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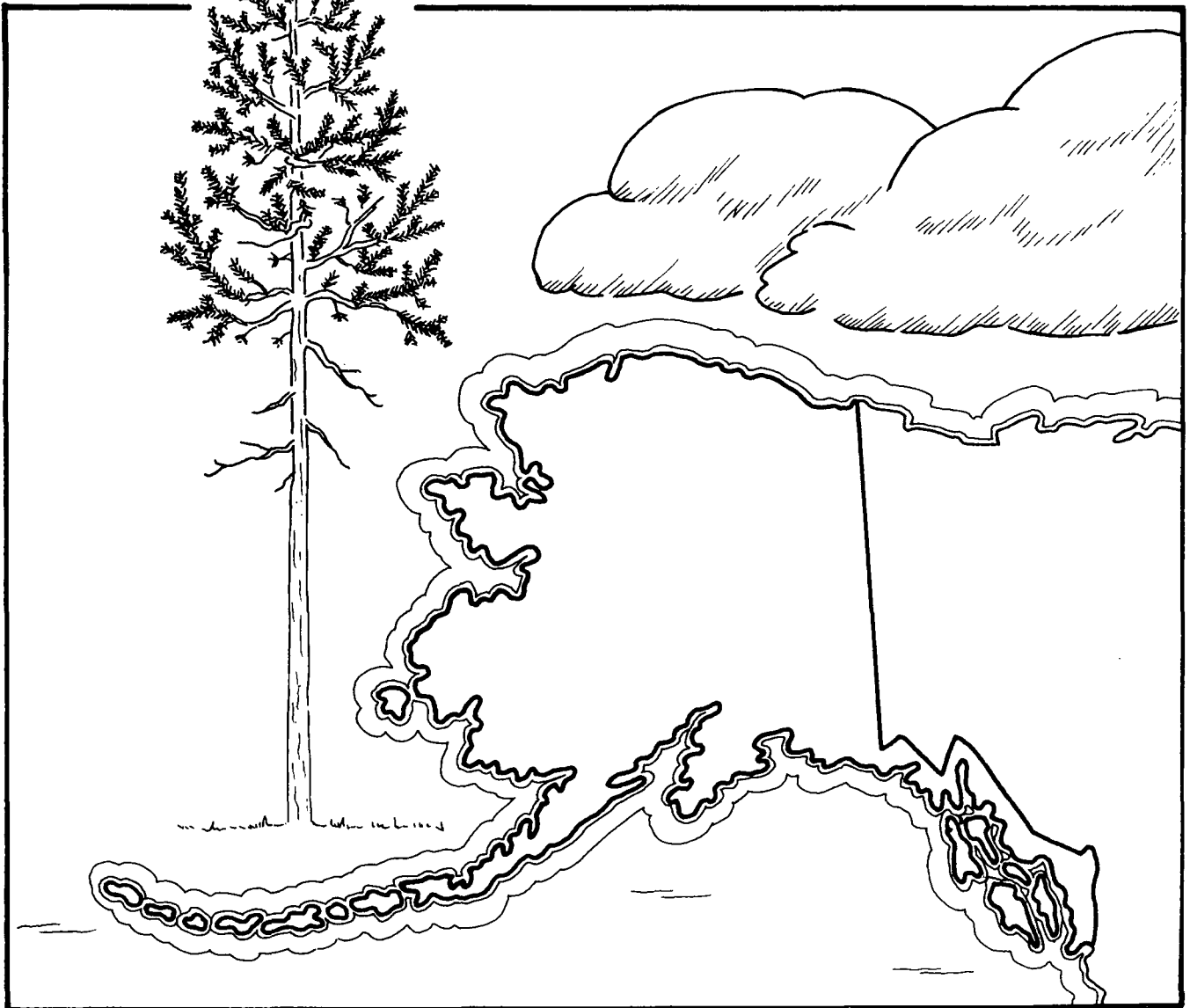
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Implications of Research on Lodgepole Pine Introduction in Interior Alaska

John N. Alden

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Abstract

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Growth, winter injury, and mortality were evaluated for 12-year-old trees of 11 subarctic lodgepole pine provenances and a jack pine provenance at Fairbanks, Alaska. Provenances from northeast British Columbia grew more than 0.003 cubic meter of wood per tree annually from 9 to 12 years after outplanting. The species sustained snow damage and winter injury, however, and could be at high risk in long-term management on severe sites in Alaska. Provenance $\times$ site interactions were not significant for mortality, tree height, and volume after the same stock grew for 10 seasons at Fairbanks and Whitehorse, Yukon.

Height and environmental injury of 3-year-old seedlings from 18 subarctic lodgepole pine and a jack pine $\times$ lodgepole pine swarm from Fort Nelson River, British Columbia, were evaluated at two sites in the interior and one site in south-central Alaska. Seedlings from high-altitude provenances grew more slowly and sustained less environmental injury after outplanting than seedlings from low-altitude provenances. More seedlings of the jack pine $\times$ lodgepole pine provenance sustained injury, but they grew taller than seedlings of the lodgepole pine provenances in the nursery and after two growing seasons in the field. Additional research is necessary to identify and determine growth and yield of superior jack, lodgepole, and jack pine $\times$ lodgepole pine provenances for a wide range of sites in Alaska.

Keywords: Lodgepole pine, *Pinus contorta*, jack pine, *Pinus banksiana*, subarctic species and provenances, hybrid/swarm, introgression, growth, survival, winter injury, Alaska.

Summary

Lodgepole pine, *Pinus contorta* var. *latifolia* Engelm., from subarctic climates of central Yukon and northeast British Columbia is genetically variable and capable of rapid juvenile growth. Variation in growth and survival traits was determined for 11 subarctic lodgepole pine provenances and a jack pine, *Pinus banksiana* Lamb., provenance after 12 growing seasons at about 2-meter spacing in Fairbanks, Alaska. Interactions among the same provenances and sites at Fairbanks, Alaska, and Watson Lake and Whitehorse, Yukon, were assessed for 10-year tree height and mortality. In addition, 9 tree species, including lodgepole pine, and 18 subarctic lodgepole pine and a natural jack pine $\times$ lodgepole pine provenance were compared for growth, mortality, and apparent environmental injury after two growing seasons at two sites in interior Alaska and one growing season in south-central Alaska.

Lodgepole pine and jack pine provenances from northeast British Columbia grew more than 0.003 cubic meter of stem wood per tree annually from 9 to 12 years at Fairbanks, Alaska. The species sustained snow damage and mild winter injury, however, and could be at high risk for long-term management on severe sites. Interactions between provenances and sites for mortality, tree height, and volume were not significant ($P < 0.05$) at Fairbanks, Alaska, and Whitehorse, Yukon, but were significant for mortality and tree height at Watson Lake and Whitehorse, Yukon, and Watson Lake, Yukon, and Fairbanks, Alaska. Height of two subarctic provenances from the upper Yukon drainage in southwest Yukon and northwest British Columbia were superior at Watson Lake and inferior at Fairbanks and Whitehorse.

Subarctic lodgepole pine provenances sustained more injury than *Larix* Mill. provenances and less injury than *Picea abies* (L.) Karst. provenances after outplanting in interior Alaska. Jack pine provenances sustained more injury than lodgepole provenances, but jack pine was taller and recovered more rapidly than lodgepole pine after the second growing season. More seedlings of a jack pine × lodgepole pine provenance from Fort Nelson River, British Columbia, were injured than seedlings of subarctic lodgepole pine provenances after 1 year at two sites in interior and one site in south-central Alaska, but they were taller than the lodgepole pine provenances after 2 years in both the nursery and in the field. Seedlings from high-altitude provenances grew more slowly and sustained less environmental injury than seedlings from low-elevation provenances.

Provenances from the northern range of jack pine and lodgepole pine and the region of species sympatry in northeast British Columbia and the Northwest Territories should be tested for a wide range of sites in interior Alaska. Techniques for acclimation of nursery-grown seedlings, site preparation, and site-specific planting stock standards need to be developed for afforestation in Alaska.

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Introduction

Lodgepole pine, *Pinus contorta* Dougl. ex Loud., is an intolerant successional forest tree species that extends from mild maritime climates of the Pacific Northwest to subarctic continental climates of the Yukon, northeast British Columbia, and the Northwest Territories (Critchfield 1985, Fowells 1965). Populations from subarctic regions, the interior subspecies (var. *latifolia* Engelm.), depend on wildfire for natural regeneration. Wildfires reduce vegetative competition, prepare seed beds, increase the active layer in permanently frozen soils, and release viable seed from serotinous cones. Subarctic populations from the Yukon and northeast British Columbia accumulate large cone crops and retain viable seed for more than 50 years.¹

Convection columns of major wildfires in the Yukon are reported to disperse seeds as far as 50 kilometers from their source (Nyland 1980). Regardless of the species' potential for rapid migration, surveys of fossil pollen indicate that lodgepole pine may have reached the southern Yukon only 4,000 years ago and arrived in central Yukon less than 400 years ago (MacDonald and Cwynar 1985). Subarctic populations nevertheless have acquired high resistance to winter injury, while retaining the inherent potential of southern populations for a long growing season and rapid height and diameter growth (Hagner 1970, Lindgren 1983).

Subarctic provenances from south-central Yukon and northeast British Columbia are capable, in the absence of competition, of rapid juvenile growth on a productive upland site in Fairbanks, Alaska (Alden and Zasada 1983). Winter injury was more severe and rates of mortality were higher for provenances from the west slopes of the Rocky Mountains in northern British Columbia and from southeast Alaska than for subarctic provenances from central Yukon and northeast British Columbia.

The climate, landform, and barriers to plant migration are complex in the subarctic region. Mean annual temperatures are below freezing, and soils are often permanently frozen (Oswald and Senyk 1977). Mean January temperatures range from -20 to -35 °C, and mean July temperatures range from 11 to 17 °C. The northern limits of lodgepole pine follow a mean annual isotherm of -5 °C (Nyland 1980). Altitudes range from 600 meters above mean sea level (m.s.l.) in central Yukon to 2400 meters above mean sea level (m.s.l.) in the Pelly-Cassiar Mountains of south-central Yukon and northern British Columbia. Eastern slopes of the Pelly-Cassiar Mountains decline to less than 300 meters above m.s.l. on the Liard flood plain of northeast British Columbia and the Northwest Territories. Annual precipitation ranges from less than 25 centimeters at low altitudes to more than 60 centimeters at altitudinal tree limits (1500 meters above m.s.l.).

