

## **Section 5.**

### **Lodgepole pine (*Pinus contorta*)**

#### **Preamble:**

The following text applies principally to lodgepole pine (*Pinus contorta* Dougl. ex. Loud.) in the most important part of its range; namely central and southern British Columbia, western Alberta, eastern Washington, eastern Oregon, Idaho, Montana, Wyoming, northern Colorado, and northern Utah. It also discusses use of lodgepole pine as an exotic.

#### **1. Taxonomy**

The genus *Pinus* L. (in the family Pinaceae) originated in the early to mid-Mesozoic about 180 million years ago, prior to the continental separation in the Laurasian region that became eastern North America and western Europe (Burdon, 2002). Some 150 million years before the present (BP), *Pinus* subdivided into hard pines (subgenus *Pinus*) and soft pines (subgenus *Strobus*). Rapid evolution, speciation, and migration occurred during the Tertiary prior to cooling climatic conditions at its end (Mirov and Hasbrouck, 1976). Lodgepole pine (*Pinus contorta* Dougl. ex. Loud.) and its close relative jack pine (*P. banksiana* Lamb.) might have evolved from a common progenitor into a western and a northern species during cooling in 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 BP.

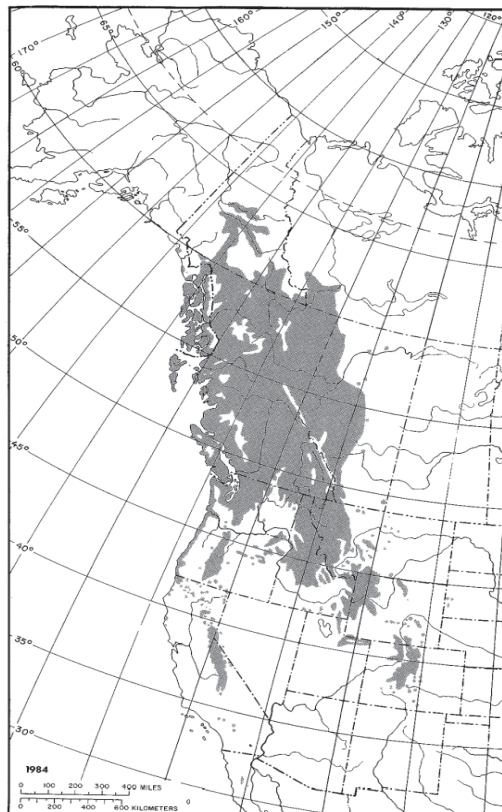
Lodgepole pine is a western North American 2-needled pine of the subgenus *Pinus* (much resin, close-grained wood, sheath of leaf cluster persistent, two vascular bundles in each needle), section *Pinus*, subsection *Contortae*, along with the North American species *P. banksiana*, *P. virginiana* and *P. clausa* (Little and Critchfield, 1969). The stiff usually twisted needles are 2.5-7.6 cm long; cones are near branch tips, each cone scale with a short spine. Lodgepole pine has evolved into several highly differentiated but interfertile geographic races that differ morphologically and ecologically. Four subspecies (Critchfield, 1957), also referred to as varieties (Little, 1979), are recognized:

- *Pinus contorta* subsp. *contorta* – a coastal, somewhat crooked shorter race, known as shore pine, coast pine, or beach pine;
- *Pinus contorta* subsp. *bolanderi* (Parl.) Critchf. – a closed-cone (serotinous) stunted local form in north-western California (Mendocino County, endemic on podzol soils), which is called Bolander pine, and by some considered a synonym under *P. contorta* subsp. *contorta* (Aitken and Libby, 1994; Kral, 1993);
- *Pinus contorta* subsp. *murrayana* (Grev. & Balf.) Critchf. – a non-serotinous, far western montane race in that Cascades (Oregon) to Mexico but primarily in the Sierra Nevada of California, which is called Sierra lodgepole pine or sometimes tamarack pine; and
- *Pinus contorta* subsp. *latifolia* (Engelm. in S. Wats.) Critchf. – the extensively distributed continental interior race, which is often straight and tall, and referred to simply as lodgepole pine or sometimes as Rocky Mountain lodgepole pine or black pine.

## 2. Natural distribution

Lodgepole pine is a commonly occurring Western North American (and marginally central North American) species with a wide latitudinal and elevational range (Wheeler and Guries, 1982a; Klinka *et al.*, 2000) (Figure 1). It grows throughout the Rocky Mountain and Pacific regions, with a range extending from approximately 31°N in Baja California north to around 64°N in the Yukon Territory, and from the Pacific Ocean east to South Dakota. Although subsp. *contorta* and *bolanderi* are not found above 610 m, the interior subsp. *latifolia* and *murrayana* together span from 490 to 3,660 m (Little, 1979). Forests dominated by lodgepole pine cover approximately 26 million ha in North America, with the majority of this area is in Canada (20 million ha) (Lotan and Critchfield, 1990; MacDonald and Cwynar, 1985; Griffin and Critchfield, 1976).

**Figure 1** The native range of lodgepole pine



Source: from Lotan and Critchfield, 1990

## 3. Reproductive biology

### 3.1. Reproductive development

Lodgepole pine is monoecious, with male and female strobili (“flowers”) usually borne separately on the same tree. Female strobili are usually at the apical end of main branches in the upper crown, while pollen strobili originate in the lower crown. Female strobili are reddish-purple and develop in whorls of two to five. Pollen cones are pale yellow to yellowish- orange and occur in crowded clusters at the base of new shoots (Lotan and Critchfield, 1990).

Buds differentiate into male, female or vegetative the summer prior to strobili emergence. Pollen strobili emerge in spring and generally mature from mid-May to mid-July (Satterlund, 1975; Critchfield, 1980). The timing of pollen maturation and female receptivity appears to be related to elevation and climate. Pollen dispersal is *via* wind. Pollen is drawn into the micropyle in a pollination drop. Fertilization occurs nearly one year after pollination, then cones complete development and mature in August, September, or October of that year (Owens and Molder, 1994). Inland and high elevation stands mature earlier than coastal or low elevation stands. At maturity, cones change from purple-green to light brown in colour (Schopmeyer, 1974).

### 3.2. Mating system and gene flow

The mating system of lodgepole pine is outcrossing, with both single and multilocus estimates of outcrossing rate ( $t$ ) based on allozymes approaching one (Yeh and Layton, 1979; Epperson and Allard, 1984). Selfing estimates based on phenotypic frequencies of progeny of open-pollinated trees carrying recessive, mutant markers indicated a selfing rate of 4.3% in the upper crown and 9.6% in the middle crown (Sorensen and Adams, 1993).

Lodgepole pine, like all pines, is wind pollinated and has pollen grains with two air sacs, facilitating long-distance dispersal, thus gene flow is generally thought to be high for this species (Yang and Yeh, 1995). Studies using paternal chloroplast and maternal mitochondrial genetic markers indicate that gene flow is higher *via* pollen than seed, as would be expected (Dong and Wagner, 1994). Gene flow is higher among central, continuous populations than among disjunct, or marginal populations (Yeh and Layton, 1979; cf. Delcourt and Delcourt, 1991; Fazekas and Yeh, 2001), and appears to be highest for subsp. *latifolia*, intermediate for subsp. *contorta*, and lowest for subsp. *murrayana*, based on indirect estimates from population differentiation statistics (Yang and Yeh, 1993).

