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GENETICS

of JACK PINE



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

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Research Summary

Jack pine is an important species for planting and direct seeding in the Lake States and throughout much of the boreal forest of Canada, where it is a major source of pulpwood, lumber, and round timber. It is highly variable in climatic adaptation, growth, and form and exhibits great genetic diversity of silvicultural significance. Although referred to early in the 20th century as a "frugal scrub," its current high economic value, genetic variability, silvicultural simplicity, and ability to grow on less fertile and drier soils than are required by other sympatric species make jack pine a prime candidate for genetic improvement by selection, breeding, and controlled seed production.

Jack pine is in the Subgenus *Pinus*, Section *Pinus*, and Subsection *Contortae* along with lodgepole pine, Virginia pine, and sand pine.

Within its natural range jack pine grows in diverse climatic conditions and on a wide variety of sites. Planting of jack pine in the past, because of its apparently very modest habitat requirements, was largely on sites too poor to support merchantable timber production of other species. However, research has shown that planting jack pine on the poorest sites was not always justifiable. On short rotations and good soil, locally adapted jack pine produces a higher volume of wood than do red pine or other sympatric species.

Nearly all the present range of jack pine was glaciated during the most recent Wisconsin stage, which reached its maximum about 18,000 years ago. Thus, the present distribution of the species results from reinvasion and migration over great distances in a short time. Available paleobotanical evidence suggests that jack pine survived the Wisconsin glacial maximum at low elevations in the Appalachian Mountains south of 34° N latitude and also in the western Ozark Mountains, migrating from these refugia to the north and east and up the Mississippi Valley.

Jack pine is monoecious with ovulate cones usually occurring in the upper tree crown and staminate cones in the lower crown. Staminate cone primordia are initiated in early or mid-July, and ovulate cone primordia in August. Under intensive culture, female flowering begins as early as 12 months of age. Time of wind-pollination varies from year to year, occurring within the period from mid-May to mid-June. Two growing seasons are required for the ovulate cones to mature. The seed is mature and viable in mid-September of the second growing season.

Controlled pollination techniques are similar to those for other pines. Cone and seed production is fairly regular and increases until crowns begin to compete. Yield of filled seed in a seed orchard can reach 1,158,000 per acre (2,860,000 per hectare) through age 8 years. Over much of its range, jack pine has serotinous, persistent cones, allowing seed to be stored on the tree for several years while retaining its viability. However, red squirrels may consume most of the seed, particularly in young stands. Cone and ovule abortion and various insects are continuing problems. Little seed dormancy is present, and germination is usually rapid.

Cuttings taken from young trees can be rooted, but rooting ability decreases rapidly as the ortet age increases. Needle fascicles, in which the intrafascicular buds are forced to develop by shearing the terminal bud, can be rooted as well. Grafting is highly successful in some clones, but graft incompatibility is evident in others. Cell culture and tissue culture have not yet resulted in successful propagation of a complete jack pine tree.

Studies of jack pine in natural stands have revealed valuable information on the great variation among and within populations in many important characteristics, including the phenotypic plasticity of the species and its adaptability to various environments.

Many tests have shown that growth of jack pine provenances is related to environmental gradients associated with latitude (photoperiod) and length and temperature of the growing season, and that the species shows clinal variation over these gradients. Trees from "local" sources usually grow as well as or better than the average of those from all sources, but provenances moved slightly northward within the same climatic zone usually outgrow the local one. However, moving provenances northward in boreal eastern Canada increases vulnerability to the North American strain of scleroderris canker. Provenance variation in resistance to both the North American and European strains of scleroderris has been noted. Twenty-year results of provenance tests in the Lake States and in Canada have shown that catastrophic losses in wood production can result from planting the wrong provenance. The provenance tests also show that evaluation of growth at about 10 years is reliable for predicting later growth and wood production.

Jack pine × lodgepole pine is the only verified interspecific hybrid in which jack pine is a parent.

The hybrids are highly susceptible to sweetfern rust and should not be planted where this disease is a problem. Natural hybrids with lodgepole pine occur in areas where the ranges of the two species meet.

Selfing results in substantial inbreeding depression, but the species is generally self-compatible, at least through the S_2 generation. Crosses among selfed lines cause heterosis and relieve inbreeding depression. Thus, applied inbreeding strategies can contribute to the future genetic improvement of jack pine.

As in other pines, the similarities among the 12 pairs of chromosomes in jack pine and their lack of morphological differentiation have made their intensive study and detailed karyotype analysis difficult.

Ionizing radiation can induce genetic changes in or kill jack pine. However, of the conifers that have been studied and could be considered for planting in areas of low radioactivity or potential radioactive materials release, jack pine is one of the most resistant to radiation.

Geographic origin should be considered first when selecting sources of seed for artificial regeneration. Once the identity of superior natural stands is known from provenance tests, these stands can be used as seed sources to meet short-term artificial-regeneration needs and as a genetic base for selection and testing to meet long-term breeding objectives. The objectives must include not only maximization of genetic gains beginning in the short term, but also long-term goals including maintenance of genetic diversity, fixation of favorable alleles, and assurance that genetic research information is kept up to date generation after generation. The flowering at an early age in jack pine and the early predictability of mature performance make possible rapid generation turnover. Therefore, jack pine has the potential for more rapid genetic improvement than is possible in most other tree species. Further basic and applied research is needed to insure continuing progress in breeding and improvement to meet future increasing demand for jack pine wood.

Genetics of Jack Pine

T. D. Rudolph ¹ and C. W. Yeatman ²

Introduction

Jack pine (*Pinus banksiana* Lamb.) is a tree of the northern forests of the United States and Canada, ranging from the Atlantic coast of Maine and Nova Scotia through the Lake States and central Canada to the valley of the Mackenzie River (fig. 1). It com-

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monly occurs as a fire species (fig. 2) in even-aged pure or mixed stands on less fertile and drier soils than those required by sympatric species (Hosie 1969) (fig. 3). In the Lake States and throughout much of the boreal forest of Canada, jack pine is an important species for planting and direct seeding and is a major source of pulpwood, lumber, and round timber (Eyre and LeBarron 1944; Cayford *et al.* 1967; Cayford and Bickerstaff 1968; Anon. 1977; Benzie 1977).

The species varies in climatic adaptation, growth, and form (Rudolf 1958; Schoenike 1962a, 1976) and exhibits great genetic diversity of silvicultural sig-

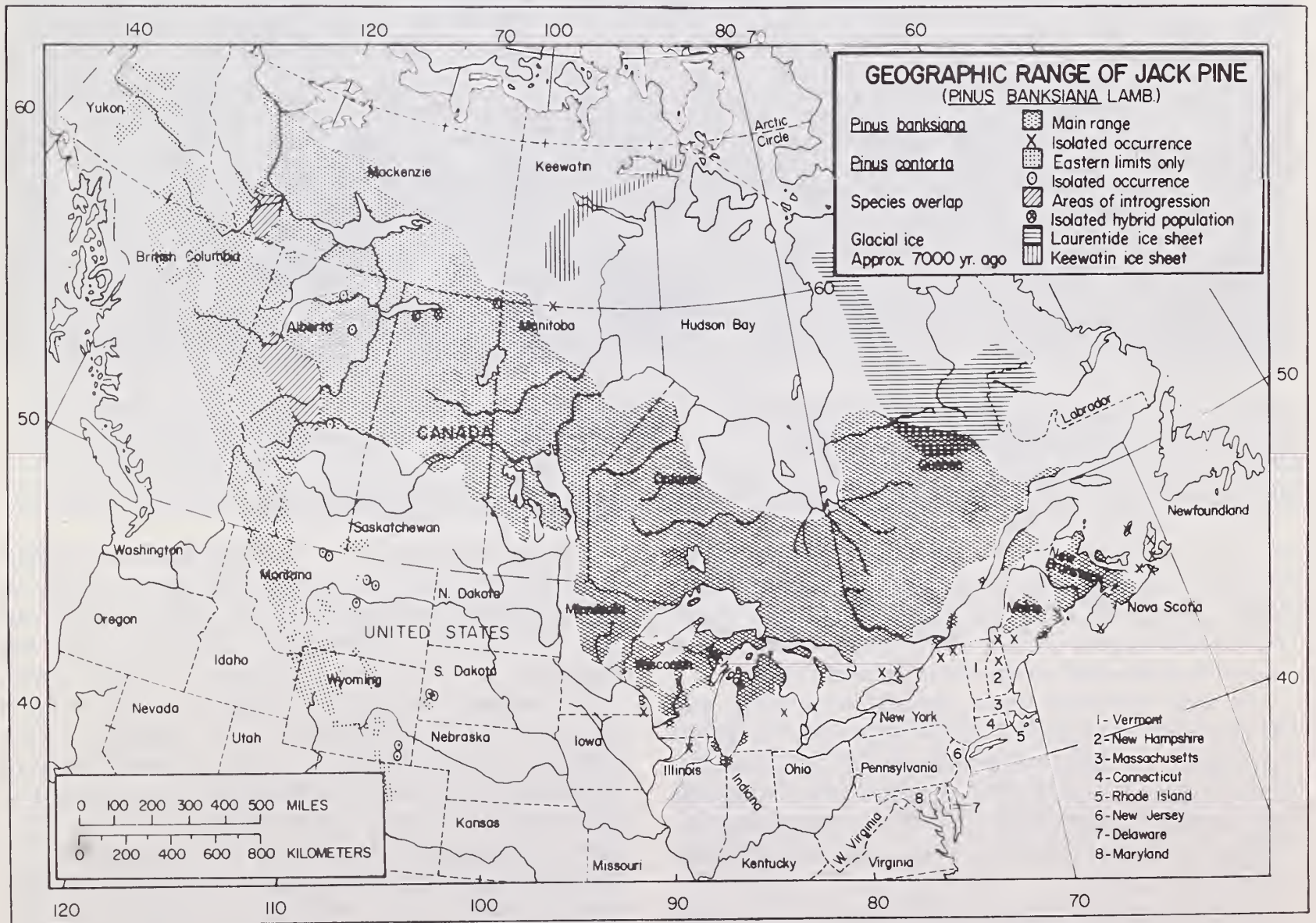


Figure 1.—The natural geographic range of jack pine (modified from Critchfield and Little 1966) showing isolated occurrences outside its main range, its relation to the eastern limits of the closely related lodgepole pine, areas of introgression, and isolated hybrid populations within the jack pine range. The relation of the present range to the Laurentide and Keewatin glacial ice sheets is also shown.



Figure 2.—Natural regeneration of jack pine near Red Lake in northwestern Ontario 12 years after a fire. The heat of a fire releases seeds from serotinous cones to exposed mineral soil and sunlight. These ideal growth conditions result in dense regeneration.

nificance (Rudolph 1964; Jeffers and Nienstaedt 1972; Yeatman 1974a) (fig. 4). Problems of seed supply and production are minimal in jack pine because it produces cones at an early age and regularly year after year; and, with some important exceptions, seed is retained for many years within closed cones that are held on the trees (Rudolf 1958).

Its high economic value, genetic variability, and silvicultural simplicity make jack pine a prime candidate for genetic improvement by selection, breeding, and controlled seed production. Programs for genetic improvement of jack pine are being initiated in the Lake States and in Canada from Nova Scotia to Alberta.

The purposes of this publication are: (1) to summarize accumulated information on the genetics of jack pine, (2) to suggest approaches to future breeding and improvement, and (3) to identify research needs.

Historical Notes

To the early French explorers and settlers, jack pine was a deformed and scrubby tree growing on rock outcrops and sterile sands. These impressions gave rise to the superstition that jack pine was poisonous to animals and capable of inducing sterility in women (Schoenike 1962a, 1976). Even early in the 20th century, Roth (1902) referred to jack pine as a "frugal scrub among the stately race of northern evergreens," undoubtedly comparing it to the majestic white (*Pinus strobus* L.) and red pine (*Pinus resinosa* Ait.) which were the foundations of the early squared-log and timber trades to European and domestic markets. Before the turn of the century, jack pine was used locally for mining timbers, railroad ties, and rough lumber. Its commercial value was first recognized in the Lake States. Pinchot (1909) stated that it "has only recently



Figure 3.—A high-quality, 50-year-old, natural stand near Baskatong Lake in western Quebec. This provenance ranked first in a local, range-wide test and is providing the foundation for subsequent improvement. Lanes were cut to remove thinnings. The stand was thinned between lanes to remove poorer phenotypes and to release the crowns of the better trees for seed production. Three hundred plus trees were systematically selected from the thinned stand and a 40-hectare seedling seed orchard was established together with progeny tests (Lamontagne 1980b).

come to be regarded as commercially important.” In an excellent early monograph on the species, Sterrett (1920) not only discussed the timber potential of jack pine but also described it in detail. Wackerman (1925) called jack pine the “Cinderella of the Lake States.” Gray (Fernald 1950) described it as a low tree usually 16 to 33 ft. (5 to 10 m) (rarely

66 ft, or 20 m) high. According to Pinchot (1909), jack pine reaches its largest size in the United States in Minnesota where trees up to 100 ft (30 m) tall and more than 25 in (65 cm) in diameter at breast height have been noted (Hansen 1937; Rudolph and Libby 1956).

Taxonomy

A. B. Lambert (1803) described jack pine in detail from cultivated specimens and named it *Pinus banksiana* in honor of Sir Joseph Banks, renowned naturalist and then president of the Royal Society of London. Schoenike (1976) thoroughly reviewed the nomenclature of jack pine, beginning with a second-hand description published in 1755 by Duhamel du Monceau. The synonym *P. divaricata* was given precedence by some authors in the past, and the subject was most recently debated by Argus (1971, 1973), Hunt (1972), and Voss (1972). It now appears that the name *P. banksiana* Lamb. will stand.

Within the genus *Pinus*, jack pine has been included in various groupings and classifications based on its apparent relation to other species. Shaw (1914) classified it in Section *Diploxylon*, Subsection *Pinaster*, Group *Insignes* with other species that bear persistent and at least partially serotinous cones. Pilger (1926) placed it in Subgenus *Diploxylon*, Section *Banksia*.

Rehder's (1949) classification was similar to Shaw's except the names of the classes were

changed. Thus, he classified jack pine in Subgenus *Eupitys*, Section *Taeda*, Series *Insignes*. Based on relations determined from species hybridization studies, Duffield (1952) reclassified part of the genus *Pinus* and included jack pine in Subgenus *Diploxylon*, Subsection *Pinaster*, Group XIII with *P. virginiana* Miller and *P. contorta* Douglas.

Little and Critchfield (1969) reviewed all previous major classifications of the genus *Pinus* and presented a revised classification containing three subgenera, five sections, and fifteen subsections. In their scheme, jack pine is in Subgenus *Pinus*, Section *Pinus*, and Subsection *Contortae*. They include *P. contorta*, *P. virginiana*, and *P. clausa* with *P. banksiana* in this Subsection. However, based upon crossability between species within the Subsection, this grouping may not represent meaningful overall relations. For example, even though *P. banksiana* and *P. contorta* are readily crossable between themselves, as are *P. virginiana* and *P. clausa*, neither *P. banksiana* nor *P. contorta* has been crossed with the latter species. *P. clausa*, on the other hand, crosses with other pines that are not



Figure 4.—Two “plus” trees (left) and two “minus” trees (right) in a natural stand near Eganville, Ontario. Plus trees were selected for predominant height, straight stem, wide branch angle, and uniform number and size of branches in whorls.

Range and Habitat

in Subsection *Contortae* (for example, see Saylor and Koenig 1967) and may be more closely related to them than to *P. banksiana*.

P. banksiana and *P. contorta* probably evolved from a common progenitor and became differentiated only after cooling of the climate and crustal uplift in western North America during the late Tertiary (Yeatman 1967). Natural hybrid populations of lodgepole and jack pine are found where ranges of the two species meet in Alberta and the Northwest Territories (Moss 1949, Scotter 1974) (fig. 1).

Named variants of jack pine are rare. Rousseau (1938) described a variant of low bush stature as forma *procumbens* found in Quebec and Nova Scotia. The low, semiprostrate provenance from Acadia National Park described by Schantz-Hansen and Jensen (1952) is probably also of this type (Schoenike 1962a). Fowler (1965a,b) and Rudolph (1966a) have described phenodeviants in seedling populations, particularly in those resulting from controlled self-pollinations. Johnson and others (1965a, 1965b, 1968a) and Johnson (1969) described dwarf seedlings that segregated in populations obtained from seeds collected from "witches' brooms." They also reported a pendulous tree in Minnesota whose open-pollinated progeny were practically all prostrate or strongly reclining (Johnson and others 1968b). Other variants have been isolated, including several types of dwarfs, and trees with variegated needle color, unusual branching characteristics, and bisporangiate strobili in natural populations and in populations with an ionizing radiation history.³

³ Data available at the Forestry Sciences Laboratory, North Central Forest Experiment Station, USDA Forest Service, Rhineland, WI 54501.

A detailed range of jack pine has been presented by Critchfield and Little (1966). The range (fig. 1) covers about 2,600 mi (4200 km) from the northwest to the southeast and more than 1,000 mi (1600 km) from north to south. It extends latitudinally from 42° N to 65° N and longitudinally from 60° W to 127° W (Schoenike 1962a, 1976). The only significant artificial extensions of this range have occurred in the Central and Northeastern States on strip-mined areas (Rudolph 1958) and on the sandhills of Nebraska (Rudolph 1958; Boldt 1969; Sprackling and Read 1975). Isolated stands occur in southeastern Minnesota (Rudolph and Libby 1956; Rudolph and others 1957; Rudolph 1960; Schoenike 1961, 1962b), northern Illinois (Schoenike 1962a, 1976), and New Hampshire (Baldwin 1959, 1961, 1979). The southernmost extension of its range occurs in northern Indiana on the south shore of Lake Michigan (Rudolph and Schoenike 1963).

Except at the eastern extremities of its range where a maritime climate prevails, jack pine grows in diverse continental climates with mean annual temperatures between 23° F and 49° F (-5° C and 9.5° C) (Schoenike 1962a, 1976) and mean minima between -5° F and -50° F (-20° C and -45° C) or lower (Rudolph 1958). The northern limits of the range closely parallel the 85° F (29.4° C) mean annual maximum isotherm, but frost may occur in some areas during any month (Rudolph 1958). Precipitation varies between 10 and 55 in (25 and 140 cm) per year with 5 to 23 in (13 to 58 cm) of this coming during the 60- to 170-day growing season (Schoenike 1962a, 1976). During the summer, there may be periods of 30 days or more without measurable precipitation in the central and western portions of the range (Rudolph 1958).

Jack pine is found at elevations from near sea level to 2,600 ft (790 m) on river flood plains, broad, level uplands, coarse-textured glacial and lake deposits, rocky seacoasts, mountain slopes, and other formations (Schoenike 1962a, 1976). Usually found on sandy, loose-textured soils, it also occurs on loamy soils, on thin soils over the granites and metamorphosed rocks of the Canadian Shield, over limestones, on peats and raw humus, and in soil over permafrost (Rudolph 1958; Cayford and others 1967; Schoenike 1962a, 1976; Rowe 1972). According to the forest cover types described by the Society of American Foresters (Eyre 1980), in the boreal forest of Canada, six subtypes of the jack pine forest cover type are recognized, and jack pine

is also a component of the black spruce, paper birch, and aspen cover types on some sites. It is also a component of the red pine and the northern pin oak cover types in the northern forest region. Some of the outliers scattered near the southern fringes of its range occur in various types of hardwood forest (Braun 1950).

Because of its apparently modest habitat requirements, jack pine has often been planted on sites too poor to support merchantable timber production of any other species (Wilde and others 1965). Thus, in comparison with other species growing on more favorable sites, it has been found to produce lower volumes of wood at comparable ages. But confining jack pine to the poorest sites has not been always

justifiable; on short rotations and better soils, jack pine can produce more wood than can red pine or other sympatric species. In Quebec, plantation-grown jack pine has produced up to double the volume of natural stands of the same age. On a similar site, rotation age was reduced from 60 to 40 years (Anon 1977). Jack pine does not grow as well as red pine on abandoned farms and old cutover land where soil compaction and deteriorated root channels prevent root penetration (MacArthur 1959; Wilde and others 1965; Bolghari 1976). But it grew much better (based on survival and average height at 10 years) than red pine on blueberry-sweetfern (*Vaccinium-Comptonia*) sites within the natural range of red pine in northern Ontario (Mullin 1975).



Figure 5.—Adjacent red and jack pine plantations (jack pine, right; red pine, left) of the same age (27 years from seed) and from a locally adapted seed origin on a sandy-gravel outwash soil at the Petawawa National Forestry Institute, Ontario. The site, typical of many where the ranges of the two species overlap, is marginal for red pine, which has some fail areas. Height of jack pine is about 43 ft (13 m); red pine about 33 ft (10 m).

Biogeography

In 24 of 25 pairs of adjacent red and jack pine plantations in the Lake States, 28 to 42 years old, the red pine mean annual volume growth exceeded that of jack pine (Alban 1978). Not considered, however, was how unadapted seed sources or the compacted soils on plantation sites influenced the species comparisons. Comparison of adjacent plantations of local adapted seed sources of the two species growing on outwash sand at Petawawa, Ontario, showed that jack pine was taller than red pine after 27 years (fig. 5).⁴ Also, planting of red pine instead of jack pine over much of Canada is not possible because the range of red pine overlaps only a portion of the jack pine range.

Growth of red pine in Wisconsin exceeded that of jack pine on nonpodzolic, coarse, sandy soils enriched in silicate minerals such as feldspar, mica, and hornblende. But on podzolized sandy loam soils or on soils derived from quartzitic parent materials, jack pine produced more than a 50-percent higher increment than red pine in some plantation comparisons. Planting of jack pine for wood production on very infertile soils cannot be justified (Wilde and others 1966). However, planting carefully selected seed sources on such soils for other nonwood production purposes, such as erosion control, may be desirable.

Soils with relatively high organic matter, phosphorus, and silt and clay content produced the best jack pine growth (Wilde and others 1965). Chrosciewicz (1963) found that the best jack pine sites in central Ontario had very fine, sandy soils with the water table within 3 to 6 ft (1 to 2 m) of the surface. Productivity of jack pine exceeded that of mixed hardwoods at ages 20 to 30 after fire on site-quality-3 till soils in New Brunswick (MacLean and Wein 1976). On quality-1 sites in Ontario, biomass production ranged from 30 to 50 t/acre (60 to 100 mt/ha) in the 25- to 60-year-old range (Hegyi 1972). Under intensive culture in Wisconsin, jack pine produced up to 26 t/acre (57 mt/ha) of biomass at age 7 years (Zavitkovski and Dawson 1978). This rapid juvenile growth and biomass production makes jack pine a desirable species for energy plantations (Zavitkovski 1979a, 1979b).

