

## The late Quaternary history of lodgepole and jack pines

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Lodgepole and jack pines (*Pinus contorta* Dougl. ex. Loud. and *Pinus banksiana* Lamb.), components of the North American boreal forest, have pioneering roles after major disturbances such as fire or glaciation. These species are closely related and hybridize in western Canada, but their fossil records and contemporary variation patterns suggest they had completely different late Quaternary histories. Several taxonomically recognized geographic races of lodgepole pine apparently survived the last glaciation without drastic modification, the northern races either persisting in far-northern refugia or migrating from the south. The uneven influence of jack pine on northern lodgepole populations implies repeated genetic contacts, but less marked introgression in the other direction could be of post-Pleistocene origin. Jack pine occupied its entire range after the last glacial maximum and lacks taxonomically recognized races. In the Great Lakes region, however, the presence of regionally distinct populations suggests the species had at least two Midwestern refugia. This hypothesis is contrary to the widely held view that jack pine occupied most or all of its range from a well-documented refugium in southeastern North America, but is supported by limited fossil evidence that pine persisted in the Midwest during the last glaciation.

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Deux pins de la forêt boréale nord-américaine, les pins tordu et gris (*Pinus contorta* Dougl. ex. Loud. et *Pinus banksiana* Lamb.) jouent le rôle de pionniers après les perturbations majeures comme le feu ou les glaciations. Ce sont deux espèces très proches qui hybrident entre elles dans l'ouest du Canada. Les fossiles et le patron des variations contemporaines des deux taxons suggèrent cependant que leurs histoires quaternaires soient complètement différentes. Plusieurs races géographiques du pin tordu auraient survécu à la dernière glaciation sans modifications majeures: les races nordiques ayant soit persisté dans les refuges du grand nord soit migré à partir du sud. L'influence inégale du pin gris sur les populations nordiques du pin tordu suppose des contacts génétiques, alors que l'introgression inverse, moins prononcée, pourrait être d'origine post-pleistocène. Le pin gris a occupé son aire entière après le dernier maximum de glaciation et ne contient pas de races taxonomiques reconnues. Cependant, dans la région des Grands Lacs, la présence de populations distinctes suggère que l'espèce a eu au moins deux refuges dans les États de la Prairie. Cette hypothèse est en opposition avec l'opinion largement répandue à savoir que le pin gris a envahi la plus grande partie de son aire à partir d'un refuge bien connu, situé dans le sud-est de l'Amérique du Nord. Quelques preuves fossiles tendent, au contraire, à prouver que durant la dernière glaciation, le pin a persisté dans les États de la Prairie.

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### Introduction

The history and attributes of lodgepole and jack pines (*Pinus contorta* Dougl. ex. Loud. and *Pinus banksiana* Lamb.) suggest that this closely related species pair, the most northern of the American pines, can be characterized as Pleistocene opportunists. Their representation in the Tertiary fossil record is sketchy (lodgepole pine) or nonexistent (jack pine), but by the end of the Pleistocene epoch they had major pioneering roles in revegetating the deglaciated north of North America. Their successful adaptation to the climatic changes of the Pleistocene is illustrated by the fact that most of the present ranges of both species were covered by ice less than 18 000 years ago. Today they are the only pines represented in the boreal forest of North America.

Pleistocene history has been drastically revised in recent years (e.g., Bowen 1979) and may have comprised as many as 16 or 18 prolonged glacial events separated by relatively short interglacial periods. The Pleistocene record of lodgepole and jack pines extends back no farther than the last of these sequences. If their recent history is representative of earlier cycles, however, these pines must have been in a state of flux

through at least the latter part of the Pleistocene, with their populations repeatedly subdividing or merging and undergoing explosive expansions or mass extinctions. Lodgepole and jack pines may also have intermittently exchanged genes, as they are doing at present. And, as Terasmae (1973) has pointed out, these kinds of events are likely to have left detectable genetic evidence that can be used to reconstruct late-glacial and post-glacial migration patterns.

Lodgepole and jack pines provide contrasting illustrations of the approach suggested by Terasmae (1973). Jack pine occupied its present range after the end of the Pleistocene and its genetic structure must have been shaped primarily by events that are recent on the scale of geological time. Its physical environment is more homogeneous than that of lodgepole pine and it lacks taxonomically recognized infraspecific units. Lodgepole pine spans a much wider environmental range, from the mild maritime climates of the Pacific coast to the cold continental climates that characterize the range of jack pine. Most of the distribution of lodgepole pine was covered by Cordilleran ice, but the species also extends south of glacial limits in three salients (Pacific coast, Cascades – Sierra Nevada, and Rocky Mountains), each occupied by a distinctive geographic race. All three races are taxonomically recog-

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nized and have at times been treated as species. The contrasts between lodgepole and jack pines suggest that late Quaternary events have had impacts on jack pine that can still be detected, whereas the geography of lodgepole pine has permitted older racial differences to survive repeated glaciations without much modification.

Two fundamentally different approaches are available in reconstructing species history: (i) inferences from the distribution and variation of living organisms and (ii) the fossil record. Both approaches have been applied to jack and lodgepole pines. Illustrating the first approach, discontinuities in the variation of jack pine in the Great Lakes region have been interpreted as evidence of two glacial refugia (Zavarin *et al.* 1969), two migration routes into the region (Skeates 1979), or the postglacial evolution of distinct races (Wright 1972). Widespread indications of jack pine influence on lodgepole pine have been attributed to contacts between the species long before postglacial time (Critchfield 1980; Forrest 1980; Wheeler 1981). And variations in northern lodgepole pine led von Rudloff and Nyland (1979) and Wheeler and Guries (1982a) to conclude that the species persisted in Yukon refugia during the last glaciation.

Historical reconstructions based primarily on the fossil record (mostly pollen) are often at odds with conclusions from contemporary populations. Most paleobotanists (e.g., Wright 1968; Davis 1981; Webb *et al.* 1983) agree that jack pine migrated into the Great Lakes region from a major late-Pleistocene refugium in eastern North America. Yeatman (1967) postulated, from pollen and other evidence, that jack pine occupied its entire range from this eastern refugium and that gene exchange with lodgepole pine is a late-postglacial phenomenon. Paleobotanists have virtually abandoned the idea that lodgepole pine had a Yukon refugium and have argued instead that it occupied its northern range from refugia between the ice sheets that covered most of western Canada in the late Pleistocene (e.g., Anderson 1970) or south of the ice.

This paper combines these approaches in an attempt to reconstruct the recent history of lodgepole and jack pines. Summaries of the literature on the biology and genetics of both species (Critchfield 1980; Rudolph and Yeatman 1982) have supplied much of the background for the next two sections of this paper and, with a few exceptions, only supplemental references are cited in these sections. Dates given as years before present (B.P.) are in radiocarbon years. In those instances where dates are not interpolated between radiocarbon determinations, their standard errors and laboratory numbers are given in the original citations. Pollen percentages are usually based on land plants only. Localities mentioned in the text are mapped in Figs. 2 and 3.

### Taxonomic context

Lodgepole and jack pines are hard pines (subgenus *Pinus* = *Diploxylon*). They are classified with two other North American species, Virginia pine (*Pinus virginiana* Mill.) and sand pine (*Pinus clausa* (Engelm.) Sarg.) in subsection *Contortae* of section *Pinus* (Critchfield and Little 1966). Subsection *Contortae* is morphologically coherent (relatively small cones and seeds, and anatomically similar needles in pairs) and has a characteristic life history. The trees are small and short lived and begin cone production at an early age. The cones of all but Virginia pine are sometimes serotinous; they remain tightly closed at maturity and often open only after exposure to high temperatures generated by forest fires. All species frequently occur on low-nutrient sites, grow rapidly in juvenile stages, and

are intolerant of shade.

The collective distribution of the group has an inverted U-shaped configuration that spans the continent (Critchfield and Little 1966). The western arm is lodgepole pine (Fig. 1). It ranges south to Baja California, north to Alaska and the Yukon, and east to Alberta and Colorado, with eastern outliers scattered from northern Alberta to South Dakota. The crossbar of the inverted U is jack pine. It is distributed from northwestern Canada to the Atlantic coast, overlapping lodgepole pine in western Canada. The eastern arm (Pennsylvania to Florida) comprises the allopatric ranges of Virginia and sand pines.

Despite the geographically central location of jack pine, analyses of both isoenzymes and seed and cone characteristics of the taxa in *Contortae* indicate that this species occupies an isolated position within the subsection (Wheeler *et al.* 1983). Genetic distance values based on isoenzymes delineated three groups in *Contortae*: Virginia and sand pines, the subspecies of lodgepole pine, and jack pine. Wheeler *et al.* (1983, p. 338) suggested that "lodgepole pine most closely resembles the ancestral taxon from which the other taxa in the subsection are derived." They did not estimate times of divergence, but implied that lodgepole and jack pines probably diverged some time during the Pleistocene. Another comparison of lodgepole and jack pine isoenzymes was restricted to Alberta populations (Dancik and Yeh 1983). Alberta lodgepole pine was more variable genetically than jack pine, with heterozygosities averaging 18.4 and 11.5, respectively. Genetic distance values provided the basis for a rough estimate that lodgepole and jack pines diverged about one-half million years ago, but Dancik and Yeh (1983) interpreted this as the minimum time of divergence. Pre-Pleistocene divergence is suggested by the finding of fossil cones "very similar but not identical to" jack pine cones (Kuc and Hills 1971), but the fossils have not yet been described (see below).

Crossability data provide a different picture of relationships within *Contortae*. Lodgepole and jack pines can be easily crossed, as can Virginia and sand pines. The crossability of lodgepole and jack pines is 31%; controlled interspecific crosses with lodgepole pine as the female parent produce about a third as many germinable seeds as crosses between lodgepole pines. In the overlap region, natural hybridization is restricted by differing ecological preferences, by these internal reproductive barriers, and by a difference in flowering time. Jack pine flowers first in natural stands; in a California plantation it peaked 2–3 weeks before lodgepole pine.

The two pairs of pines in subsection *Contortae* are separated from each other by strong reproductive barriers that have only recently been breached. Lodgepole × Virginia pine crosses have produced a few chlorotic, dwarfed offspring. A few hybrids have also been produced from crosses between sand pine and two species in subsection *Australes*, which includes most of the hard pines of southeastern North America. The genetic and morphological evidence suggest that among extant pine lineages, the *Contortae* group is most closely related to *Australes*.

Lodgepole and jack pines have a Eurasian analog in Scots pine (*Pinus sylvestris* L.) and superficial similarities among these northern two-needled pines led Clausen (1963, p. 864) to consider them "a single large gene pool." This grouping is not supported by morphology, cytology, or crossing behavior. Scots pine is classified in subsection *Sylvestres*, which includes most Eurasian hard pines and red pine (*Pinus resinosa* Ait.), the sole representative of the subsection on the North American continent. Pines in *Sylvestres* have a distinctive karyotype and

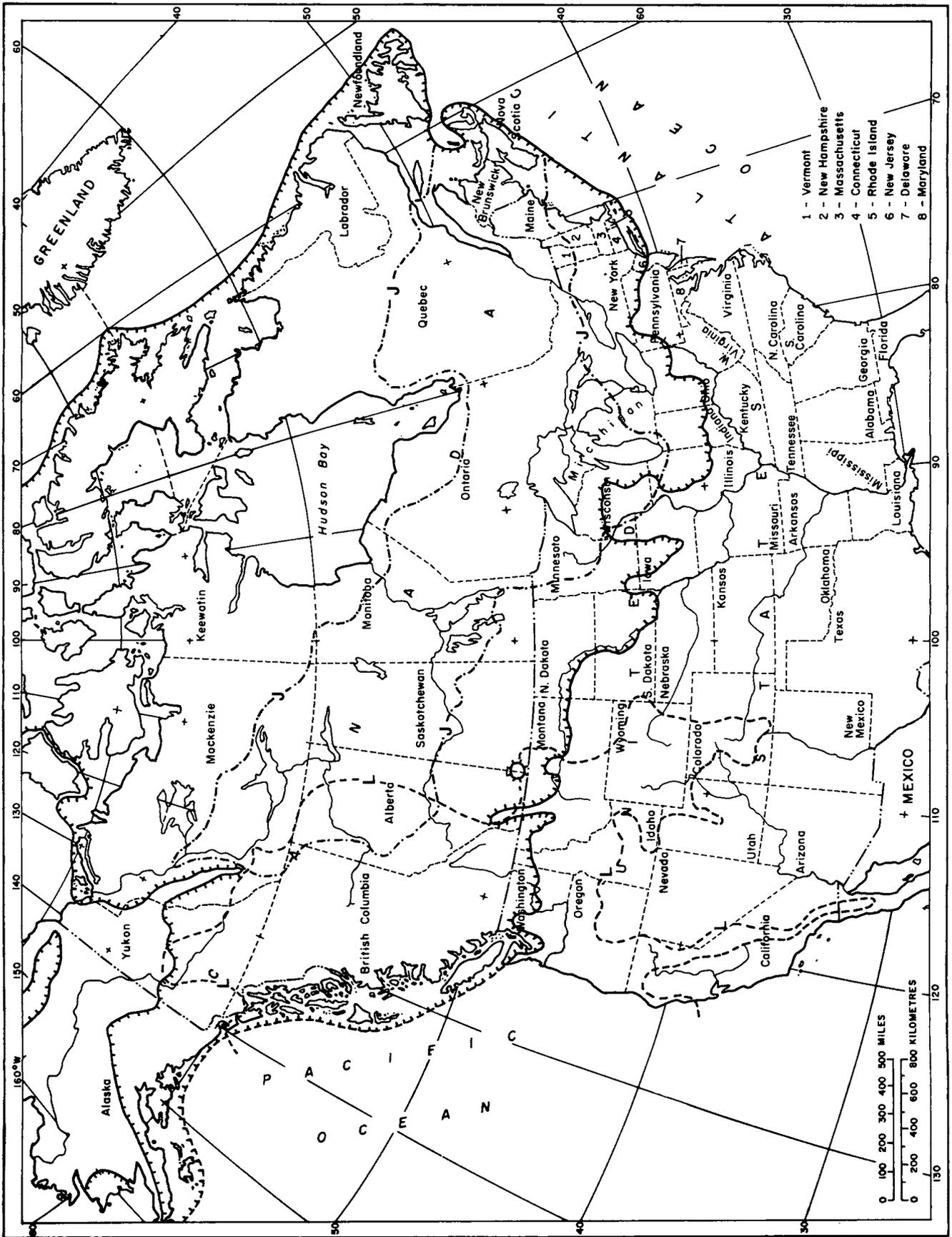


FIG. 1. Approximate limits of North American ice sheets at last glacial maximum (-----); (adapted from Péwé 1983) and distribution limits of lodgepole (L, ----) and jack (J, - · - · -) pines.

are genetically isolated from pines in other groups. In particular, many attempts to cross Scots and lodgepole pines have all been blocked by strong reproductive barriers.