¹ Data on file with: Institute of Northern Forestry, 308 Tanana Drive, Fairbanks, AK 99775-5500.

Biochemical studies indicate that lodgepole pine is genetically variable in subarctic regions. The monoterpene composition of subarctic populations is variable and distinct from southern interior populations and shore pine, subspecies or var. *contorta* (Forrest 1980, 1981; von Rudloff and Nyland 1979). Subarctic populations are genetically distinct in allozymes and allozyme frequencies (Wheeler and Guries 1982a, 1982b; Yeh and Layton 1979) but share rare alleles at several loci with coastal populations (Wheeler and Guries 1982b). Yukon and coastal populations are similar in monoterpenes of leaf resins (von Rudloff and Nyland 1979). Evidence of jack pine (*P. banksiana* Lamb.) introgression in populations from southeast Yukon and north-east British Columbia is present in monoterpene compositions of both leaf and shoot resins (Forrest 1981, von Rudloff and Lapp 1987, von Rudloff and Nyland 1979).

This report updates information on growth, winter injury, snow damage, and mortality of lodgepole pine in the 1974 provenance trial at Fairbanks. Other useful information for introduction of lodgepole pine to Alaska is reported from studies of (1) 10-year-old tree height and mortality of the same provenances and their interaction with sites at Fairbanks, Alaska, and Whitehorse and Watson Lake, Yukon; (2) mortality, growth, and apparent environmental injury of 1-0 seedlings of lodgepole pine, jack pine, and seven additional tree species after the second growing season at two former agricultural sites in interior Alaska; and (3) height and mortality of 18 subarctic provenances of lodgepole pine and one natural jack pine $\times$ lodgepole provenance after two growing seasons in the interior and after one growing season in south-central Alaska. Nursery and site preparation practices for introduction of lodgepole pine to Alaska are briefly discussed.

Procedures

T-Field Arboretum Study

Three-year-old seedlings of 29 IUFRO lodgepole pine provenances and one jack pine provenance from southeast Alaska, northern British Columbia, and the Yukon were planted at T-Field Arboretum (lat. 64°52' N., long. 147°52' W., 150 meters above m.s.l.), Fairbanks, Alaska, in June 1974 (Alden and Zasada 1983). The provenances ranged in latitude from Wendle Park, British Columbia (53°07'), to Ethel Lake, Yukon (63°18'). Three-year-old seedlings of each provenance were planted at 1.8 meters (6 ft) in nine-tree plots in each of two randomized blocks. Tree height, winter injury, and mortality were measured annually from 1974 to 1985. Average volume and increment of stem wood per tree were estimated annually for the 12 subarctic provenances from tree heights and stem diameters measured at 15 centimeters above the ground in 1980 and at 137 centimeters above the ground each year from 1982 to 1985. Trees of the 18 southern provenances were severely injured or killed above snow level and were not included in the analyses. Inside-bark stem volumes were determined by the method of Kovats (1977). Snow damage, cone production, and seed yield were measured for each provenance in 1985. Relations between mean annual height growth, winter injury, and climatic variables at Fairbanks International Airport (lat. 64°49' N., long. 147°52' W., 133 meters above m.s.l.) for 1980 to 1985, and between winter injury and average daily, minimum, and maximum bimonthly temperatures for January to May from 1975 to 1985 were examined with multiple linear-regression analysis.

Study I

Each provenance in the trial at Fairbanks was also planted in nine tree plots in each of six randomized blocks at Whitehorse, Yukon (lat. 60°51' N., long. 135°15' W., 660 meters above m.s.l.), and each of four randomized blocks at Watson Lake, Yukon (lat. 60°07' N., long. 128°49' W., 700 meters above m.s.l.), in 1974 (fig. 1). Mortality and height of each tree was measured at both sites at the end of the 10th growing season (1983). These measurements were analyzed with 1983 data from Fairbanks for significance of interaction among provenances and sites. Tree diameters were measured at Whitehorse in 1983. Average inside-bark stem volume per tree was determined for all provenances and the 12 subarctic provenances after 10 growing seasons at Fairbanks and Whitehorse. Interaction between provenances and sites at Fairbanks and Whitehorse was tested for significance in analysis of variance.

Study II

Four provenances each of lodgepole pine and jack pine were sown with seven additional species (table 1) in 66-cubic-centimeter (4-in³) cells in a greenhouse at the Alaska Forest Nursery, Eagle River, in early March 1983. The seedlings were overwintered outdoors and planted at two former agricultural sites in interior Alaska (fig. 1) in June and July 1984. Soils on site 1 were formed on a Holocene glacial outwash or moraine. The organic surface and roots of the native forest species (*Populus tremuloides* Michx. [quaking aspen], *Picea mariana* (Mill.) B.S.P. [black spruce], and *Salix* spp. [willows]) were partially removed in agricultural clearing during the late 1960's and in site preparation for the study in March 1984. Soils of site 2 were deep loess deposits that appeared nutritionally impoverished. Roots of the forest vegetation and unincorporated organic matter were removed from the soil surface in the early 1970's for production of agricultural crops. The site was not farmed, and the soils were tilled at 2- to 4-year intervals to prevent invasion of woody competition.

Each species was planted at 2-m spacing in 16-tree plots. The plots were randomized in 20 blocks at site 1 and 14 blocks at site 2. *Betula venucosa* was planted only at site 1. Four open-pollinated families each from a natural lodgepole pine × jack pine hybrid swarm on the Fort Nelson River, British Columbia (lat. 59°12' N., long. 123°25' W., 300 meters above m.s.l.) and from a Fort Simpson, Northwest Territories, provenance (lat. 61°48' N., long. 121°18' W.) at T-Field Arboretum, Fairbanks, Alaska, were included in the jack pine plots. The Fort Nelson River hybrid swarm contained both lodgepole and jack pines, but cone and seed characteristics of most trees were intermediate between the species. Lodgepole and jack pine are widely distributed north of Fort Nelson River and east of the Liard River in northeast British Columbia² (Krajina and others 1982).

Seedlings of each provenance and family were planted at random in the plots. Location and pedigree of each seedling were mapped to determine variation among families and among provenances within species. The seedlings were measured for mortality, height, animal damage, and evidence of environmental injury at the end of the first and second growing seasons. Symptoms of environmental injury included dead and chlorotic foliage, dead terminal shoots, dead buds, and animal damage.

² Personal communication: A. McLeod, British Columbia Forestry Service, Prince George, BC.

- ▲ Natural range of lodgepole pine and outlying populations
- ◇ Unconfirmed outlying populations:
West Hart River, lat. 64°45' N; and
White River, lat. 61°50' N.
- xx Region of jack x lodgepole pine hybridization and introgression.
- Southern limit of low-risk provenances for Tanana Valley, Alaska (Alden and Zasada 1983), and
subarctic provenance test zone for study III.
- ▲ Arctic tree limits for white spruce.
- ◆ Test site locations: Study I, 64°52'–147°52', 150 m. 60°51'–135°15', 660 m.
60°07'–128°49', 700 m. studies II and III, 64°00'–145°10', 420 m, and study III,
61°50'–145°10', 420 m.

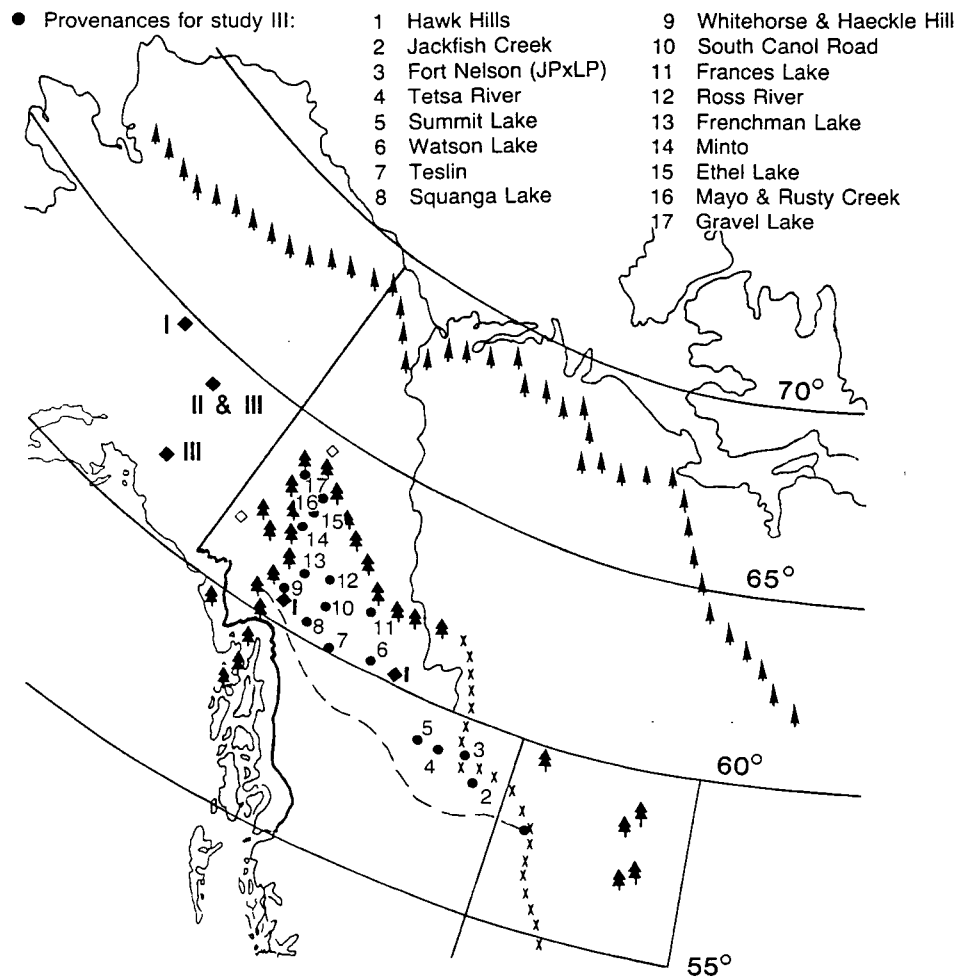


Figure 1—Northern (subarctic) range of lodgepole pine and locations of test sites for studies I, II, and III and provenances for study III.

