomensis* as is the modern forest in which *P. macrocarpa* lives from the modern communities of which *P. menziesii* is a member. This suggests that big-cone Douglas-fir in Pliocene already had a fairly restricted range.

Fossil remnants of Asian members of the genus *Pseudotsuga* have been found in Pliocene deposits of Japan (Miki 1957). Of the three fossil species distinguished, two, *P. subrotunda* and *P. gondylocarpa*, apparently became extinct during Pleistocene. The third species, ancient *P. japonica*, appears to have been almost identical in appearance to modern Japanese Douglas-fir.

The fossil record of *Pseudotsuga* in Europe is scant. Kräusel (1926) has attributed fossil wood in Miocene beds of Silesia and Styria as belonging to the genus *Pseudotsuga*. Zalewska (1961) has described cones and leaves of *Pseudotsuga* from Miocene deposits in western Poland.

The fossil record furnishes little information on the relationship between Asiatic and American members of the genus. Migration of coastal and interior types of Douglas-fir since the last ice age is discussed by Tusko (1963).

THE SPECIES IN NATURE

PRESENT DISTRIBUTION

Douglas-fir has the most extensive latitudinal range of any North American commercial conifer, from 19° to 55° N. latitude. On a map of Western North America, its range resembles an inverted V, the shorter arm extends southward from its northern limits in British Columbia to the west along the Pacific slope into California and the longer arm extends southeastward along the Rockies into Mexico. On the Pacific slopes west of the Cascade Range or Coast Ranges, continuous stands of Douglas-fir occur from their northern limit on Vancouver Island through western Washington, Oregon, and northern California in what is called the Douglas-fir region. Elevations range up to 2,500 feet (762.5 m) in the north and to 5,500 feet (1 677.5 m) in the south. Here, the species attains full development, with mature low and middle elevation stands often exceeding 200 feet (61 m) in height.

East of the Cascade and Sierra Ranges, and through the Rocky Mountains where the trees are usually under 100 feet (30.5 m) in height,

the species grows to elevations of 11,000 feet (3 355 m). These trees are often in a zone above the ponderosa pine zone and below the Engelmann spruce-subalpine fir zone, usually in mixture with coniferous associates. At the southern limit of its range, Douglas-fir is confined to north slopes and shaded areas, but at high elevations or northerly latitudes it occupies southerly aspects. Its eastern range terminates in Alberta, Montana, Wyoming, Colorado, and New Mexico. It occurs spottily southward through most of Mexico in high elevation forests. Douglas-fir grows to a markedly higher elevation in the Rocky Mountains than at the corresponding latitude on the coast. For example, at 45° N. latitude, it occurs up to about 4,000 feet (1 220 m) in the Coast Ranges and up to 8,000 feet (2 440 m) in the Rockies. Whether this is a genetic adaptation or whether it reflects climatic difference is unclear.

The detailed map of its natural range shown in figure 2 is from "Atlas of United States Trees" (Little 1971). Corrections have been

made for British Columbia, California, Arizona, New Mexico, and Mexico from advice of local authorities.²

HABITAT

Habitats of the species in Western North America are so extensive that it is more convenient to describe their limitations. Douglas-fir is adapted to almost any moist, well-drained forest habitat below midalpine zones. Its lack of occurrence is usually explained by one of its relatively few limitations (Waring 1970) or by stand history. It gives way to more cold-tolerant mountain hemlock (*Tsuga heterophylla* [Raf.] Sarg.), subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.), Engelmann spruce (*Picea engelmannii* Parry), western white pine (*Pinus monticola* Dougl.), and lodgepole pine (*P. contorta* Dougl.) at high elevations or northerly latitudes. It yields to more drought-tolerant ponderosa pine (*P. ponderosa* Laws.) and various oaks on sites below about 25 inches (63 cm) of annual rainfall and to western redcedar (*Thuja plicata* Donn), maples, alders, cottonwood, and other broadleaves on poorly drained sites. Sitka spruce (*Picea sitchensis* [Bong.] Carr.) and western hemlock predominate in the cool fog belt associated with tidal zones of the Pacific Ocean. Douglas-fir shows little tolerance for wet soils, and its anaerobic respiration system appears normally weak or inactive (Conkle 1974). As a seedling, it competes poorly with sod grasses or with overtopping broadleaves, such as red alder, which has replaced it on several million acres of the most fertile logged-over coastal sites.

Natural occurrence of Douglas-fir is mainly determined by fire. Its thick, fire-resistant, corky bark, rapid growth, and long lifespan are the main adaptations that have assured seral supremacy in a region of dry summers with catastrophic natural forest fires. On the Pacific slopes, essentially pure stands resulted from crown fires that destroyed its associates, almost all of which are thin barked, and left a seed source of pure Douglas-fir. Lesser fires resulted in a Douglas-fir overstory with a mixed even-aged Douglas-fir and western hemlock understory. Here, the species does not usually reproduce a new stand in its own shade. Except in its youth when it is reasonably shade tolerant, Douglas-fir tolerance ranks between ponderosa pine and western hemlock (Isaac 1943). In its interior range, Douglas-fir ranks intermediate in tolerance among its associates; and lodgepole pine is often the more successful fire species. Without fire, even-aged stands are gradually replaced over several centuries with more shade-tolerant western hemlocks, silver

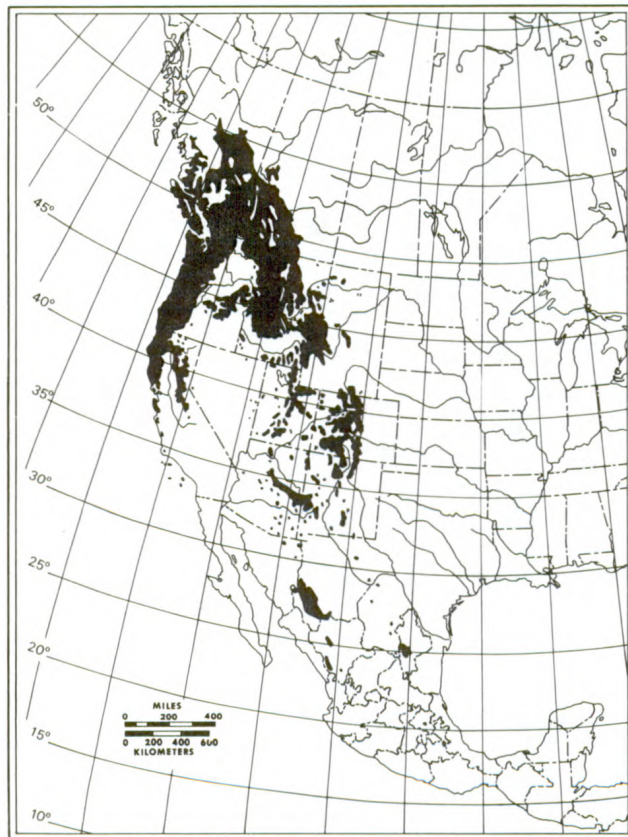


Figure 2.—Natural range of Douglas-fir.

According to 1972 compilations of R. K. Hermann, Oregon State University, Corvallis, over half a million acres of Douglas-fir forests exist in 26 countries in Europe. There are plantations in France—250,000 acres (106 000 ha), in Great Britain—116,000 acres (47 000 ha), and in Germany—110,000 acres (45 000 ha). In the southern hemisphere, New Zealand has planted 65,500 acres (26 500 ha), Australia 2,100 acres (850 ha), and Chile 5,000 acres (2 000 ha).

² R. Schmidt, British Columbia Forest Service; P. Haddock, University of British Columbia; W. Critchfield, Pacific Southwest Forest and Range Experiment Station; R. Ryker, Intermountain Forest and Range Experiment Station; M. Haysworth, Rocky Mountain Forest and Range Experiment Station; and J. Franklin, Pacific Northwest Forest and Range Experiment Station.

fir (*Abies amabilis* [Dougl.] Forbes), or grand fir (*A. grandis* [Dougl.] Lindl.), and western redcedar, although individual Douglas-firs may live over 1,300 years (McArdle and others 1961) to assure a high chance of species survival on a site.

GROWTH

Rotations of 50 to 100 years will use but a small fraction of the species' potential lifespan (1,325 years), reported height (385 ft or 126 m), diameter (15.5 or 5.1 m) (Isaac and Dimock 1965), or wood quality potential. The high growth rates, for which the species is prized, come after a period of slow growth as seedlings; 7 to 11 years are required for natural regenerating stands to surpass breast height (McArdle and others 1961).

Slow early growth in natural or nursery environments probably reflects environmental constraints. Seedlings can be grown to 2 feet (61 cm) in height in 2 years under optimum nursery conditions. When constraints were artificially removed, 8-foot-tall (2.4-m) seedlings were grown in 2 years (Copes and others 1969).

Beyond seedling stage, annual height growth can surpass 6 feet (2 m). An average of over 2 feet (61 cm) can be sustained for the next century on best sites, with periodic annual increment of about 200 cubic feet per acre (14 m³/ha). Best yields of Douglas-fir's native range, where summer droughts are common, appear to be exceeded in countries such as New Zealand (Spurr 1961), where climates are warmer at corresponding latitudes and summer rainfall is likely to be more adequate. For average coastal sites, corresponding annual height and yield figures are 1.4 feet (43 cm) and 140 cubic feet per acre (10 m³/ha) (McArdle and others 1961). Young managed stands can produce about 30 percent more volume than unmanaged stands (Curtis and others 1973). Old-growth coastal stands of 390,000 board feet per acre (5 456 m³/ha) have been recorded (Worthington 1958), and volumes of over 100,000 board feet per acre (1 400 m³/ha) are not unusual. Growth drops markedly on poorer sites. Over the interior range of Douglas-fir, heights seldom exceed 160 feet (49 m) or volumes more than 60,000 board feet per acre (840 m³/ha) (Buell 1965).

GENETICS

CROSSABILITY

The North American *Pseudotsuga macrocarpa* was hybridized with *P. menziesii* (Ching 1959). Despite many trials, particularly by Orr-Ewing (British Columbia Forest Service) who has all species of *Pseudotsuga* as flowering arboretum trees, no successful cross has been made between the Douglas-fir and Asiatic *Pseudotsuga*. Although differences in chromosome number is suspect in lack of success, this would not apply to crosses using *P. macrocarpa* as pollen. Simpler causes may be involved. Sectioned micropylar canals revealed that *P. wilsoniana* pollen expanded longitudinally only about 200 micrometers, a distance usually insufficient to contact the nucellar tissue. No barriers to racial crosses of *P. menziesii* are reported.

GENETIC MARKERS

A number of genetic markers have been discovered, and one has been found to be of prac-

tical use. The recessive gene for white cotyledons, which can be conveniently observed in dissected homozygous seed, was discovered in two unrelated trees (Sorensen 1971). Cuttings from these trees are now vegetatively propagated in several seed orchards to monitor the proportion of stray-to-orchard tree pollen and self-to-neighbor tree pollen.

The proportion of various marker types found in a study of 28 trees was estimated at 53-percent yellow foliage, 14-percent white cotyledons, 25-percent nonwhite cotyledonary lethals, 4-percent virescents, and 4-percent dwarfs. Most have been found to segregate as single gene recessive (Sorensen 1973). Piesch and Stettler (1971) reported additional mutant types that they identified as mottled and curly, the segregation ratios conformed to 9:7 and 15:1, and the expected ratios of pairs of genes showed different degrees of epistasis. In addition, dwarfing genes have been reported from inbreeding of S₁ generation parents, but segrega-

tion ratios obtained subsequently suggest a more complex inheritance (Orr-Ewing 1974).

REPRODUCTIVE DEVELOPMENT

Sufficient life cycle information to permit the geneticist to follow the germinal line has only recently been published (Allen and Owens 1972).