### Reproductive attributes

#### *Cones and seeds*

In many of the characteristics they share, lodgepole and jack pines are adapted to both rapid migration and explosive population increases. The outstanding exception is the serotinous cone. Storage of most or all of the annual seed crop on the tree augments the potential for rapid increases in population size in the event of fire, but at the expense of the ability to reproduce in the absence of fire. The two pines have resolved this problem in different ways and jack pine is the more fire dependent in nearly all respects. Paradoxically, jack pine also appears to have traveled farther and faster than lodgepole pine since the end of the Pleistocene.

Most trees of both species have predominantly open or closed cones, but neither the mechanism nor the inheritance of cone serotiny is fully understood. The resin that bonds together the scales of closed lodgepole cones has a melting point (45–59°C) that is higher than the usual range of naturally occurring temperatures and there is some evidence that cones opening at maturity have resin with a lower melting point. Progeny tests of jack pine have shown that serotiny is controlled by one or a few genes and a genetic model of a single additive gene with two alleles has been used to interpret the frequency of cone types in natural populations of both species. Although this model does not adequately explain much of the data, it is probable that a relatively simple genetic mechanism controls serotiny in both species.

Young lodgepole pines have a prolonged initial phase of open-cone production before they begin to produce serotinous cones. Trees less than 20–25 years old produce mostly open cones and trees more than 30–55 years old produce mostly closed cones. Since lodgepole pines bear cones at an early age (about 7–10 years), they produce open cones for at least one or two decades before the shift to closed cones. Jack pine is more precocious than lodgepole pine, but it is not certain whether jack pine also has an initial open-cone phase. In one Minnesota provenance test, open cones were quite general on 7- to 10-year-old trees (Schantz-Hansen and Jensen 1952) and in central Saskatchewan, where the frequency of closed-cone trees in older stands approaches 100%, Jameson (1961) observed that nearly all cones on 7- to 10-year-old trees opened at maturity. Cone serotiny is general by 16–20 years (data of Rudolph *et al.* 1959; Schoenike *et al.* 1959), so if jack pine commonly has an initial phase of open-cone production, it lasts no more than a few years.

Cone serotiny is also more widespread geographically in jack pine than in lodgepole pine and has a higher frequency in stands. Mature stands with mostly open-cone trees are common in the southern Great Lakes region and sporadic in the east (Schoenike 1962). Elsewhere, closed-cone trees are usually in the great majority, with frequencies often reaching 100%.

The geographic and edaphic races of lodgepole pine are conspicuously different in the incidence of closed cones. Closed cones are rare in the coastal race, but common on edaphically extreme sites near the coast. All cones open at maturity in the Sierra Nevada and most other mountains of California and southern Oregon. In the Rocky Mountain region, where lodgepole pine is considered a fire species, stands

with moderate to high frequencies of closed-cone trees are common but not universal. In one survey, nearly a third had less than 10% closed-cone trees and no stands had more than 90% closed-cone trees (Perry and Lotan 1979).

Trees of both species accumulate large numbers of closed cones in their crowns. Mature open-grown lodgepole pines in Alberta had a maximum of 1102 closed cones and trees in stands bore up to 376 closed cones (Crossley 1956). Mature trees in Montana averaged several hundred closed cones and one tree had 4400 closed cones (Lotan 1967). Dominant jack pines in a 40-year-old Minnesota stand had 100–200 closed cones, but 70- to 80-year-old dominants averaged 463 and one had 2356 closed cones (Roe 1963).

The number of seeds per cone is highly variable in both species, but average values are higher for jack pine. Minnesota jack pines of varying age and condition had 17–37 viable seeds per cone, with an overall mean exceeding 25 (Roe 1963). Most estimates for lodgepole pine are in the range of 11–21 sound or germinable seeds, averaging 15–18 per cone.

The size of the seed reserved in serotinous cones depends on several factors: age and composition of stand, frequency of closed-cone trees, and amount of squirrel predation. Most estimates for jack pine are in the range of 560 000 to 4 370 000 sound or germinable seed per hectare (Roe 1963). Estimates for mature lodgepole stands range considerably higher, up to 7 900 000 sound or germinable seed per hectare.

Lodgepole and jack pines have the smallest seeds of any pines. Air-dry lodgepole seeds average 2.3–3.5 mg through most of the glaciated north and 3.3–11.4 mg farther south. In jack pine samples from the Great Lakes region, the mean weight of air-dry seeds was 2.6–6.4 mg (Eyre and LeBarron 1944). Oven-dry weights of seeds from rangewide samples were 2.2–5.1 mg, with the heaviest seed in the southern Great Lakes region (Yeatman 1966).

The winged seeds have a slow rate of fall and can be dispersed for long distances by wind. The terminal velocity of lodgepole seed is 0.6–0.8 m/s, much less than that of most other western conifers. In New Zealand, where this introduced species reproduces naturally, trees have become established 16–18 km from their parents. Other possible mechanisms of long-distance dispersal are seed scudding on snow or ice and water transport of closed cones.

Jack pine and most lodgepole pine seed germinates promptly and without pretreatment. Germination of untreated lodgepole seed from most origins is essentially complete in 1–2 weeks at optimum temperatures (21–25°C). Germination of fresh jack pine seed from many Minnesota parent trees was practically complete in 7 days, with sound-seed germination averaging 95% (Schantz-Hansen 1941).

In both pines, seed stored in serotinous cones on the tree retains its viability for many years. Lodgepole seed from cones of all ages was 90% germinable in an Alberta study and averaged 91–92% of fresh-seed germination in Wyoming and Colorado. Jack pine seed of the 4–12 most recent cone crops and from undatable “old” cones, collected from many trees in several Minnesota stands, was more than 90% germinable (Schantz-Hansen 1941).

Seeds of both pines are undamaged by short exposures to temperatures higher than those needed for cone opening. Idaho lodgepole seed was not affected by 15-min exposures to temperatures up to 65°C, but germination dropped after exposure to 75°C and above (Knapp and Anderson 1980). Beaufait (1960) showed that jack pine seed survives brief exposures to

very high temperatures. Viability of extracted seed was not affected by exposure to 341°C for up to 10 s and seeds in serotinous cones were viable after exposure to the same temperature for up to 2 min. Beaufait's (1960) experiments suggest that either ground or crown fires will open serotinous cones and that fires are not likely to influence seed viability unless the cones ignite.

Fires favor the regeneration of lodgepole and jack pines in several ways: they release stored seed, reduce competition, and prepare a favorable seedbed (Eyre and LeBarron 1944). Shedding of jack pine seed from closed cones was practically complete a week after a mid-June crown fire in Minnesota. The timing of germination is important to survival; jack pine reproduction is more likely to become established after fires early in the growing season than after late summer or fall fires (Jameson 1961; Eyre and LeBarron 1944). Bare mineral soil provides the best medium for germination and survival. In Saskatchewan, jack pine reproduction was more abundant when the organic layer was destroyed than when it was lightly burned and pine seedlings grew faster on burns than on relatively undisturbed areas (Jameson 1961).

### Pollen

Pines are abundantly represented in the fossil record by their pollen, which they produce in large amounts. In a California plantation, lodgepole pines from coastal origins produced an average of 466 million pollen grains per tree in their 9th year and one tree of another origin shed an estimated 21 billion pollen grains.

Jack pine has the smallest pollen grains of any of the 12 hard pines native to the eastern United States and Canada (Whitehead 1964). Red pine, the only other hard pine in the central and eastern parts of jack pine's range, has slightly larger pollen grains. In Whitehead's (1964) extensive sampling, the internal diameter of the body of the grain (=corpus breadth) averaged about 8% larger in red pine. The pollen of both species (and all other hard pines) can be distinguished morphologically from the pollen of white pines, including eastern white pine (*Pinus strobus* L.). Reliable morphological distinctions between jack and red pine pollen have also been described (Ammann 1977), but in most palynological studies, the two species are lumped.

Lodgepole pine is the only representative of *Pinus* in the north and west of its range, but farther south and east another hard pine, the ecologically dissimilar ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.), is often present. Hansen (1947) routinely separated the two pollens by size, but the validity of this procedure was questioned by Mack (1971), who found more overlap than Hansen had reported. Hansen's (1947) reconstruction of postglacial succession in the Pacific Northwest, which assigned an important pioneer role to lodgepole pine, was challenged by R. N. Mack and his associates, and in their revision of the vegetation history of northeastern Washington they lumped lodgepole and ponderosa pollen (e.g., Mack *et al.* 1976; Mack *et al.* 1979). A different approach was taken by Alley (1976) and Hansen and Cushing (1973), who studied fossil pollen assemblages in southern British Columbia and the southwestern United States respectively. They independently worked out combinations of morphological and size criteria for separating lodgepole and ponderosa pollen, with fair to good success.

According to Hansen (1952), lodgepole pollen is somewhat larger than jack pine pollen. He did not provide sup-

porting data, nor did he attempt to separate the two species in a transect through west-central Alberta. Their pollen size can be compared from the data of Whitehead (1964) and Hansen and Cushing (1973). Internal diameter of the pollen body was measured in both studies and the same pretreatment and mounting medium were used. Jack pine pollen from 24 localities averaged 37.0  $\mu\text{m}$ , and four lodgepole samples from the southern Rockies averaged 42.5  $\mu\text{m}$ . This difference may be minimal in western Canada; Whitehead's (1964) largest jack pine pollen (40.6  $\mu\text{m}$ ) was from his westernmost collection (Saskatchewan).

Many lodgepole  $\times$  jack pine hybrids produce large quantities of aborted pollen grains, less than half the size of normal grains (Saylor and Smith 1966; Righter and Stockwell 1949, Fig. 2). Individuals with up to 42% aborted pollen are common among first-generation artificial hybrids and their descendants, compared with no more than 1–2% aborted grains in non-hybrids (Pollack 1980; Saylor and Smith 1966). One or more natural hybrids in Alberta produced about 50% aborted pollen (Moss 1949) and trees with up to 14, 27, and 28% aborted pollen were present in three stands in and near the Alberta overlap region (Pollack 1980). Hansen (1952), in his transect through this region, noted the sporadic occurrence of fossil pine pollen smaller than either lodgepole or jack pine pollen in most of the muskegs he sampled and inferred that it might be produced by their hybrids. This finding, if it can be confirmed or extended in radiocarbon-dated sections, may offer a unique opportunity to reconstruct the history of genetic interaction between these two pines in postglacial and perhaps earlier times.

### Comparison with other northern conifers

The dominant conifers of the boreal forest were ranked by Rowe and Scotter (1973, p. 448) according to "relative degree of adaptation for successful regeneration after fire." "Pine" (jack and possibly lodgepole) scored highest in several characteristics: seed retention on the tree, earliness of seed production, and seedling frost hardiness and growth rate. Pine also had the highest overall rating, followed by spruces and other northern conifers. Rowe and Scotter (1973) did not rank red pine, which is present only near the southern margins of the boreal forest, but despite its dependence on fire for successful regeneration, it would score near the bottom of the scale. Red pine is remarkably uniform genetically (Fowler and Morris 1977) and its evolutionary conservatism may be a consequence of this lack of variability.

### Lodgepole pine: variation

South of the limits of Cordilleran ice, the principal races of lodgepole pine appear to have been influenced by repeated glaciation less than most of their coniferous associates. These races are geographically isolated from each other in the south and their distinctness suggests that they have been genetically isolated for many millenia. Direct evidence that southern populations were not badly dislocated by glaciation is reviewed later, but near the end of the Pleistocene lodgepole pine is known to have occurred near the ice front in western Washington and probably in the northern Rocky Mountains. In contrast, most or all northern populations achieved their present distribution in the past 12 000 years and their genetic structure must have been more significantly impacted by recent events. Several features of these populations may provide clues to their

recent history: the distinctness of the coastal race, characteristics of Yukon populations, and evidence of introgression from jack pine.

#### *Coastal race*

Despite a linear distribution through more than 20° of latitude, this race is fairly homogeneous in many of its characteristics. The differences between it and the interior races are manifold and apparently of long standing. Lodgepole pine is widely planted outside North America and the hereditary basis of these racial differences has been demonstrated in provenance tests in northern Europe and elsewhere (reviewed in Critchfield 1980).

More direct evidence that the coastal race "has been a separate entity for a considerable period of time" is provided by a rangewide survey of allelic variation at 42 genetic loci controlling enzymes (Wheeler and Guries 1982a, p. 1808). The five coastal populations sampled (Puget Sound to southeastern Alaska) had a higher average number of rare alleles than any other geographic race, with nearly half of the rare alleles found in the species. Although the coastal race is in contact with central interior populations, it shares fewer rare alleles with this group than with either extreme northern or southern interior populations.

The overall homogeneity of the coastal race, as well as its local variations, is illustrated by the monoterpenes of cortex resin, the most thoroughly studied set of characteristics in lodgepole pine (Forrest 1980, 1981). Monoterpenes, like enzymes, are useful in biogeographical interpretations because they are usually under simple genetic control. Forrest (1980, 1981) analyzed resin from more than 2000 trees of many coastal origins, mostly growing in provenance tests in Great Britain, but including a few samples from natural populations. The cortex resin of the coastal race has the highest levels of  $\beta$ -phellandrene. Within the region, the highest percentages of this compound are in Forrest's large but uniform North Coastal region, which includes all coastal populations north of Vancouver Island, plus populations on the outer coast of Vancouver Island and a single outlier (Queets) in western Washington.

Throughout the North Coastal region, lodgepole pine grows on bogs and muskegs and trees from seed sources in the region are often slower growing, have denser crowns, and are more resistant to exposure than trees from other coastal sources (Shelbourne and Miller 1976). These authors have proposed that North Coastal populations constitute a muskeg ecotype, abruptly replaced in coastal Washington by a sand dune ecotype.

The existence of a distinct North Coastal ecotype is not supported by the distribution and variability of enzyme-controlling genes in the coastal region (Wheeler and Guries 1982a, 1982b). All five coastal populations sampled were quite distinct from each other and in a cluster analysis based on genetic distance, three stands within the North Coastal region did not segregate from the other two coastal stands (N. C. Wheeler, unpublished data).

South of Forrest's North Coastal region, most populations have somewhat lower levels of  $\beta$ -phellandrene and higher levels of  $\beta$ -pinene. Other significant variations in the coastal region include (i) uniformly high levels of 3-carene in the southernmost coastal stands and sporadically high levels in the Vancouver Island - Olympic Peninsula area, (ii) very high levels of  $\beta$ -pinene in a cluster of stands near the southern end of Puget Sound, and (iii) relatively high  $\alpha$ -pinene and

camphene in a few southern Oregon - northern California populations.