Table 1—Provenances of 9 species outplanted at sites 1 and 2 in study II, Delta Junction, Alaska, 1984

Species	Number of provenances	Region	Latitude <i>Degrees North</i>
<i>Pinus contorta</i> var. <i>latifolia</i> Engelm., lodgepole pine	4	NE BC, and YT, Canada	58-63
<i>Pinus banksiana</i> Lamb., jack pine	6 (2 hybrids)	MB, SK, NT, Canada, NE BC, Canada and Fairbanks, AK	54-63 59, 65 (T-Field)
<i>Pinus sylvestris</i> L., Scots pine	5	Estonia, Sweden, Finland	58-68
<i>Pinus flexilis</i> James, limber pine	1	Jasper N.P., AB, Canada	~53
<i>Larix laricina</i> (Du Roi) K. Koch, tamarack	5	Tanana Valley, AK	64-65
<i>Larix sibirica</i> Ledeb. and <i>L. sukaczewii</i> N. Dyl., eastern and western Siberian larch	7 (seed sources)	Altai to Archangels, USSR	52-64
<i>Picea abies</i> (L.) Karst., Norway spruce	6	Estonia, Norway, Sweden, Finland	58-64
<i>Picea glauca</i> (Moench) Voss, white spruce	4	Kenai Peninsula to Fairbanks, AK	60-65
<i>Betula verrucosa</i> Ehrh., European white birch	3	Finland	62

Study III

Three to twelve open-pollinated families from each of 18 subarctic lodgepole pine provenances and the natural lodgepole pine × jack pine hybrid swarm on Fort Nelson River, British Columbia (fig. 1), were sown in 164-cubic-centimeter (10-in³) containers in early March 1983. Families were collected from one to several stands per provenance in northeast British Columbia and south-central Yukon. Two families from a lodgepole pine stand south of Fort Nelson River were included in the Fort Nelson River provenance. Populations were small and discontinuous in central Yukon and were usually collected from one stand per provenance.

The families were randomized on a greenhouse bench at the Alaska Forest Nursery and moved outside for winter in late July 1983. Two hundred families were planted at 2-meter spacing in single-tree plots in each of 17 randomized blocks at site 1 and in 10 randomized blocks at site 2 in June and July 1984. Ten blocks were planted at site 3 in September 1984 and again in June 1985. Site 3 is on the Cooper River Plateau, south of the Alaska Range (fig. 1) and was mechanically cleared of logging slash and competing vegetation in August 1984. Sites 1 and 2, north of the Alaska Range, were prepared as described in study II. The heights of seven seedlings reserved at the nursery for each family were measured in October 1984. Height, mortality, and environmental injury were measured for all families in the field trial in September and early October 1985. Family values were averaged to compute provenance values. Altitude and location of each provenance were reported at the mid-range of family altitudes.

Differences among species, provenances, and sites in each study were tested for statistical significance by analysis of variance. Data that did not conform to a normal distribution were ranked and analyzed with nonparametric statistics (Conover 1980). When differences among species, provenances, or families were significant, multiple comparisons between means were tested for significance with the Waller-Duncan Bayes Rule (Waller and Duncan 1969). The Waller-Duncan Bayes Rule provides a measure of the seriousness of type I error to type II error; it is preferred for multiple comparisons when sample sizes are equal (Milliken and Johnson 1984; Petersen 1985).

Simple correlation (r) or Spearman's rank correlation (r_s) coefficient was calculated to show the degree of association between altitude, growth, and environmental injury of the provenances. First-order regression analyses and partial F-tests were made to examine relations between mean annual height growth of lodgepole pine and climatic variables and between winter injury and bimonthly winter temperatures at Fairbanks. Differences between treatments and associations between variables were reported as statistically significant at 0.05 probability of error or less.

Results

T-Field Arboretum Study

Mean height, diameter, and stem volume per tree, and mortality of the subarctic provenances after 12 years at Fairbanks, Alaska, are shown in table 2 and figure 2. The jack pine (Petitot River) and lodgepole pine (Jackfish Creek and Tetsa River) provenances from northeast British Columbia produced more volume than the lodgepole pine provenances from Yukon. Annual volume increment per tree for the provenances from northeast British Columbia increased from 0.001 cubic meter in 1981 to more than 0.004 cubic meter in 1985.

Table 2—Mean tree height, diameter at breast height, and volume of 11 northern (subarctic) lodgepole pine provenances and a jack pine provenance (Petitot River, BC) at T-Field Arboretum, October 1985

Location	Latitude	Longitude	Altitude	Height	Diameter	Volume ^a
	°N	°W	m	cm	mm	m ³ ·10 ⁻²
Jackfish Creek, BC	58°32'	122°42'	457	483	83.0	1.48a
Petitot River, BC	59°54'	122°05'	396	453	84.5	1.46a
Testa River, BC	58°40'	124°10'	762	448	75.0	1.30ab
Cassiar, BC	59°06'	129°44'	792	448	73.5	1.12ab
Carmacks, YT	62°14'	136°18'	670	442	72.0	1.07abc
Ethel Lake, YT	63°18'	136°28'	875	437	66.5	.98bc
Muncho Lake, BC	59°03'	125°46'	853	423	71.5	1.02abc
Hawk Hills, AB	57°23'	117°33'	716	410	69.5	.98bc
Takhini River, YT	60°41'	136°11'	746	402	66.5	.89bc
Stone Mountain, BC	58°39'	124°46'	1173	396	69.5	1.00abc
Pink Mountain, BC	57°00'	122°42'	1112	362	58	.66c
Atlin, BC	59°48'	133°47'	788	336	54	.60c

^a Differences among volumes with a common letter were not significant.

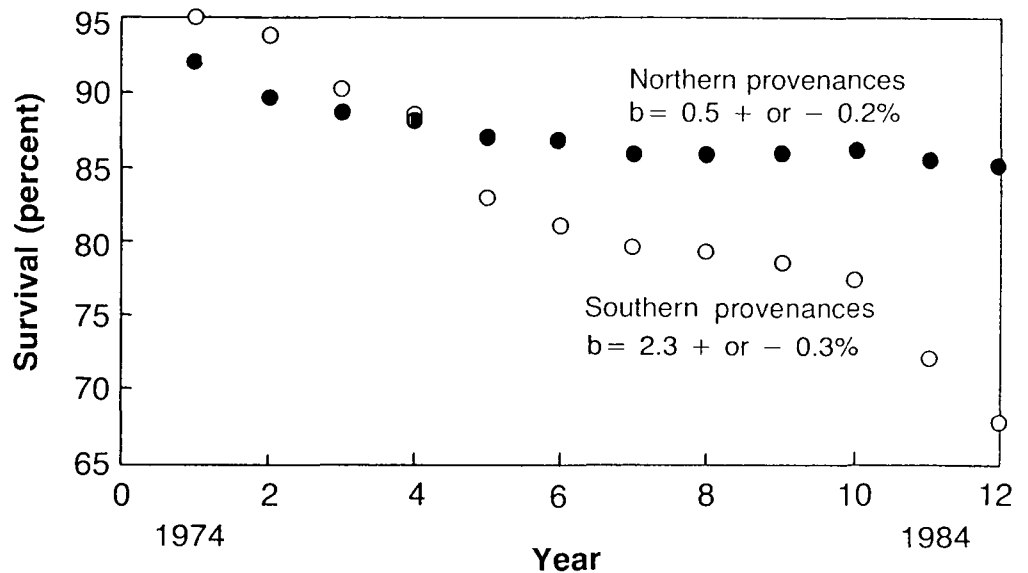


Figure 2—Average mortality rates (b) and confidence limits ($P = 0.05$) for the 12 northern (subarctic) and 18 southern lodgepole pine provenances at T-Field Arboretum.

The Carmacks and Ethel Lake provenances from central Yukon and the jack pine provenance from British Columbia sustained less winter injury in late winter 1983 than lodgepole pine provenances from northern British Columbia and Alberta (fig. 3). The only apparent injury to the central Yukon and jack pine provenances was in the foliage directly above the snow surface on south exposures. The foliage seemed to recover from this injury. Provenances from Pink Mountain and Atlin, British Columbia, were severely injured and produced significantly less volume than provenances from northeast British Columbia and the Yukon (table 2). Pink Mountain and Atlin are at the southern limit of the subarctic region. Stems, buds, and foliage of provenances south of the subarctic region were killed above snow level (fig. 4). Only stems, buds, and foliage that were covered by snow escaped injury. Mortality of the southern provenances increased (fig. 2), and mean annual height growth of all provenances decreased abruptly (fig. 5) after severe winter injury in 1983.

Annual height and diameter growth of the subarctic provenances differed greatly and were inversely related from 1983 to 1985 (fig. 5). Annual variation in height growth from 1980 to 1985 was not related to seasonal growing degree-days at a 5- °C base ($\bar{x} = 1149 \pm 69$), growing degree-days for June ($\bar{x} = 306 \pm 37$), precipitation for June ($\bar{x} = 3.4 \pm 1.7$ cm), precipitation for the May-July growing season ($\bar{x} = 10.9 \pm 2.3$ cm), precipitation for October-April ($\bar{x} = 10.5 \pm 2.7$ cm), or precipitation for August-September ($\bar{x} = 5.9 \pm 2.7$ cm) of the year before the growing season. Annual height growth was not related to the percentage of trees with winter injury.

