Section 2.
Jack pine (*Pinus banksiana*)

1. Taxonomy and use

1.1. Taxonomy

The largest genus in the family Pinaceae, *Pinus* L., which consists of about 110 pine species, occurs naturally through much of the Northern Hemisphere, from the far north to the cooler montane tropics (Peterson, 1980; Richardson, 1998). Two subgenera are usually recognised: hard pines (generally with much resin, wood close-grained, sheath of a leaf fascicle persistent, two fibrovascular bundles per needle — the diploxylon pines); and soft, or white pines (generally little resin, wood coarse-grained, sheath sheds early, one fibrovascular bundle in a needle — the haploxylon pines). These subgenera are called respectively subg. *Pinus* and subg. *Strobus* (Little and Critchfield, 1969; Price *et al.,* 1998). Occasionally, one to about half the species (20 spp.) in subg. *Strobus* are classified instead in a variable subg. *Ducampopinus*.

Jack pine (*Pinus banksiana* Lamb.) and its close relative lodgepole pine (*Pinus contorta* Dougl. Ex Loud.) are in subg. *Pinus*, subsection *Contortae*, which is classified either in section *Trifoliis* or a larger section *Pinus* (Little and Critchfield, 1969; Price *et al.,* 1998). Additionally, subsect. *Contortae* usually includes Virginia pine (*P. virginiana*) and sand pine (*P. clausa*), which are in southeastern USA. Jack pine has two quite short (2-5 cm) stiff needles per fascicle (cluster) and lopsided (asymmetric) cones that curve toward the branch tip, and the cone scales often have a tiny prickle at each tip (Kral, 1993). Non-taxonomic ecological or biological variants of jack pine have been described, including dwarf, pendulous, and prostrate forms, having variegated needle colouration, and with unusual branching habits (Rudolph and Yeatman, 1982).

1.2. Uses

Jack pine is one of the most important commercial tree species in Canada and the Lake States of USA. Its wood is moderately hard and heavy, and relative to other softwoods, of intermediate strength (Eyre and LeBarron, 1944; Hosie, 1979). It can produce merchantable stands on sites often too poor and infertile for other tree species to thrive (Cayford and McRae, 1983). It has a number of commercial applications, including pulpwood, general construction timber, railway ties, poles, pilings, mine timbers and fuel (Rudolf, 1958; Hosie, 1979; Cayford and McRae, 1983; Law and Valade, 1994). Other applications include the extraction of essential oils for aromatic agents in products such as perfumes, cosmetics and cleaners (Marles *et al.,* 2000).

There were a number of traditional aboriginal uses of jack pine (Marles *et al.,* 2000), some of which are: inner bark and needles processed to yield poultice to treat wounds and frostbite; pitch chewed as a medicinal; dried cones used in tanning of hides; roots used to make baskets, and fish hooks made from knots. The wood was used for cabins, boat planks, fishnet floats and fuelwood. Though less effective than spruce (*Picea*) pitch, pine pitch could also be used for caulking.

2. Natural distribution and migrational history

2.1. Natural distribution

Jack pine is widespread through northern North America from the Atlantic coast to the low Rocky Mountains (Figure 1). With a mainly contiguous range, it is the most widely distributed pine species in Canada, and grows farther north than any other North American pine (Cayford *et al.,* 1967; Rudolph and Laidly, 1990). The natural range extends from southeastern Canada in Nova Scotia, Prince Edward Island and New Brunswick westward through much of south-central Québec, central Ontario, Manitoba, Saskatchewan and Alberta and the extreme northeast of British Columbia northward into the Northwest Territories (extending slightly into Nunavut). Toward the south, jack pine extends into the Lake States (eastern Minnesota, northern Wisconsin and Michigan) and to northern Illinois and Indiana. Its southern limit in the eastern USA is mainly in northern New York, Vermont and New Hampshire and central Maine, with an outlying population in eastern Pennsylvania (Rudolf, 1958; Rudolf, 1965; Kral, 1993). In the Lake States jack pine generally occurs at elevations between 300 m and 460 m above sea level; in the eastern portion of its range, it grows from near sea level to 850 m in elevation (Rudolf, 1965; Elias, 1980).

2.2. Centre of origin, evolution, and migrational history

The genus *Pinus* is ancient, believed to have originated in the early to mid-Mesozoic era about 180 million years ago, prior to continental separation in the Laurasian region that became eastern North America and western Europe (Burdon, 2002). Approximately 150 million years before the present (BP), *Pinus* diverged into hard pines (subg. *Pinus*) and soft pines (subg. *Strobus*) (Yeatman, 1967). Rapid evolution, speciation, and migration occurred during the Tertiary prior to cooling climatic conditions at its end (Mirov and Hasbrouck 1976). Lodgepole pine and jack pine might have evolved from a common progenitor into western and northern species during the cooling of the late Tertiary (Pliocene), or may not have diverged until the Pleistocene (Critchfield, 1984) — Dancik and Yeh (1983) estimated that they diverged between 485,000 and 565,000 years BP.

During the Pleistocene, jack pine retreated southward ahead of the advancing ice sheet. It was extirpated from northern regions prior to *Picea* (spruce), which could withstand the cooling temperatures longer. A main glacial refugium for this species was in the Appalachian Highlands (southeastern USA). Fossil evidence suggests that it also had at least two additional refugia in the American Midwest (Critchfield, 1984, 1985). Although it has been hypothesised that jack pine was able to persist alongside lodgepole pine in an unglaciated region between ice sheets in Alaska and the Yukon Valley (Mirov and Hasbrouck 1976), conclusive evidence for a western refugium was lacking until recently (Yeatman, 1967; Critchfield, 1985). Recent mitochondrial DNA minisatellite analysis, which identified three genetically distinct populations, has led to the inference that three distinct jack pine glacial refugia occurred: one west of the Appalachian mountain range, one east of these mountains, and a third in the unglaciated coastal region of eastern Canada (Godbout *et al., in press*). This work therefore concurs with fossil evidence and supports the theory of a western refugium.

With the retreat of the last Wisconsin glaciation beginning about 18,000 years BP, *Picea* species were the first coniferous postglacial colonisers, followed by northern migration of jack pine and lodgepole pine, which were in turn followed by red pine (*P. resinosa*) and eastern white pine (*P. strobus*). Jack pine expanded rapidly (350-500 m per year between 13,000-8,000 years BP) from the Appalachians to the Great Lakes and the Maritimes (Davis, 1976). It advanced into southern Ontario between 10,500 and 9,500 years BP, and underwent rapid expansion during a warm, dry period (Fuller, 1997). The last part of the Great Lakes area to be deglaciated was the north-central shore of Lake Superior (near Marathon, Ontario), which today has one of the most genetically distinctive populations in central Canada (Critchfield, 1985). Jack pine is estimated to have reached its northern limit in northwestern Québec

near Hudson Bay (at 55° latitude) about 3,000 years BP, some 4,000 years after the region was deglaciated (Desponts and Payette, 1993). The species is believed to have become established first in sporadic stands, from which it was able to colonise additional sites after fire.

Figure 1. Main natural distribution of jack pine in North America

Pinus banksiana

500   0   500 1000 1500 Kilometers

USGS

Source: Courtesy of the Flora of North America Association

Populations from one Midwestern refugium migrated to Lower Michigan, while populations from the second refugium colonised Wisconsin and Minnesota (Critchfield, 1985). On prairie grasslands in north-central Minnesota, jack pine advance was curtailed by competition for water until about 5,000 years BP, when increased fire frequency favoured jack pine forestation (Almendinger, 1992).

Jack pine did not reach southern Manitoba until about 12,000 years BP (Jacobson *et al.,* 1987). The species expanded northwestward rapidly, extending into north-central Saskatchewan by about 8,000 years BP (McLeod and MacDonald, 1997). The rapid spread may have been in part due to the warm dry period with higher fire frequencies, favouring its regeneration. Further expansion northward continued at a reduced rate, coinciding with cooler temperatures and lower fire incidence. Jack pine reached its northwestern limit in the Northwest Territories (Upper Mackenzie River Valley) around 4,150 years BP (McLeod and MacDonald, 1997). Whereas the limiting factors in the western portion of the current range appear to be growing degree-days (>5ºC) and dominance of peat soils, the northern limit in the east appears to be caused by snow and the lack of sufficient fire (Despland and Houle, 1997; McLeod and MacDonald, 1997; Hofgaard *et al.,* 1999; Asselin *et al.,* 2003).

3. Reproductive biology

3.1. Reproductive bud differentiation

Jack pine is monoecious. It is a wind pollinated, cross-fertilising species, although some natural selfing can occur. Ovulate (female) strobili or cones ("flowers") are typically found on vigorous primary and secondary branches in the upper crown, and staminate (male) strobili on the less vigorous tertiary branches of the lower crown (Rudolph and Laidly, 1990). Like most other pines, jack pine has a 3-year reproduction cycle. Staminate cone primordia are initiated in early or mid-July, ovulate cone primordia in August (Curtis and Popham, 1972). Time of anthesis varies from year to year, ranging from mid-May to early June, and is generally synchronised with female cone receptivity (Rudolph and Yeatman, 1982). In southern Ontario, pollen shedding begins around the last week of May and continues for about a week (Ho, 1991). Ovulate cones begin to emerge from bud scales in mid-May. When fully emerged, margins of bracts are reflexed and cones at the peak of receptivity; this occurs about 25 May in Ontario (Ho, 1991; Roussy and Kevan, 2000). Following pollination, pollen tube growth and ovule development are initiated, but stop in mid-summer (Owens and Blake, 1985). They resume the following spring and fertilisation occurs about 13 months after pollination. Cones and seeds mature late in the growing season of the year of fertilisation (Rudolph and Laidly, 1990).