Most interior populations have less  $\beta$ -phellandrene than most coastal populations, but the sharpest distinction between the two groups is in the frequency of trees with moderate to high amounts of limonene. About half of the coastal provenances or natural stands sampled by Forrest had no high-limonene trees and nearly all the rest had 12% or less. The frequency of high-limonene trees in interior populations was 15-87%, with a few exceptions in central British Columbia.

Contacts with interior populations appear to have had little effect on northern coastal populations. The two races meet and intergrade in the Skeena River Valley of northern British Columbia and perhaps in other river valleys that cut through the Coast Mountains. The gradient in frequency of high-limonene trees along the Skeena River illustrates the transition from coastal to interior populations. Coastal stands near the mouth of the river had no high-limonene trees (Forrest 1980, 1981). About 100 km up the river the frequency was 12%. In another 100 km the frequency increased to about 28%, a level typical of interior British Columbia. In the same transect, the frequency of trees high in  $\beta$ -phellandrene decreased from 90% on the coast to 70 and 55% at 100 and 200 km from the coast, respectively.

Western Washington is the southernmost area where gene exchange is possible between coastal and interior populations, but the distribution of high-limonene trees provides no evidence of extensive contact. Almost all of Forrest's samples originated either at low elevations (less than 275 m) west of the Cascade crest or at moderate elevations (760-1220 m) in the Cascades. The low-elevation samples had less than 12% high-limonene trees and the montane samples had 39-69% high-limonene trees.

#### *Yukon populations*

Much of interior Alaska and part of western Yukon were not glaciated during the Pleistocene and lodgepole pine extends north to the margins of this unglaciated region (Fig. 1). This distribution led Hultén (1937) to include it among the plant species that survived glaciation in a Yukon refugium, as well as south of the ice. The fossil record does not support the possible existence of a pine refugium in the Yukon, but several recent studies have shown that populations in parts of the Yukon are sufficiently different from other northern populations to justify a reconsideration of Hultén's (1937) hypothesis.

Lodgepole pine nearly always has two needles per fascicle except in a few northern localities. Three-needled fascicles are present and sometimes common in Yukon populations in and near the unglaciated region (von Rudloff and Nyland 1979). Three-needled fascicles have also been reported in the Atlin Lake region of northern British Columbia (Garman 1973) and are common or predominant at one timberline site in the Alberta Rockies (Pollack and Dancik 1979).

In a provenance test covering the northern half of lodgepole pine's range, 2-year-old seedlings from the only two Yukon sources in or near the unglaciated region consistently differed from seedlings of other far-northern sources (Hagner 1970). Hagner (1970) studied characters that indirectly measured cold hardiness. In degree of lignification of wood cells at the end of the season and in time of terminal-bud formation, the two Yukon sources unexpectedly differed from other northern sources, resembling instead provenances 800-1300 km to the southeast. These two Yukon sources also differed from the other northern sources in other characteristics, but in the direc-

tion of greater cold hardness.

Surveys of enzyme loci provide the most conclusive evidence of the genetic distinctness of northern interior populations (Yeh and Layton 1979; Wheeler and Guries 1982a, 1982b). Yeh and Layton (1979) studied 26 loci in 15-tree samples from nine interior populations. A cluster of samples in and near the unglaciated Yukon differed from samples in north-eastern and southern British Columbia at six loci. At five loci, the western Yukon samples lacked an allele present in the others and at one locus, they possessed an allele lacking elsewhere. Wheeler and Guries (1982a, 1982b) analyzed 42 loci in larger samples (mostly 60 trees) throughout the range of lodgepole pine. In a cluster analysis based on genetic distance, eight populations in the Yukon and extreme northern British Columbia tended to cohere in a group distinct from interior populations farther south. Their strongest evidence for the distinctness of the northern group, however, was the distribution of rare alleles. At 11 loci, alleles present in two or more northern populations were absent or infrequent in the southern interior. Wheeler and Guries (1982a) concluded that northern interior populations originated from a refugium in the unglaciated part of west-central Yukon.

Northern interior populations are contiguous to the coastal populations of southeastern Alaska, but most evidence from growth and morphology indicates that the two groups have been genetically distinct for a long time (Critchfield 1980). In cortex resin composition, southeastern Alaska populations have a high frequency (76–100%) of trees high in  $\beta$ -phellandrene, but frequency in the Yukon is only 0–30% (Forrest 1980, 1981). The difference in frequency of high-limonene trees is nearly as great; the average frequency in Alaska is 6% and in the Yukon is 49%.

Two kinds of data suggest a closer affinity between coastal and northern interior populations. Coastal stands share more rare alleles at enzyme loci with the northern interior group than with other interior populations, but Wheeler and Guries (1982a) placed little biogeographical emphasis on this observation. Coastal and northern interior populations also overlap in leaf resin composition (von Rudloff and Nyland 1979). Trees on Vancouver Island and the Oregon coast had resin high in  $\beta$ -phellandrene and low in most other terpenes (their type A). Type A trees were not reported in Alberta populations (Pauly and von Rudloff 1971), but about a third of the trees in the northern interior were of this type. The authors concluded that the Yukon was a glacial refugium for lodgepole pine and speculated that this refugium may have been a long-term reservoir of genetic diversity (von Rudloff and Nyland 1979).

#### *Introgression from jack pine*

Lodgepole and jack pines overlap in Alberta and the southwest corner of Mackenzie District, N.W.T. (Fig. 1). Natural hybridization has been studied most intensively in Alberta, where it was first described (Moss 1949), but hybrids have also been noted near Nahanni Butte in Mackenzie District (Cody 1963). Stands in the Alberta overlap region range from nearly pure jack pine through hybrid swarms to nearly pure lodgepole pine (Moss 1949; Mirov 1956; Schoenike 1962; Wheeler 1981; Pollack and Dancik 1985).

Outside the overlap region, recent investigations concur with earlier observations that introgression from jack pine has taken place, but there is little agreement concerning the amount or geographic distribution of jack pine influence. In resin studies,  $\beta$ -phellandrene is a reliable indicator of lodgepole pine, but the resins of jack pine have no such diagnostic constituent. The

principal and most characteristic monoterpene in its wood resin (Zavarin *et al.* 1969; Pollack and Dancik 1985) and leaf resin (Pauly and von Rudloff 1971) is  $\alpha$ -pinene, but this monoterpene is also present in lodgepole pine resins. Consequently, even large increases in the  $\alpha$ -pinene fraction of the latter are subject to interpretations other than that of introgression from jack pine.

Introgression at considerable distances from the overlap region was first proposed by Critchfield (1957), mostly on the basis of cone orientation. Lodgepole cones are usually projecting or reflexed, their axes forming angles of 90° or more with the terminal part of the branch. This orientation hardly overlaps with the semierect or incurved cones of jack pine except in the central and northern interior. Stands between Yellowstone and Banff, Alta., had smaller mean cone angles and were significantly more variable than most other lodgepole stands (Critchfield 1957). In addition to trees with typically reflexed cones (angles, 110–120°), they included trees with cone angles of 50–60°, well within the phenotypic range of jack pine. More comprehensive data on the frequency of semierect cones showed a gradient from none in the Yukon to 14% in the southern half of British Columbia, with the highest frequencies in scattered stands in south-central and southeastern parts of the Province (K. Illingworth, personal communication, 1973). Cone angle was also measured by Wheeler (1981). In his sampling of the central and northern interior distribution, one population in southwestern Alberta and a cluster of three populations in central British Columbia had the smallest and most variable cone angles (means, 103–114°; standard errors, 35–46°). In contrast, six populations closer to the overlap region, as well as the isolated Cypress Hills population, had larger and more uniform cone angles (means, 118–130°; standard errors, 13–25°).

Variations in the composition of wood resin are inconsistent and difficult to interpret. Mirov's (1956) finding that some lodgepole pines 60–80 km from the Alberta overlap region were low in  $\beta$ -phellandrene (18–40% of total monoterpenes) was confirmed by Pollack and Dancik (1985). Their large samples from the same areas sampled by Mirov (1956) included 21 and 3% of individuals that resembled jack pine more than lodgepole pine. Among all their samples in Alberta, only the isolated eastern outlier in the Cypress Hills was completely devoid of what they interpreted as jack pine influence.

Extreme variations in a small sample in southern Montana were also interpreted as evidence of jack pine influence (Lotan and Joye 1970). A few trees had  $\alpha$ -pinene,  $\beta$ -pinene, or 3-carene as the major constituent of their wood resin and only 8–23% of  $\beta$ -phellandrene.

Wood resin of northern Rocky Mountain stands was also sampled by Smith (1983), with different results. In a transect from northeastern California to northwestern Montana, he found a trend of decreasing  $\beta$ -phellandrene (from 70 to 57%) and a corresponding increase in  $\beta$ -pinene (from 6 to 22%). The increase in  $\alpha$ -pinene, however, was trivial (from 5 to 7%). His Rocky Mountain samples (62 trees in eastern Idaho and northwestern Montana) included no trees with more than 12%  $\alpha$ -pinene or less than 39%  $\beta$ -phellandrene and provide no support for a hypothesis of extensive introgression.

The results of leaf resin studies in western Canada were initially interpreted by E. von Rudloff and his associates as evidence of widespread introgression, but questions later raised about the data by von Rudloff have not been resolved. Lodgepole pines were first sampled in the Rocky Mountains of Alberta and the Cypress Hills (Pauly and von Rudloff 1971).

TABLE 1. Geographic distribution of jack pine characteristics in lodgepole pine populations

Region	Cone orientation	Resin			Enzyme genes
		Wood	Cortex	Leaf	
Yukon	—		+	+	+
British Columbia					
Northeast	—		+		—
Central	+		+		—
Southeast	+		—		—
Alberta					
Jasper—Hinton—					
Coalspur	—	+	—	+	+
Banff region	+	+	+	+	
Cypress Hills	—	—	—	—	—
Western Montana	+	±	—		+

NOTE: +, evidence; —, no evidence; ±, contradictory evidence of jack pine influence.

The resin of most trees differed from a bulk sample of jack pine resin in about 10 constituents. Camphene, for instance, was 5.8% of the bulk sample but less than 1% in most lodgepole pines. From the Banff area north to the overlap zone, trees intermediate in composition were present at low frequency and two intermediates also resembled jack pine in lacking cone-scale prickles. Two Cypress Hills population samples showed no jack pine influence. Doubts were raised about the interpretation of these data when von Rudloff (1975) reported that some central and eastern jack pines have "intermediate" resin composition. Trees with intermediate resin were also reported at low frequencies in and near the Yukon and in the Alberta overlap region (von Rudloff and Nyland 1979).

The broadest claims for widespread introgression of jack pine genes into lodgepole pine are based on variations in cortex resin composition (Forrest 1980, 1981). As an indicator of jack pine influence, Forrest emphasized an uncommon resin composition which he called type E: "camphene relatively very high;  $\alpha$ -pinene and/or  $\beta$ -pinene high" (Forrest 1980, p. 350). No data on the composition of jack pine cortex resin have been reported, however, and Forrest's basis for comparison was the leaf resin data of von Rudloff and his associates. Camphene is present in the leaf resin of jack pine, as noted earlier, but it is essentially lacking in the wood resin (Zavarin *et al.* 1969; Pollack 1980).

Forrest's type E trees are rare or absent through most of the coastal region and the southern interior. They are common in (i) most stands in northeastern British Columbia, (ii) scattered stands in the Yukon, central British Columbia, and near Banff, Alta., and (iii) stands on the coast of southern Oregon and northern California. Groups (i) and (ii) may have been influenced by jack pine. Group (iii) is far more likely to have originated independently of jack pine, despite Forrest's (1980, p. 357) suggestion that "these populations may be an introgressed relict surviving after southerly migration induced by glaciation."

Other rare types among Forrest's monoterpene patterns may be more reliable indicators of jack pine influence. Types G, H, L, M, and N, all high in  $\alpha$ -pinene, are restricted to northeastern British Columbia, the Banff region, a few stands in central British Columbia, and the overlap zone (Forrest 1980, 1981).

Genetic variations at enzyme loci also provide evidence that jack pine genes are present in lodgepole populations remote from the range of jack pine (Wheeler 1981; Dancik and Yeh 1983). In a comparison of lodgepole and jack pine populations

in Alberta, Dancik and Yeh (1983) found six alleles unique to jack pine, but four of the six had previously been found in Yukon populations of lodgepole (Yeh and Layton 1979). Wheeler (1981) compared lodgepole populations throughout the northern interior with western jack pine, using an index value ( $M$ ) that estimated the proportion of jack pine genes in each population. This index was based on species differences in gene frequencies at 11 loci, but on the average only 6 loci contributed to  $M$  in lodgepole populations outside the overlap region. Populations in three widely separated areas had significant values of  $M$  (5.7–10.2): (i) three of five populations in and near the unglaciated part of the Yukon, (ii) one (Coalspur) in the Rocky Mountain foothills of western Alberta, and (iii) one in the Bitterroot Mountains of western Montana. Areas (i) and (iii) are 700–800 km from the overlap region; area (ii) is about 100 km from the overlap region. In all three instances, evidence of jack pine influence was lacking in populations closer to the present range of jack pine ( $M = 0.0–2.9$ , not significant). Wheeler (1981) interpreted these data as evidence of ancient hybridization complicated by displacement and subsequent migration.

These several conflicting lines of evidence point to the influence of jack pine in northern interior populations far outside the overlap zone, but not in coastal, southern interior, or Sierra Nevada – Cascade populations. Regions for which more than one kind of evidence is available are listed in Table 1. The total number of genes controlling the characteristics tabulated may be no more than 15 or 20 and the lack of agreement between different kinds of data suggests that individual jack pine genes are widely but unevenly dispersed through northern and north-eastern populations of lodgepole pine.

### Lodgepole pine: fossil history

The Tertiary record of lodgepole pine (reviewed in Critchfield 1980) is remarkably sparse, although the species often grows in habitats (bogs, lakeshores) that are over-represented in the fossil record. Convincing reports are restricted to the conifer-rich forests that extended from the Pacific Northwest to western Alaska in the late Tertiary. Lodgepole pine must have been an occasional constituent of these forests; it is represented in the late Miocene Faraday flora near Portland, OR, by a cone (J. A. Wolfe, personal communication, 1971) and in the late Miocene – early Pliocene Skonun flora of the Queen Charlotte Islands by pollen closely resembling that of indigenous lodgepole pine (Martin and Rouse 1966).

At some time in the early Pleistocene or perhaps earlier, lodgepole pine may have extended at least 100 km west and 400 km north of its present limits in the Yukon. Considerable pine pollen is present in deposits in eastern Alaska (Matthews 1970) and northern Yukon (Lichti-Federovich 1974). Both occurrences were originally thought to date to the late Pleistocene, but recent work has established that they are "pre-Pleistocene or at least very early Pleistocene" (J. V. Matthews, Jr., personal communication, 1985).