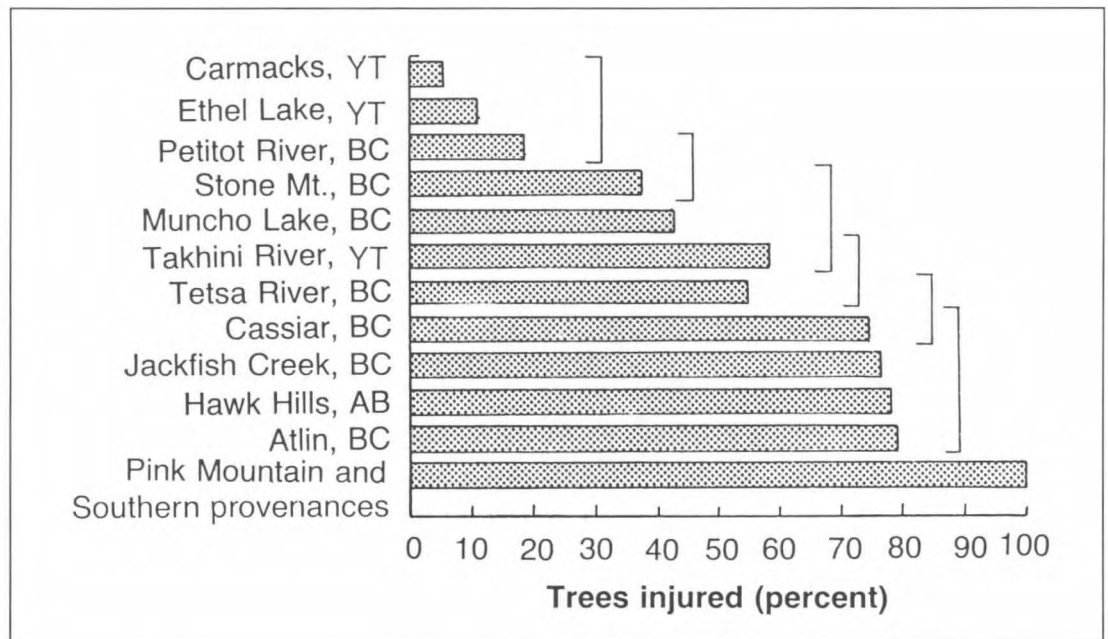


Figure 3—Winter (1982-83) injury to foliage, buds, and stems of 11 northern (subarctic) lodgepole pine provenances and a northern jack pine provenance (Petitot River, BC) at T-Field Arboretum. Differences among provenances enclosed with a common line were not significant.



Figure 4—Severe winter injury to central British Columbia provenances, Red Willow River, 54°56', 120°15', 950 meters above m.s.l.; McKale, 53°25', 120°20', 701 meters above m.s.l.; Kispiox 55°38', 127°55', 610 meters above m.s.l., in the foreground at T-Field Arboretum, Fairbanks, AK, in early May 1986. Provenances south of the subarctic region sustained frequent and severe winter injury for 12 growing seasons. Hawk Hills, AB (57°23', 117°23', 716 meters above m.s.l.) lodgepole pine (background center) and Petitot River, BC (59°54', 122°05', 396 meters above m.s.l.) jack pine (background right) rarely sustained severe winter injury.

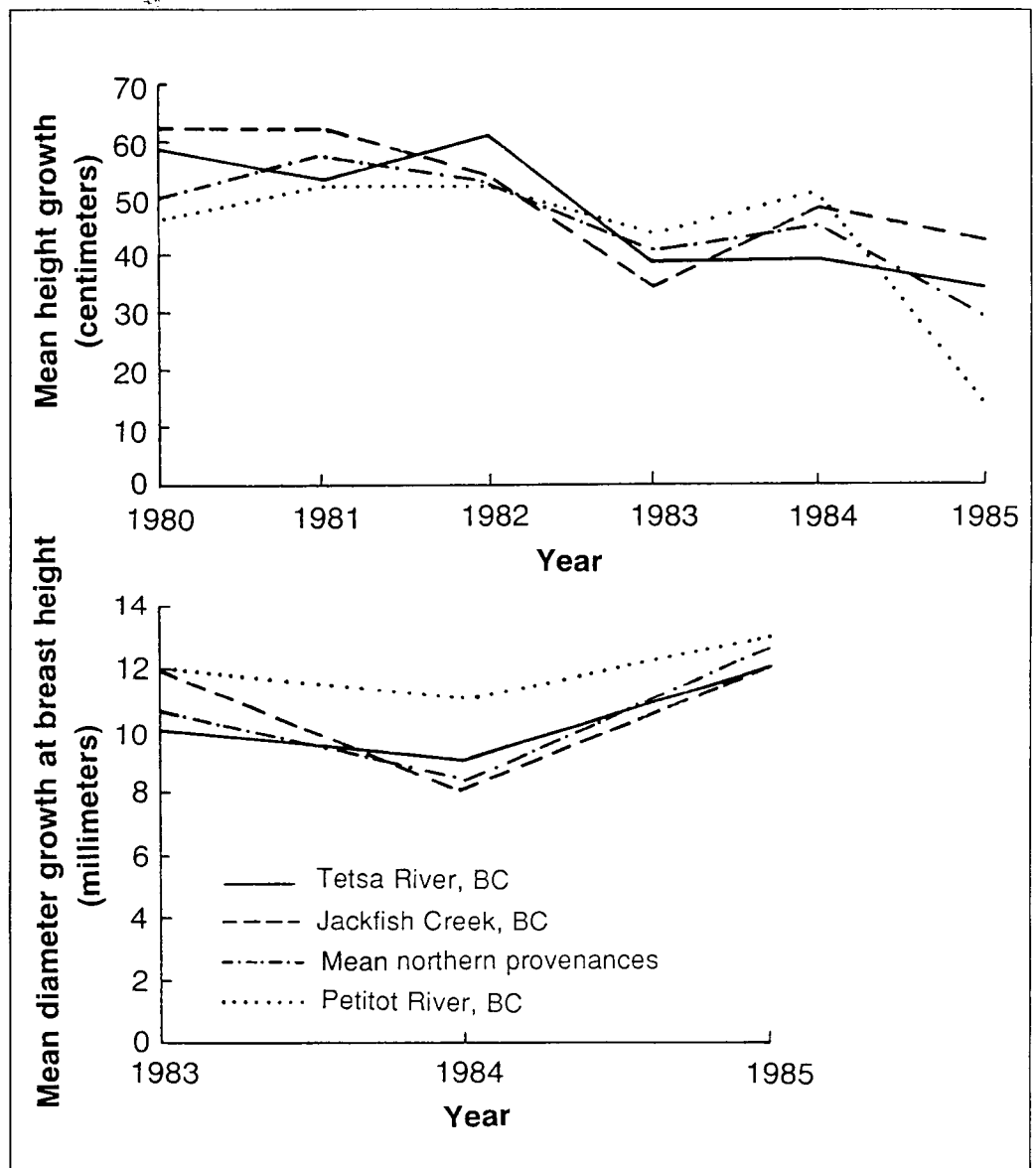


Figure 5—Average growth in height and DBH of the 12 northern (subarctic) provenances and each of 3 outstanding provenances from northeast British Columbia at T-Field Arboretum.

The percentage of trees with winter injury was not related to low temperature extremes and average daily minimum and maximum temperatures for bimonthly periods between January and May from 1975 to 1985. Injury was most severe after the 1977-78 and 1982-83 winters. Injury was not observed in fall and winter. Mean monthly temperatures from January to May were 4 °C above normal in 1978 and 3 °C above normal in 1983. Trees with injury averaged 46 percent in 1978 and 80 percent in 1983 for all provenances.

The sharp decline in height growth of the subarctic provenances in 1985 was caused by broken tree tops from heavy snow loads. More than 120 centimeters of snow containing 7.7 centimeters water equivalent fell during a 12-day period in late December 1984.³ Thirty-seven percent of the trees sustained broken leaders, stems, and limbs. Differences in snow damage among provenances were not significant, and potential loss of volume growth per tree in 1985 was offset by an increase in diameter growth.

The average number of cones per tree for the subarctic provenances increased from 6 in 1981 (Alden and Zasada 1983) to 37 in 1985. Filled seeds per cone increased from 6 in 1981 to 27 in 1985. Differences among provenances were not significant in 1985. An age-related increase in pollen production and pollination may have increased yields of filled seed.

Study I

Differences in mortality and average tree height among the subarctic provenances and the subarctic and southern provenances combined at Fairbanks, Whitehorse, and Watson Lake in 1983 (fig. 6) were significant. Snowshoe hares (*Lepus americanus* Erxleben) caused higher mortality at Whitehorse than at Fairbanks and Watson Lake.⁴ Southern provenances were more severely injured by hares than were the subarctic provenances (Ying and Illingworth 1986). Mortality at Fairbanks was caused by winter injury. Interactions between provenances and sites at Fairbanks and Whitehorse for mortality, average tree height, and volume per tree (fig. 7) were not significant.

Provenance $\times$ site interactions for mortality and 10-year height of the subarctic and southern provenances combined were significant between Whitehorse and Watson Lake and between Fairbanks and Watson Lake. Differences in mortality and height between the southern provenances and the subarctic provenances were smaller at Watson Lake than at Fairbanks and Whitehorse. Height of Atlin and Takhini River provenances were superior to other subarctic provenances at Watson Lake but inferior at Fairbanks and Whitehorse. Height of the Petitot River provenance, on the other hand, was superior at Fairbanks and Whitehorse and inferior at Watson Lake.

³ Local climatological data, National Weather Service Office, International Airport, Fairbanks, Alaska.

⁴ Personal communication: C. Ying, British Columbia Forest Service, Victoria, BC.

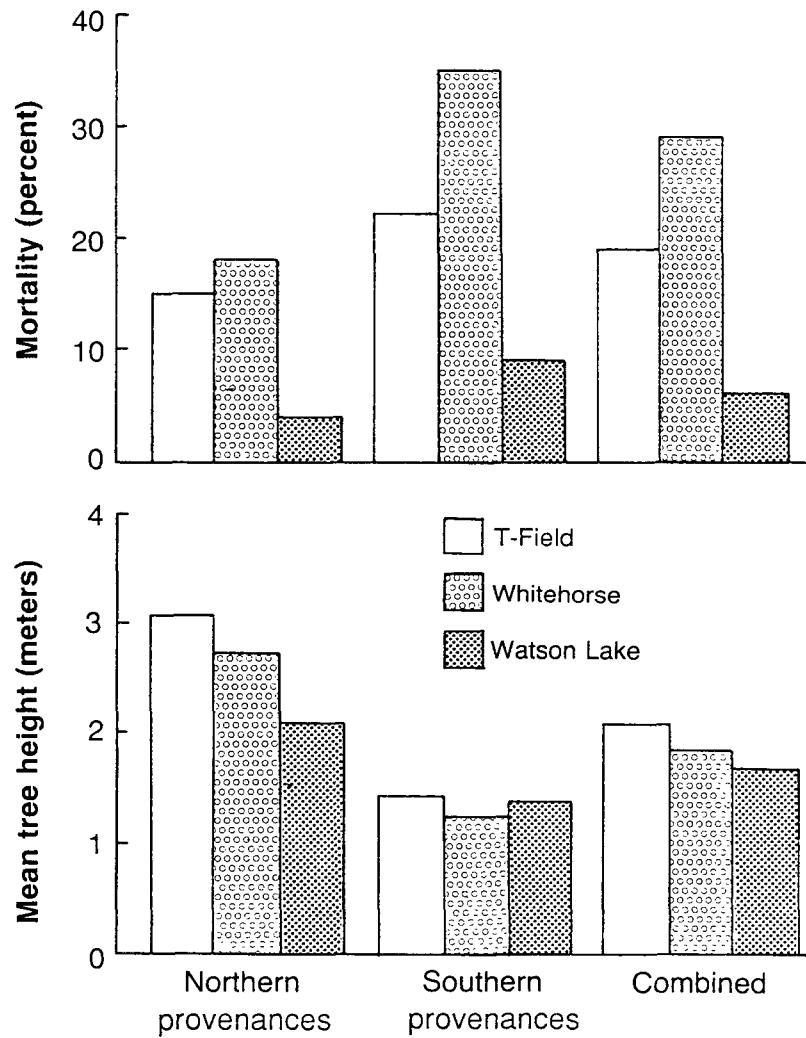


Figure 6—Percentage of mortality and mean tree height of 12 northern (subarctic) provenances and 18 southern provenances at T-Field, Whitehorse, and Watson Lake test sites in 1983 (study I).

