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THE WORKING PARTY ON CHEMICALS, PESTICIDES AND BIOTECHNOLOGY

Series on Harmonisation of Regulatory Oversight in Biotechnology No. 44

CONSENSUS DOCUMENT ON THE BIOLOGY OF LODGEPOLE PINE
(Pinus contorta Dougl. ex. Loud.)

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No. 44

Consensus Document on the Biology of Lodgepole Pine (*Pinus contorta* Dougl. *ex*. Loud.)

Environment Directorate

Organisation for Economic Co-operation and Development

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ABOUT THE OECD

The Organisation for Economic Co-operation and Development (OECD) is an intergovernmental organisation in which representatives of 30 industrialised countries in North America, Europe and the Asia and Pacific region, as well as the European Commission, meet to co-ordinate and harmonise policies, discuss issues of mutual concern, and work together to respond to international problems. Most of the OECD's work is carried out by more than 200 specialised committees and working groups composed of member country delegates. Observers from several countries with special status at the OECD, and from interested international organisations, attend many of the OECD's workshops and other meetings. Committees and working groups are served by the OECD Secretariat, located in Paris, France, which is organised into directorates and divisions.

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FOREWORD

Consensus Documents contain information for use during the regulatory assessment of a particular product. In the area of plant biosafety, these are being published on information on the biology of certain plant species, selected traits that may be introduced into plant species, and biosafety issues arising from certain general types of modifications made to plants.

This document addresses the biology of lodgepole pine (*Pinus contorta* Dougl. *ex*. Loud.). Canada served as the lead country in the preparation of this document. The draft was revised on a number of occasions based on the inputs from other member countries. This document is published on the responsibility of the Joint Meeting of the Chemicals Committee and the Working Party on Chemicals, Pesticides and Biotechnology of the OECD.

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PREAMBLE

The environmental safety/risks of transgenic organisms are normally based on the information on the characteristics of the host organism, the introduced traits, the environment into which the organism is introduced, the interaction between these, and the intended application. The OECD's Working Group on Harmonisation of Regulatory Oversight in Biotechnology decided at its first session, in June 1995, to focus its work on identifying parts of this information, which could be commonly used in countries for environmental safety/risk assessment to encourage information sharing and prevent duplication of effort among countries. Biosafety Consensus Documents are one of the major outputs of its work.

Biosafety Consensus Documents are intended to be a "snapshot" of current information on a specific host organism or trait, for use during regulatory assessments. They are not intended to be a comprehensive source of information on everything that is known about a specific host or trait; but they do address the key or core set of issues that member countries believe are relevant to risk/safety assessment. This information is said to be mutually acceptable among member countries. To date, 30 Biosafety Consensus Documents have been published. They include documents which address the biology of crops, trees and micro-organisms as well as those which address specific traits which are used in transgenic crops.

In reading the Consensus Documents, it is useful to consult two additional texts. The first, entitled *An Introduction to the Biosafety Consensus Document of OECD's Working Group for Harmonisation in Biotechnology* explains the purpose of the Consensus Documents and how they are relevant to risk/safety assessment. It also describes the process by which the documents are drafted using a "lead country" approach. The second text is *Points to Consider for Consensus Documents on the Biology of Cultivated Plants*. This is a structured checklist of "points to consider" for authors when drafting or for those evaluating a Consensus Document. Amongst other things, this text describes how each point is relevant to risk/safety assessment.

The Consensus Documents are of value to applicants for commercial uses of transgenic organisms, regulators in national authorities as well as the wider scientific community. As each of the documents may be updated in the future as new knowledge becomes available, users of Consensus Documents are encouraged to provide any information or opinions regarding the contents of this document or indeed, OECD's other harmonisation activities. If needed, a short pre-addressed questionnaire is attached at the end of this document that can be used to provide such comments.

The published Consensus Documents are also available individually from OECD's website (http://www.oecd.org/biotrack) at no cost.

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.

SECTION I. TAXONOMY

1.   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.

2.   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.

SECTION II. NATURAL DISTRIBUTION

3.   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).
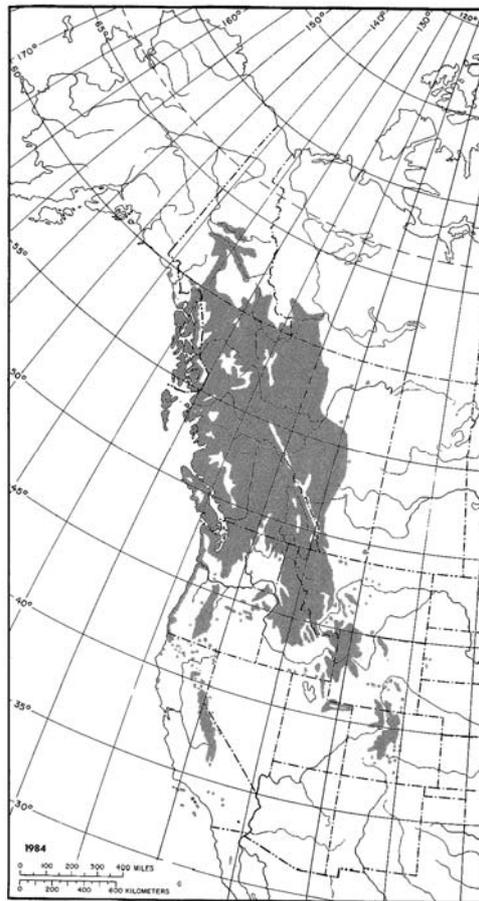