Near the end of the Pleistocene, lodgepole pine was widespread south of the ice in the western United States. In western Washington, it was intermittently common near the ice in the middle Wisconsin or earlier and was a major element of early postglacial vegetation (e.g., Heusser 1964; Hansen and Easterbrook 1974). Today, it is the only hard pine in the region except for a few stands of ponderosa pine and its identification from fossil pollen is reinforced by the presence of lodgepole needles in late glacial and early postglacial sediments of the

Puget Lowland (Barnosky 1981; Tsukada and Sugita 1982), southwestern British Columbia (Mathewes 1973), and northern Vancouver Island (Hebda 1983).

In the Rocky Mountain region, lodgepole pine was present at two upper-elevation sites by about 11 600 years B.P.: one in the Bitterroot Range in western Montana (Mehring *et al.* 1977) and the other near Yellowstone Lake in northwestern Wyoming (Baker 1976). At the latter site, its identity is verified by needles. The early, synchronous appearance of this species at about the same stage of vegetational change at two widely separated sites suggests that it was widespread in the northern Rocky Mountains at the end of the Pleistocene. By 10 000 years B.P., macrofossils (wood and cones) establish that it was part of a coniferous forest in northwest Montana near the Canadian border (Carrara and Wilcox 1984).

Lodgepole pine must have been subdivided into several isolated populations by the end of the Pleistocene. Within the lowlands of western Washington, this is suggested by marked local variations in cortex resin composition and other characteristics. The refugial status of the species in the thinly sampled interior is more difficult to reconstruct, but differences in morphology and enzyme genes between contemporary populations in (i) southeastern British Columbia and conterminous parts of the United States, (ii) the Rocky Mountains proper, and (iii) the Cypress Hills may derive from isolation in separate refugia (Wheeler and Guries 1982*a*, 1982*b*; Wheeler 1981).

Evidence concerning the origin of Forrest's North Coastal group is conflicting. Although this group occupies most of the glaciated coastal region, it is less variable in cortex resin composition than, for example, stands in the Puget Lowland or on the inner coast of Vancouver Island. One explanation of this unusual uniformity is that it originated from a single refugium. The southernmost outlier, near Queets, WA, is a few kilometres beyond the limits of Wisconsin ice in the western Olympic Peninsula. Pollen sequences from nearby sites (Hoh, Kalaloch, Humptulips) collectively establish that pine (almost certainly lodgepole pine) was present in the region from the early or middle Wisconsin until early postglacial time (Heusser 1964, 1972). This refugium could have provided the base from which the North Coastal region was recolonized.

This interpretation is not supported by the genetic diversity of North Coastal populations at enzyme loci (Wheeler and Guries 1982*a*), nor by the fossil record of lodgepole pine in this region near the end of the Pleistocene. A pollen sample at Glacier Bay, Alaska, dated 10 940 years B.P., included 19% pine pollen, suggesting that lodgepole pine was in the region soon after deglaciation (McKenzie 1970). Pine arrived at another site, near Juneau, about 10 300 years B.P. (Heusser 1960). Possible Alaskan refugia include unglaciated coastline and nunataks near outliers of lodgepole pine between Glacier Bay and Yakutat (Coulter *et al.* 1965; Derksen 1976). Parts of the Queen Charlotte Islands were also ice-free during the last glacial maximum (Warner *et al.* 1982) and abundant lodgepole pine pollen was deposited at one site by 12 200 years B.P. (Mathewes and Clague 1982). Lodgepole pine also grew at the northern end of Vancouver Island before 13 500 years B.P. (Hebda 1983), but it is not known whether it originated in hypothetical refugia on the island or migrated from the mainland. The hypothesis of multiple coastal refugia is supported by these fossil occurrences, but leaves unexplained the unusual homogeneity of North Coastal lodgepole pine in some of its characteristics.

The fossil record also conflicts with evidence from extant

lodgepole pine in the Yukon. The genetic distinctness of northern populations supports the inference that pine was present in the Yukon during the last glacial period. At the same time, paleobotanists appear to have dismissed this possibility because of the absence of pine macrofossils (Hopkins 1979) and the near absence of pine pollen in late-glacial and early postglacial deposits of this region (e.g., Hopkins *et al.* 1981). This negative evidence would be more decisive if the studied sites were near stands of lodgepole pine in unglaciated parts of the Yukon. The closest are two lakes 75–85 km north of the present known limits of the species. Chapman Lake has only traces of pine pollen in late- and post-Pleistocene sediments (Terasmae 1973). A late-glacial pollen assemblage from Hart Lake was briefly described by Vernon and Hughes (1966) as including "very little pine." At Antifreeze Pond, about 120 km west of the nearest lodgepole pines, Rampton (1971) found no identifiable pine pollen in cores covering the last 30 000 years.

Other negative evidence is the recent arrival of pine at sites 100–300 km southeast of the unglaciated region. From pollen data, pine reached a site 30 km west of Whitehorse only 640 years B.P. and L. Cwynar (personal communication, 1983) has concluded that "a pine refugium in southwest or central Yukon seems out of the question." Farther south, at several sites near Atlin Lake, significant quantities of pine pollen are recorded 2000–4200 years B.P., several thousand years after the arrival of spruce (Anderson 1970). It can be argued that pine migrating the relatively short distance from a refugium in the unglaciated part of the Yukon would have spread throughout this region much earlier and would have reached the vicinity of Whitehorse before it arrived in the Atlin Valley.

Another possible source of northern lodgepole pine is the Alaskan coast, via the river valleys that cut through the Coast Mountains (Anderson 1970). The strongest argument against this alternative is the overall distinctness of northern coastal and interior populations.

A third possible source of this far-northern pine is a refugium in northeastern British Columbia or western Alberta, in ice-free areas between the Laurentide and Cordilleran glaciers. This alternative was favored by Anderson (1970). It requires a migration of 1000–2500 km and is in better agreement with the recent arrival of pine in the Atlin region and southern Yukon.

The problem of an ice-free corridor or ice-free areas between the two ice sheets was reviewed by Ritchie (1980). The available geological and fossil data are so limited and contradictory that they can be interpreted as supporting opposite conclusions. Compare, for example, "The latest evidence I am aware of suggests that at the very least there was no corridor between 25 000 B.P. and 10 000 B.P. . . and that the ice barrier may have been in place much longer" (Hoffman 1981, pp. 31–32) and "Alaska and central North America may have been connected, then, by an ice-free corridor during most of the last glacial period . . ." (Hopkins 1979, p. 19). Recent radiocarbon dates and fossil pollen data tend to support the existence of extensive ice-free regions in western Alberta during the late Wisconsin. For a site in the Rocky Mountain foothills southwest of Calgary, Mott and Jackson (1982) reported dates of 18 400 and 18 500 years B.P. just below a pollen assemblage indicating tundra or grassland. At a site near Watino in the Peace River region, dates of 27 400 to >38 000 years B.P. were associated with a pollen assemblage suggesting open vegetation with scattered spruce trees (Westgate *et al.* 1972). Sediments of Lake Wabamun, 40 km west of Edmonton, record vegetation for the past 16 000 years B.P. (Holloway

*et al.* 1981), but Hickman *et al.* (1984) consider that some radiocarbon dates of that study may be in error by more than 3 000 years.

An ice-free corridor or a series of ice-free areas in which scattered pines survived might help to explain the apparent asymmetry of introgressive influences in lodgepole and jack pines. Indications of introgression in western jack pine, reviewed later, are sparse and possibly of recent origin. In this part of Canada, the prevailing winds during pollen shedding are westerly and the occasional long-distance transport of a cloud of lodgepole pollen could account for scattered hybrids and hybrid derivatives within the range of jack pine. Or, as Rudolph and Yeatman (1982) proposed, lodgepole pine was more widely distributed in early postglacial time and its eastern outliers and scattered hybrid populations are relicts of that distribution.

The influence of jack pine on northern and northeastern populations of lodgepole pine is more difficult to explain in the context of postglacial time. This influence has been detected at greater distances from the overlap region and on both sides of the Rocky Mountains. The most probable explanation is that it is the result of genetic contacts long before the last glacial period. Supporting this interpretation is the dispersed and uncorrelated nature of jack pine influence. An alternative explanation, suggested by the rough correspondence between regions of pronounced jack pine influence and the suture between Cordilleran and Laurentide ice, is that introgression occurred in populations between the ice sheets and these populations provided a base for the colonization of the northern interior range of lodgepole pine.

The few sites in the region with pollen data do not provide a critical test of these alternatives, nor has pine pollen at most of these sites been assigned to either pine species. A minimum date for lodgepole pine in the Canadian interior is 9660 years B.P., when pollen deposition is first recorded at a bog near Jasper, Alta. (Kearney and Luckman 1983). A more complete sequence is available for Lake Wabamun (Holloway *et al.* 1981) in the overlap region near a stand that Moss (1949) described as predominantly jack pine but including lodgepole pine and intermediates. Pine and other conifers replaced tundra-like vegetation at this site, but the dates are in question (Hickman *et al.* 1984). Pine arrived at two sites northeast of Edmonton (Lofty Lake, Alpen Siding Lake) between 9500 and 7500 years B.P. (Lichti-Federovich 1970, 1972), at Eaglenest Lake in the Birch Mountains of northeastern Alberta about 7300 years B.P. (Vance 1984), and at John Klondike Bog in the southwest corner of the Mackenzie District, N.W.T., about 6700 years B.P. (Matthews 1980). At all of these sites the pine could have been jack or lodgepole or both. The Alberta sites are within the distributional limits of lodgepole pine and the trees at Eaglenest Lake are putative lodgepole  $\times$  jack hybrids (Vance 1984). Neither pine now grows at the Mackenzie site (Matthews 1980), but both species are present in the region, near the margins of their respective distributions.

### Jack pine: variation

#### Great Lakes region

Multivariate analyses of the characteristics of jack pine in natural stands (Schoenike 1976) and provenance tests (Hyun 1979) have established that much of the geographically ordered variation in the species is in the Great Lakes region. Hyun's (1979) cluster analyses, based on 10-year-old trees grown in

Minnesota from seed of 90 widely scattered origins, produced only one geographically coherent cluster. It included all samples from the Lake States: Minnesota, Wisconsin, and Michigan. Schoenike's (1976) analysis, unlike Hyun's (1979), included samples in northeastern Minnesota. These northern samples clustered with samples in western Ontario and were excluded from Schoenike's (1976) two Lake States clusters. One cluster comprised lower Michigan and a few southern outliers and the other included the other Lake States samples: central and eastern Minnesota, most of Wisconsin, and upper Michigan.

Underlying the results of both analyses is a pronounced north-south gradient in cone characteristics in the Great Lakes region. The existence of this gradient was first mentioned by Eyre and Le Barron (1944). They noted that most trees in the northern Lake States have serotinous cones, but that cones are mostly not serotinous in the south and near the prairie border in Minnesota. Later observations in natural stands (Schoenike 1962) and a provenance test (Schoenike *et al.* 1959) confirmed the existence of the gradient, showed that corresponding gradients exist in cone shape and orientation, and established that these variations have a genetic basis.

Reinterpreting these data, Zavarin *et al.* (1969) observed that in Minnesota, the gradient in cone characters is not a gradual one, but is largely concentrated in a zone extending across northern Minnesota (Fig. 3). This zone coincides with cluster boundaries of Hyun (1979) and Schoenike (1976); stands north of a line from Cloquet (near the western end of Lake Superior) to Red Lakes (at the western limit of jack pine) have predominantly serotinous, curved cones, attached to the branch at small or negative angles (the latter owing to extreme cone curvature). Stands south of this line have mostly open cones with straight axes, attached to the branch at relatively large angles. Zavarin *et al.* (1969) observed that this cline does not coincide with any abrupt environmental change and suggested that the two populations might have migrated into Minnesota from different glacial refugia. The cline is relatively steep, with a maximum width of about 100 km, and Red Lakes may be near its northern edge (data of Rudolph and Libby 1956).

East of Minnesota this multicharacter cline gradually disappears, as the north-south gradients in different cone characteristics diverge from each other (Critchfield 1984; Figs. 3A-3D). The change from mostly serotinous to mostly open cones occurs in a discrete zone across northern Wisconsin and the Lower Peninsula of Michigan, but the gradients in cone curvature and orientation tend to flatten out, separate, and shift to the north.

A second population discontinuity in the Great Lakes region has been described and interpreted by Wright (1972). He proposed that distinct races of jack pine (among other conifers) have evolved on the Upper and Lower peninsulas of Michigan, with gene exchange between the races restricted or prevented by the 7-km gap across the Straits of Mackinac (Fig. 3). The evidence is from a large-scale test of jack pine seed sources throughout the Lake States, planted at many sites through the region. In some plantations, height growth at ages 5 (Arend *et al.* 1961), 10 (King 1966), and 20 years (Jeffers and Jensen 1980) showed the same pattern: seed sources from the Lower Peninsula consistently grew faster than Upper Peninsula sources. The Upper Peninsula has a generally colder climate and shorter growing season and Wright (1972) concluded that natural selection and geographic isolation are responsible for the postglacial evolution of these races. Genetic differentiation

within each race, Wright (1972) suggested, is minimized by continuous gene exchange.

This racial distinction is supported and extended by data from Schoenike's (1962) study of jack pine in natural stands and by his later analysis (Schoenike 1976), which placed the two groups in different clusters. Schoenike's two Upper Peninsula and four Lower Peninsula samples differ most in mean values of three leaf and cone characters (two-thirds or more of sample means compared between regions are significantly different at  $p = 0.05$ ):

	Lower Peninsula	Upper Peninsula
Needles		
Width (mm)	1.44–1.47	1.56
Hypodermal layers	1.62–1.68	2.03, 2.04
Cones		
Knobiness (classes)	1.8–2.4	2.8

The two sets of samples also show less marked differences in cone orientation, curvature, and weight and in the proportion of trees having cones with prickles. These differences in leaves and cones are less likely than differences in growth to have evolved during postglacial time under the influence of natural selection. An alternative hypothesis to that of Wright (1972) is that the divergence of Upper and Lower Peninsula populations is due in part to differences in origin and migratory history.

A minor break extending northwest from Lake Nipigon in western Ontario was observed by Skeates (1979) in an Ontario-wide provenance test (Fig. 3). Four provenances east of this break averaged 5.8–6.2 m tall at 20 years; four provenances to the west were 6.4–6.9 m tall. Schoenike's (1962) samples from the two regions differ in mean number of branches per whorl (a sample from Marathon, Ont., unlike any other in central Canada, is omitted from this comparison): 2.5–3.1 in the west and 1.7–2.3 in the east. The two groups also show minor differences in cone orientation and curvature and in length of cone apophysis.

Two needle characteristics also change in the vicinity of Lake Nipigon, although not quite along Skeates' (1979) boundary. Schoenike's (1962) four samples west of the lake had fewer stomata (63–66/mm<sup>2</sup> on adaxial face) and more widely spaced teeth (6.3–6.8/mm) than three samples east of the lake (78–79 stomata/mm<sup>2</sup>, 7.1–7.4 teeth/mm).

