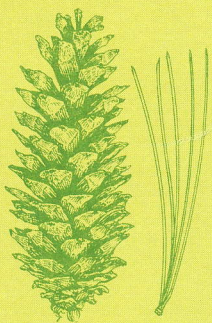


# GENETICS

of WESTERN WHITE PINE



# CONTENTS

	Page		Page
SUMMARY ABSTRACT .....	iii	Crossability .....	9
INTRODUCTION .....	1	Deleterious Recessive Genes and Other Genes .....	10
Paleobotanical and Present Range .....	1	Variation in Natural Stands .....	10
Speciation .....	3	Monoterpenes .....	10
Habitats .....	3	Growth .....	10
Growth .....	4	Insect Resistance .....	11
SEXUAL REPRODUCTION .....	4	Induced Mutation .....	11
Chromosomes .....	4	Blister Rust Resistance .....	11
Flowering .....	4	Physiology of Resistance .....	12
Cone and Seed Bearing .....	5	IMPROVEMENT PROGRAM .....	13
Pollen Storage .....	6	Breeding for Blister Rust Resistance .....	13
ASEXUAL REPRODUCTION .....	6	Tandem Selection for Blister Rust, Resistance and Growth Rate .....	13
Rooting .....	6	LITERATURE CITED .....	13
Grafting .....	7		
GENETICS AND BREEDING .....	7		
Taxonomy .....	7		

Issued December 1971

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.

## SUMMARY ABSTRACT

More than 20 years of investigation on the inheritance of white pine blister rust (*Cronartium ribicola*) disease resistance, growth, and other features of the paleobotany, flowering, seed yield, and inbreeding of western white pine (*Pinus monticola*) are summarized.

Megafossil collections indicate that the progenitor of *P. monticola* (the fossil species *P. wheeleri*) has been present in and around the present distribution of *P. monticola* since the early Pliocene to mid-Eocene eras, and that the species has withdrawn into four western North American subpopulations. Special significance is placed upon three megafossil cone collections from eastern Siberia, authoritatively identified as *P. monticola*. These collections indicate that *P. monticola* has had opportunity for gene-exchange with other Asiatic white pines that have evolved near the gene-center for *C. ribicola*.

*P. monticola* is monoecious, precociously female as early as age 7 and remaining so through age 20. Under wide spacing in a cultivated, irrigated, and fertilized seed orchard, grafts produced nine cones per tree 12 years after grafting; in a comparable arboretum seedlings produced 4½ cones at age 11, and 20 cones at age 18. Anthesis (♂) and receptivity (♀) are simultaneous, with ample overlap for self-pollination. Long-term average yields for 25- to 70-year-old trees are 28 cones; seed produced by these cones include 104 filled seed per wind-pollinated cone, 88 filled seed per controlled cross-pollinated cone and 47 filled seed per self-pollinated cone. Yields vary greatly between mother trees, localities, and seed years. Selfing results in lower cone and seed yields, and a growth reduction of 30 to 40 percent below that of outcrossed progenies.

Needle bundles and cuttings from young trees can be rooted with fair to good success. Greenhouse grafting is highly successful, but in northern Idaho field grafting meets with scant success.

*P. monticola* appears to be noncrossable with *P. balfouriana* and *P. aristata* of Subsection *Balfourianae*, but with at least three species of Subsection *Cembrae*, sound seed of unverified hybridity have been produced repeatedly. Within Subsection *Strobi*, repeated crossings with six other species have been successful, but repeated crossings with *P. armandii* and *P. lambertiana* have failed. Thus there is good prospect for obtaining white pine blister rust resistance-genes from resistant Eurasian species like *P. cembra*, *P. sibirica*, *P. koraiensis*, *P. griffithii* and *P. peuce*. Growth of individual hybrids varies widely depending on the particular parental combinations.

The genetic load of *P. monticola* includes deleterious recessive genes for albinism, dwarfing, curly needles, and a variety of chlorophyll deficiencies. Monoterpenes are under strong genetic control. Variation in growth associated with elevation of seed source appears to occur, especially at the extreme upper and lower elevations. Heritability of height growth is low (5 to 30 percent); heritability of blister rust resistance is high (65+ percent). Four races of *C. ribicola* characterized by foliage lesion types are recognized, and several recessive and dominant resistance-genes are either recognized or hypothesized.

Relative abundance and variety of white pine blister rust resistance factors present in *P. monticola* strengthens the hypothesis that *P. monticola* and *C. ribicola* have made contact in the past, or that gene-exchange has occurred between *P. monticola* and resistant Asiatic white pines. Breeding for blister rust resistance is eminently possible. A first-stage program for mass-producing partially resistant F<sub>2</sub> seed is now in the seedling-seed orchard planting stages; a second-stage program has been started for the purpose of further improving and stabilizing the level of resistance and to incorporate improvement of growth.

# Genetics of Western White Pine

R. T. Bingham, R. J. Hoff, and R. J. Steinhoff<sup>1</sup>

## INTRODUCTION

Western white pine (*Pinus monticola* Dougl.) is among the prized conifers native to the western United States. Its stately, clean-boled form (fig. 1), its soft, white, easily machined and valuable lumber, its ability to reproduce itself naturally, its relatively rapid and long-continued growth, and its occupancy of sites often not favorable for other commercial conifers all have combined to make this species a favorite of the forest manager throughout the species' range.

Now the introduced, epidemic white pine blister rust disease (pathogen *Cronartium ribicola* J.C. Fisch. ex Rabenh.) has rendered management of western white pine uneconomical over all but the southern part of its California-Sierra Nevada Mountain distribution. Thus, for the last 20 years, forest geneticists have been preoccupied largely with the survival trait (blister rust resistance) for this species. Improvement of other western white pine qualities is also underway.

### Paleobotanical and Present Range

The Cenozoic era progenitors of *P. monticola* Dougl., represented by four- to five-needled fascicles, winged seeds, and occasionally by cone fossils have been grouped under one wide ranging and morphologically variable fossil species, *Pinus wheeleri* Cockerell, by Chaney and Axelrod (1959); this species also may include the progenitors of *Pinus albicaulis* Engelm., *Pinus aristata* Engelm., *Pinus flexilis* James, *Pinus lambertiana* Dougl., and *Pinus strobiformis* Engelm. or *Pinus strobus* var. *chiapensis* Martinez (the soft or white pine classification of Critchfield and Little (1966) is followed). Distribution of these megafossils along with that of fossil and bog pollens and the pertinent references are shown in figure 2. Potassium-Argon dates determined for the fossil-bearing stratum

of six of the megafossil localities (Axelrod 1966a; Evernden and James 1964) place their age at 10.7 million years (early Pliocene) through 55 million years (mid-Eocene). Radio-carbon and other dating techniques place the age of bog pollens at from 2,000 to 18,000+ years (Hansen 1942c; 1947a; 1967).

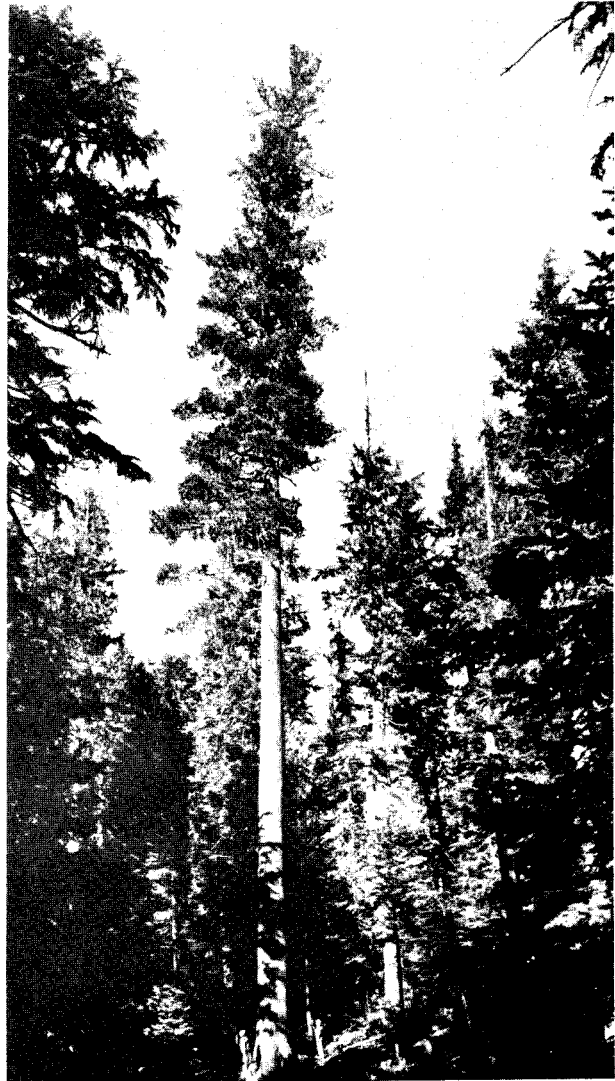
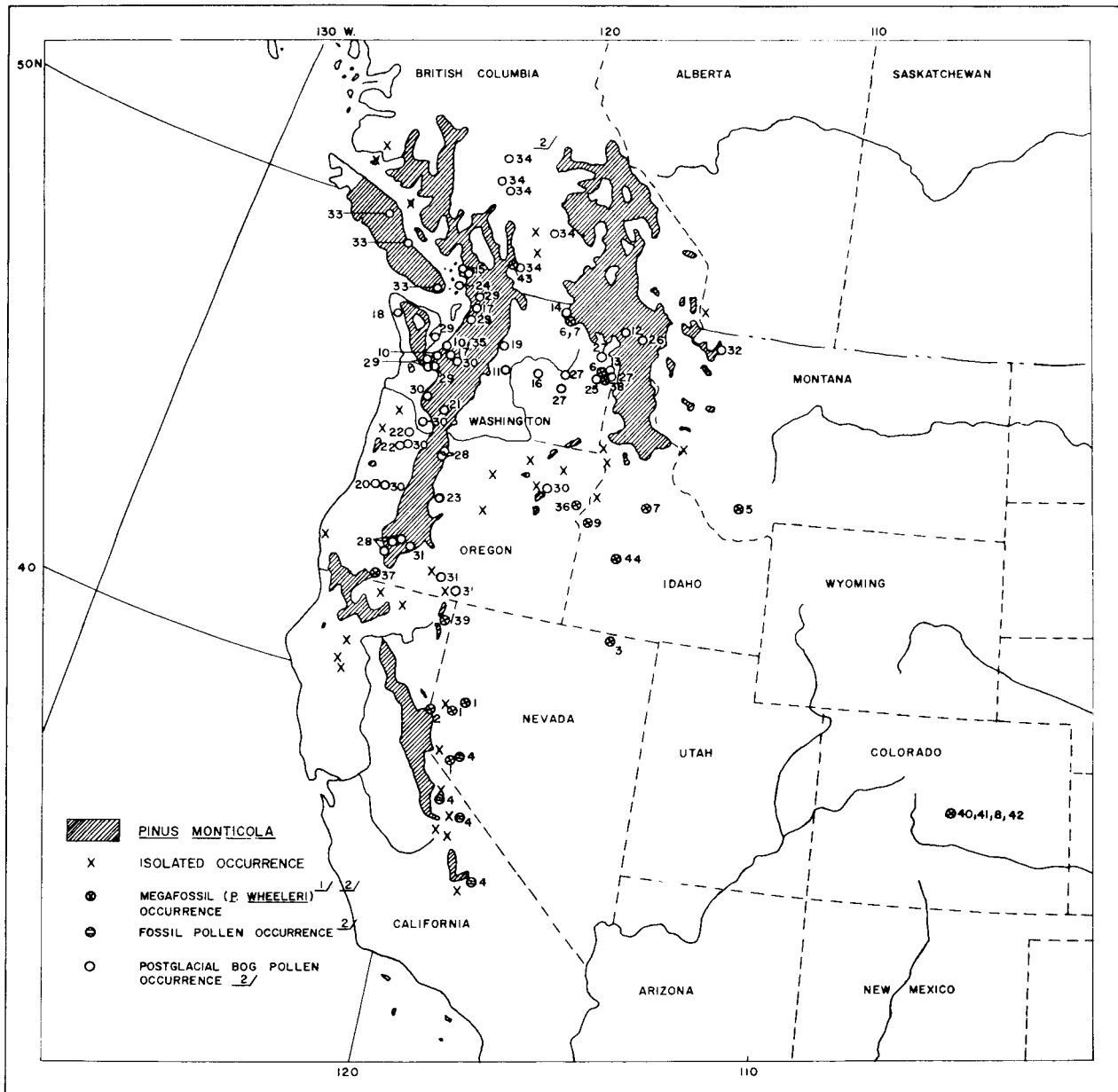