3.2. Natural seed production and dissemination

Jack pine is an early and prolific seed producer. Rudolph (1979b) observed ovulate strobili on plantation trees only 17 months in age. Typically, cone production begins at 5 to 10 years of age among open-grown trees and 10 to 25 years in closed stands; optimum seed production occurs between 40 to 90 years, varying with site and stand conditions (Roe, 1963; Rudolf, 1965). Annual seed production varies (*e.g.* Houle and Filion, 1993); some seed is usually produced each year (Rudolph and Laidly, 1990), with good cone crops occurring every 3 to 4 years (Eyre and LeBarron, 1944; Roe, 1963). A cone may produce 17 to 40 filled seeds (Roe, 1963; Cayford *et al.,* 1967; Jeffers, 1972; Houle and Filion, 1993; Greene and Johnson, 1999).

Over most of its range, jack pine bears serotinous cones, an adaptation that can result in significant quantities of viable seed dispersal following fire. In the absence of fire, cones may remain closed for more than 25 years (Roe, 1963). Seeds within closed cones maintain high viability for at least 5 years; even after 20 years, average germination may reach 50% (Rudolf, 1965; Cayford and McRae, 1983). In the southern part of its range, jack pine produces non-serotinous cones, which soon open without fire (Ahlgren, 1974). Trees may have 10 or more annual cone crop cohorts (Greene and Johnson, 1999; Greene *et al.,* 1999). Consequently, jack pine can maintain a substantial aerial seedbank; estimates for well-stocked stands range from 1 million to 4 million seeds per ha (Rudolf, 1965; Greene *et al.,* 1999). Fires of suitable intensity and duration cause the cones to open and release seed, while leaving most seed undamaged and viable (de Groot *et al.,* 2004). Seed may be released within the first few days following fire (Eyre and LeBarron, 1944); the majority of seed is released within 3 or 4 years (Greene and Johnson, 1999), often leading to post-fire stands that are even-aged. The extent of early regeneration and establishment on a site may correlate to the pre-burn basal area, reflecting the size of the aerial seed bank (Greene and Johnson, 1999; Arseneault and Sirois, 2004).

3.3. Natural regeneration

3.3.1.   Seedling regeneration

Jack pine seed does not require stratification (Yeatman, 1984). It has epigeal (aboveground) germination. Favourable seedbeds include mineral soil, decomposed organic layers less than a few centimetres thick, and burned or scarified duff (Rudolf, 1965; Cayford and McRae, 1983; Greene

et al., 1999). Feather mosses and herbaceous, grass and shrub litter make poor seedbeds (Cayford, 1963a). Undisturbed surface humus may hinder seed germination and seedling survival (Chrosciewicz, 1970). Partial shade may enhance germination and early establishment (Eyre and LeBarron, 1944; Rudolf, 1958; Cayford, 1963b); however, full sunlight is subsequently required for optimal growth and survival (Rudolf, 1965). Most germination occurs promptly following seed dispersal, if temperature and moisture conditions are suitable (Cayford and McRae, 1983). Establishment is better when seed dispersal is in spring and early summer rather than autumn (Rudolf, 1958; Chrosciewicz, 1988b). A proportion of seed may not germinate until one or two growing seasons after dispersal (Ahlgren, 1959; Thomas and Wein, 1985); St-Pierre *et al.,* (1992) found that 95% of seedlings were established within 3-years following fire.

Forest fire may enhance seedbed quality by reducing accumulated organic layers, reducing plant competition and pest populations, and providing nutrients (Cayford, 1963b). Prescribed burns that reduce surface litter and raw humus depth, while exposing mineral soil and reducing aerial parts of competing vegetation, improve stocking and subsequent height growth (Chrosciewicz, 1970, 1988b). Scarification to expose mineral soil and reduce the thickness of litter following harvesting may enhance germination (Cayford, 1959). The level of rainfall can affect the quality of the seedbed in a manner that varies with soil type and level of the water table (Rudolf, 1958; Chrosciewicz, 1988b); early seedling height growth may be affected by vegetation competition and the soil moisture regime (Chrosciewicz, 1970). The importance of an appropriate seedbed becomes more pronounced when weather conditions are less favourable for germination and early growth (Benzie, 1977). Early seedling mortality due to heat and drought can be substantial, particularly on dry sites, although mitigated by shade (Cayford *et al.,* 1967).

3.3.2. *Vegetative propagation*

Jack pine does not naturally reproduce through vegetative propagation (Rudolf, 1958).

3.4. Mating system and gene flow

Jack pine is monoeceous, with a mixed mating system. While it is mainly outcrossing, self-pollination also occurs. Selfing rates of between 7% and 12% have been reported (Sittmann and Tyson, 1971; Rudolph 1979a; Cheliak *et al.,* 1985). Most of the genetic variation resides within populations (regardless of the distance between sampled populations). Outcrossing rate estimates generally range from 88 to 98% (Dancik and Yeh, 1983; Danzmann and Buchert, 1983; Cheliak *et al.,* 1985; Snyder *et al.,* 1985; Ross and Hawkins, 1986; Misenti and DeHayes, 1988; Fu *et al.,* 1992; Gauthier *et al.,* 1992; Godt *et al.,* 2001; Saenz-Romero *et al.,* 2001).

Very weak patterns of family substructuring have been observed in jack pine stands (Cheliak *et al.,* 1985; Xie and Knowles, 1991; Saenz-Romero *et al.,* 2001). Dong and Wagner (1994) found that maternally inherited mitochondrial DNA showed higher levels of population subdivision than paternally inherited chloroplast DNA. No differences in isozyme variation were detected between natural and plantation stands (Knowles, 1985).

Jack pine seed and pollen are windborne. Seed does not disperse beyond about 30 m from the parent tree (Rudolf, 1965). However, gene flow through pollen dissemination is extensive. A jack pine pollen grain is only about 50 µm wide (including the two air-bladders) (Di Giovanni *et al.,* 1995), and is therefore able to travel long distances. Di Giovanni *et al.,* (1996) obtained samples of its pollen 300 m above the ground; in a steady wind of 5 m per sec, they estimated that the pollen could drift about 60 km. Saenz-Romero *et al.,* (2001) estimated gene flow to be more than 11 migrants per year whereas Godt *et al.,* (2001) obtained a rate of 16.9 migrants per year, both thus indicating that extensive migration has a large influence on the species' genetic structure.

Xie and Knowles (1991) suggested that short seed dispersal distances may cause small-scale non-random genetic spatial patterns but these would not occur over a large scale. They suggested that high gene flow resulting from long-distance pollen migration overwhelms forces (such as genetic drift) that promote subpopulation differences, and causes the lack of variation observed between populations.

4. Hybridisation

Jack pine and lodgepole pine (*P. contorta* subsp. *latifolia*) share a sympatric region in Canada in central and northwestern Alberta to the Northwest Territories. Genetic remnants of lodgepole pine within the jack pine population in Saskatchewan have also been detected (Rudolph and Yeatman, 1982; Dong and Wagner, 1993). Where the species coexist, natural hybridisation occurs. More widespread hybridisation is prevented by phenological differences in female strobili receptivity and pollen shed in these species, with jack pine flowering 2 to 3 weeks earlier (Critchfield, 1985). Some artificial F_1 hybrids have high levels of pollen abortion, but F_1 to F_3 hybrids produced some sound seed (Critchfield, 1980). Zavarin *et al.,* (1969) described the introgression of jack pine genes into lodgepole pine stands 150 km south of the hybrid zone, and lodgepole pine genes into jack pine stands 150 km north of the closest lodgepole pine stand. Yet the genetic distance between jack pine and lodgepole pine populations in Alberta based on allozymes averages 20 times greater than among populations within each species (Dancik and Yeh, 1983). In the sympatric region, jack pine is xerophytic, and often found on well-drained, sandy sites, whereas lodgepole pine is mesophytic, tolerant of heavier, wetter clay soils, and more typical at higher elevations; hybrids commonly occupy intermediate sites (Wheeler and Guries, 1987; Yang *et al.,* 1999).

Artificial hybrids reportedly have been made between jack pine and Virginia pine and loblolly pine respectively. Artificial hybridisation has also been reported with Japanese black pine (*P. thunbergii*). Nonetheless, the only artificial hybrid sufficiently verified is with lodgepole pine (Rudolph and Yeatman, 1982). Crossing between members of different *Pinus* subsections typically does not occur, because of genetic barriers (Critchfield, 1975). Artificial crosses and backcrosses between jack pine and lodgepole pine were carried out in many early programs in an attempt to combine the fast growth and relative pest resistance of jack pine with the stem form of lodgepole pine.

