

814—820 (1961). — CONKLE, M. T.: Growth Data for 29 Years from the California Elevational Transect Study of Ponderosa Pine. *Forest Science* 19: 31—39 (1973). — DONOVAN, G. A., E. M. LONG, J. P. VAN BUIJTENEN, J. F. ROBINSON and R. A. WOESSNER: Introduction to Practical Forest Tree Improvement. Texas Forest Service a part of the Texas A and M University System. Circular 207 (1976). — FALCONER, D. S.: Introduction to Quantitative Genetics 365 p. Ronald Press, New York, New York (1960). — HANSON, W. D.: Heritability. In: Statistical Genetics and Plant Breeding. A Symposium and Workshop sponsored by the Committee on Plant Breeding and Genetics of the Aricultural Board at North Carolina State College. (HANSON, W. D. and R. F. ROBINSON, eds.). National Academy of Science - National Research Council, Washington, D. C. Publication 982 (1963). — LEVINS, R.: Theory of Fitness in a Heterogeneous Environment. II. Development Flexibility and Niche Selection. *American Naturalist* 97: 75—90 (1963). — LEVINS, R.: Dormancy as an Adaptive Strategy. Symposia of the Society for Experimental Biology. Academic Press, New York, New York (1969). — MADSEN, J. L. and G. M. BLAKE: Ecological Genetics of Ponderosa Pine in the Northern Rocky Mountains. *Silvae Genetica* 26: 1—8 (1977). — NAMKOONG, G.: Introduction to Quantitative Genetics in Forestry. USDA Forest Service Technical Bulletin # 1588 (1979). — REHFELDT, G. E.: Genetic Gains from Tree Impro-

vement of Ponderosa Pine in Southern Idaho. USDA Forest Service Research Paper INT-263. Intermountain Forest and Range Experiment Station (1980a). — REHFELDT, G. E.: Genetic Variation in Southern Idaho Ponderosa Pine Progeny Tests after 11 Years. USDA Forest Service, General Technical Report INT-75. Intermountain Forest and Range Experiment Station (1980b). — SNEDDECOR, G. W. and W. G. COCHRAN: Statistical Methods. The Iowa State University Press, Ames, Iowa (1968). — SQUILLACE, A. E. and R. R. SILEN: Racial Variation in Ponderosa Pine. *Forest Science Monograph* 2 (1962). — STEINHOFF, R. J.: Northern Idaho Ponderosa Pine Racial Variation Study - 50 Year Results. USDA Forest Service Research Note INT-118. Intermountain Forest and Range Experiment Station (1970). — WEIDMAN, R. H.: Evidences of Racial Variation in a 25-year Test of Ponderosa Pine. *Journal of Agricultural Research* 59: 855—868 (1939). — WELLS, O. O.: Geographic Variation in Ponderosa Pine. I. The Ecotypes and Their Distribution. *Silvae Genetica* 13: 89—103 (1964a). — WELLS, O. O.: Geographic Variation in Ponderosa Pine. II. Correlations between Progeny Performance and Characteristics of the Native Habitat. *Silvae Genetica* 13: 126—164 (1964b). — WRIGHT, J. W. and W. I. BULL: Geographic Variation in Scotch Pine. *Silvae Genetica* 12: 1—25 (1963). — WRIGHT, S. S.: Correlation and Causation. *Journal of Agricultural Research*. XX (7): 557—586 (1921).

Variation in growth and branching characteristics of *Pinus attenuata*

By A. G. BROWN and J. C. DORAN

Division of Forest Research, CSIRO,
PO Box 4008, Canberra, A.C.T. 2600, Australia

(Received 1st October 1984)

Abstract

Seed of *Pinus attenuata* from natural stands in western North America was sown in Canberra in 1960. Seedlings from 39 seedlots were planted in 1961 at an altitude of 770 m in the Australian Capital Territory.

After 12 years growth the heights and diameters were weakly inversely correlated with latitude of seed source. There was also a weak inverse correlation between tree height and the altitude of seed source. Differences in growth and branch characteristics among the seed sources were substantial. While statistically significant, the phenotypic correlations among these traits were not strong. The most vigorous trees, which also displayed relatively fine branches, were from the Coast Ranges of California below altitudes of 1000 m. Subsequent infection by *Dothistroma* caused an appreciable loss of foliage, but some provenances were little affected and the ranking on growth was little changed at 20 years of age.

Key words: *Pinus attenuata*, knobcone pine, provenances, growth, branching, variation, *Dothistroma*.