Various environments over its wide range have provided jack pine ample opportunity for differentiation and natural selection. Analysis and interpretation of genetic variation in jack pine require an understanding of the origin, evolution, and migrational history of the species.

Jack pine probably evolved as a species distinct from lodgepole pine during the late Tertiary. The species migrated south as the arctic climate cooled during the Pliocene/Pleistocene. Subsequently, it survived the four major glacial periods of the Pleistocene in peripheral refugia, reinvading the glaciated territory during the interglacial periods. During these intervals, jack pine probably occurred in environments similar to those of today and was as widely distributed (Raup 1941a, 1941b; Schuchert and Dunbar 1941; Rosendahl 1948; Dorf 1960; Terasmae 1960; Heinselman and Roe 1963; Yeatman 1967; Zavarin and others 1969; Critchfield 1978).

Virtually the entire present range of jack pine was glaciated during the most recent Wisconsin stage, which reached its maximum some 18,000 years ago (Flint 1957; Prest 1970). The present distribution of the species (fig. 1) therefore results from reinvasion and migration over great distances in a relatively short time, estimated at 15,000 years since the retreat of the ice began (Cushing 1967). The probable number and locations of the most recent (Wisconsin) glacial refugia of jack pine are questions of particular interest in relation to the interpretation of the present geographic variation.

Schoenike (1962a, 1976) made a thorough morphological study of jack pine populations from most of the species' range. He concluded that the variation in most traits studied is continuous and shows a mixture of clinal trends and random or highly intricate patterns. The major clinal trends appeared in an axis extending from the lower Great Lakes region to the western parts of the species' range. Furthermore, there were three end points of differentiation in jack pine: The east coast, the southern Great Lakes region, and the western border of the species' range.

In Minnesota, a very steep cline or partial discontinuity in several cone characteristics appears to exist from the northeast to the southeastern, south-central, and western portions of this small part of the species' range (Rudolph and Libby 1956; Rudolph and others 1957; Schoenike and others 1959; Rudolph 1960; Schoenike 1962a, 1976;

⁴ Data on file at the Petawawa National Forestry Institute, Canadian Forestry Service, Chalk River, Ontario, Canada.

Zavarin and others 1969). In northeastern Minnesota, cones are predominantly serotinous, curved, and attached to the branch at very acute angles. But to the south and southwest, the cones are predominantly open, straight, and attached to the branch at wide angles. This steep cline does not coincide with any obvious abrupt environmental change. Also, in the southern and southwestern portions of its range in Minnesota, jack pine appears to be more shade tolerant than elsewhere, and a tendency toward uneven-aged stands is evident (Rudolph and Libby 1956). Two possible explanations for this steep cline or partial discontinuity in traits of jack pine in Minnesota are that the populations originated from two different glacial refugia or from a single refugium by divergent migrational routes. The two, long-isolated lineages showing distinctly different characteristics migrated here in postglacial times and have not yet lost their individuality through interbreeding or "introgression" (Zavarin and others, 1969).

Based on fossil evidence, Wright (1964b) inferred that the late-glacial forests of the Great Lakes region were dominated by spruce and that pine was absent. He also hypothesized that jack pine migrated into the region from its Appalachian glacial refuge as the spruce deteriorated after the climate moderated.

Yeatman (1967) also concluded from a review of published paleobotanical evidence that jack pine survived the Wisconsin glaciation in only one major eastern refugium south of the ice margin. From this refugium it migrated north and west during the late-glacial and postglacial periods.⁵ This view conflicted with the earlier conclusion of Löve (1959), who found floristic evidence that jack pine survived glaciation to the west as well as to the east of the Lake Agassiz basin in Manitoba. More recently, Ritchie and others (Ritchie and Haddon 1975; Ritchie 1976; Ritchie and Yarranton 1978) interpreted extensive palynological evidence from the Prairie Provinces as supporting the hypothesized western origin for jack pine growing west of Lake Winnipeg today. Zavarin and others (1969) also argued in favor of "two glacial refugia, one central

or eastern and one northwestern" based on morphological and biochemical evidence of introgression of jack pine into lodgepole pine. They regarded the current exchange of genetic material in Alberta (Moss 1949, 1953) as only the most recent of a series of such events that may have occurred in previous interglacial and possibly pre-pleistocene times.

Critchfield (1978) concluded that evidence of preglacial contacts of lodgepole pine with jack pine is both limited and conflicting, resting mainly on the single morphological character of cone orientation. He also observed that although lodgepole pine and jack pine hybridize in regions of sympatry in Alberta and the Mackenzie Valley (Critchfield and Little 1966), there is not much to indicate introgression in lodgepole pine bordering the overlap zones. This is also consistent with Yeatman's personal observation of foothills lodgepole pine in Alberta along some 248 mi (400 km) of the forestry trunk road from the South Saskatchewan River northwest to Grand Prairie. Variation of lodgepole pine towards jack pine in cone orientation and crown conformation was observed only towards the western edges of the zone of species introgression near Coal Valley, Hinton, and Edson.

There is clear morphological evidence of introgression of lodgepole pine into jack pine in northern Saskatchewan (Argus 1966; Argus and Raup 1982) (fig. 1). The restricted occurrence of introgression in this area (G. W. Argus, personal communication 1980) indicates that it is of postglacial origin. The same conclusion applies to the hybrid population reported from the South Nahanni River, near its confluence with the Liard River in the Northwest Territories (Cody 1963; Scotter 1974).

The marked difference between jack pine and lodgepole pine in their constituent monoterpenes (Mirov 1956) has been used by some authors to characterize the two species and to examine populations for evidence of introgression (Zavarin and others 1969; Pauly and von Rudolff 1971; Critchfield 1978; Pollack 1979). The influence of natural hybridization on turpentine composition has been demonstrated for trees from the region of species overlap in Alberta. Components attributable to jack pine have been detected as far west as Jasper and the Sunwapta Falls in Jasper National Park. Resins from pine populations growing at Kananaskis, west of Calgary, and in the Cypress Hills of southeastern Alberta and southwestern Saskatchewan are all

⁵ The division between the late-glacial and postglacial periods in continental North America is generally taken to coincide with the rapid change towards a warmer and drier climate between 12,000 and 10,000 years B.P. (before present). The change occurred earlier in southern latitudes than in northern ones (Wright 1964a; Dreimanis and Karrow 1972; Saarnisto 1974).

characteristic of pure lodgepole pine. Resin samples from populations in central Saskatchewan and near Cold Lake, eastern Alberta, are characteristic of jack pine.

To hypothesize a western refugium for jack pine, one must first identify a region and suggest an environment in which the species could have survived separately from lodgepole pine during the last glacial maximum.

On the other hand, three questions arise about the proposed eastern origin of jack pine in western Canada. How and when did jack pine overcome the physical barrier to migration presented by glacial Lake Agassiz, which occupied southern Manitoba and southwestern Ontario and extended south into North Dakota and western Minnesota during late-glacial and early postglacial times (Brophy 1967; Prest 1970)? Was there enough time and adequate environmental opportunity for jack pine to migrate over 930 mi (1,500 km) from the Agassiz (Lake Winnipeg) basin to the Mackenzie Valley? Can the suggested west-east time sequence of earliest fossil pollen in northern Saskatchewan and Manitoba, as summarized by Ritchie (1976), be compatible with a proposed southeast-northwest migration of jack pine?

The following conclusions came from Yeatman's (1982) detailed re-examination and update of the literature.

Western Refugia

The glacial record precludes the possibility that jack pine or lodgepole pine survived in Alberta throughout the Wisconsin glacial interval (Prest 1970). To the north, jack pine is a relatively recent species in the Mackenzie basin in the northwest extremity of its range (Raup 1933, 1941a, 1946), and evidence for the survival of lodgepole pine in unglaciated areas of the Yukon (Hultén 1937) remains inconclusive (Critchfield 1978). The present distribution of lodgepole pine (Critchfield and Little 1966), together with palynological, morphological, and biochemical evidence, indicate that only lodgepole pine persisted south of the ice in the Rocky Mountains and eastern foothills of the northwest United States (Hansen, 1949a, b; Heusser 1969; Licht-Federovitch 1970; Mack and others 1978a, b). From this general refugium, lodgepole pine migrated north during the late-glacial period to the foothills and lands of western and central Alberta vacated by

ice and free of glacial water. The existence and distribution of eastern outliers of lodgepole pine and hybrids with jack pine (Critchfield and Little 1966; Argus 1966; Argus and Raup 1980) indicate that in the early postglacial period lodgepole pine migrated far to the east in northern Saskatchewan as it followed the receding front of the Keewatin glacial mass. Lodgepole east of the foothills was unable to survive the dryness of the hypsithermal period, except at a few widely scattered locations with favorable environments at high elevations in Alberta or on well-drained, moist microsites near lakes in Saskatchewan (fig. 1). The evidence suggests that jack pine did not arrive in northern Saskatchewan until 6,000 to 5,000 years ago and formed small hybrid populations with the relict lodgepole pine stands.

Eastern and Southern Refugia and Migration

From an examination of glacial retreat records and paleobotanical studies, one can reconstruct the westward migration of jack pine. The species survived the Wisconsin glacial maximum in eastern North America south of the tundra zone, bordering the glacial margin, and at low elevations in the Appalachian Mountains to at least 34° N latitude (Delcourt 1979). As the glaciers receded, jack pine migrated north and east into eastern Canada and west toward continental North America (Wright 1968a). The route to the west passed south of the Great Lakes, following the moraines, outwashes, and eskers left by the retreating ice, and following the meltwater streams and shorelines created by fluctuating glacial lakes. Jack pine reached western Minnesota and the southern shore of Lake Agassiz some 11,000 to 10,000 years ago (McAndrews 1967a). By about 9,500 years ago, it had migrated around or across the southern end of the Lake Agassiz basin to the western shore. During the final Campbell (high water) phase of the lake, jack pine grew on the sands of the Sheyenne Delta in North Dakota (McAndrews 1967b).

During the time of the mammoth (*Mammuth americanum*), horse (*Equus*), and muskox (*Symbos*), the mid-Wisconsin interstadial before 25,000 to 20,000 years B.P., jack pine grew in the pine-parkland forests of the western Ozarks (King, J. E. 1973). Spruce was apparently absent in western Missouri, but interstadial pollen deposits from northern and central Illinois are characteristic of a

boreal forest that included spruce, pine and a few deciduous trees (Wright 1968b; Gröger 1972a, b).

As full glacial extension approached, jack pine declined, and for several millenia, spruce dominated the forests of central North America, from north-eastern Kansas and northern Nebraska to the Appalachians (Wright 1968a, b, 1970; King, J. E. 1973). The full glacial populations of jack pine centered in the southern Appalachians were separated from those in the Ozarks to the west by mesic, cool temperate, deciduous and coniferous forests. These forests were apparently influenced by the cooling effect of glacial meltwaters flowing down the Mississippi Alluvial Valley (Delcourt 1979). The demise of jack pine populations between 34° and 37° N latitude in the Southeast occurred about 12,500 years B.P. (Delcourt and Delcourt 1979; Delcourt and others 1980). In the North, spruce forests reoccupied glaciated territory as the ice receded from the Central States. These forests differed from the modern boreal forests of Canada because of the absence of pine and an apparent admixture of ash, oak, and elm together with openings in which *Artemisia* was abundant (Amundson and Wright 1979).

However, several factors suggest that pack pine may have survived near the Ozark refugium and migrated north by way of the fluvial sands and gravels of the Mississippi Valley, which were created by the great meltwater rivers flowing south from the receding glacial fronts.

During the late-glacial period, the climate became warmer and drier throughout the Mid-Western States. Spruce was replaced by deciduous forest in the South or directly by prairie formations in the West (Wright 1968a, 1970). The trend accelerated from about 12,000 years B.P. to culminate in the postglacial hypsithermal, 8,000 to 5,000 years B.P. By this time, the prairies extended eastward within the Prairie Peninsula to include most of Illinois and northwestern Indiana below Lake Michigan (Wright 1968b).

This sequence is evident from pollen records dating from 14,500 years B.P. in Iowa (Brush 1967; Durkee 1971) and southeastern Minnesota (Wright and others 1963). Relative frequencies of jack pine pollen greater than 30 percent together with high counts of pollen grains per unit volume led Durkee (1971) to conclude that *Pinus* (probably *P. banksiana*) grew in the forests of the upper Des Moines River in north-central Iowa 12,000 to 11,000 years B.P. Subsequently, pine failed to survive the early

postglacial period in Iowa as prairie grasses and herbs completely dominated the vegetation. At Kirchner Marsh, located within the St. Croix moraine south of Minneapolis and about 5 mi (8 km) west of the Mississippi River, pine was insignificant (less than 2 percent of total pollen assemblage) within the spruce pollen zone of basal sediments dating from about 13,300 years B.P. (Wright and others 1963). Spruce declined rapidly after 11,000 years B.P. to be replaced by ash, birch, and alder before pine pollen appeared in quantity and rose dramatically to a peak of more than 30 percent at about 10,000 years B.P. During a later short interval, the pine declined to 10 percent or less when elm, oak, grasses, and herbs dominated the pollen assemblage.

In contrast, jack pine apparently did not reach the territory between the Des Moines and Mississippi Rivers, according to two pollen records from southern Minnesota. Jack pine was an insignificant component of late to postglacial assemblages recovered from Madelia and Spring Valley (Jelgersma 1962; S. Jelgersma reported by Cushing 1967). Madelia is close to a tributary of the Minnesota River, north-east of the Des Moines River watershed. Spring Valley is in the upper reaches of the Root River, a small tributary in southeastern Minnesota that meanders some 59 mi (95 km) west to the Mississippi River. Today, the only natural jack pine trees west of the Mississippi in southeastern Minnesota are found in isolated stands in the Root River area some 25 mi (40 km) west of the Mississippi and to the north in Winona County (fig. 1) (Rudolph and others 1957; Rudolph 1960; Schoenike 1961; Rudolf and Schoenike 1963).

The present southern and southwestern extremities and outliers of jack pine in the Lake States (fig. 1) are all associated with the Mississippi River or its northern and eastern tributaries, including (from south to north) the Illinois, Rock, Wisconsin, Black, Chippewa, and St. Croix Rivers. The abrupt differentiation between open- and closed-cone types of jack pine from south to northeast and north within Minnesota was reported by Rudolph and Libby (1956) and confirmed by Schoenike (1962a, 1976) in studies of variation *in situ*. In a study of all-range jack pine provenances growing together at Cloquet, Minnesota, Hyun (1979) found the clearest differentiation to be for a cluster of southern and southwestern sources from the Lake States, including an isolated stand towards the southern end of Lake

Huron in Ontario. These aspects of the past and present distribution of jack pine together with the morphological and genetic distinction of Lake States jack pine suggest that the species may have migrated north from the Central States as well as east from the Appalachians. The latter migration may have come before the former, and the two populations may have met in Minnesota and north-central Wisconsin late in the postglacial period.

From the Sheyenne Delta, jack pine may have migrated northwestward, following the shores of the Lake Agassiz along the Manitoba Escarpment to reach the area of Porcupine Hills and the outlet to the Saskatchewan River 7,000 years B.P. (Nichols 1969; Ritchie and Haddon 1975). This 435 mi (700-km) distance would have been traversed in about 2,500 years at an inferred average migration rate of somewhat less than 19 mi per 100 years (30 km per 100 years). More rapid rates must have occurred during late-glacial expansion of jack pine in the Lake States.

Prairie flora dominated the land west of Lake Agassiz. The prairie grasses rapidly replaced the pine from south to north (Ritchie 1966) as the southern shores of the lake retreated northward (Elsion 1967), and the regional and local moderating effects of the lake declined and disappeared (Shay 1967). Retreat to the north and lowering of the lake level during the interval of 10,000 to 8,000 year B.P. resulted from the differential crustal uplift in the south and the opening of progressively lower outlets to the east into the Superior basin and finally to the north into Hudson Bay (Prest 1970).

After reaching the boreal region of northwestern Manitoba and adjacent Saskatchewan, jack pine could have spread rapidly north and west, traversing and occupying the coarse deposits and moraines that paralleled the edge of the Canadian Shield (Douglas 1970, Maps 1253A, 1254A). The species was present in northern Manitoba and northeastern Saskatchewan between 6,500 and 5,500 years B.P. (Ritchie 1966) and reached west-central Alberta by about 4,500 years B.P.

Small, introgressed lodgepole \times jack pine populations discovered in northern Saskatchewan are interpreted in works by Argus (1966) and Argus and Raup (1980) as evidence of an early postglacial extension of lodgepole pine to the east in the direction of the wasting Keewatin ice sheet (fig. 1). Only few, small, isolated stands of lodgepole pine remained when jack pine arrived 2 or 3 millenia later to occu-

py the more xeric sites and dominate the regional pollen cloud. The hybrid offspring of the lodgepole pine trees were probably better adapted to the climate of the time than were the pure lodgepole pines. Now, some 40 to 80 generations later, only traces of the lodgepole pine remain in these isolated populations.

As the climate cooled after 4,000 years B.P., jack pine probably moved south and west in central Alberta to meet lodgepole pine east of the foothills in the principal area of introgression. At the same time, jack pine continued north and west to reach its present limits near Great Slave Lake and the upper Mackenzie and lower Liard and Nahanni Rivers, where the two species meet to form a second small zone of introgression.

Sexual Reproduction

Reproductive Development

Jack pine, a monoecious species, has ovulate cones that usually occur on primary and secondary branches in the upper tree crown. The staminate cones occur on tertiary branches lower in the crown. Ovulate cones are modified long shoots, and staminate cones are modified dwarf shoots (Doak 1935). In northeastern Wisconsin, bud initiation for the following year's shoot system begins in late June or early July. Staminate cone primordia are initiated in early or mid-July, but the ovulate cone primordia are not initiated until August. By early September, the staminate cone primordia are about 0.04 in (1 mm) long and remain that size until spring. Then they elongate to about 0.2 in (5 mm) by the middle of May and early June, when pollen is shed. Time of anthesis varies considerably from year to year. Ovulate cones in long branch terminal buds are generally not visible to the naked eye during the fall and winter, but can be identified microscopically (Curtis and Popham 1972). Cecich (1979) has described the ultrastructure of the 1st-year jack pine ovule. The ovulate cones usually begin to emerge in mid-May, and pollination occurs soon after, when the cone scales are about perpendicular to the cone axis (Curtis and Popham 1972) (fig. 6).

The male gametophyte develops slowly after pollination, a pollen tube emerges, and the generative cell divides to form a stalk cell and a body cell. Also during the first season of development, and prior to winter dormancy, the megaspore within the nucellus enlarges and produces up to 32 nuclei by free nuclear divisions. In the spring, the free nuclear divisions in the female gametophyte continue until up to 2,000 nuclei are formed and cell wall formation begins. Several archegonia are initiated during this time before the female gametophyte is completely cellular. The egg cell arises after a series of divisions in the archegonium. Also in the spring, the stalk and body cells of the male gametophyte move down into the pollen tube. Shortly before fertilization, the nucleus of the body cell divides to form two sperm nuclei of unequal size. The pollen tube continues to grow through the nucellus toward the female gametophyte. Here, it enters the neck cells of the archegonium and discharges into the egg cell the two male gametes, the tube nucleus, and the stalk cell. The egg nucleus is fertilized by the larger of the two male gametes, and the other three nuclei disinte-



Figure 6.—Female flowers (strobili) of jack pine at the receptive stage. At optimum receptivity, the scales are opened at right angles to the cone axis.

grate. Fertilization occurs about 13 months after pollination, when the female cone is approaching its maximum size (Ferguson 1904).

The zygotic nucleus divides three times to produce an eight-celled proembryo (Beal 1934; Buchholz 1931). After another division, the proembryo becomes organized into an apical tier, a suspensor tier, and a rosette tier. Up to four apical tiers per archegonium develop into embryos, but the rosette tiers may also give rise to embryos. Although polyembryony does occasionally occur (Buchholz 1931; Gravatt and others 1940), usually only one embryo survives to maturity. Subsequent development of the embryo includes differentiation of the root apex, cotyledons, and provascular tissue.

The pollinated ovulate cones need two growing seasons to reach maturity. At the end of the first season, the ovulate cones are about 0.24 in (6 mm) wide and 0.39 in (10 mm) long. By September of the next year, the mature cones are up to 1.2 in (3 cm) wide and 2.4 in (6 cm) long (Curtis and Popham 1972).

Natural Pollination

Under natural conditions, jack pine is normally a wind-pollinated, cross-fertilizing species. The wide genetic variation in the species suggests large, effective breeding populations; heterozygosity for many alleles; and strong natural selection against self-fertilization and increased homozygosity.

Although separation of the male and female cones within the crown helps to limit the amount of self-pollination, some overlap does occur within the mid-tree crown, particularly in open-grown trees. Anthesis is generally synchronized with ovulate cone receptivity (fig. 6). On the average, three trees had 12.8 percent self-fertilization in the upper crowns and 25.9 percent in the lower crowns (Fowler 1965a). Rudolph (1966a) found up to 25 percent natural selfing on the basis of deviant seedlings in open-pollinated progenies. Because of increased homozygosity of recessive lethal genes, however, embryo development failure after selfing may be more frequent than after open pollination. As a result, self-pollination probably occurs much more often than the above percentages indicate. But because natural selection acts against semilethal and other deleterious characteristics, it would severely limit the number of selfed seedlings that survive under natural conditions (Rudolph 1979a). Teich (1970) used inheritance of cone serotiny characteristics to determine inbreeding coefficients of 0.27 to 0.67. Sittman and Tyson (1971) suggested that misclassification of mixed cone types inflated the coefficients and that self-fertilization was about 10 percent.

Controlled Pollination

The basic techniques for controlled pollination of jack pine are similar to those reported for other pines by Cummings and Righter (1948), Mergen and others (1955), and Wright (1976). These methods have been modified to suit local conditions and meet specific breeding objectives. The "double bagging" technique used to isolate ovulate cones is satisfac-

tory for most purposes. A bag made of sausage casing is placed over the end of the branch bearing ovulate cones, the bottom is sealed with a wad of cotton, and the bag is tied with a 12 in. (30-cm) piece of 21-gauge copper wire. A size 1250 "Pollen-tector" kraft paper bag is then placed over the sausage casing.⁶ The kraft bag prevents excessive heat buildup (fig. 7).