Floral bud structure and development following initiation closely resemble *Larix*. Douglas-fir normally produces male and female strobili on the same twig (fig. 3). Females are subterminal; males usually occur on the basal two-thirds of outer twigs and over the full length of interior twigs, although intermingling does rarely occur.



Figure 3.—A Douglas-fir twig with megasporangiate and microsporangiate strobili at pollination stage.

The reproductive cycle of Douglas-fir for Victoria, B.C., is diagrammed in figure 4 (from

Owens 1973). Floral buds arise in April on low elevational trees from cells in axils of embryonic leaves (Owens and Smith 1964). The vegetative shoot develops within the bud for about 6 weeks before the bud bursts, at which time embryonic buds are detected with a hand lens (Silen 1967a). Floral buds cannot be distinguished from vegetative buds visually or histochemically until mid-May, about 10 weeks after onset of growth (Owens 1969). However, male and female bud numbers are correlated well enough that a profusion of basal buds seen with a hand lens in April provides the earliest practical indicator of a possible cone crop 17 months later (Silen 1967a).

Floral buds continue to enlarge as they gradually differentiate from early July through November. Dissection permits certain identification by September. By November, the larger size and non-waxy bud scales permit easy external distinction from the wax-covered vegetative buds. Overwintering seedcone buds contain visually recognizable trident bracts and scales with embryonic seed (Allen 1942a, Allen and Owens 1972).

Floral buds burst in April, over a month ahead of vegetative flush, the females quickly becoming upright and the males pendant. Color variation from deep red to light green is a strongly inherited trait (Tusko 1963, Ching and others 1966, Copes 1972). Floral and vegetative bud burst is poorly correlated for individual trees (Griffith 1968, Sorensen and Campbell 1971). Female strobili have been found to be already receptive to pollen at bud burst and to continue so until they begin to turn downward, a 20-day period. This surprisingly long receptive period provides opportunity for a tree to receive pollen from trees over a considerable elevational range in mountainous topography, which enhances Douglas-fir's potential adaptation over a greater range of sites (Silen 1967c).

Pollen dispersal follows a J-shaped distribution of frequency with distance from source. The majority of pollen from a tree falls within 400 feet (122 m) (Wright 1952), but this is accompanied by a high level of background pollen over the Douglas-fir region in good pollen years (Silen 1962b). Enough pollen is shed even in short drying periods (Ebell and Schmidt 1964) that adequate seed set is accomplished despite prolonged rainy periods (Silen and Krueger 1962).

Pollination at low elevations occurs in mid-April and advances upslope about 77 feet (23 m) per day (Silen 1963). Anthesis and recep-

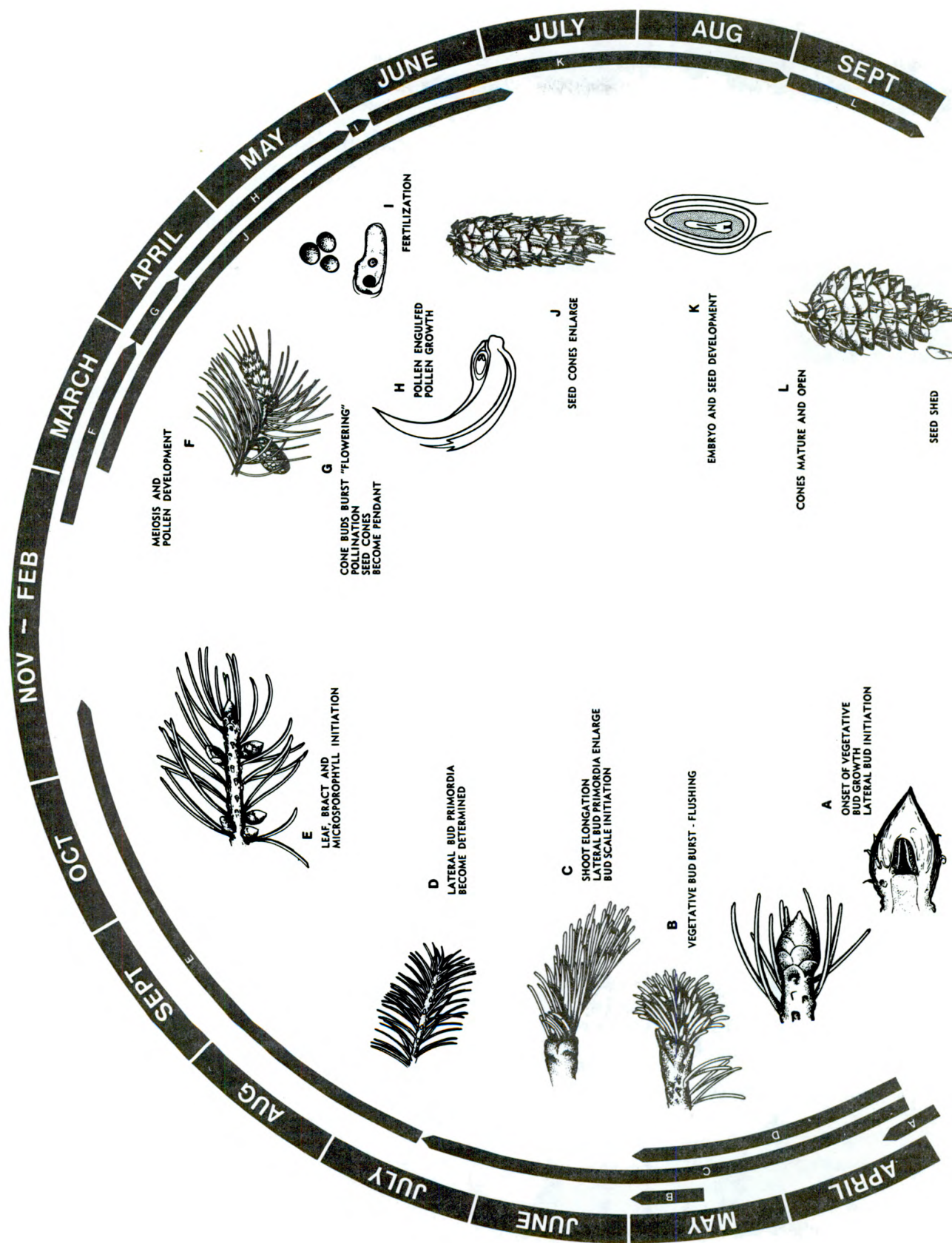


Figure 4.—The reproductive cycle of Douglas-fir extends over 17 months. Letters A and L represent various stages and a brief description of these stages. The approximate time each stage occupies in the reproductive cycle is represented by an arrow. (Reproduced from Owens (1973), with permission.)

tivity normally occur together, events that are sensitive to cumulative temperatures (Silen and Keane 1969, Campbell 1974).

Although one-fourth to three-fourths of the pollen catch is a tree's own pollen, only about 7-percent self-pollinated seedlings occur in an average seed lot, which leads to an average inbreeding depression of 1.5–2.0 percent in 1st-year seedlings (Orr-Ewing 1954, Sorensen 1973). About one-third of the trees produce less than 2-percent selfed seed and rarely do more than 20-percent filled seed originate from self pollen (Sorensen 1973, Sorensen and Miles 1974). About a third of the conelets ultimately abort (Griffith 1968). About 16 percent (range 0–49 percent based on a 12-tree sample) of the normal-size seed halt embryo development and appear as flattened seed.

Bracts are arranged to capture and carry pollen efficiently to stigmatic areas. Pollen grains falling on the stigmatic surface are curled inward into the micropylar canal by a sea-anemone-like movement caused by differential growth of the stigmatic area (Barner and Christiansen 1962, Allen and Owens 1972). The large round pollen grain (90–100 micrometers) has a thick, smooth exine layer that breaks on imbibition to expose a mechanically strong plastic intine layer. Before producing a pollen tube, the grain swells to about 500 micrometers longitudinally, but only a small amount in cross section to bridge the space in the micropylar canal between the stigmatic end and the nucellar cap. A rigid pollen grain is essential because the micropylar canal is dry rather than liquid-filled as in *Pinus*. Up to nine pollen grains (average 1.8, basis 343 wind-pollinated seed) may elongate within a micropylar canal.

Male gametophytes develop through the normal sequence of cell divisions, mostly prior to pollen release, to produce a five-cell structure (Allen and Owens 1972). Male gametes are released after the swelled grain contacts the nucellus. Only then is a pollen tube formed which dissolves its way through the nucellar tissue to one of four-to-six archegonia. Several embryos may develop per seed after fertilization in June, but mature seed with double or triple embryos are uncommon. Unusual features for Douglas-fir are the brief opportunity for intermingling or possibly even pairing of homologous chromosomes during syngamy and the absence of cleavage polyembryony which permits from any one of up-to-four cells of the free nucleate state to contribute genes to the resulting embryo

(Allen and Owens 1972). No abnormality is apparent in pollen growth, fertilization, and early embryo development from self pollination, but most such embryos collapse within a few weeks, probably because of increased homozygosity of deleterious recessive genes (Orr-Ewing 1956, 1957a).

Because of numerous pollen grains per micropylar canal—four-to-six archegonia—and at least three patterns of embryo development from the free-nucleate stage embryos, the opportunity for both gamete selection and genetic diversity in the development of a single seed is apparent. This poses potential complexities for breeding.

Flowering

Douglas-fir ordinarily retains its juvenile, nonflowering condition from 5 to 12 years (Allen 1942b); however, flowering in the second year has been observed (Oregon State University 1974). Flowering before age 15 is light and markedly favors female production, a factor of some consequence in planning for adequate early pollination in seedling seed orchards. Attempts at stimulating precocious flowering by doubling the yearly growth cycle (Ching and Lavender 1970) or applying fertilizer (Allen 1963) have not been successful, but applications of hormones have been successful (Pharis 1974). The inheritance of flowering tendencies appears strong as evidenced by consistently poor or good early production from progeny when both types of parents were systematically crossed at the Dennie Ahl Seed Orchard. Flowering of 5-year-old seedlings among crosses in a 6 × 6 diallel mating at our laboratory provided a family heritability estimate of 0.68.

Cone crop differences arise from a combination of many causes. The most important causes are variation in numbers of primordial floral buds or their subsequent losses, induced latency of immature buds, overwinter killing of developed buds, freezing of conelets, and insect attacks on seeds and cones. Average number of buds initiated per shoot is quite consistent from tree to tree (Griffith 1968), from year to year (Owens 1969), and between elevations (Silen 1967c). Climatic events of the previous year appear to affect number of floral buds that develop (Lowry 1966, van Vredenburg and La-Bastide 1969, Silen 1973a, Eis 1973). Effects of 1 year's heavy production can carry over to depress the next crop (Owens 1969) and reduce growth of shoots (Puritch 1972) and roots (Rook and Sweet 1971). Conversely, removal of

a crop of female buds enhances cone production the next year (Silen and Copes 1972). Number of floral buds that develop may be greatly influenced by lifting, girdling, shading, debudding, defoliating, and fertilizing trees from a few weeks to 15 months before buds begin to differentiate (Ebell 1971; Silen 1967c, 1973b; Stoate and others 1962; Pharis 1974, 1976). Most of these treatments appear to increase or decrease the proportion of immature buds that become latent rather than to initiate new bud primordia. Such treatments are often most effective when applied at onset of spring growth.

The physiology involved with varying proportions of floral buds to vegetative buds is still obscure. The relatively less polar gibberellins, particularly combinations of GA4, GA7, and GA9, have enhanced floral bud number, especially in combination with auxin. Four-year-old seedlings as well as mature grafts have responded to treatment, with evidence of differential male and female effects (Pharis 1974, Ross and Pharis 1976). The switching between floral and vegetative stage is usually complete, except for rare poliferated cones that show various combinations of female, male, and vegetative sectors. Even here the line between sectors is sharp, sometimes resulting in a single scale with pollen and seed on opposite sides. Switching between sets of developmental genes has been suggested as an underlying mechanism (Silen 1973a).