Skeates (1979) speculated that the ancestors of the western group migrated south and west of the Great Lakes into western Ontario, while the slower-growing eastern group passed through a filter of harsh environments in its migration north of the Great Lakes. Lake Nipigon itself and a scarcity of jack pine sites in the region are partial barriers that maintain this discontinuity, according to Skeates (1979).

Several other patterns are evident in or reinforced by Schoenike's (1962) descriptive statistics on natural populations of jack pine.

(1) The importance of Lake Huron as a major boundary is obvious in both cluster analyses (Hyun 1979; Schoenike 1976). The most pronounced differences in mean values between Schoenike's (1962) Lower Peninsula samples and three samples in southwestern Ontario (Georgian Bay and vicinity) are as follows:

	Lower Peninsula	Southwest Ontario
Crown width (m)	6.7–7.6	5.5–5.8
Bark thickness (mm)	10.4–14.2	7.9–9.1
Leaves		
Width (mm)	1.44–1.47	1.51–1.69
Hypodermal layers	1.62–1.68	2.27–2.48
Cones		
Curvature (%)	10–16	30–36
Angle (°)	47–60	5–23
Knobiness (classes)	1.8–2.4	2.6–3.3

The magnitude of these differences between populations growing in much the same range of environments suggests that they have been isolated from each other longer than postglacial time. A corollary to this interpretation is that lower Michigan could not have been colonized by jack pine from Ontario, either across Lake Huron or around its southern end.

(2) An important boundary is evident is Schoenike's (1962) data between the Upper Peninsula and contiguous populations extending from central Wisconsin to central Minnesota. Schoenike's (1976) analysis excluded small clusters (two or three samples) and this break was not identified in either his or Hyun's (1979) analysis. Upper Peninsula samples differ from five Wisconsin–Minnesota samples most conspicuously in mean values of these characteristics:

	Upper Peninsula	Wisconsin–Minnesota
Bark thickness (mm)	9.7, 11.7	13.2–16.0
Branches per whorl	1.8, 2.0	2.6–3.2
Needles		
Length (mm)	31, 34	40–45
Stomata per mm <sup>2</sup> (abaxial face)	67, 72	52–60
Hypodermal layers	2.03, 2.04	2.40–2.72
Open-cone trees (%)	0, 15	65–90

Although the Upper Peninsula is separated from lower Michigan and Ontario by narrow water gaps, Upper Peninsula jack pine resembles populations in both of those regions more closely than it does the contiguous Wisconsin–Minnesota race. In most characteristics that differentiate it from the Lower Michigan population, it is intermediate between the latter and Ontario jack pine and may be a mixture of the two. On the basis of phenotypic similarity, these two regions are more probable bases for jack pine's colonization of the Upper Peninsula than is Wisconsin.

(3) Schoenike's (1962) sample from Marathon, Ont., on the northeast shore of Lake Superior, is the most distinctive in central Canada. This anomalous stand differs from others in northern Ontario in many characteristics and in its low cone specific gravity and high frequency of open-cone trees it resembles stands 400 km or more to the south and southwest. The possibility that this stand was planted is not supported by its age range (32–94 years), but sampling intensity in the region is too low to establish whether it represents a small enclave or an extensive north-shore population.

To summarize, several regional populations of jack pine can be identified in the Lake States: (i) Lower Peninsula of Michigan, (ii) Upper Peninsula, and (iii) central Wisconsin –

central Minnesota. A cline across northern Minnesota separates population *iii* from populations in northernmost Minnesota and central Canada. In Canada, Lake Nipigon marks a poorly defined line of separation between western and central Ontario populations and a stand near Lake Superior (Marathon) differs from all other sampled populations in central Canada.

#### Western Canada

Outside the Great Lakes region, jack pine is fairly uniform through most of its range, from eastern Alberta to Québec (Schoenike 1976). Variability increases in the east (Maritime Provinces, New England), where the distribution is fragmented, and in the far west, where introgression from lodgepole pine may be a factor.

The degree and extent of introgression in jack pine are hard to assess, partly because most investigations in the western interior of Canada have emphasized lodgepole pine. From the available data, the influence of lodgepole pine appears to be patchy and sporadic. There are convincing reports of hybrids, or jack pines with some lodgepole characteristics, up to 400 km from the nearest known lodgepole pine, but interspersed are stands of apparently pure jack pine. Moss (1949) observed hybrids or hybrid derivatives in some but not all jack pine stands he studied in eastern Alberta. Cody (1963) reported hybrids about 50 km north and east of the known limits of lodgepole pine in the Mackenzie District. G. W. Argus found a few putative hybrids in jack pine stands south of Lake Athabaska, together with many trees having some lodgepole characters (H. M. Raup, personal communication, 1981). In north-eastern Alberta, intermediates between lodgepole and jack pines were reported in the Christina Highlands (Achuff and LaRoi 1977) and at Eaglenest Lake in the Birch Mountains (Vance 1984) and several of Schoenike's (1962) jack pine samples tend to resemble lodgepole pine in some respects, to show increased variability, or both: Fort Simpson, Mackenzie District, N.W.T.; McMurray and Conklin, Alta.; Cree Lake and Glaslyn, Sask. (Fig. 2).

Other western jack pine stands sampled by Schoenike (1962) show little or no lodgepole influence in either character means or variability. Examples in northern and eastern Alberta include Fort Fitzgerald, Fort Vermilion, and Bruderheim (Fig. 2). The Bruderheim stand, only 80 km east of the overlap zone, was also studied by Moss (1949), who found no hybrids there, and Mirov (1956), who analyzed the turpentine (low boiling point) fraction of the wood resin. The principal constituent,  $\beta$ -phellandrene, is lacking or present in trace amounts in jack pine wood resin. The Bruderheim stand was pure jack pine in turpentine composition, as well as in morphology. Another Alberta stand lacking lodgepole influence is at Cold Lake, near the Saskatchewan border (Pollack 1980). A large (64-tree) sample was pure jack pine in both turpentine composition and morphology. A smaller sample from Fort Vermilion also had only trace amounts of  $\beta$ -phellandrene in its wood resin.

Genetic variation at enzyme loci provides evidence of limited gene flow from lodgepole pine (Wheeler 1981). One of three jack pine populations surveyed in eastern Alberta showed a low but significant level of lodgepole influence. This population, near McMurray, Alta., is 90 km from the nearest known outliers of lodgepole pine in the Christina Highlands and Birch Mountains, all of them discovered in the past two decades (Critchfield 1980; Vance 1984).

#### Jack pine: fossil history

Because the pollen of jack pine is not usually separated from

that of associated hard pines, macrofossils provide a more reliable basis for reconstructing its history. Abundant cones from late-Tertiary deposits in the Canadian Arctic were "very similar to but not identical with *Pinus banksiana*" (Kuc and Hills 1971, p. 1093), but these collections have not been described. Apart from this preliminary report, the macrofossil record of jack pine may extend back no farther than the last interglacial interval of the Pleistocene. Jack pine wood was found at two northern Minnesota sites in deposits that are definitely or probably interglacial; one deposit was later dated >36 000 years B.P. (Heinselman 1973). At another northern Minnesota site, jack pine wood and two closed cones "similar to *Pinus banksiana*" were associated with cones of black spruce (*Picea mariana* (Mill.) B.S.P.) and wood of spruce, fir (*Abies*), larch (*Larix*), alder (*Alnus*), and poplar (*Populus*) in deposits dated >38 000 years B.P. (Heinselman and Roe 1963).

During a prolonged, warm interstadial in the mid-Wisconsin, jack pine was the principal tree at a cluster of sites in the Ozark Mountains of Missouri. Its identification is based on detached cone scales, pollen in the size range of jack pine pollen (King 1973), and a single cone in a deposit dated 48 900 years B.P. (F. B. King 1981). Forests dominated by spruce grew at these sites after 25 000 to 20 000 years B.P., but pine may have been present as late as 17 000 to 18 000 years B.P. (King 1973). Farther east in the Ozark region, jack pine may have persisted through the late Pleistocene. Pollen of spruce and jack or red pine was abundant at a site in southeastern Missouri until 12 500 to 10 000 years B.P. (Smith 1984).

East of the Mississippi, a pine identified as jack pine was common at several sites by 23 000 to 17 000 years B.P.: eastern Tennessee (Delcourt 1979), northern Georgia (Watts 1970), and South Carolina (Watts 1980). The first identification of jack pine in this region was made by Watts (1970), who eliminated from consideration red pine and nearly all of the southeastern hard pines on the basis of pollen size and needle number, size (width, thickness), and structure. Watts (1970) overlooked or omitted sand pine, but this species is not a promising alternative to jack pine: its needles are smaller (Harlow 1947; Lanyon 1966) and its pollen is larger (Whitehead 1964). Jack pine disappeared from these southeastern sites between 16 400 and 13 000 years B.P., at the end of the full-glacial period. Shortly thereafter (12 800 to 11 300 years B.P.), a pine that Watts (1979) identified as jack pine arrived at three sites in central and southeastern Pennsylvania and grew there until 11 000 to 9 700 years B.P. This identification, based on needle fragments, is probable but not certain; Virginia pine cannot be eliminated in the absence of pollen-size measurements. The needles of jack and Virginia pines have no reliable differences in structure or stoutness (Harlow 1947; Lanyon 1966), but Virginia pine has larger pollen grains than jack pine (diameters, 45.6 and 37.0  $\mu\text{m}$ ; Whitehead 1964). The history of Virginia pine is unknown, but the species now reaches its northern limits in north-central Pennsylvania.

No pine macrofossils assignable to the late Wisconsin have been recovered in the region west of the Appalachians and north of Tennessee. They appear in this region about 10 000 to 11 000 years B.P., at the start of the postglacial period. All pine macrofossils of earliest postglacial time have been identified as jack pine and it is now widely accepted that jack pine is the species that dominated the early postglacial pine forests of the central and southern parts of the Great Lakes region. At Van Nostrand Lake, near Toronto, Ont., jack pine needles were recovered from sediments dated 9 700 to 10 500 years B.P.

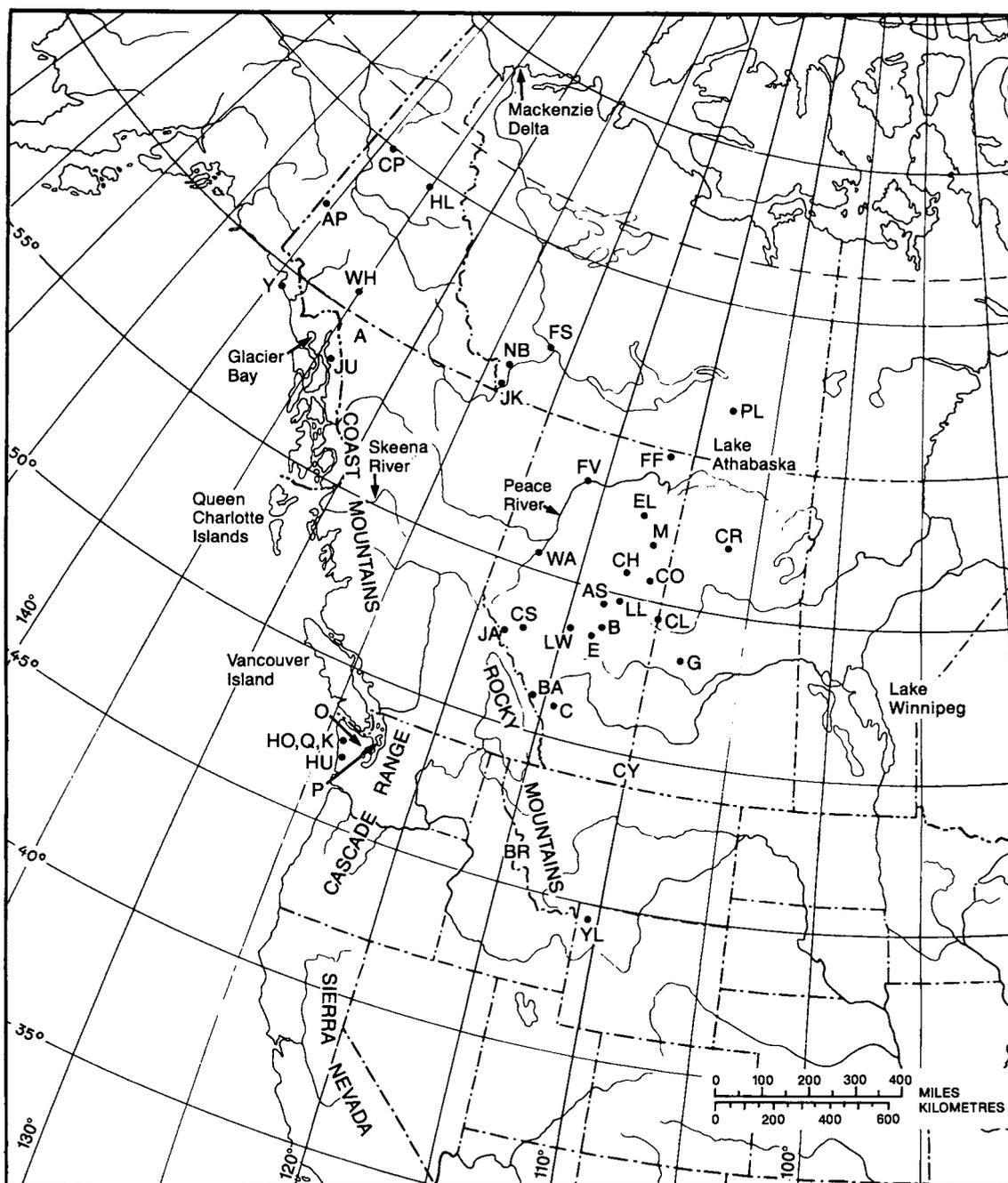


FIG. 2. Location map of western North America. A, Atlin Lake, Atlin Valley; AP, Antifreeze Pond; AS, Aspen Siding Lake; B, Bruderheim; BA, Banff; BR, Bitterroot Range; C, Calgary; CH, Christina Highlands; CL, Cold Lake; CO, Conklin; CP, Chapman Lake; CR, Cree Lake; CS, Coalspur; CY, Cypress Hills; E, Edmonton; EL, Eaglenest Lake; FF, Fort Fitzgerald; FS, Fort Simpson; FV, Fort Vermilion; G, Glaslyn; HL, Hart Lake; HO, Hoh; HU, Humptulips; JA, Jasper; JK, John Klondike Bog; JU, Juneau; K, Kalaloch; LL, Lofty Lake; LW, Lake Wabamun; M, McMurray; NB, Nahanni Butte; O, Olympic Peninsula; P, Puget Sound, Puget Lowland; PL, Porter Lake; Q, Queets; WA, Watino; WH, Whitehorse; Y, Yakutat; YL, Yellowstone Lake.