### 3.3. Seed production

Lodgepole pine is a highly fecund species, and trees commonly start producing viable seed at 5 to 10 years, with the percentage of germination as high as that of mature trees. Female and male strobili have been observed on two year-old seedlings. This high and early fecundity contributes to lodgepole pine's ability to naturalize and become invasive in some foreign environments such as New Zealand (Ledgard, 1993; Richardson and Higgins, 1998). Good cone crops usually occur at 1- to 3-year intervals, with light crops in between. Only squirrels (*Sciuridae*) and coreid insects are significant seed predators (Lotan and Critchfield, 1990).

Lodgepole pine seeds are relatively small compared to other species of pine. The number of cleaned seed per kg ranges between 200,000 and 300,000, depending on subspecies (Lotan and Perry, 1983). Seed weights vary considerably and increase from north to south. The number of cleaned seeds averaging 207,000 per kg for subsp. *latifolia*, 258,000 per kg for subsp. *murrayana* and 298,000 per kg for subsp. *contorta* (Critchfield, 1980). Filled seed per cone can range from 5 to 45, and averages around 20 (Critchfield, 1980).

Individual dominant and codominant trees can produce from a few hundred to a few thousand cones per tree (Lotan, 1975). Annual production for subsp. *latifolia* may run from 173,000 to 790,000 seeds per hectare with half to one-third available for annual seedfall and the remaining held viable in closed serotinous cones (Fowells, 1965; Critchfield, 1980). In New Zealand, subsp. *latifolia*, *murrayana* and *contorta* have all been introduced, but subsp. *contorta* produced seed earlier and more prolifically than the other subspecies, contributing to its role as a "noxious weed" (Ledgard, 1993). Cones are persistent and the majority are serotinous for mature trees in more northern areas of subsp. *latifolia*. Closed cones can accumulate for decades. Juvenile subsp. *latifolia* produce mostly non-serotinous cones. In Oregon, where cones are primarily non-serotinous, seedfall ranges from about 35,000 to over 1.2 million per ha

(Dahms, 1963). In the serotinous cones of subsp. *latifolia*, stored seeds are in the millions per hectare and the number of seeds stored is probably 10 times that of seeds produced annually (Lotan, 1975).

The serotinous cone habit varies over a wide range of geographic scales (Lotan, 1975). While this habit is typical of most of the range of subsp. *latifolia*, trees of this subspecies in eastern Oregon are mostly non-serotinous (Lotan and Critchfield, 1990). Serotinous cones are also rare in coastal populations (subsp. *contorta*), and absent in the Sierra Nevada and southern California and Baja California populations (subsp. *murrayana*), but are found in Bolander pine (subsp. *bolanderi*) (Critchfield, 1980). The scales of serotinous cones cannot flex open due to a resinous bond. These bonds break on exposure to temperatures between 45° and 60°C (Perry and Lotan, 1977). After resinous bonds break, cone scales can flex open hygroscopically and release seeds. Closed cones at or near the soil surface (less than 30 cm depth) are subjected to insolation temperatures sufficient to break resinous bonds, and may provide seed for natural regeneration in harvested areas. The potential for weedy invasiveness of lodgepole pine as an exotic may be affected by cone serotiny and the presence or absence of fire (Ledgard, 1993; Richardson and Higgins, 1998). In northern Europe, subsp. *latifolia* originating from the northern portion of the range with predominantly serotinous cones has not proven weedy or invasive, with only limited naturalization despite wide scale planting, whereas in New Zealand subsp. *contorta* has spread rapidly from seed dispersed from cones opening at maturity (Ledgard, 1993).

Lodgepole pine is a fire-maintained, subclimax species. Its ability to regenerate to extremely high densities and exclude other species can be attributed to the closed cone habit. Millions of seeds per hectare held in reserve for many years are readily available to germinate. In addition to opening cones, fire prepares an ideal seedbed. It appears that fire is a strong agent of natural selection favouring serotinous cones (Perry and Lotan, 1979). It is possible that the serotinous cone habit could be lost if landraces develop where subsp. *latifolia* has been introduced as an exotic in environments with low fire frequency and intensity, e.g., northern Europe.

Seeds remain viable in serotinous cones for years. Viability can be maintained as long as cones or seeds are not on the ground. Once cones are on the ground, they open. Damping-off fungi may infect the seed, rodents may feed on the seeds, or germination may occur. Seeds are not stored in soil seedbanks (Lotan and Critchfield, 1990).

### 3.4. Natural regeneration

Lodgepole pine is best maintained using even-aged silvicultural systems (Lotan, 1975). Clear cutting followed by either planting or natural regeneration is common. Although success of natural regeneration is high, planting allows for initial stocking control and genetic improvement. Natural regeneration requires an adequate seed source, an appropriate seedbed, and suitable microsites to succeed.

For non-serotinous cones that disperse seeds from standing trees, the density of seedfall 20 m from the timber edge is only 10 to 30% of that at the stand edge in the Rocky Mountains (Lotan and Perry, 1983). Dispersal of sufficient seed to adequately restock an area often only occurs within 60 m of the seed source (Dahms and Barrett, 1975; Lotan, 1975). Prevailing winds, thermal effects, or scudding on snow or ice may disperse seeds far beyond these distances, however. For example, in New Zealand the furthest documented seedling establishment from a seed source is 30 km (Ledgard, 1993). The annual seedfall from the non-serotinous cones of initial colonizers helps to fully occupy sites. Seedfall can also restock stands following relatively minor disturbances in a stand and maintain lodgepole pine in mixed stands. There are usually some trees with non-serotinous cones in most stands. Most seeds in mature non-serotinous cones are released in fall and winter (Fowells, 1965).

When stands are harvested and the resulting slash contains large numbers of serotinous cones, appropriate slash treatments can result in sufficient seed dispersal for natural regeneration. If cones become detached from the slash, they can open with normal summer soil surface temperatures (Lotan,

1964). The seed supply will be largely destroyed if slash to be burned is piled before cones have had a chance to open (Lotan, 1975). After sufficient cones have opened, piling slash scatters seeds and helps prepare the seedbed. Most seed is released from serotinous cones near the ground during the first year. Serotinous cones that are suspended well above the ground will remain closed, and the seed they contain will remain viable for years. Broadcast burning can be used to accelerate the release of seeds from such cones or from those with limited exposure to sunlight. Some seeds will be destroyed; however, the amount will vary with fire intensity.

### 3.5. *Vegetative reproduction*

Lodgepole pine vegetatively reproduces only rarely in nature. Some natural sprouting has been observed in the Bitterroot National Forest in Montana. Branches on stumps from thinning often become leaders. Lodgepole pine is regularly grafted into seed orchards, but the success of grafting can depend on the clone (Critchfield, 1980). Juvenile lodgepole pine cuttings are relatively easy to root, but rootability varies with clone and declines with donor age (Fries and Kaya, 1997a). Seedlings can be hedged to maintain juvenility and provide cuttings (Fries and Kaya, 1997b). Many needle fascicles (short shoots) can be stimulated to produce long shoots by pinning seedlings horizontally along the soil, then the shoots produced can be cut and easily rooted (S.N. Aitken, University of British Columbia, unpublished data). Callus tissue cultures and liquid cell suspensions have been produced from seedling hypocotyl tissue, excised embryos, and actively growing shoots (Cole, 1975). There are no published reports regarding somatic embryogenesis in lodgepole pine, but other *Pinus* species have been successfully cloned in this manner so it is highly likely that this technology could be developed, providing an effective system within which transformation and regeneration of transgenic emblings could be achieved.

