Pinus banksiana Lamb. Jack Pine

Pinaceae Pine family

T. D. Rudolph and P. R. Laidly

Jack pine *(Pinus banksiana),* also called scrub pine, Banksian pine, or Hudson Bay pine, is a small- to medium-sized coniferous tree of the northern forests of the United States and Canada, where it is an important source of pulpwood, lumber, and round timber *(1,10,15,16).* It grows farther north than any other American pine and is the most widely distributed pine species in Canada. It is a pioneer species in succession and invades areas where mineral soil has been exposed by major disturbances such as fires. It usually grows in even-aged pure or mixed stands on less fertile and drier soils than those required by other native species in its range (38).

Habitat

Native Range

The major portion of the jack pine range (fig. 1) is in Canada where its northern boundary extends eastward from the Mackenzie River in the Northwest Territories across the country to Cape Breton Island, NS. The range then extends southwest through Maine, New Hampshire, northern New York, central Quebec and northern Ontario, Michigan, extreme northwest Indiana, northeast Illinois, then northwest through Wisconsin, Minnesota, Manitoba, Saskatchewan, central Alberta, to extreme northeast British Columbia (72).

Within its range, jack pine is widely but not continuously distributed. In Canada it is most abundant in Ontario, and in the United States, the largest acreages are in Minnesota, Wisconsin, and Michigan (74). The only significant artificial extensions of the jack pine range have been on strip-mined areas in the central and northeastern States *(61)* and on the sand hills of Nebraska (II).

Climate

In the eastern part of its range, jack pine grows in a maritime climate but elsewhere it is found in diverse continental climates characterized by short, warm to cool summers, very cold winters, and low rainfall. The average January and July temperatures range from -29" to -4" C (–20° to 25" F) and from 13° to 22° C (55° to 72° F), respectively. Average annual maximum temperatures range from 29" to 38° C (85" to 100" F), and average annual minimum temperatures are from -21" to -46" C (-5" to -50" F) (61). Mean annual temperatures range between -5" and 4" C (23" and 40" F) (74). The northern limits of the range closely parallel the 29" C (85" F) mean annual maximum isotherm. Frost may occur in some areas during any month and in the Northwest the range extends into the permafrost zone. *(61).*

Average annual precipitation ranges from 250 to 1400 mm (10 to 55 in) but 380 to 890 mm (15 to 35 in) are more usual. The average warm season precipitation ranges from 150 to 640 mm (6 to 25 in). Annual snowfall is from 76 to 508 cm (30 to 200 in), but over much of the range it is between 102 and 254 cm (40 to 100 in). Summer droughts are common in the south-central and western portions of the range *(61).*

The average date of the last killing spring frost ranges from April 30 to about July 1; and the average date of the first killing fall frost ranges from about August 10 to October 20. The frost-free period averages from 50 to 173 days but is usually from 80 to 120 days. Generally, temperature, rainfall, and frost-free period increase from the northwestern toward the southeastern part of the range *(61).*

Soils and Topography

Jack pine is usually found on sandy soils of the Spodosol and Entisol soil orders *(81).* It also grows on loamy soils, on thin soils over the granites and metamorphosed rocks of the Canadian Shield, over limestones, on peats, and on soil over permafrost *(16,61,74).*

Jack pine can grow on very dry sandy or gravelly soils where other species can scarcely survive, but it grows best on well drained loamy sands where the midsummer water table is from 1.2 to 1.8 m (4 to 6 ft) below the surface. Jack pine does not grow naturally where the surface soil is alkaline, but it does grow on soils overlying limestone. It can grow on calcareous soils (pH 8.2) if a normal mycorrhizal association is present. In southeastern New Brunswick, owing to a long fire history, jack pine occupies vast areas of clayey soils and it is more common than red pine on xeric sites that have high nutrient levels *(61).*

In well stocked stands in Minnesota and central Wisconsin, available moisture-holding capacity in the

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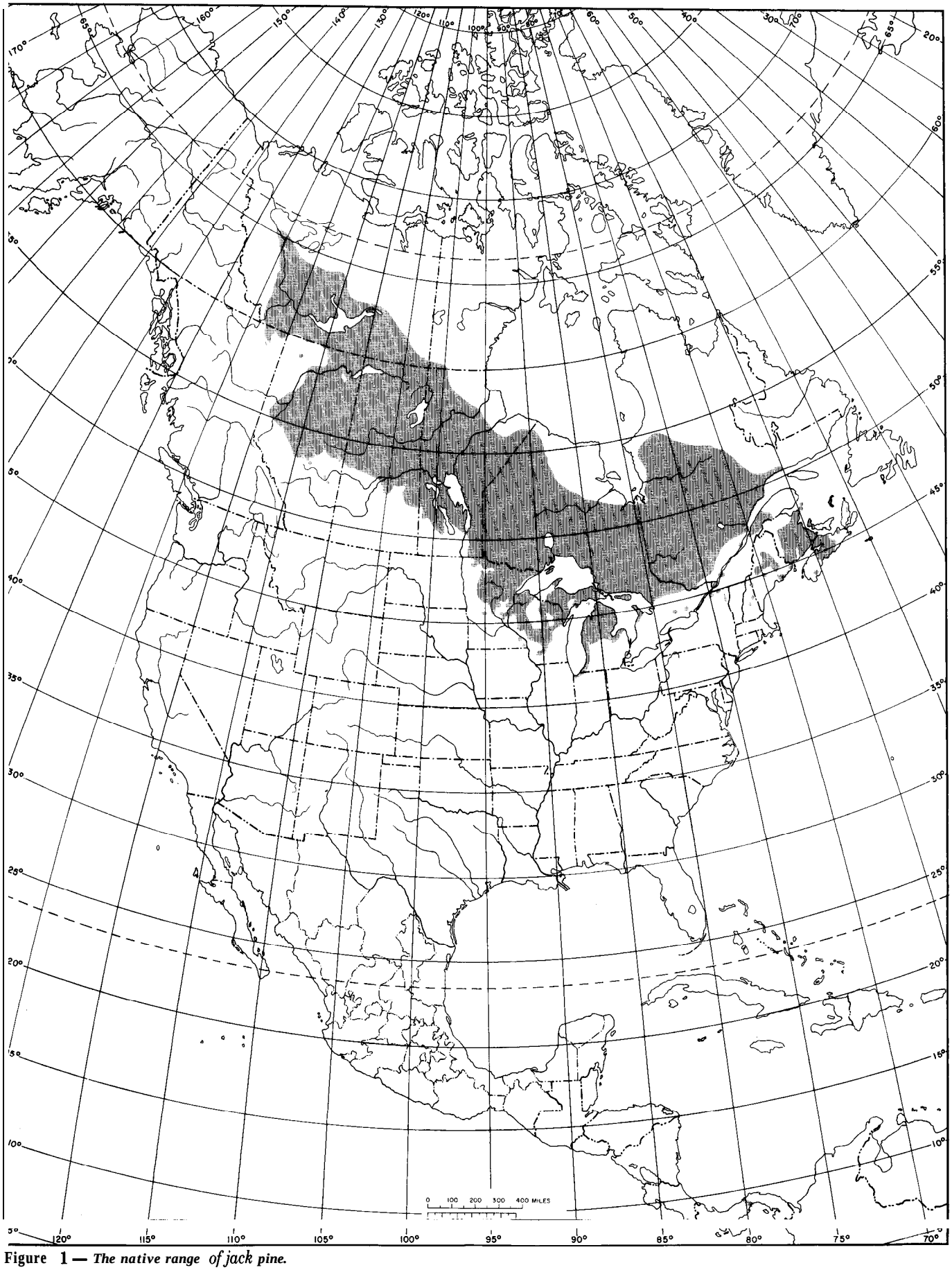