Even though lodgepole pine is more genetically variable than jack pine (Dancik and Yeh, 1983), it is more susceptible to sweetfern rust (*Cronartium comptoniae*) and western gall rust (*Endocronartium harknessii*) and eastern gall rust (*Cronartium quercuum*) (Anderson and Anderson, 1965; Yeatman, 1974, Yang *et al.,* 1998, 1999). Unfortunately, the pines' hybrids were also more susceptible to western gall rust than was jack pine (Yang *et al.,* 1999). As lodgepole pine resistance to western gall rust, needlecast (*Davisomycella ampla*), stalactiform blister rust (*Cronartium coleosporioides*), and Sequoia pitch moth (*Synanthedon sequoiae*) increases clinally with proximity to the jack pine range (Wu *et al.,* 1996; Wu and Ying, 1998), it appears that introgressed jack pine genes are conferring resistance to lodgepole pine. However, other explanations can be proposed for the clinal trends in lodgepole pine resistance. Yang *et al.,* (1997) have questioned whether the introgression interpretation is valid for western gall rust; neither study sampled non-hybrid jack pines.

Numerous morphological traits such as needle length, cone characteristics and turpentine composition appear intermediate in hybrids (Moss, 1949; Mirov, 1956; Keng and Little, 1961; Zavarin *et al.,* 1969; Rudolph and Yeatman, 1982). Rudolph and Nienstaedt (1962) found that hybrid resistance to winter injury was intermediate between the hardy jack pine and less hardy lodgepole pine. Whereas early hybrid growth and survival is considered generally to be intermediate to that of jack pine and lodgepole pine (Lotan, 1967; Yeatman and Holst, 1972; Garrett, 1979; Yang *et al.,* 1999), little difference in performance was noted by age 15 to 20, which led Rehfeldt and Lotan (1970) to conclude that lodgepole pine × jack pine hybrid breeding programs were not warranted.

Hybridisation, backcrossing and introgression have been characterised by allozyme variation (Wheeler and Guries, 1987; Dancik and Yeh, 1983) and randomly amplified polymorphic DNA (RAPD) variation (Ye *et al.,* 2002). Paternally inherited chloroplast DNA exhibits atypical, novel variants in the zone of sympatry (Wagner *et al.,* 1987, 1988, 1991; Govindaraju *et al.,* 1988). Maternally inherited mitochondrial DNA distinguished between each species and their hybrids, and was found much less variable in jack pine than in lodgepole pine (Dong and Wagner, 1993).

5. Genetics

5.1. Cytology

The diploid (2*n*) chromosome number of jack pine (and all members of the genus *Pinus*) is 24. Saylor (1972, as summarised by Rudolph and Yeatman, 1982) found that 11 of the chromosomes had median centromeres, but the 12th and shortest chromosome was heterobrachial; the chromosomes varied in length by a factor of 0.6. The diploid DNA genome size of jack pine has been estimated to be 29.8 picograms (Rake *et al.,* 1980), with variability per cell and among genetic families (Miksche, 1968; Wyman *et al.,* 1997).

5.2. Inbreeding depression

Inbreeding depression caused by self-pollination has been expressed by lower seed set, mortality, abnormal germination, abnormal phenotypes, chlorophyll deficiencies, lower water-use efficiency, lower growth rates, delay in initiation of flowering, and lower fecundity (Fowler, 1965a, 1965b; Rudolph 1966a, 1981b; Blake and Yeatman, 1989). Rudolph (1981a) observed inbreeding depression in tree height between 18 to 24% in selfed S_2 progeny.

Fowler (1965b) observed about 13% selfing in the upper crown and 26% in the lower crown of seed orchard trees. However, many selfed progeny would not be expected to survive; Sittmann and Tyson (1971) estimated an inbreeding rate due to selfing of 5% per generation for a population in Hardy-Weinberg equilibrium. As jack pine retains its serotinous cones for years, comparisons can be made between seed of the same tree produced in different years (Teich, 1970). Higher rates of selfed seed are found in the latest seed (Cheliak *et al.,* 1985; Snyder *et al.,* 1985); it appears that selection against inbred seed is occurring at a linear rate, with a loss of viability of selfed seed.

5.3. Genetic variation

5.3.1. Population-level variation

Jack pine provenance testing has been carried out on a regional and a rangewide basis, and included growth chamber, greenhouse, nursery, and field experiments. Besides being tested throughout its natural range in Canada and USA, its seed has been distributed to Great Britain, The Netherlands, New Zealand and Japan for testing (Rudolph and Yeatman, 1982). Numerous investigations have described a pattern of clinal variation, usually associated with temperature (growing degree-days) and photoperiod (latitudinal) effects, particularly where cold temperatures and growing degree-days are not limiting. When grown in a common environment, northern provenances which originate in areas with colder temperatures and fewer growing degree-days are typically smaller in height, diameter and volume than southern sources (Schantz-Hansen and Jensen, 1952; Giertych and Farrar, 1962; Sweet and Thulin, 1963; Yeatman, 1974; Canavera, 1975; Skeates, 1976; Hyun, 1979; Jeffers and Jensen, 1980; Rudolph and Yeatman, 1982; Magnussen and Yeatman, 1988b; Bolstad *et al.,* 1991; van Niejenhuis and Parker, 1996). This trend was observed from the early seedling stage through to age 20, although differences lessened with age (Yeatman, 1974).

Jeffers and Jensen (1980) found more variability in volume among sources than height, diameter or survival; volume was not correlated with growing degree-days, unlike the other traits. Magnussen and Yeatman (1979) observed a larger amount of within-population than between-population variation for height. Survival was correlated to the similarity in climatic conditions between source origin and test site (Jeffers and Jensen, 1980). Higher mortality resulted in less competition, and subsequently increased growth rates (Jeffers and Jensen, 1980).

Seedling leaf, root, and total dry weights were also found to vary in relation to growing degree-days of the source (Giertych and Farrar, 1962). Aboveground biomass was strongly related to water availability, except for provenances from warmer climates suspected of being more tolerant to water stress or having more efficient water usage (Strong and Grigal, 1987). There was greater variability between provenances on more adverse sites. Dry weights of 4-month-old seedlings correlated with height after 4 years (Yeatman and Holst, 1967).

Under environment chamber conditions, seed source differences between jack pine seedlings were most readily observed under short photoperiods (Mergen *et al.,* 1967). Northern provenances were more responsive to changes in photoperiod than southern sources (Giertych and Farrar, 1962; Yeatman, 1974). In field trials, more variability between populations in height growth was observed at milder test sites (Jeffers and Jensen, 1980). Taller provenances were found to retain higher photosynthetic rates into autumn than slower-growing sources (Logan, 1971). However, no provenance differences were detected in stem respiration (Lavigne, 1996).

Southernmost provenances typically begin flowering at a younger age (Sweet and Thulin, 1963). Western provenances bear smaller cones with fewer seeds (Jeffers, 1972; Schoenike, 1976). Most of the total variation in cone and seed traits resided between populations. Climatic variables were related to chemical components in embryo and megagametophyte, although environmental preconditioning may have influenced nutrient levels in the megagametophyte (Durzan and Chalupa, 1968). Maternal effects of seed weight have been observed on germinants, but diminished by the time seedlings were 3 months old (Yeatman, 1974). No differences between sources were noted in timing or rate of germination (Yeatman, 1966). Seed weight is highest in populations from regions with longer and warmer growing seasons.

Southern provenances are slower to flush in spring, set bud at the end of the growing season, and form secondary needles than northern provenances (Yeatman, 1974). Budburst is strongly associated with colder mean January temperatures (Steiner, 1979). Coastal populations burst bud later than more continental sources. Significant provenance differences have been observed in lammas growth (second, late-season terminal shoot extension) and proleptic growth (second, late-season extension of the lateral buds at the base of the terminal bud) (Rudolph 1964). Cessation of cambial activity was found to be under strong genetic control, but there was less control over initiation of cambial activity (Kennedy, 1971). Provenance differences have been noted in foliar nitrogen, phosphorus, potassium and calcium (Mergen and Worrall, 1965; Giertych and Farrar, 1962; Strong and Grigal, 1987). Foliar nitrogen content correlated with growing degree-days (Giertych and Farrar, 1962), with northwestern provenances having the highest foliar nitrogen (Mergen and Worrall, 1965). Strong and Grigal (1987) hypothesised that foliar macronutrient provenance differences were slight because jack pine is efficient in using available nutrients.

Northern provenances develop winter foliage colouration more rapidly and attain a deeper hue than southern provenances (Canavera, 1975; Rudolph and Yeatman, 1982; vanNiejenhuis and Parker, 1996). The purpling is attributed to at least five anthocyanin pigments, which are produced after the first autumn exposure to freezing temperatures (Nozzolillo *et al.,* 2002). Young seedling foliage turns purplish in autumn, but as seedlings age, winter colouration becomes a yellow-bronze. Northern sources are older than southern sources before making the transition between purple and bronze foliage (Canavera and Wright, 1973). Northern provenances develop cold hardiness earlier in autumn (Yeatman, 1974). Sources from warmer climates have wider annual rings, wider earlywood and latewood rings,

and slightly lower specific gravity (Kennedy, 1971). Provenance differences were observed in both tracheid length and wood specific gravity, with a larger between-stand than within-stand component (King, 1968). Northern Canadian provenances and sources from Nova Scotia had the slowest growth, shortest tracheid length and highest specific gravity, whereas U.S. populations from Michigan, Wisconsin and Minnesota had the fastest growth, longest tracheid length and lowest specific gravity. Crown width and bark thickness are negatively correlated with latitude (Hyun, 1979). One Atlantic coast source from Maine (USA) was noticeably prostrate by age 4, similar to its parental types, when grown in Minnesota (Schantz-Hansen and Jensen, 1952).