## 4. Genetics

### 4.1. *Cytology*

*Pinus contorta* has a haploid complement of  $n=12$  chromosomes, like all species in the genus *Pinus* and most in the family Pinaceae (Wright, 1962). Aneuploids and polyploids are unknown in this species. The inheritance of cytoplasmic organelles has been studied using genetic markers, and like other species in the Pinaceae, mitochondria are inherited largely maternally with some paternal leakage, whereas chloroplasts are inherited paternally (Wagner *et al.*, 1991a; Dong *et al.*, 1992; Dong and Wagner, 1994).

### 4.2. *Genetic variation*

#### 4.2.1. *Population-level variability*

The results of numerous allozyme studies of among and within subspecies and population variation are compiled in Table 1. Wheeler and Guries (1982b) compared seed and cone morphology with allozyme frequencies and found that while 38% of the variation in morphology was due to differences among subspecies, and 19% due to variation among populations within subspecies, for allozymes just 3% of the variation was among subspecies and 6% among populations within subspecies. The strong morphological differences among subspecies support Critchfield's 1957 taxonomic treatment (Wheeler and Guries, 1982b; Newman and Jancey, 1983). Marginal (disjunct or peripheral) populations show a higher degree of population differentiation than core populations, presumably due to reduced gene flow (Fazekas and Yeh, 2001; Yeh and Layton, 1979). Populations separated by short distances (one or two km) differ very little genetically (Knowles, 1984).

Highly variable microsatellite markers (SSR, single sequence repeats) and randomly amplified polymorphic DNA (RAPD) markers have been developed for lodgepole pine (Hicks *et al.*, 1998). Expected heterozygosities for these markers range from 0.67 to 0.77 for SSRs and 0.39 to 0.47 for



RAPDs (Thomas *et al.*, 1999). For both types of markers, over 94% of variation was found within populations. Planted stands did not differ significantly from naturally regenerated stands for expected heterozygosity.

The apparent discrepancy between selectively neutral genetic markers showing little population genetic differentiation, and polygenic morphological or physiological traits showing strong differentiation, is typical of widespread conifers. This is due in part to the homogenizing effects of long-distance gene flow *via* pollen and post-Pleistocene range expansions from glacial refugia on selectively neutral genetic markers, and in part to the strong effects of environment-dependent selection on adaptive traits (Cwynar and MacDonald, 1987; Delcourt and Delcourt, 1991). Yang *et al.* (1996) compared population differentiation for quantitative traits and allozymes for five populations of subsp. *latifolia*. They concluded that two branching traits which showed a low degree of population differentiation similar to allozyme (<6%), were likely selectively neutral (as allozymes are assumed to be), while size and wood specific gravity, with >13% of variation among populations, were under divergent selection.

**Table 1. Summary of genetic diversity estimates for *Pinus contorta***

Populations Sampled <sup>3</sup>	Expected heterozygosity ( $H_e$ ) within populations	% polymorphic loci	Population differentiation ( $F_{st}$ or $G_{st}$ )	Reference
<i>Allozymes</i>				
Rangewide (4 subsp.)			0.061 <sup>1</sup> 0.032 <sup>2</sup>	
Subsp. <i>latifolia</i>	0.118	69		Wheeler and Guries, 1982b
Subsp. <i>contorta</i>	0.126	65		
Subsp. <i>murrayana</i>	0.124	73		
Subsp. <i>bolanderi</i>	0.109	58		
Subsp. <i>latifolia</i>	0.194	69	0.034	Yang and Yeh, 1993
Subsp. <i>contorta</i>	0.180	62	0.057	
Subsp. <i>murrayana</i>	0.196	63	0.076	
Subsp. <i>contorta</i> , CA	0.119	38	0.057	Aitken and Libby, 1994
Subsp. <i>bolanderi</i>	0.105	28	0.044	
Subsp. <i>latifolia</i> – nearby populations CO	0.135	44	0.008	Knowles, 1984
<i>Randomly Amplified Polymorphic DNA</i>				
Subsp. <i>latifolia</i> , BC				Fazekas and Yeh, 2001
Central populations	0.160		0.081	
Intermediate populations	0.153		0.076	
Marginal populations	0.143		0.139	

<sup>1</sup> Location: USA - CA = California; CO = Colorado; Canada - BC = British Columbia

<sup>2</sup> Differentiation among populations within subspecies

<sup>3</sup> Differentiation among subspecies

Provenance testing and seedling genecological experiments are extensive for *Pinus contorta*, due to its widespread distribution, economic importance and use as an exotic. An enormous provenance trial established in British Columbia in the 1970s by the British Columbia Ministry of Forests included 142 populations and 60 field test sites (Xie and Ying, 1995; Rehfeldt *et al.*, 1999). A total of 158 seed lots were distributed around the world for International Union of Forest Research Organizations (IUFRO) provenance trials (summarized in K. Lindgren, 1993), but most of these trials contain only

a subset of provenances from a limited geographic area. The British Columbia provenance trial has been the focus of many published studies, and the trees under test are now over 20 years old. Population variation in growth rate, insect and disease resistance, shoot phenology, snow breakage and wood properties have been studied in these trials (Ying *et al.*, 1985; Ying and Hunt, 1987; Yanchuk *et al.*, 1988; O'Reilly and Owens, 1989; Xie and Ying, 1995; Wu *et al.*, 1996; Rehfeldt *et al.*, 1999). Most of the focus in this trial has been on subsp. *latifolia*, as survival and growth of the other subspecies is poor in the continental climate of interior British Columbia.

The results of the British Columbia provenance trial and seedling studies indicate that *P. contorta* is an adaptive specialist with locally adapted populations and relatively steep genetic clines, particularly associated with elevation of origin (Rehfeldt, 1987; Xie and Ying, 1995; Rehfeldt *et al.*, 1999). As the trees in the British Columbia field provenance trial aged, genetic clines became steeper over time with a greater proportion of the total variation due to differences among populations (Ying *et al.*, 1989; Xie and Ying, 1995). Seedling genecological studies have provided additional information on provenance variation in subsp. *latifolia* for adaptive traits including shoot growth components (phenology and rate of elongation), and cold hardiness (Rehfeldt, 1987, 1989; Lindgren and Nilsson, 1992; Chuine *et al.*, 2001). Genetic clines are strongly associated with source climate, with temperature rather than moisture variables accounting for the most population variation (Rehfeldt *et al.*, 1999). Populations originating from lower elevations have higher growth rates, longer growing seasons, greater resistance to needle cast and are more susceptible to snow breakage than those from higher elevations (Rehfeldt, 1987). Latitudinal clines are significant, but much weaker than those associated with elevation, with similar levels of differentiation observed for populations separated by 1000 m of elevation or 7° of latitude (Rehfeldt, 1987; Xie and Ying, 1995). Higher rates of height growth are related to a greater number of predetermined stem units, which result from a higher rate of initiation of primordia in buds during the previous growing season rather than a longer duration of initiation (Cannell and Willett, 1975; Chuine *et al.*, 2001).