Figure 1 — *The native range of jack pine.*

upper 30 cm (12 in) ranges from 3 to 17 percent by weight. Site index improves with an increase in fine sand and silt and clay in the upper soil layer, an increase in water-holding capacity (up to a point after which it levels off), and an increase in cation exchange capacity in the A and B horizons *(61)*. Similar relations between these soil factors and site index were found for plantations in Wisconsin (82).

In a jack pine forest in northeastern Minnesota about 2580 to 3140 kg/ha (2,300 to 2,800 lb/acre) ovendry weight of organic matter was returned to the soil annually The quantity of nutrient elements, expressed in percentage of dry weight, in freshly fallen jack pine litter averages as follows: calcium, 0.61; potassium, 0.16; phosphorus, 0.04; nitrogen, 0.58; and ash, 4.15. The litter is acid with a pH of 3.8 to 4.3 *(61)*. Accumulated biomass of vegetation in jack pine stands more than 50 years old in northeastern Minnesota was 89 000 kg/ha (79,400 lb/acre) on shallow soils over bedrock, and 152 800 kg/ha (136,300 lb/acre) on deep till soils. Biomass of the forest floor was 35 200 kg/ha (31,400 lb/acre) on shallow soils and 50 300 kg/ha (44,870 lb/acre) on deep till soils. Nutrients in the vegetation, forest floor, and soil were similarly higher on the deep till soils (33). The above values largely agree with those found on other sites for jack pine forest floor biomass, litter fall, and nutrient transfer from jack pine forest to soil *(28,49,78)*.

In the Lake States and Canada, jack pine grows most commonly on level to gently rolling sand plains, usually of glacial outwash, fluvial, or lacustrine origin. It occurs less commonly on eskers, sand dunes, rock outcrops, and bald rock ridges. In the Lake States jack pine is found chiefly at elevations between 300 and 460 m (1,000 and 1,500 R), with a maximum of about 610 m (2,000 ft) above sea level. In the East, jack pine grows on a variety of sandy sites from near sea level up to about 610 m (2,000 ft), with an outlier in New Hampshire at 760 m (2,500 ft) *(61)*.

Associated Forest Cover

The Jack Pine forest cover type (Society of American Foresters Type 1) *(26)* typically originates after forest fires. It is found in pure, even-aged stands or as a majority of the stocking over vast areas of Canada and to a much lesser extent in the Lake States and the northeastern United States *(61)*. In the boreal forest jack pine is also a component of three other forest cover types-Black Spruce (Type 12), Paper Birch (Type 18), and Aspen (Type 16). In the northern forest region it is a component of two forest cover types-Red Pine (Type 15) and Northern Pin Oak (Type 14). Outliers near southern fringes of the species' range are found in various types of hardwood forest *(12)*.

Associated tree species, listed in order of presence on dry to mesic sites, include northern pin oak *(Quercus ellipsoidalis)*, bur oak *(Q. macrocarpa)*, red pine *(Pinus resinosa)*, bigtooth aspen *(Populus grandidentata)*, quaking aspen *(P. tremuloides)*, paper birch *(Betula papyrifera)*, northern red oak *(Quercus rubra)*, eastern white pine *(Pinus strobus)*, red maple *(Acer rubrum)*, balsam fir *(Abies balsamea)*, white spruce *(Picea glauca)*, black spruce *(P. mariana)*, tamarack *(Larix laricina)*, and balsam poplar *(Populus balsamifera)*. In the boreal forest the most common associates are quaking aspen, paper birch, balsam fir, and black spruce. In the northern forest they are northern pin oak, red pine, quaking aspen, paper birch, and balsam fir. Associates are nearly always subordinate to jack pine except for aspen, paper birch, and red pine which may be coordinate *(26,61)*. Infrequent associates in the northeastern United States and adjacent Canada include white oak *(Quercus alba)*, pin cherry *(Prunus pensylvanica)*, gray birch *(Betula populifolia)*, red spruce *(Picea rubens)*, and pitch pine *(Pinus rigida)* *(61)*.

In Canada, six subtypes of jack pine may be recognized based upon the edaphic and climatic conditions where they are found and on associated species as follows: jack pine-balsam fir-black spruce (subtype a); jack pine-feather moss (subtype b); jack pine–sheep laurel (subtype c); jack pine-sphagnum (subtype d); jack pine-labrador-tea (subtype e); jack pine-lichen (subtype f) (26).

The preceding subtype descriptions apply primarily to eastern Canada. However, jack pine forests in Saskatchewan bear close resemblance to some of the subtypes described above *(43)*.

Subtypes, as such, are not recognized in the Lake States. There are, however, certain variants of the type, including jack pine-black spruce, jack pine-red pine, and northern pin oak-jack pine (26).