Zusammenfassung

Im Jahre 1960 wurden Samen aus natürlichen Beständen von *Pinus attenuata* in Nordwest-Amerika in Canberra ausgesät. Im Jahre 1961 wurden die aus 39 Samenproben angezogenen Sämlinge in 770 m Höhe im Bereich der Hauptstadt Australiens ausgepflanzt. Nach 12 Jahren ergab sich eine schwach negative Korrelation zwischen Baumhöhe bzw. Baumdurchmesser und der geographischen Breite der Saatgutherkunft. Die Baumhöhe und die Höhe ü. NN der Saatgutherkunft waren ebenfalls schwach negativ korreliert. Es gab erhebliche Unterschiede im Wachstum und im Zweigcharakter zwischen den Herkünften. Trotz statisti-

scher Signifikanz waren die phänotypischen Korrelationen unter diesen Merkmalen nicht streng. Die leistungsstärksten Bäume, die auch verhältnismäßig feine Äste aufwiesen, stammen aus dem kalifornischen Küstengebirge aus Höhen unter 1000 m. Nachträglich auftretender *Dothistroma*-Befall bedingte einen bemerkenswerten Laubverlust, aber einige Provenienzen wurden wenig angegriffen, und die Klassifizierung nach der Wuchsleistung blieb im Alter 20 nur wenig verändert.

Résumé

On a semé à Canberra en 1960 des semences de *Pinus attenuata* pris dans des peuplements naturels de la région occidentale de l'Amérique du Nord. Les plantes résultant de 39 lots de semences ont été établies en 1961 à une élévation de 1.000 m au Territoire Capital australien.

Au bout de 12 années de croissance on a trouvé qu'il existait une corrélation faiblement inverse entre la hauteur et le diamètre des arbres et la latitude d'origine des semences. Les différences relatives à la croissance et aux caractéristiques qui existaient entre les provenances étaient importantes. Quoique statistiquement significatives, les corrélations phénotypiques entre ces traits n'étaient pas étroites. Les arbres les plus vigoureux, qui montraient également de relativement belles branches, provenaient de la Chaîne Littorale de Californie, d'élévations de moins de 1.000 m. L'attaque ultérieure de *Dothistroma* a entraîné une perte considérable de feuillage, mais quelques provenances demeuraient peu affectées et la classification selon la croissance ne s'était changée que peu à l'âge de 20 ans.

Introduction

The Californian closed-cone pines, *Pinus attenuata* LEMM., *P. radiata* D. DON and *P. muricata* D. DON, form a

distinct taxonomic group within the genus. All three species occur in discontinuous stands on the western coast of temperate North America, extending from southern Oregon to northern Baja California, Mexico, and to the islands of Santa Rosa, Santa Cruz, Guadalupe and Cedros (NEWCOMB 1962; CRITCHFIELD and LITTLE 1966; GRIFFIN and CRITCHFIELD 1972). While *P. radiata* and *P. muricata* have an essentially maritime distribution, *P. attenuata* is more widespread, being scattered throughout much of montane California from which it extends north into Oregon and south to near Ensenada, Baja California, Mexico. The eastern limit is the Sierra Nevada foothills and the western limit the coast of California. It occurs at 200–2000 m elevation in colder and drier climates than either of its relatives and on soils which are frequently shallow and classified as unsuitable for commercial timber production (NEWCOMB 1962). Nowhere does *P. attenuata* grow with *P. muricata*, but it does have a zone of contact with *P. radiata* at Point Ano Nuevo (DUFFIELD 1951). While putative natural hybrids resembling the controlled cross '*P. × attenuata*' (STOCKWELL and RIFTER 1946) have been reported by LINDSAY (1932), NEWCOMB (1962) and others, recognisable hybridisation in the field is limited (STEBBINS, quoted in BANNISTER 1958; DE LA PUENTE 1960; NEWCOMB 1962; FORDE 1964). Hybrids between *P. attenuata* and *P. radiata* may be useful for sites too dry or cold for *P. radiata*. In field trials on marginal timber sites at elevations of 670 m and 990 m in northern California, hybrids were found to be more promising than either of the parent species after three years of growth (GRIFFIN and CONKLE 1967). CONKLE (1970) outlined a hybrid breeding program for the two species. L. O. HUNT (pers.

comm. 1978) reported that he had been conducting trials of the hybrid for a decade in southwest Oregon.