Insect and disease resistance for a variety of pests including western gall rust (*Endocronartium harknessii*), stalactiform blister rust (*Cronartium coleosporioides*), needle cast (*Lophodermella concolor*) and Sequoia pitch moth (*Synanthedon sequoiae*) varies significantly among provenances and increases with proximity to the natural range of *Pinus banksiana* (jack pine), indicating that introgression may provide genetic variation for pest defenses to *P. contorta* (Wu *et al.*, 1996). Susceptibility to all of these pests except sequoia pitch moth also increases with provenance elevation (Ying and Hunt, 1987; Yanchuk *et al.*, 1988; Wu *et al.*, 1996).

One test site in the British Columbia provenance trial was located on southern Vancouver Island in a location mild enough to allow for the survival and growth of all four subspecies. Even in this relatively mild location, the narrow adaptation of populations was observed, with all populations except those from Vancouver Island and nearby populations on the eastern tip of the Olympic Peninsula exhibiting poor growth or survival and declining vigour (Ying and Liang, 1994).

#### 4.2.2. *Variation among individuals within populations*

Like most widespread conifers, there are high levels of within-population genetic variation in lodgepole pine for both genetic markers and quantitative traits. For allozyme loci, 91% of the total genetic variation resides within populations of lodgepole pine, while for many morphological and quantitative traits, a substantially greater proportion of variation is due to among-population variation (Wheeler and Guries, 1982b; Yang *et al.*, 1996; Table 1). Average expected heterozygosity estimates are typical of gymnosperms (Hamrick *et al.*, 1992). Expected heterozygosities within populations are similar for subsp. *latifolia*, subsp. *contorta* and subsp. *murrayana*, and lower for subsp. *bolanderi* (Wheeler and Guries, 1982b; Yang and Yeh, 1993; Aitken and Libby, 1994).

Nursery and field progeny trials for breeding programs of *P. contorta* subsp. *latifolia* have revealed significant variation among families within populations for height and diameter growth, branch length, angle and diameter, wood specific gravity, western gall rust infection and severity, stalactiform blister rust, needle cast, Sequoia pitch moth, ramicorn branch frequency, cold hardiness in North America, and weather injury and scleroderris canker (*Gremmeniella abietina*) infection in Sweden (Yanchuk *et al.*, 1988; Fries, 1989, 1991; Ericsson *et al.*, 1994; Ericsson and Danell, 1995; Wu *et al.*, 1995, 2000; Yang *et al.*, 1996, 1998; Ericsson and Andersson, 1997; Wu and Ying, 1997; Wang *et al.*, 1999, 2000). A sample of representative individual heritability estimates is provided in Table 2.

Early selection for growth and adaptive traits has been an area of interest to lodgepole pine breeders. Nursery-field and age-age correlations have been variable and often poor for growth (Wu *et al.*, 1997), cold hardiness (Ericsson and Andersson, 1997) and resistance to western gall rust (*Endocronartium harknessii*) (White *et al.*, 2000). However, combining early seedling nursery performance with field results may enhance selection efficiency and genetic gain (Wu *et al.*, 2000).

**Table 2. Individual heritability estimates for growth and pest resistance traits in *Pinus contorta* subsp. *contorta* (lodgepole pine)**

Trait	Location <sup>1</sup> and trial type	Individual heritability estimate or range	References
Height	Field progeny tests BC, AB, S	0.14-0.50	Rehfeldt, 1985; Ericsson and Danell, 1995; Xie and Ying, 1996; Yang <i>et al.</i> , 1998; Wu <i>et al.</i> , 2000
Height	Seedling greenhouse, BC	0.61	Wu <i>et al.</i> , 1995
Diameter	Field progeny test, BC	0.33-0.40	Xie and Ying, 1996; Wu <i>et al.</i> , 2000
Diameter	Seedling greenhouse, BC	0.46	Wu <i>et al.</i> , 1995
Harvest index	Field progeny test, BC	0.34	Wu <i>et al.</i> , 2000
Fall cold hardiness	Field progeny test, ID	0.10	Rehfeldt, 1989
<i>Endocronartium harknessii</i> infection	Field progeny test, BC and AB	0.12-0.50	Wu and Ying, 1997; Yang <i>et al.</i> , 1998
<i>Cronartium coleosporioides</i> infection	Field progeny test, BC	0.32	Wu and Ying, 1997
<i>Lophodermella concolor</i> impact	Field progeny test, BC	0.30	Wu and Ying, 1997
<i>Synanthedon sequoiae</i> damage	Field progeny test, BC	0.21	Wu and Ying, 1997
Injury/cankers, mainly <i>Gremmeniella abietina</i>	Field progeny test, S	0.12	Ericsson and Danell, 1995

<sup>1</sup> AB = Alberta, S = Sweden, ID =Idaho, BC = British Columbia

### 4.3. Inbreeding depression and genetic load

Self-fertility is low in lodgepole pine. Just 12% as many seeds on average were produced by controlled self-pollination as by controlled outcrossing, indicating very low self-fertility and high inbreeding depression for embryo survival, even for a conifer. This is likely a result of a high genetic load of recessive lethal alleles (Sorensen and Adams, 1993). In the same study, the relative self-fertility of a stand containing a small proportion of lodgepole pine in an ecologically marginal location for this species was almost twice that of more typical stands with higher proportions and densities of



this species, suggesting perhaps that mating system could shift to more self-pollination in a population with few founders through purging of recessive, deleterious alleles, *e.g.* following introduction as an exotic. The genetic load may be too high in particular cases for this to occur.

## 5. Hybridization

*Pinus contorta* subsp. *latifolia* hybridizes and introgresses with jack pine (*P. banksiana*) in both western Alberta and the Northwest Territories where the two closely related species are sympatric (Critchfield, 1980). The natural hybrid zone in northwestern Alberta has been studied for traits including cone orientation, curvature and prickles (Moss, 1949; Wagner *et al.*, 1991b), needle length (Keng and Little, 1961), chemical composition of turpentine (Mirov, 1956; Zavarin *et al.*, 1969) and a variety of allozyme and nuclear and organelle-based genetic markers (Wheeler and Guries, 1982b, 1987; Dancik and Yeh, 1983; Dong *et al.*, 1992; Wagner *et al.*, 1987, 1991b; Govindaraju *et al.*, 1988; Ye *et al.*, 2002). Despite the interspecific gene flow that introgression facilitates, the two species have remained quite distinct genetically in areas near the introgression zone. More widespread hybridization is prevented by phenological differences in female stroboli receptivity and pollen shed in these species, with lodgepole pine flowering 2 to 3 weeks later (Critchfield, 1985). The genetic distance between lodgepole pine and jack pine populations in Alberta based on allozymes averages 20 times greater than the genetic distance among populations within either species (Dancik and Yeh, 1983). Hybrids may have reduced reproductive rates relative to parental species: some artificial F1 hybrids of jack and lodgepole pine have high levels of pollen abortion, but F1 to F3 hybrids produce some sound seed (Critchfield, 1980). Each species does, however, show some influence of introgression from the other in natural populations near the introgression zone (Zavarin *et al.*, 1969). Some Alberta and Saskatchewan jack pine populations show lodgepole pine influence in morphology, chemistry, or mitochondrial DNA, but the degree of influence does not appear to be well correlated with distance from lodgepole pine (Critchfield, 1980; Dong and Wagner, 1993). Resistance of lodgepole pine to some insects and diseases is highest in the introgression zone and declines significantly with distance to the nearest populations of jack pine, suggesting that introgression may increase resistance in lodgepole pine (Wu *et al.*, 1996; Wu and Ying, 1998; Yang *et al.*, 1999). However, other explanations can be proposed for the clinal trends in lodgepole pine resistance. Yang *et al.* (1997) questioned whether the introgression interpretation is valid for western gall rust; neither study sampled non-hybrid jack pines. The extent to which introgression between these species occurred prior to, or since, the last glacial period is unclear (Critchfield, 1985; Dancik and Yeh, 1983).