Successful enhancement of cone crops is presently limited to the practices of providing sunny, somewhat droughty locations for seed orchards, removing competing vegetation, and applying nitrate fertilizers in early spring (Steinbrenner and others 1960, Sloate and others 1962, Allen 1963). Drought stress, girdling (Ebell 1967, 1971), and tree lifting (Silen 1973b) have also increased cone production and are used for special genetic purposes. Gibberellins and auxins are already used to enhance flowering and permit earlier cross pollinations, but technologies for large-scale use are still to be developed. A typical response of all such practices has been to multiply the number of cones produced. Greatest increases usually occur with large crops or on prolific trees. Small effects or no effects are usually experienced with small crops or on poor flowering trees (Silen and Copes 1972).

Seed

Seed ripens from late August at low elevations to late October at high elevations. Natural

shedding takes place over several months as cone scales open successively wider after each wetting (Allen and Owens 1972). An average of one viable seed per cone remains unshed as late as March. Unlike pines, cones develop without pollination to produce normal size but empty seed. Even as late as mid-July before gametophytes collapse, the unpollinated seed appears full, leading to possible overestimates of seed yields from early cone crop surveys. Distribution of nutrients and photosynthate during cone development has been extensively studied (Ching and Ching 1962). Cones harvested and dried more than 20 days before maturity produce seed of substantially reduced germination, a major cause of light seed and weak seedlings (Olson and Silen 1975). Artificial ripening of seed in cool, moist storage is, however, possible up to 30 days before maturity (Silen 1958). Seed removed from green cones up to a month before seedfall will germinate (Ching and Ching 1962). Normal seedlings up to 10.4 inches (26 cm) tall have been grown from such immature seed before winter in our laboratory as a potential way of gaining a season's growth.

Wind-pollinated seed of most parent trees germinated at time of seedfall show no dormancy. Dry, stored seed of some parents continue to be nondormant, but the germination rate of others drops off rapidly.

Seed crops are irregular (Garman 1951); nonetheless, seed is produced on some trees in most localities each year. Some trees produce cones nearly every year, others remain barren for long intervals. Cones are produced on sunlit branches, more are found on southerly quadrants of the crown (Winjum and Johnson 1962). Good crops are seldom spaced more than 3 years apart in low elevation, dry, sunny areas like the Willamette Valley; however, severe seed shortages occur from less frequent good crops over large portions of Douglas-fir's range. As many as 10 years may pass without a good cone crop in some high elevation stands. This irregularity of crops can seriously lengthen tree improvement programs and has contributed to disgenic use of the more plentiful low elevation seed at higher elevations.

Yields vary greatly by crop, age of tree, and cone size (Garman 1951, Kozak and others 1963). Yao (1971) reported that seed weight decreases with latitude. Willis and Hofmann (1915) observed that younger trees produce larger cones having larger, heavier seed than older trees, with similar yields of about one-half pound per bushel in a good crop year. Av-

erage yields were 16 seeds per cone and 1,000 cones per bushel. From our own observations of 697 trees in the Oregon and Washington Cascades, we recorded an average of 17.3 seeds per cone from collections covering three seasons, with a maximum of 52.5 for the best yielding tree. Filled-seed yields of 309 trees harvested at Vernonia, Oreg., in the bumper crop of 1966 averaged 25.6 seeds; filled seed on individual trees ranged from 7.2 to 53.7. Corresponding seed yields were experienced in New Zealand (Sweet and Bollman 1972), but lower yields were reported in Europe (Otto and Kleinschmit 1975). Artificial pollination can more than double average yields, although occasional trees produce few filled seed.

VARIATION

Survival

Survival through a rotation becomes a major consideration when Douglas-fir ecotypes are moved to an environment where they are unadapted. Incentive for faster growth is strong to use ecotypes with genes that have developed in more mesic and temperate sites than the local source. Losses have been dramatic where seed movements have obviously exceeded the genetic amplitude of the ecotype. Killing of coastal sources by deep cold in eastern Europe (Schober 1963) or in the Eastern United States (Baldwin and Murphy 1956, Wright and others 1971) are classic examples. In Europe, and lately in New Zealand (Wilcox 1974), the common outcome has been a slow decimation by diseases native to the Douglas-fir range, or by frost.

Within the species range, similar but less dramatic examples have been numerous. Coastal Douglas-fir planted in the interior of its range is eventually killed by unseasonal low temperatures. Conversely, plantings of interior sources west of the Cascades (Silen and Woike 1959, Silen 1962c, Haddock and others 1967) have gradually failed over several decades, primarily from endemic needle diseases of little consequence to local trees.

Within the Douglas-fir region, similar survival problems have been associated with seed movement but have developed over a longer time span than most genetic studies. Several large commercial plantations established in western Oregon and Washington before 1920 appeared thrifty for decades but now exhibit obvious survival problems. Practically all are from coastal but nonlocal seed. All five experimental plantations of the Douglas-fir Heredity

Study planted in 1913 and still maintained by the Forestry Sciences Laboratory, Corvallis, Oreg., have several of the 13 races obviously failing. The study sources and plantations are localized to western Oregon and Washington.

Initial survival of trees on all five sites was over 90 percent. Survival of trees by age 17 was still generally over 80 percent (Munger and Morris 1936); it now varies from 24 to 64 percent. On the highest and most severe site at 4,600 feet (1,400 m), severe decimation of some low elevation races was apparent in the first decade. By age 60 only three high elevation races survived in sufficient numbers to make a stand, the most local race was clearly superior in both growth and survival. On three other exposed sites ranging from 1,100 to 2,000 feet (330–610 m) in elevation, decimation of non-adapted races began after age 30. All three have several races now seriously understocked as well as growing poorly. On a sheltered site at 2,600 feet (800 m), however, all but two races have full stocking, the decimation of the two occurred mainly in the last decade. Thus, relative exposure of the site is a major element in time needed to uncover unadapted races. Large differences in survival have also developed between families within races in every plantation. The decimating agents are often mystifying and are different at each site. Before dying, trees often display a gradual decline in vigor. Much mortality or damage also dates from climatic extremes such as freezes, heavy snow loads, ice storms, winter exposure above snow, hurricanes, and probably drought. Surrounding natural stands were usually damaged less and recovered better than the races tested. Natural selection, continued over this 60-year timespan, appears to favor genotypes similar to those occurring in natural stands. Thus, seed movement can involve risks of unacceptable mortality that appear over a longer period than spanned by the career of the geneticist. Risks are lessened by shorter rotations, by seed movement involving only modest environmental changes, or by choice of sheltered sites. Too intensive selection even within the local stand may be subject to the same risks.

Growth

Genetic variation of a magnitude expected for so wide-ranging and long-lived a species as Douglas-fir has been documented for a number of phenological, growth, form, and resistance traits (table 1). As with other western conifers (Hamrick and Libby 1972), most traits display

clonal variation but a few vary ecotypically. A westwide, clinal pattern of inherent growth of Douglas-fir over its range has long been obvious, as has a generalized inverse relationship between growth and cold-hardiness or drought resistance.

Collectively, the documentation of genetic variation in Douglas-fir suggests that selection from among these and many other traits has been stabilized by several thousand years of similar climate into populations having a sensitive adaptation to local environments. A major feature of recent literature on genetic variation is that populations, sometimes only a few miles apart, maintain measurable genetic differences in growth and phenology despite pollen exchange.

Geographic Variation.—A westwide pattern of inherent growth rates similar to the one reported earlier for ponderosa pine (Squillace and Silen 1962) is also apparent for Douglas-fir. Three features of the annual precipitation pattern in the range of Douglas-fir appear important in its development. One feature is the decrease in precipitation and humidity behind successively higher north-south mountain ranges from the Coast Ranges through the Rocky Mountains. A second feature is a characteristic summer drought that begins in spring across the Southwest United States and advances slowly northward over most of the species range by early July. Thus, long severe moisture deficiencies can occur any summer in any part of the range. For example, even as far north and in as maritime a climate as Vancouver, B.C., where annual precipitation ranges from 66 to 107 inches (1.7–2.7 m), a 74-day rainless period occurred in the 1951 growing season. In such droughty years survival depends primarily on moisture within the soil and the tree at the onset of growth. A third feature is that relief from summer drought by rains from thunderstorms is usually of minor importance in the high rainfall northwest portion of Douglas-fir's range, but these rains constitute a major part of the low annual precipitation in the drier southern and eastern portions.

Selection response to this precipitation pattern has been that highest inherent rates of growth characterize races along the Pacific slopes of Washington, Oregon, British Columbia, and California where annual moisture is generally more plentiful and yearly recharge of the soil is dependable. Races from interior British Columbia and western Idaho are generally of intermediate growth. Slowest growing

TABLE 1.—*Traits exhibiting genetic variation in Douglas-fir*

Trait	Estimated genetic control ¹	Literature citation or source ²
Total height	W-M	Campbell 1964 (0.10); Campbell 1972 (0.10–0.30); Namkoong and others 1972 (0.24–0.50); Kleinschmit and others 1974
Stem diameter	M	Campbell 1964 (0.20)
Stem straightness	M	Orr-Ewing 1967; Wilcox 1974
Dry weight	W	Campbell and Rediske 1966 (0.09)
Branching	W-M	Campbell 1961, 1963 (0.05–0.30)
Stockiness	M-S	Silen (see text "Form") (0.26)
Wood specific gravity	M-S	Nicholas 1963 (0.17–0.52)
Wood trachied length	M	Nicholas 1963 (0.11–0.27)
Percent summerwood	M	McKimmy 1966 (0.00–0.66)
		Nicholas 1963; McKimmy 1966; Wilcox 1968, 1974
Percent heartwood	W	Wilcox 1968, 1974
Wood permeability	W	Miller and Graham 1963; Bramhall 1955
Wood extractives		Hancock and Swan 1965
Terpene composition	MS	Zavarin and Snajberk 1973; von Rudloff 1972
Spiral grain	MS	Campbell 1964
Frost resistance	M	Bellmann and Schönbach 1964; Schönbach and Bellmann 1967; Campbell and Sorensen 1973
Disease resistance	M	Larsen 1946; Meyer 1954; Brandt 1960; Schober 1963; von Stephan 1973; Wilcox 1974
Insect resistance	M	Mitchell and Nagel 1969
Animal resistance	MS	Radwan 1969; Dimock and others 1976
Rooting		Black 1973
Cotyledon number	M	Sziklai 1963, 1965; Sorensen 1966
Graft incompatibility	S	Copes 1973 (0.81)
Cone production	S	Allen 1963 (see text "Seed")
Top injury		Anderson and Wilson 1970
Survival	M-S	Bialobok and Mejnartowicz, 1970; (see text "Survival")
Fertilizer response	W	Rediske and others 1968
Floral color	S	Ching and others 1966; Copes 1972
Seed	W-M	Allen 1960, 1962
Foliar nutrients		van den Driessche 1973

¹ Figures cited by authors are mainly broad sense heritability or upper limit estimates: (W) weak (h^2 less than 0.1), (M) moderate ($h^2 = 0.1-0.3$), (MS) moderately strong ($h^2 = 0.3$ to 0.5), (S) strong (h^2 above 0.5).

² Heritability estimates are shown in parentheses.

races characterize the interior basin and east slope of the Rocky Mountains, where spring-time soil moisture may be seriously deficient and cyclic droughts can extend over several years. Arizona and New Mexico sources range from slow to moderately fast growing under the influence of more plentiful summer rains. An index of the westwide seasonal moisture distribution pattern, September-through-June precipitation as a percent of annual precipitation, has been correlated with racial growth differences in both ponderosa pine (Squillace and Silen 1962) and Douglas-fir (Sorensen 1967).

Such a generalized clinal pattern of inherent rate of growth is seen in table 2 in which average height as a percent of study plot mean of races in each geographic region is pooled from four rangewide studies conducted in Western North America and western Europe. Mature natural stands over the West also display a similar relationship in comparative heights, which lends credence to the pattern.