In Ontario, single isolation bags made with woven terylene and transparent window inserts have been satisfactory for most controlled pollinations. These bags may be reused once under normal conditions, but should then be discarded.

The optimum time for pollination is when the scales of the ovulate cones are fully opened and at right angles to the cone axis (fig. 6). However, the time of maximum receptivity varies not only between locations and among trees within a location, but also between ovulate cones on the same tree. If it is not possible to apply pollen more than once to span the range of receptivity, it is most practical to pollinate when most ovulate cones on a tree are receptive.

Pollen collection must be carefully timed. Usually, staminate cone-bearing branches can be collected, and pollen release can be forced a few days before the normal time for pollen shedding. In a warm spring or in a hot spell after a long, cool spring, pollen may ripen and shed in 1 or 2 days. Collections made too early will result in shriveled staminate cones and little or no viable pollen. In general, the pollen is mature enough to collect when squeezed staminate cones produce a bright yellow exudate. At this time, the individual strobili comprising a cluster will be independently loose rather than a rigid unit. Before being placed in the extraction container, the pollen-bearing branches should be washed in running water to remove any possible contaminative pollen.

Staminate cones can be dried for pollen extraction in various ways to prevent contamination. A simple method is to place the freshly washed staminate cones in "Pollen-tector" bags, insert a wad of cotton into the mouth of the bag before tying, and dry in a circulating oven at 80° F (27° C) to 90° F (32° C) until pollen sheds freely. The pollen can be ex-

⁶ The use of trade, firm, or corporation names in this publication is for the information and convenience of the reader and does not constitute an endorsement by the U.S. Department of Agriculture of any product or service to the exclusion of others that may be suitable.



Figure 7.—Controlled pollinations being made on 17- and 23-month-old seedlings at the beginning of their second growing season in the nursery after 6 and 10 months, respectively, of initial growth in the greenhouse. Flowering at a young age enables rapid generation turnover in jack pine breeding.

tracted and cleaned by sifting it through an 80-mesh screen. Although pollen is best when used fresh, it can be stored at 32° F (0° C) in a desiccator over calcium sulfate or silica gel for at least 1 year.

Germinability of the pollen can be tested in distilled water at 75° F (24° C). Germination or pollen tube growth can be scored after 72 hours. However, pollen tube formation *in vitro* does not necessarily insure nuclear viability and fertilizability. Stairs and Houston (1969), for example, found that for several coniferous species, exposing pollen to gamma radiation levels up to 400,000 R did not inhibit pollen tube growth *in vitro* but rendered the pollen completely inviable in terms of fertilizability and seed production. Thus, *in vitro* pollen germination tests may not be entirely reliable.

Cone and Seed Production

In Placerville, Calif., jack pine trees were among the youngest of 55 species and varieties of pine to flower, producing both ovulate and staminate cones at 3 years (Righter 1939). Jack pine typically begins to flower at 5 to 10 years when open-grown but not until 10 to 25 years in closed stands (Roe 1963). Widely spaced jack pine seedlings in a well-watered nursery can be expected to flower after 3 years (Wright 1964). However, in standard nursery beds

in Lower Michigan, 3-year-old seedlings flowered at a frequency of only about 0.3 percent (Rudolph 1966b).

When near-optimum growing conditions in the greenhouse and nursery are provided, female flowering can be induced in a small percentage of seedlings as early as 12 months after seed sowing (Rudolph 1979c). In older seedlings grown under these conditions, the percentage of flowering trees increases to 16 to 23 percent at 17 months, 62 percent at 23 months, and 71 percent after 4 years (Rudolph 1966b; Jeffers and Nienstaedt 1972). Production of male strobili in seedlings 3 years and younger was practically nonexistent in contrast to Righter's (1939) report of equal frequencies of males and females on 3-year-old seedlings in California. Continuous variation among full-sib progenies in percentage of seedlings producing ovulate cones at 17 months indicated that early flowering is under additive genetic control and not under the control of a single major gene or recessive genes (Jeffers and Nienstaedt 1972).

Photoperiod may influence flowering. Because female and male strobili are initiated at different times during the growing season, different photoperiods may be needed for each type of flower initiation (Larson 1961; Giertych 1967).

Once cone production in jack pine begins, it is fairly regular and increases until crown competition becomes a factor (Roe 1963). In 5-year-old nursery-grown trees, 6.7 female strobili per tree were produced, and, allowing for 50 percent abortion, 10,700 cones or about 108,000 seeds per acre (267,000 seeds per ha) could have been harvested the next year (Jeffers 1976). Six-year-old trees growing at initial seed orchard spacing of 2.44×2.44 m (8×8 feet) produced comparable yields of more than 10 cones per tree and about 119,000 filled seeds per acre (310,000 filled seeds per ha). Based on conelet counts in the summer of the 7th year, an average of 38 cones per tree was projected at age 8, resulting in a total yield of 1,158,000 seeds per acre (2,862,000 filled seeds per ha) of seed orchard during the first 8 years (Rudolph 1979a).

Analysis of 25 years of seed production data from the Argonne Experimental Forest in northeastern Wisconsin showed that jack pine seed crops were good 42 percent of the time, medium 35 percent of the time, and fair 23 percent of the time (Godman and Mattson 1976).

In a natural, medium-stocked stand, 70 to 80 years old, Roe (1963) found an average of 335 cones per tree. Cone production per acre (ha) was more than twice as high in thinned stands as in unthinned ones. Cone production in natural stands was best at 40 to 50 years. In well-stocked plantations, seed production per acre (ha) was twice as high in 9-year-old trees as in those 13 years old, apparently because of crown closure. In the boreal region of Quebec, 65-year-old jack pine produced the highest seed yields (10.7 lbs/acre, 12 kg/ha; 1,214,000 seeds/acre, 3 million seeds/ha) at densities of 325 to 485 stems per acre (800 to 1,200 stems per ha) (Popovich and others 1970). At the Petawawa Forest Experiment Station in eastern Ontario, 15-year-old trees growing at 14×14 ft (4.27×4.27 m) spacing had more than four times more conelets on the average (83+ per tree) than at a 7×7 ft (2.13×2.13 m) spacing (19 per tree). Because there were fewer trees, however, the number of conelets per acre (ha) was only 10 to 20 percent greater at the wider spacing. Because of rapid crown closure at the narrower spacing, this advantage in conelet production at the wider spacing is expected to increase.⁷

Seed yields per cone vary from about 15 to 75 (Schantz-Hansen 1941; Rudolf 1958; Roe 1963; Rudolph 1966b, 1967, 1976; Jeffers 1972; Baker 1980). Seed yields of more than 30 seeds per cone are rare from open-pollinated cones. Cone borers (*Laspeyresia* spp.) can reduce average seed yield to 10 or fewer per cone.⁷ In a study of jack pine growing in natural stands in northeastern Ontario, Baker (1980) observed great variation in fecundity from tree to tree. Some trees had many cones almost every year, while others were consistently unproductive, even though they were of similar age and crown size. Trees with heavy annual cone crops did not necessarily have the greatest number of filled or viable seeds per cone.

Strongly curved cones yield fewer seeds than do straight cones (Schantz-Hansen 1941; Jeffers 1972; Baker 1980) (fig. 8), and cone shape appears to be highly heritable and easily recognized (Schoenike and others 1959) (fig. 9). Ovulate abortion on the inside curvature is twice that on the outer curvature (Cecich 1979). Therefore, trees with strongly curved cones should be avoided as plus trees, when other characteristics are equal (Yeatman 1975b). The average number of cone scales per cone in 11 provenances was 84, but only a little more than one-third of the scales in the upper ends of the cones bore seeds (Jeffers 1972). Percentages of filled seed vary depending on many environmental factors and probably on some genetic factors. Average filled-seed yields of 20 to 30 per cone are common. Overmature trees produce smaller cones with fewer filled seeds per cone (Roe 1963).

Cone characteristics such as cone volume, cone length, scale number, number of scales to first ovule, and number of scales to first seed are under stronger genetic control than such characteristics as ovule number, seed number, and filled-seed number (O'Loughlin 1973).

Cone and seed characteristics were evaluated for 15 provenances growing at six locations in the North Central United States (Rudolph and Cecich 1979). Cone volume, seed size, number of seeds per cone, number of filled seeds per cone, percentage of total seed filled, and germination percentage differed significantly among the six plantation locations as well as among provenances (see page 29). Plantations at Lake Tomahawk, Wisc., and Platts-

⁷ Data on file at the Petawawa National Forest Institute, Canadian Forestry Service, Chalk River, Ontario, Canada.

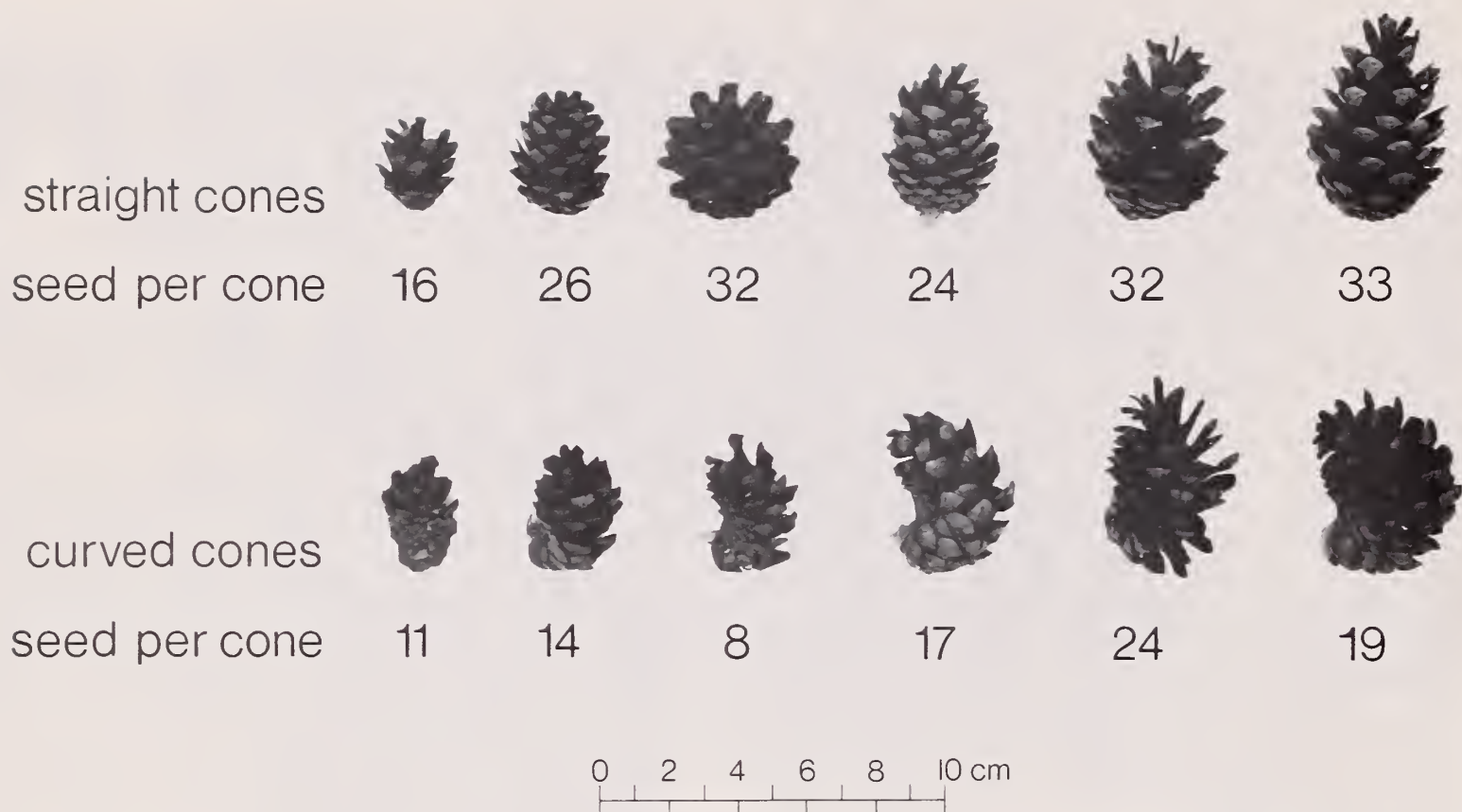


Figure 8.—Differences in jack pine seed yields due to cone curvature and size. Curved cones yield less seeds than do straight cones of the same size. Cone size and shape appear to be highly heritable.

mouth, Nebr. ranked best for most of the seed yield and quality characteristics; a Grand Rapids, Minn., plantation was intermediate; and plantations at Kellogg Forest, Mich., Black River Falls, Wisc., and Columbia, Mo., had low yields of viable seeds per cone. The variation among locations appeared to be related to site quality but not to latitude or longitude. Thus, selecting seed orchard locations for jack pine must emphasize choosing the best possible site for the species where growing-season length is not limiting. Locating seed orchards somewhat south of the locations of the provenances being grown may result in greater seed yields and better seed quality as long as unsuitable regional pollen does not significantly contribute to pollination within the orchard.

Because jack pine has serotinous, persistent cones over much of its natural range, seed can be stored on the tree over an extended time while retaining its viability (Rudolf 1958). However, viability may be significantly reduced after 5 to 10 years; only cones 6 years old or less are recommended for seed collection for nursery or container stock production

(Baker 1980). Total seed stored per acre can reach more than 13 lb (14.6 kg per hectare) (estimated at over 1,620,000 seeds per acre, over 4 million per hectare) in well-stocked mature stands (Eyre and Le Barron 1944). The amount of viable seed stored in the cones varied from 560,000 per hectare in a 40-year-old, unthinned stand to 1,875,000 in a thinned stand of the same age (Roe 1963). Intermediate amounts of 941,000 and 1,179,000 seeds per hectare were stored in 70- to 80-year-old stands and plantations, respectively. In northeastern Ontario, Baker (1980) recorded yields of filled seeds ranging from 526,000 to 6,040,000 per hectare. This variation was related to stand age (30–80 years), but not to stocking. In areas with nonserotinous or partially serotinous cones, seed may be disseminated during any season (Rudolf 1958).

In selection, the serotinous cone habit should be favored for two reasons: Economy of seed collection and insurance against fire (Yeatman 1975b). First, seed can be stored in the closed cones for several years and collected in quantity as needed. Second,

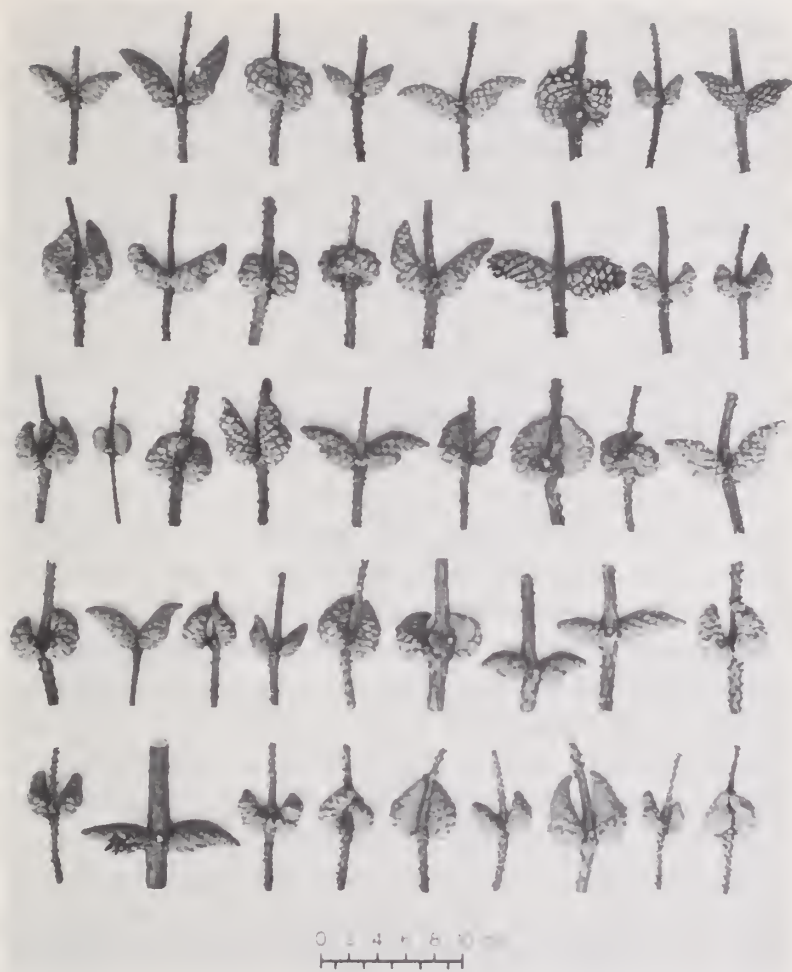


Figure 9.—A sample of the variation in cone size, shape, curvature, and angle with the branch found in a jack pine rangewide test plantation near Lake Tomahawk, Wisc.

in the event of fire, the closed cones release the stored seed and insure natural regeneration.

The serotinous cone character is highly heritable. But because it is difficult to classify trees having both open and closed cones, the number of genes controlling the trait remains debatable (Rudolph and others 1959; Teich 1970; Sittmann and Tyson 1971). The melting temperature of the resinous bonding material of the cone scales has been reported as 122° F (50° C) (Cameron 1953), but it is likely that the bonding resin softens at lower temperatures in the nonserotinous cones in the southern portions of the species' range (Rudolph 1958).

The number of dewinged and commercially cleaned seeds ranges between 71,000 and 250,000 per lb (156,000 and 550,000 per kg) with an average of 131,000 per lb (288,000 per kg). More than 94 percent of the seeds are filled (USDA, Forest Service 1948). Proportions of filled seed in jack pine may be ascertained by nondestructive methods such as

X-radiography (Rudolph 1967), by flotation in liquids such as ethyl alcohol or diethyl ether (Brown 1967a), or by blowing out the empty seeds.

Cone and seed crops in jack pine may be reduced by a number of agents that have been summarized by Rudolf (1958). Rainy weather at time of pollination may reduce seed set. Low-vigor trees may produce much pollen but little seed. Red squirrels and other rodents may destroy cones and consume seeds. Cone and seed insects may also cause serious losses. Oak-pine rust damages trees, resulting in smaller and aborted ovulate cones. Birds may also be important consumers of jack pine seed.

Cone production and seed production are also reduced by cone and ovulate abortion. In controlled cross-pollinations, conelet and cone abortion ranges from about one-third to two-thirds of the strobili pollinated.⁸ The abortion rate in selfing of S₁ trees to produce S₂ seed was 75 percent (Rudolph 1976). Therefore, in controlled breeding, it is necessary to pollinate additional strobili to compensate for abortion. Within a cone, all ovules near the base of the cone abort, and the frequency of abortion decreases toward the tip (Cecich 1979).

Seed Germination and Seedling Development

Jack pine seed occasionally exhibits some dormancy but usually germinates to capacity within 15 to 60 days under favorable conditions (Rudolph 1958). Some seeds require more than 100 days to germinate, however. (Rudolph, personal observation). Delayed germination has also been observed in trials of direct seeding of jack pine in Ontario. Increases in stocking between the 1st and 3rd years after sowing were observed and were often substantial (Riley 1980). Ahlgren (1959) suggests that fire may stimulate germination through the action of heat, which breaks the partial dormancy. On the other hand, fire has been observed to delay germination (Beaufait 1962), prompting Roe (1963) to suggest that extreme heat may induce dormancy. Seeds from cones exposed to 900° F (482° C) for 30 seconds germinated normally, but longer exposures killed the seeds (Beaufait 1960).

⁸ Data available at the Forestry Sciences Laboratory, North Central Forest Experiment Station, USDA Forest Service, Rhineland, WI., and at the Petawawa National Forestry Institute, Canadian Forestry Service, Chalk River, Ontario, Canada.

Asexual Reproduction

Exclusion of light reduced germination at temperatures ranging from 60° to 80° F (15.6° to 26.7° C). Germination was promoted by either a single, short exposure to light or by daily exposures longer than a minimum period (8 hours) (Ackerman and Farrar 1965). Light did not effectively "trigger" germination until a threshold moisture content was reached equivalent to about 30 minutes imbibition.

Under forest conditions with adequate moisture, seeds germinate when air temperatures reach 64° F (18° C) (Rudolf 1958). Germination is best on mineral soil but can also occur on the moist duff that usually follows fire. Associated species were shown to affect germination, survival, and growth differentially in laboratory and field tests (Brown 1967b).

Cecich and Horner (1977) used microspectrophotometry and electron microscopy to describe the cytochemical and ultrastructural changes during the first few days of germination. During the first 48 hours of germination, increase in volume is due entirely to cell enlargement, because cell division does not begin until 52 hours. DNA synthesis begins at 43 hours. The first leaf primordia appear between adjacent cotyledons at 72 hours. Protein and starch digestion occurs before the leaves appear. Heterochromation increases in the nuclei during germination, and Golgi bodies increase in number after the first cell divisions.

Young seedlings can grow in as little as 2 percent of full sunlight, but they grow tallest in intensities greater than 52 percent of full sunlight (Rudolf 1958). Under forest conditions, seedlings attain a height of about 2 in (5 cm) the first year, 6 in (15 cm) at 2 years, and 1 to 3.3 ft (0.3 to 1 m) at 4 years (Rudolf 1958). In the greenhouse, seedlings can grow to more than 8 in (20 cm) tall in 10 weeks (Rudolph 1976). Age of the trees from which cones are collected and age of the cones do not affect the early development of jack pine (Rudolf and Ralston 1953).

Rooting of Cuttings

Jack pine cuttings can be rooted, especially when taken from young trees, but rooting ability decreases rapidly as ortet age increases. Cuttings taken from 4-month-old seedlings gave 76 percent rooting (Armson and others 1975), but average rooting was only 7.4 percent in cuttings from 6-year-old ortets and 5.4 percent in those from 10-year-old ortets (Zsuffa 1974). Variation in rooting percentage among clones ranged from 0 to 31 percent. Rooting was best in cuttings from ortets with long, heavy branches but did not differ between second- and third-order branches. Cuttings of medium length (1 to 3 in, 2.6 to 7.5 cm) produced the best results. Cuttings rooted in tubes developed better root systems than those planted in an open bed.

Recent research has shown that aryl esters of indole auxins can enhance rooting of jack pine cuttings. Phenyl indole-3-butyrate (P-IBA) treatment caused 12 percent more jack pine cuttings to initiate roots than did treatment with indole-3-butyric acid (IBA) and up to 30 percent more than did no treatment. The two auxin treatments did not differ in their effects on the number of roots initiated nor on the length of the longest root per cutting (Haissig 1979).