Figure 1.—An overmature western white pine (age 300+, height 185 feet, diameter 52 inches), growing on the Kaniksu National Forest, northern Idaho.

<sup>1</sup> Research Plant Geneticists, USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, Utah 84401; stationed in Moscow, Idaho, at the Forestry Sciences Laboratory, maintained in cooperation with the University of Idaho.

Genetics of western white pine--figure 2.  
 --Bingham, Hoff & Steinhoff  
 WO Forest Service Research Paper



1/ MEGAFOSSIL OCCURRENCES INCLUDE THOSE OF ALL SPECIES CONSIDERED SYNONYMOUS WITH *PINUS WHEELERI* COCKERELL, BY CHANEY AND AXELROD, 1959. CONTEMPORARY RANGE IS THAT OF MAP 6, CRITCHFIELD AND LITTLE, 1966.

2/ NUMBER ACCOMPANYING MEGAFOSSIL OR POLLEN OCCURRENCE IDENTIFIES THE AUTHORITY FOR THE OCCURRENCE, AS SHOWN BY CORRESPONDING NUMBER IN THE LITERATURE CITED.

Figure 2.—Past and present range of *Pinus monticola* Dougl.

There are reports of *P. monticola* (not *P. wheeleri*) megafossils from four different localities in northeastern and eastern Siberia (Hopkins, MacNeil, Merklin, and others. 1965; Vashkovsky 1959; Sukachev 1910; and Krish-tofovich 1941). The first three of these reports are based upon cones—the first two on sectioned cones (thus on seeds with wings, or their traces, on adaxial surfaces of cone scales, along with cone morphology),<sup>2</sup> and the third, according to Mirov (1967), on cone and branch material “preserved so well in frozen strata that it was identified without any difficulty as *P. monticola*.” These megafossils are dated merely “Tertiary” (Mirov 1967), or late Pliocene to early Pleistocene.<sup>3</sup> These Siberian megafossils seem to be correctly identified and thus lead to the following alternative hypotheses: (1) that progenitors of *P. monticola* crossed the Bering Land Bridge (probably eastward, Mirov 1967) from Siberia and retreated southward in North America before the evolution of the blister rust fungus; (2) that the pine and rust met somewhere in northeast Asia, but that the rust was somehow incapable of following the pine in its retreat to North America; or (3) that the pine and rust were present simultaneously in northeast Asia yet never met, the pine, via pollen, having exchanged genes with resistant Asian pines so that it carried away some resistance genes in its retreat across the Bridge.

Considering North American megafossil and fossil pollen occurrences, it would seem that the present range of *P. monticola* is very similar to its range during the Pliocene. However, the species never quite regained the range it occupied prior to glaciation; for the most part it failed to repopulate the now dry areas at the fringes of the present range. The occurrence of *P. wheeleri* fossils at Florissant, Colorado (the type locality, Cockerell 1908) is somewhat difficult to reconcile with the distribution of most of the other fossils attributed to that fossil species; it is also difficult to reconcile this occurrence with the present range of *P. monticola*. The type specimen, however, has needles which are exceptionally long (12+ cm.) in respect to other collections of *P. wheeleri*, or for that matter to present-day *P. monticola*. Thus, there is a possibility it might be a progenitor of the present-day *P. strobus* var. *chiapensis*, or *P.*

*strobiformis*, both of which often have needles of this length.

In any event, *P. monticola* seems to have withdrawn into four major gene centers that are now more or less isolated. This is shown by Map 6 of Critchfield and Little (1966) and in figure 2 which is an adaptation of that map. The four subpopulations (Inland Empire, Cascade Mountains-Vancouver Island, Siskiyou Mountains, and Sierra Nevadas) appear to have been isolated for at least several thousand years, and possibly much longer. Latitudinal spread of the species is relatively great, almost 17½°. The southernmost outlier of *P. monticola* is probably in Onion Valley north of Siretta Peak, California<sup>4</sup> and the northernmost near Quesnel Lake, B. C. (Can. Dep. Resources and Develop. 1950).

No range-wide study of genetic variation has yet been undertaken; however, in view of the geographic, climatic, topographic, and edaphic diversity of the present major population centers, plus outliers, interpopulation variation can be expected to be great.

## Speciation

A study of Maps 5 through 8 in Critchfield and Little (1966) also gives rise to speculation concerning natural hybridization and/or introgression of *P. monticola* with other North American white pines. *P. monticola* is isolated by more than 1,000 miles from *P. strobus* L., with which, however, it remains quite crossable. But at some localities (extreme southeastern British Columbia, Blue Mountains of northeastern Oregon, and in the central and southern Sierra Nevadas of California) *P. monticola* occurs close to crossable *P. flexilis* and we may presume a limited but continuing gene exchange. *P. monticola* and *P. albicaulis* are sympatric over an even greater portion of their ranges. Although these latter species appear to cross only with difficulty, there exist even more possibilities for gene exchange. *P. lambertiana* is another western North American white pine with a partly sympatric range, but it has proved to be noncrossable with *P. monticola* (see section on crossability, page 9).

## Habitats

Over most of its range (fig. 2), *P. monticola* is fire-perpetuated, seral, and frequently is a pioneer species. In the north (Inland Empire

<sup>2</sup> Personal communication, A. P. Vashkovsky, 1968, through Dr. David M. Hopkins.

<sup>3</sup> Personal communication, Dr. David M. Hopkins, 1968; A. P. Vashkovsky, 1968, through Dr. Hopkins.

<sup>4</sup> Personal communication, W. B. Critchfield, 1967.

and Vancouver Island-Puget Sound area) it ranges over a broad elevational belt from 1,000 to 6,000 feet in the Inland Empire, and from sea level to 5,000 feet on the Pacific Coast (Wellner 1962). To the south, in the Cascades and Sierra Nevadas, however, it is often narrowly belted between Douglas-fir—western hemlock and Pacific silver fir forest-cover types (Society of American Foresters 1954) at 5,000 to 7,500 feet in southern Oregon, between Douglas-fir—western hemlock and red fir types at 6,000 to 7,500 feet in the northern Sierras of California, and between ponderosa pine, sugar pine, fir-Jeffrey pine types at 8,500 to 10,000 feet in the southern Sierras of California. Even though *P. monticola* is narrowly belted in the southern part of its range, the species displays aggressiveness and tenacity in this transition zone between mid- and high-elevation types.

Climatically, on the north, stream-bottom types persist although they may receive as little as 25 inches of annual precipitation. In areas where 35 to 40 inches of precipitation is received, the distribution of *P. monticola* is general. On western Vancouver Island *P. monticola* grows in 110-inch precipitation areas (Wellner 1962). Growing seasons on the north range from less than 70 to more than 225 days (Wellner 1962), and an elevationally associated variation in growing season length of as much as 40 to 80 days may occur between stands only a few miles apart. Little is known about soil requirements of *P. monticola*; however, in northern Idaho best growth occurs on deep, well drained, medium to fine textured soils overlying a variety of parent materials (Wellner 1962).