Results reported from tests conducted in other climates or latitudes can be broadly interpreted from the pattern (Hermann and Ching 1975). In Eastern United States, where frost-sensitive coastal races are killed in winter, races from New Mexico and Arizona grow best (Wright and others 1971), presumably responding to an adaptation for a summertime rainfall pattern as well as cold winters. In the continental climate of eastern and northern Europe, races from southwestern British Columbia, western Washington, and northern Oregon are best (Jahn 1955, Rohmeder 1956).

In maritime western Europe, races from Vancouver Island and western Washington are preferred; but in southern Europe, races from Oregon and California appear better suited (Schober 1963). In New Zealand (Wilcox 1974) better performance is displayed by coastal fog-belt races of California and southern Oregon. Such experience suggests importance of day length as well as climatic adaptation.

Improvement strategies using racial variation for faster growth rates generally seek the genes developed in a milder and more mesic part of the range than the intended planting site. Such strategies must generally balance better growth against poorer hardiness.

Local Variation.—The pronounced genetic differences in growth and other traits of geographic races apparently grade clinally so that differences between local populations only a few kilometers apart are detectable.

Several studies along a transect near 45° N. latitude in western Oregon show that sharp changes in local climate are accompanied by correspondingly sharp changes in inherent rates of growth or phenological expression. From seed collections grown in different years at Corvallis, Irgens-Moller (1957, 1967) and Sorensen (1967), for example, report a 2-week-later average bud burst and a 13- to 17-percent superiority in height for low elevation seedlings from the coast hills seed over those from a seed of similar elevation on the west side of the Willamette Valley separated by only 11 and 15 miles (18 and 24 km). The latter presumably was adapted to less spring rainfall and earlier onset of seasonal drought. Sorensen (personal

TABLE 2.—Comparative height growth of Douglas-fir and ponderosa pine from different geographic regions tested in the Douglas-fir region of the United States and in western Europe¹

Region of origin	Douglas-fir				Ponderosa pine
	Western Oregon ² (14 years)	Western Washington ³ (20 years)	Denmark ⁴ (21 years)	Germany ⁵ (44 years)	Western United States ⁶ and New Zealand (25–43 years)
West of Cascade Mountains	⁷ 176 (2)	141 (3)	127 (3)	136 (2)	118 (5)
West of Sierra Mountains	114 (1)	81 (1)	111 (1)	109 (3)	137 (3)
Interior British Columbia	—	—	95 (1)	95 (1)	97 (6)
Northern Rocky Mountains	79 (3)	102 (3)	95 (2)	95 (3)	107 (13)
Southern Rocky Mountains	95 (2)	102 (1)	—	93 (3)	80 (7)
East slope Rocky Mountains	48 (1)	67 (1)	76 (1)	70 (1)	70 (2)
Intermountain	41 (1)	20 (1)	77 (2)	74 (5)	76 (6)

¹ Height growth of provenance trees as a percent of average height of plantation trees.

² Data from plantation at Corvallis, Oregon.

³ Data from plantation at Wind River Experimental Forest, Wash.

⁴ Lundberg (1957).

⁵ Schober (1959).

⁶ Squillace and Silen (1962) reporting on three studies.

⁷ Numbers in parentheses are numbers of regional average provenances.

correspondence 1974), using seed collections at 7-mile intervals along the Willamette Valley and Coast Ranges portion of the transect, found significant differences in bud burst and other phenological traits between some adjacent stations. A consistent pattern has been displayed between other stations along the transect. Even on the floor of the Willamette Valley along the transect, west- and east-side populations are clearly different. In a study by our laboratory of 50 wind-pollinated families tested on eight low elevation sites in western Oregon and Washington, families from the more mesic east-side Willamette Valley floor averaged 12.1 percent greater average height at 5 years than families from the drier west side.

A similar experience is reported from Europe (Schober 1963) with seed from the transition zone between coastal and interior British Columbia. Races from the grasslands east of the coastal mountains are susceptible to *Rhabdocline* and are slow growing compared with nearby types to the east and west in higher moisture regimes (see also Kleinschmit and others 1974).

On a single ridge in southern Oregon, Hermann and Lavender (1968) found genetic differences among seedling traits of north and south slope populations in nursery and growth chamber studies. Sweet (1965), studying clinally varying seedling traits of 22 coastal sources from California, Oregon, and Washington, observed predictable differences between races that differed more than 1,000 feet (305 m) in elevation at the same latitude, or somewhat more than a degree of latitude at the same elevation. Von Rudloff (1972) in British Columbia and Zavarin and Snajberk (1975) in California, studying ratio of terpene fractions in leaf oils or resin blisters, found populations that differed measurably between short sampling intervals, particularly in situations where accompanying climatic changes were abrupt in mountainous topography. Rehfeldt (1974b), studying seedling populations originating at 2,950, 3,700, and 4,260 feet (900, 1,125, and 1,300 m) from two valleys in northern Idaho 10.5 miles (17 km) apart, found differences in various phenological and growth traits among most of the six populations.

Using racial seed collections of coastal Douglas-fir at 44 weather stations, Campbell (1974) generalized that the predicted date of seedling bud burst in a common environment was later

¹ Campbell, Robert K. Genecology of Douglas-fir in an Oregon Cascades watershed. Unpublished data on file, Forestry Sciences Laboratory, Corvallis, Oreg.

by 5 days per 400-foot (122-m) rise in source elevation, the same elevational delay rate reported by Silen (1963) for pollen shedding in western Oregon and Washington. Campbell also found an average delay of 4 days per degree of latitude as predicted by "Hopkins law" to suggest that phenological adaptation of the 44 races to the local climate was very exacting. His more recent growth data³ sampling 193 locations within a single Cascade Range drainage show that different genetic populations were present to conform closely with each change of landform (Campbell 1976). Speculations about the way such population differences can be maintained despite pollen exchange usually involve effective selection for each generation from among the large seedling populations (Silen 1967b, Fryer and Ledig 1972, Rehfeldt 1974b).

Within-stand variation.—Variation among family means of parents within a locality or stand can approach the same order as racial differences (Rehfeldt 1974a). Table 3 provides examples from my studies of local growth variation of families at various ages. Typically, the range in average height of families from a single locality is one-third to one-half the general average. Coefficients of variation in average family height are large for seedlings but drop to the 3- to 6-percent range in older seedlings and mature trees, most of which reflects the smaller ratio of living crown to bole length in older stands. Variation in family volume per hectare is larger, with the coefficient of variation remaining in the 8-percent range at age 50 for the half-sib families cited. Other data from the Douglas-fir Heredity Study (table 4) suggest that top performing families in each race, in addition to producing a larger average tree, survive about 11 percent better than average.

Form

Though Douglas-fir stands appear superficially straight stemmed and of good form, a surprising amount of sweep sinuosity, roughness, excessive limbiness, and undesirable crown form is normal. In stands marked commercially for piling, where only slight deviations from straightness are permissible, selection seldom exceeds 20 percent of the trees.

Potential for improvement in bole straightness, stockiness, and crown and limb characteristics appears certain. Inheritance of poor or good form was clearly demonstrated by Orr-Ewing (1967). Moderately strong inheritance

TABLE 3.—*Examples of variation in height and volume among wind-pollinated families of Douglas-fir originating from a single stand or locality*

Age	Source	Elevation	Number of parents	Mean family height or volumes	Range of family means	Coefficient of variation	Test details
<i>Years</i>		<i>Feet</i>		<i>Centimeters</i>		<i>Percent</i>	
<i>HEIGHT</i>							
2	Vernonia, Oreg.	300	300	33	17-47	15	4 replications of 50 seedlings/replication
5	Corvallis, Oreg. (West Willamette Valley)	250	31	118	107-140	4	8 sites, 3 replications/site
5	Lacomb, Oreg. (East Willamette Valley)	900	19	133	119-145	4	8 sites, 3 replications/site
5	Shelton, Wash.	400	33	113	104-130	5	8 sites, 3 replications/site
5	McLeary, Wash.	400	17	120	114-150	6	8 sites, 3 replications/site
50	Gates, Oreg.	1,000	17	116.6	112-118	3	100 per parent on 5 sites
50	Santiam, Oreg.	3,400	12	116.7	113-118	3	100 per parent on 5 sites
<i>VOLUME</i>							
				<i>Cubic feet</i>			
50	Gates, Oreg.	1,000	17	10.2	8-11	8	100 per parent on 5 sites
50	Santiam, Oreg.	3,400	12	8.1	7-9	8	100 per parent on 5 sites

TABLE 4.—*A comparison of individual tree volumes at 50 years of age for the average family, best family, and best 1/4 of the families at five plantations in the Douglas-fir Heredity Study*¹

Plantation:	Wind River	Hebo	Mount Hood	Mount Baker	Mount Hood
Elevation (feet):	1,100	2,000	2,600	2,000	4,600
Number of parents in source:	9	7	11	8	12
Cubic feet					
Average family	12.5	17.8	5.3	37.9	2.8
Best family ²	15.9	22.7	7.4	62.8	4.8
	(27)	(28)	(40)	(66)	(71)
Best 1/4 of families ²	14.7	20.9	6.7	57.4	4.3
	(18)	(17)	(26)	(51)	(53)

¹ Data are presented for the seed source most nearly local to the plantation site.

² Numbers in parentheses are the percent gain over the average tree.

of straightness is suggested by the same order of family ranking at 5 years in each of the five plantations of the Douglas-fir Heredity Study (see also Wilcox 1974).

Inheritance of stockiness also appears fairly strong but may be difficult to predict. From a 3 × 6 factorial mating of randomly chosen parents, individual tree heritability was estimated at 0.27 for 8-year-old seedlings based on ratio of height to diameter at one-fourth the height. Most of the variance is additive. Phenotypic selection of parent trees was ineffective in upgrading the portion of desired stocky, tall families. Nursery rankings of families for stockiness were poorly related with stocky families at 8 years. No data exist on whether as many stocky trees as slender trees can be grown per unit area.

Campbell's (1961) measurements of repeatability on 100 trees suggest substantial inheritance for several crown characteristics, such as limb size, crown width, and ratio of width to height of top 10 whorls.

Bole imperfection from cold damage varies greatly by family. Cambial freezing, such as occurred during the record 1955 severe early freeze in the Northwest, caused major wounds and stem rotting. In every race in the Douglas-fir Heredity Study, certain families were much more damaged or resistant than average. Similarly, family differences in ice or snow breakage that caused offset stems were repeatedly experienced in the study. Both types of wounds become more damaging with time as the stem, weakened by rot in the wound, often breaks again years later below the live crown and the tree dies.

Phenology

Only growth has received more genetic study than phenological traits. Long-term phenological records have been made at many weather stations.⁴ (Griffith 1968). Phenology is intimately associated with adaptation and survival, but it appears less well related to tree height growth (Munger and Morris 1936, Griffith 1968).

Bud burst is an easily studied, sharply delineated phenological event of high heritability (Silen 1962c). Its variable occurrence from 30 to 45 days after onset of cambial growth and 11 to 34 days after flowering (Griffith 1968), however, reduces its interpretive value as an indicator. Unlike the less variable onset of cambial growth (Griffith 1968), bud burst varies yearly in response to summations of heat above growth thresholds (Campbell 1974). Its control appears to be mediated by gibberellins (Lavender and others 1973).

Many observations of bud burst inheritance come from early studies of races. For 13 races grown at five locations, a common order of bud burst was always observed even though bud burst occurred 2 months later at the highest site than at the lowest (Munger and Morris 1936, Haddock and others 1967). The same burst order was noted in observations 30 years apart (Morris and others 1957). Bud burst occurred earliest for races from broad valley origins, followed elevationally by those on open slopes. Races from the floors of narrow valleys characterized by cold air drainages, however, burst relatively late, an important feature since they also display good inherent growth rates.