Relatively strong reproductive barriers exist between both lodgepole pine and jack pine and the two other species in subsection *Contortae*, *P. virginiana* (Virginia pine) and *P. clausa* (sand pine), both native to the southeastern United States. Controlled crosses between lodgepole and Virginia pine have yielded only a few dwarfed, chlorotic hybrid progeny (Critchfield, 1985). Lodgepole pine has not been successfully hybridized with pines from any other subsections or continents. Repeated efforts have been made to hybridize *Pinus contorta* with *Pinus sylvestris* (subsection *Sylvestres*), but these have resulted in only empty or inviable seed (Duffield, 1951/1952; Critchfield, 1980). Attempts with other species in subsection *Sylvestres*, as well as western American hard pines in other subsections, have also failed (Duffield, 1951/1952; Critchfield, 1980). These strong barriers to hybridization prevent contamination of native pine gene pools in Europe, where *Pinus contorta* has been widely planted.

## 6. Ecology

### 6.1. Climate

Within its native range, lodgepole pine grows predominantly within boreal, temperate and mesothermal climates (Klinka *et al.*, 2000). Minimum temperatures range from 7°C on the coast at

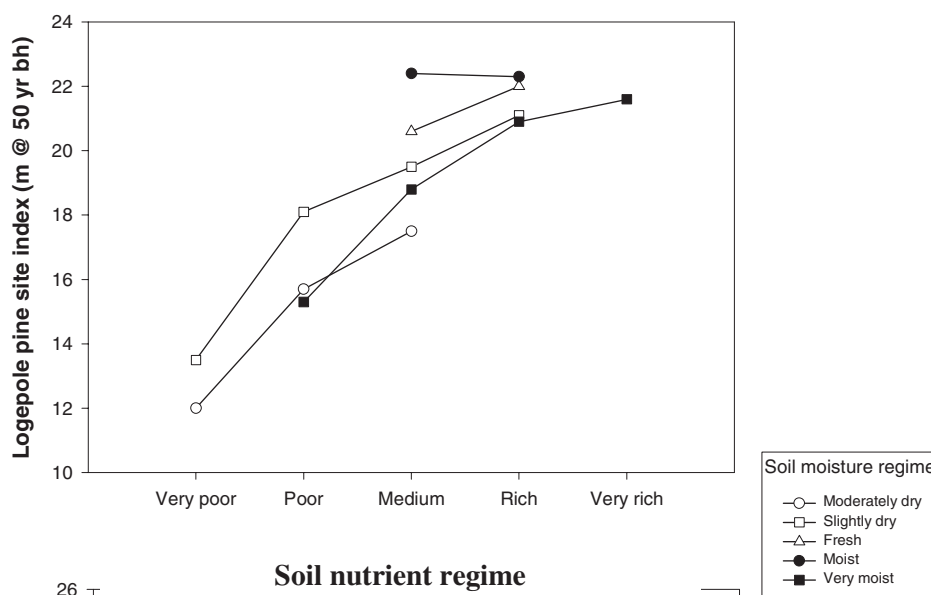
the southern edge of the species range to  $-57^{\circ}\text{C}$  in the Northern Rocky Mountains (Lotan and Critchfield, 1990). Maximum temperatures range from  $27^{\circ}\text{C}$  for subsp. *contorta* along the coast and at high elevations to well over  $38^{\circ}\text{C}$  at low elevations for subsp. *latifolia* in the interior. Average July minimum temperatures are frequently below freezing at high elevations (Lotan and Critchfield, 1990). Lodgepole pine seedlings are cold hardy compared to many conifers, and can survive in low-lying ‘frost-pockets’ in some locations where other species do not (Cochran and Berntsen, 1973; Lotan and Perry, 1983). At low elevations in the interior, subsp. *latifolia* can grow in areas receiving as little as 250 mm of mean annual precipitation, whereas subsp. *contorta* receives more than 5,000 mm along the northern coast. Many subsp. *latifolia* and subsp. *murrayana* sites have low summer precipitation. Melting snow provides most of the soil water used by subsp. *latifolia* and *murrayana*, for rapid growth in early summer (Lotan and Critchfield, 1990).

## 6.2. Soils

Lodgepole pine grows across nearly the entire range of soil moisture conditions (from very dry to very wet) and soil nutrient conditions (from very poor to very rich), but the most productive growth occurs on fresh to moist, rich soils. Compared to many other tree species, it tolerates water-deficient, water-surplus, and nutrient-deficient soils well (Krajina, 1969; Klinka *et al.*, 2000).

Relationships between potential site index of lodgepole pine and analytical and categorical measures of site quality have been studied in the Sub-boreal Spruce (SBS) zone of British Columbia (Wang *et al.*, 1994; Klinka *et al.*, 1994, Kayahara *et al.*, 1995), and in the Boreal White and Black Spruce (BWBS) zone of the Upper Foothills natural subregion of Alberta (Brisco, 2001). Lodgepole pine site index (i) increased with increasing soil water supply from water-deficient to fresh and moist sites and then decreased with increasing water surplus, and (ii) increased from very poor through very rich sites with the rate of increase decreasing with increasing nitrogen availability. Increase in site index along the soil nutrient gradient was consistently steeper than along the soil moisture gradient (Figure 2).

**Figure 2. Site index of lodgepole pine at 50 years ( $n = 235$ ) in relation to soil nutrient regime (x axis) and soil moisture regime (symbols) across the Sub-boreal Spruce zone of British Columbia (from Kayahara *et al.*, 1995)**



Lodgepole pine site index appears to improve with increasing nitrogen availability even on water-deficient sites. All the trends in site index–site quality relationships are supported by regression analysis indicating that each soil moisture and nutrient regime had a strong relationship with site index. The best quantitative soil measure related to site index of lodgepole pine was forest floor and mineral soil C/N ratio, which explained about 40% in the variation of site index.

Brisco (2001) characterized soil nutrient regimes by several, predominantly nitrogen related measures (i.e., total N, mineralizable N, and forest floor C:N ratio and phosphorus, P) and determined foliar nutrient levels in young lodgepole pine stands across a range of sites. He found (i) significant differences in needle mass and foliar levels of N, P, and sulphur, S, between soil nutrient regimes, and (ii) a strong correlation between soil and foliar nutrient variables. In a relatively dry montane boreal climate (mean annual precipitation = 343 mm), soil moisture regime accounted for 63% and soil nutrient regime for 32% of the variation in lodgepole pine site index.

It can be concluded that both soil moisture and nitrogen are major determinants of tree growth in the SBS and BWBS zones, and that lodgepole pine will respond to nitrogen fertilization, with the response likely decreasing with increasing soil water surplus and available nitrogen. In general, lodgepole pine responds favourably to additions of nitrogen, and has shown a relatively consistent response to fertilization with various sources of nitrogen (Cochran, 1975; Cochran *et al.*, 1979; Yang, 1985; Brockley, 1989, 1990, 1996, 2001). On some sites nitrogen fertilization may induce sulphur or boron deficiencies.