Only small experimental plots of *P. attenuata* and its hybrid with *P. radiata* have been established in Australia. The growth of *P. attenuata* from a number of provenances and several different hybrids in arboreta in the Australian Capital Territory was described by ROUT and DORAN (1974): the height growth of *P. attenuata* was usually less than 90% of that of *P. radiata* of the same age; the growth of the hybrid was intermediate between that of the parent species. The stem form of *P. attenuata* and the hybrid was quite poor.

Early introductions of *P. attenuata* into Australia were made without any detailed knowledge of variation within the species. The trial which provided the data for this paper was established to study, under Australian Capital Territory conditions, the growth and form of a wider range of *P. attenuata* provenances and to provide material for the production of hybrids with *P. radiata* for testing on sites too dry for the optimum development of *P. radiata*. This paper is a report on the first of these two objectives.

Materials and Methods

Seed from populations of *P. attenuata* in California and Oregon was received in Canberra in August 1960 via the Institute of Forest Genetics at Placerville. The seed was from the 1956 crop. In some populations the seed had been collected from a single tree; in other cases it was obtained from two or more trees. Details of the seed origins are given in Appendix 1 and Figure 1.

Appendix 1. — Seed source data, *Pinus attenuata*.

| Seedlot No. + | Origin | | Latitude (N) | Longitude (W) | Altitude (m) | Number of mother trees in seedlot | Replicates |
|---------------|-------------------|-------------------------------|--------------|---------------|--------------|-----------------------------------|------------|
| | County++ | Place Name | | | | | |
| 2 | Orange | Pleasants Park | 33°51' | 116°37' | 1067 | >1 | 3 |
| 4 | San Bernardino | City Creek Road | 34°11' | 117°14' | 957 | >1 | 3 |
| 5 | San Luis | Cuesta Summit | 35°19' | 120°36' | 823 | >1 | 3 |
| 6 | Santa Cruz | Big Basin | 37°13' | 122°09' | 686 | >1 | 3 |
| 7 | Santa Cruz | Bonny Doon Ridge | 37°03' | 122°08' | 549 | >1 | 3 |
| 10 | Napa | Mt St Helena | 38°39' | 122°37' | 1158 | 5 | 1 |
| 11 | Lake | Bettla Rock | 38°54' | 122°47' | 823 | 5 | 3 |
| 12 | Lake | Bettla Rock | 38°54' | 122°47' | 792 | 1 | 3 |
| 13 | Lake | Reister Road | 39°09' | 122°38' | 914 | 6 | 3 |
| 15 | Lake | Little Horse Mountain | 39°15' | 122°48' | 716 | >1 | 3 |
| 16 | Lake | South of Long Ridge | 39°18' | 122°49' | 975 | 5 | 3 |
| 17 | Colusa | Goat Mountain | 39°16' | 122°44' | 1829 | 1 | 3 |
| 19 | Colusa | Below Old Mill Camping Ground | 39°18' | 122°38' | 1036 | >1 | 1 |
| 20 | Glenn | Long Point Lookout | 39°41' | 122°42' | 1143 | >1 | 3 |
| 22 | Trinity | Hayfork Creek | 40°28' | 123°04' | 975 | >1 | 3 |
| 23 | Trinity | Junction City | 40°43' | 123°03' | 488 | >1 | 2 |
| 24 | Humboldt | Hoopa Res. | 41°05' | 123°36' | 1067 | 5 | 3 |
| 25 | Del Norte | Gordon Mountain | 41°48' | 123°52' | 1250 | >1 | 2 |
| 26 | Del Norte | Red Mountain | 41°31' | 123°55' | 1097 | >1 | 1 |
| 27 | Siskiyou | Scott River | 41°44' | 123°01' | 488 | 1 | 1 |
| 29 | Siskiyou | West Branch | 41°57' | 123°30' | 914 | 5 | 3 |
| 30 | Siskiyou | Bartle | 41°18' | 121°46' | 1341 | >1 | 3 |
| 31 | Siskiyou | Everett Hill | 41°16' | 122°13' | 1433 | 5 | 3 |
| 32 | Siskiyou | Duzel Rock | 41°30' | 122°43' | 1585 | >1 | 2 |
| 33 | Siskiyou | Tennant | 41°33' | 121°57' | 1585 | >1 | 3 |
| 35 | Josephine, Oregon | O'Brien Creek | 42°07' | 123°15' | 1280 | 6 | 3 |
| 37 | Josephine, Oregon | Chrome Ridge | 42°32' | 123°42' | 1219 | >1 | 3 |
| 38 | Josephine, Oregon | Onion Ridge | 42°24' | 123°38' | 1219 | >1 | 3 |
| 39 | Josephine, Oregon | Oregon Caves | 42°06' | 123°24' | 1372 | >1 | 3 |
| 40 | Josephine, Oregon | O'Brien P.O. | 42°04' | 123°43' | 457 | >1 | 1 |
| 41 | Jackson, Oregon | Palmer Peak | 42°09' | 123°10' | 1372 | 2 | 2 |
| 42 | Mariposa | Briceburg | 37°32' | 119°59' | 914 | >1 | 1 |
| 44 | Eldorado | Whaler Creek | 38°51' | 120°42' | 1036 | >1 | 3 |
| 45 | Eldorado | Pennsylvania Point | 38°59' | 120°42' | 975 | >1 | 3 |
| 46 | Placer | Forest Hill | 39°01' | 120°49' | 975 | >1 | 3 |
| 47 | Placer | Gold Run | 39°10' | 120°52' | 975 | >1 | 1 |
| 48 | Placer | Blue Canyon | 39°16' | 120°43' | 1402 | >1 | 3 |
| 49 | Placer | Blue Canyon (poor site) | 39°16' | 120°43' | 1433 | >1 | 3 |
| 50 | Nevada | Lake City | 39°22' | 120°57' | 914 | >1 | 3 |