Rooting of Needle Fascicles

The rooting of needle fascicles can potentially establish large clones in a short time. Removal of the terminal apical bud induces the fascicular buds to differentiate and develop shoots. Rudolph and Nienstaedt (1964) rooted fascicles from 2- and 5-year-old jack pine seedlings on which the terminal buds had been sheared. Shearing the terminal buds in early July, when height growth was largely completed, resulted in the development of up to 30 fascicular buds per 5-year-old seedling and up to 21 buds on the 2-year-old ones. Fascicles without a visible bud did not develop shoots even when they rooted. Exposure to cold before rooting hastened the breaking of dormancy in the fascicular buds. Fascicles from 2-year-old trees root more readily than those from 5-year-old trees. Best rooting (70 percent) was obtained from fascicles that had been treated with indolebutyric acid (0.1 percent) and that came from sheared 2-year-old trees propagated in a heated rooting medium under 20-hour photoperiod. Treatment with 0.8 percent indolebutyric acid hindered fascicle survival.

Grafting

Little information is available on grafting of jack pine. Holst and Santon (1958) attempted reciprocal grafts of jack, red, and Scotch pine to test for graft compatibility and possible stimulation of growth or flowering. Combinations of jack and red pine failed, but combinations of jack and Scotch pine survived. Some of the jack pine ramets on Scotch pine rootstocks are now more than 25 years old and show no ill effects of the interspecific graft union. However, Yeatman (1974a) has concluded that there are no long-term practical advantages to interspecific grafting with jack pine.

Some graft incompatibility has been noted with wide-ranging differences between clones (Rudolph, personal observation). Grafts in some clones soon fail, but others do not fail until several years later. Attempts to graft scions on rootstocks raised from seed from the same parent trees gave inconclusive results. Grafting is more successful when done just as the rootstock resumes growth in the spring. Yeatman (personal observation) has noted that some failures in grafting jack pine plus trees could be attributed to the condition of scions collected at various times in the winter and held in frozen storage (0° F, -18° C). The survival rate was very poor when the scions were thawed too quickly. Scions stored in the freezer for 12 months and thawed in a cold room (35° F, 2° C) did not survive when grafted, but some scions survived after storage for 6 months. Grafting scions from young trees was more successful than from older trees. However, more research is needed on the causes of grafting failure and on the factors involved in graft incompatibility.

Cell and Tissue Culture

Durzan and Campbell (1974) presented optimistic prospects for eventual mass production of improved forest trees by cell and tissue culture. They reviewed not only the potential of cell and tissue culture in vegetative propagation per se, but also the possibility of using these techniques to propagate selected genotypes for direct use in regeneration. However, neither callus tissue nor cell suspension culture has resulted in successful propagation of complete jack pine plants.

In a series of seven reports in 1976 in the *Canadian Journal of Botany*, Durzan and his colleagues examine the chemical factors and growth data that characterize proliferation of callus and cell suspensions of jack pine seedling tissues. The reports of Durzan and his coworkers contain much fundamental information needed to develop cell and tissue culture methods to propagate jack pine (Chalupa and others 1976; Durzan and Bourgon 1976; Durzan and Chalupa 1976a, 1976b, 1976c, 1976d; Durzan and others 1976).

Genetics and Breeding

In situ Variation

In situ investigations have provided valuable information on the amount and types of variation among and within populations of jack pine for many characteristics, and on the reaction range or phenotypic plasticity of the species and its adaptability to various environments. *In situ* investigations can only provide information on naturally occurring phenotypes, but the environmental and genetic components of the observed variation cannot be separated. The most comprehensive study, made by Schoenike (1962a, 1976), involved on-site measurements and sampling of 20 trees in each of 90 areas representing an estimated 75 percent of the total range of the species. Data were collected on 33 traits of tree crown, bark, wood, foliage, and cones of mature trees.

All of the characteristics Schoenike studied varied significantly with geographic origin; an average 37 percent of the variation was due to origin. Variation between localities was strongest for bark thickness, needle length and width, number of stomata per leaf surface and cone serotiny, and was weakest for needle curvature, needle thickness, and number of resin ducts.

Variation patterns in most characteristics were clinal, especially from the Lake States to the northwest, although irregular patterns occasionally existed within the species' range. Important correlations were noted between certain environmental factors and individual traits including precipitation/bark thickness, precipitation/needle length, latitude/needle volume, number of stomata/latitude, temperature/cone serotiny, and temperature/cone knobiness.

In grouping the traits according to magnitude for multiple range analysis, some groups overlapped, but most localities within any group were from the same geographic area. Clinal gradients, further defined by multivariate analysis, were steepest in an area from northwest of Lake Superior toward the northwestern portions of the range in Canada. But variation from the species norm increased in all directions from this center to maximum phenotypic variability on the east coast, in the southern Lake States, and at the western border of the species. Cluster analysis, which identified eight clusters, showed that neighboring clusters were more similar than distant ones, adding further evidence of the general clinal variation pattern.

Coefficients of variation among trees in stands were determined, and, although large differences were found between stands, no geographic patterns emerged. Samples from western Alberta substantiated that natural hybridization has occurred there with lodgepole pine. No other locality showed enough differentiation to suggest that a separate population occurred.

Schoenike's investigation suggests that environmental factors are the dominant selection forces responsible for the natural variation within the current jack pine range. Mutations have generally been considered of minor importance in population variation. However, the importance of mutations in natural variation may be greater in jack pine than in most other northern forest tree species, because jack pine has both a short sexual-generation time and the ability to regenerate prolifically after fire and other environmental disturbances. Schoenike concluded that genetic drift was inconsequential in jack pine natural variation. Introgression with lodgepole pine is of major importance only in the northwestern extremities of the species' range.

The area of optimum development of jack pine is north of the Great Lakes in Ontario and Quebec (Chrosiewicz 1963; Le Blanc and Conway 1974). There is also where Schoenike (1962a, 1976) found most traits to be intermediate and least differentiated relative to the extremes of variability. The species is very abundant there and occurs on a wide range of sites. Whether this area could be considered a "center of variability" for the species remains debatable.

Other studies of variation in natural stands of jack pine have covered only portions of its range. In a survey of the variation in jack pine native to Minnesota, a clear differentiation was noted from predominantly closed cones in northeastern Minnesota to open cones in the southern and southwestern portions of the range in Minnesota (Rudolph and Libby 1956; Rudolph and others 1957; Rudolph 1960). Lammas growth and prolepsis in four natural stands in Minnesota occurred most often in the south and in exposed situations (Rudolph 1961, 1964).

Provenance Variation

The many *ex situ* studies of variation in jack pine have included controlled environment chamber, greenhouse, nursery, and field experiments. They have included trees grown from seed collected in natural stands or provenances over the species' range and tested at various locations (table 1).

Growth.— Growth is the characteristic most fre-

quently emphasized in *ex situ* provenance studies, particularly in relatively mild climates. Tree growth is also paramount in boreal environments, but only among cold-hardy and disease-resistant seed sources. In environments where growing season and low temperatures are not limiting, growth usually follows a clinal pattern associated with environmental gradients of latitude (photoperiod), and length and temperature of the growing season.

Table 1.—*Provenance tests of jack pine*

Provenance locations	No. of provenances	Test Location	Year established	Published results
Maine to Alberta	32	Cloquet, MN	1942-43	Schantz-Hansen and Jensen 1952, 1954; Rudolph and others 1959; Schoenike and others 1959; Schoenike and others 1962; Schoenike and Brown 1963; Jensen and Brown 1965.
Minnesota, Wisconsin, Michigan	29	17 sites in Minnesota, Wisconsin, Michigan	1951	Stoekeler and Rudolf 1956; Jensen and others 1960; Arend and others 1961; Batzer 1961; Rudolph 1961, 1964; King 1966, 1968, 1971; King and Nienstaedt 1965; Alm and others 1966; Alm and Jensen 1969; Sutherland 1972; Jeffers and Jensen 1980; Zavitkovski and others 1980.
Minnesota, Wisconsin, Michigan	16	Chalk River, Ontario	1951	Morgenstern and Teich 1969.
Ontario	14	Chalk River, Ontario	1951	Holst and Yeatman 1961; Yeatman 1974a.
Ontario Quebec	6	New Zealand	1955	Sweet and Thulin 1963.
Ontario Quebec	9	Chalk River, Ontario	1957	Yeatman 1974a.
Rangewide	99	Canada, Holland U.S., Great Britain	1962	Giertych and Farrar 1962; Yeatman 1964, 1965, 1966a, 1966b, 1967, 1971, 1974a, 1976a, 1976b; Holst 1967; Mergen and Worrall 1965; Mergen and Thielges 1967; Mergen and others 1967; Durzan and Chalupa 1968; King 1968; Miksche 1968; Holst and others 1969; Teich and Smerlis 1969; Kennedy 1969, 1971; Schnare 1969; Chiba and Nagata 1970; Logan 1971, 1974; Logan and Pollard 1971; Chalupa and Durzan 1972; Canavera and Wright 1973; Jeffers 1972; Kriek 1973; Mergen and others 1974; Sprackling and Read 1975; Tauer 1976, 1978; Hyun 1979; Rudolph and Cecich 1979; Tobolski 1979.

With some exceptions, trees from "local" provenances have ranked among the best in growth in field tests. In one of the earliest tests at Cloquet, Minn., the relatively fast-growing local provenance was exceeded in average annual height growth by at least six other provenances during the first 8 to 10 years (Schantz-Hansen and Jensen 1952, 1954). Wright (1972) reported that Lower Peninsula jack pine was superior to trees of Upper Peninsula origin when grown in both parts of Michigan. A few tests (Alm and Jensen 1969) have failed to demonstrate clinal variation patterns or have been interpreted as showing ecotypic variation (Arend and others 1961). The clinal pattern, however, predominates in the published information on provenance test growth.

Differences in growth among provenances from the jack pine range have been demonstrated, beginning in young seedlings grown under the same conditions. An all-range provenance study including 99 seed sources was begun by the Petawawa Forest Experiment Station in 1962 with nursery tests in the United States and Canada and field tests in the United States, Canada, and Great Britain (Holst 1967). In a study of nine of the provenances in controlled environments, northern provenances were more responsive to change in photoperiod than southern ones (Giertych and Farrar 1962). In 115-day-old seedlings, total dry weight, height, dry weights of foliage and roots, and dry weight per unit of nitrogen content were all positively correlated with degree-days of the seed origin. Trees from 50 provenances from the entire range were grown in nine controlled environments in combinations of three photoperiods and three temperatures (Yeatman 1964, 1965, 1966b). Growing degree-days (base 42° F, 5.6° C) best accounted for growth after 3 months. At the cotyledon stage, growing degree-days and seed weight accounted for about equal amounts of the 76 percent of variation in seedling size among provenances (Yeatman 1966a). At the end of 3 months, however, the effect of seed weight on seedling size was insignificant. Based on regressions of seedling weight on growing degree-days, Yeatman (1966b) distinguished between western and eastern populations with the dividing line at 91° W longitude. The relation was stronger in the west than in the east.

Among trees from these provenances, differences in dry weight, shoot length, and needle characteristics were better expressed in photoperiods of 15

hours or less than in 20-hour photoperiods (Yeatman 1966b; Mergen and others 1967). Photoperiod was four times as important as temperature in accounting for variation in growth characteristics. Yeatman and Holst (1967), studying 38 of the provenances in controlled environments for 4 months and in the nursery for 4 years, found a strong correlation ($r = 0.85$) in the seedling dry weight in the laboratory and seedling height in the nursery. Height growth at 4 years in an Ontario nursery was best correlated with mean daily temperature during the growing season of the seed origin (Holst and others 1969).

Study of seedling phenology in relation to seed origin and cultural environment showed that spring growth initiation depended primarily on temperature. Seedlings in northern provenances had a lower temperature threshold than did seedlings of southern origin. In most environments, northern provenances also formed buds earlier than did southern provenances, but strong provenance \times environment interactions were evident. Bud formation was usually promoted by high temperatures and short photoperiods, but was delayed by longer photoperiods and lower temperatures (Yeatman 1966b).

A test in Missouri of 30 provenances from the rangewide study showed trees from northern sources to be shorter than those from southern ones after two growing seasons (Schnare 1969). Tree height was correlated with climatic variables associated with latitude. Photoperiod at the origin was cited as an important variable at this location, which has a shorter photoperiod during the growing season than is found over any part of the jack pine range.

In a Michigan test of the rangewide provenances, trees from Lake States sources were up to three times as tall after 3 years as those from the Northwest Territories and northeastern Quebec. Correlations between 1-, 2- and 3-year heights were highly significant as were those between 3-year nursery heights and 4-year field heights (Canavera and Wright 1973).

After 9 years in a Nebraska test of the rangewide collection, the tallest trees, which exceeded the plantation mean by about 15 percent, originated from Fort Coulonge, Quebec, and Mosinee, Wisc. (Sprackling and Read 1975). The shortest trees were from Wrigley, Northwest Territories, and reached only 61 percent of the plantation mean height. Annual height growth varied from 12 to 24 in (30 to 60

cm) among provenances.

These results show that provenances representing the range of the species vary in height growth with latitude and the length and temperature of the growing season. Southern provenances generally grow more rapidly, at least where photoperiod and growing season are not limiting.

Tests of provenances from within regions may also show a relation between height growth and latitude of origin, but other environmental factors influencing growth differences become more apparent with more intensive sampling of provenances in a region. Yeatman (1975a) tested collections made from two stands in each of five areas along a 60-mi (97-km) transect in the Ottawa Valley. Tree height after 6 years at 3 test sites in the Valley showed differences among progenies from trees within stands but not from trees among stands or areas. Yeatman concluded that, in terms of early height growth, jack pine, within this relatively small area, is not differentiated by ecotypic variation or by isolation of stands. Therefore, selection for height could be made throughout the area as though all trees were from the same provenance.

Ontario and Quebec provenances tested at Chalk River, Ontario, showed a significant positive correlation between 17- to 19-year height and growing degree-days (Holst and Yeatman 1961; Yeatman 1974a). Also, 53 percent of the variation among provenances in tree volume was accounted for by growing degree-days. Trees from a source 40 mi (65 km) away from the local source and test site but in the same climatic region grew as much as 10 percent more. This shows that variation within climatic regions may justify regional sampling, testing, and selection for genetic improvement.

Performance of a 7-year-old trial of six Ontario and Quebec sources on two New Zealand test sites showed provenance differences in height; the taller sources originated in milder climates (Sweet and Thulin 1963). The study, however, did not include sources from the warmest climates in the natural distribution of the species, and the authors suggest that such sources would probably have more rapid early growth in New Zealand.

After 2 years in the nursery, average seedling height in 29 provenances from within the Lake States was negatively correlated with latitude and positively correlated with seed-origin degree-days over 50° F (10° C). Clinal variation also occurred (Stoekeler and Rudolf 1956).

The 29 provenances were planted on 17 test sites in the Lakes States in 1954. Ten-year mean height of the 29 sources among 11 of the 17 test plantings in Minnesota, Wisconsin, and Michigan ranged from about 9.6 ft (2.9 m) on the Chippewa National Forest site to 15.2 (4.6 m) on the Marinette County Forest in northeastern Wisconsin (King 1966). The widest range in height among sources was found in the Mosinee Industrial Forest planting, in Washburn County, Wisc. Here, trees from the poorest source (northern Minnesota) were 25 percent below the plantation mean. The best provenance (western Lower Michigan) was 17 percent above the plantation mean height and 6 percent above the local provenance. Hence, planting of the poorest provenance instead of the best would, in this case, result in more than 40 percent less height growth after 10 years. Overall, in Michigan and Wisconsin tests, provenances from Lower Michigan grew best; in the northern Minnesota plantings, provenances from north-central Minnesota were in the top rank. Other studies have shown similar seed source × plantation interactions.

Morgenstern and Teich (1969) analyzed the individual provenance contribution to seed source × plantation interaction among 16 of the 29 provenances to calculate the phenotypic stability of height growth at the age of 12 years. They found that sources from north of 47° N latitude and south of 45° N contributed heavily to the interaction while the central sources contributed little, probably because they were closer to the test planting sites. Analysis of such seed source × planting site interactions to determine height growth stability will help in selecting superior seed sources for improvement breeding.

Ten-year height at the Petawawa Forest Experiment Station in Ontario showed significant differences among 16 of the Lake States provenances, but only moderate geographic separation was evident. Trees from Lower Michigan provenances were among the tallest (Yeatman 1974a).

In a planting of the 29 provenances near Cloquet, Minn., height variation among provenances at 15 years showed no relation to site quality, age of parent stand, or geographic location (Alm and Jensen 1969). The shortest provenance, from the eastern part of the Upper Peninsula of Michigan, was 78 percent as tall as the tallest, which was from the eastern part of Lower Michigan. The provenance closest to the test plantation ranked fourth in

height and second in diameter.

Thus, the 10- and 15-year results of the Lake States provenance tests show that height growth of Lower Michigan provenances is among the best where length of the growing season is not limiting. Southern Lake States provenances also had the most rapid height growth when tested on coal strip-mine banks in southwestern Indiana, where growing seasons are much longer than those of the seed origins (Williams and Beers 1959).

Table 2.—*Jack pine seed origins included in Lake States provenance test*¹

Seed source	County	Latitude	Longitude	Growing degree-days ²	Average January temperature
		°N	°W		°F
Minnesota					
1589	Cass	47.4	94.4	9,200	5
1590	Cass	47.0	94.6	9,400	7
1591	Itasca	47.5	94.1	9,100	5
1592	Lake	47.7	91.2	7,400	10
1593	Cook	48.0	90.3	6,700	14
1594	St. Louis	48.1	92.4	8,500	5
1595	Pine	46.0	92.6	9,500	10
1596	Pine	46.4	92.8	9,000	9
1597	Becker	47.1	95.4	8,900	4
1600	Cass	46.8	94.4	9,400	6
1601	Beltrami	47.5	95.0	8,600	5
1602	Itasca	47.8	93.3	8,800	6
Wisconsin					
1605	Bayfield	46.7	91.0	9,000	13
1606	Forest	46.0	88.9	8,500	12
1608 ³	Burnett	45.9	92.1	10,000	10
1609	Marinette	45.2	88.3	9,600	14
1610	Oneida	45.8	89.8	9,000	10
1611	Wood	44.4	89.7	10,000	13
Michigan (Upper Peninsula)					
1612	Gogebic	46.2	89.2	8,500	12
1613	Ontonagon	46.6	89.0	8,800	15
1614	Alger	46.3	86.7	8,100	15
1615	Chippewa	46.3	84.8	8,000	15
1621	Luce	46.6	85.4	7,900	16
Michigan (Lower Peninsula)					
1616	Manistee	44.2	86.2	10,100	22
1617	Ogemaw	44.2	84.1	9,600	19
1618	Alpena	45.0	83.5	9,000	19

¹ Data from Stoeckeler and Rudolf (1956).

² Normal annual sum of average daily temperatures of 50° F or higher.

³ Not planted at University of Minnesota CFC (Plantation 6).

Twenty-six provenances common to 14 test plantations (fig. 10, tables 2 and 3) in the Lake States provenance study were remeasured for height and diameter at age 20 (Jeffers and Jensen 1980). Aver-

age tree volume was determined from sample trees harvested from each of 10 provenances in two Wisconsin plantations and one Michigan plantation. The Pillsbury State Forest planting in north-central Minnesota (3) had the greatest mean height 33.3 ft (10.2 m) for all sources. The plantation at the University of Michigan Biological Station in the northern Lower Peninsula (15) had the shortest mean height, 18.9 ft (5.8 m). Differences in height among sources were significant in all plantations except that at Cloquet, Minn. (6). The widest mean-height variation among provenances was found in the Mosinee Industrial Forest plantation in Washburn County, Wisc. (8). Here, the two shortest provenances from Lake and St. Louis Counties in northeastern Minnesota (1592, 1594) were only 71 percent as tall as the plantation mean. The tallest source, from Manistee County in Lower Michigan (1616), was 17 percent taller than the plantation mean. These results show that a large loss in production can result from reforesting an area with the wrong provenance. Over all plantings, three provenances from Lower Michigan (1616, 1617, 1618) ranked highest in mean height, followed by the Pine County, Minn. provenances (1595, 1596). Those from northeastern Minnesota were consistently ranked lowest. The provenances from Lower Michigan appear to have a broad adaptive range within the Lake States and may be best for planting on a wide range of sites in this region. However, the Pine County, Minn. jack pine appears to also do well over a wide range of locations in the Lake States, except those with a short growing season. Mean diameter growth at 20 years of the 26 provenances in 14 plantations, ranging from 3.2 to 4.7 in (8 to 12 cm), shows about the same variation patterns as height. Significant differences among provenances were found in all plantations except the three in northern Minnesota. Provenances from Lower Michigan and Pine County, Minn. again ranked highest.