Lodgepole pine grows well in many topographic positions. It grows well on both gentle slopes and in basins, but stands are also found on steep slopes, ridges, in rocky terrain and on a gravel substrate. The growth of lodgepole pine is better on northern and eastern slopes than on southern and western aspects (Alexander, 1974).

Lodgepole pine grows best where soil parent materials are derived from granites, shales, and coarse-grained lavas (Fowells, 1965). It is relatively rare on soils derived from limestone that tend to be dry; however, extensive stands occur on calcareous glacial tills (Smithers, 1961). Lodgepole pine grows well on glacial tills in Alberta, and it appears glacial drift provides a favourable balance of moisture and porosity. Highly calcareous soils derived from dolomitic limestone parent material in Montana usually do not support lodgepole pine (Lotan and Critchfield, 1990).

In the U.S. System of Soil Classification (U.S. Soil Conservation Service, 1975), extensive stands of *P. contorta* subsp. *latifolia* occur on Inceptisols and Alfisols in interior forests. Boralfs and Ochrepts probably support better tree development than Andepts, although lodgepole pine is common on the latter (Lotan and Critchfield, 1990). *Pinus contorta* subsp. *contorta*, is often found on Histosols (peat bogs or muskegs) in the hypermaritime forests of southeastern Alaska, coastal British Columbia, and western Washington, and on Inceptisols, Alfisols, and Ultisols on dry, sandy, or gravelly sites in more southern coastal areas (Lotan and Critchfield, 1990).

Lodgepole pine grows on wet flats and poorly drained soils, and can tolerate high water tables. These conditions often favour lodgepole pine over other tree species. In the Sierra Nevada, eastern Oregon, and coastal California, soils with an underlying hardpan support lodgepole pine and exclude species such as ponderosa pine (*Pinus ponderosa*), redwood (*Sequoia sempervirens*), or Douglas-fir (*Pseudotsuga menziesii*). On level sites in British Columbia, Alberta and central Oregon, the frost tolerance of lodgepole pine during germination allows its establishment but excludes other species (Lotan and Critchfield, 1990).

### 6.3. Synecology

Lodgepole pine grows predominantly in even-aged, post-fire forests in pure or, less often, mixed-species stands. It is a pioneer species on rock outcrops and in ombrotrophic wetlands, and is present in early and mid-stages, and occasionally late stages, of secondary succession across a wide range of sites.

Owing to its wide climatic amplitude, lodgepole pine is a minor or major component in many regional ecosystems (climatic/vegetation zones); for example, in British Columbia, it occurs in all 12 forested biogeoclimatic zones (Krajina, 1969; Meidinger and Pojar, 1991). Given its wide edaphic amplitude, lodgepole pine is a minor or major but temporary component of many local ecosystems (plant associations, site types, habitat types, or forest cover types) (Krajina, 1969; Franklin and Dyrness, 1973; Eyre, 1980; Lotan and Critchfield, 1990; Meidinger and Pojar, 1991; Klinka *et al.*, 2000).

Lodgepole pine grows in extensive, pure stands delineated by the Lodgepole Pine forest cover type (Eyre, 1980), and is a component in 27 of the 55 western forest cover types. In montane boreal climates, it is represented in White Spruce (Type 201), White Spruce–Aspen (Type 251), White Spruce–Paper Birch (Type 202), Paper Birch (Type 252), and Black Spruce (Type 204) cover types. In subalpine boreal climates it is a component in all six high-elevation cover types: Mountain Hemlock (Type 205), Engelmann Spruce–Subalpine Fir (Type 206), Red Fir (Type 207), Whitebark Pine (Type 208), Bristlecone Pine (Type 209), and California Mixed Subalpine (Type 256). In cool temperate climates it is a minor component of seven other types: Interior Douglas-fir (Type 210), Western Larch (Type 212), Grand Fir (Type 213), Western White Pine (Type 215), Blue Spruce (Type 216), Aspen (Type 217), Limber Pine (Type 219), and Interior Ponderosa Pine (Type 237). In mesothermal climates it is a component in Coastal True Fir (Type 226), Western Redcedar–Western Hemlock (Type 227), Western Redcedar (Type 228), Douglas-fir–Western Hemlock (Type 230), Port Orford-Cedar (Type 231), Redwood (Type 232), and Jeffrey Pine (Type 247).

The cover and composition of understory vegetation in all these forest cover types varies and depends on site (climate and soil), associated tree species, stand developmental stage, and stand density. Relative to other tree species, light interception by lodgepole pine canopies is intermediate, thus providing light conditions for the development of diverse understory vegetation.

### 6.4. Stand dynamics

Lodgepole pine is intolerant of shade and competition from other tree species. Occasionally, seedlings establish and persist under a forest canopy and in small gaps, but these individuals rarely survive. In spite of its shade intolerance, lodgepole pine can survive in excessively dense stands for long periods, often for 50 years or more. Lodgepole pine typically regenerates after stand-destroying fires and develops even-aged, single-storied, single- or mixed-species stands. Four basic successional roles have been recognized by Pfister and Daubenmire (1975):

1. Minor seral: a component of even-aged stands rapidly being replaced by shade-tolerant associates in 50 to 200 years.
2. Dominant seral: the dominant component of even-aged stands with a vigorous understory of shade-tolerant species that will replace lodgepole pine in 100 to 200 years.
3. Persistent: the dominant component of even-aged stands with little evidence of replacement by shade-tolerant species.
4. Climax: the only tree species capable of growing in a particular environment; lodgepole pine is self-perpetuating (e.g., in the Sub-boreal Pine – Spruce zone of British Columbia (Meidinger and Pojar, 1991) and in the *Pinus contorta* zone of Oregon (Franklin and Dyrness, 1973).

In the absence of fire, lodgepole pine is usually succeeded by its more tolerant associates, such as white spruce (*Picea glauca*), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*). Succession proceeds at variable rates, and is particularly slow in some high elevation forests. Pure stands of lodgepole pine persist for varying lengths of time. Low-elevation stands begin to break up at 80 to 100 years, while high-elevation stands last for several hundred years. For example, pure stands in and around Yellowstone National Park contain 300 to 400-year-old trees, with several groups of younger even-aged trees. These stands originated as even-aged stands but have been breaking up for centuries (Lotan and Critchfield, 1990). A typical lifespan of some lodgepole pines can be 250 to 600 years.

The ability of lodgepole pine to regenerate at the expense of other species is due to cone serotiny, seed viability, germinative energy, rapid juvenile growth, and ability to survive a wide variety of climate, microsite and soil conditions (Lotan, 1976). Lodgepole pine responds positively to thinning at an early age (Cole, 1975). Heavily stocked managed stands must be thinned to prevent stagnation. Overstocked stands on poor sites should be thinned as early as age 10.