Life History

Reproduction and Early Growth

Flowering and Fruiting--Jack pine is a monoecious species. Ovulate cones are usually borne on primary and secondary branches in the upper tree crown and staminate cones are usually borne on tertiary branches lower in the crown. Ovulate cones are modifed long shoots and staminate cones are modifed dwarf shoots *(24)*.

In northeastern Wisconsin, bud initiation for the following year's shoot systems begins in late June or

early July. Staminate cone primordia are initiated in early or mid-July but ovulate primordia are not initiated until August. By early September the staminate cone primordia are about 1 mm (0.04 in) long and remain that size until spring. Then they elongate to about 5 mm (0.2 in) by the middle of May and early June just before pollen is shed. Rapid elongation up to several more millimeters occurs as the pollen is shed. Time of pollen shedding (anthesis) varies greatly from year to year depending on the weather (23).

Fertilization occurs about 13 months after pollination when the female cone is approaching its maximum size (27). Jack pine is normally a wind-pollinated, cross-fertilizing species but up to 25 percent or rarely more natural selling can occur *(29,64)*. Under natural conditions, however, survival of selfed and other inbred seedlings is severely reduced by natural selection against the semilethal and other deleterious characteristics carried by the inbred seedlings (67).

Cones mature and the seeds ripen late in the growing season of the year after pollination. Various cone and seed characteristics, including cone color, volume, fresh and dry weight, specific gravity, scale color, seed color, and embryo length, can aid in determining seed ripeness. In northeastern Wisconsin the best indicators of cone and seed ripeness are cone color, 75 percent brown; insides of the cone scales, reddish brown; seeds, dark brown or black; and cone moisture content, less than 45 percent of fresh weight. These indicators of cone and seed ripeness coincide with the beginning of cone harvesting by squirrels about September 10. Because specific gravity of the serotinous cones usually remains above 1.0 at least until February, flotation techniques cannot be used to evaluate cone and seed ripeness in jack pine *(18)*.

Seed Production and Dissemination—Jack pine trees, particularly under good early growing conditions, begin to flower at a younger age than most other pine species *(41,65,68)*. Under near optimum growing conditions in the greenhouse and nursery, female flowering can be induced in a small percentage of seedlings as early as 12 months from seed sowing (68). Male flowering under these conditions usually does not begin until the fourth year. An accumulated yield of 2,861,000 filled seeds per hectare (1,158,000/acre) can be produced through the first 8 years in plantations with 2.4 m (8 ft) between trees *(67)*.

In naturally regenerated stands, jack pine typically begins to flower at 5 to 10 years under open-grown conditions but not until later in closed stands *(61)*. Once cone production in jack pine begins, it is fairly regular and increases until crown competition becomes a factor. Seed production differs from year to year but some seed is usually produced every year and total crop failures are rare *(31,61)*.

Seed yields per cone range from about 15 to 75 (72). Strongly curved cones yield less seed than straight ones (72). Ovulate abortion on the inner curvature of cones is twice that on the outer curvature (17). The average number of scales per cone can be more than 80 but usually only a little more than one-third of the scales, those in the upper end of the cones, bear seeds (72).

Over much of its natural range jack pine bears predominantly serotinous cones, but in the southern part cones are nonserotinous. Total seeds stored on the trees in serotinous cones can reach more than 14.6 kg or 4 million seeds per hectare (13.0 lb or 1.6 million/acre) in well stocked mature stands *(61)*. As viability after 5 to 10 years may be significantly reduced, however, only cones 6 years old or less should be collected (8). Commercially cleaned seeds range between 156,500 and 551,000/kg (71,000 and 250,000/lb) with an average of 288,800/kg (131,000/lb) *(45)*.

Well-stocked, mature stands in the Lake States dispersed an annual average of 6,670 to 25,950 seeds per hectare (2,700 to 10,500/acre) over 5 years; much of the total crop remained in the unopened cones. In areas with nonserotinous or partially serotinous cones, seed may be disseminated during any season. The effective range of seed dissemination, as measured by established seedlings, is about two tree heights although it is low beyond one tree height *(61)*.

The melting temperature of the resinous bonding material of the cone scales is 50" C (122" F), but it is likely that the bonding resin softens at lower temperatures in the nonserotinous types in the southern portion of the species' range. The mechanism of cone opening in both serotinous and nonserotinous cones is hygroscopic. Once the bonding material of the cone scales is broken, the quantity of water in the scales is the limiting factor in scale movement and flexing outward under drying condition *(35,61)*.

Jack pine cones open most readily during dry weather when the temperature is at least 27" C (80° F), although many of them remain closed until they are exposed to fire or high temperatures near the ground after wind breakage or logging. Over most of its range where serotinous cones are common, up to 50 percent may open on the sunny part of the crown. Cones may also open in very cold winters when the temperature is -46" C (– 50° F) or colder *(61)*.

Cone and seed crops in jack pine may be reduced by numerous agents *(61).* Rainy weather at time of pollination may reduce seed set. Cone and seed production are also reduced by cone and ovulate abortion *(17,66),* but the severe losses previously attributed to abortion may be partially the result of insect attacks. Within a cone, all the ovules near the base of the cone abort and abortion decreases toward the tip *(17).*

Seedling Development-Germination is epigeal (45). Jack pine seed usually germinates within 15 to 60 days under favorable conditions *(61),* but some seeds require more than 100 days to germinate (72). Delayed germination of direct seeding increased stocking between the first and third year after sowing (60).

Under forest conditions with adequate moisture, seeds germinate when air temperatures reach 18" C (64" F) but light also influences germination *(2,61).* Under continuous light, germination was complete at a range of temperatures from 16" to 27" C (60" to 80" F) (2). Germination was markedly reduced at all temperatures when light was excluded. The shade cast by slash and snags on burned-over or cut-over areas to reduce surface temperature and drying undoubtedly contributes substantially to the good germination often observed on such areas (16).