## Growth

Early height growth of *P. monticola* is very slow, unlike that of its near relatives *P. strobus* and *Pinus griffithii* McClell. (blue pine or Hima-

layan white pine). At an age of 1 year the nursery seedlings average only 3 to 5 cm. in height (Squillace and Bingham 1954); they average 5 to 10 cm. at age 2 (Squillace and Bingham 1958a). Transplants in three northern Idaho field plots ranged from: 11 to 17 cm. in height at age 3 (Bingham, Squillace, and Patton 1956; Squillace and Bingham 1958a); 17 to 25 cm. at age 4 (Squillace, Bingham, Namkoong, and others. 1967); and they averaged 57 cm. in height at age 9.<sup>5</sup> In natural stands *P. monticola* does not commence rapid height growth until about age 15, although rapid growth may begin as early as age 10 under wide spacing in cultivated, watered, and fertilized plantations (Bingham 1967). Thereafter height growth continues at 1 to 3 feet per year, often for more than 100 years on the better sites. Maximum heights of 220 to 240 feet, and diameters (d.b.h.) of 81 to 84 inches are recorded (Anonymous 1956; Otter 1933), probably for 400- to 500-year-old veterans.

Another characteristic of western white pine growth that contributes to the difficulty of its establishment in plantations and arboreta, especially outside its natural range, is its youthful sensitivity to winter injury. Where nursery seedlings are not under deep snow or otherwise protected from frost-heaving and exposure to drying winter winds, they may be killed outright, and transplants up to 10 years of age may be almost completely defoliated.

Added to these problems is another one concerning seed dormancy. Early fall sowing (October), or long periods of stratification (90 to 120 days) help to overcome seed coat and embryonic dormancies but even these treatments often fail to assure good germination.<sup>5</sup>

For successful greenhouse manipulation of potted seedlings, at least 14 weeks of chilling at 40° F. is required before seedlings will resume normal growth (Steinhoff and Hoff in preparation).

## SEXUAL REPRODUCTION

### Chromosomes

Saylor and Smith (1966) studied chromosome behavior in *P. monticola*, showing the typical number ( $n = 12$ ) of chromosomes and relatively minor meiotic irregularities in the species or in its hybrids with *P. strobus* and *P.*

*griffithii*. R. J. Hoff<sup>5</sup> later confirmed the number  $n = 12$ .

### Flowering

*P. monticola* is monoecious. Like many pines it is precociously female; in a northern Idaho arboretum it produces female strobili as early



as age 7 (Bingham 1967). Righter (1939) also reported female strobili in this species at age 7 at a Placerville, California, arboretum, and Olson (1932) observed mature cones in the field in northern Idaho at age 10. *P. monticola* remains predominantly "female" through age 20 or more; in a Moscow, Idaho, arboretum during a bumper "flowering" year, at age 15–18 years, 90 percent of the trees produced female strobili but only 10 percent produced male strobili (Bingham 1967).

Five years of cultural treatments with young and with reproductively mature trees in the field (watering, fertilizing, and cultivating) had little effect on strobilus production. Neither did grafting 6-year-old seedling scions on reproductively mature stocks induce earlier or heavier flowering in young plants (Barnes and Bingham 1963). However, wide spacing of 5- to 7-year-old transplants and continued cultivation and irrigation with filtered and processed sewage effluent gave good results in a Moscow, Idaho, arboretum. Female strobili borne annually on 11- to 18-year-old trees increased from 4.5 per tree in 1964 to 20.2 per tree in 1967, and filled seed per cone ranged from 60 to 136 (Bingham 1967). Meanwhile, in a grafted seed orchard at Sandpoint, Idaho, up to 8 years after grafting on 5-year-old stocks, strobili per scion averaged less than one; 12 years after grafting, cones per scion averaged 9.2.<sup>5</sup>

Exact time of production of female cone initials is unknown in *P. monticola*, but apparently, like those of *P. strobus*, they are not visible until April or later in the year when they are pollinated (Ferguson 1904; Stephens 1962). Stephens (1962) did find differentiated male strobili of *P. strobus* by mid-November, but none at the end of August.

Bingham and Squillace (1957) summarized time of anthesis and maximum ovulate strobilus receptivity for a 6-year period on a number of *P. monticola* trees in northern Idaho as follows:

Elevation (feet)	Average date	
	Anthesis ♀	Strobilus receptivity
2,700 – 3,300	June 27	June 29
5000	July 8	July 7

Throughout this elevational range, for the 6 years observed, earliest pollen release was June 10; latest was July 12. The earliest receptive female strobili were found June 10; latest were found July 14. Certain individual trees in the same area were consistently early or late, and the sequence of flowering between areas was

firmly fixed. On a single area, over the 6 years, periods for maximum anthesis varied as much as 3 weeks; timing of anthesis was closely associated with average May and June temperatures. Generally, *P. monticola* is synacmous, i.e., there is no phenological barrier to selfing.

One convenient feature of *P. monticola* "flowering" is that unpollinated female strobili in sausage-casing bags may remain receptive for as long as 10 days to 2 weeks. After remaining receptive for this period, unpollinated strobili may abort and dehisce within another week.

Data are lacking on fertilization in *P. monticola*, but if the process is like that in *P. strobus*, it takes place in June, about 1 year after pollination (Ferguson 1904), and the maturing, second-year female strobili then elongate rapidly, reaching full size by mid-July.

## Cone and Seed Bearing

Large *P. monticola* cones ranging from 20 to 25 cm. in length have the potential for bearing more than 300 seeds, of which more than 225 filled seeds have been known to develop under wind pollination. Records over an 18-year period on more than 25,300 cones from 380 25- to 70-year-old trees at 13 localities in northern Idaho and northwestern Montana gave the cone and seed yields shown in table 1 (Bingham and Rehfeldt 1970).

TABLE 1.—Cone and seed bearing in young *P. Monticola* trees

Type of cones or seeds	Average	Maximum	Total trees observed
	<i>Number</i>		
Mature cones per tree	28	400+	380
Filled seed per cone:			
Wind-pollinated cones	104	226	172
Controlled cross-pollinated cones	88	222	329
Self-pollinated cones	47	161	202
Hollow seed per cone:			
Wind-pollinated cones	22	—	209
Controlled cross-pollinated cones	13	—	209
Self-pollinated cones	58	—	209

Good first-year female strobilus ("flower") crops occur once every 3 to 4 years, with the major cycle being 4 years. Autoregression techniques involving flowers of the four previous seasons accounted for 47 percent of the variation in current-season flower crops. Similar regressions extended to moisture stress (which

integrates temperature and precipitation) during June to mid-September indicated that warm, dry "stress" periods in the early summers of the 2 years prior to flower emergence favored flower production; on the other hand, stresses in the late summer of the year prior to emergence, or during the period of emergence, depressed flower production (Rehfeldt, Stage, and Bingham In preparation).

Mother trees, localities, and years in which the cones were born significantly affect yields of cones and seeds. Individual mother trees vary among themselves, but from year to year are consistent in their capacity to bear cones or set seed. To illustrate this variation, total annual seed-setting capacity for five low-yielding trees (average 20 cones per tree) observed 5 to 8 years was 4,250 filled seed; for five high-yielding trees (average 77 cones per tree) observed 5 to 15 years, the capacity was 55,600 filled seed (Bingham and Rehfeldt 1970). Different localities, seed years, and mother-tree microsites confound the preceding results; thus, it is impossible to prescribe extent of genetic control on cone and seed bearing.

Squillace (1967) studied the variability in length of cones from five trees where mean cone length ranged from 17 to 21 cm. He found that cones from a single tree varied as much as 12 cm. in length, although the maximum difference in average cone length between trees was only 13 cm. He also found that strobili on upper branches on the south and west sides of the tree produced higher yields of heavier seed. The largest *P. monticola* cone ever seen here was almost 36 cm. long, and the smallest was less than 5 cm. long.

Cone and seed insects, especially *Conophthorus monticolae* Hopk., *Eucosma rescissoriana* Hein., and *Dioryctria abietella* (D. and S.), cause partial to almost complete failures of cone crops in otherwise poor to fair crop years

(Barnes, Bingham, and Schenk 1962; Schenk and Goyer 1967).

Selfing of *P. monticola* produces lower yields of sound seeds, higher yields of hollow seed, and slower growing seedlings. On the average, the production of filled seed in self-pollinated cones averages only 55 percent of the yield in controlled cross-pollinated cones; furthermore, hollow seed yields are more than 2.5 times as great in the selfed as in the crossed cones (table 1). Selfed seedlings show a depression in height growth that seems to increase up to about age 10, then it levels off to a growth rate that is only 60 to 70 percent that of seedlings from outcrossed progenies of the same parent trees (Bingham and Squillace 1955; Squillace and Bingham 1958b; Barnes 1964).

A selective fertilization mechanism discriminating against self pollen, when in competition with outcross pollen, is probably effective in reducing natural selfing in *P. monticola*. Some western white pines were found to be highly self-fertile, but the majority were essentially self-sterile. This, along with lower selfed seed yields and lower survival of selfed seedlings, led to the conclusion that very small proportions of the seed produced by wind pollination in multiclone seed orchards would be selfs (Bingham and Squillace 1955; Barnes, Bingham, and Squillace 1962).

## Pollen Storage

Air dried pollens stored at 0° to 5° F. in a household deepfreeze unit retain for 3 years or more their ability to set useful quantities of sound seed. Callaham and Steinhoff (1966) showed only 20 percent reduction in seed-setting ability of 3-year-stored vs. fresh pollens, and Bingham and Wise (1968) later confirmed these results, showing about 50 percent filled seed yields for 3-year-old pollens.

## ASEXUAL REPRODUCTION

### Rooting

Cuttings from western white pine trees more than 4 to 5 years old are difficult to root.<sup>5</sup> Despite this handicap, Deuber (1942) obtained 11 rooted cuttings from a total of 196 taken from a 56-year-old tree; however, he later reported no success with 120 cuttings from a 45-year-old tree. Cuttings from 3-year-old seedlings have been rooted with fair success (20 to 30+ per-

cent).<sup>3</sup> These cuttings were collected during March, treated with rooting hormones, and planted in Palouse silt loam soil : peat moss : sand, or in pure sand.