### 6.5. Damaging agents

Lodgepole pine is host to a large number of insects and diseases. The mountain pine beetle (*Dendroctonus ponderosae*) is the most severe insect pest of lodgepole pine. The epidemics that periodically occur in many lodgepole pine stands seriously impact long-term yield. Adult beetles attack trees in July or August, introducing blue stain fungi (Amman, 1978). The mature insects form egg galleries in the phloem, and larvae feed in these galleries. The beetles and fungi together girdle and kill trees. Larvae over-winter in the tree, complete development, and emerge as adult beetles in the spring. Harvesting has been considered a means of preventing mountain pine beetle epidemics (Cole, 1978), and no mortality occurred in heavily thinned stands in Oregon where vigour ratings were high (Mitchell *et al.*, 1981). However, mountain pine beetle has killed lodgepole pine across a wide range of stand ages and densities in the epidemic that started in the late 1990s in British Columbia. The mountain pine beetle has played an historic role in the dynamics of lodgepole pine ecosystems. Through periodic epidemics, large amounts of fuel are produced, which eventually burn, generating favourable conditions for lodgepole pine regeneration (Brown, 1975; Lotan, 1976).

There are a number of other insects that can damage lodgepole pine locally. The lodgepole terminal weevil (*Pissodes terminalis*) destroys elongating terminal leaders. Larvae of the Warren's collar weevil (*Hylobius warreni*) girdle roots and the root collar. Larvae of the weevil *Magdalis gentilis* mine and kill branches. Lodgepole pine is host to a number of sucking insects, including the pine needle scale (*Chionaspis pinifoliae*), the black pineleaf scale (*Nuculaspis californica*), and the spruce spider mite (*Oligonychus ununguis*). Several insects defoliate lodgepole pine, including lodgepole sawfly (*Neodiprion burkei*), the lodgepole needle miner (*Coleotechnites milleri*), the sugar pine tortrix (*Choristoneura lambertiana*), the pine tube moth (*Argyrotaenia pinatubana*), and the pandora moth (*Coloradia pandora*) (Amman, 1975; Lotan and Critchfield, 1990). In plantations in central Europe, pine shoot moths (*Rhyacionia buoliana* and other related species) are important insect pest (Stephan, 1980).

Lodgepole pine is seriously affected by the parasite dwarf mistletoe (particularly *Arceuthobium americanum*) (Baranayay, 1975; Hawksworth, 1975). Sticky dwarf mistletoe seeds are forcibly ejected as far as 9 m, and adhere to the foliage of neighbouring trees. The proportion of trees infected can increase rapidly over time (Hawksworth, 1975). Dwarf mistletoe can spread in young stands at 0.3 to 0.5 m per year, with the fastest spread in dense stands. In many areas, over 50% of lodgepole pine forests are infected (Lotan and Critchfield, 1990). Infections reduce growth and vigour, increase mortality, reduce wood quality, and decrease seed production. Dwarf mistletoe can be managed by clearcutting units designed to reduce infection of regeneration from surrounding stands. Fire can also limit spread of dwarf mistletoe by eliminating sources of infection. (Lotan and Critchfield, 1990).



Lodgepole pine is subject to attack by many fungal pathogens that can reduce growth and cause mortality (Krebill, 1975). *Atropellis piniphila* causes a stem canker that is one of the most serious diseases in lodgepole pine, and renders stems useless for most solid wood uses. Rust fungi causing stem cankers result in mortality, reductions in growth, and log defects. Comandra blister rust (*Cronartium comandrae*) is the most serious of these. Western gall rust, caused by the fungus *Peridermium harknessii*, causes trunk cankers that result in log culls and seedling and sapling mortality. This rust does not have an alternate host, thus can directly re-infect pines. Needle casts are caused by fungi including *Elytroderma deformans* and *Lophodermella concolor*. Lodgepole pine is susceptible to root rots caused by fungi including *Armillaria ostoyae* and *Heterobasidion annosum*. Wood decay results from fungi such as *Phellinus pini* and *Peniophora pseudo-pini*. The fungus *Gremmeniella abietina* is an important damaging agent of lodgepole pine in Europe, causing stem cankers (Karlman, 1993; Witzell and Karlman, 2000).

Warm, dry Chinook winds following extremely cold weather occasionally cause winter desiccation, known as red belt injury, particularly in Canada and Montana. The resulting defoliation of trees is common, and mortality can occur over large areas. Heavy snow can break or bend trees, particularly in dense stands. Thinning of dense stands can increase snow breakage (Lotan and Critchfield, 1990).

## 7. Forestry practices

### 7.1. Deployment of reforestation materials

Lodgepole pine is one of the most commonly regenerated trees in Western North America. The area planted, primarily using containerized seedling stock, surpasses that regenerated naturally. It can be grown in single- or mixed-species stands, preferably with shade-tolerant species. Depending on site and management objectives, clearcutting and patch-cutting systems are viable silvicultural systems for the establishment and growth of the species (Burns, 1983). Propagation by seed is currently the primary method for regenerating lodgepole pine. Techniques for collection, processing, testing, and storage of seed are given in Schopmeyer (1974). The annual planting of lodgepole pine as of 1992 was 70 million seedlings in British Columbia, 8 million in Alberta, 3 million in Idaho and Montana combined, and small programs in the Pacific Northwestern United States and Alaska (D. Lindgren, 1993). Planting in British Columbia has increased since that time.

Lodgepole pine was first introduced to Europe in 1832. It was planted in arboreta, parks, and on a minor scale in forests. In 1950, lodgepole pine became a major species for afforestation of peatlands in Britain, Ireland, Sweden, and Finland. Today, lodgepole pine plantations also exist in the Netherlands, Denmark, Island, Norway, Germany, Poland, and the former Soviet Union. The country with the largest share of exotic plantations of lodgepole pine is Sweden due to the superior growth and cold hardiness of this species compared to *Pinus sylvestris* (K. Lindgren, 1993). Interest in lodgepole pine as an exotic has declined in recent years for a variety of reasons, including naturalization and invasiveness in New Zealand (Ledgard, 1993), insect problems in the Netherlands (de Vries, 1993), and changes in policy regarding exotic species and risks in Sweden (Lindgren *et al.*, 1993).

### 7.2. Provenance transfer

Lodgepole pine is considered an adaptational specialist rather than generalist, meaning that populations differ genetically over fairly short physical or environmental distances (Rehfeldt, 1988; Xie and Ying, 1995). Thus, the seed transfer limits for this species are relatively conservative. In British Columbia, natural stand seed of *Pinus contorta* subsp. *latifolia* can be moved 2° latitude to the north, 1° south, 3° longitude to the west, 2° east, 300 m up in elevation and 100 m down in elevation from the location of collection to the planting site. Seed transfer guidelines are asymmetrical since results from provenance trials indicate that sources from slightly milder locations (lower elevation or farther south)

show slightly superior growth rates with no increase in mortality compared to local provenances. If seed is transferred between seed planning zones, it must be moved to the same ecosystem type it was collected from. Six superior provenances have been identified in British Columbia based on provenance trial results, and allowable seed transfer distances are greater for these than for other provenances (BC Ministry of Forests, 1995; Xie and Ying, 1995).

In Alberta, natural stand seed collected for reforestation from all forest tree species including lodgepole pine must be used within 80 km and 150 m elevation of the collection site. In Sweden, forest tree seed is managed within six seed zones, defined by latitude and elevation, and seed orchards are designated for each zone (Ericsson, 1993). Parent trees of seedlings in seedling seed orchards or grafted clones in clonal orchards for different Swedish zones originate from different geographic areas in British Columbia and Yukon Territory.