+ Placerville

++ Counties are in California unless otherwise stated

The field trial was planted in June 1961 at Blue Range (35° 17' S, 142° 42' E), 22 km west of Canberra at a spacing of 2.5 × 2.5 m. The design used square plots containing 25 trees arranged in randomised blocks. There were three replications of seedlots for which sufficient stock was available, but fewer replications of others (*Appendix 1*).

The trial site formerly carried dry sclerophyll forest (*Eucalyptus macrorhyncha* and *E. rossii*) which was pulled down and burnt shortly before planting. The site has a slight slope with an easterly aspect and an altitude of 770 m. The mean annual rainfall is about 1000 mm. The mean minimum temperature of the coldest month (July) is about 1° C and the mean maximum temperature of the hottest month (January) about 27° C.

The soil is duplex with poor internal drainage in the lower horizons. The levels of total nitrogen and phosphorus were moderately low (N = 1500 ppm, P = 227 ppm, P. SNOWDON pers. comm.).

Adjacent *P. radiata* had a predominant height of 15 m at age 12 years (SQ V, SINDEN 1967).

The total height and diameter (at 1.3 m) of the survivors of the nine internal trees in each plot were measured at

ages of 8 and 12 years. At age 8 data on morphological characteristics were also collected — the number of branch clusters on the stem 30 cm or more above the ground and the number of cone clusters on the stem were counted, and the diameter and angle of the two largest branches in the cluster nearest breast height were measured, as well as the length of the longest branch in this cluster. At age 20 (1981) the diameter and density of the foliage of the nine internal trees in each plot were assessed, and the survivors from all 25 trees in each plot were counted.

Results and Discussion

Survival and health

The overall survival was 87% a year after planting, when most plots were refilled. Although in the 11 subsequent years the trees experienced competition from bracken and some browsing by kangaroos, many of the deaths which reduced the average survival among the inner 9 trees in each plot to 76% appear to have been caused by a species of *Armillaria* (W. STAHL, pers. comm.). The survival varied between seedlots, from 33% to 100% and was positively correlated with height ($r = 0.53^{***}$). Between the assessments at ages 12 and 20 years, *Dothistroma* needle blight became widespread in Australia (EDWARDS and WALKER 1978). *P. attenuata* is 'most susceptible' to this fungus (GILMOUR 1967), and the trial became heavily infected. By age 20, most dead foliage had fallen leaving apparently-healthy crowns, the density of which varied appreciably ($P < 0.01$) between seedlots. On the empiric 3-point scale used to assess foliage density (1 = sparse, 2 = medium, 3 = dense) the range extended from seedlots with mean scores of 1.2 to a maximum value of 2.6 (*Table 1*). Seedlots with larger diameter at age 20 also tended to have dense foliage ($r = 0.48^{**}$). The average survival among the inner 9 trees in each plot was 62%: clearly lower than at age 12, but sufficient to provide 'reasonable' stocking. Survival in several seedlots exceeded 90%.