Needle bundles taken from 2-year-old western white pine seedlings have been rooted successfully (Hoff and McDonald 1968; McDonald and Hoff 1969). These needle bundles were collected during February or early March, and were (1) treated with rooting hormones or left untreated

and (2) placed in washed river sand or a mixture of this sand with peat moss and forest soil (1:1:1). Highest rooting success (81 percent) was with a treatment of rooting hormones and a forest soil: peat moss: sand culture medium. In one experiment involving 318 budded needle bundles (Hoff and McDonald 1968) 45 of the bundles rooted and eight of these produced shoot growth.

## Grafting

*P. monticola* is relatively easy to propagate by grafting at all ages (Bingham 1966; Barnes and Bingham 1963). Several types of grafts have been used with good success including bottle, whip-and-tongue, side, approach, and wedge grafts. Early spring grafting prior to flushing is most successful, and yet scions collected during early winter and stored in a freezer grafted nearly as well as those collected fresh. Furthermore, scions taken from a variety of places in the tree crown graft with equal success (Hanover 1962).

Grafting conducted under greenhouse conditions, including high humidity control, consistently gives the best results (85 to 95 percent success in securing unions and new growth on scions), whereas the success of field grafting varies depending upon weather conditions. On the West Coast, and in some interior valleys of the Inland Empire, grafting success has been good—probably because of high humidity during and after grafting. But in the hotter, drier regions of the Inland Empire such as at Moscow and Sandpoint, Idaho, field grafting is a chancy operation. Success is only 30 percent, or less, even when a plastic bag with an aluminum foil covering is used over the graft.

There may be clonal differences in ability to graft (Hanover 1962). Two hundred and fifty greenhouse grafts were made for each of 13 ortets. Four months after grafting, survival rates ranged from 97 down to 55 percent; but after two seasons in a greenhouse and one in the field, survival rates ranged from 83 to 13

such as observed in older grafts of southern percent. Hanover concluded that this was due to an early incompatibility, possibly associated with the vigor of ortets. Latent incompatibility pines and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) recently also has been observed in *P. monticola* grafts, 12 years after grafting.<sup>5</sup>

Subsequent growth of grafts has ranged between good (Bingham 1966) on northern Idaho field plots to fair or poor in a Moscow arboretum.<sup>5</sup> Growth records at a grafted seed orchard at Sandpoint, Idaho (Bingham, Hanover, Hartman, and others. 1963), show that within 3 years after grafting most grafts were developing into normal upright trees.

Although root grafting has been commonly reported for most forest species, there are only a few reports of root grafts for western white pine: C. D. Leaphart<sup>5</sup>; Rigg and Harrar 1931; McMinn 1955. This is probably due to a lack of reporting and not to a lack of observation. Two natural intertree branch-to-stem grafts in *P. monticola*, one of these grafts involving a *Thuja plicata* Donn, have been observed by C. A. Wellner.<sup>6</sup>

Interspecies grafting of *P. monticola* scions on other white pine rootstocks has been generally successful. R. T. Bingham and A. E. Squillace<sup>5</sup> successfully grafted *P. monticola* on *P. strobus* and on western white pine interspecies hybrid rootstocks (*P. monticola* X *P. strobus* and *P. monticola* X *P. griffithii*). Dr. J. W. Duffield,<sup>7</sup> successfully grafted *P. monticola* on *P. lambertiana*, *P. griffithii* and *Pinus ayacahuite* Ehrenb. rootstocks; also, he successfully grafted *P. monticola* on the *P. monticola* X *P. strobus* hybrid rootstock. And Bingham and Squillace<sup>5</sup> attempted interspecies grafts with *P. monticola* scions on *Pinus ponderosa* Laws., *Pinus contorta* Dougl., *Picea engelmannii* Parry, *Pseudotsuga menziesii*, and the interspecies hybrid *Pinus contorta* X *Pinus banksiana* Lamb. A few grafts of all of these latter combinations made weak unions and remained alive 4 to 5 months, but thereafter all scions died during the winter.

## GENETICS AND BREEDING

### Taxonomy

*P. monticola* (according to Critchfield and Little 1966) has been placed in Subgenus *Strobus*, Section *Strobus*, Subsection *Strobi*. This classification is equivalent to Shaw's (1914

and 1924) placement of the species in Section *Haploxyylon*, Subsection *Cembra*, Group *Strobi*. Thus, *P. monticola* belongs among the five-

<sup>5</sup> Personal communication, 1968.

<sup>6</sup> Personal communication, 1968.

<sup>7</sup> Personal communication, 1951.

TABLE 2.—Summary of hybridization efforts within portions of the Subgenus *Strobos* Section *Strobos* of the Genus *Pinus*.<sup>1</sup>

Table 2.--Summary of hybridization efforts within portions of the Subgenus *Strobos* Section *Strobos* of the Genus *Pinus*.<sup>1/</sup>

Subsection	<u>CEMBRAE</u>	<u>pumila</u>	<u>sibirica</u>	<u>koraiensis</u>	<u>albicaulis</u>	<u>flexilis</u>	<u>strobiformis</u>	<u>armandii</u>	<u>ayacahuite</u>	<u>lambertiana</u>	<u>parviflora</u>	<u>peuce</u>	<u>griffithii</u>	<u>strobos</u>	<u>monticola</u>
Subsection <u>CEMBRAE</u>															
<u>P. cembra</u> L.															
<u>P. pumila</u> Regel															
<u>P. sibirica</u> Du Tour															
<u>P. koraiensis</u> Sieb. & Zucc.	F-1 <sup>2/</sup> 1,3 <sup>3/</sup>														
<u>P. albicaulis</u> Engelm.	U-2-a 3,4	U-1-a 4	U-1-a 3	F-2 3,4,10											
Subsection <u>STROBI</u>															
<u>P. flexilis</u> James	F-1 3,4,10	F-1 4	F-1 3	F-1 3,4,10	U-2-a 4										
<u>P. strobiformis</u> Engelm.					F-1 4	H-1-a 6									
<u>P. armandii</u> Franch.	F-1 3		F-1 3	U-1-a 10	F-1 3,4	F-1 4,10	F-1 10								
<u>P. ayacahuite</u> <sup>4/</sup> Ehrenb.	F-1 10				F-1 4	H-1-b 10									
<u>P. lambertiana</u> Dougl.	F-1 3			H-2-a 10	F-1 10	F-1 4,10	F-1 10	H-3-a 3,4,10	F-1 4 <sup>5/</sup> ,10						
<u>P. parviflora</u> Sieb. & Zucc.	F-1 3,10				F-1 3,4	F-1 3,4,10				F-1 3,10					
<u>P. peuce</u> Criseb.	F-1 1			F-1 1,10		F-1 3,4				F-1 10	H-1-a 10				
<u>P. griffithii</u> McClell.	F-1 10		F-1 3	F-2 3		H-2-a 3,10	F-1 4	H-1-a 10	F-1 10	H-1-b 3,10	H-2-a 3				
<u>P. strobus</u> L.	F-1 1,10			U-2-b 1,8	F-1 10	H-2-a 5,10	F-1 10	H-2-b 9,10	F-2 3,5,10	H-2-b 3,5,8,10	H-2-a 1,3,5,10	H-3-b 3,5,10			
<u>P. monticola</u> Dougl.	U-1-a 2			U-2-a 2,10	U-1-a 2	H-2-c 2,6	H-1-a 4,7 <sup>6/</sup>	F-2 2,4,10		F-2 2,4,10	H-2-c 2,3,10	H-2-c 2,3,6	H-3-c 3,10	H-3-c 2,3,5,10	

<sup>1/</sup> This table is adapted from Wright (1959). It includes his information through that date, plus new information (footnoted) obtained from the same and additional stations through 1968.

<sup>2/</sup> F = failure, U = uncertain--sound seed or seedlings produced but hybrids not yet authenticated, H = hybrids verified.  
1 = less than 20 crosses attempted, 2 = 20-50 crosses attempted, 3 = more than 50 crosses attempted.  
a = less than 1 filled seed per cone, b = 1-5 filled seeds per cone, c = more than 5 filled seeds per cone.

<sup>3/</sup> Numbers refer to the following references: 1. C. E. Ahlgren, 1967, personal communication. 2. Table 3, this paper. 3. C. Heimburger, 1967, personal communication. 4. Breeding record files, Inst. Forest Genetics, Placerville, Calif. 5. H. B. Kriebel, 1967, personal communication. 6. Little and Righter, 1965. 7. Righter and Duffield, 1951. 8. H. Saho, 1968, personal communication. 9. E. J. Schreiner 1967, personal communication. 10. Wright, 1959.

<sup>4/</sup> Some of the reports listing *P. ayacahuite* probably refer to variety *brachyptera* which is synonymous with *P. strobiformis*.

<sup>5/</sup> Originally reported as H in Wright, 1959.

<sup>6/</sup> Originally reported as *P. monticola* x *P. ayacahuite*.

needed white pines having deciduous needle sheaths, unarmed, terminal cone-scale umbos, with cones that open and liberate the seed, and with seeds having either well-developed or rudimentary wings.

Critchfield and Little (1966), whom we follow, list 14 species in the Subsection *Strobi*. We will consider here only 10 of these Subsection *Strobi* species which are those having a substantial botanical range and with which interspecies hybridization has been attempted more than a few times. In addition, we will consider five white pines in Subsection *Cembrae* and two in Subsection *Balfourianae*.

### Crossability

From the taxonomic standpoint crossability of *P. monticola* with all species of the Subgenus *Strobis* would be of interest. But from the practical, tree improvement standpoint, its crossability with those species in Section *Strobis*, or in Section *Parrya*, Subsection *Balfourianae* (i.e., the five-needled white pines), is of greatest interest for improving blister rust resistance or other qualities of *P. monticola*.