Type of seedbed is an important factor affecting jack pine seed germination *(16,61).* In northeastern Minnesota, germination under clearcut and partially cut jack pine stands averaged 60 percent on mineral soil, 49 percent on burned duff, 47 percent on scarified and shaded duff, and 17 percent on undisturbed duff *(61).* The poor germination on litter and humus is caused by poor moisture conditions and it can be satisfactory in years of above normal precipitation. Germination may be delayed by spring drought *(16).* Associated species can affect germination, survival, and growth of jack pine differentially, probably as a result of allelopathy *(13).*

Survival on various seedbeds shows the same trend as germination (61). Optimum conditions for jack pine seedling establishment and survival are provided by mineral soil and burned seedbeds where competition from other vegetation is not severe *(16),* the water table is high, and there is some shade *(61).* Competition from shrubs and herbaceous vegetation, together with smothering by fallen leaves, are important causes of seedling mortality on sandy soils in Ontario. On clay soils in Manitoba and Saskatchewan, competition from aspen and hazel are responsible for poor survival. On similar soils in western Manitoba competing grasses kill many seedlings (16).

Most of the older jack pine stands appear to have been established following fires *(61).* Although jack pine seed usually germinates following fire, most of the seedlings die unless the organic matter left on the soil is less than 1.3 cm (0.5 in) thick. Most germination occurs the first and second season following fire, with most mortality between the first and second growing season. Unless conditions for germination and early survival are favorable, good regeneration does not necessarily follow burns (20,61).

Young seedlings grow tallest in full sunlight *(48),* although under stands their initial abundance may be greatest in light intensities of 11 to 30 percent of full sunlight, but no seedlings are found at 60 percent and higher crown cover (61).

Under forest conditions, seedling growth is slow in the first 3 years but increases rapidly beginning in the fourth and fifth years. Seedlings attain a height of about 5 cm (2 in) the first year, 15 cm (6 in) at 2 years, and 30 to 90 cm (12 to 36 in) at 4 years. Early growth of 2-O seedlings in plantations is more rapid, amounting to 30 to 45 cm (12 to 18 in) per year on medium sites (61).

Shoot growth begins in late April and early May at Cloquet, MN, and Chalk River, ON *(62,63,80),* and about May 10 in the Upper Peninsula of Michigan *(61).* Essentially all height growth is completed in 61 to 68 days at the three locations. Maximum growth rate approaches 1 cm (0.4 in) per day in both Minnesota and Ontario. Although shoot growth in jack pine ceases long before the end of the frost-free season, the remaining time may be necessary to complete latewood growth, lignification, terminal bud development, and hardening off to resist frost (SO).

If favorable moisture conditions prevail in late summer, jack pine frequently has a second period of shoot elongation and produces lammas and proleptic shoots *(62,63).* Trees with lammas shoots had a longer growth period than those without them but did not grow significantly less the following year. The late growth does not result in detectable increases in diameter growth and it may or may not result in false rings. Fall frost injury resulting in frost rings, however, may be frequent in the current shoots of trees with lammas growth.

Vegetative Reproduction-Under natural conditions jack pine does not reproduce vegetatively. Jack pine cuttings from young trees can be rooted but rooting ability decreases rapidly with increasing ortet age. Cuttings from 4-month-old seedlings gave 75 percent rooting (7) but average rooting was only 7 percent in cuttings from g-year-old ortets and 5 percent in those from lo-year-old ortets (90). Clonal variation in rooting percentage ranged from 0 to 31.

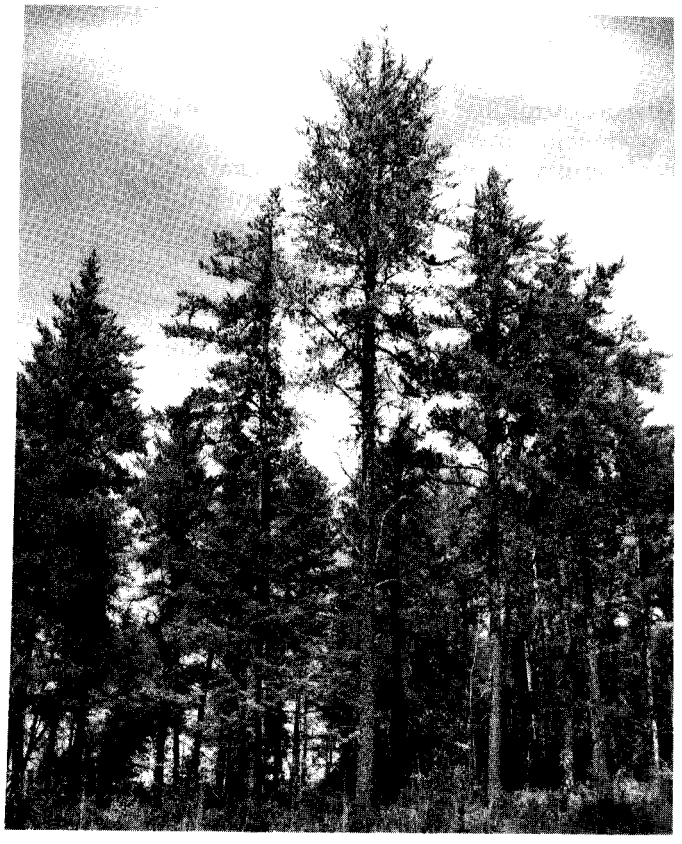

Figure *2 -A stand of jack pine in Minnesota.*

Aryl esters of indole auxins can enhance rooting of jack pine cuttings taken from young seedlings. Phenyl indole-3-butyric (P-IBA) treatment caused 12 percent more jack pine cuttings to root than did treatment with indole-3-butyric acid (IBA), and up to 30 percent more than no treatment (34).

Rooting needle fascicles has potential for establishing large clones in a short time. Shearing the terminal buds on trees up to 5 years old induces the fascicular buds to differentiate and develops shoots. Treating such shoots from 2-year-old trees with IBA (0.1 percent) and placing them in a heated rooting medium under a 20-hour photoperiod resulted in up to 70 percent rooting *(71).*

Jack pine can be grafted, most successfully using dormant scions and when grafting is done just as the rootstock resumes growth in the spring. Both early and delayed graft incompatibility may occur; the causes are unknown (72). No complete jack pine plants have yet been propagated from either callus tissue or cell suspension cultures (72).