Variation in volume growth at 20 years among trees from the 26 sources over the 14 plantations was even more striking than that for height and diameter. For example, in the Mosinee Industrial Forest plantation in Wisconsin (8), trees from the Lake County, Minn. source (1592) produced only 52 percent of the plantation mean volume per tree; the Pine County, Minn. trees (1595) produced 36 percent more volume than the plantation mean. In many of the plantations, trees from the Lower Michigan provenances exceeded the plantation

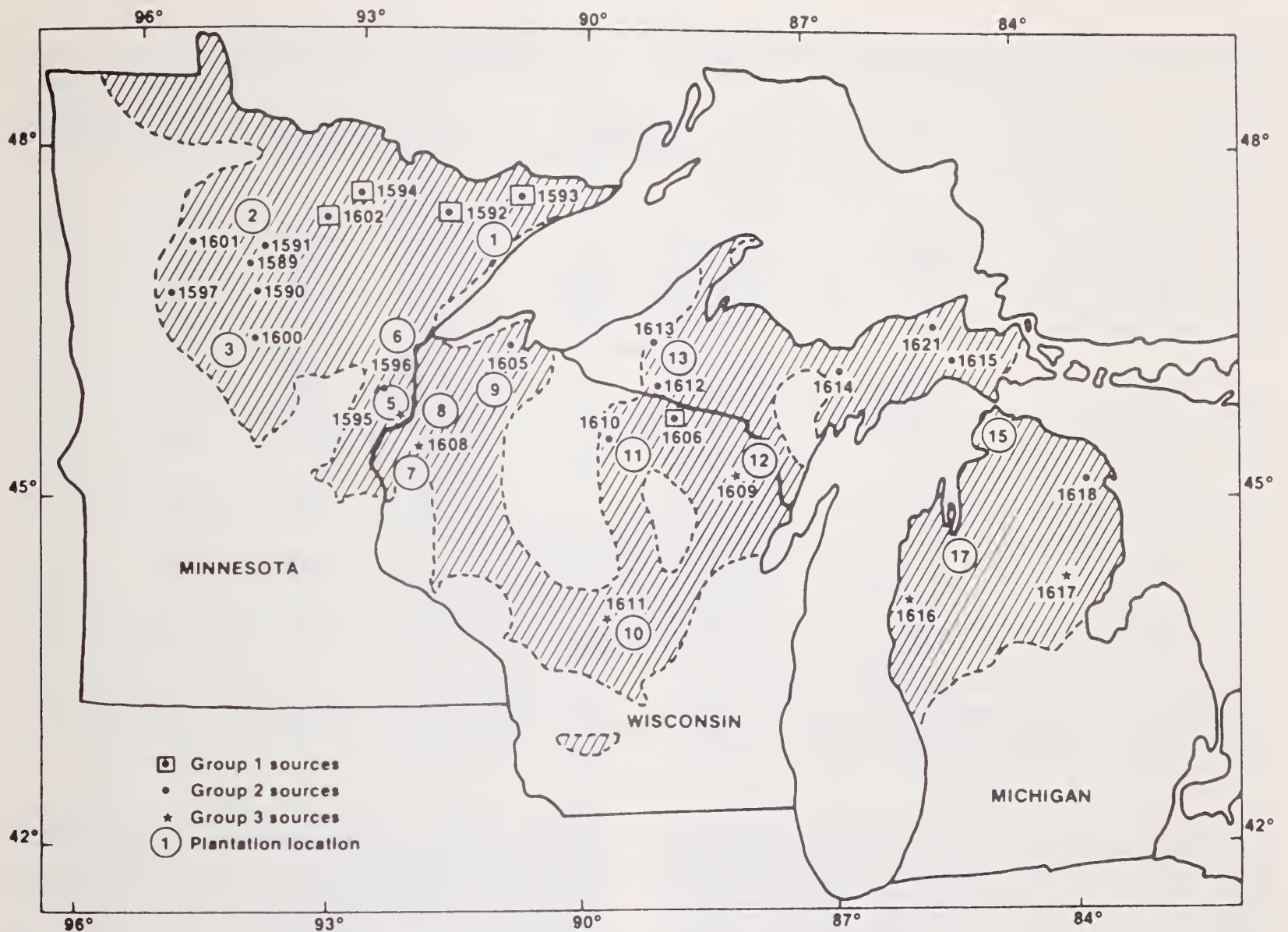


Figure 10.—Location of seed sources and plantations included in 20-year measurements of the Lake States jack pine provenance test. Shaded area shows the natural range of jack pine in the Lake States as described by Rudolf and Schoenike 1963. Assignment of the provenances into three groups according to performance results is also indicated (Adapted from Jeffers and Jensen 1980).

mean by 20 to 40 percent and usually ranked highest in volume per tree.

In terms of volume of solid wood produced per acre (hectare), where survival in the plantations is taken into account, variation among plantations and the 26 provenances within plantations is even greater. The range in volume produced among plantations was 1,041 to 2,012 cu ft per acre (73 to 141m³ per ha). Within plantations, the greatest range among sources in volume per hectare was from 38 percent to 187 percent of the plantation mean. Potential volume production losses of this magnitude, which were caused by planting the wrong provenance, should be of great concern to those responsible for jack pine reforestation.

Jeffers and Jensen (1980) assigned each of the 26 provenances to one of three groups based upon correlations among them for degree-days; average January temperature; and height, diameter, and volume per tree. Trees from group 1 sources were from northeastern Minnesota (fig. 10), the region with the shortest growing season and the lowest average January temperatures, and grew slowest in all plantations within the same climatic zone except in the Superior National Forest plantation (1). Differences in growth among the three provenance groups were generally greater the farther south the plantation. The greatest range in volume produced per acre (hectare) occurred in a central Wisconsin plantation where group 3 provenances produced 245 percent as

Table 3.—Locations of jack pine plantations included in the Lake States provenance test ¹

Number	Forest	County	Plantation establishment	Latitude	Longitude	Growing degree-days	Average January temperature
				°N	°W		°F
Minnesota							
1	Superior NF ²	Lake	U.S. For. Serv.	47.6	91.1	7,400	10
2	Chippewa NF	Beltrami	U.S. For. Serv.	47.4	94.5	8,600	5
3	Pillsbury SF	Cass	Minn. Conserv. Dept.	46.4	94.5	9,400	6
5	General Andrews EF	Pine	Minn. Conserv. Dept.	46.4	92.8	8,700	9
6	Univ. Minn. CFC	Carlton	Univ. of Minn.	46.7	92.5	8,500	8
Wisconsin							
7	Burnett CF	Burnett	Burnett Co.	45.6	92.8	10,000	10
8	Mosinee IF	Washburn	Mosinee Pap. Co.	46.2	92.0	10,000	10
9	Chequamegon NF	Bayfield	U.S. For. Serv.	46.3	91.4	9,000	13
10	Nepco IF	Wood	Nekoosa-Edwards Pap. Co.	44.2	89.8	10,000	13
11	Argonne EF	Forest	U.S. For. Serv.	45.8	89.0	8,500	12
12	Marinette CF	Marinette	Marinette Co.	45.7	88.0	9,600	14
Michigan (Upper Peninsula)							
13	Ottawa NF	Ontonagon	U.S. For. Serv.	46.3	89.2	8,500	12
Michigan (Lower Peninsula)							
15	Univ. Mich. BS	Emmet	Univ. of Mich.	45.5	84.7	8,700	17
17	Fife Lake SF	Grand Traverse	Mich. Conserv. Dept.	44.5	85.4	9,700	18

¹ Data from Jeffers and Jensen (1980).

² NF = National Forest; SF = State Forest; EF = Experiment Forest; CFC = Cloquet Forestry Center; CF = County Forest; IF = Industrial Forest; BS = Biological Station

much volume as that of group 1. In the plantations with longer growing seasons, growth in height, diameter, and volume was usually less the farther north the seed origin and increased with degree-days of the origin. Such correlations were poor or insignificant in the plantations with a short growing season.

The 20-year results of the Lake States provenance study by Jeffers and Jensen (1980) show that provenances originating closest to the planting sites grew as well as or better than the average for all provenances; but many others, especially those moved slightly northward, outgrew the local provenance. Thus, although wide latitudinal movement of provenances is not suggested, movement up to 100 mi (160 km) northward in the Lake States can increase growth. Selection of superior provenances within latitudinal belts of similar climate should make substantial genetic gains possible. Also, the results clearly show that planting the wrong provenance can cause catastrophic losses in wood production.

Biomass production in 24- and 25-year-old plantings of four of the Lake States provenances at three locations ranged from about 1.2 to 2.7 tons/acre/yr

(2.6 to 6.0 mt/ha/yr) (Zavitkovski and others 1981). The highest mean annual biomass production was 63 percent greater than the maximum reported in the literature. Total biomass and mean annual biomass production were negatively related to latitude of the plantation. The average whole-tree biomass production was almost 60 percent greater at Pembine in northeastern Wisconsin and 30 percent greater at Watersmeet in the southern Upper Peninsula of Michigan than at Isabella in northeastern Minnesota. Similar comparisons in stem biomass showed even greater differences between plantation locations, with relatively more biomass being incorporated into stems at warmer locations. A significant interaction between provenances and plantation locations was present. For example, a Lower Michigan provenance produced the greatest biomass in the plantations in northeast Wisconsin and on the Upper Peninsula of Michigan; an Upper Peninsula source produced the least. In the short-growing-season location in northeastern Minnesota, the Lower Michigan provenance ranked poorest and the Upper Peninsula provenance was best. This suggests that moving provenances slightly northward

within climatic zones may increase biomass production, but moving from warmer to colder short-growing-season zones results in poor growth.

The height growth results over the 14 plantations after 20 years (Jeffers and Jensen 1980) show variation patterns that are strikingly similar to the 10-year results presented by King (1966), particularly with regard to the good overall performance of the Lower Michigan provenances. Correlations between 10- and 20-year height were significant in all plantations. Correlations between 5- and 20-, 5- and 10-, and 10- and 20-year heights among provenances were also generally greater in the plantations located in warmer areas. Among Ontario provenances grown at the Petawawa Forest Experiment Station in Ontario, 5-year height was not effective in predicting 19-year height. However, height at 11 years accounted for 71 percent of the variation in height at 19 years (Holst and Yeatman 1961; Yeatman 1974a). Differences among provenances became smaller as age increased, particularly among the fast-growing ones. For the 29 provenances in the Cloquet planting in northeast Minnesota, comparison of average heights at 15 years from seed with those at 8 years showed that trees from the five best provenances maintained their rank (Alm and Jensen 1969). The above relations indicate that height growth at about 10 years is reliable for predicting later height growth. This information increases confidence in early evaluation of performance tests and helps in roguing seedling seed orchards.

There are small, but significant, differences among provenances in the date of height-growth initiation in the spring. Trees from northern sources flushed up to 1 week earlier than those from southern sources, both at Cloquet, Minn., and Chalk River, Ontario (Rudolph 1961, 1964; Teich and Holst 1969). Date of height-growth cessation varied among provenances from late June to mid-July. Northern provenances ended height growth earliest and also had the shortest period of growth. The mean duration was 61 days in Ontario and 67 to 68 days in Minnesota.

Growth rate in Ontario varied among provenances from 0.13 to 0.37 in/day (3.3 to 9.3 mm/day), and the average maximum growth rate during the season at Cloquet, Minn. also approached 0.39 in/day (1 cm/day). Teich and Holst (1969) pointed out that although leader growth in jack pine stops long before the end of the frost-free season, the re-

maining time may be necessary to complete late-wood growth, lignification, setting of terminal buds, and hardening off to attain frost resistance. Rudolph (1961, 1964) reported frost injury to shoots on trees with lammas growth, particularly on those in which height growth was artificially extended by lengthening the photoperiod. These results suggest that selection for height growth should be made on the basis of the highest rate of growth that occurs during a moderately long period of growth.

Provenance variation has also been found in second flushes of growth or lammas growth (in terminal shoot) and prolepsis (in lateral shoots at base of terminal bud) (Rudolph 1961, 1964). The occurrence also varied significantly between plantations and from year to year, indicating that these late shoots have a wide range of reaction to environmental conditions in addition to the genetic influence shown by the provenance differences. Frequency of the late shoots increased with more southern latitude of seed origin, increase in degree-days of origin, and higher average July temperature of the origin. A clinal variation pattern was apparent, and control by multiple genes was suggested. Trees with lammas growth did not grow much less the next season than those with normal growth, although the difference approached significance at the 5-percent level. Lammas growth and prolepsis appear to have no significant advantage in terms of height growth but often result in deviations from normal shoot development and tree form. Therefore, seed collection from trees and stands with these growth types should be avoided (Rudolph 1961, 1964).

Tree Form. — Stem form of jack pine is highly variable and often poor, particularly in trees growing at wide spacings (fig. 4). Branch angle with the stem also varies greatly but is commonly less than 40 degrees. (Rudolph and Libby 1956; Yeatman 1957b). In one of the earliest provenance studies established in 1942-43 at Cloquet, Minn., Schantz-Hansen and Jensen (1952, 1954) rated fewer than 10 percent of the trees in the good and fair form classes combined. However, Schantz-Hansen and Jensen (1952) suggested that many of the undesirable form characteristics would disappear as the trees got older and that trees previously classified as having poor form may ultimately prove to be entirely satisfactory crop trees. Trees in the most rapidly growing provenances appeared to have somewhat better form than those in slow-growing

provenances, such as shrubby trees from Bar Harbor, Maine.

Schoenike and others (1962) examined the branching characteristics in the same Cloquet plantations when the trees were 15 to 16 years old. The average number of branches per whorl among provenances ranged from 3.1 to 4.0, but most provenances had 3.5 to 3.8 branches per whorl. The range in branch angle among provenances was from 44 to 70 degrees. Crown diameter averaged only 43 percent of total height in a narrow-crowned provenance from western Wisconsin. Branch diameter, expressed as a percentage of the stem diameter at the point of branch attachment, varied among provenances from 34 percent to more than 57 percent. The variation in these branching characteristics showed no consistent trends with geographic location of the provenance.

Sprackling and Read (1975) evaluated 28 provenances for their potential as windbreaks, Christmas trees, and landscaping trees in Nebraska. Fast-growing trees with dense crowns and upright branching habits were the preferred type for these purposes. Slow-growing trees from northern origins had the lowest rating and fast-growing trees from southern origins were best. Trees from Petawawa, Ontario, ranked best and ones from Nipekamaw River, Saskatchewan, ranked worst.

Wood and Bark Properties. — King (1968) found provenance differences in both tracheid length and specific gravity. Tracheid length varied in a 5-year-old rangewide test from 0.044 to 0.064 in (1.12 to 1.62 mm). Specific gravity ranged from 0.321 to 0.389. The slow-growing, more northern provenances generally had the higher specific gravity and the shorter tracheids. The between-provenance variation was much greater than the within-provenance variation. Juvenile selection for tracheid length may result in genetic gains, but specific gravity of young trees may have little value in predicting the density of mature trees.

Significant differences among provenances occur in other xylem characteristics including ring width, earlywood width, latewood width, percentage of latewood, rate of annual ring formation, and date of latewood initiation (Kennedy 1969, 1971). Wider rings and greater widths of earlywood and latewood were associated with provenances from regions of more growing degree-days. Latewood percentage was not systematically related to provenance and

showed considerable genotype \times environment interaction.

Bark thickness in 18- to 21-year-old trees showed a continuous pattern of variation among 25 provenances tested in Minnesota (Schoenike and Brown 1963). Trees with thick bark were found in provenances from the southern and western portions of the Lake States. Trees with thin bark were mostly from far northern and east coast provenances. Bark thickness on trees from Minnesota provenances decreased rapidly and uniformly from the southwest to the northeast. Similarly, in Michigan provenances, bark thickness decreased from south to north. Schoenike and Brown concluded that bark thickness is a trait under moderately strong genetic control, and that selective breeding for bark thickness may be feasible.

Cold Hardiness. — Variation among jack pine provenances in winter injury was noted by Schantz-Hansen and Jensen (1952, 1954) in the oldest seed source test at Cloquet, Minn., after the severe 1947-48 winter. The most heavily damaged provenances were from Baldwin and Wellston in Lower Michigan. Some trees died, and up to 93 percent showed some injury. Most Minnesota and Canadian provenances showed little or no winter injury. Therefore, trees should not be moved from areas with long, warm growing seasons to those with short growing seasons and more severe winters.

Trees with lammas shoots are subject to injury in years with early, severe autumn frost (Rudolph 1961, 1964). Because lammas shoots occur more frequently in trees from southern origins when moved to more northern sites, care must be taken when moving provenances to minimize such potential frost injury.

Yeatman (1966b) demonstrated that jack pine provenances differ in cold hardiness and associated morphological and physiological characteristics. Within a uniform environment, such differences are related to latitude of seed origin when considered over the full range of the species. Tolerance to spring frost was not related to seed origin because growth initiation in the spring depended primarily on temperature.

Cold hardiness in a number of jack pine provenances, provenance hybrids, and lodgepole pine \times jack pine hybrids back-crossed to jack pine planted near Hillsport in northern Ontario, was clearly associated with germplasm of northern origin both in

pure jack pine and in hybrids with lodgepole pine (Yeatman and Holst 1972). Trees containing germ-plasm of southern origin were susceptible to winter injury at this northern location. There was no evidence that either provenance hybrids or hybrids with lodgepole pine were more or less winter hardy than natural jack pine populations of similar geoclimatic origin. California lodgepole pine \times Lake States jack pine hybrids were intermediate in frost hardiness between the parental populations of the two species with a polygenic mode of inheritance indicated (Rudolph and Nienstaedt 1962).

Winter hardiness is critical to survival and growth of planted jack pine in the colder boreal climates of Canada (Yeatman 1976a). No long-term advantage in growth is to be expected by moving provenances north in such climates, and the risk of winter injury and susceptibility to disease is increased.

Fall Coloration. — Young jack pine seedlings change from green to a purple or purplish bronze in autumn (Stoekeler and Rudolf 1956). Both rate of change and color intensity vary with age and depend on seasonal temperatures and provenance. Among 29 Lake States provenances in a Wisconsin nursery, trees from northern provenances showed an earlier and more intense color change than those from southern provenances. The positive correlation with latitude was significant in 1-, 2-, and 3-year-old seedlings. A weaker but significant positive correlation with average January temperature of the origin was also noted. On the average, color change was more intense in the 1-year-old seedlings than in the other age classes. There was no relation between color change and length of the frost-free period of the seed origins. Yeatman (1966b) observed similar color changes during the fall and winter in seedlings of three latitudinal groups (45° N, 50° N, and 55° N+) grown at New Haven, Conn. (latitude 41° N). Seedlings grown at the same time in a greenhouse in New Haven developed less intense coloration and developed more slowly in the fall. In evaluating 95 provenances from the range-wide collection in a Lower Michigan test, Canavera and Wright (1973) noted that the color change in trees from the northernmost provenances persisted to age 7, but the color changed from green to yellow rather than from green to purple. Canavera (1975) also reported a north-south trend in color change among progenies from stands in Lower Michigan. In

2-year-old trees of 11 provenances from the range-wide collections tested in Hokkaido, Japan, the northern provenances were most purple in mid-October, but the southernmost provenances remained green (Chiba and Nagata 1970).

Seed Yield. — Differences among provenances grown at the same location have been noted in cone size and in seed yield and quality (Rudolph and Cecich 1979). Cone volume, seed size, number of seeds per cone, percentage of total seed that was filled, and germination percentage differed significantly among 15 Canadian and Lake States provenances grown at six locations in the North Central United States. No relation to latitude or longitude of the provenances was found. The largest cones (0.366 to 0.427 cu in (6 to 7 cc) and seeds (0.629 cu in/1000 seeds, 10.3 cc/1000 seeds) were produced by three Quebec provenances and one Wisconsin provenance (Nekoosa); the smallest (0.0281 cu in and 0.467 cu in/1000 seeds, 4.6 cc and 7.6 cc/1000 seeds), by a New Brunswick provenance (Grand Lake). Highest average yields of seeds per cone (31) were produced by the Nekoosa, Wisc. provenance and the lowest (18) by a Saskatchewan provenance. Percentage of total seed filled ranged from 44 in the New Brunswick provenance to 78 in the Murray Bay, Quebec, and Brainerd, Minn., provenances. It should be noted that the Grand Lake, New Brunswick provenance represents a small population of probably highly inbred trees that have consistently performed poorly in provenance tests. Plantation location \times provenance interactions, which indicate changes in provenance rank due to plantation location, were highly significant for all these cone and seed characteristics except for percentage of total seed filled and percentage of germination. On the average, larger cones had larger seeds, more seeds, more filled seeds, and a higher percentage of germinating seeds. The seed crop evaluated (1978) was preceded by severe droughts in 1976 and 1977, which may have lowered seed yield and quality. Those provenances that produce least under drought stress may be average producers when receiving adequate moisture. However, because their seed yields are reduced by stress, their long-term average production will be lower.

Disease and Insect Resistance. — Evidence of genetic variation in susceptibility or resistance to some diseases and insect pests has been observed in jack pine provenance tests. Differences among Lake

States provenances in incidence of white-pine weevil (*Pissodes strobi* (Peck)) have been noted in Michigan and Minnesota tests (Arend and others 1961; Batzer 1961; King 1971). Provenances with the most weeviled trees in the Michigan plantations were also among the most weeviled in the Minnesota plantations.

In 11 test locations in the Lake States, provenances showed significant variation in the incidence of eastern pine shoot borer (*Eucosma gloriola* (Heinrich)) and eastern gall rust (*Cronartium quercum* (Bark)) (King 1971). In three Michigan tests, provenances varied in susceptibility to red-headed pine sawfly (*Neodiprion lecontei* (Fitch)) and bark beetle (*Pityophthorus* spp.) (Arend and others, 1961). Other pests were present, but no provenance differences could be detected. The relation between the geographic location of the seed origin and pest incidence was random. Thus, it was not possible to predict the provenances that would produce the least susceptible trees. Resistance to one pest was not related to resistance to other pests. Therefore, care must be taken to insure that selection for resistance to one pest does not increase susceptibility to other pests. Ten-year height-growth ranking of the provenances was little affected by heavy pest infestations. However, trees from the provenances most severely attacked by the white pine weevil were all above average in height and those least weeviled were below average.

King and Nienstaedt (1965) found differences among provenances in susceptibility to needlecast fungus (*Davisonmycella ampla* (Dav.) (Dark.)) infection in two 10-year-old plantations of 29 Lake States provenances. Because the differences remained constant from year to year and in two environments, they were considered to have a direct genetic basis. The rate of symptom development, however, differed not only among origins but also between years and locations and was considered not to be under strong genetic control. In the two plantations investigated, provenances from Lower Michigan showed the highest resistance to the needlecast fungus, and those from northeastern Minnesota showed the lowest.

In northern Wisconsin, differences in incidence of eastern pine shoot borers among 90 provenances were significant and were highly correlated with variation among provenances in height growth (Jeffers 1978 a,b). Borer incidence was related to length

of the terminal shoot at the time of female oviposition. Trees in provenances that flushed later than average were tallest and had shorter new terminal shoots at the time of oviposition and lower borer incidence. Borer incidence is apparently under strong genetic control. Selection for resistance can begin at age 4 years.

Jack pine has some resistance to the fungal disease scleroderris canker (*Gremmeniella abietina* (Lagerberg) Morelet), and to the European strain recently discovered in New York, New England, and adjacent areas of Canada (fig. 11). By the 5th growing season, 7 of 92 provenances had more healthy trees than could be attributed to chance alone in a nursery test infected with the North American strain of scleroderris at Longlac, northern Ontario (Teich 1967). Subsequent artificial inoculation of five of the partially resistant provenances growing at Petawawa (three from Quebec and two from Ontario) proved that trees from the Quebec provenances were relatively resistant to the North American strain of scleroderris (Teich and Smerlis 1969).