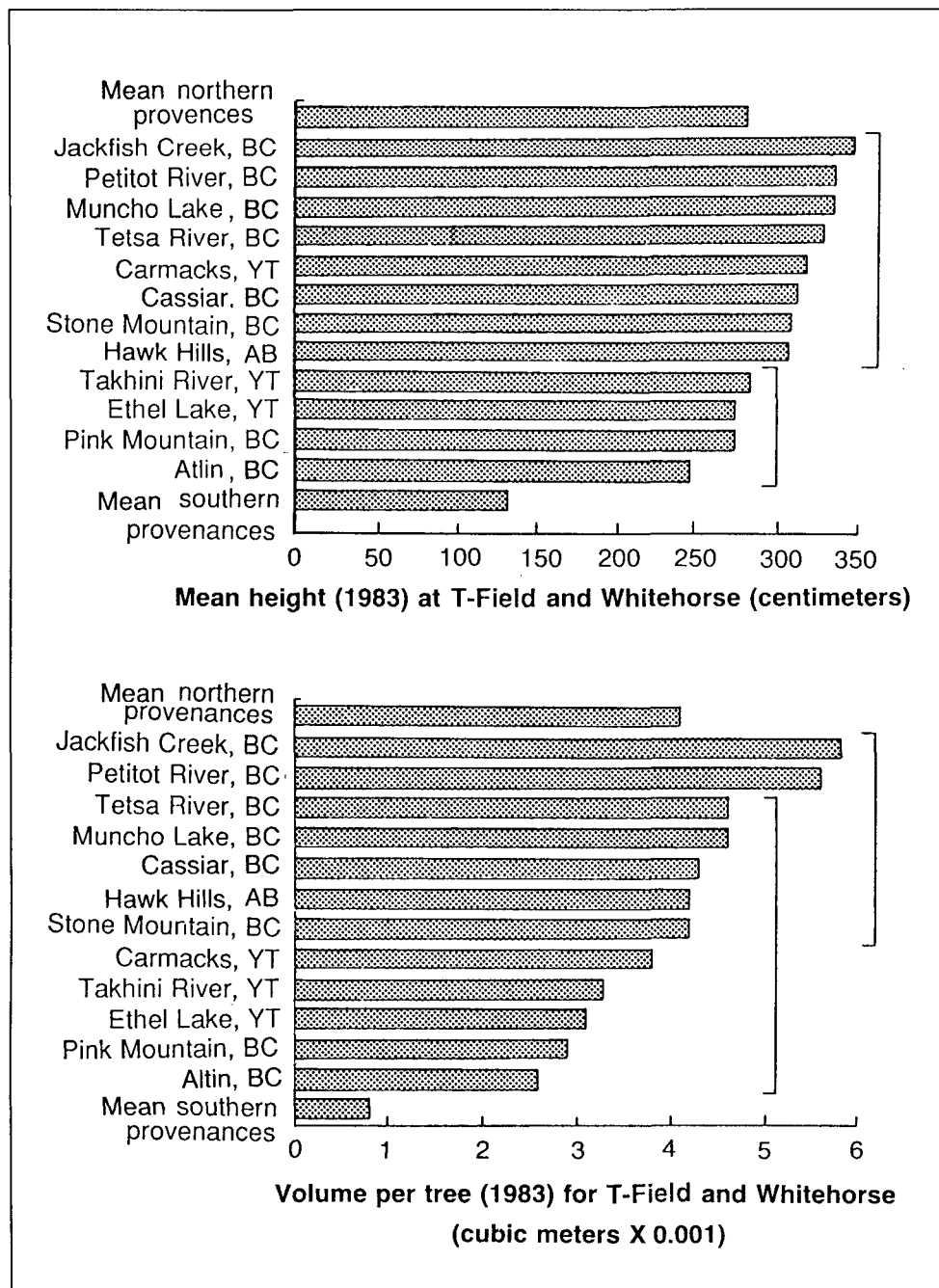


Figure 7—Average height and volume per tree for each of the 11 northern (subarctic) lodgepole pine provenances and the Petitot River, BC, jack pine provenance after 10 growing seasons at T-Field Arboretum and Whitehorse test sites (study I). Mean height of the northern and southern provenances are top and bottom bars, respectively. Differences among provenances enclosed with a common line were not significant.

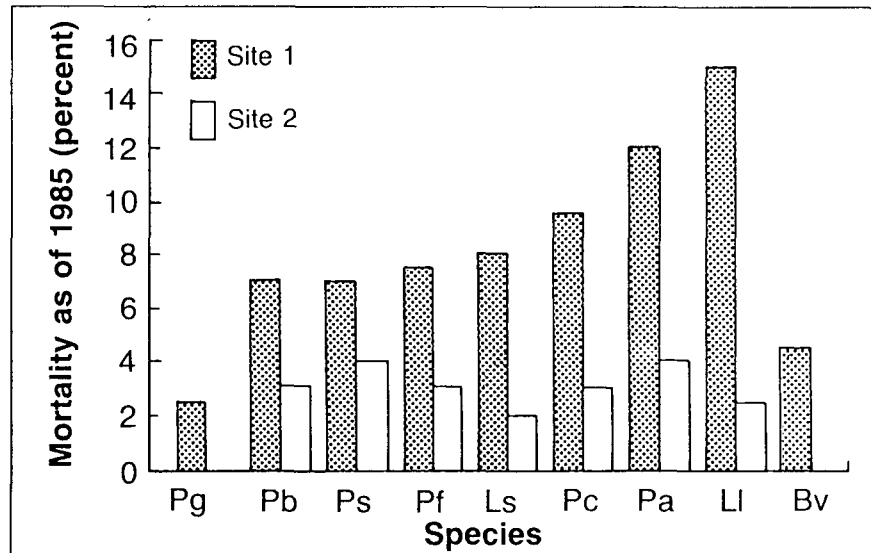


Figure 8—Mortality as of 1985 of nine tree species after the second growing season at sites 1 and 2 of study II in interior Alaska. Differences between sites were significant. Pg = *Picea glauca*, Pb = *Pinus banksiana*, Ps = *Pinus sylvestris*, Pf = *Pinus flexilis*, Ls = *Larix sibirica/sukaczewii*, Pc = *Pinus contorta*, Pa = *Picea abies*, LI = *Larix laricina*, and Bv = *Betula verrucosa* (site 1 only).

Study II

Height and condition of lodgepole pine and eight other species were compared after the first (1984) and second (1985) growing seasons at two sites in interior Alaska. Differences in mortality of seedlings among species at both sites were not significant after the 1985 growing season (fig. 8). Mortality was significant between sites, however. Mortality averaged 8 percent at site 1 (woody competition) and 3 percent at site 2 (grass competition). Differences in apparent environmental injury among species and between sites were also significant after the second growing season (fig. 9). Seventy-two percent of the seedlings at site 1 and 54 percent of the seedlings at site 2 showed symptoms of injury. Only *Picea abies* seedlings sustained more injury than *Pinus* seedlings. Differences in environmental injury among the pine species were not significant in 1985, but fewer seedlings of lodgepole pine (60 percent) showed symptoms of injury than seedlings of jack (97 percent) and Scots (87 percent) pines after the 1984 growing season. More jack and Scots pine seedlings than lodgepole pine seedlings recovered from injury in 1985, however (fig. 10). Injury to lodgepole pine seedlings increased 16 percent; injury to jack and Scots pine seedlings decreased 10 percent each. Additional analysis is necessary to determine if injury to jack and Scots pine seedlings was less severe than injury to the lodgepole pine seedlings.

Clipping of stems by voles (*Clethrionomys* and *Microtus* species) and snowshoe hares, and browsing or trampling of seedlings by moose (*Alces alces*) were major causes of damage. More lodgepole pine (9 percent) than jack and Scots pine (3 percent) seedlings were clipped by voles at site 2 in 1984, but the difference was not significant ($P = 0.09$). Injury from voles declined to 5 percent for lodgepole pine, 2 percent for jack pine, and 1 percent for Scots pine in 1985. Only European white birch sustained serious animal damage from moose browse at site 1.