When grown in a common environment, races bordering the cool Pacific Ocean are generally late, whereas those from high elevations or interior portions of Douglas-fir's range burst early and are prone to frost damage (Irgens-Moller 1968) and *Rhabdocline* attack (Liese 1936, Haddock and others 1967). With such exceptions, bud burst is earliest for southerly coastal races, with each degree of latitude contributing a delay of about 1.8 days in inherent bud burst (Sweet 1965). Racial bud burst tends to be progressively earlier with distance from the Pacific Ocean, the greatest change occurring within the first 30 miles (50 km) (Campbell 1974).

⁴Morris, W. G. 1952. Average day of year on which given phenological development occurred in given species at points in Oregon and Washington. 7 p. Unpublished report on file at Pacific Northwest Forest and Range Experiment Station, Portland, Oreg.

Terminal buds are usually last to burst on a tree. Relative delay between lateral and terminal buds was progressively longer for seedlings of southerly races in a west coast transect study (Sweet 1965).

For races grown in a common environment, bud set is earliest in the interior provenances. For coastal sources, northern provenances (Kleinschmidt and others 1974) and high elevations (Bialobok and Mejnartowicz 1970) cease growth earliest. Inherent variation in bud set provides an evasion mechanism against fall frosts (Campbell and Sorensen 1973, Griffin 1974) and early onset of summer drought.

The inherent seasonal rhythm of phenological events persists when plants are moved to new environments. Adjustment to the new environment is believed to occur primarily at one end of the growth period. Offsite plants thus poorly utilize the growing season and may be delayed in meeting physiological requirements for dormancy and growth (Campbell 1974).

Resistances

Pests.—In its natural range, Douglas-fir is relatively free from serious pests, although it is attacked by numerous biotic agents. Of these, only resistance to browsing by deer and clipping by hare have been pursued with a sustained research effort (Dimock and others 1976). A useful level of variation in resistance was found among nine parents. Inheritance of their resistance in crosses was primarily additive. Laboratory studies of factors related to animal resistance are promising (see "Physiological Variation").

Outside the range of Douglas-fir, selection for resistances to the needle diseases *Rhabdocline pseudotsuga* and *Phaeocryptopus gaumannii*, both of little consequence to natural stands, has been a key to successful introduction. In northern Europe, for example, races from areas in western Washington characterized by high humidities often show high resistance to *Rhabdocline* attack. Those from the more arid interior are usually susceptible (Schober 1963). Present epidemics of *Phaeocryptopus* in New Zealand stands have exposed much within-stand variability to indicate potential resistance (Wilcox 1974). Resistance to root rots has not been demonstrated.

Resistance to a number of other pests has been suggested or demonstrated in published reports (table 1). These include midges, *Contarinia* sp. (Mitchell and Nagel 1969), the twig weevil, *Cylindrocopturus furnissi* (V. Allen,

personal communication, 1975), the gall insect, *Chermes cooleyi* (Wheat 1965), and the limb gall, *Bacterium pseudotsugae*.

Cold.—The relative cold hardiness of interior races has long been used in choice of seed sources for introductions into continental climates of Europe (Schober 1963, Bellman and Schönbach 1964) and the United States (Baldwin and Murphy 1956, Wright and others 1971). Unfortunately, cold hardiness appears loosely correlated with reduced growth rate.

For coastal races, inherent resistance to fall frosts was shown to be related to both early bud set, an evasion mechanism, and to a physiological sensitivity related to latitude. In provenance collections grown at Corvallis, Oreg., races from the mild climates of Puget Sound, the Willamette Valley, and the Oregon coast were most sensitive (Campbell and Sorensen 1973). The same two factors explained most of the sensitivity to damage in another study of 10 California races (Griffin 1974).

Within the amplitude of a single race, individual families display wide differences in cold sensitivity. For example, in a study of 309 wind-pollinated families from Vernonia, Oreg., grown at Corvallis, a severe spring frost completely defoliated 94 percent of the year-old seedlings. The 10 least defoliated families averaged 28 percent uninjured plants, and in one family 49 percent were uninjured. Likewise, in the record November 15, 1955, cold, the 13 races and 120 families of the Douglas-fir Heredity Study, then 42 years old, sustained an interesting family and racial damage pattern. Heavy killing of trees in all crown classes occurred at only two of the five plantations (Hebo, Oreg., and Verlot, Wash., both at 2,000 feet (600 m)) still having active cambial growth. In both, all races sustained some killing; but low elevation races were most damaged. Every race also had some families with no damage interspersed with families with up to 38 percent dead trees. The pattern was related to proportions of trees whose cambiums were still active in late November, a phenological characteristic of the family.

Drought.—Douglas-fir seedlings have been shown to have both drought avoidance and drought hardiness differences related to seed origin. Seedlings from seed from the Rocky Mountains and from dry sites in the Cascade Range consistently have lower transpiration rates and show more sensitive stomatal control than seedlings from wet sites of the Cascade and Coast Ranges (Ferrell and Woodard 1966; Pharis and Ferrell 1966; Unterschuetz and

others 1974; Zavitkovski and Ferrell 1968, 1970). Seedlings from dry sites also have more rapid root growth than those from wetter sites (Heiner and Lavender 1972). Data indicate that populations on adjacent north and south slopes display significant local differences in drought avoidance (Ferrell and Woodard 1966). There are fewer drought hardiness data, but they indicate inherent differences between populations in this characteristic as well (Pharis and Ferrell 1966).

Physiological Variation

Genetic variation has been revealed in many studies of physiological traits of Douglas-fir such as photoperiod, thermoperiod, photosynthetic rate, or with chemical determinations of monoterpenes, isoenzymes, and DNA (deoxyribonucleic acid) content.

The species light requirement is satisfied by a short light break during the night (Irgens-Moller 1962). A considerable period of short days is required to force dormancy. Despite long days, Douglas-fir also normally goes dormant during the summer dry period. Sensitivity to photoperiod is greater with interior sources (Irgens-Moller 1958, 1962). A thermoperiod of 75°F (24°C) soil temperature combined with an 18-hour photoperiod maximizes dry weight increment for the species, but interior sources are less affected by lower than optimum temperatures and have lower shoot-root ratios (Lavender and Overton 1972). Interior races respond differently in photosynthetic rates and saturation points than do coastal races (Campbell and Rediske 1966, Krueger and Ferrell 1965), particularly to seedling preconditioning (Sorensen and Ferrell 1973). Cell nuclear volumes and DNA content are strongly correlated with increasing latitude and appear higher for coastal sources than for interior sources (El-Lakany and Sziklai 1971, 1973); this finding was of use in determining origin of plantations (Berny 1972).

Distinctions between adjacent populations have been most successful with studies of oleoresins (von Rudloff 1972; Zavarin and Snajberk 1973, 1975; Snajberk and others 1974). Differences between genotypes are easily demonstrated for at least 10 enzymes. Application of isoenzyme investigations to studies of racial variation (Muhs 1974), individual genotypic differences, grafting incompatibility, mutations, and flowering are in progress in several laboratories in Western North America.

Attempts to relate animal damage resistance to chemical content of foliage by genotype have

led to investigations of tissue digestability, essential oils, and several chemical constituents. Resistance is related to lower dry matter content and cellular digestabilities, essential oils with greater inhibitory action on rumen, more monoterpenes in vapor from foliage, and lower levels of chlorogenic acid, the last being the most promising screening chemical for animal-damage-resistance types (Radwan 1969). Chlorogenic acid content is a highly heritable trait showing primarily additive variation (Radwan 1975, Radwan and Ellis 1975).

Wood

Prospect of breeding for specific wood traits is promising. Study of wind-pollinated Douglas-fir families at age 46 has indicated family heritabilities range from 0.17 to 0.52 for specific gravity (McKimmy 1966) and 0.11 to 0.27 percent for tracheid length (Nicholas 1963). Measurements of juvenile wood were of low reliability for estimating traits in mature wood in this study, but good correlations with mature wood were reported by Reck and Sziklai (1973). Ranking of average specific gravity and fiber length was essentially the same for five wind-pollinated families on three widely separated coastal plantations of the Douglas-fir Heredity Study, indicating considerable stability for these wood traits (McKimmy 1966). A more recent study of Douglas-fir at age 9 years based on 54 full-sib families in a hierarchical mating design provided an individual tree heritability for specific gravity of 0.61. No interactions were found between the two test sites, and a highly significant parent offspring correlation of 0.51 was calculated.⁵ Bramhall (1955) reports racial differences in permeability of wood to preservations.

AGE OF TRAIT EXPRESSION

Meaningful expression of genetic variation can occur early for some traits but requires many decades for several that are commercially important. Traits of germinants involve single-gene mutants for at least five chlorophyll deficiencies and three needle irregularities (see "Genetic Markers"). Seedlings 1 to 5 years of age have shown genetic variations in seven phenological traits, four growth traits, three

forms of cold injury, two forms of drought resistance, animal browsing, photoperiod, thermoperiod, transpiration, respiration, and photosynthetic rate. Young trees have been used to display differences in form and resistances to at least two needle diseases and two insects, as well as to needle shedding after cutting. Observations of mature trees are required to evaluate resistance to some wood pathogens, mortality from long term-climatic extremes, certain gene-environment interactions, and differences in mature volume growth per acre.

The 1912 Douglas-fir Heredity Study (Munger and Morris 1936, USDA Forest Service 1963), based on seed from 120 wind-pollinated parents from 13 localities in western Oregon and Washington, illustrates various time requirements. Bud bursting order has remained essentially unchanged since young trees were evaluated (Morris and others 1957). Frost susceptibilities were accurately recorded on young trees. Early expressions of differences in straightness and taper changed slowly with stand development. Likewise, wood sampled earlier than 25 years showed little relationship to mature wood traits (McKimmy 1966). Ranking of races in growth reported at age 17 (Munger and Morris 1936) practically all changed by age 50 (Silen 1966a). Even correlation of early height growth of individual trees with mature heights was very low (2 years with 50 years, $r = 0.005$; 11 years with 50 years, $r = 0.112$; and 22 years with 50 years, $r = 0.47$ (Silen 1965)). Gene-environment interactions, of minor consequence at 17 years, were large at age 50 for both families and for races. An especially clear case is illustrated in figure 5. Survival differences between races, minor at 17 years, were about 2:1 at 50 years, the greatest differences occurring on most severe sites. Survival differences, appreciably favoring adapted races, developed within a decade on the most severe site but only recently have become noticeable on the most sheltered site. Unfortunately, the relative severity of the five sites would have been difficult to predict in the study since severity of the site is only weakly related to site quality or to elevation (Silen 1966a).

Similar trends through time began to appear in a 1958 regional study of 16 reciprocally planted races (Rowe and Ching 1973). Likewise, comparison of 2-year heights versus 10-year heights on 26 full-sib families from parentage of the Dennie Ahl Seed Orchard provides generally low relationships ($r = 0.01$ to 0.46).

⁵ Campbell, Robert K., Robert Echols, and Roy Stonecypher. Heritabilities of volume and specific gravity and expected gain from early selection in Douglas-fir. Unpublished data on file, Forestry Sciences Laboratory, Corvallis, Oreg.