Unfortunately, the Subsection *Balfourianae* pines (*Pinus balfouriana* Grev. and Balf. and *P. aristata*), both of which are moderately resistant to blister rust, appear not to be cross-

able with *P. monticola*.<sup>8</sup> In the Subsection *Cembrae* and *Strobi* pines, however, crossability is fair to good, as shown in table 2.

*P. monticola* has proved to be easily crossable with six of the other nine important white pines of Subsection *Strobi*, including the moderately resistant *P. peuce* and the highly resistant *P. griffithii*. Failure to produce the *P. monticola* X *P. armandii* hybrid has been disappointing, since the southeastern Asian *P. armandii* is probably the world's most blister rust resistant white pine. Conversely, probable success of inter-Subsection crosses between *P. monticola* and moderately to highly resistant *P. cembra* and *P. koraiensis* encourages the resistance breeder.

More than 180 controlled pollinations attempting to produce interspecies hybrids between *P. monticola* and other white pines in Subsections *Strobi*, *Cembrae*, and *Balfourianae* have been made by the Intermountain Forest and Range Experiment Station, Moscow, Idaho, as part of the project for investigation of blister rust resistance. Results of these crossings are outlined in table 3; they confirm the general findings on crossability shown in table 2.

<sup>8</sup> Unpublished data: USDA Forest Service, Institute of Forest Genetics, Placerville, California, and the Intermountain Forest and Range Experiment Station, Moscow, Idaho.

TABLE 3.—*Pinus monticola* interspecies hybrids attempted 1950–1968

Pollen parent	Number of different crosses attempted	Total number strobili pollinated	Total number cones collected & extracted	Number of crosses producing filled seed	Average number of filled seed per mature cone	Total number of filled seed all crosses	Total number of seedlings produced
Section <i>STROBUS</i>							
Subsection <i>CEMBRAE</i>							
<i>P. albicaulis</i>	5	165	112	5	0.5	74	0 <sup>1</sup>
<i>P. cembra</i>	7	121	97	5	1–	73	3
<i>P. koraiensis</i>	19	441	286	5	trace	43	10
Subsection <i>STROBI</i>							
<i>P. armandii</i>	14	344	90	2	trace	2 <sup>2</sup>	0
<i>P. flexilis</i>	26	680	428	24	19.9	5,168	2,000±
<i>P. lambertiana</i>	5	152	105	2	trace	3 <sup>2</sup>	not sown
<i>P. parviflora</i>	13	374	269	13	31.4	9,790	445
<i>P. peuce</i>	20	467	273	20	17.0	5,154	700+
<i>P. strobus</i>	35	585	327	32	18.9	4,645	2,000±
<i>P. griffithii</i>	28	676	271	8	0.9	568	175±
Section <i>PARRYA</i>							
Subsection <i>BALFOURIANAE</i>							
<i>P. aristata</i>	7	224	161	1	trace	2 <sup>2</sup>	0
<i>P. balfouriana</i>	6	212	182	1	trace	1 <sup>2</sup>	0

<sup>1</sup> Seed collected in 1968—not yet planted.

<sup>2</sup> Possibly resulting from contaminating *P. monticola* pollens accidentally getting into pollination bags.

## Deleterious Recessive Genes and Other Genes

Several single recessive genes are recognized in *P. monticola* self-pollinated progenies. Among 150 trees represented by S<sub>1</sub> progenies, we recognize the following: 15 carriers of an albino gene; another 10 or more trees carrying chlorophyll-deficiency genes (deficient seedlings show various shades of yellow-green foliage); one or two trees having a curly-foilage gene; and at least one tree having a dwarfing gene. Selfed progenies of five or more trees contain chlorophyll-deficient types where segregation is not clearly in a 3:1 ratio, and one selfed progeny that contains a very low proportion of types having green cotyledons but albino epicotyls. One tree carries the albino, the curly-needle, and the dwarfing gene. Crossed albino carriers do not necessarily produce albinos—i.e., two or more loci for the recessive albino gene are involved.

### Variation in Natural Stands

Phenotypic variation among trees along an elevational transect from 2,500 to 4,600 feet was studied by Barnes (1967). He found that trees from 2,500 to 4,000 feet grew at approximately the same rate, but that trees at 4,600 feet grew significantly slower. Growth at an additional plot at 5,200 feet was much reduced, but part of the reduction appeared to be caused by more severe infection by blister rust. Branch angle increased regularly as elevation increased.

### Monoterpenes

The production of monoterpenes in *P. monticola* appears to be under strong genetic control. Hanover (1966a) found the inheritance of alpha-pinene, beta-pinene, 3-carene, limonene, and an unknown terpene to be mainly controlled by additive gene action. In another study Hanover (1966b) found the production of 3-carene to be controlled primarily by a single gene.

### Growth

Research aimed at improving the growth and quality of *P. monticola* has proceeded along with the work to secure blister rust resistance. However, because of the problem of securing sufficient test materials that would survive continued exposure to blister rust, the program

and results have been rather restricted. The first two nursery and field tests (1952 and 1953) for rust resistance were also used to get an early idea of height growth potential of the selected trees. At the end of 1 year's growth in the nursery, the correlation between periodic annual growth of the individual parents and height growth of their seedlings was found to be 0.30; in a second experiment the next year this correlation was 0.84 (Squillace and Bingham 1954). In further studies of the heritability of juvenile growth rate of the same seedlings in field plots (Squillace, Bingham, Namkoong, and others. 1967), average heritability of fourth-year height increment was approximately 6.6 percent. It was predicted that possible genetic gain, based on several combinations of selection and progeny testing, would range from 4 to 12 percent. In another investigation of height growth in 1-year-old seedlings, Hanover and Barnes (1963) found that heritability values for epicotyl length ranged from a low of 5 percent (based on female-parent variance) to 31 percent (based on male-parent variance).

Squillace and Bingham (1958a) found that the progeny from trees on moist, north-facing slopes grew faster than the progeny from trees growing on adjacent dry, south-facing slopes under nursery and field conditions. They also found that the foliage of progenies from high elevation trees had a higher dry matter content than those from low elevation trees. The progeny of low elevation trees grew faster at a low elevation nursery site than high elevation progenies, but slower than high elevation progenies in a high elevation planting. Information from another series of plantings indicates that some progenies perform about the same regardless of the site while others may do well on one site but poorly on another.<sup>5</sup>

As indicated by the crossability data presented earlier (table 3), numerous hybrids involving *P. monticola* have been produced. Several workers have reported hybrid vigor for seedlings of the cross between *P. monticola* and *P. strobus* (Buchholz 1945; Righter 1945; Duffield and Righter 1953; Heimburger 1953; Riker and Patton 1954; and Bingham, Squillace, and Patton 1956). After 8 years of growth in northern Idaho, hybrid trees were slightly more than twice as tall as *P. monticola* progenies from the same female parents (Barnes and Bingham 1962). At age 14, however, the *P. monticola* seedlings were about 75 percent as tall as the hybrids;<sup>5</sup> this indicates that the expected fast early growth of hybrids is being

offset as *P. monticola* finally commences its period of rapid growth. This same phenomenon was observed by Bingham, Squillace, and Patton (1956); the height advantage of some hybrids disappeared so that they were, in time, intermediate in height between their parents.

Hybrids between *P. monticola* and *P. griffithii*, *P. flexilis*, and *P. strobiformis* have shown considerable promise at Placerville, California, by exceeding the growth of *P. monticola* (Duffield and Righter 1953, and unpublished data, Institute of Forest Genetics, Placerville, California). However, the test plantings are located about 3,000 feet below the elevational range of *P. monticola*, so a direct comparison may not be justified.

### Insect Resistance

Many entomologists and geneticists are investigating the possibility of using *P. monticola* as a source of resistance to the white-pine weevil (*Pissodes strobi* (Peck)) in eastern North America. Wright and Gabriel (1959) found that 15- to 25-year-old plantation trees were attacked much less severely than adjacent plantings of *P. strobus* of comparable age. When seedlings were subjected to attack by weevils in cages, *P. monticola* seedlings had fewer feeding cavities than *P. strobus* seedlings, but on older trees, *P. monticola* had twice as many cavities as *P. strobus* (Gerhold and Soles 1967).

### Induced Mutation

Techniques for inducing mutations that could provide new sources of disease resistance also have been investigated. Hanover (1965) found that ethyl methanesulfonate applied to seeds after stratification produced somatic mutations in one of the resulting seedlings.

Hanover and Hoff (1966b) tested another method of applying the same mutagen and found that sound seed were produced by pollen in water suspensions containing the mutagen.

### Blister Rust Resistance

After 40 years, in 1967, the USDA Forest Service finally abandoned blister rust control in northern Idaho, northeastern Washington, and northwestern Montana. This longstanding control program was abandoned due to existence of a particularly difficult set of control conditions: the high susceptibility of the *P. monticola* host; the abundance and susceptibil-

ity of the alternate *Ribes* spp. hosts; the extremely favorable climate for rust spread; and the difficult working terrain. These conditions have led to development of the world's most spectacular blister rust epiphytotic; under these conditions, blister rust resistance in *P. monticola* may be a survival trait.

For the resistance breeder, the massive epiphytotic and accompanying intense infection is a decided help. Rust-free trees, where persisting at levels of less than one in 10,000 trees, are easily located. Under clonal testing, most rust-free phenotypes prove to be resistant (Bingham 1966). However, since vegetative propagation of other than very young materials is unreliable and expensive, mass propagation of resistant varieties will be by seed. Thus, it is transmission of resistance that is the important character.

Work on inheritance of blister rust resistance in *P. monticola* began in 1950, with controlled matings between trees in a group of 20 phenotypically resistant parents; these parents, called "candidates," were 25- to 70-year-old rust-free trees in natural stands which had been exposed to the rust for 25 years or more. An irregular mating scheme was used. The 2-year-old progenies from these crossings were subjected to intense, artificial exposure to the rust. Examinations 4 years after inoculation disclosed that most candidates transmitted some resistance to their F<sub>1</sub> offspring. On the average, these progenies from candidate X candidate matings contained 12.6 percent more resistant seedlings than control progenies. More important, about one-fourth of the candidates exhibited general combining ability (g.c.a.), and about 30 percent of the seedlings from matings between such "g.c.a.-trees" survived the intense exposure to the rust (Bingham, Squillace, and Wright 1960).