(McAndrews 1970; J. H. McAndrews, personal communication, 1977; Buckley and Valdes-Pages 1981). On the Upper Peninsula of Michigan, needles were deposited in Canyon Lake as early as 9500 years B.P. (Davis 1978, 1981). At Wolf Creek, in central Minnesota, rare needles of jack pine were present to the base of the pine pollen zone in sediment variously dated 10 200 to 10 500 years B.P. (Birks 1976; Amundson and Wright 1979). Near Lake Itasca in northwestern Minnesota, four jack pine cones were found by C. T. Shay at Nicollet Creek Bog, but the three older cones are of uncertain age and stratigraphic position. They were first assigned to the pine pollen zone that initiates the postglacial period (McAndrews

1966), but later to the prairie-oak savanna zone that succeeds the pine zone in this area (Shay 1971). The radiocarbon dates of the pine zone at Nicollet Creek are 9 500 to 7 550 years B.P. (Shay 1971), but the same zone at nearby Bog D is dated 11 000 to about 8 500 years B.P. (McAndrews 1966). The Nicollet Creek cones are the only cones of jack pine reported in early postglacial sediments, but because of these discrepancies in radiocarbon dates and an incomplete record at this site, they cannot be closely dated.

Quaternary macrofossils of red pine are fewer, more recent, and more restricted in distribution than those of jack pine. None are recorded for Pleistocene time. The oldest are seeds depos-

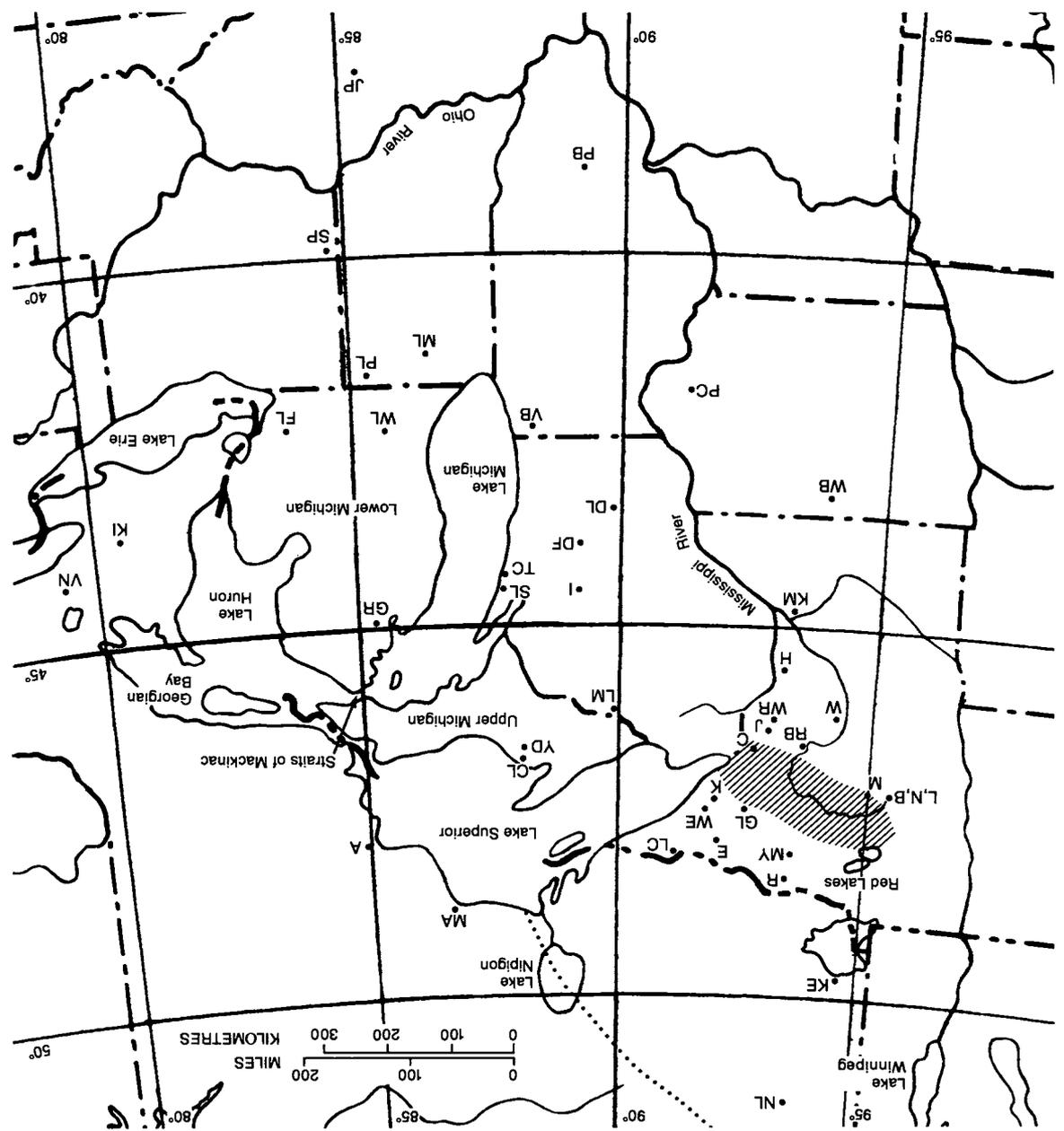


FIG. 3. Location map of Great Lakes region. The cline across northern Minnesota is hatched (▨) and the dotted line through Lake Nipigon is the break between Skates' (1979) central and western Ontario populations. A, Alfies and Antioine lakes; B, Bog D; C, Cloquet; CL, Canyon Lake; DF, Disterhaft Farm Bog; DL, Devils Lake; E, Ely; FL, Frains Lake; GL, Glatich Lake; GR, Green Lake; H, Horseshoe Lake; I, Iola Lake; JM, Jackson Pond; K, Kylan Lake; KE, Kenora; KI, Kitchener; KM, Kitchner Marsh; L, Lake Itasca; LC, Lake of the Clouds; LM, Lake Mary; M, Martin Pond; MA, Marathon; ML, Myers Lake; MY, Myrtle Lake; N, Nicolle Creek Bog; NL, Nungesser Lake; PB, Pittsburg Basin; PC, Pioneer Creek; PL, Pretty Lake; R, Ray; RB, Rossburg Bog; SL, Seidel Lake; SP, Sunbeam Prairie Bog; TC, Two Creeks; VB, Volo Bog; VN, Van Nostrand Lake; W, Wolf Creek; WB, Woden Bog; WE, Weber Lake; WL, Wintergreen Lake; WR, Willow Run Pond; YD, Yellow Dog Pond.

1000-1900 years. With a few exceptions, the pollen record corroborates the limited macrofossil record that pine trees were either absent or present in small numbers in the late-glacial forests of the Midwest. This unexpected situation was first noticed by Wright (1964), more fully documented a few years later (Wright 1968), and periodically updated (Wright 1971, 1981). The pollen record has also established that diploxylon pine (jack or red pine) appeared in large numbers throughout much of this region between 11 000 and 10 000 years B.P., replacing spruce as the dominant conifer in forests south of the receding glacial margin. Both spruces now present in the Great Lakes region, were found in sediments probably deposited within the past

8900 years B.P. in a bog in Kitchener, southern Ontario (Anderson 1982). The next oldest occurrences are not far apart: a single red pine needle in sediments dated 8500 years B.P. at Lake Mary, WI, near the Michigan border (Webb 1974), and needle fragments and a few seeds scattered through sediments dating back to about 8200 years B.P. at Jacobson Lake in eastern Minnesota (Wright and Watts 1969). Other red pine fossils are more recent. At Canyon Lake, upper Michigan, red pine needles are present only in sediment younger than 3200 years B.P. (Davis 1981). At two sites in the Lake Itasca region, a cone (Shay 1971) and needle fragments (McAndrews 1966)

white spruce (*Picea glauca* (Moench) Voss) and black spruce, were present in the late-glacial forests replaced by pine. The decline of spruce and the often synchronous expansion of pine regionally define the end of the Pleistocene and the beginning of the postglacial period (Wright 1964).

H. E. Wright has consistently favored the view that pines were absent from the late-Pleistocene boreal forests of the Midwest, and since 1968 has argued that all three pines of the Great Lakes region migrated there from the eastern United States at the end of the Pleistocene. Both parts of this hypothesis have been widely accepted. Maps assembled by Davis (1976, 1981) show both eastern white pine and diploxylon pine (based on jack or red pine pollen and jack pine macrofossils) migrating west from the Appalachians into the Great Lakes region at the end of the Pleistocene. The most striking feature of the 1981 map is the apparently simultaneous appearance of diploxylon pine from southern Ontario to Minnesota within a 1000-year period, with little indication of an east-west progression in date of arrival.

The alternative to a massive and extremely rapid immigration of pine into the Midwest is that pine was never eliminated from the late-glacial vegetation of the region. Wright (1968, p. 949) spelled out this rejected alternative: "... pine ... occurred in stands so small that its pollen did not show up in the pollen rain, but large enough to provide local seed sources when the opportunity came for expansion." Summarized below are (i) problems with the migration hypothesis and (ii) evidence supporting the alternative view that the sudden abundance of diploxylon pine pollen and jack pine macrofossils at the start of the postglacial period reflects a population explosion rather than immigration.

#### Migration routes

Wright (1968) first proposed and later discarded the area north of the Great Lakes as a migration route for pine from the east into northern Minnesota. Glacial ice extended as far south as the northeast shore of Lake Superior as recently as 9000 to 9500 years B.P., according to geological and pollen evidence (Saarnisto 1974; Maher 1977; Landmesser *et al.* 1982; Clayton 1983), long after pine arrived in northern Minnesota and western Ontario. This part of the Lake Superior shoreline, centered around Marathon, Ont., was the last part of the Great Lakes region to be deglaciated. Perhaps coincidentally, Marathon is also the location of a strikingly distinct jack pine population, as noted earlier. The minimum time of ice retreat from the Marathon area is 9000 years B.P. (Saarnisto 1974).

The pollen record also provides little support for the migration of pine south of the Great Lakes into the Midwest. Critical recent data, including estimates of pollen influx, are mostly lacking for Ohio, but in older pollen diagrams spruce is usually replaced by hardwoods rather than pine (Kapp and Gooding 1964; Ogden 1966). Shane (1980) referred to "the sequential migrations of red/jack and white pines that swept through Ohio between about 10,400 and 10,000 BP"; but, in her transect of generalized pollen diagrams, pine appeared earlier in western than in northern or northeastern Ohio.

The ineligibility of migration routes north and south of the Great Lakes led both Wright (1971) and Davis (1981) to favor a central route for the westward migration of the pines. The axis of hard pine migration mapped by Davis (1981) extends from southern Ontario across lower Michigan and Lake Michigan into Wisconsin. Wright (1971) also proposed a migration route north of Lake Erie. This central route presents two important problems.

(1) Allowing for the imprecision of radiocarbon dating, the sequence of hard pine appearance is the reverse of that predicted. Its arrival in southern Michigan and Indiana apparently preceded its arrival in Ontario. Most dates for the appearance of jack pine in southwestern Ontario are 10 600 years B.P. or later (McAndrews 1970; Karrow *et al.* 1975; Anderson 1982). By this time, hard pine may already have replaced spruce farther west. At two sites in southern Michigan (Frains Lake, Kerfoot 1974; Wintergreen Lake, Manny *et al.* 1978) and one in northeastern Indiana (Pretty Lake, Williams 1974), both pollen percentages and influx data support pine arrival dates of 10 800 to 10 600 years B.P.

The arrival of hard pine in the region west of Lake Michigan may also have preceded its arrival in and near lower Michigan. Pollen diagrams for Disterhaft Farm Bog (West 1961; Webb and Bryson 1972) and Devils Lake (Maher 1982) show that hard pine abruptly replaced spruce 11 000 years B.P. at these sites in south-central Wisconsin. Both hard pine and white pine reached the Volo Bog area in northeastern Illinois about 10 900 years B.P. (J. E. King 1981). At Devils Lake and Volo Bog the succession from spruce to pine is documented by pollen influx as well as percentage data.

(2) Differences among Ontario, lower Michigan, and Wisconsin-Minnesota populations appear to be too great to have evolved in the past 10 000 years. Ontario and lower Michigan populations were compared earlier. The latter differ from Wisconsin-Minnesota populations primarily in vegetative characteristics (Schoenike 1962; mean values):

	Lower Michigan	Wisconsin-Minnesota
Branches per whorl	1.5-1.7	2.6-3.2
Leaves		
Length (mm)	33-35	41-45
Width (mm)	1.44-1.47	1.61-1.68
Stomata per mm <sup>2</sup> (abaxial face)	52-60	73-77
Hypodermal layers	1.62-1.68	2.40-2.72

#### Late-glacial records of pine in the Midwest

Pine contributed no more than 2-10% to the pollen rain of the central United States during late-glacial time, with a few exceptions (Wright 1968). The exceptions are mostly concentrated in and south of lower Michigan. At two sites in central lower Michigan, updated pine peaks of about 45 and 55%, respectively, preceded the late-glacial spruce zone (Gilliam *et al.* 1967; Kapp 1977). These early pine peaks were attributed by the authors to long-distance wind transport of pine pollen. A similar pine peak of about 50% at Green Lake, in the northern part of the Lower Peninsula, has an estimated date of more than 13 000 years B.P. (Lawrenz 1975) and must have been deposited soon after the site was deglaciated. (The partial pollen diagram for this site published in Webb *et al.* 1983 (Fig. 10.2) is in error: the vertical scale is based on uncorrected radiocarbon dates and the final spruce decline is shown at about 12 000 years B.P., at least 1 200 years too early.) In western Ohio, a pine peak of 35% preceded the spruce zone in an undated core at Sunbeam Prairie Bog (Kapp and Gooding 1964). The date of this peak, estimated from a shorter radiocarbon-dated core, was more than 11 700 years B.P. At Jackson Pond, a site in central Kentucky, pine pollen was 30-70% of total tree pollen between the glacial maximum and the start of the Holocene, with spruce codominant (Wilkins

1984).

High relative frequencies of pine pollen during late-glacial time were also found in an undated core from Myers Lake, IN (Frey 1959). The spruce zone is preceded by three sharply defined peaks of 60–65% pine pollen. Frey (1959) reviewed earlier pollen diagrams for northern Indiana, some of them also showing late-glacial pine peaks, and concluded that “a large representation of *Pinus* in late-glacial time apparently was not regional for northern Indiana, but was controlled more by local conditions” (p. 138). This conclusion is illustrated by the 14 000 year record at Pretty Lake, 120 km northeast of Myers Lake. The representation of pine pollen at this site, expressed as either relative frequency or pollen influx, was trivial before 10 800 years B.P. (Williams 1974).