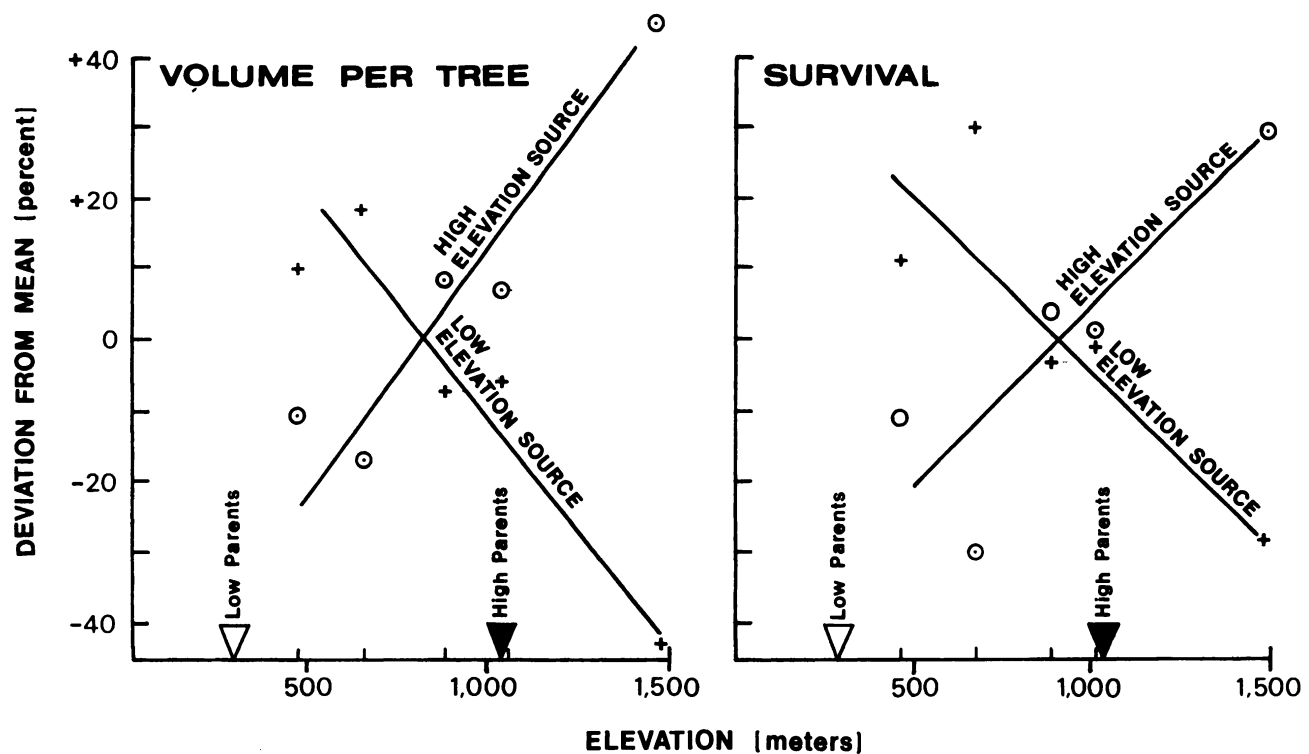


Figure 5.—Gene-environment interactions at age 50 of a high elevation source and a low elevation source collected in 1912 from the Santiam Valley, Oregon Cascades, grown at five sites in western Oregon and Washington. Volume per tree and percent survival are shown as percent deviation from their common means. The low elevation source (Gates, 1,000 feet or 300 meters, represented by four parents—○) shows superiority in both traits at low elevations, whereas the high elevation source (Santiam, 3,500 feet or 1 070 meters, represented by five parents—+) shows superiority at high elevations. Note that switching of both traits occurs at the middle elevation plantation. Plantings in 1915 were represented by 100 progeny per parent per site.

GENETIC TECHNIQUES

Initially dependent on technologies developed for pines, Douglas-fir tree improvement now incorporates many additional technologies specifically adapted for the species.

SELECTION

Growth

The mountainous topography of the West provides mainly natural stands of variable age rather than plantations for selection. Great difficulties have been experienced in statistically setting aside enough environmental variability or stand developmental effects to make confident selections for inherent growth rates.⁶ Consequently, most selections are now tested for

field performance of their progeny, using wind-pollinated seed (see "Testing"). In most phenotypic selection programs most trees in a stand are ocularly eliminated in choosing a few straight, well-formed candidates. Stands are

⁶ The largest known comparison of selected versus random parent trees was done by Crown Zellerbach Corporation and State of Oregon, each in a 300-parent program. Each marked 100 groups of 10 parent trees in 30- to 40-year stands, from which a random, a best, and a second-best were selected for volume growth. Progeny mean diameters of 100 families in each group were:

	Best in 10 (mm)	Best in 5 (mm)	Random (mm)
Crown Zellerbach Corporation (at 10 years)	35.7 ± 0.30	35.5 ± 0.25	35.6 ± 0.26
State of Oregon (at 8 years)	20.9 ± 0.20	21.0 ± 0.15	21.0 ± 0.14

sometimes strip cruised for this purpose. Candidate trees are usually compared with neighboring trees on some basis that attempts to account for differences in age and growing space. Sometimes such comparisons are further refined for differences in developmental history as evidenced by limb growth and age of neighboring trees (Krueger 1960).

A refinement in systematically setting aside the environmental component in phenotypic field selection, developed at Weyerhaeuser Company by R. K. Campbell, recorded coordinate location and diameter of each tree in a stand and computed growing space in a computer program that selected trees for their efficient use of space in terms of volume growth. Developmental history was then evaluated to further improve the selected group of parents.

Form

Selecting only straight and unbroken trees—traits that are universally desired and have a useful degree of inheritance—as candidates is practical for the species. Although selections for most seed orchards have prized trees of slender form, there is evidence that volume-per-acre improvement may be enhanced by tall but stocky types. Snow breakage, a concern west of the Cascade Range where heavy, wet snows are common, as well as ice breakage, is also less among stocky tree types. Although inheritance of stockiness appears at least moderate, the unreliability of phenotypic selection, the low reliability of a nursery to predict the trait in older trees (see “Form” under “Variation”), and the correlation with larger limb size limit present selection opportunities.

Horizontal branching was emphasized in early selection guides as desirable for reducing knot size (Isaac 1955). Few limbs per whorl or better limb spacing at the whorl has been suggested as a selection criterion to prevent structural weakness in wood. Both traits have been used only sporadically.

Phenology

Despite almost certain relationships of phenology with such traits as frost, drought, insect resistance, and possibly wood and growth, little use has been made to date of selection for phenological differences of parent trees. Undoubtedly, phenological differences will become of much use as seed orchardists seek better control of pollen and insects, as progeny families are evaluated, and as the extensive pheno-

logical researches now underway are better correlated to specific tree traits.

Resistances

With few serious pests in the mesic parts of Douglas-fir's natural range, present selection guides simply concentrate on healthy undamaged trees. Frost and cold resistance as expressed in progeny families are, however, crucial selection traits where the species is introduced and are of growing importance in selections for its interior native range. Seed mixes of parentage whose progeny display frost resistance is an obvious practical genetic application for planting frost-prone areas. Any parentage displaying resistance to browsing by deer and hare may have similar application in areas of heavy animal pressure.

CONE PRODUCTION

Early selection guides recommended trees with evidence of cone bearing. Although a heavy seed crop reduces a tree's growth, a negative relationship between inherent heavy cone bearing and growth rate has not been established. Besides seed production, cone and seed damage and germination rates are possible traits for selection as factors causing parental contribution to vary in seed orchard seed.

CONTROLLED POLLINATION

Early publications (Orr-Ewing 1956, Ching 1960) still provide useful guidelines. New products and technologies, however, have simplified procedures.

The expanding seed cone buds are isolated in bags in early March after pollen cone buds are removed. Most easily missed are a ring of tiny buds at the base of the shoot. Bags with an observation window are expensive. Pollination programs now generally use low cost, cool, kraft windowless bags (Wilson 1969) that can be left in place from March to September for both isolation and protection against insects. They are often too deteriorated from needle abrasion by September, however, to assure holding shed seed.

Pollen collection, extraction, and handling differ little from that developed for pines (Duffield 1954), although Douglas-fir's large pollen grain is more convenient for handling. Pollen must be air dried to below a 10-percent moisture content for preservation in cold storage or in freeze drying (Livingston and Ching

1967), but drying to a moisture content below 3.5 percent is harmful (Rediske 1977). Moisture-sensitive colored paper strips are helpful in monitoring desired moisture levels. Pollen may be ripened ahead of normal shedding. Hsin and Daniels (1977) reported on a variety of methods using potted 6- to 10-year-old grafts that advanced shedding up to 50.6 days. All treatments reduced pollen viability, but forcing in a greenhouse or in polyethylene bags after dormancy gave acceptable pollen about 2 weeks ahead of normal shedding.

In ordinary pollen testing in water or on agar, no pollen tube forms. Shedding of exine on imbibition followed by grain elongation of 200 to 500 micrometers is used, instead, as an indicator of pollen vigor.⁷ Such elongation requires 24 to 48 hours in ordinary testing methods (Ho and Sziklai 1972). Adenosine triphosphate determinations have been developed by Ching and Ching (1972, 1976) as a quick test with reported high reproducibility. Another quick test in our laboratory uses a 0.15-percent H_2O_2 solution. Viable pollen grains fully elongate 1 to 2 hours, then burst. The test is reasonably reliable in evaluating seed set of Douglas-fir.⁸

Maximum set of seed averaging about 37 seeds per cone is obtained when good pollen is liberally applied to fully expanded conelets. Seed set of over 20 seeds per cone, however, is obtained from pollen applied at any time over the 14-day period from bursting until the conelets begin to turn horizontally. Some seed set is obtained from pollen applied before buds have burst or as the cones bend downward.

When rigorous isolation is needed, pollen is applied with a syringe, either dry or in water suspension (Allen and Sziklai 1962). As in corn breeding, for most large-scale practical programs where evaluations are based on average growth of a large family, the bag is carefully removed for a brief time while pollen is poured over each conelet. Our laboratory has determined that seed set is enhanced if bracts on all

sides of the conelet are poured full. Scarce pollen may be diluted up to five times its volume with dead pollen and still provide a good set of filled seed. Success of such dilution is possible because the micropylar canal can accommodate up to nine pollen grains, only one of which need be successful.

Supplemental pollen has been successfully applied to seed orchard trees with a mist blower (Karlsson 1977). A vacuum cleaner with a rake attachment was used to obtain large quantities of pollen. Seed yields were increased 21 percent.

TESTING

Field testing for growth performance is often made difficult by mountainous topography. With thousands of parent trees now under field tests, technology has rapidly developed. A typical commercial testing procedure begins with growing test seedlings, usually 100 to 250 per parent, in special nursery beds for 2 years, or in container nurseries for 1 year. Seedlings are shipped from these facilities to the test sites, individually labeled, and segregated into replicates.

A typical improvement program testing 300 or more parents will use 6 to 12 sites of 5 to 15 acres (2–6 ha) in size, sampling the range of sites in the forest ownership (fig. 6). The needed uniform within-plot conditions in typical rugged topography of the region often limits choice to small sites. Scarification or herbicides are ordinarily required to control plant competition, and fences to keep out deer and elk. Trapping, baiting, and individual screening, however, have also been needed to control hare or mountain beaver. Randomized block designs in rectangular plots are most commonly used, although wheellike designs on flat ground have been used. Single tree plots are used more frequently than row plots. In instances of more than 60 parents in a test, sets of 30 to 60 parents are tested separately, with or without common or standard parentage. Spacing is usually about 10 feet (3 m). No evidence of a spacing-genotype interaction was observed in studies by Campbell and Wilson (1973). One early Oregon program testing 900 parents used three spacings—8-, 12-, and 15-ft (2.4-, 3.7-, and 4.6-m). Growth is measured either at regular time intervals or before a good seed year to provide means of updating the ranking of parents selected for seed collections or crossings. Information on animal injury and frost damage is usually recorded for possible use in resistance breeding. With over 125 such test

⁷ Christiansen (1969) found that some dead pollens elongate. This must be a rare occurrence as no seed set has yet been obtained with any pollen lot judged to be dead by pollen germination tests in our laboratory.

⁸ Fresh, 1-year-old, 2-year-old, and killed pollen were first compared for percent elongated pollen using 14-percent sucrose-agar and 0.15-percent H_2O_2 against germinated pollen counts seen in hand-sectioned micropylar canals. Later they were compared with percent filled seed per cone. Very poor or very good pollen lots were identified to the same accuracy with either agar or H_2O_2 tests. Weak lots were highly variable in seed set in all tests, probably because micropylar canals hold several grains.