Sapling and Pole Stages to Maturity

In well-stocked stands, jack pine (fig. 2) develops into a short to medium-tall, slender tree with a narrow, open crown covering 30 to 45 percent of the stem *(61)*. Crown ratios from 10 to 20 percent are not uncommon in dense stands. Open-grown jack pine develops a stocky stem of poor form and a wide, spreading crown with persistent branches, often to the ground. Overstocked stands produce weak, spindly stems that are susceptible to breakage by wind, ice, and snow *(10).*

Growth and Yield-During the first 20 years, jack pine in its native range is the fastest growing conifer other than tamarack *(61).* Seedlings reach 1.4 m (4.5 ft) tall in 5 to 8 years, depending on site. In the Lake States, 20-year-old stands with 2,470 trees per hectare (1,000/acre) on sites ranging from site index 12 to 21 m (40 to 70 ft) average between 5.5 and 9.8 m (18 and 32 ft) tall, 6.7 and 20.0 m^2 (29 and 87 ft^2) in basal area, 5.8 and 10.2 cm (2.3 and 4.0 in) in d.b.h. *(46),* and 14 600 and 62 800 kg/ha (13,000 and 56,000 lb/acre) in ovendry weight of aboveground biomass (3).

The generalized equations used to derive these biomass estimates (3) give results similar to biomass production reported in other natural jack pine stands *(22,32,37,51)*. Mean annual biomass production of 43-year-old natural jack pine stands in Quebec ranged from 1.42 to 2.47 t/ha (0.63 to 1.10 tons/acre) *(28)*; in 7- to 57-year-old jack pine in New Brunswick from 0.94 to 2.76 t/ha (0.42 to 1.23 tons/acre) *(51);* and in 20- to loo-year-old stands in Ontario from about 1.17 to 3.38 t/ha (0.52 to 1.51 tons/acre) (45). In 24- and 25-year-old plantations in the Lake States, the highest mean annual biomass production was 58 percent higher than the maximum reported in the literature, when seed source and site were properly matched (89).

Annual height growth on medium sites (site index 17 m (55 ft)) in the Lake States averages from 33 cm (13 in) at age 30 to 23 cm (9 in) at age 50. At age 80 years, annual height growth is only 13 cm (5 in) *(46)* On typical sand plains sites, growth is about one site quality better where the water table is 1.2 to 1.8 m (4 to 6 ft) from the soil surface than where it is deeper *(61).*

Normally, mature trees are about 17 to 20 m (55 to 65 ft) tall and 20 to 25 cm (8 to 10 in) d.b.h., although some trees have attained 30 m (100 ft) in height and 64 cm (25 in) in d.b.h. *(46,61)*, and one tree listed by the American Forestry Association in 1982 measured 73.4 cm (28.9 in) in d.b.h. and 25.6 m (84 ft) tall. Stand basal areas seldom exceed 37

Table l-Yields of unmanaged jack pine stands in the Lake States and in Saskatchewan by age and site index

Age	Height[1]	Basal area	Total volume	Merchantable volume
yr	*m*	*m²/ha*	*m³/ha*	*m³/ha*
		Lake States		
Site index[2] 12.2 m				
30	8.2	12.2	41	31
40	10.4	15.8	67	52
50	12.2	18.4	92	71
60	13.7	20.4	114	88
Site index 18.3 m				
30	12.2	23.0	115	89
40	15.5	27.3	174	134
50	18.3	30.1	224	173
60	20.4	31.7	265	206
		Saskatchewan		
Site index 10.1 m				
30	5.8	11.7	45	10
40	8.2	14.0	66	34
50	10.1	15.8	85	56
60	11.9	17.0	102	75
Site index 17.4 m				
30	11.6	19.3	112	61
40	14.6	23.2	140	98
50	17.4	26.2	168	134
60	19.8	28.2	195	165
	ft	*ft²/acre*	*ft³/acre*	*ft³/acre*
		Lake States		
Site index 40 ft				
30	27	53	580	448
40	34	69	956	736
50	40	80	1,311	1,008
60	45	89	1,631	1,264
Site index 60 ft				
30	40	100	1,647	1,272
40	51	119	2,484	1,920
50	60	131	3,194	2,472
60	67	138	3,789	2,936
		Saskatchewan		
Site index 33 ft				
30	19	51	645	150
40	27	61	940	485
50	33	69	1,210	800
60	39	74	1,460	1,070
Site index 57 ft				
30	38	84	1,600	865
40	48	101	2,000	1,403
50	57	114	2,405	1,910
60	65	123	2,785	2,360

[1] Mean height of dominants and cc-dominants.
[2] Height of dominants and codominants at 50 years.

m^2/ha (160 $ft^2/acre$) (46). Jack pine stands begin to disintegrate after 80 years on the best sites and after 60 years on the poorest sites. Vigorous trees 185 years old have been found in northwestern Minnesota, however. The oldest tree reported-230 years old-was found east of Lake Nipigon in Ontario *(61)*.

Growth is somewhat slower, but maintained longer, in Canada. Average stocking on sites having a site index range of 14 to 17 m (45 to 55 ft) in southern Manitoba produces a culmination of mean annual increment at 50 to 60 years with 1.6 to 3.2 m^3/ha (23 to 46 $ft^3/acre$) of merchantable material *(9)*. For average site (site index 14 m (45 ft)) and stocking in Saskatchewan, mean annual increment culminates at about 70 years with 2.0 merchantable m^3/ha (28 $ft^3/acre$) (42). In fully stocked stands on average sites (site class 2) in Ontario, mean annual increment culminates at about age 60 with 2.7 m^3/ha (38 $ft^3/acre$) of merchantable material (54).

Yields from well-stocked, unmanaged jack pine stands in the Lake States at 60 years are shown in table 1 *(46)*, along with yields from well-stocked unmanaged stands in Saskatchewan (42). Rotation age of 40 to 50 years is recommended to produce pulpwood and 60 to 70 years is recommended to produce poles and sawtimber.

Rooting Habit—Jack pine frequently develops a taproot as a seedling and maintains it to maturity. During the first growing season under natural conditions the seedling root system penetrates to a depth of 13 to 25 cm (5 to 10 in). By the end of the second growing season jack pine seedlings on typical sandy soils in the open have a dry weight between 1 and 2 g (0.04 and 0.08 oz), have developed 8 to 10 cm (3 to 4 in) tops, and have root systems from 28 to 33 cm (11 to 13 in) deep and from 46 to 61 cm (18 to 24 in) wide. On a moist sandy soil with the water table about 76 cm (30 in) below the surface in Upper Michigan, roots penetrated to 53 cm (21 in) in 2 years but only to 61 cm (24 in) by 7 years; the lateral spread, however, increased from 0.9 to 1.2 m (3 to 4 ft) at 2 years to 4.3 to 4.9 m (14.0 to 16.2 ft) at 7 years. In the 7-year-old trees the average volume of the top, stem, branches, and foliage was about 4000 cm^3 (244 in^3) as compared to 1200 cm^3 (73 in^3) for the root system *(61)*.