Later, in tests conducted annually during the years 1960 through 1965, a more sensitive, four-tester mating scheme was used to confirm g.c.a. and levels of resistance in 400 candidate trees. Each of the four test crosses was represented by from 100 to 140 F<sub>1</sub> seedlings, divided among 10-row plots in a randomized block design used in planting each test in the rust resistance test nursery. Tests in which seedlings were 2 years old when inoculated and 4 years old when scored confirmed the earlier findings; about one-fourth of the candidates exhibited g.c.a., and progenies from crosses among g.c.a.-trees survived at near the 30 percent level.<sup>5</sup>

However, when we attempted to shorten the test rotation by inoculating seedlings at 1 year

of age and scoring them 2 years after inoculation, average survival levels in progenies of g.c.a.-trees dropped to 15 to 20 percent above controls (Bingham, Olson, Becker, and others, 1969). Other workers have noted similar host-age resistance phenomena in young white pines, resistance decreasing markedly with reduction in host age (Heimbürger 1958; Patton 1961; Patton and Riker 1966).

In any event, in test trees inoculated at 1 year of age, heritability of blister rust resistance in *P. monticola* is quite high. Bingham, Olson, Becker, and others (1969) computed narrow-sense  $h^2$  for the pertinent "selection units" (the four half-sib candidate X tester families upon which selection of g.c.a.-trees was based) as ranging from 64 to 100 percent, in three successive tests planted in 1960, 1962, and 1963. In these same tests ratios of general-to-specific combining ability averaged 2:1 in the better candidate trees and 10:1 in four testers previously selected for g.c.a. Candidate X tester progenies averaged only 4 to 7 percent greater survival than controls in these tests, but progenies of the better g.c.a.-trees averaged 13 percent above controls. And genetic gain in the next, or  $F_2$  generation (i.e., to be realized in the  $F_2$  seedlings, coming from orchards planted with resistant  $F_1$  trees of g.c.a.-tree matings) was estimated at 10 to 24 percent. It was anticipated that had inoculation been withheld to seedling age of 2 years, and final scoring to 3 years after inoculation (age 5 years), indicated first and second generation gains would have been higher.

Major genes may be implicated in blister rust resistance of *P. monticola* and a number of these with additive effects is hypothesized. There is evidence that in certain testers and candidates, frequency of needle lesions is controlled by a single gene with the two alleles nondominant and at equal frequency (Hoff and McDonald In preparation). Also, there is newer evidence that failure of foliar infections to become bark infections may reflect action of at least two independent, recessive genes (McDonald and Hoff, in preparation). Other new work by McDonald and Hoff indicates presence of at least four races of the rust pathogen, characterized by four foliage lesion types. Expression of the four types (races) may be controlled by three rust alleles. Also, one dominant and one recessive resistance gene in host foliage may control resistance to all four races of the pathogen.<sup>5</sup> In any event, there are two or more seats of resistance, in foliage and bark (Bingham, Squillace, and Wright 1960); this supports

the multiple gene hypothesis.

The relative abundance and variety of resistance factors currently present in *P. monticola* was an unexpected occurrence. Perhaps the hypotheses (2 and 3, page 3) that *P. monticola* and *C. ribicola*, or *P. monticola* and resistant Asian white pines, made contact in prehistoric times, provide an answer.

## Physiology of Resistance

Hanover's (1963a) analysis of several chemical constituents of the foliage and bark of resistant and susceptible *P. monticola* failed to reveal significant qualitative differences between phenotypically resistant and susceptible trees. Among nonsignificant differences observed were the following: a higher level of one polyphenol in resistant trees (Hanover 1963b; Hanover and Hoff 1966a); a slightly higher level of protein amino acids in susceptible trees; a higher amount of an unknown organic acid in resistant trees; higher levels of glucose in susceptible trees; higher levels of leucoanthocyanin in susceptible trees; a higher level of chlorophyll in resistant trees; a higher average dry matter content for susceptible trees; and a higher ash content for susceptible trees. Followup work on some of the above findings has been completed. The difference in the level of the polyphenol was not substantiated, but the same "almost significant" differences were found in dry matter content (Hoff 1968). Susceptible trees in both studies above were infected in varying degrees; therefore, it was hypothesized that the differences in dry matter content might be due to the infection level instead of being related to susceptibility. Later Schütt and Hoff (1969) found no significant differences in dry matter content between infected and noninfected full-sibs nor between noninfected grafts of resistant and susceptible trees. Because of a lack of knowledge concerning the precise sites, and genetic mechanisms of resistance, further followup work on earlier findings has been virtually stopped.

Hoff (1970) found that needle resistance of *P. monticola* could possibly be partly explained by an inhibitory compound(s) present in an ether fraction of an alcoholic extract of pine foliage. The ether fraction of six out of 16 resistant trees and one out of 16 susceptible trees decreased basidiospore germination of *C. ribicola*. This inhibitory action may be correlated with an observed needle resistance factor that was investigated by Hoff and McDonald (In preparation).



# IMPROVEMENT PROGRAM

## Breeding for Blister Rust Resistance

Because resistance to blister rust is the most important trait for *P. monticola* in the Inland Empire (northeastern Washington, northern Idaho, northwestern Montana and south-central British Columbia), and in coastal British Columbia, Washington, Oregon, and northern California, work on other traits largely has been held in abeyance awaiting results of resistance testing.

Now it appears that testing candidates for g.c.a. in respect to resistance (i.e., test crossing phenotypically resistant candidates and artificially inoculating test cross progenies), followed by remating of the best 25 percent of the g.c.a.-trees, artificially inoculating these progenies, and planting their surviving  $F_1$  seedlings so they will cross in seed orchards will give two-step gains perhaps producing up to 50 percent resistant  $F_2$  planting stock.

This is the practical "first-stage" program now underway in northern Idaho and in the western Washington and Oregon Cascade Mountain populations of *P. monticola*. In northern Idaho, first-stage orchards of resistant  $F_1$  seedlings will be planted beginning in 1971. Significant production of resistant  $F_2$  seedlings is anticipated by about 1985. Plans to control problems arising from elevational variation include remating g.c.a.-trees only from within the same elevational zones, and thereafter planting

resistant stock only onto sites within the pertinent zones.

## Tandem Selection for Blister Rust Resistance and Growth Rate

A "second-stage" selection program aimed at obtaining more highly resistant, possibly rust race buffered, and faster growing materials is just getting underway in northern Idaho. The first job of greatly expanding the genetic base of phenotypically resistant candidate trees was commenced in 1967. Almost 2,700 new candidate trees out of a goal of 2,800 have been located in 1967 through 1969.

Now that the second stage base has been selected, plans call for: (1) more meaningful, genecological classification of candidates according to habitat types and/or aspect and elevation to further preclude planting maladaptation; and (2) dual selection among 500- to 800-candidate groups in perhaps four to six ecological zones for both resistance and growth rate. The same or higher levels of resistance, along with 5 to 10+ percent increase in growth rate is anticipated from this second-stage work.

Mixed pollen crosses (Bingham 1968), improvement of inoculation methods, and securing higher progeny test efficiency are applied breeding objectives for the future.

## LITERATURE CITED

- Anonymous.  
1956. These are the champs. Part II. Amer. Forests 62: 33-40.
- (1)<sup>10</sup> Axelrod, D. I.  
1956. Mio-Pliocene floras from west-central Nevada. Univ. Calif. Pub. Geol. Sci. 33: 1-322.
- (2) \_\_\_\_\_  
1962. A Pliocene Sequoiadendron forest from western Nevada. Univ. Calif. Pub. Geol. Sci. 39: 195-268.
- \_\_\_\_\_  
1966a. Potassium-Argon ages of some western Tertiary floras. Amer. J. Sci. 264: 497-506.
- (3) Axelrod, D. I.  
1966b. The Eocene Copper Basin flora of northeastern Nevada. Univ. Calif. Pub. Geol. Sci. 59: 1-83.
- (4) \_\_\_\_\_, and W. S. Ting.  
1960. Late Pliocene floras east of the Sierra Nevada. Univ. Calif. Pub. Geol. Sci. 39: 1-118.
- Barnes, B. V.  
1964. Self- and cross-pollination of western white pine: a comparison of height growth of progeny. USDA Forest Serv. Res. Note INT-22, 3 p.
- \_\_\_\_\_  
1967. Phenotypic variation associated with elevation in western white pine. Forest Sci. 13: 357-364.

<sup>10</sup>Numbers in parentheses identify authorities for megafossil and fossil pollen occurrences of figure 2.