Figure 6.—A typical progeny test site. Established in 1970, this is one of eight similar plantations testing 170 parent trees for a 70,000-acre (29 000 ha) cooperative tree improvement program in western Oregon. The wind-pollinated progeny are 6 years old (photo courtesy Starker Forests, Corvallis, Oreg.).

sites established in the Douglas-fir region, all informational phases depend heavily on computers.

Most commercial testing has been designed for minimizing costs. In such minimal-cost tests, a progeny family must display generally superior performance over all sites, or a site-related trend, to be statistically detectable for selection. The concept of segregating parentage from the tests that trend toward better performance on good or poor sites, high or low elevations, or north or south slopes, provides opportunities to enhance the selection of families adapted for specific sites.

ASEXUAL REPRODUCTION

Information on asexual reproduction is comparatively well developed for Douglas-fir because of its early dependence on grafted seed orchards. The species does not ordinarily re-

produce naturally by asexual means, although two instances of viable seed produced from unpollinated cones are reported (Orr-Ewing 1957b, Allen 1942c).

Douglas-fir is easily grafted, but it ranks among the most troublesome species for graft incompatibility, a major factor influencing tree improvement strategies. It roots readily from cuttings or air layers of juvenile trees, but no instances of stump sprouting, suckering, or natural air layering are recorded. It is rooted with greater difficulty after ortets reach 10 years of age (Black 1973), an obstacle to consideration of clonal forests of superior mature trees. Reproduction from single cell and genetic combinations using protoplast fusions are, as yet, unsuccessful (Winton and others 1974), but whole plants have been produced from pieces of cotyledons (Cheng 1975).

Grafting

Information on grafting has been developed to meet seed orchard needs (Orr-Ewing and Prideaux 1959). Over 90-percent initial success is usually attained from careful field grafting in springtime without bag protection, using cleft, veneer, and sometimes other common graft types (Copes 1969). Grafting can be done at any season in the greenhouse or by enclosing the grafts in protective bags to prevent desiccation or overheating of grafts. Scions are usually collected during winter dormancy and can be stored in polyethylene bags at 32° F (0° C) for at least 4 months if desiccation and molding are controlled. Major factors influencing successful grafting are condition of scions, time of grafting, length of graft union, and weather conditions immediately before and after grafting (Copes 1967b, 1970). Scions collected from the major branch tips in the top whorls of mature trees are more prone to grow upright than are branch tips or scions collected from a lower position in the tree. Scions of the latter type often show plagiotropic growth for many years. Use of vigorously growing rootstocks, however, greatly reduces the period of plagiotropic growth.

Graft rejection, or grafting incompatibility, is a major problem. An average of 35 percent of all grafts are ultimately rejected by understock tissue (Copes 1969). Percentage of rejection for clones has ranged from 5 to 95 percent. The incompatibility problem was serious enough to slow major new investment in Douglas-fir tree improvement for several years (Silen and Copes 1972). Solutions were found, based on

early recognition of symptoms and evasion (Copes 1967a). By 13 months after the grafting, a characteristic incompatibility symptom in the xylem is seen microscopically in incompatible unions. In one evasion technique, two grafts of a clone are made per rootstock and one graft is sacrificed and inspected after thin sectioning and tissue staining. A different scion clone is substituted on the rootstock if the characteristic incompatibility symptom appears in the sacrificed union. This technique results in variable seed orchard spacing. For uniform spacing, another technique with the same incompatibility symptom is used to detect and select understocks compatible with each scion clone. Enough grafts of each scion clone are made to insure at least one compatible stock-scion combination for every clone. The young compatible rootstocks can then be easily propagated by rooted cuttings in quantities sufficient for orchard understock requirements of each specific scion clone. Present research is aimed at producing highly compatible understocks through breeding and use of rooted cuttings. Breeding work is based on the finding that inheritance of graft compatibility is fairly high and primarily additive (Copes 1973, 1974). Thousands of highly compatible rootstocks are routinely produced yearly.

Rooting

Douglas-fir roots less readily than western hemlocks, spruces, or firs. Erratic and low rootability of cuttings from mature trees led to an early reputation as a difficult species to root. The finding that seedling cuttings rooted readily has led to increased use of rooting for asexual reproduction. Decreasing rootability with age is seen in a compilation of experience at Corvallis, Oreg. Success from rooting cuttings in sweatboxes without mist or bottom heat has averaged about 90 percent for 1-year seedlings, 60 percent for 4-year seedlings, 20 percent for 8-year seedlings, and less than 10 percent for mature trees.

Knowledge developed mainly within the last decade has more than doubled rooting success from cuttings from 10- to 50-year-old trees (Brix and Barker 1969, 1971; Black 1973; Cornu 1973; Copes 1977). It appears that cuttings must have satisfied auxin, chilling, and day length requirements for best success; but auxin can partially substitute for lack of chilling (Roberts and Fuchigami 1973; Bhella and Roberts 1974, 1975). Rooting of mature tree cuttings is still erratic. Best success has been achieved with a buried inarch technique in which adult cuttings are grafted to lower stems of young seedlings (Wheat 1964, Brix and Barker 1971).

Best results are reported with collections made in the December-to-March period (Roberts and Fuchigami 1973). Use of IBA (0.5 percent best according to Cornu (1973)) appears to maximize rooting as well as to enhance shoot growth (Ross 1975). Intermittent mist and bottom heat are considered advantageous, but soil moisture control is essential to reduce fungal attack. Fibrousness of roots is influenced by the rooting media, with a 2:1 peat-sand mixture recommended by Copes (1977) when mist and bottom heat are used. Number of cuttings obtained from young seedlings is greatly enhanced by shearing (Ross 1975). Under all conditions, results can vary greatly among clones.

Techniques of growing plantlets through tissue culture techniques have recently defined plant growth regulator for each developmental state (Cheng and others 1977). Adventitious root development following formation of shoots required 0.05–0.25 micrometer NAA (naphthaleneacetic acid). Shoot formation required only basal medium. Adventitious bud formation required 5 micrometers BAP (N_6 -benzylamino-purine) plus 0.5–5.0 micrometers NAA, or 5 micrometers BAP and 0.25–5.0 micrometers each of IBA (indole-3-butyric acid) and IAA (indole-3-acetic acid).

APPLIED PROGRAMS

HISTORY

A variety of practical tree improvement programs has evolved to accommodate the serious technical problems with the species. Although most large landowners established seed production areas or seed orchards during the late

1950's, many abandoned them out of discouragement or reduced tree improvement financing during the mid-1960's. This discouragement arose from problems associated with mountainous topography, small seed zones, animal dam-

age, brush competition, planting failures, high establishment costs, and need for skilled staffs and special seed orchard sites. Additionally, the unanswered technical questions of heavy pollen contamination, uncertainty of selection, difficult rooting, and the slow, erratic or unequal seed production of clones cooled early optimism. The species proved to be among the worst of the major species in expressing latent mortality from grafting incompatibility.

By the mid-1960's, planting, which earlier had been practiced on only a modest scale, was greatly expanded. Better data on potential genetic gains began to restore confidence. Proposed use of wide crossing of races and a concept that avoided need for grafted seed orchards engendered hope. By 1970 most of the early seed orchard problems were being solved with evasion techniques (Silen and Copes 1972). Fueled by favorable changes, an exponential expansion in program acreage that spread to most of the Douglas-fir region was underway by 1970 and is still rapidly expanding over other parts of the West.

The systematic search for suitable races of Western North American species, occasioned by the seed collection of the International Union of Forest Research Organizations (IUFRO) and other European seed collections and by seed collections appropriate for trial in the southern hemisphere, has also led to expanding improvement programs of Douglas-fir as an exotic.

SEED CERTIFICATION

Need to assure landowners of the source of Douglas-fir region better natural seed collections led to the establishment of a system of certification in Oregon and Washington in 1962. Overall guidance of the program is by the Northwest Forest Seed Certifiers, Inc., composed of major seed-using landowners and commercial seedsmen. British Columbia instituted a program in 1971 (Piesch and Phelps). Actual field certification is done by Washington Crop Improvement Association, Oregon State University Extension Service, and British Columbia Forest Service.

SEED PRODUCTION AREAS

Some early programs used seed production areas that had been rogued of pole-size stands to leave widely spaced, good dominants to produce wind-pollinated seed. Most seed production areas have been phased out in favor of more genetically efficient and financially effi-

cient programs, or because too high a proportion of seed originated from relatively few parents.

SEED ORCHARDS

As the only available tree improvement concept initially, the grafted, general-combining-ability seed orchard program was widely adopted in the Douglas-fir region. By 1965, 20 Douglas-fir orchards totaling over 200 acres (80 ha) had been started. About 20 more orchards and over 700 acres (280 ha) have since been added (fig. 7), but 10 of the original 20 earlier ones are no longer maintained. Genetic gain was based on utilizing the additive component of genetic variance from intensive phenotypic selection. Plus-tree selections ranged from 15 to 100 per seed zone, with 10 to 80 ramets of each parent grafted to understock seedlings. Most orchard spacing is now about 40 trees per acre. Only recently have any seed orchard programs begun systematic and comprehensive field testing of progeny to assess performance of individual parents.



Figure 7.—An 8-year-old Douglas-fir seed orchard, at Colton, Oreg. (photo courtesy of Bureau of Land Management, Salem, Oreg.).

Discovery of evasion techniques has provided major breakthroughs for solutions to most early seed orchard problems. Graft incompatibility research has provided a method of producing an orchard virtually free of the problem (see "Grafting"). Widely compatible rootstocks are now being bred (Copes 1973, 1974).

The perplexing problem of heavy contamination from outside pollen has also been solved by another evasion technique. Spraying the orchards with cold water prior to bud burst delays floral buds from bursting until the peak period of local pollen shed has passed (Silen and Keane 1969). The contamination problem itself dissi-

pates with time. Pollen production in orchards more than a decade old becomes so abundant that it reduces the contribution of outside pollen to a minor component. Even so, some early flowering clones may be poorly pollinated or late flowering ones may be pollinated mainly by outside sources.

Lack of cone production was a persistent problem for early orchards located in high rainfall portions of the Douglas-fir range. Sunny localities in the Willamette Valley-Puget Sound trough and on the Sannich Peninsula of Vancouver Island have been sought for newer orchards. In such locations the problem of slow and erratic early cone production usually changes to overproduction for the intended seed zone after about a decade. During the bumper crop year of 1971, the three oldest Douglas-fir orchards, started over a decade earlier, produced 20 to 30 pounds (9-13.5 kg) of seed per acre. In two of these, seed needs for the breeding zone were exceeded.

The problem of unequal seed production of clones in Douglas-fir is serious. For example, records of the first two good seed crops at the Dennie Ahl Seed Orchard show that, of 35 clones, about eight-tenths of each seed crop was produced by the same 9 clones (V. Allen, personal communication). Much of the orchard pollen is also from a few clones.

Seed orchard concepts have undergone many changes. Phasing grafted orchards into long-term breeding programs has taken several patterns. Sophisticated breeding designs have been incorporated. For example, one of the earliest large seed orchard programs was on Vancouver Island. A cooperative effort of all landowners has led to crossing of over 400 parents in a mating scheme of small partial diallels for genetic evaluations and future seed orchards.

Early orchards with few clones have usually incorporated new selections for a larger genetic base. In one program, five additional field selections are being crossed as males onto each orchard clone. Seed from the crosses serve three purposes: testing genetic worth of clones for possible orchard roguing, selecting seed within families from which a next generation of selections can be made, and establishing a seedling seed orchard for production of seed for the next generation. Many Northwest seed orchard owners have combined progressive programs (see "Progressive Programs") with their orchard programs to obtain early seed before their orchards begin to produce, to reduce inbreeding, and to correct deficiencies in the genetic base of their programs.