Numerous studies have reported jack pine resistance at the population level to various pests (Yeatman and Teich, 1969). Southern sources growing on northern test sites had a higher incidence of scleroderris canker (*Gremmeniella abietina)*, with best resistance from Québec sources (Yeatman and Morgenstern, 1979). Taller trees were found to have a higher incidence of eastern gall rust infection (Bolstad *et al.,* 1991). However, in Minnesota southern Lake States sources were less susceptible to eastern gall rust than northern sources (King, 1971; Jeffers and Jensen, 1980). Other pests for which resistance has been reported include white pine weevil (*Pissodes strobi*) (Arend *et al,.* 1961; King, 1971), bark beetles (*Pityophthorus* spp), redheaded pine sawfly (*Neodiprion lecontei*) (Arend *et al.,* 1961; Schantz-Hansen and Jensen, 1952), eastern pine shoot borer (*Eucosma gloriola*) (King, 1971) and needlecast (*Davisomycella (Hypodermella) ampla*) (King and Nienstaedt, 1965).

Most studies involving interprovenance crosses have found that these intraspecific hybrids are approximately intermediate to the parental types. Traits showing this include height, stem characteristics, crown characteristics (Magnussen and Yeatman, 1988b; Bolstad *et al.,* 1991), survival (Magnussen and Yeatman, 1988a), and shoot extension periodicity (Magnussen and Yeatman, 1979). However, Magnussen and Yeatman (1988a) observed significant heterosis (departure from midparent value) in height at all test sites except the northernmost, where provenance differences were not significant. No significant reciprocal cross effects have been found (Magnussen and Yeatman, 1988a; Bolstad *et al,.* 1991).

Provenance by environment interactions have been observed in many traits of jack pine. Source by temperature and source by photoperiod interactions in number of primary needles produced were noted in a controlled-environment seedling experiment (Mergen *et al.,* 1967). Provenance by site interactions occurred in aboveground total biomass production of six provenances grown at eight sites throughout the Lake States (Strong and Grigal, 1987). While no provenance by site interaction was noted in height at two test sites in New Zealand (Sweet and Thulin, 1963), many studies located within jack pine's natural range have described strong provenance by site interactions for height, diameter, volume, and survival from seedling stage through to age 20 (Jeffers and Jensen, 1980). Northern and southern provenances appear to contribute more to these source by environment interactions than midlatitude provenances (Morgenstern and Teich, 1969; Jeffers and Jensen, 1980; Magnussen and Yeatman, 1988b), perhaps due to the greater distance between origin and planting site for those populations (Morgenstern and Teich, 1969).

Age 3 was considered too young for selection of wood quality traits, in particular specific gravity (King, 1968). Provenance trials have indicated that age-5 height is not reliable for predicting height at age 20 (Yeatman, 1974; Jeffers and Jensen, 1980). However, by age 10 to 15, height effectively predicted growth at age 20, and could reliably be used to develop seed source recommendations (Yeatman, 1974; Jeffers and Jensen, 1980). Magnussen and Yeatman (1988b) suggested that height after 8 to 10 years could be used as a reliable indicator of later performance when testing was carried out on favourable sites, but on adverse sites, decisions regarding seed source selections should be delayed until the tests are older.

5.3.2. Within-population variation

High levels of genetic variation in jack pine growth have been documented in numerous studies. Table 1 lists a sampling of individual and family heritabilities reported for height growth from sites in the central to eastern range (Manitoba [MB], Ontario [ON], Wisconsin [WI] and New Brunswick [NB]).

Table 1. **Examples of jack pine individual (h^2_i) and half-sib family (h^2_f) heritabilities for height.**

Reference	location	# families	# sites	age	h^2_i	h^2_f
Klein, 1989b	MB	216	3	10	0.1	0.49
Klein, 1995	MB	215	3	20	0.34	0.68
Magnussen & Yeatman, 1990	ON	100	3	6	0.13	0.42
" "	"	"	"	14	0.18	0.48
Morris *et al.,* 1992	ON	369	1	3	0.17	0.26
Riemenschneider, 1988	WI	102	1	7	0.2	–
Adams & Morgenstern, 1991	NB	104	4	7	0.17	0.74
Park *et al.,* 1989	NB	162	4	10	0.26	0.81

Estimates of the amount of total variation due to family are below 20% (Canavera, 1975; Klein, 1989b; Park *et al,.* 1989). Genetic gain is typically low; height gains of seedlings aged 2 or 3 range from 0.4 to 5.1% (Canavera, 1975; Rudolph *et al.,* 1989; Adams and Morgenstern, 1991). At age 20, Klein (1995) estimated a genetic gain of 5.7% for height; Simpson and Steel (1995) reported a height gain of 3.2% in a seed orchard after 14 years and three roguings.

Riemenschneider (1988) proposed that early selection based on young seedling performance might be efficient in improving growth over a rotation. Carter *et al.,* (1990) found that accelerated-grown seedlings that underwent two growing cycles were adequate for roguing out the poorest families prior to installation of field tests, although some misclassification in family ranking occurred in comparison to height at age 7. Genetic correlation for height between age 6 and age 14 was estimated at 0.71 (Magnussen and Yeatman, 1990). Jeffers and Jensen (1980) found that height at age 10 reliably predicted height at age 20.

Clonal and/or family variation was observed for a number of cone and seed production traits, including cone volume, number of empty seeds, and seed potential (Todhunter and Polk, 1981; de Groot and Schnekenburger, 1996). While variation has been observed in cotyledon number and length and timing of budset (Saenz-Romero and Guries, 2002), lammas growth was not related to height and did not differ between families (Canavera, 1975). The latter study also found no family differences in the age when flowering first occurred.

Maley and Parker (1993) intensively studied the region in northwestern Ontario around Lake Nipigon (north of Lake Superior), which is known for its east-west discontinuity in the clinal variation of many jack pine traits. Van Niejenhuis and Parker (1996) noted that irregularities in clinal patterns from this area correspond to irregularities in local climate patterns. Most of the variation in cone and needle traits was within stand or within tree, not between stands. Results were inconclusive in differentiating between the hypothesis that separate lineages migrated in opposite directions around Lake Superior post-glaciation, and evidence that the patterns are caused by adaptation to an abruptly changing climate within the region.

As observed in many species, wood quality traits of jack pine appear to be more highly heritable than growth traits. Family heritability estimates for wood density of trees aged 5 to 20 range from 0.40 to 0.73, and individual heritabilities between 0.31 and 0.93 (Okwuagwu and Guries, 1980; Ernst *et al.,*

1983; Villeneuve *et al.,* 1987a, 1987b; Park *et al.,* 1989; Magnussen and Keith, 1990; Klein, 1995). Family heritability for tracheid length is also high (0.50) (Okwuagwu and Guries, 1980). Stem straightness is also highly heritable, with an estimated h^2_i of about 0.3 (Magnussen, 1990; Klein, 1995). Conversely, while the number of leaders was variable, there was no genetic component to the variability (Morris *et al.,* 1992). Most of these estimates were based on single-site analyses, and thus possibly inflated, but it is evident that wood quality traits are highly heritable.

Relative density decreased from the pith to between age 9 to 12, then rapidly increased to age 15, after which increases were more gradual (Villeneuve *et al.,* 1987b). It has been suggested that wood density could be selected for by age 6 or 7 (Villeneuve *et al.,* 1987b). The Pilodyn tester was considered reliable enough for low-intensity selection to rogue out families with the lowest wood density (Villeneuve *et al.,* 1987a), but not recommended for selection of the best genotypes (Zhang, 1995).

General combining ability, but not specific combining ability, was significant for both juvenile wood specific gravity and tracheid length (Okwuagwu and Guries, 1980). Wood density and stem taper were found to have low phenotypic variation (as expressed by the coefficient of variation), compared to high phenotypic variation observed in stem volume, percent heartwood, and dry fiber weight (Magnussen and Keith, 1990; Zhang and Chui, 1996). Most of the phenotypic variation in wood density resides within families, with between 7% and 11% due to family differences (Villeneuve *et al.,* 1987b; Park *et al.,* 1989; Magnussen and Keith, 1990; Zhang and Chui, 1996).

Jack pine growth traits are negatively correlated with wood quality traits, in particular stem straightness, and branch angle, length and diameter (Park *et al.,* 1989; Adams and Morgenstern, 1991; Morris *et al.,* 1992). Park *et al.,* (1989) described a negative relationship between growth and wood density. However, others have found that stem volume and wood density were either not correlated or positively correlated (Magnussen and Keith, 1990; Zhang, 1995; Zhang and Chui, 1996), implying that breeding programs based on selection for growth would not necessarily cause a reduction in wood density. Stand spacing also affects growth and wood quality, with wide spacing producing poor stem and branch form, and dense spacing causing reduced growth due to crown closure and suppression (Magnussen and Yeatman, 1987).