Farther west, pine may have been present in the Pittsburg Basin of south-central Illinois as late as about 14 000 years B.P. (Grüger 1972). In Iowa, most late-glacial pollen assemblages include very little pine (Baker *et al.* 1980), but peaks of hard pine pollen (30 and 37%) are recorded about 10 700 years B.P. and before 10 800 years B.P. at Woden Bog (Durkee 1971) and Pioneer Creek (Szabo 1980).

Pollen influx data are lacking at the above sites except Pretty Lake and it can be argued that if influx were sufficiently low, even small numbers of pine pollen grains transported for long distances could account for these high pine percentages. This argument does not apply to a late-glacial episode of relatively high pine pollen deposition at Wolf Creek in central Minnesota (Birks 1976). At a single level dated 13 500 years B.P., pine influx (mostly diploxylon pollen) reached 500 grains/cm<sup>2</sup> per year. This may be an accident of sampling or radiocarbon dating, but throughout the rest of the long late-glacial record pine influx values were mostly in the range of 30–100 grains/cm<sup>2</sup> per year. By comparison, modern pine influx in the beech–maple region of southern Michigan averages about 400 grains/cm<sup>2</sup> per year (Davis *et al.* 1973). Commercial pine forests (natural and planted) cover only 0.2–1.4% of the land area near the lakes studied by Davis and her co-workers (Ostrom 1967), but the lakes are all within 120 km of extensive pine forests in central lower Michigan. The late-glacial pine peak at Wolf Creek is too small to establish that pines were growing in the vicinity, but it is too high to account for by wind transport 1000 km or more from pine stands in the Rocky Mountains or the Southeast, except perhaps under rare meteorological conditions.

A third kind of evidence that pines may have been in the Midwest before 11 000 years B.P. is the presence of a fossil pine cone beetle (*Conophthorus*) in the well-known Two Creeks forest bed, on the Wisconsin shoreline of Lake Michigan (Morgan and Morgan 1979). Several radiocarbon dates for Two Creeks are all near 11 850 years B.P. *Conophthorus* is restricted to pines and most species are cone predators. Morgan and Morgan (1979) were certain of the genus and tentatively identified the species as *C. coniperda*, which breeds exclusively in cones of eastern white pine. Other species of *Conophthorus* in the Great Lakes region occur in the cones of jack and red pines and the twigs of jack pine (Hedlin *et al.* 1980). There is no other evidence of pines in the late-glacial vegetation west of Lake Michigan; pine pollen is rare in late-glacial sediments at Seidel Lake (West 1961), a few kilometres north of Two Creeks, and at other sites in eastern Wisconsin (Schweger 1969). Pine is not recorded in the region until more than 800 years later, when it appeared at sites south and west of Two Creeks (Volo Bog, Disterhaft Farm Bog, and Devils Lake). Possibly, this fossil insect fragment was transported

to Two Creeks by wind or water from pine stands in lower Michigan or elsewhere in the southern Great Lakes region.

These limited data, together with the variation pattern of jack pine in this region and the absence of a plausible migration route from the east, support the tentative conclusion that small numbers of jack pine trees persisted in the Midwestern boreal forest through full- and late-glacial time. What little is known of the full-glacial vegetation of the region (e.g., Wright 1981) provides few clues to the whereabouts of these small pine populations 18 000 years ago. The distinctness of contemporary populations in lower Michigan and Wisconsin–Minnesota suggests that at least two populations must have survived south of the limits of late-Wisconsin glaciation; one later colonized lower Michigan and the other eventually occupied most of Wisconsin and Minnesota as far north as the Cloquet – Red Lakes line. From the late-glacial pollen record, one refugial area may have been in the central Ohio River Valley (southwestern Ohio, central Kentucky). A second possible refugium, suggested by the occurrence of isolated southern outliers of jack and red pines in northern Illinois (Little 1971), and the early arrival of pine in northeastern Illinois and southeastern Wisconsin, is the unglaciated Driftless Area to the west.

#### *Mechanism of jack pine expansion*

The climatic warming that ended the Pleistocene is reflected in a decline in spruce pollen and a simultaneous increase in hard pine pollen through a broad band extending across the Great Lakes region from southern Ontario to northwestern Minnesota (Itasca region). At most sites, the succession from spruce to pine took place in about 100–600 years (Wright 1968), but at some sites it lasted longer and at others it may have occurred in much less than 100 years. These extremes are illustrated by two lakes in eastern Minnesota. At Jacobson Lake, pine gradually replaced spruce between 10 400 and 9 000 years B.P. (Wright 1968; Wright and Watts 1969). At Horseshoe Lake, in contrast, pine replaced spruce within a single sampling interval of about 5 cm (Cushing 1967). In this interval, spruce pollen declined from 38 to 5% and pine increased from 5 to 55%. Cushing's (1967) diagram is undated, but Wright (1968) estimated that this 5 cm of sediment represented about 140 years. This period places an upper limit on the change at Horseshoe Lake. The lower limit may be much shorter, as Bryson *et al.* (1970, p. 71) pointed out: “if drought-abetted fire were a major immediate agent of vegetational change, such declines might be even faster—one year, for example.”

Other sites scattered through the region also show a major shift in percentages of spruce and pine pollen within a single sampling interval (5–20 cm):

	Spruce decrease	Pine increase
Minnesota		
Nicollet Creek Bog (Shay 1971, Fig. 36)	43–10	18–54
Bog D (McAndrews 1966)	35–10	5–45
Wisconsin		
Iola Bog (Schweger 1969)	43–10	20–72
Disterhaft Farm Bog (West 1961)	39–13	30–67
Lower Michigan		
Frains Lake (Kerfoot 1974)	45–25	2–60
Indiana		
Myers Lake (Frey 1959)	37–7	10–68

The disappearance of the spruce forest was interpreted by Wright (1968) as a direct response to climatic warming. According to this interpretation, spruce ceased to regenerate, and the spruce forest survived only as long as the life-span of its younger age-classes. Meanwhile, the forest eroded away as openings were created by windthrow and localized fires. These openings were occupied by jack pine and other forest trees able to regenerate in the warmer postglacial climate. In Wright's (1968) view, the arrival of jack pine in the region at the time of the spruce decline was fortuitous and fire played only a minor role in opening up the decadent spruce forest.

An alternative interpretation is that the two extraordinary events marking the beginning of postglacial time, the disappearance of spruce and its replacement by jack pine, were not independent, but were causally linked by large-scale forest fires. Conflagrations would have a strong selective effect in the ecological sense, selecting against the fire-prone spruce forest and selecting for fire-adapted jack pine if it were already present in small numbers in the late-glacial boreal forest. An intermediary role of fire was tentatively advanced as an explanation for the abrupt change from spruce to pine at Iola Bog, WI (Schweger 1969). Beyond the range of jack pine, Wells (1970, p. 1581) proposed that regional forest fires, triggered by the warming trend near the end of the Pleistocene, were responsible for the "catastrophic elimination of the highly combustible and ill-adapted spruce forests" of the northern Great Plains.

Of the two spruces represented in the late-glacial forest of the Midwest, white spruce is restricted to upland sites and black spruce is characteristic of but not restricted to wetter sites (Wright 1964). They differ greatly in their response to fire and variations in their frequency in late-glacial forests could help to explain site differences in the rate of spruce replacement: from a hypothetical single season to as long as 1400 years. White spruce is highly vulnerable to fire killing and poorly adapted to regeneration after fires (Lutz 1956; Viereck 1973; Zasada 1971). The trees have thin bark and shallow roots and in Alaska, white spruces with fire scars are uncommon. White spruce stands develop a mantle of organic matter from 10 to as much as 30 cm thick. Regular cone production does not begin until the trees are about 40 years old and annual crops in interior Alaska range from complete failures to nearly 40 million seeds/ha. In Alaska, about 86% of all fires occur before the seed matures. The oldest stands (up to 350 years) grow in fireproof habitats such as islands in flood plains. Individual trees 400–500 years old are not rare in parts of Alaska and in the Mackenzie River Delta (Cropper and Fritts 1981; Giddings 1947) and the oldest white spruce reported, more than 589 years old, grew on a river terrace in the Mackenzie River Delta (Giddings 1947). In relation to fire, black spruce differs most notably from white spruce in having a guaranteed source of seed for postfire regeneration (Vincent 1965). Much of the seed is retained in partially closed cones for at least 2 or 3 years after the cones mature and large quantities are released after fire.

If warming temperatures at the close of the Pleistocene were accompanied by periodically severe droughts, conditions would be created for a massive accumulation of fuel in the spruce forests. The thick organic layer of the forest floor would dry out and some trees might be killed by drought. White spruces under stress are vulnerable to killing by bark beetles and these and other losses of drought-stressed trees to insects and diseases would add to the fuel load.

The North American boreal forest has a natural fire regime of large-scale, high-intensity fires that recur at long intervals

in periods of severe drought (Heinselman 1981). Under these climatic conditions, much of the spruce forest could have been destroyed in less than the life-span of spruce. Whitehead *et al.* (1982) estimated that 11 000 years ago, the boreal forest of eastern North America (east of 100° W) had an area of  $2.1 \times 10^6$  km<sup>2</sup>. Midwestern spruce forests replaced by pine in the next 1000 years made up perhaps one-quarter of the total, or 500 000 km<sup>2</sup>. Historical precedents exist for the destruction of forests of this extent in a few catastrophic fire seasons. In Siberia, fires burned about 142 000 km<sup>2</sup> of boreal forest and other vegetation during the dry summer of 1915, in a region of  $1.8 \times 10^6$  km<sup>2</sup> (Shostakovich 1925). In northern Canada, radiocarbon-dated charcoal layers and buried forest soils north of the tree line in Keewatin suggest that fires have periodically destroyed spruce forests over areas at least 200 km across (Sorenson *et al.* 1971). In presettlement times, some severe fire years are known to have been synchronous over much of northern North America east of the Rocky Mountains (Heinselman 1981).

The adaptations of closed-cone jack pine for regeneration after high-intensity fires led Rowe and Scotter (1973, p. 452) to conclude that "jack pine must have evolved as a component of a fire-prone ecosystem." The large supply of germinable seed stored in the cones enables jack pine to increase explosively in population size. Even a few trees established in a new site could expand rapidly in numbers if (i) an initial open-cone phase is a general phenomenon in jack pine or (ii) fires recur after cone-bearing begins. The seed stored in closed cones also enables jack pine to regenerate after a fire at any time during the growing season. The other pines of the Great Lakes region, in contrast, can regenerate after hot fires only if the fires are late in the growing season of years with good cone crops.

In the event of fire, a single jack pine might easily release 10 000 germinable seeds and a pine grove covering 0.1 ha might release from 50 000 to more than 400 000 germinable seeds. The seeds are shed rapidly after the cones are opened by fire and germinate promptly. An intense fire would prepare a seedbed by consuming the organic layer and reducing or eliminating competition.

Through much of this region, the jack pine that replaced spruce must have differed from contemporary jack pine in one important respect: a higher frequency of closed-cone trees. The Cloquet – Red Lakes zone across northern Minnesota, extended southeast to the "thumb" of lower Michigan, separates southern populations with less than 35% closed-cone trees from northern populations with 70–100% closed-cone trees (Schoenike *et al.* 1959; Schoenike 1962). (Outside a narrow transition zone, the only exception is the Marathon, Ont., sample, with 45% closed-cone trees.) Cone serotiny is under simple genetic control and would be expected to shift rapidly even between generations under the strong selective influence of changing fire regimes. High-intensity fires at short intervals would select for higher frequencies of closed-cone trees and low-intensity fires at long intervals would favor open-cone trees.

Charcoal stratigraphy provides a direct test of the hypothesis that fires were primarily responsible for the destruction of spruce forests and their replacement by jack pine. It has been studied at only a few sites, however, and most are outside the region where this succession marked the end of the Pleistocene. At Nicollet Creek Bog, near the northwestern end of this region, abundant charcoal fragments in the spruce zone suggested to Shay (1971) that forest fires were "relatively frequent and/or intense" in the spruce forest compared with the pine

forest that abruptly replaced it. The spruce forest at this site may have been dominated by the more fire-susceptible white spruce; the ratio of white spruce to black spruce cones is 7.1 in the spruce zone.

The most intensively studied site in this region is Wolf Creek, in central Minnesota. Birks (1976) counted pollen at intervals of 2–20 (mostly 10) cm through a core covering the period from 20 500 to 9 150 years B.P. and sampled macrofossils in another core. The abrupt decline of spruce at this site is documented by both pollen (percentage and influx values) and macrofossil numbers. Both white and black spruces were present in the spruce zone and (in much smaller numbers) in the succeeding pine zone. The appearance of jack pine in small numbers coincided with the decline of spruce. Jack pine needles were present in sediments directly above the spruce zone, before diploxylon pine pollen reached its early postglacial peak.

The transition from spruce to pine at Wolf Creek was analyzed more closely by Amundson and Wright (1979), who resampled at intervals of 1–2 cm a portion of Birks's (1976) core covering more than 1000 years. In the uppermost 5 cm of the spruce zone they found a large peak in charcoal concentration, exceeding by 30 to 35% the charcoal levels in their other samples. Amundson and Wright (1979, p. 13) concluded that "no strong case can be made . . . for attributing the change from spruce forest to pine forest to a greater incidence of fire," but their data and that of Birks (1976) are consistent with a different interpretation. The high charcoal peak at the top of the spruce zone suggests that much of the spruce forest may have been destroyed by one or a series of high-intensity fires and the immediate appearance of jack pine implies that it was already present at or near the Wolf Creek site. The increase in pine pollen over a period of several hundred years suggests that the population was initially small and increased gradually in size, perhaps influenced by the recurrent fires reflected in the charcoal record of this period.

The decline of spruce was also reanalyzed by Amundson and Wright (1979) at Kirchner Marsh, a much-studied site in southeastern Minnesota close to or beyond the southern limits of jack pine's postglacial range. The rapid elimination of spruce at this site was accompanied by high levels of charcoal; three peaks during the spruce decline represent charcoal concentrations two to four times as great as the charcoal level in the late-glacial spruce forest. Mixed hardwoods replaced spruce at this site. Pine trees, if they were present at all, were a later, transitory component of the early postglacial hardwood forest, contributing a maximum of 25% diploxylon pine pollen. Amundson and Wright (1979, p. 13) concluded that the destruction of spruce and the later appearance of pine at Kirchner Marsh cannot "be attributed with confidence solely to fire," but fire does present a reasonable alternative to other interpretations.

#### *The cline across northern Minnesota*

The range of jack pine in the Midwest began to contract at almost the same time that it reached its maximum extent at the close of the Pleistocene. At Volo Bog, northeastern Illinois, the influx of hard pine pollen decreased abruptly as early as 10 600 years B.P. (J. E. King 1981). At most other sites south of the present range of jack pine, hard pines persisted until 9400 to 8500 years B.P.