In northern Minnesota, root growth begins when the temperature reaches 4" C (40" F) in the upper 15 cm (6 in) of soil, usually within a week of the onset of shoot growth. Root growth ceases in the fall when soil temperature drops to 7" C (45" F) for 6 days or more. In some years root growth may begin in April and continue to late October. Seven-year-old trees elongated their lateral roots an average of 38 cm (15

in) in 1 year ***(61).*** In Manitoba, root development of jack pine growing on dry and fresh sands was confined mainly to the taproot for the first 1 to 3 years, but lateral branching became increasingly common on 3- to 4-year-old seedlings. Mycorrhizae were found on l-year-old seedlings ***(16).***

On deep, well-drained soils the roots may penetrate below 2.7 m (9 ft). Trees without distinct taproots usually have lateral roots that turn and grow downward as they approach other trees. The bulk of the root system, however, consists of laterals confined largely to the upper 46 cm (18 in) of soil; much of the root system is in the upper 15 cm (6 in) of soil. In 25-year-old jack pine stands in central Wisconsin, the dry weight of all roots in the upper 1.5 m (5 ft) of soil was 10 980 to 13 790 kg/ha (9,800 to 12,300 lb/acre) ***(61).*** A 40-year-old stand of jack pine in northern Minnesota produced 28 000 kg/ha (24,978 lb/acre), ovendry weight, of roots greater than 0.5 cm (0.2 in) and stumps less than 15 cm (6 in) tall (73).

Reaction to Competition-Jack pine is one of the most shade-intolerant trees in its native range. It is the least tolerant of its associated pine species and is slightly more tolerant than aspen, birch, and tamarack. Jack pine may be more tolerant in the seedling stage and often requires some shade on dry sites to reduce surface temperatures and evapotranspiration. Soon after seedlings are established, however, they should receive full sunlight to assure survival *(10,61)*. Overall, jack pine can most accurately be classed as intolerant of shade.

Overstocked jack pine seedling and sapling stands with 4,950 or more trees per hectare (2,000/acre) should be weeded or cleaned (precommercial thinning) to improve growth and development. Otherwise such stands may stagnate because natural thinning in jack pine stands is slow except on the best sites *(10)*. A study in northern Minnesota, wherein direct seeding produced a stand averaging 32,100 trees per hectare (13,000/acre) at age 5 years, compared the growth of no thinning with thinning to square spacings of 1.2, 1.8, and 2.4 m (4, 6, and 8 ft). Twenty-two years later the treatments averaged 9, 10, 13, and 15 cm (3.7, 4.1, 5.1, and 5.8 in) in d.b.h., respectively ***(14).*** Planting, direct seedings, and precommercial thinnings should have a goal of 2,000 to 3,000 trees per hectare (800 to 1,200/acre) by age 10 years *(19,30)*.

Jack pine is a pioneer species on burns or other exposed sites. In the absence of fire or other catastrophes, jack pine is succeeded by more tolerant species, but on the poorest, driest sites it may persist and form an edaphic climax. In loamy sands and sandy loams in northern Minnesota, the usual succession is from jack pine to red pine to eastern white pine to a hardwood type composed of sugar maple *(Acer* ***saccharum),*** basswood *(Tilia* ***americana),*** and northern red oak. Frequently, the red pine and white pine stages are absent and jack pine is followed by speckled alder *(Alnus* ***rugosa),*** American hazel *(Corylus* ***americana),*** beaked hazel *(C.* ***cornuta),*** paper birch, and quaking aspen. This stage is followed by either the sugar maple-basswood association or spruce-fir. On loamy soils in northeastern Minnesota and parts of Canada, jack pine is succeeded by black spruce, white spruce, balsam fir, and paper birch. Eventually, the paper birch is eliminated from this association. In parts of northwestern Canada, jack pine may be replaced directly by white spruce; in parts of eastern Canada, the immediate succession may be to pure black spruce *(10,26,61)*.

Damaging Agents--Jack pine is subject to many agents that cause damage or mortality. Young jack pines are especially susceptible to early spring fires. Severe drought may kill many seedlings, particularly on coarse soils. All young jack pines less than 1.5 m (5 ft) tall and 55 percent of those from 1.5 to 3.7 m (5 to 12 ft) tall were killed by 123 days of flooding in northern Minnesota. Heavy populations of white-tailed deer can kill young jack pines up to 2.1 m (7 ft) tall, retard total height growth to half its potential, and deform most trees so they have little future value for timber products. Snowshoe hares can severely damage jack pine reproduction, particularly in dense stands in trees less than 4 cm (1.5 in) in d.b.h. *(16,61)*. Jack pine seedlings are greatly damaged by elk in western Manitoba when animal populations are high, and meadow voles cause occasional damage and mortality by gnawing the bark off main stems and lower branches ***(16).*** Porcupines can cause extensive damage in older stands *(74)*.

Numerous insects affect the survival and growth of jack pine seedlings (83). The more important groups of these are as follows: (1) root borers such as the pales weevil ***(Hylobius pales),*** pine root collar weevil *(H. radicis)*, pine root tip weevil *(H.* ***rhizophagus),*** and Warren's collar weevil *(H. warreni)*; ***(2)*** shoot and stem borers such as the northern pine weevil ***(Pissodes approximatus),*** the white pine weevil *(P.* ***strobi),*** and the Allegheny mound ant ***(Formica exsectoides);*** (3) leaf feeders such as numerous sawflies ***(Neodiprion sertifer, N. pratti banksianae, N. swainei, N. nigroscutum, N.*** *compar,* ***N. lecontei, N. dubiosus, N. nanulus*** *nanulus),* ***Diprion similus,*** jack pine budworm, pine chafer *(Anomala* ***oblivia),*** and pine webworm *(Tetralopha* ***robustella);*** (4) needle miners such as ***Argyrotaenia tabulana, Exoteleia***

pinifoliella, and ***Zelleria haimbachi;*** (5) root feeders including primarily white grubs ***(Phyllaophaga*** spp.); and (6) sucking insects such as two midges ***(Cecidomyia reeksi,*** and ***C. piniinopis),*** scale insects ***(Nuculaspis California, Chionaspis pinifoliae,*** and ***Toumeyella parvicornis),*** spittlebugs ***(Aphrophora parallela*** and ***A. saratogensis),*** and a wooly aphid *(Pineus* ***coloradensis).***