Isozyme variability in jack pine has been well documented (*e.g.* Dancik and Yeh, 1983; Danzmann and Buchert, 1983; Cheliak *et al.,* 1985; Snyder *et al.,* 1985; Wheeler and Guries, 1987; Xie and Knowles, 1991; Fu *et al.,* 1992; Gauthier *et al.,* 1992; Godt *et al.,* 2001; Saenz-Romero *et al.,* 2001). Variability has also been observed in RAPD (Nkongolo and Gratton, 2001; Ye *et al.,* 2002) and sequence-tagged-site (STS) (Perry and Bousquet, 1998) markers, chloroplast DNA (Wagner *et al.,* 1987, 1988, 1991; Govindaraju *et al.,* 1988), and mitochondrial DNA (Dong and Wagner, 1993). Variability in the amount of DNA per cell has been observed (Miksche, 1968), with superior families having less embryo and megagametophyte nuclear DNA than inferior families (Wyman *et al.,* 1997). Superior families were also more amenable to producing viable plants from *in vitro* culture (Briand *et al.,* 1998). Gene transfer in jack pine has been accomplished using electroporation (Tautorus *et al.,* 1989), microprojectile bombardment (Hay *et al.,* 1994), and *Agrobacterium rhizogenes* (McAfee *et al.,* 1993).

Family differences have been observed in water-use efficiency (Cantin *et al.,* 1997) and carbon isotope discrimination (Zhang and Cregg, 2096). Jack pine is more tolerant of soil salinity and alkalinity than lodgepole pine, white spruce (*Picea glauca*), poplar (*Populus*) and alder (*Alnus*). Genotypic differences within species were noted in response to salinity by Khasa *et al.,* (2002), who suggested developing breeding programs for salt-tolerant genotypes for reclamation of oil sand deposits.

5.3.3. Resistance to pests

Differences between sources in resistance to white pine weevil have been reported (Batzer, 1961, 1962; King, 1971; Hodson *et al.,* 1982; de Groot and Schnekenburger, 1999). Batzer (1962) and de Groot

and Schnekenburger (1999) observed that local sources may be the most weevil-resistant, best-adapted populations. King (1971) and Hodson *et al.,* (1982) found that the tallest trees were the most heavily weeviled.

Northern jack pine populations were more susceptible to the eastern pine shoot borer (King, 1971; Jeffers, 1978; Hodson *et al.,* 1982, 1986). Jeffers (1978) observed that incidence was correlated with length of the terminal shoot during the period of borer oviposition in May, with longest terminals having highest incidence and shortest terminals the lowest. Source variability was also described for resistance to the northern pitch twig moth, but was not related to latitude (Hodson *et al.,* 1982, 1986).

Northern jack pine populations are more susceptible to eastern gall rust than southern populations (King, 1971; Hodson *et al.,* 1982, 1986). King (1971) proposed that southern populations may have been subjected to more intense infestations and so developed resistance. As eastern gall rust is morphologically indistinguishable from western gall rust, King (1971) proposed that resistance may be conferred against both rusts.

Jack pine needlecast fungus ranges from Wisconsin to Nova Scotia. Source differences were found in susceptibility to it, and consistent over years and across sites, when tested in the Lake States (King and Nienstaedt, 1965). The most resistant jack pine populations were from Lower Michigan, the least resistant from northeastern Minnesota.

Jerome and Ford (2002) studied the relationship between *Arceuthobium americanum* (lodgepole pine dwarf mistletoe), which is primarily western in range, and its two host species, lodgepole pine and jack pine. There were three genetic races of the parasite, but genetic distances revealed that hosts were divided into only two groups: one being lodgepole pine, and the other jack pine and its hybrids with lodgepole pine. The mistletoe strain on jack pine had twice as much population differentiation as that of the host.

King (1971) proposed that heavy infestations of pests may not affect tree height, as laterals quickly assume dominance if the terminal shoot is damaged. However, Hodson *et al.,* (1982) observed that eastern gall rust, pine shoot borer, white pine weevil and redheaded pine sawfly infestations all caused height decreases by age 15.

6. Tree growth and phenology

Jack pine is a relatively small tree, often up to 20 m tall with a dbh of 30 cm, occasionally reaching 25 m tall with a dbh of 35 cm. The bark is thin, reddish-brown to gray, becoming dark brown and flaky with age. Eyre and LeBarron (1944) noted the following factors as contributors to optimum early growth: (1) full sunlight; (2) fertile, well-drained but moist soils; (3) moderate summer temperatures; and (4) freedom from pests and competition. Young seedlings are very sensitive to shade and root competition. Compared to associated conifer species in the Lake States, juvenile growth rates are high (Eyre and LeBarron, 1944). With the exception of tamarack (*Larix laricina*), growth rate for the first 20 years is generally greater than for any other conifer in its natural range (Rudolf, 1965). In 5-year-old New Brunswick plantations, average height ranged from 1.2 to 1.4 m (Barteaux and Bailey, 1986). In Manitoba, 5-year-old seedlings averaged 0.5 to 1.2 m; growth was poorest on dry sites, better on fresh sites, and best on moist sites (Cayford, 1963a).

Shoot growth begins from late April to early May at sites in Minnesota, Michigan and Ontario, and is largely completed in 61 to 68 days (Rudolph and Laidly, 1990). In Wisconsin shoot elongation begins in the first week of May and is complete by mid-July; differentiation of lateral bud primordia occurs from early July to September (Cecich, 1983b). First year seedlings may exhibit continuous height growth into autumn as long as the temperature and moisture conditions are favourable (Eyre and LeBarron, 1944).

Jack pine may develop a taproot that is maintained into maturity. Where a distinct taproot is lacking, lateral roots may turn and grow downward in the proximity of other trees (Rudolf, 1958). On deep soils, roots may reach a depth of 270 cm or more, but more often the bulk of roots occur within the upper 46 cm (Rudolph and Laidly, 1990).

Jack pine is generally rather short-lived, with individuals living up to 180 to 200 years. Stands may survive to 100 years (Benzie, 1977), although they usually begin to disintegrate after 80 years on good sites and 60 years on poor sites (Rudolf, 1965). In Ontario, jack pine grows rapidly for the first 40 years, then shows growth reduction at rates that vary with stand and site conditions (Galloway, 1986). Height and diameter growth of stands vary with a number of factors, including soil moisture regime, soil texture and petography, and regional macroclimate; in northern Ontario, site indices decreased from the mid-humid warm-boreal climate (Hills Site Region 4E) to the dry-humid mid-boreal climate (Site Region 3W) (Chrosciewicz, 1963). The best growth and development in Canada is achieved in a wide area to the north and west of Lake Superior (Hosie, 1979).

Jack pine exhibits an intermediate self-pruning capacity in dense stands. On better sites, stands can undergo considerable mortality during intermediate stages of development because of natural thinning (Galloway, 1986; Kenkel *et al.,* 1997). On poorer sites, however, natural thinning may be slow (Benzie, 1977). Open-grown trees and those on poor sites may be short and shrub-like, developing undesirable branch and form characteristics (Eyre and LeBarron, 1944; Galloway, 1986). In well-stocked stands, trees develop a narrow crown that may cover 30 to 45% of the stem (Rudolf, 1965).

Under favourable conditions, jack pine may exhibit both lammas and proleptic growth. Rudolph (1964) found that trees exhibiting lammas growth had a longer growing period and greater total growth than individuals that exhibited normal growth, although the resulting shorter internodes adversely affected wood quality. Lammas growth may be more susceptible to autumn frost injury.

7. Ecology

7.1. Habitat

7.1.1.   Climate

Across its broad range, jack pine tolerates a wide range of climatic conditions. Though the eastern portion of its range has a maritime climate, most of the range is inland and continental, with warm to cool summers, very cold winters, and low rainfall (Rudolf, 1965). Rudolph and Laidly (1990) have described the climate: Average temperatures range from -29ºC to -4ºC in January and 13ºC to 22ºC in July. Average annual minimum and maximum temperatures range from -46ºC to -21ºC and 29ºC to 38ºC respectively, with annual mean temperatures ranging from -5ºC to 4ºC. Average total annual precipitation ranges from 250 to 1,400 mm, with 380 to 890 mm more common. Summer droughts are common in the Lake States and western portion of the range (Rudolf, 1958).

The northern limit of the species' range closely follows the 29ºC mean annual isotherm (Rudolph and Laidly, 1990; Despland and Houle, 1997), extending into the permafrost zone in the northwest (Rudolf, 1958). The frost-free period typically averages 80 to 120 days, with extremes ranging from 50 to 173 days (Cayford *et al.,* 1967; Rudolph and Laidly, 1990). The date of the last killing spring frost ranges from 30 April to 1 July, and of the first killing autumn frost from 10 August to 20 October (Rudolf, 1958).

7.1.2.   Soils and site types

Across its range, jack pine occurs on a variety of soils and site types, although most characteristically on sandy soils (Spodsols or Entisols) (Rudolph and Laidly, 1990). Typical sites include dry sand plains

developed on glacial outwash, morainic, aeolian and lacustrine deposits (Cayford and McRae, 1983). It is also found on fresh to moist sands, on tills, and thin soils overlying rock outcrops. In Ontario it can be found on glacio-fluvial plains, eskers, dunes and kames of sandy acidic soil, and occasionally on lowland sands and clays (Chrosciewicz, 1963). In the Lake States, it typically occurs on acidic sand plains of glacial-outwash origin, with low moisture and fertility, and a level or gently rolling topography (Eyre and LeBarron, 1944; Rudolf, 1963). In the eastern to central range, jack pine is also found on the thin moderately fertile rock-outcrop soils that overlay the Canadian (or Precambrian) Shield (sometimes called the Laurentian Plateau). In northwestern Canada, it may also grow on morainic hills (Rudolf, 1958).