- Barnes, B. V., and R. T. Bingham.  
 1962. Juvenile performance of hybrids between western and eastern white pine. USDA Forest Serv., Intermountain Forest and Range Exp. Sta. Res. Note 104, 7 p.  
 \_\_\_\_\_ and \_\_\_\_\_
1963. Flower induction and stimulation in western white pine. USDA Forest Serv. Res. Pap. INT-2, 10 p.
- \_\_\_\_\_, \_\_\_\_\_, and J. A. Schenk.  
 1962. Insect-caused loss to western white pine cones. USDA Forest Serv., Intermountain Forest & Range Exp. Sta. Res. Note 102, 7 p.  
 \_\_\_\_\_, \_\_\_\_\_, and A. E. Squillace.
1962. Selective fertilization in *Pinus monticola* Dougl. II. Results of additional tests. *Silvae Genet.* 11: 103-111.
- (5) Becker, H. F.  
 1961. Oligocene plants from the Upper Ruby River Basin, southwestern Montana. *Geol. Soc. Amer. Memoir* 82, 127 p.
- (6) Berry, E. W.  
 1929. A revision of the flora of the Latah formation. U.S. Geol. Surv. Prof. Pap. 154-H: 225-264.
- Bingham, R. T.  
 1966. Breeding blister rust resistant western white pine. III. Comparative performance of clonal and seedling lines from rust-free selections. *Silvae Genet.* 15: 160-164.
- \_\_\_\_\_  
 1967. Possibilities for production of blister rust resistant tree seed in the Moscow Research Arboretum. USDA Forest Serv., Intermountain Forest and Range Exp. Sta. Office Rep. August 23, 18 p.
- \_\_\_\_\_  
 1968. Breeding blister rust resistant western white pine. IV. Mixed pollen crosses for appraisal of general combining ability. *Silvae Genet.* 17: 133-138.
- \_\_\_\_\_, J. W. Hanover, H. J. Hartman, and Q. W. Larson.  
 1963. Western white pine experimental seed orchard established. *J. Forest.* 61: 300-301.
- \_\_\_\_\_, R. J. Olson, W. A. Becker, and M. A. Marsden.  
 1969. Breeding blister rust resistant western white pine. V. Estimates of heritability, combining ability, and genetic advance based on tester matings. *Silvae Genet.* 18: 28-38.
- \_\_\_\_\_, and G. E. Rehfeldt.  
 1970. Cone and seed yields in young western white pines. USDA Forest Serv., Res. Pap. INT-79, 12p.
- Bingham, R. T., and A. E. Squillace.  
 1955. Self-compatibility and effects of self-fertility in western white pine. *Forest Sci.* 1: 121-129.  
 \_\_\_\_\_ and \_\_\_\_\_
1957. Phenology and other features of the flowering of pines, with special reference to *Pinus monticola* Dougl. USDA Forest Serv., Intermountain Forest and Range Exp. Sta. Res. Pap. 53, 26 p.  
 \_\_\_\_\_, \_\_\_\_\_, and R. F. Patton.
1956. Vigor, disease resistance, and field performance in juvenile progenies of the hybrid *Pinus monticola* Dougl. X *Pinus strobus* L. *Ztschr. f. Forstgenet. u. Forstpflanzenzucht.* 5: 104-112.  
 \_\_\_\_\_, \_\_\_\_\_, and J. W. Wright.
1960. Breeding blister rust resistant western white pine. II. First results of progeny tests including preliminary estimates of heritability and rate of improvement. *Silvae Genet.* 9: 33-41.  
 \_\_\_\_\_ and K. C. Wise.
1968. Western white pine cones pollinated with 1- to 3-year-old pollens give good seed yields. USDA Forest Serv. Res. Note INT-81, 3 p.
- (7) Brown, R. W.  
 1937. Additions to some fossil floras of the western United States. U.S. Geol. Surv. Prof. Pap. 186-J: 163-186.
- Buchholz, J. T.  
 1945. Embryological aspects of hybrid vigor in pines. *Science* 102: 135-142.
- Callahan, R. Z., and R. J. Steinhoff.  
 1966. Pine pollens frozen five years produce seed. P. 94-101 *in*, Second Forest Genet. Workshop. Proc., USDA Forest Serv. Res. Pap. NC-6, 110 p.
- Canada Department Resources and Development.  
 1950. Native trees of Canada. 4th Ed. Can. Dep. Resources and Develop., Forest. Br. Bull. 61, 293 p.
- Chaney, R. W., and D. I. Axelrod.  
 1959. Miocene floras of the Columbia Plateau, Part 2. Systematic considerations. Carnegie Inst. Wash. Pub. 617: 135-237.
- (8) Cockerell, T. D. A.  
 1908. Fossil flora of Florissant, Colorado. *Bull. Amer. Mus. Natur. Hist.* 24: 71-110.
- Critchfield, W. B., and E. L. Little, Jr.  
 1966. Geographic distribution of the pines of the world. USDA Forest Serv. Misc. Pub. 991, 97 p.
- Deuber, C. G.  
 1942. The vegetative propagation of eastern white pine and other five-needle pines. *J. Arnold Arb.* 23: 198-215.

- (9) Dorf, E.  
1938. A late Tertiary flora from southwestern Idaho. Carnegie Inst. Wash. Pub. 476 (II): 73-124.
- Duffield, J. W., and F. I. Righter.  
1953. Annotated list of pine hybrids made at the Institute of Forest Genetics. USDA Forest Serv., Calif. Forest and Range Exp. Sta., Forest Res. Note 86, 9 p.
- Evernden, J. F., and G. T. James.  
1964. Potassium-Argon dates and the Tertiary floras of North America. Amer. J. Sci. 262: 945-974.
- Ferguson, M. C.  
1904. Contributions to the knowledge of the life history of *Pinus* with special reference to sporogenesis, the development of the gametophytes, and fertilization. Wash. Acad. Sci. Proc. 6: 1-202.
- Gerhold, H. D., and R. L. Soles.  
1967. Weevil attacks on caged seedlings of three white pine species. P. 51-59 in, 14th Northeastern Forest Tree Impr. Conf. Proc., 91 p.
- Hanover, J. W.  
1962. Clonal variation in western white pine. I. Graftability. USDA Forest Serv., Intermountain Forest and Range Exp. Sta. Res. Note 101, 4 p.
- 1963a. Comparative biochemistry and physiology of western white pine (*Pinus monticola* Dougl.) resistant and susceptible to infection by the blister rust fungus (*Cronartium ribicola* Fischer). Ph.D. Thesis, Wash. State Univ., 166 p.
- 1963b. New developments in breeding western white pine. II. Biochemistry of rust resistance. P. 77-78 in, Forest Genet. Workshop Proc. Southern Forest Tree Impr. Comm. Pub. 22, 97 p.
1965. Effect of the chemical mutagen ethyl methanesulfonate on western white pine. Silvae Genet. 14: 23-26.
- 1966a. Genetics of terpenes. I. Gene control of monoterpene levels in *Pinus monticola* Dougl. Heredity 21: 73-84.
- 1966b. Inheritance of 3-carene concentration in *Pinus monticola*. Forest Sci. 12: 447-450.
- \_\_\_\_\_, and B. V. Barnes.  
1963. Heritability of height growth in year-old western white pine. P. 71-76 in, Forest Genet. Workshop Proc., Southern Forest Tree Impr. Comm. Pub. 22, 97 p.
- \_\_\_\_\_, and R. J. Hoff.  
1966a. A comparison of phenolic constituents of *Pinus monticola* resistant and susceptible to *Cronartium ribicola*. Physiol. Plant. 19: 554-562.
- \_\_\_\_\_ and \_\_\_\_\_  
1966b. Pollination of western white pine with water suspensions of pollen—a technique for chemical mutagen treatments. Forest Sci. 12: 372-373.
- (10) Hansen, H. P.  
1938. Postglacial forest succession and climate in the Puget Sound region. Ecology 19: 528-542.
- (11) \_\_\_\_\_  
1939a. Paleoecology of a central Washington bog. Ecology 20: 563-568.
- (12) \_\_\_\_\_  
1939b. Pollen analysis of a bog in northern Idaho. Amer. J. Bot. 26: 225-228.
- (13) \_\_\_\_\_  
1939c. Pollen analysis of a bog near Spokane, Washington. Bull. Torrey Bot. Club 66: 215-220.
- (14) \_\_\_\_\_  
1940a. Paleoecology of a montane peat bog at Bonaparte Lake, Washington. Northwest Sci. 14: 60-69.
- (15) \_\_\_\_\_  
1940b. Paleoecology of two peat bogs in southwestern British Columbia. Amer. J. Bot. 27: 144-149.
- (16) \_\_\_\_\_  
1941a. A pollen study of post-Pleistocene lake sediments in the Upper Sonoran life zone of Washington. Amer. J. Sci. 239: 503-522.
- (17) \_\_\_\_\_  
1941b. Further pollen studies of post-Pleistocene bogs in the Puget Lowland of Washington. Bull. Torrey Bot. Club 68: 133-148.
- (18) \_\_\_\_\_  
1941c. Paleoecology of a bog in the spruce-hemlock climax of the Olympic Peninsula. Amer. Midland Natur. 25: 290-297.
- (19) \_\_\_\_\_  
1941d. Paleoecology of a montane bog near Lake Wenatchee, Washington. Northwest Sci. 15: 53-65.
- (20) \_\_\_\_\_  
1941e. Paleoecology of a peat deposit in west central Oregon. Amer. J. Bot. 28: 206-212.
- (21) \_\_\_\_\_  
1942a. A pollen study of a montane peat deposit near Mount Adams, Washington. Lloydia 5: 305-313.
- (22) \_\_\_\_\_  
1942b. A pollen study of lake sediments in the lower Willamette Valley of western Oregon. Bull. Torrey Bot. Club 69: 262-280.