Figure 1. The native range of lodgepole pine (from Lotan and Critchfield, 1990).

SECTION III. REPRODUCTIVE BIOLOGY

A. Reproductive development

4.   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).

5.   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).

B. Mating system and gene flow

6.   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).

7.   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).

C. Seed production

8.   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).

9.   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).

10.   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).

11.   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).

12.   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.

13.   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).

D. Natural regeneration

14.   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.

15.   For non-serotinous cones that disperse seeds from standing trees, the density of seedfall 20m 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).

16.   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.

E. Vegetative reproduction

17.   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.

SECTION IV. GENETICS

A. Cytology

18.   *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).

B. Genetic variation

B.1 Population-level variability

19.   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).

20.   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.

21.   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 [3]	Expected heterozygosity (H_e) within populations	% polymorphic loci	Population differentiation (F_{st} or G_{st})	Ref.
Allozymes				
Rangewide (4 subsp.)			0.061 [1]	Wheeler and Guries, 1982b
			0.032 [2]	
Subsp. *latifolia*	0.118	69		
Subsp. *contorta*	0.126	65		
Subsp. *murrayana*	0.124	73		
Subsp. *bolanderi*	0.109	58		
Subsp. *latifolia*	0.194	69	0.034	Yang and Yeh, 1993
Subsp. *contorta*	0.180	62	0.057	
Subsp. *murrayana*	0.196	63	0.076	
Subsp. *contorta*, CA	0.119	38	0.057	Aitken and Libby, 1994
Subsp. *bolanderi*	0.105	28	0.044	
Subsp. *latifolia* – nearby populations CO	0.135	44	0.008	Knowles, 1984
Randomly Amplified Polymorphic DNA				
Subsp. *latifolia*, BC Central pops.	0.160		0.081	Fazekas and Yeh, 2001
Intermediate pops.	0.153		0.076	
Marginal pops.	0.143		0.139	

[1]Location: USA - CA = California; CO = Colorado; Canada - BC = British Columbia
[2]Differentiation among populations within subspecies
[3]Differentiation among subspecies

22.   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.

23.   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).

24.   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).

25.   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).

B.2 Variation among individuals within populations

26.   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).

27.   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.

28.   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[1] 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 *et al.*, 1998; Wu *et al.*, 2000
Height	Seedling greenhouse, BC	0.61	Wu *et al.*, 1995
Diameter	Field progeny test, BC	0.33-0.40	Xie and Ying, 1996; Wu *et al.*, 2000
Diameter	Seedling greenhouse, BC	0.46	Wu *et al.*, 1995
Harvest index	Field progeny test, BC	0.34	Wu *et al.*, 2000
Fall cold hardiness	Field progeny test, ID	0.10	Rehfeldt, 1989
Endocronartium harknessii infection	Field progeny test, BC and AB	0.12-0.50	Wu and Ying, 1997; Yang *et al.*, 1998
Cronartium coleosporioides infection	Field progeny test, BC	0.32	Wu and Ying, 1997
Lophodermella concolor impact	Field progeny test, BC	0.30	Wu and Ying, 1997
Synanthedon sequoiae damage	Field progeny test, BC	0.21	Wu and Ying, 1997
Injury/cankers, mainly *Gremmeniella abietina*	Field progeny test, S	0.12	Ericsson and Danell, 1995

[1] AB = Alberta, S = Sweden, ID =Idaho, BC = British Columbia

C. Inbreeding depression and genetic load

29.   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.

SECTION V. HYBRIDIZATION

30.   Pin*us 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).

31.   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.

SECTION VI. ECOLOGY

A. Climate

32.   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°C in the Northern Rocky Mountains (Lotan and Critchfield, 1990). Maximum temperatures range from 27°C for subsp. *contorta* along the coast and at high elevations to well over 38°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).

B. Soils

33.   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).

34.   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).

35.   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.