The more productive sites in Ontario include silty sands, loamy sands and loams (Chrosciewicz, 1963), although competition from other species may limit its occupation. Productivity studies carried out in Québec, Ontario, Manitoba and Saskatchewan show that jack pine generally achieves best growth on fresh to somewhat moist upland till sites of fine sand to clay texture, as well as on moist sands (Cayford *et al.,* 1967). Best growth in the Lake States occurs in Minnesota, where despite lower rainfall than other states of the region, soils are generally more fertile (Eyre and LeBarron, 1944). Poorer sites include dry, weakly podzolised sands and wet poorly drained soils (Cayford *et al.,* 1967). Because of its modest moisture and nutrient requirements, jack pine can grow on sites too dry, shallow or infertile for competing tree species to survive.

7.2. Synecology and associated species

Jack pine typically establishes after fire, often forming pure, even-aged stands. Frequently, however, it is associated with other tree species. Throughout the boreal forest, it commonly occurs with black spruce (*Picea mariana*) on moist to fresh sites, and with trembling or quaking aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*) on silty sands, loamy sands and loams; and less commonly with balsam fir (*Abies balsamea*) and white spruce (*P. glauca*) (Chrosciewicz, 1963; Rudolph and Laidly, 1990). In the Great Lakes–St. Lawrence Forest Region, it also occurs with northern pin oak (*Quercus ellipsoidalis*), bur oak (*Q. macrocarpa*), eastern white pine and red pine (Cayford *et al.,* 1967). Where it occurs in mixtures it is often dominant, or codominant with trembling aspen, birch and sometimes red pine. Additional associated species on dry to mesic sites may include northern pin oak, bur oak, bigtooth aspen (*P. grandidentata*) and balsam poplar (*Populus balsamifera*) (Rudolph and Laidly, 1990). Less common associates include red maple (*Acer rubrum*), red oak (*Q. rubra*) and white oak (*Q. alba*) (Rudolf, 1958). In the east, it may be found infrequently with white oak, pin cherry (*Prunus pensylvanica*), gray birch (*B. populifolia*), red spruce (*P. rubens*) and pitch pine (*P. rigida*) (Rudolf, 1965; Greenwood *et al.,* 2002).

A variety of herbs and shrubs, ferns, mosses, and lichens are associated with jack pine, varying in distribution with soil type and moisture regime. Common on many site types across much of its extensive range are Virginia strawberry (*Fragaria virginiana*), late low-bush blueberry (*Vaccinium angustifolium*), common red bearberry (*Arctostaphylos uva-ursi*), short-awn mountain-rice (*Piptatherum pungens*), prickly rose (*Rosa acicularis*) and in the east sweetfern (*Comptonia peregrina*) (Cayford, 1963a, 1963b; Chrosciewicz, 1970, 1988b). On fresh to moist sites, the shrubs include alders (*Alnus viridis* subsp. *crispa* and *A. incana* subsp. *rugosa*), willows (*e.g.* gray willow [*Salix bebbiana*]), choke cherry (*P. virginiana*), pin cherry and beaked hazelnut (*Corylus cornuta*). Other common species on moist sites include Canadian bunchberry (*Cornus canadensis*), arctic sweet-coltsfoot (*Petasites frigidus* var. *palmatus*), bluejoint (*Calamagrostis canadensis*), rusty Labrador-tea (*Ledum groenlandicum*), American twinflower (*Linnaea borealis* subsp. *americana*) and common red raspberry (*Rubus idaeus* subsp. *strigosus*) (Chrosiewicz, 1983). Associated ferns may include northern bracken fern (*Pteridium aquilinum*). On drier sites, associates include reindeer-mosses (*e.g. Cladonia rangiferina*) and other lichens, Canadian small pussytoes (*Antennaria howellii* subsp. *canadensis*) and sometimes prairie redroot (*Ceanothus herbaceus*) (Chrosciewicz, 1983), while a shrub layer may be

lacking (Rudolf, 1958). Throughout much of its range, Schreber's moss (*Pleurozium schreberi*) is a common associate on many sites; other mosses and club-mosses may include juniper-leaf hair moss (*Polytrichum juniperinum*), glittering feather moss (*Hylocomium splendens*), ostrich-plume feather moss (*Hypnum crista-castrensis*) and stiff ground-pine (*Lycopodium annotinum*) (Rudolf, 1958; Cayford, 1963b; Chrosciewicz, 1970, 1988a, 1988b). In the eastern portion of its range, rhodora (*Rhododendron canadense*) is a common associate (Rudolf, 1965).

7.3. Competition, succession, and stand structure

Jack pine is a shade-intolerant, early-seral, relatively fast-growing and short-lived species. It is slightly more tolerant than aspen, birch and tamarack, but less so than many other conifers it is associated with such as black spruce, white spruce and balsam fir. Throughout much of its range, the major causes of catastrophic tree mortality and stand loss are fire in the west, and a mix of fire and budworm in the east. Jack pine stands are particularly susceptible: they commonly occur on drier sites, foliage is highly combustible and the bark thin. Indeed, the species may be adapted to facilitating fire spread (Kelsall *et al.,* 1977). Trees are often girdled and killed by fire (Cayford and McRae, 1983). In the central and northern portions of its range, jack pine succession is closely linked to forest fire regimes (Conkey *et al.,* 1995). With its serotinous cones, multi-cohort aerial seed banks, and early rapid growth, the species is well adapted to re-establishing sites following fire (Greene *et al.,* 2004). It can recolonise very large burns where it was present in the pre-fire landscape (Greene *et al.,* 1999). As most seedlings establish within 2 or 3 years of a fire, the result is often extensive even-aged stands. Greene and Johnson (1999) found that jack pine re-establishes roughly in proportion to its pre-fire basal area, reflecting in part the available seed bank. It may be found to occupy a broad range of site types after a burn, from muskeg (peatland) to ridge tops (Farrar, 1995; Pellerin and Lavoie, 2003).

Fire frequency is critical in determining jack pine population dynamics. Long-term maintenance of local populations depends on fire return intervals that are less than the average lifespan of individual trees (Desponts and Payette, 1992), but long enough for the development of adequate seed banks. A frequency of less than 15 to 20 years may result in local elimination, because of inadequate seed banks and the loss of potential future seed producers (Farrar, 1995; Greene and Johnson, 1999). Frequent fires in the Lake States may result in its elimination in favour of oaks such as northern pin oak (Rudolf, 1965). Conversely, at the limits of its range in northern Québec, jack pine is succeeded by black spruce in areas with long fire intervals (Desponts and Payette, 1992). The absence of the natural fire regime would result in elimination of jack pine from parts of its range, to be replaced by more shade-tolerant competitors (Cayford and McRae, 1983).

In the absence of fire in the Boreal and the Great Lakes–St. Lawrence Forest Regions, jack pine is often succeeded by the more tolerant black spruce, white spruce and balsam fir (Cayford *et al.,* 1967). On productive sandy sites in Minnesota, it may be succeed by red pine, then white pine and mixed hardwoods; in some cases succession is directly to hardwoods such as white birch and trembling aspen (Rudolf, 1965). In the Boundary Waters Canoe Area of northern Minnesota, succession may be to black spruce – feather moss forest types, or balsam fir – white birch – white spruce types (Cayford and McRae, 1983).

In some parts of its range jack pine is self-replacing even in the absence of fire, typically because of an ability to survive on sites too harsh for competitors. Desponts and Payette (1992) found in northern Québec that it was able to regenerate on sites of exposed mineral substrates. Among marginal disjunct coastal populations in Maine, Conkey *et al.,* (1995) observed continuous regeneration on sites too poor and shallow for other species; cone serotiny was low in these populations (negating the need for fire to achieve seed dispersal). In the southwestern part of its range, jack pine may continuously regenerate on very dry sites (Cayford *et al.,* 1967).

7.4. Species interactions and dynamics

A variety of insects affect the survival and growth of jack pine. Jack pine budworm (*Choristoneura pinus pinus*) is one of the most significant defoliators in central Canada and the Lake States (Howse, 1984). It feeds mainly on new growth, preferring male strobili clusters and new foliage, and can cause growth loss, top kill and mortality (Conway *et al.,* 1999). Swaine jack pine sawfly (*Neodiprion swainei*) is also an economically important pest, particularly in eastern Canada. Feeding on needles, it causes top kill, and if populations are sufficient, tree mortality occurs within 1 year or more typically 3 to 4 years (Howse, 1984).

In jack pine seed orchards in Wisconsin, the mirid *Platylygus luridus* has caused conelet abortion at rates of 51 to 87% (Rauf *et al.,* 1984). De Groot and Schnekenburger (1999) found that white pine weevil and eastern pine shoot borer respectively damaged 14.5% and 26.6%, of trees in an open-pollinated family test in Ontario. These two pests may significantly reduce height growth in the Lake States (Hodson *et al.,* 1982). Other damaging insects include root borers (*e.g.* pales weevil, *Hylobius pales*), shoot and stem borers (*e.g.* northern pine weevil, *Pissodes approximatus*), needle miners (*e.g. Argyrotaenia tabulana*) and root feeders (*Phyllophaga* spp.) (Rudolph and Laidly, 1990).