### 7.3. *Breeding programmes*

There are active breeding programs for lodgepole pine (*P. contorta* subsp. *latifolia*) in British Columbia, Alberta, the Inland Empire of the United States and northern Europe. The largest program is in British Columbia, with six active breeding programs for different geographic areas (breeding zones), and 14 seed orchards serving these areas (Forest Genetics Council of B.C, 2001). There are 100 to 500 parent trees undergoing progeny testing in each of these zones. The primary trait for improvement is stem volume, accomplished through indirect selection on tree height due to the much higher heritability of height than diameter or volume, while maintaining density is a secondary goal (Wang *et al.*, 1999). Current gains for volume range from 6 to 11% (Forest Genetics Council of B.C, 2001). Most seed orchards are located in the Okanagan Valley, a warm, arid region, and early seed production was lower than expected due to a climate-related pollination or fertilization problem.

In Alberta, there are five breeding zones with a total of approximately 1,100 phenotypically selected parent trees, and most of these have included progeny tests (Dhir and Barnhardt, 1993). Two additional breeding zones are under development (N. Dhir, Alberta Forest Service, pers. comm.). A combination of seedling and grafted clonal seed orchards have been established to produce improved seed from selected parent trees. In addition to survival, growth and wood density, susceptibility to western gall rust (*Endocronartium harknessii*) is being evaluated (Yang *et al.*, 1997).

In Idaho and Montana, the Inland Empire Tree Improvement Cooperative has had an ongoing breeding program since 1978. Approximately 1,000 phenotypically-selected parent trees are represented in open-pollinated progeny tests. A series of short-term nursery trials of additional phenotypic selections were established in 1992 (D. Lindgren, 1993).

In Sweden, the breeding program is based on approximately 1,100 open-pollinated families of subsp. *latifolia* established in both seedling seed orchards and progeny trials (Ericsson *et al.*, 1994; Ericsson and Danell, 1995). Seedling and grafted clonal seed orchards were established, with 140 ha of seed orchards as of 1992. Seed production from these orchards exceeds current planting requirements in Sweden to the point where seed could be exported (Lindgren *et al.*, 1993). Field tests are evaluated for health, height, and ramicorn branch frequency at 8 to 12 years of age, while damage caused by the fungus *Gremmeniella abietina* and weather-related injuries are evaluated on harsh sites (Ericsson and Danell, 1995). Roguing orchards based on the results should produce genetic gains of 2 to 6%.

D. Lindgren (1993) summarized the status of breeding programs of lodgepole pine around the world. At that time there were small breeding programs in Norway (subsp. *latifolia*), Ireland (subsp. *contorta*), Britain (subsp. *contorta*) and Finland (subsp. *latifolia*). There was a substantial program underway in the Pacific Northwestern United States (subsp. *latifolia*), but with a shift away from even-aged management and artificial regeneration, this program has been reduced. There are no known breeding programs for subsp. *murrayana* or subsp. *bolanderi*.

#### 7.4. Conservation of genetic resources

Lodgepole pine is a widespread species with high fecundity and high population densities. Natural regeneration is relied upon extensively in some portions of its range. It is well-represented in parks and ecological reserves throughout its native range. Thus, threats to genetic diversity are low for this species. Lester and Yanchuk (1996) concluded that subsp. *latifolia* and subsp. *contorta* were both well-protected in existing protected areas in British Columbia, with the exception of the Tatshenshini Basin, Alberta Plateau and Fort Nelson Lowland in northern BC; protected areas in the province have nearly doubled since that assessment. Sierra Nevada lodgepole pine, subsp. *murrayana*, is in high-elevation areas of the Sierra Nevada Mountains of California, an area that is well-represented in National Parks and US Forest Service Wilderness Areas, and otherwise undergoes little harvesting. Bolander pine, subsp. *bolanderi*, endemic to the Mendocino pygmy forest, is not harvested for wood but is under some pressure due to residential development. There is a substantial ecological reserve as well as a California state park and a privately owned conservation reserve in this small area for *in situ* gene conservation. Shore pine, var. *contorta*, is represented in coastal parks and ecological reserves from California to Alaska, and is not harvested commercially over much of its range. Additionally, the extensive provenance trials, other genetic tests, breeding arboreta and seed banks provide *ex situ* gene conservation, particularly for subsp. *latifolia*. Climate change may result in maladaptation of populations in reserves, but Rehfeldt *et al.* (1999) predicted that lodgepole pine populations would adapt to predicted levels of climate change in 4 to 12 generations as a result of natural selection.

### 8. Summary

Lodgepole pine has one of the widest ecological amplitudes of any conifer in North America and is one of the important and valuable timber crop species in Western North America and northern Europe. Across most of its range, it is a pioneer and early seral, short-lived, and fire-adapted species. Because of the rapid growth rate, low taper, thin bark, and relatively narrow crown, it produces a higher volume of wood sooner than many of its associates. It has low nutrient requirements and is easy to regenerate and grow. A common problem of regenerating lodgepole pine is overstocking, which may result in growth stagnation in early stand development on water-deficient, nutrient-poor sites.

The ecology of lodgepole pine is diverse as a result of its large geographic distribution. Although it typically occurs in pure, even-aged stands, lodgepole pine associates with a great number of shade-tolerant tree species, especially in late seral stages, and is a minor or major component in many ecosystems in many climatic zones in Western North America. Lodgepole pine is not only an important timber species, but is also a major tree species in many scenic and recreational areas, and on critical watersheds. It provides a large area of wildlife habitat and is widely associated with grazing and range allotments.

Lodgepole pine is an adaptive specialist, with populations varying with climatic gradients in temperature, and to a lesser extent, moisture. Appropriate seed transfer distances are short for all except a few more broadly adapted provenances. Breeding programs must start with well-adapted, local populations in order to obtain genetic gain. Genetic variation within populations is high, offering opportunities for obtaining genetic gain in growth and wood quality traits. While variation for disease and insect resistance is high, the use of locally adapted populations and planting of this species on appropriate sites will adequately manage pest problems from a genetic standpoint in most cases. The genetic resources of this species are generally well-protected by *in situ* reserves throughout its natural range, although adaptation of these populations to a rapid change in climate may take several to many generations.

Lodgepole pine has received relatively little study in terms of genetic transformation. While methods for genetic engineering and regeneration of transgenic plants through somatic embryogenesis developed for short-rotation pines could likely be adapted for this species, the long rotation lengths and use of locally-adapted populations, as well as a lack of single-gene traits of interest, make the use of this technology unlikely for operational reforestation in the near future.

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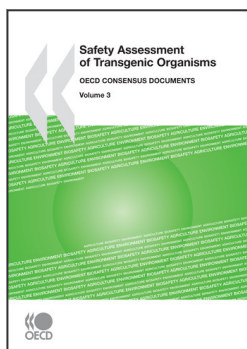
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**From:**  
**Safety Assessment of Transgenic Organisms,**  
**Volume 3**  
OECD Consensus Documents

**Access the complete publication at:**  
<https://doi.org/10.1787/9789264095434-en>

**Please cite this chapter as:**

OECD (2010), "Section 5 - Lodgepole pine (*Pinus contorta*)", in *Safety Assessment of Transgenic Organisms, Volume 3: OECD Consensus Documents*, OECD Publishing, Paris.

DOI: <https://doi.org/10.1787/9789264095434-9-en>

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