The jack pine tip beetle ***(Conophthorus banksianae)*** causes extensive shoot tip mortality, preferring sapling-size trees. The lodgepole terminal weevil ***(Pissodes terminalis)*** attacks and destroys the new terminal bud of jack pine in Saskatchewan *(61,83).*

Several sawflies attack jack pine. Trees are often killed because the sawflies feed on both old and new needles. The pine tussock moth ***(Parorgyia plagiata)*** commonly defoliates large areas of sapling- and pole-size jack pine. The jack pine budworm is the most important defoliator of jack pine in the northeastern United States *(61,84).*

Several diseases commonly attack young jack pines and reduce survival and growth. A needle rust fungus ***(Coleosporium asterum)*** causes some defoliation of seedlings. Diplodia blight ***(Diplodia pinea)*** frequently results in a shoot blight of jack pine seedlings under nursery conditions. Sirococcus shoot blight ***(Sirococcus strobilinus)*** has also caused seedling losses in Lake States nurseries. Scleroderris canker ***(Gremmeniella abietina)*** causes serious losses in both nursery stock and young plantations. Before nursery control programs for this disease were instituted in the Lake States, this fungus killed an average of 40 percent of seedlings in plantations established with infected stock (77).

Jack pine is susceptible to a number of rust fungi that cause both growth loss and tree mortality Many of these rusts are disseminated by infected nursery stock. The sweetfern blister rust ***(Cronartium comptoniae)*** sometimes kills many young seedlings and reduces the growth of survivors. More prevalent is the pine-oak (eastern) gall rust ***(Cronartium quercuum),*** which may infect up to 50 percent of young seedlings, killing many of the seedlings with galls on the main stem. Young jack pine in Minnesota have been severely cankered by stalactiform rust *(Cronartium* ***coleosporioides).*** In recent years the pine-to-pine (western) gall rust ***(Endocronartium harknessii)*** has been found throughout the Lake States in young jack pine stands. The importance of this rust is its potentially rapid rate of spread. This rust can infect directly from pine to pine without spending parts of its life cycle on an alternate host as do all the previously mentioned rusts (77).

Sapling- and pole-size jack pine frequently show severe needlecast *(Davisomycella* ***ampla).*** This fungus often causes loss of all but the current year's needles. Although affected trees suffer growth loss, the disease seldom causes mortality. Diplodia blight frequently kills branches and often the entire tree. This disease appears to be stress related and may reach epidemic status following drought. The European strain of scleroderris canker is currently killing many jack pine in northern New York and will cause serious losses if it reaches the major range of jack pine (77).

The rust fungi mentioned under seedling disease also cause extensive mortality in pole-size stands. The pine-oak (eastern) gall rust has caused severe losses in jack pine stands in northern Wisconsin. In some pole-size stands the disease is so prevalent that the stands have become worthless and have been destroyed (77).

The major root-rot fungi include the shoestring fungus ***(Armillaria*** *mellea)* and annosum root rot ***(Heterobasidion annosum) (77).***

The principal wood decay organisms are ***Phellinus*** *pini,* ***Phaeolus schweinitzii,*** and ***Fomitopsis pinicola*** (77).

Windthrow is not a serious problem in jack pine stands except on shallow soils or when more than one-third of the stand basal area is removed in thinnings. Stem breakage from wind, ice, and snow is more common *(10).*

Cone and seed production can be decreased by numerous factors. Red squirrels and other rodents destroy cones and consume seeds *(18,61,69,72).* Low-vigor trees may produce much pollen but little seed. Pine-oak (eastern) gall rust damages trees resulting in smaller and aborted ovulate cones. Birds may be important consumers of jack pine seeds that fall to the ground or are directly sown ***(61).*** Cone and seed insects may cause serious losses. In one study in northeastern Wisconsin, numerous insect species were found attacking conelets and cones (57). The jack pine budworm ***(Choristoneura*** *pinus pinus)* destroyed 12 percent of the conelets. A mirid ***(Platylygus*** *luridus)* was observed piercing conelets as well as shoots and needles and was apparently responsible for a severe but unknown conelet abortion rate. The most prevalent insect attacking cones was the cone borer ***(Eucosma monitorana)*** which killed 10 percent of the cones. Other insects responsible for a total of about 4 percent cone mortality were the webbing coneworm *(Dioryctria* ***disclusa),*** red pine cone beetle ***(Conophthorus resinosae),*** jack pine budworm, and cone midges ***(Lestodiplosis*** *graddator,* ***Resseliella silvana,*** and ***Asynapta hopkinsi)*** (57).

Other insects that directly damage jack pine conelets, cones, or seeds, or that decrease their numbers by damaging potential cone-bearing shoots include the jack pine tip beetle ***(Conophthorus banksianae)***, shield-backed pine seed bug ***(Tetyra bipunctata),*** Virginia pine sawfly ***(Neodiprion pratti pratti)***, a moth ***(Holcocera immaculella),*** eastern pine seedworm ***(Laspeyresia toreuta),*** Nantucket pine tip moth ***(Rhyacionia frustrana)***, European pine shoot moth ***(R. buoliana), fir*** coneworm ***(Dioryctria abietivorella),*** and spruce coneworm ***(D. reniculelloides) (36).***

Special Uses

The most notable special use for jack pine is as a breeding area for the Kirtland's warbler, a rare and endangered species. The Kirtland's warbler requires homogeneous stands of jack pine between 1.5 and 6 m (5 to 20 ft) tall (about 7 to 20 years old); stands are preferably larger than 32 ha (80 acres) *(52)*.

Jack pine stands can be an important part of the visual resource for recreation areas; they stabilize watersheds, produce areas for blueberry picking, and provide food and shelter for wild game species, including the snowshoe hare and the white-tailed deer *(10)*.

Genetics

The various environments in which jack pine grows over its wide range have provided ample opportunity for differentiation and natural selection *(72)*.