Seedling seed orchards established from full-sib families are a major element of several programs to provide second-generation seed. Orchards established on farmland use the same practices and have the same problems of differential cone production and pollen management as the grafted orchards. Some have been established with seedlings in large pots to accelerate early cone production and breeding and to permit flexible management.

WIDE CROSSINGS

Programs aimed at genetic gains from heterosis or at better growth from genes found in more mesic and mild portions of the range have been started in Germany (Schönbach and Bellmann 1967); British Columbia (Orr-Ewing and others 1972); Colorado, Idaho, and Oregon (Rowe and Ching 1973). The programs require a search to find best performers by race and by local percentage. The British Columbia experience since 1963 has narrowed the range-wide search to Oregon and Washington parents because of poor growth of crosses resulting from interior or low latitude parentage. Adaptation risks of such programs may be reduced by including wide-cross planting stock mixed with native stock. If the progeny do not perform to expectation, seedlings of local parentage will make the final crop (Orr-Ewing and others 1972). These programs are in the testing stages.

CLONAL PROGRAMS

Since Douglas-fir roots in satisfactory percentages as seedlings, clonal forestry becomes possible. A program to use clones of best parental combinations of adapted races is being developed in West Germany by the Escherode Tree Breeding Station. Similar concepts are being explored in New Zealand by the geneticists at the Rotorua Station. A substantial American research effort is in progress to produce plants from cotyledons (Cheng 1975) and from single cell culture (Winton and others 1974).

PROGRESSIVE PROGRAMS

Initially designed for small Douglas-fir ownerships, versions of progressive programs have spread to over 15 million acres (6 million ha) centered in the Douglas-fir region. These programs (Silen 1966b) feature a large genetic

base, dependence on family selection from tests using wind-pollinated seed, immediate use of seed from parent trees for commercial planting, rapid phasing from phenotypic to genotypic selection, and early crossing of parent trees in the forest for second-generation seed orchard stock. Advanced versions of the program consist of three distinct phases.

The first phase usually begins during a good seed year. Breeding zones, usually under 250,000 acres (100 000 ha) are delimited. Enough parent trees are selected, usually three parent trees per 1,000 acres (400 ha), to satisfy seed needs of the landowner. A wide range of selection intensity has been used. The program, however, depends primarily on gains from family selection based on testing of progeny. Wind-pollinated seed are collected from every parent for a genetic test. All seed from the best one-fourth of the parents are collected for commercial planting. The following year, 6 to 12 field progeny tests of the parents are installed (see "Testing").

The second phase, aimed at providing seed from years 15 to 30 of the program, consists of establishing second-generation seed orchards by year 5 of the program. Usual crossing design has been a single-pair mating of all parents to provide half as many crosses as number of parents. Full-sib progeny are planted in orchards at close spacing. No field tests of these crosses are considered essential since the parental ranking for general combining ability is established by the wind-pollinated test. Final intent is to remove 15 or 16 planted trees when the best one-fourth of the families and best one-fourth of the progenies are known, allowing panmixia among the final seed orchards at an irregular spacing averaging 36 feet (10 m). Costs of phases one and two in 1975 were \$3.50 per forested acre of ownership.

The third phase is initiated between years 15 and 20 of the progressive program. This calls for selection of the best individual trees of the best wind-pollinated families for second generation crossing. Seed from these crosses would be field tested as well as used in a seedling seed orchard for the following generation.

Many variations of the program now exist. They aim to eliminate steps such as a grafted seed orchard, a multiple cross-mating design, and an initial field test of full-sib crosses. Reduced genetic efficiency from control over only one parent in the first decade is a trade-off for the low cost and rapid pace with which a landowner can advance with a very large genetic base in a long-range breeding program by the

second decade. For example, in a span of 2 to 4 years, a landowner begins fulfilling seed needs from phenotypically selected parents, establishes a field test of parents, crosses them, and establishes a seedling seed orchard for the next generation of seed. Assurance of a seed supply from known parents has been the most immediate benefit.

The program involves nearly 10,000 parent trees. Sixteen cooperatives of private, State, and Federal landowners in Oregon and Washington have been formed to share parentage, to test programs, to cross parents, and to establish seedling seed orchards. Such cooperatives range from 70,000 to 560,000 acres (28 000 to 242 000 ha). The cooperatives receive overall guidance from the Forest Service, U.S. Department of Agriculture, and Industrial Forestry Association geneticists. Special greenhouse facilities have been established by private, State, and Federal landowners for growing containerized seedlings for the progeny tests (fig. 8).

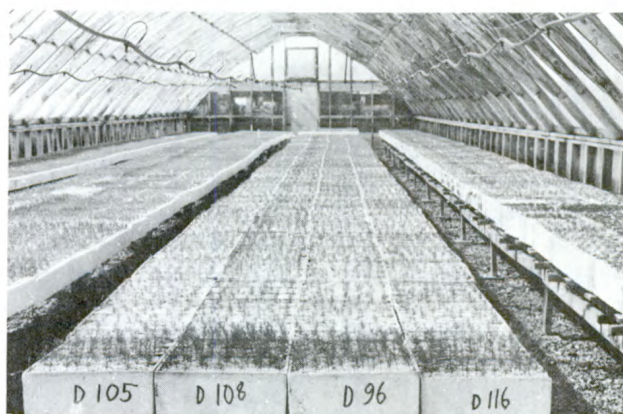


Figure 8.—A regional facility developed for the progressive program to grow progeny-test seedlings in containers for tree improvement cooperatives. Seedlings are produced from about 1,500 parents yearly for test sites which already surpass 125 in number in Oregon and Washington (photo, courtesy of Industrial Forestry Association).

A small progressive program was started in 1964 to improve Christmas trees. It was based on wind-pollinated seed of 100 randomly selected parent trees tested on eight plantations from Roseburg, Oreg., to Shelton, Wash. By 1974 the trees were harvested and sold. Of the 100 parents, the best 10 provided an average value gain of 18 percent, the top parent produced a 28-percent value gain. The top 11 parents have been crossed in a 6×11 mating to initiate a second generation program.

STRATEGIES

Strategies depend on objectives. A minor crop with a short rotation, such as Christmas trees, can have a relatively unsophisticated, economically defined objective. For a major long-term crop, like timber, the entire local or regional natural gene pool can become permanently altered. Tree improvement objectives and strategies for a major species like Douglas-fir are complicated by adaptational considerations (Silen and Doig 1976). Tree improvement strategies depend on whether or not the program begins with an adapted population.

SOURCES OF VARIATION

Beginning improvement strategies are understandably different where Douglas-fir is introduced, as contrasted to programs in its native range. Where it is an introduced tree, emphasis is on sampling enough races from appropriate climatic zones in the Douglas-fir range to find fastest growing adapted strains or in simply using seed from earlier importations (Heybroek 1974). Hardiness and resistance to disease are critical. In the Eastern United States, Europe, and New Zealand, the exact location of the best source is being sought from screenings of hundreds of collections of races from Douglas-fir's native range (Kriek 1974, Kleinschmit and others 1974). An important strategy for western Europe involves use of late bursting, rapid growing, low elevation races from narrow valleys of the Cascades, which are naturally selected for frost resistance to avoid freezing air draining from large mountainous basins. Once good races are found, utilization of the large range of phenology exhibited in every race to find particularly adapted individuals is a further logical step (Sweet 1965, Bialobok and Mejnartowicz 1970).

In contrast, in the most mesic, mild, and fastest growing part of its native range, the so-called Douglas-fir region, initial emphasis on improvement is usually confined to individuals from adapted populations within localities smaller than 250,000 acres (100 000 ha). The rationale is that potential gains from adapted pest-resistant local parents are adequate and risk free, whereas seed movement involves demonstrated risks. Moreover, the high expenses of testing nonlocal races can prudently be delayed. In a few years when tree improvement programs will have reduced selected populations to only a few percent of numbers now being tested in each locality, such testing will

be much more efficient. Adequate local variation permits good initial gains. The basic aim is to enhance growth without changing adaptation, particularly to keep the buffering qualities of the adapted population.

In the more xeric or cooler parts of Douglas-fir's range where greater hardiness is accompanied by slower inherent growth, improvement strategy combines testing of local parentage while incorporating genes for faster growth from races in milder or more mesic locations. The strategy is further intended to capitalize on occurrence of hybrid vigor from new gene combinations of previously separated populations (see "Wide Crossings").

In all strategies, customs have changed dramatically from use of small numbers of selected parents per seed zone to use of very large numbers of parents to provide for adequate selection differential after the tests and to buffer losses from poor adaptation. An ownership testing more than 1,000 parents is no longer rare. Screening of such large numbers became economically feasible with wind-pollinated tests.

The long period required for testing growth, survival, and wood quality in the species has prompted new strategies. Since short rotations enhanced predictability of juvenile-mature correlations, growing of short rotation products (pulp, Christmas trees, for example), and periodic application of fertilizers to speed growth are used as evasion strategies. Another strategy involves use of early traits that may be correlated with later good growth, such as photosynthetic efficiency (Campbell and Rediske 1966) or stockiness (Silen and Rowe 1971). The strategy is to rogue all but tall-stocky or high-photosynthetic families and to carry along large numbers of such families in field tests and later roguing for long-term adaptation. Neither strategy has become operational.

GAINS

Strategies aimed at maximizing gain per year are incorporated into several programs. One company is growing large numbers of wind- and cross-pollinated seedlings in large pots under a semicontrolled environment to reduce the breeding and testing cycle to about 5 years.

A widespread practice is to eliminate about 15 years dead time between first- and second-generation seed. Crosses involving all selections

are made soon after field testing of parents is underway. The full-sib progeny are immediately planted so they will reach seed-producing age about the same time that the field tests can confidently evaluate best parentage, in both cases thought to be about 15 years. All but the best fortuitous crosses will be rogued by this time to leave a full-sib seed orchard.

Clones provide several opportunities to shorten programs. Replicated tests of relative growth by individual trees are possible, and the growing of forest mixes of best clones is a powerful potential technique.

ADAPTATION

Of all the Douglas-fir strategy questions the most serious concern long-term adaptation. No geneticist will ever be able to use as expensive and effective methods, involving virtually infinite time and numbers of trees, as were employed in natural selection for adaptation to the local environment and climate. The trends of data on long-term adaptation suggest that with decreasing site severity, a concept still poorly defined, the geneticist has increasing opportunity to successfully increase growth. But even then he seems to be taking advantage only of an increasing time scale between climatic or biologic events that have struck the past genetic balance found in the local gene pool. The geneticist strikes a different balance to achieve gains. Hence, he must properly appraise any maladaptation in his product and exercise control over how and where it is used.

Again, evasion techniques may become useful strategies. Changing local populations only to the extent needed to achieve gains in commercial traits may continue the buffered balance between trees and endemic pests. The time period when many selective events occur may be avoided if large seedlings are planted. Early harvesting may avoid others. Enhancing moisture and fertility with silvicultural practices may permit the landowner to control still others. But a major part of any strategy may simply be to judiciously confine genetically improved Douglas-fir to the less severe sites. On severe sites where Douglas-fir has difficulty even to survive, the purportedly superior tree from a genetics program should not be expected to survive for long, let alone produce superior growth.

Agriculture experts long ago learned that only part of most land areas were economic for intensive culture. In the natural state, almost any square mile of the forested West was a mosaic of sites in which various species and species mixtures found ecological niches which they successfully dominated by specializations. To bring in an artificial population of a different species like Douglas-fir to generally replace them would seemingly require a more complex breeding program than was ever envisioned.

Genetically improved and locally adapted Douglas-fir, confined to favorable sites, should contribute significantly to the economy of temperate zone forests of the world.

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Reference Abstract

Silen, Roy R.

1978. Genetics of Douglas-fir. USDA For. Serv. Res. Pap. WO-35, 34 p.
Summarizes the natural distribution, habitat, taxonomy, life history, genetic variation, genetic techniques, programs, and strategies for Douglas-fir.

KEYWORDS: Natural variation, taxonomy, genetic programs, reproduction.

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