Subsequent observations of scleroderris infection in the same provenances growing at northern test sites in Ontario and Quebec verified the critical role of provenance in disease tolerance (Yeatman 1976 a,b). Trees from southern provenances suffered up to 86-percent infection and 52-percent mortality by age 12 compared with 15 percent infection and no mortality of the best provenance from western Quebec. Trees from provenances most seriously infected were also subject to winter injury. Climatic adaptation appeared to be a major factor in resistance of planted jack pine to scleroderris canker, but soil fertility and microsite also strongly influenced susceptibility to infection in these plantations (C. W. Yeatman, personal observation). In a supplementary test of four provenances planted in 1972 on a flat, open site near the Longlac nursery, scleroderris and winter injury all but eliminated the Petawawa, Ontario, provenance 8 years after planting; the local (Caramat, Ontario) source had 49-percent survival, with only 11 percent uninfected. Two eastern Quebec provenances, La Sault au Cochon and Little Calumet River, had 83- and 88-percent survival with 57 and 74 percent uninfected, respectively. Survival in the first year after planting averaged 96.5 percent over all four provenances. Trees from the disease-tolerant Quebec provenances demon-



Figure 11.—Demonstrated variation in resistance to the European strain of scleroderris canker disease in test plots in upper New York State. Two Michigan provenances are shown; the one on the left shows almost total resistance and the one on the right is highly susceptible. Similar provenance variation in resistance has not been found in such tests nor in older plantations of red pine in New York. Inoculation tests are made by placing infected branches on a wire grid directly above the seedling plots. Host-range studies like these are being conducted by the North Central Forest Experiment Station and cooperators.

strated a clear advantage when planted on this difficult site in a boreal climate with a short growing season and severe winter conditions.⁹

Resistance to sweetfern rust (*Cronartium comptoniae* Arth.) in jack pine is highest in provenances from the southern parts of the range (Tauer 1976, 1978). Phenotypic selection for resistance is ineffective, and progeny testing is necessary to verify resistance. Rust resistance appears to be controlled by both additive and nonadditive gene action. Breeding aimed at developing resistance would be practical, particularly because screening for resistance can be done in young seedlings 7 or 8 weeks after inoculation.

⁹ Data on file at the Petawawa National Forest Institute, Canadian Forestry Service, Chalk River, Ontario, Canada.

Isozymes. — Analysis of enzyme systems by starch gel electrophoresis can be used to study geographic differentiation in jack pine. Megagametophyte (endosperm) tissue from seeds of individual trees sampled in 33 provenances of the rangewide test analyzed for seven polymorphic enzymes revealed 29 isozyme variants controlled by 10 loci. Geographic patterns in the frequencies of several alleles were suggested by the results, but analyses of additional provenances and samples would be necessary to verify them. Unique variants for several isozymes were recovered from trees of Whitecourt, Alberta origin, where jack pine and lodgepole pine are known to hybridize. These variants may be the product of genetic introgression (Tobolski 1979). Determining the mode of inheritance of isozymes

will be valuable in studying genetic variation in populations.

Variation Within Seed Origins

Genetic variation in jack pine has also been investigated in various types of one- and two-parent progeny tests (Rudolph and others 1959; Fowler 1965b; Rudolph 1966a, 1967, 1976, 1979a; Jeffers and Nienstaedt 1972; Polk 1974; Canavera 1975; Yeatman 1975a).

Growth. — At 2 years, height of individual families ranged from 73 to 117 percent of the mean for all 64 families that resulted from crosses between individual trees selected in several Lake States provenances (Jeffers and Nienstaedt 1972). Variation in 2-year seedling height was associated with individual female parents, but height of families was also influenced by the male. Families resulting from crosses with males from certain provenances were consistently tall. When these males were crossed with "good" females, the progenies were always above average. Jeffers and Nienstaedt concluded that the variation among families in seedling height is continuous and probably under additive genetic control.

When measured as 2- and 3-year-old seedlings in the nursery, the best of 382 families from 60 stands in the northern half of Lower Michigan were 27 percent taller than the experiment average, and the poorest were 28 percent shorter than average (Canavera 1975). Variation in height of progenies was not related to seed weight. The seed parents accounted for 39 and 17 percent of the variation in height in 2- and 3-year-old seedlings, respectively. The fact that progenies of trees selected for superior height were not significantly taller than those of trees selected for inferior height growth suggests that parental phenotypic selection for height growth is ineffective. Similarly, progenies from the tallest stands were not the tallest. However, a negligible portion of the total variance in seedling height was due to stands. Progenies from central Lower Michigan were about 2 percent taller than those from northern Lower Michigan. Part of the reason for the apparent ineffectiveness of phenotypic selection for height may be that many of the stands from which seed was collected originated after fires. Undoubtedly, they were initially extremely dense, so natural selection in the intervening decades had eliminated the slow-growing genotypes.

Also, some of the stands had been selectively thinned to remove the smaller trees, further reducing the variation within stands.

Tree Form. — Variation in form of jack pine trees may result from abnormal growth habits such as lammas growth and prolepsis that vary in frequency among provenances and plantation sites (Rudolph 1961, 1964). The influence on potential tree form depends on the combinations of types of late shoot development and on their magnitude. Lammas growth without prolepsis generally results in a short internode with too many branches per unit length of stem. Prolepsis without lammas growth causes at least temporary forking or competition for dominance and long, thick, upright branches. Lammas growth along with prolepsis in only one lateral frequently results in a permanently coarse, acute-angled branch called a "ramicorn." Other types of malformations also result from other combinations of late shoot types. Because occurrence of late shoots is under at least some genetic control, trees with these growth habits should be avoided in seed collections for reforestation.

Polk (1974) selected 12 phenotypes with form traits that are desirable in Christmas trees among about 20,000 trees included in a wide range of plantation experiments in Missouri. The traits studied included vigor; straight, unforked stem; long needle retention; symmetrical and balanced crown; dense crown; low crown taper; and good winter foliage color. Subsequent breeding of these phenotypes and analyses of the progenies showed that many of the traits contributing to a desirable form were highly heritable. Therefore, breeding for Christmas trees has great potential (fig. 12). In a Christmas tree marketability test in Sault Ste. Marie, Ontario, jack pine trees were competitive with Scotch pine (Cameron and McPhee 1979).

Wood and Bark Properties. — Schoenike¹⁰ examined diameter, bark thickness, and bark thickness-diameter relations among 119 progenies representing 11 progeny groups and 8 provenances of jack pine in a plantation at Cloquet, Minn. The progenies had been planted in two planting seasons, 21 and 22 years before measurement. Progeny

¹⁰ R. E. Schoenike. Variation patterns and heritability estimates for diameter and bark thickness among open-pollinated progenies of jack pine. Unpublished manuscript, March 1965.

AGE



3 years



6 years



12 years



Figure 12.—Contrast in branching habit and crown form among representative trees in the F_1 generation of two families after 3, 6, and 12 (top to bottom) growing seasons in the field. These traits persist with age and selections for them can be made among young trees. (Adapted from Polk 1974; photographs by R. Brooks Polk, School of Forestry, Fisheries, and Wildlife, University of Missouri-Columbia.)

groups accounted for about 21 percent of the variation in diameter and 16 percent of the variation in bark thickness. The amount of variation in bark thickness differed widely within different progenies, which suggests that progenies may differ in the amount of heterozygosity for genes controlling bark thickness. Heritability estimates ranged from 13.3 to 26.7 percent for diameter and 30.4 to 60.9 percent for bark thickness. Thus, some progress can be expected by selecting for diameter and bark thickness in jack pine.

Fall Coloration. — Foliage color change in autumn from green to purple was examined in 2-0 jack pine representing S_2 , $S_1 \times S_1$ -mix, S_1 open-pollinated, and S_0 open-pollinated progenies in a nursery in northeastern Wisconsin. Purple coloration was initiated on the average in the 2d week of October and was completed by November 11. Inbreeding and increased homozygosity resulted in larger interfamily but smaller intrafamily color variation. Crosses among S_1 genotypes restored patterns of variation in foliage coloration that were similar to the ancestral outcrossed condition. Genotypic variation in the earliness and potential amount of autumn foliage coloration was clearly demonstrated. No relation between tree height and coloration was evident either among or within families (Rudolph 1980).

Disease and Insect Resistance. — Henson and others (1970) tested the susceptibility of several pine species to damage by sawfly (*Neodiprion* spp.). Jack pine showed little damage and little variation in susceptibility among trees (genotypes). In marked contrast, Scots pine was highly vulnerable to feeding and also showed extreme variation between genotypes. Ikeda and others (1977) determined that two chemical constituents (13-keto-8(14)-podocaren-18-oic acid and dihydro-abietic acid) in juvenile foliage of jack pine deter feeding by two species of sawfly (*N. rugifrons* Midd. and *N. swaini* Midd.). By late summer, the content of these chemicals decreases in the current year's foliage to permit oviposition before winter. The larvae feed only on mature foliage.

Dwarfism. — Johnson and his colleagues have described several dwarf types originating from seed collected from nonpathologic, bud sport "witches' brooms" found in the crowns of jack pine trees (Johnson and others 1965a, 1968a, 1968b; Johnson 1969). The brooms are usually dense, spherical

masses of slow-growing branches that produce much smaller cones than normal branches of the same tree. Seeds from the diminutive cones on brooms are extremely small and weigh less than half as much as seeds from normal cones on the same tree. None of the brooms has ever been found to produce pollen.

Seedlings grown from open-pollinated seed collected from brooms show a segregation ratio of 1:1 for normal growth and dwarfism. Johnson and his colleagues concluded that the 1:1 segregation ratio was consistent with a simple Mendelian dominant gene for dwarfism. This conclusion was further supported by the absence of male strobili on the brooms so that fertilization would have to be by normal pollen recessive for the dwarf factor.

Various types of dwarfs have been noted in seedling populations grown from seed of controlled cross- and self-pollinations as well as open-pollinated collections (Rudolph 1979a). Segregation ratios observed in these populations suggest a more complex mode of inheritance than a single dominant gene because the proportion of dwarfs is always too low to fit this simple model. However, the segregation ratios may be distorted because of linkage between dwarfism and some lethal factors.

Other Properties. — A survey of jack pine in Minnesota that looked for trees of potential interest to forest genetics research and tree improvement (Rudolph and Libby 1956; Rudolph and others 1957; Rudolph 1960) found several exceptional trees, including one with extreme fastigate branching, a multistemmed tree, and several 185-year-old trees. Trees that showed apparent resistance to the jack pine budworm (*Christoneura pinus* Freeman) and to eastern gall rust (*Cronartium quercum* (Berk.) Mayabe ex Shirai) were also found. Variation among clones in incidence of two, unidentified, needle-miner species has also been noted.¹¹

¹¹ Data on file at the Forestry Sciences Laboratory, North Central Forest Experiment Station, Rhinelander, Wisc.

Hybridization

Putative hybrids have been reported between jack pine and Virginia pine, and loblolly pine (*P. taeda* L.) and Japanese black pine (*P. thunbergiana* Franco) (Williford and others 1977). However, jack pine × lodgepole pine is the only *verified* interspecific hybrid in which jack pine is a parent. The first hybrid by controlled pollination was made in 1939 at the Institute of Forest Genetics in Placerville, Calif. (Righter and Duffield 1951), and was initially described and named X *Pinus Murraybanksiana* by Righter and Stockwell (1949). The initial cross was made with jack pine pollen from Michigan on lodgepole pine from Eldorado County, Calif. Only 6 percent of the hybrid seed was viable, but the hybrid seeds germinated earlier and the seedlings grew more rapidly than open-pollinated seed from the lodgepole female parent. At 7 years, the hybrid seedlings were still significantly taller than the open-pollinated lodgepole pine seedlings. The hybrid seedlings began to flower at 2 years. Pollen from the hybrid plants was 40- to 50-percent aborted. Seed production on the hybrids was similar to that of the parent trees. Fourth-generation progenies of these original lodgepole × jack pine hybrids produced female strobili as early as 10 months after germination (Johnson and Critchfield 1978).

Characteristics of the hybrids resembling the lodgepole parent were stiff, straight branches, non-serotinous cones, and prickles on the cones (Righter and Stockwell 1949). Characteristics similar to the jack pine parent or intermediate included predominantly glabrous spring shoots, cone length, and cone diameter.

Embryos in the seed of the newly created hybrids were no larger than the mean between the parent species, but they did show hybrid vigor in a more rapid growth rate during development and after germination (Buchholz 1945).

In 5 and 10 years of testing, the California-developed hybrids in Montana did not exceed the height growth of Montana lodgepole pine. They were superior on an Idaho site where the Montana-origin trees were not indigenous (Lotan 1967). For these areas, hybrids having Montana and Idaho lodgepole female parents were superior to those with California lodgepole female parents. This ranking did not change after 15 to 20 years (Rehfeldt and Lotan 1970). Thus, statements about hybrid vigor must be qualified, and the origin of

parent stocks and place of testing carefully specified (Duffield and Snyder 1958).

Tests of the California-developed F₁ hybrids, F₂, backcross progeny, and the two parent species in northern Wisconsin and at Petawawa, Ontario, showed that winter injury ranged from very severe in the lodgepole pine from California to none in the jack pine. In the hybrids, severity of winter injury was associated with degree of affinity to one or the other parent, a pattern that indicated polygenic inheritance. The backcross breeding method was suggested for developing lines that would be suitable for environments tolerated by the hardier parent (Rudolph and Nienstaedt 1962; Yeatman and Holst 1972). Crosses between natural hybrids from Alberta and local Petawawa jack pine were more hardy.

The hybrids and the lodgepole pine parent were more susceptible to sweetfern rust and to eastern gall rust than was local jack pine in test plantings in Minnesota, Wisconsin, Michigan (Anderson and Anderson 1965), and Ontario (Yeatman 1974a). Hybrid trees were shorter and had darker green needles, a bushier growth habit, and thicker phloem than the local jack pine. Anderson and Anderson (1965) suggested that the hybrids could have some potential as Christmas trees but not as forest trees. However, Yeatman (1974a) recommended that lodgepole pine and its hybrids with jack pine should not be planted or direct-sown in eastern and central Canada because of their high susceptibility to sweetfern rust and their capacity to genetically degrade future generations of jack pine through dispersal of pollen. Based on widely scattered tests of F₂ hybrids from a seed orchard of lodgepole-jack pine hybrids at Placerville, Calif., Duffield (1954) suggested that such hybrids could be rapid pulpwood producers in the Pacific Northwest, the Lake States, and the Rocky Mountain region.

Natural hybrids between jack pine and lodgepole pine occur in areas of contact in central and northwestern Alberta, the principal areas where introgression has occurred (Moss 1949; Critchfield and Little 1966; Scotter 1974). Strong evidence of introgression is also reported from Mt. Watt, Alberta, and Thompson Bay and Yakow Lake on the southern shore of Lake Athabaska, Saskatchewan (Argus and Raup 1982), and in the area of Hasbala Lake in the northeast corner of Saskatchewan (Argus 1966) (fig. 1). Moss (1949) described the

range of intermediate forms found in the area of introgression in west-central Alberta. Cone morphology provides the strongest diagnostic features for distinguishing hybrids in the field, although foliage and branching habit are also used to identify them. Mature lodgepole pine cones are typically ovoid or conical, and spreading or reflexed on the branches. The scales are conspicuously umbonate, and each scale is armed with a recurved prickle. In contrast, jack pine cones are commonly directed towards the apex of the shoot, sometimes spreading, or they may be incurved or straight, and the scales are unevenly thickened and unarmed (Moss 1949) (fig. 9). One-year-old cones of lodgepole pine have pronounced prickles extending from the cone scales, unlike the small prickles borne by jack pine conelets (fig. 13).



Figure 13.—One-year-old conelets of jack pine (left), lodgepole pine (right), and hybrids (center). The lodgepole pine conelets have pronounced prickles extending from the cone scales in contrast to slight to very small prickles borne by the jack pine conelets. The hybrids, on the average, have intermediate prickles.

The needles of lodgepole pine are longer, and the vegetative buds larger than those of jack pine (Moss 1949; Argus 1966; Pollack 1979) (fig. 14). The foliage of lodgepole pine is a brighter green than the greyish tinge of jack pine ("pin gris" in French Canada). Open-grown lodgepole pine has a symmetrical crown form with semierect to horizontal branches; open-grown jack pine has an irregular crown (Moss 1949) with branches of variable size, length, and angle with the stem. Older, wide-crowned jack pine trees have the drooping branches

for which the species is well known from artists' portrayals.



Figure 14.—Vegetative buds and needles of jack pine (left), lodgepole pine (right), and hybrids (center). Lodgepole has larger buds and longer needles than jack pine; the hybrids are intermediate for both characteristics.

Natural hybrid populations are characterized by both a range of intermediate morphological variants that exhibit various combinations and expressions of the parental phenotypes and by trees typical of one or both parental species. Individual characteristics such as needle length, cone angle, or small spine on the umbo vary considerably within each species (Critchfield 1957, 1978; Schoenike 1962a, 1976), but do not appear in the combinations typical of the introgressed hybrid forms.

The turpentine composition of the two species is distinctly different. Mirov (1956) found that the turpentine of jack pine consists almost entirely of alpha- and beta-pinene, but that of lodgepole pine is mostly beta-phellandrene with small amounts of 3-carene and the two pinenes. The artificial hybrid between the two species contained turpentine consisting of about one-fourth beta-phellandrene and three-fourths pinenes. Thus, in the F_1 the bicyclic terpenes of jack pine dominated over the simpler monocyclic terpene of lodgepole pine in a 3:1 ratio. In the area of natural hybridization in Alberta, none of the trees identified as jack pine contained the phellandrene characteristic of lodgepole pine. Trees in the area that appeared to be lodgepole pine contained either mostly phellandrene or a mixture of phellandrene and the jack pine pinenes. Trees that appeared to be morphologically intermediate between the parent species were also intermediate chemically.

Studies of the lodgepole and jack pine parent species, backcrosses to jack pine, F_1 , F_2 , and F_3 hybrids, and natural hybrids suggested segregation for turpentine components (Zavarin and others 1969). However, the results were not definitive enough to formulate a genetic model for the inheritance of these compounds. The differences in turpentine composition between the two species are probably controlled primarily by a limited number of genes with major effects. Development of a mode of inheritance model was hampered by the fact that beta-phellandrene could not be recovered in the F_2 and F_3 hybrids at levels comparable to those found in lodgepole pine.

In an analysis of oleoresins and morphological characteristics of the jack pine-lodgepole pine complex in Alberta, Pollack (1979) found that the morphology of a tree did not always correlate with its monoterpene composition. Discrimination between lodgepole pine and putative hybrids was best accomplished with monoterpenes, which showed the zone of transition between the species to occur farther west than previously reported. Similar evidence of gene flow of lodgepole pine into jack pine was found in putative jack pine \times lodgepole pine hybrid stands.

Inbreeding

Controlled self-pollination of jack pine frequently results in lower yields of filled seed, poorer seed germination, lower survival of seedlings, and increased frequency of deviant types (Fowler 1965a; Rudolph 1966a, 1967, 1976). However, genotypic variation among trees is found for all these factors (Fowler 1965b; Rudolph 1966a, 1967, 1979a). Compared with cross-pollinations, self-pollinations on five trees resulted in a higher percentage of empty seed, poorer seedling survival, and shorter hypocotyls but more cotyledons (Fowler 1965a). No differences were found between self- and cross-pollinations in percentage of cones set and matured, cone length, seeds per cone, weight of full seed, and percent germination, all of which are dominantly subject to maternal influence. Rudolph (1967), however, found that, although total seeds per cone did not differ significantly between cones selfed and outcrossed, percent of germination of the selfed seed was only half that of the outcrossed seed because fewer of the selfed seeds were filled. In a complete

diallel crossing scheme involving seven trees, Yeatman¹² recorded an average of seven filled seeds per cone for self combinations compared with an average of 26 seeds per cone for the cross combinations. Reverse germination was more frequent in seed from self-pollinations than in seed from cross-pollinations (Fowler 1965b).

About one-fourth of the trees in a population carried genes recessive for chlorophyll deficiencies (Rudolph 1966a). Segregation ratios for these and other deviant types varied greatly from the simple, single-gene, 3:1 ratio. The deviations from this ratio may result from linkage with lethal genes or from multiple gene control of the deviant characteristics. Such deviant characteristics are useful markers in genetic studies (fig. 15). For example, in 848 families from open-pollinations and 106 families from controlled self-pollinations in the same population, screened for marker seedlings, estimates could be made of the percentage of natural self-pollination, the seedlings produced from natural selfing, and the percentage of selfs that were lethal (Rudolph 1979a). The frequency of natural self-pollinations on individual trees ranged up to 34 percent, but on the average, more than half of the resulting embryos were lethal. So, only about 7 percent of open-pollinated seedlings resulted from natural self-pollination. Thus, in seed orchard management, removing trees that show high selfing percentages and carefully culling poorer seedlings grown from orchard seed before field planting would reduce to a minimum the impact of natural selfing on wood yield.

In controlled self-pollinations on S_1 trees to produce S_2 progenies, cone abortion sometimes reaches 100 percent. However, repeated pollinations would be necessary to ascertain whether self-incompatibility exists. In one study, average abortion reached 69 percent of the S_1 selfed cones by the end of the 1st year and 75 percent by the time of cone maturity (Rudolph 1976). The S_1 self-pollinations yielded less than half as many filled seeds per cone as cross-pollinations, but germination and seedling survival of filled seed were similar. Inbreeding depression in seedling height of the S_2 progenies averaged 15 percent after 10 weeks (Rudolph 1976) and increased to

¹² Data on file at the Petawawa National Forestry Institute, Canadian Forestry Service, Environment Canada, Chalk River, Ontario, Canada.