Armillaria root rot (*Armillaria mellea*) frequently kills seedlings and juvenile stands. Infection by sweetfern blister rust results in cankers that reduce the commercial value of trees; volume growth can be reduced by 20%, and younger trees killed (McGauley and Gross, 1984). *Scleroderris* canker occurs throughout the range of jack pine and often causes mortality of infected seedlings. Common foliar diseases include needle rust (*Coleosporium asterum*), needlecast and Diplodia tip blight (*Sphaeropsis sapines*).

A number of vertebrate species may damage or kill jack pine. Chrosciewicz (1988a) found that snowshoe hares (*Lepus americanus*) clipped tops of more than 40% of natural and seeded seedlings, although most damaged plants survived. In western Manitoba, seedlings may be damaged by elk (*Cervus canadensis*) when its population levels are high (Rudolph and Laidly, 1990). Jack pine is generally considered a food of medium preference for deer (*Odocoileus*) (Cayford and McRae, 1983). Red squirrels (*Tamiasciurus hudsonicus*) frequently harvest jack pine cones; Rauf *et al.,* (1985) reported losses of 10% of conelets and 30% of cones.

Essential to Kirtland's warbler (*Dendroica kirtlandii*), pure young jack pine stands in north-central Michigan provide the only nesting habitat used by this endangered bird (Benzie, 1977; Farrar, 1995).

8. Reforestation practices

8.1. Provenance transfer

Where the jack pine range overlaps that of lodgepole pine in the west, the latter is preferred for commercial purposes. Extensive jack pine provenance testing has been carried out in eastern Canada and the Lake States. In numerous studies, local seed sources have typically performed well, but provenance transfer may further enhance performance.

The best sources within Saskatchewan were from the province's west and south (Klein, 1989a). Jack pine rangewide provenance testing in Manitoba found that better sources were from western and central Ontario and Québec, Minnesota and Manitoba, whereas poorly performing provenances included populations from eastern Ontario and Québec, northeastern USA, the Maritimes, and Michigan, Saskatchewan, Alberta and the Northwest Territories (Klein, 1990). For eastern Canada, Magnussen and Yeatman (1988b) recommended the use of well-defined breeding zones, and larger breeding zones in southern, milder areas. Matyas and Yeatman (1992) developed an ecological distance index based upon heat sum units and latitude for recommending transfer distances in Ontario. Using this index, a moderate northward transfer was recommended.

In the Great Lakes region including Ontario and the Lake States (Michigan, Wisconsin and Minnesota), for best growth Morgenstern and Teich (1969) recommended moving northern provenances 2-3° southward, and southern provenances 1-2° northward. Within this region, northern provenances generally grew better when transferred southward, but best growth on southern sites was from southern provenances (Yeatman, 1974). Local sources often were among the best performers, except for slow-growing populations from east of Lake Nipigon and north of Lake Superior in Ontario (Yeatman and Morgenstern, 1979).

Rudolf and Yeatman (1982) summarised various early studies. Schnare (1969) found that southern provenances grew taller in Missouri. In a Nebraska test, best sources were from Ontario and Québec, and shortest trees from the Northwest Territories (Sprackling and Read, 1975). Sources from Lower Michigan exhibited the best performance in Michigan, Wisconsin, Minnesota and Petawawa, Ontario (King, 1966; Alm and Jensen, 1969; Canavera and Wright, 1973; Yeatman, 1974). Local sources were also superior (Schantz-Hansen and Jensen, 1952; King, 1966; Jeffers and Jensen, 1980; Rudolph and Yeatman, 1982). Rudolph and Yeatman (1982) recommended that movement of sources up to 160 km northward could increase growth in the Lake States region. Jeffers (1971) had recommended using only local seed in Lower Michigan and in Minnesota, and using a mixture of local and Lower Michigan seed in Wisconsin and Upper Michigan.

Hyun (1979) used cluster analysis to analyze rangewide populations tested in Minnesota. He obtained five clusters, with the Lake States cluster and the Northwest Territories–Alberta–northern Québec cluster being the most distinct. Jeffers and Jensen (1980) assembled populations tested at fourteen Lake States sites into three groupings. The northernmost group was from the area with the harshest climates, and these sources had the worst performance and highest eastern gall rust incidence. The southernmost group, with the mildest climate, had best performance and lowest eastern gall rust incidence.

Six provenances from Ontario were tested in New Zealand at two sites (one on the North Island, one on the South Island) (Sweet and Thulin, 1963). The tallest and earliest to flower sources were the southernmost from the mildest climates.

8.2. Breeding programs

Jack pine breeding programs have been established throughout much of its natural range. Tree improvement programs are particularly important in the Lake States and central and eastern Canada. Jack pine is considered a minor timber species in Nova Scotia and Prince Edward Island, but the second most important in New Brunswick, which has completed establishment of second generation programs (Tosh and McInnis, 2000). Ontario is establishing second generation progeny tests (Boysen *et al.,* 2000), while Manitoba was planning to establish third generation tests (Klein, 1998). Lodgepole pine is of greater interest than jack pine within Alberta. However, Alberta has made both jack pine and jack pine × lodgepole pine hybrid wild stand selections and established a clonal jack pine seed orchard for the northeastern boreal region, and is testing wood density and fibre length of superior parent trees (Hansen *et al.,* 1997). Minnesota and Michigan have established second generation seed orchards (Rudolph 1984; Stine *et al.,* 1995), and seed orchards are also in place in Wisconsin and Maine (Rudolph 1984; Carter and Simpson, 1985).

Selection is primarily based upon growth and stem quality traits; pest resistance may also be important. Commonly selection is based upon age-10 measurements, although New Brunswick makes selections on height at age 7 (Fowler, 1986), and selections are made in Manitoba and Saskatchewan tests based on measurements at age 20 (Klein, 1998). First generation programs are usually based on open-pollinated family selection. Sometimes, as in Minnesota, progeny tests are rogued for conversion to seed orchards after measuring (Stine *et al.,* 1995). Second generation breeding strategies are more diverse, and typically include stratified breeding populations. New Brunswick uses a combination of polycrossing for breeding value estimation and single-pair assortative mating to produce full-sib crosses,

which are assigned to sublines (Fowler, 1986). Saskatchewan (Sande and Corriveau, 2000), Manitoba (Klein, 1998) and the Lake States (Rudolph 1984) are also using sublined breeding populations. Ontario is using a nucleus breeding system, with the breeding population substructured into an elite population produced by single-pair mating and an open-pollinated infusion population (Joyce and Nitschke, 1993).

Provenance tests generally provide information on which the breeding zone delineation and program establishment are based. Ontario has numerous jack pine breeding zones, but has amalgamated a number of them in the northwestern part of the province based on Focal Point Seed Zone methodology (Parker and van Niejenhuis, 1996). New Brunswick comprises only one breeding zone (Fowler, 1986); there are three in Manitoba and Saskatchewan (Klein, 1982).

New Brunswick is using accelerated growth cycles at the greenhouse stage to rear grafts prior to assigning them to sublines, and is experimenting with miniaturised jack pine meadow seed orchards, which have been established using accelerated-grown stock (Simpson, 1997). Supplemental mass pollination using the best clones as pollen sources is used within the meadow orchards to increase amounts of filled seed (Simpson, 1997). Realised gain trials have also been established (Simpson and Tosch, 1997).

8.3. Reproductive propagation

8.3.1. Flower induction

Jack pine is one of the youngest pines to flower, and under natural conditions may produce male and female strobili at 3 years of age (Righter, 1939), albeit at low frequencies (Rudolph 1966b). Johnson and Critchfield (1978) found female strobili on 10-month-old seedlings of a precocious lodgepole pine × jack pine hybrid cross. More typically, jack pine begins to reproduce at 5 to 10 years when open-grown, and 10 to 25 years in closed stands (Roe, 1963). Production of first male strobili usually lags 2 to 3 years behind that of female strobili, and may contribute to poor seed yield (Cecich, 1983a).

Strobili production can be enhanced using cultural practices. Rudolph (1966b) applied an accelerated-growth regime that included a 20-hour photoperiod in a greenhouse environment prior to transplanting seedlings to a nursery bed. Up to 62% of 23-month-old seedlings produced strobili, averaging 2 per tree, of which 51% developed into mature cones yielding an average of 26 seeds per cone and 77% germination. Rudolph (1979a) induced female strobili on 1% of 12-month-old seedlings that had been given 10 weeks of favourable greenhouse conditions prior to transplanting. Male strobili production did not respond as readily to accelerated-growth treatments (Rudolph 1966b, 1979a). Cecich and Bauer (1987) used artificial photoperiod and temperature regimes to apply a compressed reproductive cycle to 2-year-old seedlings, which produced seed 9 months after the pollination of female strobili (rather than the natural 16 months), although the yield of filled seeds was low. Moisture stress applied as three drying cycles from June to August yielded four times more female strobili on 12-month-old accelerated-growth seedlings than controls (Riemenschneider, 1985). In contrast, Fogal *et al.,* (1995) found that moisture stress slightly reduced female strobilus production. Nitrogen deficiency enhanced pollen strobilus production on 2-, 3- and 6-year-old seedlings (Fogal *et al.,* 1994, 1995).