Height

Average heights 8 years after planting are shown in *Table 1*. The ranking of the seedlots, and especially the tallest 10, was almost unchanged 4 years later, when the 10 tallest seedlots averaged 7.9 m high. On both occasions the 10 tallest seedlots came from the Coast Range of California. The shortest four seedlots came from the Klamath Mountains or the Cascade Range; the average height of this group at age 12 years was 4.0 m. The differences between seedlots were highly significant.

Simple correlations between the heights at age 12 and the latitude and altitude of the seed source were modest and negative (-0.45^{**} and -0.34^* respectively). The multiple correlation of height with latitude and altitude was similar (-0.51^{***}): southern, low-altitude seedlots tended to be taller than northern high-altitude ones. These correlations with latitude and altitude are consistent with the observations of NEWCOMB (1962) on a number of other characteristics. Clearly factors other than geographic location of the maternal parents contribute greatly to the large variation in height growth of the progeny: they may include the adequacy of the sample from the maternal stand, possible genetic drift or founder effects in small isolated stands, and adaptive responses to environmental factors (e.g. fire, aspect, topographic location and edaphic conditions) poorly correlated with latitude and altitude.

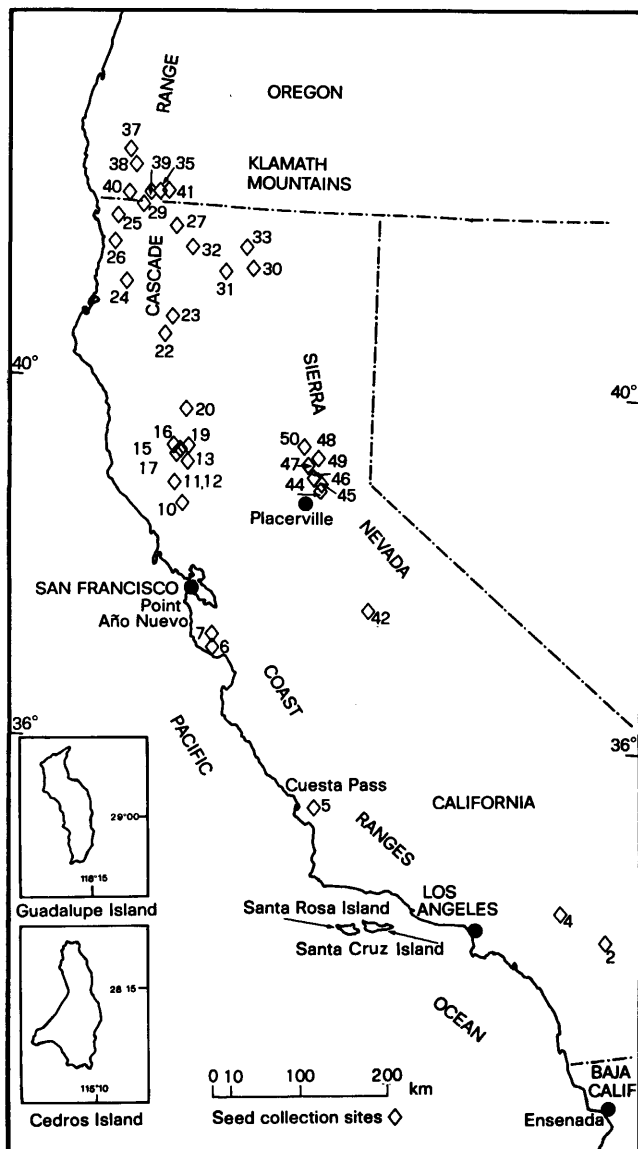


Figure 1. — Localities from which seed of *P. attenuata* was collected in natural stands.

Table 1. — Height, diameter and branch and cone characteristics of *Pinus attenuata* seedlots 8 year after planting, and foliage density score 20 years after planting. Seedlots ranked in order of height.