The contraction of jack pine's range in the Great Lakes region climaxed during the Hypsithermal or "prairie period," a

drier and warmer interval that lasted from about 8000 to 4000 years B.P. (Wright 1971, 1976). Except in the north, hard pine pollen percentages decreased sharply from their early postglacial highs, but it is uncertain whether hard pines persisted in much reduced numbers or were eliminated from the vegetation. Wright (1968) concluded that jack and red pines were extirpated throughout Minnesota except in the northeast; a hiatus of a few thousand years in the macrofossil records of both species provides some support for this conclusion. In the Itasca region, near the prairie-forest boundary in early postglacial time and at present, the latest date for deposition of jack pine cones in early postglacial sediments at Nicollet Creek Bog is 6800 years B.P. (Shay 1971), but the cones may be much older. At Jacobson Lake, eastern Minnesota, red pine macrofossils were deposited before 7200 years B.P. and after 3900 years B.P., but not in the intervening period (Wright and Watts 1969).

A few sites in the north provide evidence of the continuing presence of hard pines. At Lake of the Clouds, northeastern Minnesota, hard pine pollen percentages were 25–60% during this period (Craig 1972). Pollen percentages and influx values at Yellow Dog Pond, on Michigan's Upper Peninsula, led Brubaker (1975) to conclude that jack pine was present throughout postglacial time. At Willow River Pond near Jacobson Lake, hard pine pollen exceeded 20% for most of the period sampled (7900 to about 5000 years B.P.) and Jacobson (1979) concluded that jack pine dominated the vegetation throughout this interval.

It is not clear whether jack pine reoccupied central Minnesota after the prairie period or whether it expanded in numbers from stands that had survived this period on favorable sites. If it reoccupied the region, the morphological coherence of central Minnesota and Wisconsin populations suggests that it must have migrated from the east (Wisconsin, possibly eastern Minnesota). The available dates of hard pine arrival (or expansion) in central and northwestern Minnesota form no discernible pattern, however, and provide no support for the migration hypothesis. Red pine macrofossils reappeared in sediments at Jacobson Lake about 3900 years B.P. and a few jack pine seeds ("*Pinus* cf. *banksiana*") were deposited less than 2000 years B.P. (Wright and Watts 1969). An increase in hard pine pollen at Rossburg Bog, about 70 km to the west, must have taken place about 1000–2000 years B.P., although it cannot be closely dated (Wright and Watts 1969). At two central Minnesota sites near the southwest edge of jack pine's present range, hard pines may have arrived as recently as 500–1000 years B.P. (Jacobson 1979).

The Itasca region is near the southern edge of the cline in cone characters that extends across northern Minnesota from Red Lakes to Lake Superior (Fig. 3). Hard pines reappeared (or increased in numbers) at several sites near Lake Itasca about 1000 years B.P. (McAndrews 1966; Shay 1971). In contrast to the early postglacial pine forest at Itasca, which probably included only jack pine, all three pines native to Minnesota are represented in recent sediments. Cones of jack, red, and eastern white pines were found at Nicollet Creek Bog (Shay 1971) and needles of all three species were found at Martin Pond (McAndrews 1966).

Jack pine may have been abundant in the north by the time it reoccupied central Minnesota. An increase in hard pine pollen percentages is dated 4000 years B.P. at Weber Lake (Fries 1962; Wright and Watts 1969) and 4700 years B.P. at Myrtle Lake (Janssen 1968). Near the northern edge of the cline, at a site in the Red Lake peatland, hard pine pollen is

abundant to the base of the peat, which began to accumulate 3170 years B.P. (Griffin 1977).

The late date of the arrival or expansion of jack pine in central Minnesota implies that northern and southern populations came together within the past 2000 years, initiating the cline that now forms the transition between them. Unless gene flow across the cline has been counteracted by natural selection or by isolating barriers, this "immature" cline can be expected to widen and flatten and eventually to disappear as a discrete zone.

#### *Jack pine in northern Minnesota and western Ontario*

Although the differences between jack pine populations north and south of the Cloquet – Red Lakes line are striking, the available data are insufficient to establish either the timing or the route of jack pine's migration into the northern region. No pine macrofossils have been reported in this region and it has not been demonstrated that jack pine had the same role in early postglacial forest succession in the north that it did farther south. At the single northern site (Kylan Lake) where hard pine pollen was identified to species, the pine that replaced spruce in the early Holocene was red pine rather than jack pine (Birks 1981).

Whatever the identity of the first hard pine to invade the region north of the Cloquet – Red Lakes line, it reached most sites there between 10 000 and 10 300 years B.P. (Lake of the Clouds, Craig 1972; Weber Lake, Fries 1962; Myrtle Lake, Janssen 1968). The earliest date in the region is 10 800 years B.P., when hard pine reached a site 60 km east of Kenora, Ont. (Buckley and Valdes-Pages 1981; J. H. McAndrews, personal communication, 1977) and the latest is 8800 years B.P., when it reached Nungesser Lake, 200 km farther north (Terasmae 1967).

This early postglacial invader must have entered the region from the south. Migration routes from the north and east were still blocked by ice 10 000 years B.P. and Glacial Lake Agassiz was a formidable barrier to the west (Prest 1970).

Compared with the succession from spruce to jack pine farther south, the hard pine that invaded this region had a variety of ecological roles. At some sites it replaced spruce, as in the south: Glatsch Lake (Wright and Watts 1969), Myrtle Lake (Janssen 1968), and a few bogs near Ely, MN (undated diagrams of Potzger 1953). Succession was less predictable at other sites, including Lake of the Clouds (Craig 1972), several bogs in extreme northeastern Minnesota and in western Ontario (Potzger 1953), and Kylan Lake (Birks 1981).

Lake of the Clouds and Kylan Lake have similar pollen diagrams. At the former, hard pine pollen was 10–20% of the total for a prolonged period, perhaps 1000 years, ending 9400 years ago (date based on counts of annual laminations). Within the next 300 years, hard pine increased to 65%, spruce declined from 30 to 5%, and the influx of charcoal tripled (Swain 1973). At Kylan Lake, jack pine pollen was 10–17% of total pollen from 10 300 years B.P. to the top of the profile at 8 400 years B.P. (Birks 1981). These percentages are too small to establish that jack pine grew at the site, but are probably too large for the pollen to have been transported 75 km or more from stands south and southwest of Lake Superior. Charcoal fragments were also consistently present from about 10 300 years B.P. Red pine appeared at the site about 9250 years B.P. and within a few hundred years it largely replaced spruce: its pollen increased from 5 to 40% at the same time that spruce pollen decreased from 23 to 3% (Birks 1981).

The assumption that jack pine was the principal hard pine that entered this region from the south 10 000 years ago is not in accord with two features of contemporary jack pine populations: (i) the morphological similarity of jack pine across central Canada, including western Ontario and northernmost Minnesota, and (ii) the distinctness of populations north and south of the Cloquet – Red Lakes line. Both features are illustrated by Schoenike's (1976) comparisons of jack pine in northern Minnesota and adjacent Ontario with jack pine of other regions, using multivariate techniques that incorporated 33 characteristics into a measure of overall phenotypic similarity. The degree of dissimilarity between jack pine growing at Ray, MN, near the Canadian border, and samples 260–550 km to the south (central Minnesota and Wisconsin) could be matched only in comparisons of the Ray sample with western Canadian samples 1100–2400 km from Ray and with samples in eastern Canada and northeastern United States, 1600–2600 km from Ray. In another comparison, a cluster of samples in western Ontario was about equally dissimilar to sample clusters in (i) central Minnesota and Wisconsin, (ii) Alberta and Mackenzie District, and (iii) Maine and Nova Scotia. The inference from these data is that the principal migration of jack pine into the region north of the Cloquet – Red Lakes line took place after 10 000 years B.P. and from some direction other than the south. If there were also jack pine entrants from the south at 10 000 years B.P., they could have been eliminated during the Hypsithermal or assimilated in the later migration.

The alternative early invader in the north is red pine. Apart from the history of the vegetation at Kylan Lake, the evidence supporting this identification is fragmentary. The earliest macrofossils of red pine in the western part of the Great Lakes region (8200 and 8500 years B.P.) are in the area just to the south (Jacobson Lake, Lake Mary). Also, the present range of red pine in central Canada does not extend much beyond a northern salient that was ice-free by 10 000 to 10 500 years B.P., but bordered on the north, east, and west by glacial ice or water (Prest 1970). This part of red pine's distribution is separated from its distribution in eastern Ontario by a gap of more than 200 km in which only scattered outliers are present (Little 1971).

If red pine was the first hard pine in most or all of this northern region, jack pine migrating from the east could have joined it there by 8000–9000 years B.P. Hard pine reached recently deglaciated sites near the northeast shore of Lake Superior no later than 8600–9000 years B.P. (Alfies and Antoine lakes; Saarnisto 1974). If jack pine migrated into western Ontario from the west, however, it could not have arrived until much later. Jack pine did not reach sites north and west of Lake Winnipeg, Man., until 5500–6500 years B.P. (Ritchie 1976) and this region is 600–1000 km northwest of the Minnesota–Ontario border.

#### *Jack pine in western Canada*

Pine arrived in the region from central Saskatchewan to central Manitoba between 5500 and 7500 years B.P. (Ritchie 1976; Ritchie and Yarranton 1978), but the dates form no readily interpretable east–west sequence. The species was almost certainly jack pine; this region is remote from the ranges of all other pines. From this area, jack pine migrated both north and south. About 5000 years B.P. it reached Porter Lake, near the northern edge of its range in the Mackenzie District (Ritchie 1980). It later migrated south and by about 4000–2500 years

B.P. it reached several sites near the southern edge of its range in Saskatchewan and southwestern Manitoba (Ritchie 1976).

These recent data do not provide a conclusive answer to the much-debated question of whether jack pine had a western refugium. The existence of a refugium in western Canada was first proposed by Löve (1959) from ecological and distributional data. Ritchie and his co-workers (Ritchie and Hadden 1975; Ritchie 1976; Ritchie and Yarranton 1978) have interpreted their pollen data as support for Löve's (1959) proposal. They and others (Webb *et al.* 1983) have endorsed Löve's (1959) view that western jack pine migrated no farther east than Manitoba, where it met jack pine from the east in the area formerly covered by Glacial Lake Agassiz.

The opposing view, that jack pine occupied its western range from a refugium in eastern North America, was advanced by Yeatman (1967) and endorsed by Schoenike (1976). Yeatman's (1967) proposal was based on several kinds of evidence (some of it later reinterpreted by Zavarin *et al.*, 1969), but emphasized the limited geographic extent and apparent immaturity of introgression between jack and lodgepole pines. This description fits what is known of the influence of lodgepole on jack pine, but it does not apply to introgression in the opposite direction. From the evidence reviewed earlier, jack pine genes appear to have been dispersed far beyond the region of overlap and influenced lodgepole pine through much of its northern and northeastern distribution.

If jack pine had a western refugium, the range of possible locations has increasingly narrowed. Refugia in the "corridor" region east of the Rocky Mountains must have been isolated from lodgepole pine, at least in part. Many stands of western jack pine, even near the overlap region, show no discernable influence of lodgepole pine. Nor is there evidence of a jack pine refugium in the northern Great Plains. Sites in southern Saskatchewan (Ritchie 1976) and the Dakotas (Wright 1970) lack significant amounts of pine pollen throughout late-glacial and early postglacial time. The Cypress Hills are a remote possibility. They were not glaciated in the last glacial period and as Ritchie (1980) has noted, nothing is known of the late-Quaternary vegetation history of this isolated upland. The genetic evidence is negative, however. The Cypress Hills are occupied by a lodgepole pine outlier that lacks any trace of jack pine influence (Table 1), so if the latter had a refugium there it must have been eliminated before lodgepole pine arrived.

The strongest argument against a western refugium of jack pine is the continuity of variation across Canada, contrasting with the discontinuities between regional populations in the Lake States. The single break across central Canada is in the Lake Nipigon region. This zone is rather broad and is not of sufficient magnitude to have been identified in either cluster analysis of jack pine (Hyun 1979; Schoenike 1976). Whether eastern and western populations of jack pine came together near Lake Nipigon during postglacial time, after a separation of perhaps 100 000 years, is a question that should be answerable by future analyses of pollen and macrofossils in this little-studied part of Canada.

West of Lake Nipigon, there are no identifiable discontinuities in jack pine's variation until the overlap zone with lodgepole pine is reached. If jack pine from eastern and western refugia came together in the region of Glacial Lake Agassiz, as postulated by Löve (1959) and Ritchie (1976), this event left no detectable mark on jack pine across Manitoba (data of Schoenike 1962). The more probable limits of eastward migration from a hypothetical refugium in the west are Lake Nipigon and the cline across northern Minnesota.

## Conclusions

The history of jack pine is more amenable to reconstruction than that of lodgepole pine for several reasons. Since jack pine was displaced from its present range as recently as 13 000 years ago, its genetic structure is likely to have been shaped primarily by events that date back no farther than the last interglacial interval. Lodgepole pine, on the contrary, seems not to have been much influenced by glaciation in its distribution south of the ice. The continuity of variation patterns that may have evolved long before the last interglacial appears to have been preserved through the last glacial period and projected northward during postglacial time. Also, because the physical environment of jack pine is more homogeneous than that of lodgepole pine, its variation patterns are less obscured by a kind of "background noise" that can be attributed, in lodgepole pine, to local adaptation to a remarkably wide range of maritime and montane environments.

Variation patterns of jack pine are also more easily interpreted because they have been more fully described. Schoenike's (1962) description of 33 morphological and growth characteristics of 1790 jack pines growing in 90 localities provides a base of phenotypic data that is matched in few other species. Other studies of variation in jack pine have also been concentrated in the Great Lakes region and this happens to be the only part of its range where jack pine is subdivided into several phenotypically distinct populations.

The late Quaternary fossil record has also been more thoroughly investigated in the Great Lakes region, particularly Minnesota, than almost any other part of North America, primarily owing to the efforts of H. E. Wright, Jr. and his colleagues and students. Compared with this region, northwestern North America is still relatively unknown territory.

Taken together, this wealth of fossil and contemporary evidence supports the conclusion that jack pine survived the last glaciation in at least two refugia in the midcontinent, in addition to its well-known southeastern refugium. No firm conclusion can be reached concerning the long-standing problem of a western refugium. The almost unbroken continuity of variation across most of Canada, however, supports Yeatman's (1967) hypothesis that jack pine migrated to the western interior of Canada from eastern North America during the Holocene.

The recent history of lodgepole pine is obscure by comparison, although it is certain that it reoccupied parts of deglaciated northwestern North America from refugia south of the ice. The available evidence has, however, brought into sharper focus the principal problems: the origin or origins of the North Coastal race, the possible existence of a lodgepole refugium in the Yukon, and the extent and antiquity of introgression from jack pine.

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