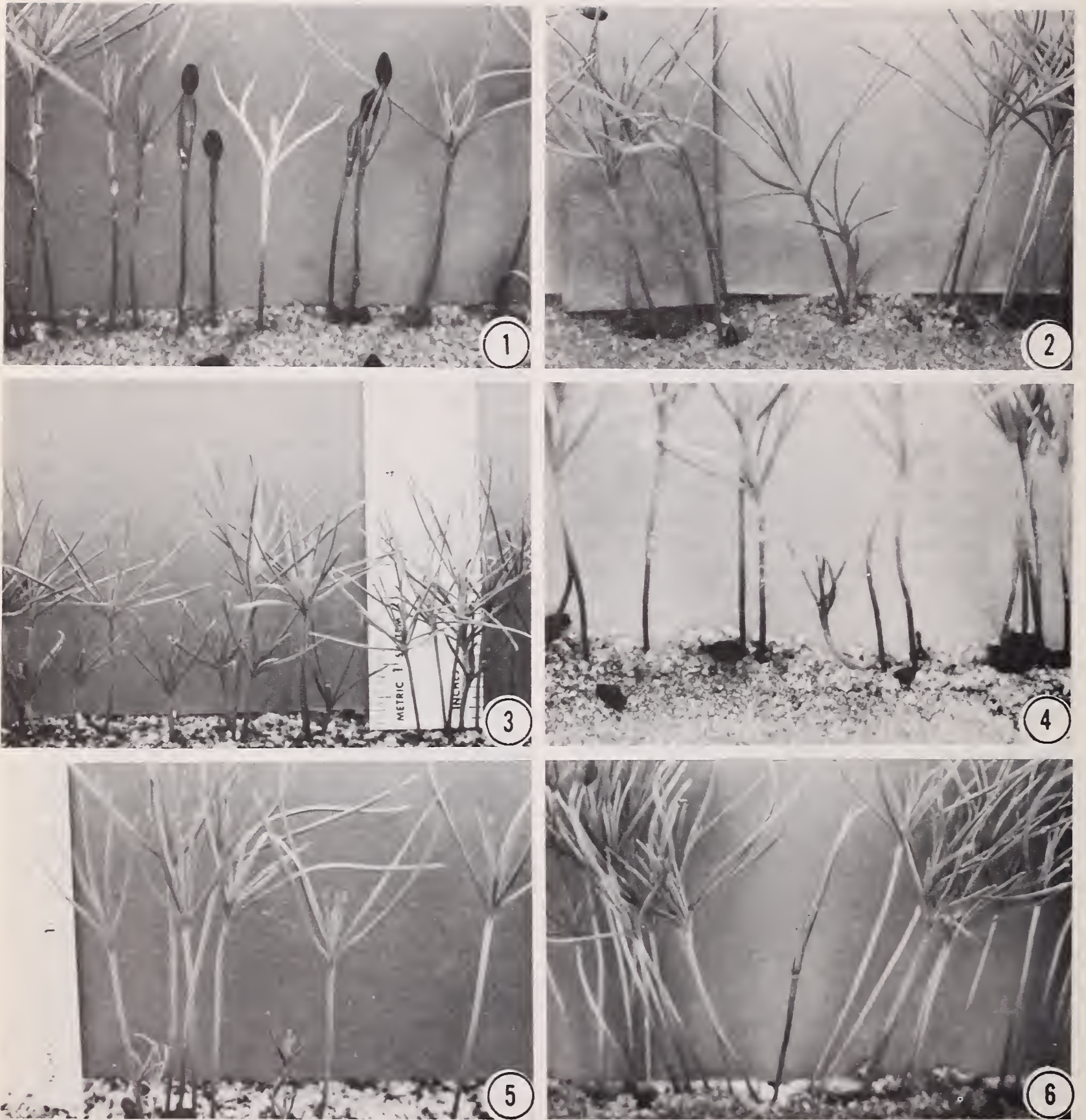


Figure 15.—Examples of seedling genetic marker types in jack pine resulting from selfing. (1) Chlorophyll deficient or abino seedling, usually lethal; (2), (3), (4), (5) various types of dwarfs; (6) cotyledons spiraled and completely fused except at extreme tips; the new shoot forces emergence through a small rupture at base of cotyledons. Such marker characteristics, identifiable in very young seedlings, are useful in various genetics and breeding studies.

20 to 25 percent at 4 years (Rudolph 1981). Variation in height within families was similar for the S_0 open-pollinated, $S_1 \times S_1$ -mix, S_1 open-pollinated and S_2 progeny groups. However, variation among families was much greater in the S_2 group than in the crosses. After 4 years, standard error of the S_2 group was about twice that of the crosses. Heterosis in the $S_1 \times S_1$ -mix and S_1 open-pollinated crosses relieved inbreeding depression and restored vigor to at least that of the ancestral outcrossed condition (Rudolph 1981). The S_2 progeny group also had the most variation among families in fall coloration but had the least within-family variation (Rudolph 1980). Fall coloration is apparently more heritable and controlled by fewer genes than is height growth (Rudolph 1981).

Attempts to use inbreeding to develop breeding populations for the potential improvement of the pines have been limited by the apparent difficulty and high cost of producing inbred material (Snyder 1968; Franklin 1969). However, many tree breeders have suggested using inbreeding and outcrossing of inbreds for improvement (see, for example, Rudolph 1976). Jack pine may be a choice species in which to test inbreeding strategies for improvement because of: (1) its potentially rapid generation turnover time (Rudolph 1966b, 1979c; Jeffers and Nienstaedt 1972), (2) its adequate seed yield and quality in inbreds (Rudolph 1966b, 1967, 1976), and (3) the ineffectiveness of phenotypic selection for growth rate (Canavera 1975), which makes the use of outcrossed progenies of inbreds appealing. Because of the short time between generations in jack pine, use for selection of the large genetic variance provided by inbreeding need not be restricted to the S_1 or S_2 generations as suggested for other species by Lindgren (1975a, 1975b). As selfing continues into later generations, homozygosity in the inbreds increases, and greater hybrid vigor in crosses between the inbreds becomes possible. With continued selfing, most lethal genes would be eliminated. Therefore, high yields of viable seeds and potential heterosis in growth would be expected after crosses and double crosses between such inbred lines. Even without selection for vigor, heterosis in progenies resulting from crosses between S_1 lines restored growth performance at least to that of the parental lines (Rudolph 1976, 1981). Thus, applied inbreeding strategies are likely to contribute to the future genetic improvement of jack pine.

Cytogenetics

The somatic chromosome number in jack pine is $2N = 24$ (Sax and Sax 1933) (fig. 16). Saylor (1972) reported that 11 of the chromosomes in jack pine have median centromeres, but the twelfth, the shortest one, is heterobrachial. He found that chromosomes 2 and 4, arranged in decreasing length of the shorter or *a* arm, had medial constrictions in their longer or *b* arm and chromosome 5 had a distal constriction in its *a* arm. Chromosomes 5, 7, and 9 showed exceptions to the descending order of *b* arm lengths; 4, 6, and 8 had the highest *a/b* arm ratios. The chromosomes varied in relative length from shortest to longest by a factor of 0.6. Characteristics of the karyotypes of the four species in subsection *Contortae* (jack pine, lodgepole pine, Virginia pine, and sand pine) were very similar, suggesting that sand pine and Virginia pine should be

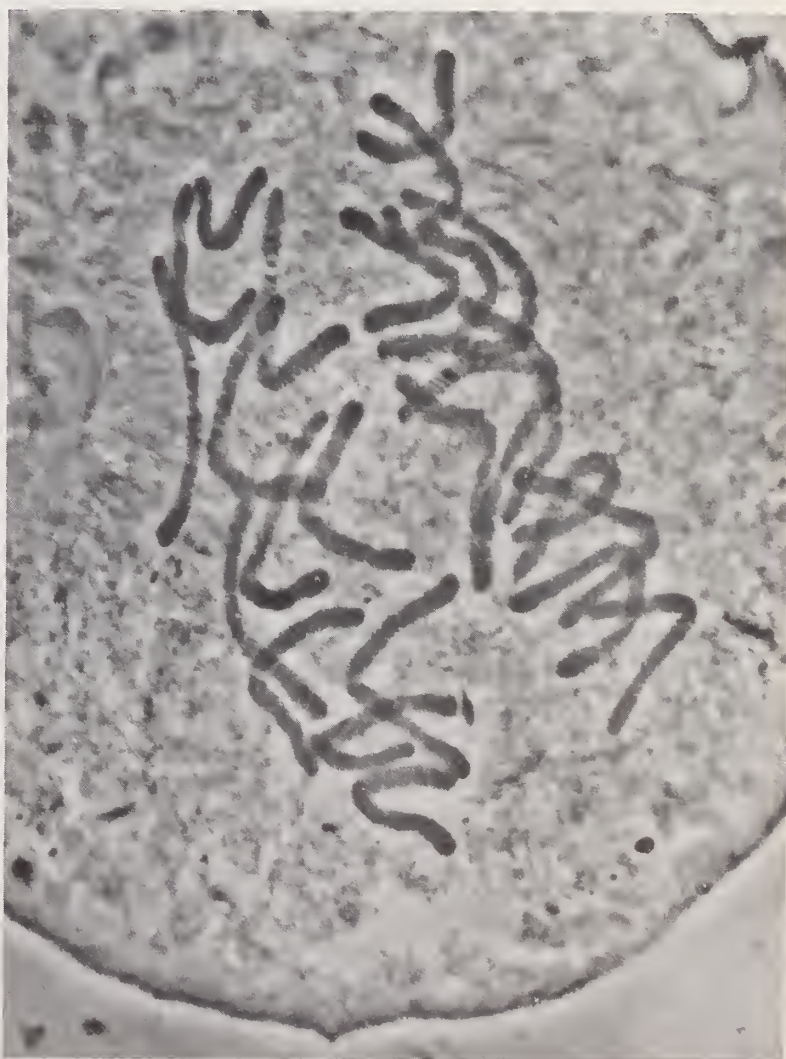


Figure 16.—The chromosomes of jack pine shown as a side view of early anaphase. The chromosomes are relatively large but highly uniform and difficult to identify individually. (1550x).

kept in the subsection even though they do not hybridize with jack or lodgepole pine. The similarity between chromosomes in the pines and their lack of morphological differentiation have made intensive study of them and detailed karyotype analysis difficult.

Kormutak (1975a) found four secondary constrictions in jack pine karyotypes, but Saylor (1972) found only three. Kormutak reported two short pairs of chromosomes, the shorter of which had a heterobrachial centromere location. Kormutak (1975b) also presented cytological evidence that jack pine and mugo and Scotch pine were incompatible because of complete inhibition of pollen tube growth in the nucellus after such pollinations.

The mitotic cycle time in jack pine is 25.7 hours (Miksche 1967a). The time intervals of interphase are: G_2 — 1.4 hours, S — 7.6 hours, and G_1 — 15.3 hours. Nuclear volume of root meristem cells was $714 \mu^3$ (Miksche and Rudolph 1968) and $1356 \mu^3$ (Miksche 1967b). The difference may be due to differences in histological preparation.

As is the case in the living cells of all plants and animals, deoxyribose nucleic acid (DNA) is the active genetic material in jack pine. Organized into genes which control cellular activities, DNA provides the bridge of genetic information from one generation of jack pine to the next. DNA content per cell, determined by chemical extraction methods, was 69.2 picograms (Miksche 1967b; Miksche and Rudolph 1968). Using chicken erythrocyte nuclei as internal standards in direct comparative cytophotometry, Rake and others (1980) found that the diploid amount of DNA per cell in jack pine was 29.8 picograms, considerably less than that determined by the earlier chemical extraction methods. Differences in DNA per cell among 11

provenances of jack pine varied from the lowest to the highest amount by a factor of 1.5 but were not related to latitude of the provenance (Miksche 1968). This does not necessarily mean that within-species variation occurs in gene number. However, multiple and variable numbers of copies of the genes may be present (Miksche and Hotta 1973; Hall and others 1974).

Miksche and Hotta (1973) reported that only 20 percent of the DNA in jack pine is unique and that 80 percent is repetitious or redundant. Hall and others (1974) concluded that to ignore the redundancy and its variation is to ignore 80 percent of the available genetic information. They suggest that a greater knowledge of variation in DNA content and its redundancy can enhance our understanding of coniferous genomes including their mechanisms of adaptation to the environment, influences on quantitative inheritance, determinants of chromosome structure, aspects of meiosis and mitosis, and new methods of karyotype analysis. Preferential staining of redundant sequences within chromosomes may make it possible to consistently identify each of the jack pine chromosomes. This would facilitate study of evolutionary relationships, genetic migration between populations, hybrid verification, and correlation among chromosome characteristics and morphological and physiological traits.

Rake and others (1980) reported 12.9×10^9 nucleotide base pairs in the jack pine genome. The percentage of total DNA that hybridized to rRNA varied little among jack pine, red pine, white spruce (*Picea glauca* (Moench) Voss), and northern white cedar (*Thuja occidentalis* L.). Close, interspecific homology in the rRNA prompted Hotta and Miksche (1974a, 1974b) to suggest these species as suitable candidates for somatic hybridization.

Effects of Ionizing Radiation

Ionizing radiation can induce genetic changes in or kill jack pine. Of the coniferous species that have been studied, however, jack pine is among the most resistant to ionizing radiation. The LD₅₀ (exposure resulting in 50-percent inhibition) gamma radiation exposure for seed tested in the greenhouse ranged from more than 11 kR (thousands of roentgens) to over 14 kR (Yim 1963, 1964; LaCroix 1964; Rudolph and Miksche 1970). The mean LD₅₀ gamma radiation seed exposure for the four early seedling characteristics — germination, survival, hypocotyl length, and cotyledon length — was about 9.7 kR, whereas that for four seedling-root and shoot-growth characteristics was 11.4 kR (Rudolph and Miksche 1970).

Among nine gymnosperm species, including jack pine, no relation was found between seed radiosensitivity and either DNA quantity per cell or nuclear volume (Rudolph and Miksche 1970).

Jack pine seeds appear to be much more sensitive to neutron than to gamma radiation. Yim (1963, 1964) reported an LD₅₀ for germination of only 850 rads after neutron irradiation. This was less than 10 percent of the LD₅₀ reported after gamma irradiation.

Seeds given an X-ray exposure of 800 R during a 45-minute period showed the highest rate of chromosome aberrations (in 4.1 percent of the cells) on the 1st day that cell division was observed during germination (about 5 days after sowing). The percentage of cells with aberrations decreased to less than 0.5 percent on the 7th day after cell division began. Radicle length was not related to aberration frequency (McMahan 1963). Seeds X-irradiated at 1,000 to 4,000 R and tested in nursery and field plantings showed no survivors at the 4,000 R exposure level after 1 year (Rudolph 1967). The LD₅₀ exposure of the seed, determined on the basis of seedling survival, decreased as the seedlings aged; 2,022 R at 40 days, 1,710 R at 130 days, and 700 R at 14 months. Survival in the X₁ generation (trees grown from X-irradiated seed) and the quantity and quality of X₂ (second generation following seed X-irradiation) seed produced on the X₁ trees showed that the reproductive capacity decreased when seed was X-irradiated at 1,000 R. Reproductive capacity was reduced to more than 10 percent in cross-pollinated X₂ seed production and to less than 5 percent after self-pollination. Phenodeviant seedlings were observed in the X₂ progenies, but it was not possible

to determine whether any had resulted from the seed X-irradiation (Rudolph 1966a).

Clark and others (1965) irradiated seeds of several gymnosperms, including jack pine, during 96 hours at a decreasing dosage rate to simulate the gamma component in an early fallout field. Jack pine germinated at all dosages, including the highest — 8.64 kR. The LD_{100/120} (100-percent lethal dose at 120 days) for field-grown seeds was 4.73 kR for jack pine. A constant rate exposure LD_{100/120} was 8.64 kR for jack pine. Clark and his colleagues suggested that in any exposure to ionizing radiation, degree of recovery depends both on the total dose (total injury) and the dosage rate (rate of injury).

Clark and others (1968) also irradiated seeds of jack pine and other gymnosperms for 1 to 250 days at a dosage rate of 0.035 R per minute for total doses to 12.6 kR. The LD₅₀ for germination after 30 days was 6.31 kR for jack pine, the most resistant of the species tested. Survival after 1 year gave an LD₅₀ of 2.95 kR.

Ten years after jack pine seed gamma irradiation, some persistent, radiation-induced, genetic damage was evident: height growth and production of viable seed were reduced at parent seed gamma-radiation exposure levels greater than 4.80 kR (Rudolph 1979b). However, seed germination and early seedling survival were good, rapid indicators of radiosensitivity, because threshold effects and LD₅₀ levels could be relatively well defined for these endpoints.

Seedlings that were gamma irradiated shortly after germination were nearly 20 times more sensitive to gamma radiation than were seeds (Rudolph 1971). Most sensitive of the four seedling endpoints was shoot dry weight at 50 days with a 50-percent inhibition exposure of 280 R.

Replicated groups of 3-year-old potted jack pine seedlings were gamma irradiated each week during the growing season — from early May to September — to receive 0, 150, 300, 600, or 900 R within a 20-hour period (Rudolph 1972). Mortality of the terminal shoots present at the time of irradiation ranged up to 98 percent; tree mortality ranged up to 24 percent in seedlings exposed to 900 R. Terminal-shoot elongation and needle elongation were completely inhibited for the remainder of the growing season immediately after exposure to 600 and 900 R. The most radiosensitive stage of the growing season occurred at the time of shoot-growth cessation

Genetic Improvement Programs

and initial differentiation of the shoot primordia for the following season.

Information on the radiosensitivity of jack pine seed and seedlings can serve as a guide for exposures in mutation induction and genetic studies. However, mutation induction might be more efficiently done by using irradiated pollen rather than seeds and seedlings, so that mutations can be recovered in the immediate progeny. Unfortunately, no information is available on jack pine pollen radiosensitivity. In any case, mutation induction and breeding in jack pine should only be considered supplements to other breeding methods, not replacements for them. Relative to other conifers, the low radiosensitivity of jack pine makes it a candidate for planting in areas of low radioactivity.

Basis for Selection

Conclusive evidence has shown that growth of jack pine provenances is related to environmental gradients associated with latitude (photoperiod) and length and temperature of the growing season, and that such growth shows clinal variation over these gradients. Migration in the postglacial period combined with natural selection have led to clear patterns of adaptive variation over the nearly transcontinental range of the species. Therefore, when selecting sources of seed for artificial regeneration and breeding, geographic origin should be considered first. "The immediate need is . . . to ensure [sic] that for future plantations we have seedlings as good as those that formed the natural forest before we began to harvest it" (Vallee 1979). Local seed collected from large natural populations is the safest and best first choice in the absence of direct evidence to the contrary. Once provenance tests identify superior natural stands, the stands can immediately be used as sources of seed for artificial regeneration.

Early gains in height growth of 10 percent or more may be obtained in this way (J. P. King 1973; Yeatman 1974a, b). When translated into volume growth per unit area, the gains would be substantially greater (Jeffers and Jensen 1980). Until selection and progeny testing produce further genetic gains, it is important to prevent contamination from other seed origins and to maintain and improve the gene pools in superior natural stands used as sources of seed for regeneration (Yeatman 1972a, b, 1974a). By the same token, it cannot be emphasized too strongly that losses of up to 50 percent, and even to 100 percent in boreal Canada, of the potential volume production may be incurred by using an improper seed source or moving seed beyond the limits of recognized ecological zones (Yeatman 1976a, b; Jeffers and Jensen 1980). Furthermore, these losses will be perpetuated in future generations that are derived from suboptimal plant or seed stock. The first step in maintaining and improving genetic quality of jack pine is to identify stands for collection and production of seed and to institute a management program on the basis of forecasted seed requirements.

Selection and testing of "plus trees" from the superior, adapted stands is the next step towards improving genetic quality. Selection should be concentrated within even-aged, young-to-mature stands

growing on good jack pine sites. Stands that are small, isolated, juvenile, overmature, unthrifty (such as low site quality), or understocked or overstocked to jack pine should be avoided. Candidate plus trees show superior growth and health. Emphasis in selection should be on stem and crown form characteristics with high heritability. Plus trees should have straight stems, wide branch angle, and uniform number and size of branches within and between whorls (fig. 4). Trees with straight, closed cones are preferred (Yeatman 1975b). Wood quality may be an additional criterion for selection. In practice, selection is a process of elimination based on the premise that poor genotypes will not produce good phenotypes. The effective improvement of both growth and quality characteristics will require much broader genetic foundation material than breeding for single factors alone (Raulo 1979). The logistics of an improvement program that includes several independent characteristics must be carefully planned.

Testing

Both clonal and open-pollinated progeny tests of the selected trees are desirable. The clonal tests can provide for early comparison among clones in highly heritable traits such as stem and crown form, and they can also provide breeding material for controlled pollinations among the initial parental selections (Yeatman 1974b). Based on the evaluated performance of the clones and progenies, the poorest genotypes can be rejected for further breeding, and their progenies can be eliminated from seedling seed orchards. To provide for comparison of performance in different environments and to create a sound basis for family selection, progeny tests should be planted on sites within the region where the genetically improved stock will eventually be used.

Seed Orchards

Jack pine is well suited for the seedling seed orchard approach because of its rapid early growth, seed production at a young age, consistent flowering year after year, and cone serotiny (Rudolph 1979a; Yeatman 1979). Grafted jack pine trees are at a disadvantage for seed production in quantity because they are relatively slow to develop large, cone-bearing crowns (fig. 17), and they are considerably more costly than seedlings. Graft incompat-

ibility may also eliminate some genotypes entirely. Grafted clones may produce seed by controlled pollination to increase the potential genetic gain in a first-generation seedling seed orchard beyond the gain possible in a first level orchard established with open-pollinated seed from the original plus trees. Seed orchards in the second and subsequent generations will be planted with pedigreed trees (seedlings, grafts, or cuttings) derived from selected lines and individuals.

Many schemes for establishing jack pine seedling seed orchards have been proposed (J. P. King 1973; Yeatman 1974b, 1979; Klein 1974; Canavera 1975; Jeffers 1976; Kang 1980). Each may have a place in specific improvement programs in a given region, but all are new and unproven.

In a plan to improve Lake States jack pine, J. P. King (1973) proposed that areas of preferred seed source be identified for each planting region on the basis of provenance tests. For each planting region, 300 to 400 parent trees should be selected, with no more than 15 trees selected per stand. Open-pollinated seed from these trees would be tested in the nursery for 2 years and then the 200 fastest growing families would be selected for field test plantings on two or three sites in the planting region. When the trees are 7 to 8 years old and flowering prolifically, the field plantings would be converted to seed orchards by removing all below-average family seedlots and the poorer trees in above-average seedlots. After 12 to 14 years, the plantings would be thinned to leave only one of the best four trees in the best 25 seedlots. The advantages of this scheme are that it begins with a broad genetic base and it incorporates germplasm from nonlocal sources that have performed well in the comparison test plantings. However, the proposed scheme for subsequent selection and thinning drastically reduces the genetic base and reduces the potential genetic gains by not taking into account and making full use of within family, intrastand, and intra-source variation.

Yeatman (1974b, 1979) proposed a scheme that requires extensive initial effort to supply seed with some genetic gain that will meet immediate and short-term needs. Also, a sustained program is needed to supply substantially improved seed to meet the long-term needs (fig. 18). Initially, stands selected for seed production would be thinned to remove the poorest phenotypes and open the canopy.