| Seedlot No. | Height (m) | Diameter (cm) | No. clusters of - | | Branch - | | | Foliage density (1) |
|-------------|------------|---------------|-------------------|-------|---------------|-----------|-------------|---------------------|
| | | | branches | cones | diameter (cm) | angle (°) | length (cm) | |
| 19 | 5.06 | 8.64 | 18.8 | 6.41 | 2.41 | 60 | 170 | |
| 12 | 4.82 | 7.62 | 16.9 | 5.04 | 2.47 | 64 | 189 | 1.8 |
| 7 | 4.69 | 7.06 | 16.2 | 3.42 | 2.74 | 62 | 221 | 2.5 |
| 13 | 4.50 | 8.23 | 18.1 | 4.69 | 2.56 | 60 | 182 | 1.9 |
| 20 | 4.28 | 6.73 | 15.8 | 4.45 | 2.52 | 63 | 177 | 1.4 |
| 6 | 4.16 | 7.70 | 16.4 | 4.17 | 3.06 | 65 | 230 | 1.9 |
| 16 | 3.86 | 6.91 | 16.3 | 4.69 | 2.55 | 62 | 181 | 1.6 |
| 5 | 3.79 | 6.60 | 15.7 | 4.23 | 2.58 | 64 | 200 | 1.9 |
| 4 | 3.77 | 7.24 | 15.7 | 2.60 | 3.15 | 58 | 229 | 1.5 |
| 17 | 3.77 | 6.76 | 16.3 | 5.31 | 2.73 | 59 | 180 | 1.8 |
| 15 | 3.71 | 6.40 | 16.9 | 4.79 | 2.62 | 64 | 187 | 1.4 |
| 24 | 3.63 | 6.50 | 17.7 | 3.48 | 2.84 | 61 | 167 | 2.5 |
| 10 | 3.48 | 6.17 | 16.0 | 3.79 | 2.58 | 65 | 167 | 1.9 |
| 45 | 3.44 | 6.20 | 16.0 | 4.12 | 2.76 | 66 | 187 | 1.6 |
| 47 | 3.43 | 5.79 | 15.3 | 4.52 | 3.10 | 46 | 198 | 2.0 |
| 42 | 3.39 | 5.28 | 14.7 | 2.20 | 2.21 | 49 | 165 | |
| 40 | 3.37 | 5.59 | 15.7 | 4.83 | 2.43 | 64 | 162 | 2.6 |
| 11 | 3.31 | 5.89 | 15.3 | 4.16 | 2.54 | 70 | 177 | 1.8 |
| 35 | 3.21 | 5.89 | 16.6 | 2.19 | 2.62 | 64 | 142 | 1.6 |
| 22 | 3.19 | 5.59 | 15.8 | 4.13 | 2.37 | 67 | 152 | 1.3 |
| 26 | 3.17 | 5.79 | 16.9 | 4.58 | 2.37 | 61 | 154 | 2.4 |
| 29 | 3.03 | 5.79 | 15.8 | 3.60 | 2.29 | 70 | 147 | 1.6 |
| 46 | 2.99 | 6.22 | 16.8 | 4.41 | 2.96 | 58 | 196 | 1.4 |
| 49 | 2.94 | 6.07 | 14.8 | 2.00 | 3.16 | 58 | 182 | 1.5 |
| 44 | 2.91 | 4.65 | 12.7 | 4.63 | 2.73 | 62 | 175 | 1.4 |
| 50 | 2.87 | 4.88 | 13.9 | 3.21 | 2.41 | 58 | 149 | 1.2 |
| 39 | 2.80 | 4.85 | 15.4 | 3.28 | 2.17 | 62 | 125 | 2.3 |
| 31 | 2.78 | 5.77 | 15.0 | 2.20 | 2.00 | 70 | 124 | 1.6 |
| 41 | 2.69 | 6.22 | 17.0 | 6.03 | 3.36 | 60 | 187 | |
| 23 | 2.60 | 4.34 | 12.7 | 1.22 | 2.10 | 66 | 127 | 1.4 |
| 25 | 2.55 | 3.68 | 15.8 | 3.21 | 2.54 | 64 | 148 | 2.1 |
| 32 | 2.48 | 4.32 | 15.0 | 3.47 | 1.74 | 68 | 106 | 1.5 |
| 33 | 2.41 | 4.62 | 13.5 | 1.03 | 1.92 | 80 | 114 | 2.0 |
| 48 | 2.41 | 5.33 | 14.0 | 1.10 | 2.53 | 60 | 142 | 1.5 |
| 2 | 2.25 | 3.84 | 11.8 | 1.31 | 2.53 | 65 | 132 | 1.6 |
| 38 | 2.23 | 4.37 | 14.3 | 1.32 | 2.07 | 66 | 120 | 1.7 |
| 37 | 2.22 | 4.11 | 14.7 | 1.62 | 2.42 | 64 | 121 | 1.5 |
| 30 | 2.20 | 3.45 | 13.2 | 1.15 | 1.61 | 62 | 100 | 1.2 |
| 27 | 1.96 | 4.88 | 17.5 | 2.45 | 2.15 | 60 | 133 | |
| Mean | 3.24 | 5.78 | 15.6 | 3.49 | 2.51 | 64 | 163 | 1.7 |

(1) Estimates on an empiric 3-point scale: 1 = sparse, 2 = medium, 3 = dense.