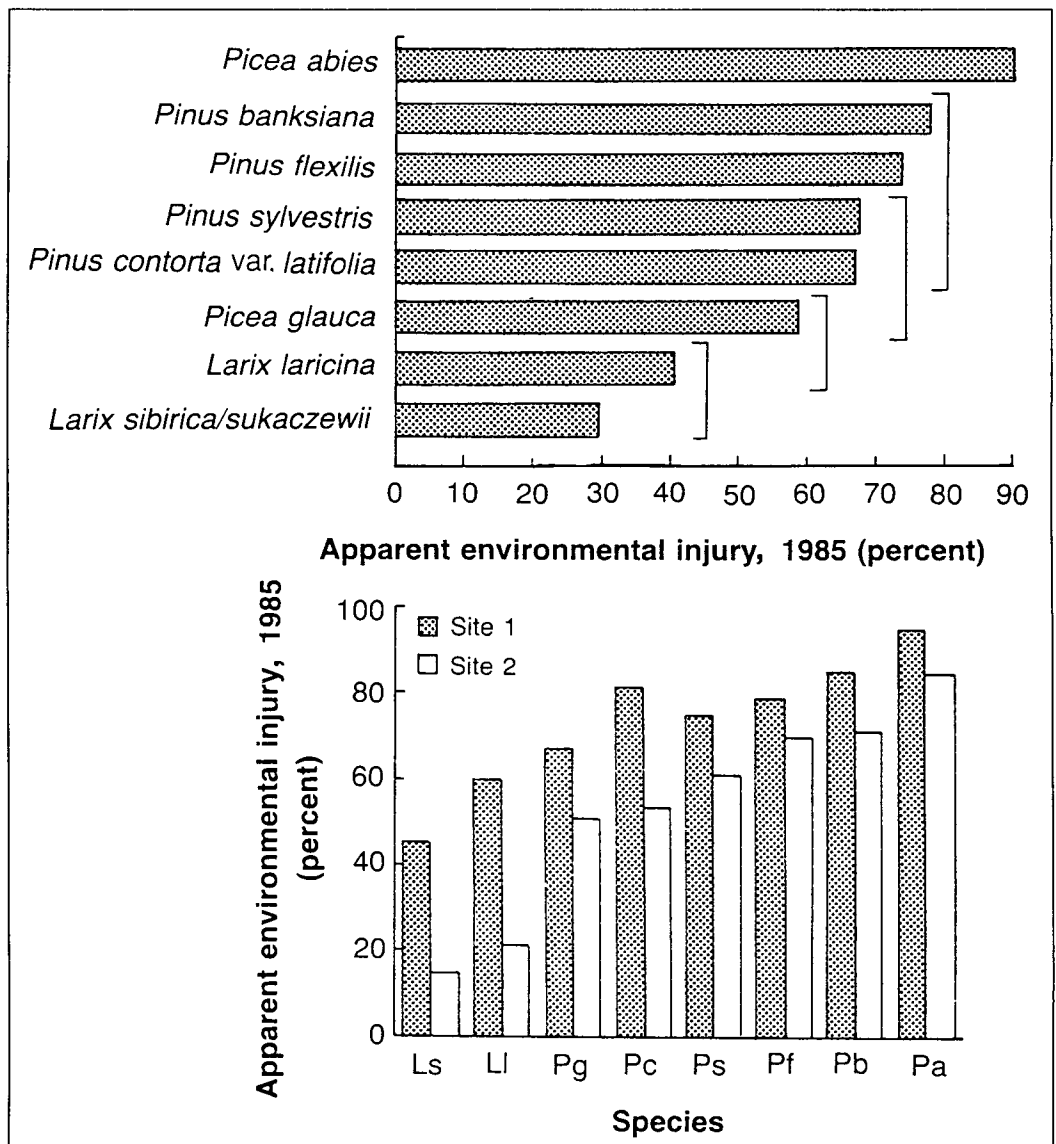


Figure 9—Percentage of surviving trees with environmental injury by species and site after two growing seasons at sites 1 and 2 of study II in interior Alaska. Differences among species and sites were significant. Differences among species enclosed with a common line were not significant. Pa = *Picea abies*, Pb = *Pinus banksiana*, Pf = *Pinus flexilis*, Ps = *Pinus sylvestris*, Pc = *Pinus contorta* var. *latifolia*, Pg = *Picea glauca*, LI = *Larix laricina*, Ls = *Larix sibirica/sukaczewii*.

Mean seedling height after the 1985 growing season was significantly greater for jack pine than for lodgepole and Scots pine (fig. 11). Seedling height of jack pine was significantly less than the mean seedling height of the *Larix* species. Field height in 1985 was related to nursery height in 1984 ($r_s = 0.85$, $P = 0.02$). All species grew significantly faster at site 2 than at site 1, but they were not significantly taller after the 1985 growing season. Species $\times$ site interaction for 1985 height growth was significant.

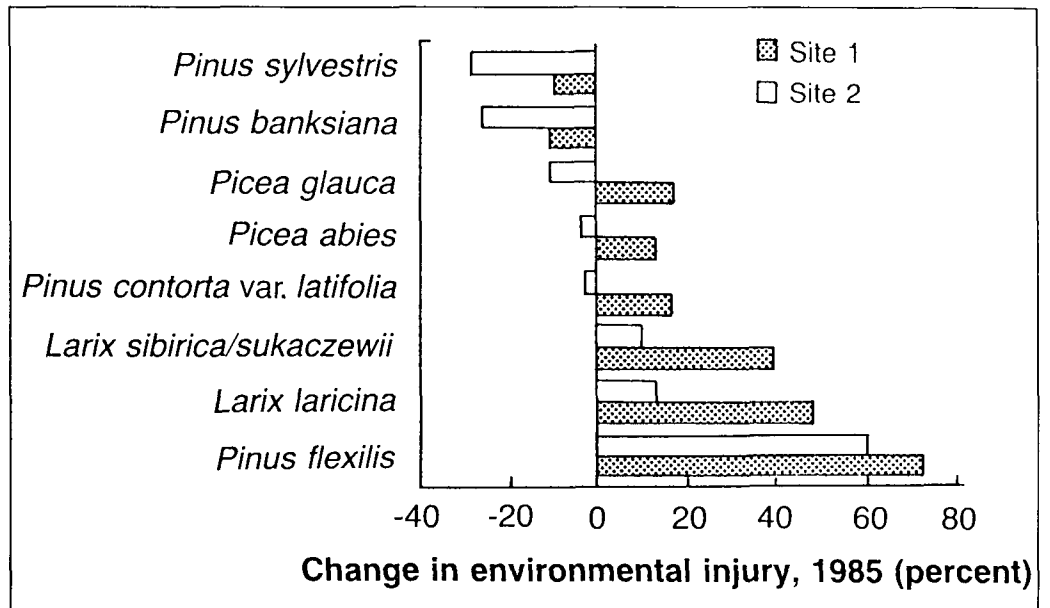


Figure 10—Percentage of change in environmental injury of eight species during the second growing season (1985) after outplanting at sites 1 and 2 of study II in interior Alaska.

The *Larix* species grew significantly more in height than the *Pinus* and *Picea* species at site 2 in 1985. Differences in height growth among the *Pinus* species were not significant. Height of Norway spruce, lodgepole pine, and European white birch decreased at site 1 in 1985. European white birch was browsed by moose, and shoots of Norway spruce and lodgepole pine continued to die back in 1985. Differences in height among lodgepole pine and jack pine provenances were significant only for the jack pine provenances at site 2 (fig. 12). Wrigley, Northwest Territories, was the only provenance significantly taller than the Fort Nelson River hybrid provenance in 1985.

Study III

Differences in average family height among provenances from the subarctic region at each of the three sites in Alaska were significant in 1985 (table 3). Provenance $\times$ site interactions for 1985 seedling height and mortality were significant. Differences in seedling height and mortality among the provenances averaged for all sites were not significant. Average field height in 1985 was correlated with 2-0 nursery height in 1984 ($r = 0.92$; $P < 0.001$). Seedlings of parents with jack pine $\times$ lodgepole pine characteristics from the Fort Nelson River, British Columbia, provenance exceeded all lodgepole pine provenances in height and in apparent environmental injury. The percentage of seedlings with environmental injury was positively correlated with 1985 field height ($r_s = 0.73$; $P = 0.003$) and negatively correlated with altitude of their provenance ($r_s = -0.68$; $P = 0.005$). Average 1985 field height of the seedlings also decreased with increasing altitude of their provenances ($r = 0.81$; $P < 0.001$).

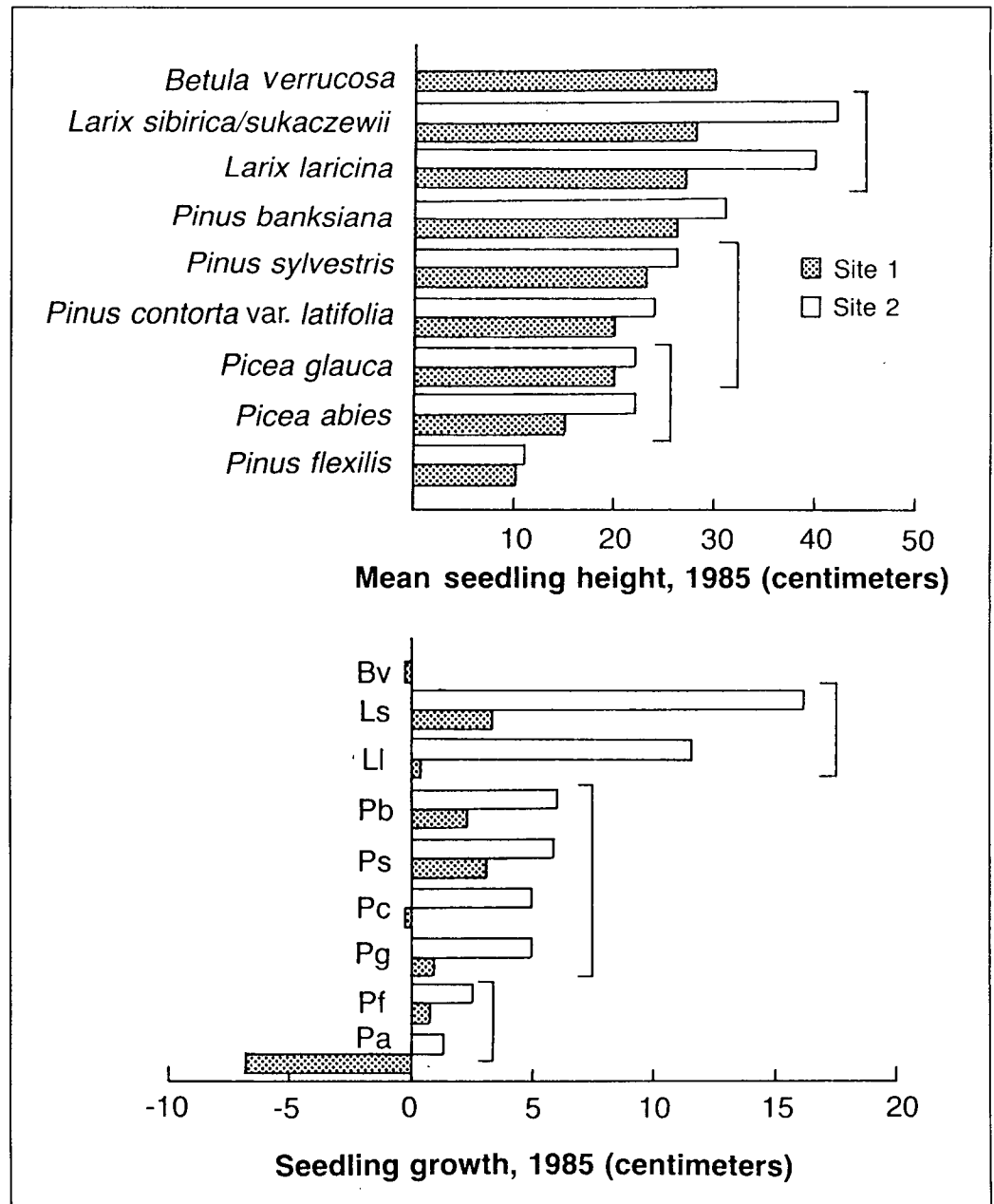


Figure 11—Mean seedling height and second-year growth (1985) of nine species at site 1 and eight species at site 2 of study II in interior Alaska. Differences among species enclosed with a common line for height and for growth at site 2 were not significant. Bv = *Betula verrucosa*, Ls = *Larix sibirica/sukaczewii*, Ll = *Larix laricina*, Pb = *Pinus banksiana*, Ps = *Pinus sylvestris*, Pc = *Pinus contorta* var. *latifolia*, Pg = *Picea glauca*, Pa = *Picea abies*, and Pf = *Pinus flexilis*.