Figure 17.—Comparison of the development of jack pine seedling progenies (left) and grafted clones (right) of the same age growing in the breeding arboretum at the Petawawa National Forestry Institute in Ontario. Grafts are slow to develop large, cone-bearing crowns; are more costly than seedlings; and are thus at a disadvantage for early seed production in quantity in orchards. Graft incompatibility is occasionally a problem as well.

This would encourage seed production on the better dominant trees by freeing the crowns from competition and by reducing the pruning effect of mutual abrasion. Fertilizer might be applied to further enhance flowering, and protective measures might be undertaken to reduce potential losses from pests and wildfire.

Sections of seed-production area cut for cone collection would be converted to seed orchard by replanting with seedlings grown from seed produced from plus trees selected in the local populations. Two levels of seed orchard management, types "A" and "B", might best satisfy the separate requirements of planting and seeding for a given program of artificial regeneration.

Relatively large areas could be planted with bulked progeny of plus trees to create type "B" orchards for mass production of improved seed for direct seeding. Close initial spacing and roguing by mass selection to retain the best phenotypes would favor a modest level of genetic gain.

Type "A" seedling seed orchards could have fewer trees to supply seed for planting and to contribute genetic material for advanced generation breeding. The identity of separate progenies would be retained in small plots (four to nine trees) to permit family selection on the basis of associated progeny clone tests. Phenotypic selection would be exercised within family plots. Close initial spacing and arbitrary grouping of families into subsets (10-30 prog-

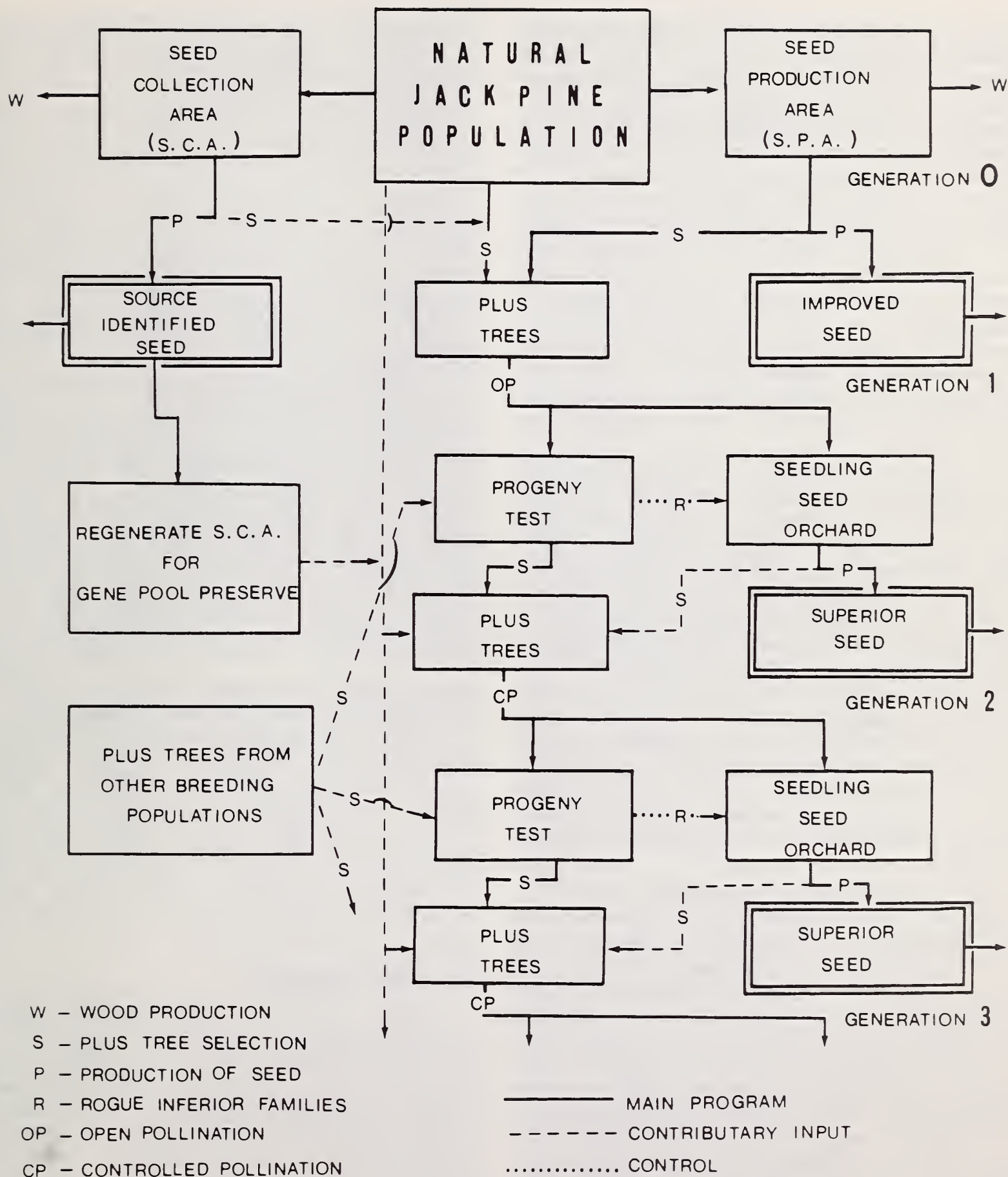


Figure 18.—Flow chart outlining the strategies for jack pine seed production and genetic improvement at a single location within a regional breeding program. The plan can be modified to meet the specific needs and means of other regions.

enies/set) would be essential to keep a functional spatial distribution of crop trees in the final orchard. Orchard blocks, including all subsets and families, would be replicated as many times as needed to meet specified seed production goals. Seed from plus trees identified in the orchard might be used to create the next generation of type "B" orchard. The larger, direct-seeding regeneration programs would thereby benefit in successive generations from genetic gains made in the breeding populations that were developed in conjunction with smaller, intensively managed type "A" orchards. Exchange of pedigreed genetic material (scions, seed, or pollen) among environmentally related subpopulations would maintain a broad genetic base within the larger breeding populations and would prevent development of unacceptably high levels of inbreeding.

An example of converting a natural stand to a seed production area and eventually to a seed orchard is found in western Quebec (Brown 1974; Yeatman 1976b; Bitto 1977; Lamontagne 1980b). The Baskatong Lake provenance (fig. 3), ranked first in the local rangewide test, provided the foundation for subsequent improvement by thinning, plus-tree selection, and establishment of a 99-acre (40-ha) seedling seed orchard that included 300 progenies. Associated progeny tests were also established to control family selection in the orchard. The practical difficulty of maintaining the identity of progenies over such a large area was recognized by Lamontagne (1980b). It gave rise to a suggestion — to rely on mass selection orchards for bulk seed production within each generation (Yeatman 1979).

Klein (1974) proposed an open-pollinated seedling seed orchard of novel design for use in Manitoba and Saskatchewan. The orchard would involve 20 parent-tree collections from each of 11 compact-area seed source locations in a 220-family test. An experimental seed orchard was established in 1972 with 24 blocks, each containing 1 tree from each of the 220 families. The blocks were divided into 11 plots of 20 trees, each plot representing a single seed-source location. Subsequent thinning, based on early performance, would reduce the 20 trees in each plot to 1 tree. Thus, selection would leave trees that have little or no co-ancestry and would provide for mating, predominantly between sources. Although this scheme would provide for a broad

genetic base within a defined geographic area, it would take no account of family performance within sources, thus reducing the potential for genetic gain that could otherwise be achieved.

A point that may be questioned in these seedling seed orchard schemes is the strong emphasis that is placed on *average* family and stand progeny performance while ignoring the *range* of variation and *distribution* of performance (skewed negatively or positively) *within* stand or family progenies. This type of selection limits the genetic base within a given breeding program and may not permit attainment of the full potential genetic gain that more deliberate consideration of within seedlot variation might provide.

Canavera (1975) proposed a seedling seed orchard scheme that could maximize genetic gain through selection among 382 Lower Michigan jack pine half-sib families. Selection would be based on average family performance combined with the range of variation and the type of distribution for performance within families. This scheme would keep superior individuals in some families skewed positively, or to the right. Normally, these individuals would have been removed because of the below-average mean. It would mean keeping more families, but having fewer trees per family. Thus, a broader genetic base would be maintained, and, less mating among related individuals would result.

Jeffers' (1976) seedling seed orchard scheme is an extension of J. P. King's (1973) proposal, modified toward the selection scheme proposed by Canavera (1975). Open-pollinated progenies from selections made in provenance tests are grown, and a combined selection index based on average family performance and on individual tree performance within families is applied to select the best individual trees to keep in the orchards.

Current Programs

Genetic improvement of jack pine is underway throughout much of its commercial range in Canada and in the Lake States. Programs vary widely in extent and intensity. Various programs in their initial stages provide much opportunity for development as knowledge and understanding of the objectives become more widespread, practical field experience is gained, and the benefits begin to be realized.

The New Brunswick Tree Improvement Council supports a cooperative tree-improvement program

that includes jack pine. It is designed to initially insure supplies of well-adapted seed for current reforestation and subsequently to produce improved seed to meet projected requirements of member companies and the provincial forest service (Coles 1979, 1980; Fowler and others 1980; Mathews 1980).

The need and opportunities for improvement of jack pine in Quebec were reviewed extensively by the Quebec Council for Forestry Research and Development (Anon. 1974). The Council concluded that a regional approach should be adopted and a seven-stage program instituted within each region, starting with the use of local seed and progressing to the establishment of seedling seed orchards and progeny tests. Another in-depth report on managing jack pine in Quebec (Anon. 1977) estimated gross merchantable volume of jack pine in Quebec to be 48,552,000 cords (176 million m³), of which 90 percent is located in three regions. Jack pine accounts for about 10 percent of the total annual cut in Quebec. Progress in genetic improvement to date includes tighter control of seed collection and stock distribution, establishment of seed production areas, and plantings of seed orchards and progeny tests (Beaudoin and others 1980; Lamontagne 1980a).

In Ontario, genetic research and applied improvement for management of jack pine are progressing as expanding regeneration programs create even greater demands for quality tree seed (Scarratt 1979). Jack pine constitutes 13 percent of the primary growing stock, or over 137,931,000 cords (500 million m³), and contributes some 30 percent of the total annual harvest in Ontario (Morgenstern and Wang 1979). Emphasis on direct seeding of jack pine (Cayford 1973; Buchert 1980) calls for an extensive approach to the mass production of genetically improved seed. The smaller quantities of seed produced in intensively managed seed orchards will be reserved for planting.

Major jack pine concentrations can be delineated and mapped quickly and accurately using satellite imagery as demonstrated for a portion of northern Ontario (Buchert 1979). This information will guide sampling for systematic investigation of jack pine population structure in Ontario (Buchert 1980). Earlier scattered provenance samples indicate that three major divisions of jack pine exist in Ontario, northwestern and northeastern regions separated

by a north-central region to the north of Lake Superior (Skeates 1979). Provenances from north of Superior are consistently slower growing than other boreal population samples (Yeatman 1976a; Skeates 1979) and are susceptible to scleroderris canker (Teich 1967; Yeatman 1981b). Consistent growth differences found between geographically close provenances justify more intensive sampling needed to clarify broad population boundaries (breeding zones) and to identify the most productive provenances for seed collection and breeding.

A proposed plan for seed production and improvement at a single location is illustrated in fig. 18. It proposes a breeding and seed production unit within a regional breeding program that is designed to include a number of independent but environmentally and operationally related subpopulations (Yeatman 1979). This plan has been initiated in the Gogama District in central Ontario where about 1,980 acres (800 ha) of 50-year-old jack pine is being managed for long-term seed production and improvement (Oldford and others 1979). Additional programs have been initiated in northern Ontario, and others are anticipated (R. M. Rauter, pers. comm.).

Three regional breeding populations are well advanced in Manitoba and Saskatchewan (Klein 1969, 1971a, 1971b, 1975, 1976, 1978, 1980). The program was initiated in 1967 when three breeding districts — eastern, central, and western — were defined, and breeding plans were established. Virtually all accessible commercial jack pine land in the region is included in the program. Family tests (open-pollinated progeny tests) and clone banks were established for each district between 1970 and 1976, each based on more than 200 selections. Gains of 10 to 15 percent in height growth are predicted from early (5-year) results of family tests in the eastern zone where the first production orchard is planned. West of Edmonton, Alberta, a consolidated clone bank is being established for future breeding.

The province of Manitoba has a breeding program that includes jack pine (Segaran 1978, 1980). Preliminary seed zones have been defined from provincial provenance tests begun in 1973. Seed production areas have been established to supply current seed requirements.

The Prince Albert Pulpwood Co. began a jack pine improvement program in 1978, in cooperation with the Government of Saskatchewan and the Canadian Forestry Service Northern Research Centre in Ed-

monton (Orynik 1980). Its first objective is to establish a 20-acre (8-ha) clonal orchard for early gain. The second phase calls for progeny tests of some 200 plus trees as the foundation for future orchards. This will be followed by advanced generation breeding for further improvement.

A new system combining both short- and long-term breeding objectives in multiple populations has been inaugurated in the Lake States (Kang 1980). Based on the Coordinated Population Concept, it includes index and breeding populations, and will eventually include production populations (seed orchards). Its objectives include not only maximization of genetic gains beginning in the short term, but long-term goals including the maintenance of genetic diversity, fixation of favorable alleles, and assurance that genetic research information continues to be pertinent as generations are turned over.

The base population for the new breeding system consists of 400 half-sib families from trees selected to represent all jack pine areas in the Lake States except extreme northeastern Minnesota and the eastern Upper Peninsula of Michigan. The excluded areas have colder climates and much shorter growing seasons than the rest of the broad jack pine range in the Lake States. The base population of 400 families was randomly divided into 20 populations of 20 families each. One or more index populations consisting of one set of 20 families each have been planted by the University of Minnesota, the University of Wisconsin, Michigan State University, and the Forestry Sciences Laboratory at Rhineland, Wisc. The index populations are used to monitor the progress of breeding activities. Because each is a random sample of the base population, the research results will apply to the total coordinated population.

Breeding population plantations that also consist of random sets of 20 families have been established by the Departments of Natural Resources in the three Lake States, by forest industry cooperators, and by the National Forest System of the USDA Forest Service. The index populations will be used to predict the average performance of the breeding populations and to develop general breeding prescriptions for following generations. In the index populations, emphasis will be on rapid generation-turnover time, providing opportunities for early evaluation of various breeding schemes, selection methods, age-to-age performance correlations, and

other breeding activities. Cooperators will use these results to manipulate their own breeding populations and develop production populations or seed orchards for mass production of improved seeds to meet regeneration needs in their areas.

Complementary Breeding Schemes

Improvement selection and breeding should not be limited to the best provenances. Crosses may be made between the better provenances for a given planting region, as proposed by Jeffers and Nienstaedt (1972). Crosses made between geographically separated origins that are within similar ecologic zones may prove superior to local or other individual seed origins. This was Klein's assumption (1969, 1974) in designing a breeding program for jack pine in the prairie Provinces. Analyses of cooperative provenance hybrid tests now being planted in the Lake States and Canada (Yeatman 1980) are designed to provide guidance in this respect. At the very least, the expected exchange of pedigreed material among environmentally related breeding populations will insure that a broad genetic foundation is maintained and inadvertent inbreeding is minimized.

The possibility of developing inbred lines in jack pine for outcrossing and double crossing to produce hybrid vigor cannot be discounted. The technique has proven highly successful for improvement of some agricultural crops. Inbreeding increases the heritability of the breeding population and can help the breeder identify and select superior genotypes. Inbreeding can also be used to remove deleterious genes from breeding populations. Rudolph (1976) noted a correlation between S_2 and $S_1 \times S_1$ -mix progenies in seedling height along with much within- and especially between-progeny variation, which suggests that selection for growth in inbred lines will be possible for improvement breeding in jack pine. Heterosis in $S_1 \times S_1$ -mix and S_1 open-pollinated crosses, even without selection, relieves inbreeding depression and restores vigor to at least the average original ancestral condition (Rudolph 1981).

As noted before, hybrids between lodgepole and jack pine have lost favor because of their extreme susceptibility to sweetfern rust. Careful selection of the parents' origin and testing of the hybrids in environments inbetween those of the parents may prove these hybrids superior to either parent on

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sites where alternate hosts for sweetfern and sweetgale rusts, are absent.

Costs and Benefits

Costs of tree improvement programs and the higher costs of producing genetically improved seed for artificial reforestation are frequently questioned. Projected cost/benefit estimates from tree improvement programs have been determined by Lundgren and King (1965) and Carlisle and Teich (1975). They concluded that yield increases of 2 to 4 percent would more than cover the cost of developing and producing improved seed. Much greater potential increases in yield have been projected from performance results discussed earlier. Seed costs have been over emphasized in the past, but, in reality, they are a small proportion of the total cost of artificial reforestation and management of the tree crop to harvest.

Synopsis

In summary, the long-term improvement and breeding of jack pine must depend upon several factors: searching out the best natural stands within ecological regions, selecting and testing the best individual parents within such stands to develop first generation seed orchards, selecting and breeding the best progenies from such stands based on clonal and progeny tests for second and future generation seed orchards, and developing pedigreed populations from such schemes without excluding crosses between provenances of similar ecologic regions or lines developed from crosses between inbred lines. Artificial regeneration of jack pine will be necessary after harvesting over extensive areas that are now occupied by the species. Maintaining the genetic base found in such populations is important for future breeding and reforestation. The importance of the species and the large forest areas involved call for avoiding errors in selecting the seed source and for genetic improvement as rapidly as resources and trained manpower will allow.

Past research related to the genetics, breeding, and improvement of jack pine has resulted in a considerable body of knowledge, as illustrated in the preceding summary of available information. Our current knowledge of jack pine points to a high potential for genetic improvement and to possible rapid progress in making genetic gains, but also to the need for more information to expedite breeding and improvement. Further basic and applied research is needed to provide the information that will insure continuing progress in breeding and improvement to meet future increasing demands for jack pine wood.

We do not attempt to establish research priorities here — these will depend upon the means, capabilities, and objectives of research organizations and the demands of their research users. We do point out many unanswered questions that should challenge current and future researchers.

Genecology

The post-glacial migrational patterns of jack pine are interesting but not yet entirely clear, and a better understanding of the genecology of the species is needed. Variation patterns in areas showing steep clinal gradients such as from the southwestern to the northeastern portions of the range in Minnesota need to be investigated in greater depth to shed more light on possible origins of the present-day populations.

Ecological seed zones need to be better defined to facilitate selection of the best possible provenances for reforestation within the zones and to avoid movement of seed beyond such zones. Provenance hybridization trials between separated origins within ecologic zones need to continue to broaden adaptive variation of seed for reforestation. Applied research by regions will be necessary to discover the best natural populations for long-term gene-pool conservation, production of improved seed, and a continued source of breeding stock for specific breeding zones.

We need to know more about the possible disease and insect resistance at the population level that is becoming apparent in tests dealing with the European strain of scleroderris canker. Although breeding for insect and disease resistance in jack pine may not be feasible in the foreseeable future, testing and using resistance in natural populations must be considered.

Although much information on provenance variation is available, we need to know more about the limits of provenance transfer and the possible genetic gains it can produce.

Seed Production and Orchard Management

More information is needed on where seed orchards should be located, how they should be designed, and how they should be managed for maximum production of high-quality seed. The relative efficiency of seedling versus grafted clonal orchards for seed production needs to be determined both for the short and the long term. Problems of graft incompatibility need to be resolved. Information is lacking on self-compatibility in the species and how it may influence seed orchard designs. The possible use of inbred lines in seed orchards must be tested. Practically no information is available on cone and seed insects that affect cone and seed yield in jack pine.

The causes of variation in the production of reproductive structures with age and their premature abscission and/or abortion need to be determined so that seed yields in orchards may be increased. Better information is needed on the variation in the phenology of anthesis and female receptivity and how it relates to potential seed production in seed orchards. Means of bringing about flowering at a younger age, particularly the earlier production of male strobili, must be developed to provide for even more rapid generation turnover and selection and breeding opportunities.

Periodicity in the amount of flowering in jack pine and factors influencing it are not known. Cultural treatments that increase seed production and minimize periodicity of flowering should be investigated.

Genetic Components of Growth

Information is needed on the identification of components and characteristics that influence growth and wood yield in jack pine. To facilitate the potential gains possible with rapid generation turnover time, we need to determine the mode of inheritance of these characteristics and find early predic-

tors of mature growth. Thus, we need to develop juvenile-mature correlations in characteristics that are components of wood yield and determine general and specific combining abilities of the selections we make for these characteristics. Genotype and environment interactions, particularly as they relate to future intensive-culture plantations, need to be studied.

Basic Genetics

Detailed analyses of marker genes are needed to facilitate study of the mode of inheritance of economically important characteristics, the degree of natural selfing, and crossing patterns in seed orchards. Eventually, the analyses will help determine possible linkage between genes controlling specific characteristics. Chromosome morphology and banding characteristics must be investigated to aid in the genetic analysis of the species. Isozyme composition of trees in research and breeding populations, together with DNA and other cell parameters, would be useful in population analyses including population structure and relatedness and, potentially, in assessing growth potential and predicting performance.

Breeding Strategies

Much remains to be learned about selection criteria and methods in jack pine. Can multiple trait or some form of tandem selection be used? With the potential for rapid generation turnover in jack pine, what long-term breeding strategies would be most efficient and produce the greatest genetic gains? Jack pine can possibly serve as an "experimental" species to develop genetic models that may be applied to breeding and improving other species as well.

Information is needed on potential genetic gains and rates of gain per generation not only for planning long-term operational research and breeding programs, but also for making forest management decisions concerning the species. More refined cost-benefit analyses of planned breeding and improvement programs are needed to support these plans and the future management of jack pine.

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Reference Abstract

Rudolph, T. D. and C. W. Yeatman. Genetics of jack pine. Res. Pap. WO-38. Washington, DC: Forest Service, U.S. Department of Agriculture; 1982. 64 p.

Reviews characteristics of jack pine including taxonomy, range and habitat, biogeography, reproduction, genetics and breeding, and effects of ionizing radiation. Discusses existing and recommended genetic improvement programs. Suggests additional research needed to expedite breeding and insure continuing progress in genetic improvement.

KEYWORDS:

Pinus banksiana, range and habitat, biogeography, sexual reproduction, asexual reproduction, genetics and breeding, *in situ* and *ex situ* variation, hybridization, inbreeding, cytogenetics, ionizing radiation effects, improvement programs.