Diameter and Volume

Of the 10 seedlots of largest diameter at age 20, 7 had been present in that group at age 12 and 5 at age 8. All 3 of the seedlots which moved into the group between ages 12 and 20 appeared to do so because low stocking in one or more plots permitted rapid diameter growth of the surviving trees. Two of the poorly-stocked seedlots had lighter than average crowns, but the 8 others were above average, further indicating that foliage loss through *Dothistroma* tended to be least in the most vigorous seedlots, thus assisting them to maintain their leading position. A similar observation on the inverse relationship between the height of plants (*P. radiata* × *P. attenuata*) and the degree of infection by *Dothistroma* was reported by BOE (1971).

Information on diameters, survival and height at 12 years was used to calculate an index of stand volume ($V = 0.3 \times \text{height} \times \text{plot basal area}$). The seedlots differed markedly in volume production: Seedlots 7 and 12 were best with index values of 66 and 61 $\text{m}^3 \text{ha}^{-1}$ while 27 was poorest with only 4 $\text{m}^3 \text{ha}^{-1}$. The 5 best seedlots came from the Coast Ranges of California while the 5 poorest included 3 from the Klamath Mountains and 1 each from the Cascade and Peninsular Ranges. (Routine plantings of *P. radiata* of the same age adjacent to the trial had a volume index value exceeding 100 $\text{m}^3 \text{ha}^{-1}$).

Branch characteristics and cone production

The mean number of branch and cone clusters on each stem, the mean diameter and angle of the two largest branches in the cluster nearest breast height, the length of the longest branch in this cluster together with mean height and diameter at age 8 are given in Table 1 for each seedlot. Analysis of variance showed very highly significant differences between seedlots in all characters assessed. The correlation coefficients between the treatment means are —

| | (2) | (3) | (4) | (5) | (6) | (7) |
|-------------------------|------|------|------|------|-------|-------|
| Stem diameter (1) | 0.91 | 0.76 | 0.62 | 0.57 | -0.23 | 0.80 |
| Height (2) | | 0.71 | 0.71 | 0.50 | -0.25 | 0.80 |
| No. branch clusters (3) | | | 0.68 | 0.37 | -0.15 | 0.52 |
| No. cone clusters (4) | | | | 0.43 | -0.30 | 0.62 |
| Branch diameter (5) | | | | | -0.67 | 0.85 |
| Branch angle (6) | | | | | | -0.52 |
| Branch length (7) | | | | | | |

(A value of 0.34 is significant at P 0.05, 0.42 at P 0.01 and 0.52 at P 0.001)

Although the correlations between branch diameter and stem diameter (and height) are statistically significant, these relationships account for less than half the variance in branch thickness (and much less in branch angle), suggesting that it would be possible, for example, to find

among the vigorous seed sources some (e.g. No. 19) which has the relatively thin obtuse branches which would be desirable in a plantation.

Sources of variation

Eight years after planting the fraction of variance attributable to seed source ranged from a high value of 31% for height, through 28% for branch length, 26% for the number of cone clusters, 19% for stem diameter, 12% for branch diameter, 11% for the number of branch clusters to 10% for branch angle. Plots accounted for a small fraction of the total variance (ranging from 18% for height to 1% for branch diameter); most variance was associated with individual trees. The much greater contribution of seed source to variation in height than in stem diameter is consistent with several examples reported by MATHESON (1973) in another genus. Branch length and diameter exhibit a pattern similar to that of stem height and diameter. The seed source is rather more important for the number of cone clusters than for the number of branch clusters. These data, together with the wide range of mean values given in Table 1, indicate the great importance of the choice of seed source in any planting or breeding of this species.

Principal component analysis

Three significant factors were identified among the 7 attributes at age 8 in Table 1 and survival. The first factor (42% of variance, after rotation) was an expression of tree size, the second of branch size (especially diameter) (29%) and the third of survival and cone production (16%). These results support the conclusion drawn earlier from the correlation matrix that an appreciable fraction of the variation in the branching attributes was independent of tree size. When for the 35 better replicated provenances the scores for the first two factors are plotted against each other, the segment of the swarm of points combining vigour and slender obtuse branches is composed almost entirely of seedlots from the Coast Ranges north of San Francisco, i.e. Seedlots 12, 13, 15, 16, 20, 22 and 29.