- (23) Hansen, H. P.  
1942c. The influence of volcanic eruptions upon post-Pliocene forest succession in central Oregon. *Amer. J. Bot.* 29: 214-219.
- (24) \_\_\_\_\_  
1943a. A pollen study of two bogs on Orcas Island, of the San Juan Islands, Washington. *Bull. Torrey Bot. Club* 70: 236-243.
- (25) \_\_\_\_\_  
1943b. Paleocology of a bog in east central Washington. *Northwest Sci.* 17: 35-40.
- (26) \_\_\_\_\_  
1943c. Post-Pleistocene forest succession in northern Idaho. *Amer. Midland Natur.* 30: 796-803.
- (27) \_\_\_\_\_  
1944. Postglacial vegetation of eastern Washington. *Northwest Sci.* 18: 79-87.
- (28) \_\_\_\_\_  
1946. Postglacial forest succession and climate in the Oregon Cascades. *Amer. J. Sci.* 244: 710-734.
- (29) \_\_\_\_\_  
1947a. Climate versus fire and soil as factors in postglacial forest succession in the Puget Sound Lowland of Washington. *Amer. J. Sci.* 245: 265-286.
- (30) \_\_\_\_\_  
1947b. Postglacial forest succession, climate, and chronology in the Pacific Northwest. *Amer. Phil. Soc. Trans.* 37: 1-130.
- (31) \_\_\_\_\_  
1947c. Postglacial vegetation of the northern Great Basin. *Amer. J. Bot.* 34: 164-171.
- (32) \_\_\_\_\_  
1948. Postglacial forests of the Glacier National Park region. *Ecology* 29: 146-152.
- (33) \_\_\_\_\_  
1950. Pollen analysis of three bogs on Vancouver Island, Canada. *J. Ecol.* 50: 270-276.
- (34) \_\_\_\_\_  
1955. Postglacial forests in south central and central British Columbia. *Amer. J. Sci.* 253: 640-658.
- \_\_\_\_\_
1967. Chronology of postglacial pollen profiles in the Pacific Northwest. *Rev. Paleobot. & Palynol.* 4: 103-106.
- (35) \_\_\_\_\_, and J. H. Macklin.  
1940. A further study of interglacial peat from Washington. *Bull. Torrey Bot. Club* 67: 131-142.
- Heimbürger, C.  
1953. The breeding of white pine (*Pinus strobus* L.) in Canada. *Abstr.*, p. 307 in, *Int. Congr. Bot. Proc.* 7, 899 p.
- Heimbürger, C.  
1958. Forest tree breeding and genetics in Canada. p. 41-49 in, *Gen. Soc. Can. Proc.* 3, 83 p.
- Hoff, R. J.  
1968. Comparative physiology of *Pinus monticola* Dougl. resistant and susceptible to *Cronartium ribicola* J. C. Fisch. ex Rabenh. Ph.D. Thesis, Wash. State Univ. 76 p.
- \_\_\_\_\_
1970. Inhibitory compounds of *Pinus monticola* Dougl. resistant and susceptible to *Cronartium ribicola* J. C. Fisch. ex Rabenh. *Can. J. Bot.* 48: 371-376.
- \_\_\_\_\_, and G. I. McDonald.  
1968. Rooting of needle fascicles from western white pine seedlings, USDA Forest Serv. Res. Note INT-80, 6 p.
- Hopkins, D. M., F. S. MacNeil, R. L. Merklin, and O. M. Petrov. 1965. Quaternary correlation across Bering Strait. *Science* 147: 1107-1114.
- (36) Hoxie, L. R.  
1965. The Sparta Flora from Baker County, Oregon. *Northwest Sci.* 39: 26-35.
- (37) Knowlton, F. H.  
1900. Fossil plants associated with the lavas of the Cascade Range. P. 36-64 in, *U.S. Geol. Surv. Annu. Rep.* 20 (Pt. 3). 595 p.
- (38) \_\_\_\_\_  
1926. Flora of the Latah formation of Spokane, Washington, and Coeur d'Alene, Idaho. *U.S. Geol. Surv. Prof. Pap.* 140: 17-81.
- Krishtofovich, A. N.  
1941. Prodomus florae fossilis. *Paleontologia S.S.S.R. (Paleontology of the U.S.S.R.)* Vol. XII. Supplement *Akad. Nauk S.S.S.R. Paleontology Inst.* 494 p.
- (39) LaMotte, R. S.  
1936. The Upper Cedarville Flora of northwestern Nevada and adjacent California. *Carnegie Inst. Wash. Pub.* 455(V): 57-142.
- (40) Lesquereux, L.  
1874. The lignitic formation and its fossil flora. P. 363-425 in, *U. S. Geol. & Geog. Surv. of the Territories Annu. Rep.* 1873 (Part II). 718 p.
- (41) \_\_\_\_\_  
1878. Contributions to the fossil flora of the Western Territories. Part 2, the Tertiary flora. *U.S. Geol. Surv. of the Territories Rep.*, Vol. 7 (Part 2). 366 p.
- Little, E. L., Jr., and F. I. Righter  
1965. Botanical descriptions of forty artificial pine hybrids. *USDA Forest Serv. Tech. Bull.* 1345, 47 p.

- McDonald, G. I., and R. J. Hoff.  
1969. Effect of rooting mediums and hormone application on rooting of western white pine needle fascicles. USDA Forest Serv., Res. Note INT-101, 6 p.
- McMinn, R. G.  
1955. Studies on the root systems of healthy and pole blight affected white pine (*Pinus monticola* Dougl.). Interim Report, Forest Biology Laboratory, Victoria, B. C. Can. Dep. Agr. Sci. Serv., Forest Biol. Div. mimeo, 31 p.
- (42) MacGinitie, H. D.  
1953. Fossil plants of the Florissant beds, Colorado. Carnegie Inst. Wash. Pub. 599: 198 p.
- Mirov, N. T.  
1967. The genus *Pinus*. New York, Ronald Press. 602 p.
- Olson, D. S.  
1932. Germinative capacity of seed produced from young trees. *J. Forest.* 30: 871.
- Otter, F. L.  
1933. Idaho's record trees. Univ. Idaho Forest. 15: 37-39.
- Patton, R. F.  
1961. The effect of age upon susceptibility of eastern white pine to infection by *Cronartium ribicola*. *Phytopathology* 51: 429-434.
- \_\_\_\_\_ and A. J. Riker.  
1966. Lessons from nursery and field testing of eastern white pine selections and progenies for resistance to blister rust. P. 403-414 in, Gerhold, H. D., et al. (Eds.), *Breeding pest-resistant trees*. Oxford, Pergamon Press. 505 p.
- (43) Penhallow, D. P.  
1908. Report on Tertiary plants of British Columbia. Can. Dep. Mines, Geol. Surv. Br. Pub. 1013, 167 p.
- Rigg, G. B., and E. S. Harrar.  
1931. The root systems of trees growing in sphagnum. *Amer. J. Bot.* 18: 391-397.
- Righter, F. I.  
1939. Early flower production among the pines. *J. Forest.* 37: 935-938.
- \_\_\_\_\_  
1945. The relationship of seed size and seedling size to inherent vigor. *J. Forest.* 43: 131-137.
- \_\_\_\_\_, and J. W. Duffield.  
1951. Interspecies hybrids in pines. A summary of interspecific crossings in the genus *Pinus* made at the Institute of Forest Genetics. *J. Hered.* 42: 75-80.
- Riker, A. J., and R. F. Patton.  
1954. Breeding of *Pinus strobus* for quality and resistance to blister rust. *Univ. Wisc. Forest. Res. Note* 12, 2 p.
- Saylor, L. C., and B. W. Smith.  
1966. Meiotic irregularity in species and interspecific hybrids of *Pinus*. *Amer. J. Bot.* 53: 453-468.
- Schenk, J. A., and R. A. Goyer.  
1967. Cone and seed insects of western white pine in northern Idaho: Distribution and seed losses in relation to stand density. *J. Forest.* 65: 186-187.
- Schütt, P., and R. J. Hoff.  
1969. Foliage dry matter of *Pinus monticola*; its variability with environment and blister rust resistance. USDA Forest Serv. Res. Note INT-102, 6 p.
- Shaw, G. R.  
1914. The genus *Pinus*. *Arnold Arb. Pub.* 5. 96 p.
- \_\_\_\_\_  
1924. Notes on the genus *Pinus*. *J. Arnold Arb.* 5: 225-227.
- (44) Smith, H. V.  
1941. A Miocene flora from Thorn Creek, Idaho. *Amer. Midland Natur.* 25: 473-522.
- Society of American Foresters.  
1954. Forest cover types of North America (exclusive of Mexico). *Soc. Amer. Forest. Comm. on Forest Types Rep.*, 67 p.
- Squillace, A. E.  
1957. Variations in cone properties, seed yield and seed weight in western white pine when pollination is controlled. *Mont. State Univ. Sch. Forest. Bull.* 5, 16 p.
- \_\_\_\_\_ and R. T. Bingham.  
1954. Breeding for improved growth rate and timber quality in western white pine. *J. Forest.* 52: 656-661.
- \_\_\_\_\_ and \_\_\_\_\_  
1958a. Localized ecotypic variation in western white pine. *Forest Sci.* 4: 20-34.
- Squillace, A. E., and R. T. Bingham.  
1958b. Selective fertilization in *Pinus monticola* Dougl. I. Preliminary results. *Silvae Genet.* 7: 188-196.
- \_\_\_\_\_, \_\_\_\_\_, G. Namkoong, and H. F. Robinson.  
1967. Heritability for juvenile growth rate and expected gain from selection in western white pine. *Silvae Genet.* 16: 1-6.
- Stephens, G. R., Jr.  
1962. Initiation of strobili primordia in *Pinus strobus* L. P. 41-43 in, 9th Northeastern Forest Tree Impr. Conf. Proc., 74 p.

- Sukachev, V. N.  
 1910. Nekotoryia dannyia k dolednikovoi flore severa sibirii. (New data on the preglacial flora of the north of Siberia). Akad. Nauk Geologicheskii mesei imeni Petra velikago Trudy 4: 55-62.
- Vashkovsky, A. P.  
 1959. A brief essay of vegetation, climate, and Quaternary chronology on the Upper Kolyma and the Upper Indigirka Rivers and on the northern coast of the Okhotsk Sea. P. 510-555 *in*, Markov, K. K. and A. J. Popov (Eds.), *Lednikov'y Period na territorii Europeiskoi Chasti S.S.S.R. i Sibiri.* (Ice age in the European section of the U.S.S.R. and in Siberia.) State Lomonsov Univ. Moscow, Geol. Faculty and Museum of General Geography, Moscow. 559 p.
- Wellner, C. A.  
 1962. Silvics of western white pine. USDA Forest Serv., Intermountain Forest and Range Exp. Sta., Misc. Pub. 26, 24 p.
- Wright, J. W.  
 1959. Species hybridization in the white pines. *Forest Sci.* 5: 210-222.
- and W. J. Gabriel.  
 1959. Possibilities of breeding weevil-resistant white pine strains. USDA Forest Serv., Northeastern Forest Exp. Sta., Sta. Pap. 115, 35 p.