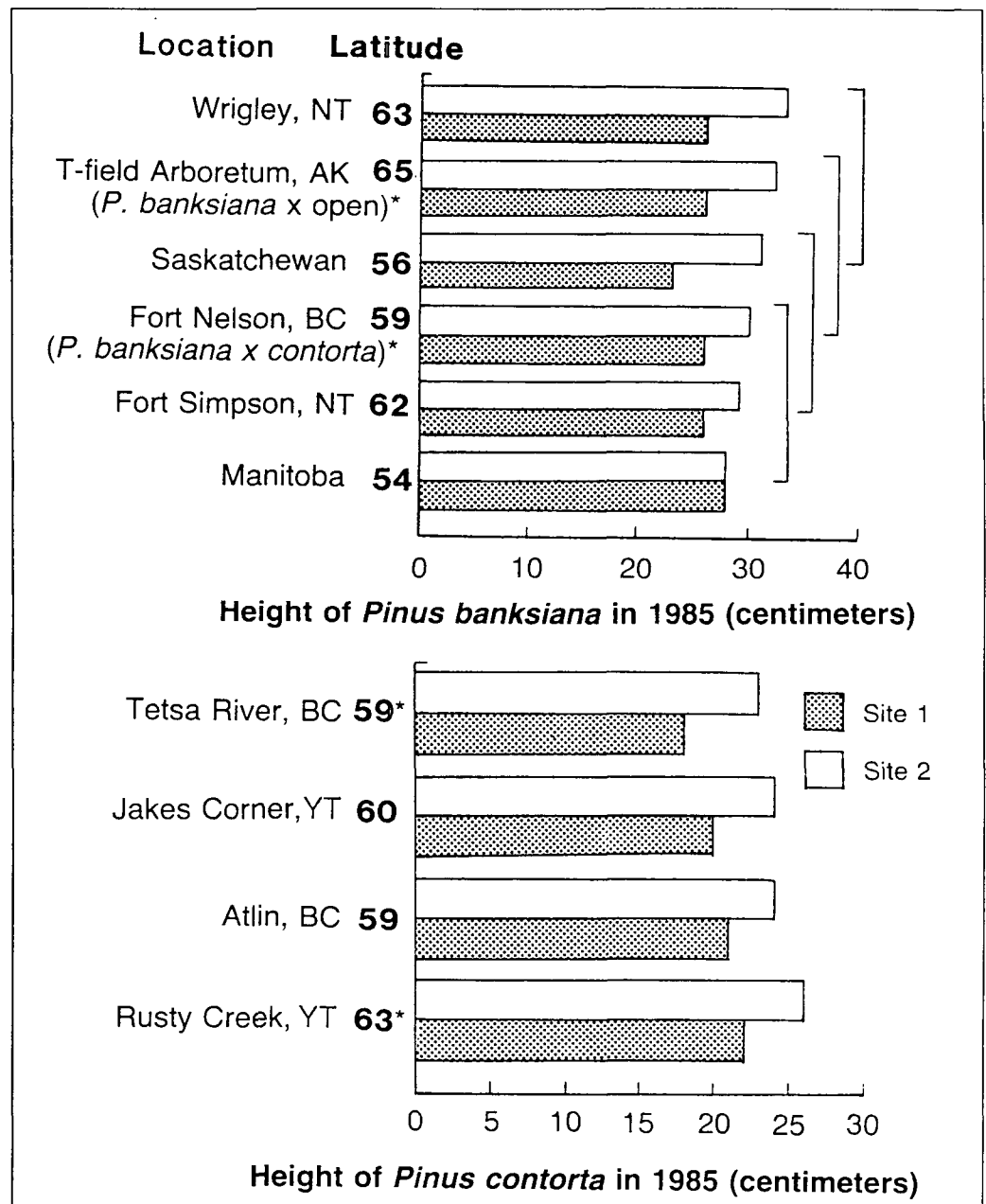


Figure 12—Variation among lodgepole pine and jack pine provenances in average seedling height in study II. The hybrid swarm (Fort Nelson River, BC) and possible hybrids (T-Field Arboretum) were included in the jack pine plots. Provenances with an asterisk are the means of four open-pollinated families each. The provenance for jack pine families at T-Field Arboretum was Fort Simpson, Northwest Territories (lat. 61°48' N., long. 121°18' W.). Only differences among *P. banksiana* and hybrid provenances at site 2 were significant. Differences among provenances enclosed with a common line at site 2 were not significant.

Table 3—Height, injury, and mortality of 18 northern (subarctic) provenances of lodgepole pine and 1 jack pine × lodgepole pine provenance (Fort Nelson River, BC) after 2 growing seasons in the nursery, 2 growing seasons at sites 1 and 2 in interior Alaska, and 1 growing season at site 3 in south-central Alaska

Provenance	Geographical location		Altitude	1984 nursery height ^a	Seedling field heights ^a				Mean environmental injury	Mean mortality
	Latitude	Longitude			Site 1	Site 2	Site 3	Mean		
	'N	'W	Meters		Centimeters				Percent ^b	
Fort Nelson River, BC	59°12'	123°25'	300-640	35.0	30.5	33.0	41.0	35.0	66	6
Jackfish Creek, BC	58°35'	122°40'	460	31.5ab	25.5abc	28.5a	37.5ab	30.5	49b	9
Ethel Lake, YT	63°15'	136°22'	640-1010	31.5ab	27.0a	29.0a	34.5de	30.0	42ab	2
Mayo, YT	63°33'	136°12'	520-580	30.5abc	25.5ab	28.5a	35.5cd	30.0	42a	2
Rusty Creek, YT	63°29'	136°28'	610-760	31.5ab	25.5abc	27.5ab	36.0c	29.5	46b	2
Minto, YT	62°30'	136°42'	520-790	31.0abc	26.0a	27.5ab	35.0cde	29.5	43b	4
Frenchman Lake, YT	62°05'	135°35'	760	30.0bc	26.0ab	28.0ab	34.5def	29.5	40a	3
Hawk Hills, AB	57°23'	117°35'	700	31.5a	24.0bcde	27.5ab	36.5b	29.5	49b	7
Watson Lake, YT	60°08'	129°30'	760-850	30.0bc	24.0bcd	28.0ab	35.0cd	29.0	40ab	4
Teslin, YT	60°00'	132°13'	730-850	30.5abc	25.5ab	27.0ab	34.5def	29.0	43b	3
Frances Lake, YT	61°32'	130°00'	850-975	32.0a	22.5de	27.0ab	36.5b	29.0	45b	4
Gravel Lake, YT	63°57'	138°38'	670-700	30.5abc	25.0abc	27.5ab	32.5g	28.5	42ab	1
Ross River, YT	62°10'	133°30'	730-850	29.5c	23.5cde	26.0bcd	33.5fg	27.5	37a	2
Whitehorse, YT	60°44'	135°12'	700-820	29.5c	23.0cde	26.5abc	33.0g	27.5	38a	5
Tetsa River, BC	58°40'	124°10'	730-1040	29.5c	22.5de	25.5bcd	34.0efg	27.5	41ab	4
S. Canol Road, YT	61°33'	133°05'	880-1010	26.5d	23.5cde	24.5d	31.0h	26.0	35a	2
Haeckle Hill, YT	60°45'	135°15'	975-1340	27.0d	22.5de	26.0bcd	29.5h	26.0	35a	3
Summit Lake, BC	58°39'	124°40'	1130-1340	27.0d	21.5e	24.0cd	31.0h	25.5	38a	7
Squanga Lake, YT	60°27'	133°30'	~760	—	—	27.5ab	38.5a	—	—	—

^a Differences among heights with a common letter were not significant. Fort Nelson River provenance was significantly taller than the others.

^b Differences among values with a common letter were not significant from the most (a) and least (b) injury-resistant *P. contorta* provenance.

Discussion

T-Field Arboretum Study

Mortality rate of the subarctic provenances decreased from 1 percent per year in 1981 (Alden and Zasada 1983) to 0.5 percent per year in 1985, and mortality rate of the southern provenances increased from 1.9 percent to 2.3 percent per year during the same period (fig. 2). Trees sustaining mild winter injury recovered rapidly. Winter injury to lodgepole pine causes abnormal shoot phenology, delays maturation of new shoots, and increases the susceptibility of immature shoots to early frost injury in Alberta (Zalasky 1980). Injury was not observed in autumn and winter at T-Field Arboretum. Lodgepole and jack pine may not be highly susceptible to late summer frost and early winter injury in interior Alaska.

Trees susceptible to winter injury, especially those from southern provenances, apparently lost hardiness in response to above-normal winter temperatures and were killed by normal subfreezing temperatures in late March and April. Trees and shrubs from habitats with long growing seasons and mild winters often initiate growth in response to above-normal winter temperatures and are injured later by freezing in cold climates (Bachtell and Green 1985). The time for initiation of annual growth and loss of hardiness may decrease with increasing latitude of interior lodgepole pine provenances. Shoot elongation of 2-year-old Rocky Mountain seedlings was earlier and more gradual for southern provenances than for northern provenances between latitude 38° and 48° N. (Moore 1984). Time and rate of shoot elongation responded clinally to latitude of seed source.