Pinus attenuata in New Zealand

Similar trials of 48 provenances of *P. attenuata* were planted in 1961. Three of the four trials were abandoned after a few years due to severe attack by *Dothistroma*. However, results of the remaining trial at Naseby in the South Island (J. T. MILLER pers. comm.) correlate fairly well with the Australian results reported here.

Conclusions

The geographic pattern of variation of *P. attenuata* in growth characteristics is a complex one, although a modest north-south cline and a weaker altitudinal cline are discernible.

There were substantial differences in vigour and branch characteristics and the number of cone clusters on the stem of *P. attenuata* seedlots in this trial. The most vigorous trees were from the Coast Ranges of California at altitudes less than 1000 m; they include Seedlots 6 and 7 from Santa Cruz County, 12 and 13 from Lake County and 19 from Colusa County. Even material from this region, however, did not perform consistently, perhaps in part because of the very limited nature of some seed samples.

The establishment of *Dothistroma* in Australia has destroyed interest in the use of hybrids between *P. attenuata* and *P. radiata*, even though the hybrids would probably have most potential in low-rainfall areas unfavourable for the spread of the pathogen.

Acknowledgements

This trial was established by Dr. J. M. FIELDING using seed kindly provided by the Institute of Forest Genetics at Placerville. A number of other staff, especially Mr A. F. ROUT, Dr. J. W. TURNBULL and Dr. K. G. ELDRIDGE have contributed significantly to the study.

References

- BANNISTER, M. H.: Evidence of hybridization between *Pinus attenuata* and *Pinus radiata* in New Zealand. Proc. R. Soc. N. Z. 85, 217–225 (1958). — BOE, K. N.: Damage to knobcone × Monterey pine hybrids and parents by red band needle blight in California redwood sites. U. S. For. Serv. Res. Note PSW-233, 6 pp (1971). — CONKLE, M. T.: Hybridisation . . . application to pine populations. Pap. Section 22 IUFRO Raleigh N. C. August 1969. U. S. For. Serv. Sth. For. Exp. Sta., 131–133 (1970). — CRITCHFIELD, W. B. and E. L. LITTLE: Geographic distribution of the pines of the world. U. S. For. Serv. Misc. Pub. 991. 97 pp. (1966). — DUFFIELD, J. W.: Interrelationships of the California closed-cone pines with special reference to *Pinus muricata* D. Don. Ph. D. Thesis, Univ. California, Berkeley. 114 pp. (1951). — EDWARDS, D. W. and J. WALKER: *Dothistroma* needle blight in Australia. Aust. For. Res. 8, 125–137 (1978). — FORDE, M. B.: Variation in natural populations of *Pinus radiata* in California. Parts 1–4, N. Z. J. Bot. 2, 213–257, 459–501 (1964). — GILMOUR, J. W.: Distribution impact and control of *Dothistroma pini* in New Zealand. Proc. XIV IUFRO Congr. 5, 221–248 (1967). — GRIFFIN, J. R. and M. T. CONKLE: Early performance of knobcone × Monterey pine hybrids on marginal timber sites. U. S. For. Serv. Res. Note PSW-156, 10 pp. (1967). — GRIFFIN, J. R. and W. B. CRITCHFIELD: The distribution of forest trees in California. U. S. For. Serv. Res. Pap. PSW-82, 114 pp. (1972). — LINDSAY, A. D.: Knobcone pine (*Pinus attenuata* LEMMON). Commonw. For. Bur. Aust. Leaflet 14, 4 pp. (1932). — MATHESON, A. C.: Levels of genetic variation in three species of *Eucalyptus*. Pap. to ANZAAS, Perth, August 1973, 6 pp. (1973). — NEWCOMB, G. B.: Geographic variation in *Pinus attenuata* LEMM. Ph. D. Thesis, Univ. California, Berkeley. 191 pp. (1962). — PUENTE, E. J. M. DE LA: Hybridization and introgression between *Pinus radiata* and *Pinus attenuata*. Proc. 5th World Forestry Cong. Seattle, U. S. A., 2, 826–830 (1960). — ROUT, A. F. and J. C. DORAN: Arboreta in the Australian Capital Territory. For. Timb. Bur. Aust. Tech. Note 8, 87 pp. (1974). — SINDEN, J. A.: Some provisional yield tables for radiata pine. Aust. For. Res. 2 (4), 3–14 (1967). — STOCKWELL, P. and F. I. RIGHTER: *Pinus*: the fertile species hybrid between knobcone and Monterey pines. Madrono 8, 157–160 (1946).