Virtually the entire present range of jack pine was glaciated during the most recent Wisconsin stage that reached its maximum about 18,000 years ago. The present distribution of the species therefore results from reinvasion and migration over huge areas and great distances in a relatively short time, estimated at 15,000 years since the retreat of the ice began in earnest. Available paleobotanical evidence suggests that jack pine survived the Wisconsin glacial maximum at low elevations in the Appalachian Mountains south of latitude 34" N. and also in the western Ozark Mountains. From these refugia it migrated to the north and east and up the Mississippi Valley, and westward around the southern end of the Lake Agassiz basin (72).

Population Differences

The wide genetic variation found in the species suggests it has large effective breeding populations, heterozygosity for many alleles, and strong natural selection against self-fertilization and increased homozygosity (72).

A study of 33 characteristics of tree crown, bark, wood, foliage, and cones of mature trees over most of the natural range showed that all varied significantly according to the geographic origin of the populations. An average of 37 percent of the variation was due to origin (74). Environmental factors appear to be the dominant selection forces responsible for the natural variation over the present-day jack pine range. The area of optimum development of jack pine is north of the Great Lakes in Ontario and Quebec ***(19,471.***

Certain traits of jack pine have been demonstrated to be under strong genetic control including cone shape, cone serotiny, cone volume, cone length, scale number, number of scales to first ovule, and number of scales to first seed *(53,61,76,79)*. Early flowering appears to be under additive genetic control and not under the control of a single major gene or recessive genes ***(41).*** Lammas growth and prolepsis, which may be detrimental to tree form, are under some genetic control *(62,63)*, and many of the traits contributing to desirable Christmas tree form are highly heritable (55).

Races

Numerous jack pine provenance or seed source tests, established beginning in the early 1940's, have provided information on variation among provenances (72). Studies of variation have included controlled environment chamber, greenhouse, nursery, and field experiment.

Growth, the characteristic most frequently emphasized in provenance studies, has been found to follow a generally clinal pattern associated with environmental gradients of latitude (photoperiod) and length and temperature of the growing season at the seed origin (72). Differences in growth among provenances have been demonstrated beginning at the young seedling stage and by age 15 to 20 years the differences among provenances in tree growth and wood production are substantial (72). For example, in a test of Lake States provenances at 14 locations, trees of two provenances from northeastern Minnesota were only 71 percent of the plantation mean height in a central Wisconsin plantation whereas trees of the tallest source, from Lower Michigan, exceeded the plantation mean by 17 percent after 20 years (40). Translated to volume growth and considering tree survival, the volume per hectare of trees in the poorest provenances was only 38 percent of the plantation mean and that of the best was 187 percent of the plantation mean. These results

clearly show the importance of selecting and using the best provenance or seed source in jack pine reforestation efforts and the magnitude of the losses in wood production that may result when seed origin is ignored. Provenance test results in Canada have similarly shown wide differences in growth among provenances *(72,84,85,86,87)*.

Most provenance tests show that trees of provenances from areas nearest the planting sites grow as well as or better than the average of trees of all provenances (72). In the Lake States, however, trees of provenances that were moved slightly northward outgrew those of the local provenance *(40)*. Thus, although wide latitudinal movement of provenances is not suggested, movement up to 160 km (100 mi) northward in the Lake States can increase growth. Selection of superior provenances within latitudinal belts of similar climate should make substantial genetic gains possible (72).

Biomass production of trees in 24- and 25-year-old plantations of four Lake States provenances at three locations ranged from 2.7 to 6.1 t/ha (about 1.2 to 2.7 tons/acre) annually (89). Total biomass and mean annual biomass were negatively related to latitude of the plantation. Movement of provenances slightly northward within climatic zones resulted in increased biomass production of the trees but movement from warmer to colder short-growing-season zones resulted in poor growth.

Although tree growth has been the single most important trait evaluated in provenance tests, variation among provenances in other tree characteristics also has been noted. These include tree form as influenced by branching characteristics, wood and bark properties, cold hardiness, autumn foliage color variation in young seedlings, seed yield and quality, isozyme systems, and numerous instances of genetic variation in susceptibility or resistance to diseases and insect pests (72).

The vast information available from provenance test results is being applied to the establishment of seed collection zones, breeding zones, and regional jack pine improvement programs in the Lake States (44) and in Canada (72).

Hybrids

Although putative hybrids have been reported between jack pine and Virginia pine *(Pinus virginiana)*, loblolly pine *(P. taeda)*, and Japanese black pine *(P. thunbergiana) (72)*, jack pine x lodgepole pine *(P.* x *murraybanksiana* Righter and Stockwell) is the only verified interspecific hybrid in which jack pine is a parent (59).

Widely scattered tests of the artificially created hybrids have shown mixed results, probably because the origin of the parents was not always matched with the environment of the test site *(25,50,58)*. Tests of the California-developed F_1 hybrids, F_2, backcross progeny, and the two parent species in northern Wisconsin and eastern Ontario showed that winter injury was associated with affinity to one or the other parent-it ranged from very severe in the lodgepole pine from California to none in the jack pine *(70,87)*. Polygenic inheritance was indicated suggesting that the backcross breeding method might be used to develop lines suitable for environments tolerated by the hardier parent.

The hybrids and the lodgepole parent were more susceptible to sweetfern rust and to eastern gall rust than local jack pine in tests in the Lake States and Ontario *(2,84)*. The form noted in some hybrids suggested some potential as Christmas trees but not as forest trees (4). However, because of the high susceptibility to sweetfern rust reported in eastern and central Canada, the hybrids should not be planted in that region (84).

Natural hybrids between jack pine and lodgepole pine occur in areas of contact in central and northwestern Alberta *(21,61,75)* and in scattered locations in Saskatchewan *(5,6)*. Differences in cone morphology provide the strongest diagnostic features for distinguishing the hybrids in the field *(61,72)*.

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 hybrid contains one-fourth beta-phellandrene and three-fourths pinenes. Thus, in the F_1 hybrids the bicyclic terpenes of jack pine dominate over the simpler monocyclic terpene of lodgepole pine in a 3-to-1 ratio *(61)*. Further study of the segregation for turpentine components in the hybrids suggested that the composition is probably controlled primarily by a limited number of genes with major effects (88). Discrimination between lodgepole pine and putative hybrids with jack pine based on analysis of monoterpenes showed that the transition zone between the species may be farther west than previously reported (56).

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