Subarctic provenances apparently maintain the inherent characteristic of lodgepole pine for rapid early growth in competition-free plantations at high latitudes. Mean annual increment of managed stands on productive sites in Alaska and the Yukon should exceed the growth of wild lodgepole pine populations. Open stands of 30- to 80-year-old lodgepole pine are growing from 3 to nearly 6 cubic meters per hectare per year on well-drained, medium-textured soils at 800 to 1000 meters above m.s.l. in south-central Yukon (Oswald and Brown 1986).

Study I

Absence of provenance $\times$ site interaction for mortality, average height, and volume per tree at Fairbanks and Whitehorse indicated that relative growth and yield of subarctic provenances may be stable over a wide range of sites at low altitudes in interior Alaska. Subarctic provenance zones for interior Alaska may be extensive. "Provenance zones" are areas within the range of a species that have populations of acceptable adaptation to a particular environment or test site within or outside the species range (Campbell 1974). Similar environments or test sites are grouped into test regions or "plantation zones" based on wide-range provenance trials. Additional tests are necessary in each plantation zone to determine the superior provenance or provenances from the provenance zone.

Differences in relative 10-year height and mortality of provenances between Watson Lake and Whitehorse and significant provenance $\times$ site interaction indicated that the Pelly-Cassiar Mountains may form a major boundary for lodgepole pine plantation zones in the Yukon and northern British Columbia. The Pelly and Cassiar Mountains separate the Liard River (Watson Lake site) and the Yukon River (Whitehorse site) drainages. Ying and Illingworth (1986) reported differences in ranking of 10-year heights for 40 provenances at Whitehorse and Watson Lake, but provenance $\times$ site interaction was small and insignificant. Provenances from central Yukon to northeastern British Columbia were recommended for reforestation in central and southern Yukon. Provenances from northeast British Columbia grew as well as provenances from central Yukon but sustained winter injury.

Study II

Significant species $\times$ site interaction for height growth in 1985 indicated that the most productive species on the glacial soils and with shrub competition at site 1 may not be the most productive species on the loess soils and with grass competition at site 2. The decline in height and increase in environmental injury of lodgepole pine seedlings at site 1 in 1985 indicated that competition and the physical environment were more severe for establishing lodgepole pine than for establishing jack and Scots pine seedlings.

Differences in height between jack pine and lodgepole pine and between jack pine provenances and the Fort Nelson River hybrid provenance suggested that either jack pine is the major species in the Fort Nelson River population or that the vigorous early growth characteristics of jack pine dominate lodgepole pine. The range of lodgepole pine extends to latitude 62° N. on the Flat River, Northwest Territories (Scotter 1974), and lodgepole pine is found in the region of the Fort Nelson River population (Krajina and others 1982). Jack pine is also present in northeast British Columbia, but the extent of jack pine and lodgepole pine introgression are not well delineated (Critchfield 1985); however, von Rudloff and Nyland (1979) found evidence of jack pine introgression in the Liard River drainage of southeast Yukon, about 75 kilometers west of the known jack pine range in Northwest Territories. Forrest (1981) reported evidence of jack pine introgression at Fort Nelson, British Columbia. Wheeler and Guries (1987) classified populations from northwest Alberta as potential nonparental outliers of jack and lodgepole pine, and von Rudloff and Lapp (1987) found unique monoterpene composition in the Petitot River, British Columbia, provenance. Thus, jack pine introgression could be extensive in northeast British Columbia. Jack pine introgression may impart rapid early growth and winter resistance observed in lodgepole pine provenances from this region at Fairbanks, Alaska. Differences in degree of jack pine introgression in northeast British Columbia may contribute to the wide variation in survival and growth of Fort Nelson provenances observed among sites in northern Sweden.⁵

Study III

The significant relations among height, environmental injury after outplanting, and altitude of provenances indicate that lodgepole pine in the subarctic regions of Yukon and northeast British Columbia is highly structured genetically, despite fossil pollen evidence of its recent arrival (MacDonald and Cwynar 1985). The natural range of jack pine extends into northeast British Columbia (Krajina and others 1982), and evidence of wide introgression in lodgepole pine is revealed in monoterpene studies of von Rudloff and Nyland (1979), Forrest (1981), and von Rudloff and Lapp (1987) and in allozyme studies and cone and seed traits (Wheeler and Guries 1987). Evidence of shore pine introgression in Yukon populations is found in the monoterpene composition of leaf resins (von Rudloff and Nyland 1979) and allozyme frequencies (Wheeler and Guries 1982b). North coastal populations of shore pine could have crossed the Coast Range into the Yukon region during early Holocene. Pine dominated the pollen samples from bog deposits in the Atlin region of the upper Yukon more than 8,000 years ago (Anderson 1985), and lodgepole pine grows less than 100 meters below White Pass summit, British Columbia (1000 meters above m.s.l.), in the coastal mountains. Foliage and cone characteristics of Sitka spruce, *Picea sitchensis* (Bong.) Carr., endemic to the Pacific coast, can be observed in spruce populations (*P. × lutzii* Little) at about 600 meters above m.s.l. on the interior slopes of the Coast Range below White Pass.

⁵ Personal communication: K. Lindgren, Swedish University of Agricultural Sciences, Umeå, Sweden, 1986.

Lodgepole pine provenances from high altitudes grew more slowly and were less susceptible to environmental injury when transplanted from the nursery to field environments than were provenances from low altitudes. Similar results have been reported for older lodgepole pine elsewhere. Relative height and percentage of unhealthy trees decreased with increasing altitude of interior lodgepole pine provenances from latitude 52° to 63° N. after eight growing seasons in field trials in northern Sweden (Lindgren 1983). The height of 10-year-old progeny grown on an agriculture site in northern Sweden decreased as the altitude of their seed parents increased from 800 to 1250 meters (Fries and Lindgren 1986). Condition of the trees was not related to altitude of the seed parents, however. Rate of shoot growth, length of the growing period, and seasonal shoot elongation of 3-year-old seedlings decreased (Rehfeldt and Wykoff 1981), and rate of cold acclimation of 2-year-old seedlings increased with increasing altitude of 30 Rocky Mountain populations between latitude 44° and 49° N. (Rehfeldt 1980). Seven of nine families represented in the Fort Nelson River, British Columbia, provenance were from a jack pine × lodgepole pine hybrid swarm at the 300-meter altitude. Thus, natural selection for fast growth at the expense of hardiness at low altitudes, as well as jack or lodgepole pine introgression, may produce the superior height and high incidence of injury observed in the Fort Nelson River provenance.

Conclusions

Subarctic lodgepole pine provenances from central Yukon and the region of jack pine sympatry in northeast British Columbia are capable of rapid juvenile growth on productive sites in interior Alaska. Research on lodgepole pine introduction established a subarctic provenance test region in Yukon and northeast British Columbia for plantation zones in interior Alaska. Provenance research showed:

1. Lodgepole pine from the provenance test region may be highly structured genetically. Seedling height and environmental injury after outplanting were highly correlated with altitude of provenance.
2. Growth of lodgepole and jack pine provenances from northeast British Columbia averaged more than 0.003 cubic meter per tree annually from 9 to 12 years after outplanting at Fairbanks, Alaska.
3. Lodgepole and jack pine are subject to snow damage and winter injury in interior Alaska. They could be high risks in long-term forest management.
4. Seedlings of a jack pine × lodgepole pine hybrid swarm from Fort Nelson River, British Columbia, were significantly larger than seedlings of subarctic lodgepole pine provenances in a nursery and two growing seasons after outplanting in interior Alaska. Seedlings of the Fort Nelson River provenance were not larger than seedlings of several jack pine provenances.
5. More seedlings of the Fort Nelson River, British Columbia, provenance showed environmental injury after transplanting than seedlings of subarctic lodgepole pine provenances. Recovery of the Fort Nelson River and jack pine seedlings during the second growing season in a species trial was more rapid than seedlings of the subarctic lodgepole pine provenances.

6. Provenances from the northern range of jack pine and the region of introgression with lodgepole pine in northeast British Columbia and the Northwest Territories should be tested in interior Alaska. A lodgepole pine hybridization program with jack pine may enhance early growth and plantation establishment.
7. Greenhouse seedlings of *Pinus*, *Picea*, and *Larix* species, 1 to 2 years old, are subject to environmental injury after outplanting in interior Alaska. Subarctic provenances of lodgepole pine sustained more injury than *L. laricina* and *L. sibirica/sukaczewii* but less injury than *P. abies*. Techniques for acclimation of nursery-grown seedlings and complete site preparation (vegetation control and surface scarification) need to be developed for afforestation in Alaska.

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Growth, winter injury, and mortality were evaluated for 12-year-old trees of 11 subarctic lodgepole pine provenances and a jack pine provenance at Fairbanks, Alaska. Provenances from northeast British Columbia grew more than 0.003 cubic meter of wood per tree annually from 9 to 12 years after outplanting. The species sustained snow damage and winter injury, however, and could be at high risk in long-term management on severe sites in Alaska. Provenance $\times$ site interactions were not significant for mortality, tree height, and volume after the same stock grew for 10 seasons at Fairbanks and Whitehorse, Yukon.

Height and environmental injury of 3-year-old seedlings from 18 subarctic lodgepole pine and a jack pine $\times$ lodgepole pine swarm from Fort Nelson River, British Columbia, were evaluated at two sites in the interior and one site in south-central Alaska. Seedlings from high-altitude provenances grew more slowly and sustained less environmental injury after outplanting than seedlings from low-altitude provenances. More seedlings of the jack pine $\times$ lodgepole pine provenance sustained injury, but they grew taller than seedlings of the lodgepole pine provenances in the nursery and after two growing seasons in the field. Additional research is necessary to identify and determine growth and yield of superior jack, lodgepole, and jack pine $\times$ lodgepole pine provenances for a wide range of sites in Alaska.

Keywords: Lodgepole pine, *Pinus contorta*, jack pine, *Pinus banksiana*, subarctic species and provenances, hybrid/swarm, introgression, growth, survival, winter injury, Alaska.

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