Gibberellin, in particular $GA_{4/7}$, has been used to promote early and enhanced male and female strobilus production. Biweekly foliar spray applications at concentrations of 400 and 600 mg per L, timed to affect reproductive bud differentiation, have been successful (Cecich, 1983b; Fogal *et al.,* 1994; Ho and Hak, 1994). Fogal *et al.,* (1996) were able to increase production of pollen strobili but not seed strobili using stem injections of $GA_{4/7}$. The effects of accelerated-growth treatment may be enhanced by the application of $GA_{4/7}$ (Cecich, 1981, 1983a; Cecich *et al.,* 1994). Gibberellin may help to compensate for variation in flowering among families (Cecich *et al.,* 1994); treatment periods may be timed to capture family differences in phenology (Ho and Hak, 1994).

8.3.2. Vegetative propagation

Long-shoot cuttings from juvenile jack pine generally root well, with rooting frequencies of 70 to 95% reported (Armson *et al.,* 1975; Browne *et al.,* 1996, 1997a). However, attempts to root cuttings from donors greater than 5 or 6 years old have met with less success. Zsuffa (1974) achieved an average of 6.6% rooting from 6- and 10-year-old donors; Potapova (1998) got no rooting from donors 20 to 25 years old. Browne *et al.,* (1997a) were able to attain 80% rooting using 3-year-old donors, but only 20% (with same treatment) on cuttings from 7-year-old donors. They identified a transitional period at 4 to 6 years of age – between juvenility and maturity – within which rooting ability drops significantly. In addition to rooting ability, the length and number of roots produced by cuttings also show an age-related decline (Browne *et al.,* 1997a, 1997b). The change in rooting ability of juvenile and mature cuttings has been linked to differences in net photosynthetic rate, carbohydrate partitioning, and starch metabolism (Haissig, 1989). Decreases in rooting ability with increasing donor stock age are well documented in pines (*e.g.* Girouard, 1971).

Several studies have examined the potential of rooting proliferated dwarf shoots, which are needle fascicles in which the diminutive shoot apex develops into a functional long shoot (Ewers, 1983), a response often induced by pruning. Rudolph and Nienstaedt (1964) rooted needle fascicles; only those from pruned donors showed fascicular bud development, rooted well and produced normal stems. Browne *et al* (1997b) achieved 87%, 86%, 60% and 49% rooting, using 2-, 4-, 6- and 8-year-old proliferated dwarf shoots respectively, but achieved only 20 to 24% rooting of 11-year-old shoots. Browne *et al.,* (2001) significantly increased the production of proliferated dwarf shoots on pruned seedlings with foliar applications of benzyladenine (BA), although maximum rates had deleterious effects on subsequent rooting; the optimum treatment yielded 22 to 29 rooted cuttings per 6-month-old donor. Rooting of proliferated dwarf shoots may thus provide an economic means of expanding seed of superior controlled cross pollinations into production populations (Klein *et al.,* 1995).

Treatment of cuttings with growth hormones may increase rooting frequency. Naphthalene acetic acid (NAA) increases speed and abundance of adventitious root primordium development (Haissig, 1982). NAA can significantly increase rooting (Browne *et al.,* 2000), and it may delay (but not halt) the age-related decline in rooting ability (Browne *et al.,* 1997a). Synthetic auxins (IBA, NP-IBA and P-ITB) improved rooting of cuttings from young seedlings (Haissig, 1983, 1990). Rooting ability may be affected by length of cutting (Zsuffa, 1974), shoot type (dwarf shoot vs. long shoot) (Browne *et al.,* 1997b), and crown position of the cutting (Browne *et al.,* 1996, 1997a). Treatment of donor stock with chilling and moderate fertiliser levels enhanced rooting ability (Browne *et al.,* 2000), whereas shade treatment was deleterious (Haissig, 1990).

Significant genetic variation in rooting ability of jack pine exists (Zsuffa, 1974). Exceptional individuals have been observed; for example, Browne *et al.,* (1997a) noted that two 30-year-old ortets yielded 57 to 58% rooting. Although the potential for selecting for good rooting clones exists, genetic correlations between rooting and other traits of economic importance (*e.g.* volume growth) have not been reported.

The first successful attempts at using somatic embryogenesis to propagate jack pine were carried out in 1995, but jack pine is recalcitrant to *in vitro* culture (*e.g.* Briand *et al.,* 1998; Park *et al.,* 2000; Pelletier and Laliberté. 2000). Charbonneau and Laliberté (2004) achieved promising results by culturing meristematic nodules from zygotic embryos, though organogenesis has yet to be optimised.

8.4. Stock deployment

The deployment methods for jack pine vary across jurisdictions, but typically consist of a combination of manual or machine planting of bare root, transplant or container stock, and aerial or spot seeding. The principal method in New Brunswick and Nova Scotia has been manual planting of

2-0 bare root and container stock; seeding is rare (Barteaux and Bailey, 1986). Machine and hand planting of 3-0 and 2-0 stock have been used in Saskatchewan, container stock less so (Little, 1984). In Québec, planting of 3-0 and 2-0, as well as 2-1 and 1.5-1.5 transplants and container stock have been practiced, and aerial seeding and spot ground seeding used (Couture and Dancause, 1984). In Ontario, planting of bare root and container stock and aerial seeding are practiced.

8.5. Conservation of genetic resources

Jack pine is a widespread, predominantly outcrossing species with high levels of gene flow *via* pollen dispersal. Most of the genetic variation is found within populations. Differences in diversity measures between natural stands and plantations have not been observed (Knowles, 1985). However, resource exploitation, habitat fragmentation and land-use change may contribute to depletion of the genetic resource. Populations in marginal habitats, such as at the limits of its range, or those isolated and undergoing more frequent inbreeding, are most vulnerable to loss in genetic diversity. Populations with low levels of diversity may be unable to adapt to changing environmental conditions such as climate change due to global warming, which would be expected to exert strong selective pressures. Selection against genotypes may occur during cone collection, nursery seedling culture, tree improvement programs, precommercial thinning, and harvesting.

In situ conservation may include maintenance of forest reserves, protected areas, and migration corridors. Reserves sufficient to allow for natural evolutionary processes to occur such as gene flow, mating, selection, and mutation are preferred. Seed transfer and stand management practices that are managed with the goal of increasing diversity may provide other conservation measures. Populations most at risk of genetic depletion need to be identified, and steps taken to protect them. Baseline biological data and knowledge regarding population structure, such as the information from provenance studies, are needed when developing effective conservation strategies. Fowler (1986) described a reserve-stand policy for *in situ* conservation of jack pine populations in New Brunswick. Boyle (1992), in a summary of forest genetic conservation activities in Canada, listed two limestone ecotype conservation areas in Ontario that include jack pine, and reserve stands of jack pine in Québec, Ontario and Manitoba.

Ex situ conservation offers additional protection of the gene pool, and may be necessary for populations most at risk. *Ex situ* reserves include seed bank storage, germplasm cryopreservation, clone banks, arboreta, seed orchards, field trials, and plantations. Boyle (1992) listed various ongoing *ex situ* activities in Canada. Most of the Canadian provinces maintain seed banks. The National Forest Genetic Resources Centre, which includes the National Tree Seed Centre, is operated by Natural Resources Canada at the Atlantic Forestry Centre with the goal of gene conservation of native species (Simpson and Daigle, 1998). Rangewide seed collections of jack pine are being obtained. Active gene management that could be incorporated into breeding programs includes strategies such as the multiple population breeding system, which is designed to manage populations in breeding programs in such a way that genetic diversity is maintained or even increased despite reduction of the population size through ongoing selection (Eriksson *et al.,* 1993).

9. Summary

Jack pine is one of the most widespread tree species and is the most widespread pine species in North America, growing farther north than any other pine. It is of significant economic importance in Canada and in the Lake States of the USA, where it is harvested for pulp and lumber products.

The population dynamics of jack pine are closely linked to fire regimes, to which the species is well adapted. With serotinous cones, large aerial seed banks and rapid early growth, it readily re-establishes following burns. In the absence of fire, jack pine is typically succeeded by more tolerant species; however, on some poor sites in marginal portions of its range it can regenerate without fire. Although its best growth is achieved on fertile sites of fresh to moist sands and loams, jack pine can grow on very dry, shallow and infertile sites on which competing tree species cannot survive.

Jack pine is precocious and responds well to flower induction treatments, making it suitable for accelerated breeding programs. It does not root vegetatively in nature, nor respond as readily as some other conifers to rooting treatments. Although vegetative propagation may be useful for expanding specialised crosses, it currently is not practical for general stock production.

Jack pine exhibits genetic variation within and among populations in many traits, including height and diameter growth, wood quality, cone and seed characteristics, and pest resistance. Breeding programs exist throughout much of its range, and are of particular importance in the Lake States and central and eastern Canada. Selection is based primarily upon growth and stem traits, as well as pest resistance.

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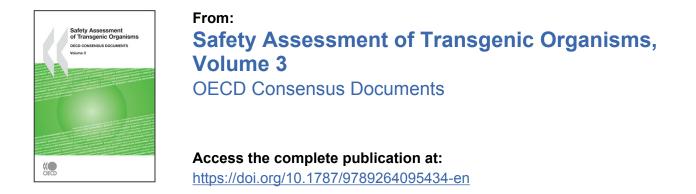
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