36.   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.
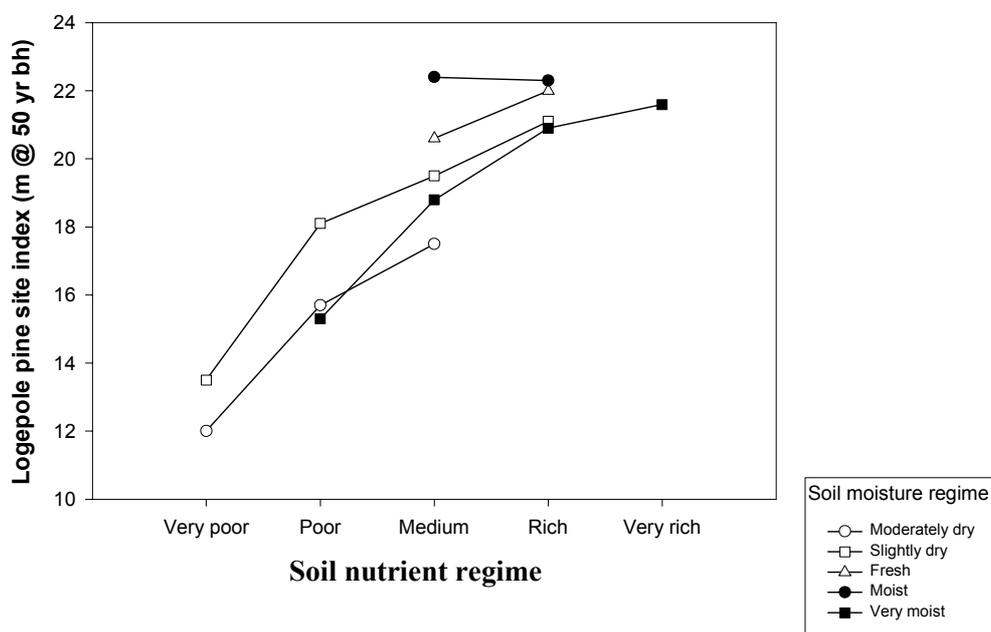
Figure 2. Site index of lodgepole pine at (@) 50 years (n = 235) in relation to soil nutrient regime (x axis) and soil moisture regime (symbols) across the Sub-boreal Spruce zone of British Columbia (from Kayahara *et al.*, 1995).

37.   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.

38.   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).

39.   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).

40.   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).

41.   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).

C. Synecology

42.   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 ombotrophic wetlands, and is present in early and mid-stages, and occasionally late stages, of secondary succession across a wide range of sites.

43.   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).

44.   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).

45.   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.

D. Stand dynamics

46.   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. <u>Dominant seral</u>: 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. <u>Persistent</u>: the dominant component of even-aged stands with little evidence of replacement by shade-tolerant species.

4. <u>Climax</u>: 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).

47.   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.

48.   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.

E. Damaging agents

49.   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).

50.   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).

51.   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).

52.   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).

53.   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).

SECTION VII. FORESTRY PRACTICES

A. Deployment of reforestation materials

54.   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.

55.   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).

B. Provenance transfer

56.   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).

57.   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.

C. Breeding programmes

58.   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.

59.   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).

60.   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).

61.   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%.

62.   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*.

D. Conservation of genetic resources

63.   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.

SECTION VIII. SUMMARY

64.   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.

65.   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.

66.   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.

67.   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.

SECTION IX. REFERENCES

Aitken, S.N. and W.J. Libby. 1994. Evolution of the pygmy-forest edaphic subspecies of *Pinus contorta* across an ecological staircase. Evolution 48: 1009-1019.

Alexander, R.R. 1974. Silviculture of subalpine forest in the central and southern Rocky Mountains: The status of our knowledge. USDA Forest Service Research Paper RM-121, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado. 88 pp.

Amman, G.D. 1975. Insects affecting lodgepole pine productivity. Pp. 310-341 *in* Proceedings, Symposium on Management of Lodgepole Pine Ecosystems, October 9-11, 1973. Washington State University, Pullman.

Amman, G.D. 1978. Biology, ecology, and causes of outbreaks of the mountain pine beetle in lodgepole pine forests. Pp. 39-53 *in* Proceedings of Symposium on Theory and Practice of Mountain Pine Beetle Management in Lodgepole Pine Forests, Washington State University, Pullman, Washington.

Baranyay, J.A. 1975. Dwarf mistletoe as a factor in the management of lodgepole pine forests in western Canada. Pp. 359-376 *in* Proceedings of Symposium on Theory and Practice of Mountain Pine Beetle Management in Lodgepole Pine Forests, Washington State University, Pullman, Washington.

Brisco, D.J. 2001. Relationships between stand and site factors in naturally established fire-origin lodgepole pine stands in the Upper Foothills of Alberta. M.Sc. thesis, University of British Columbia, Vancouver, B.C. 83 pp.

British Columbia Ministry of Forests. 1995. Seed and vegetative material guidebook. Forest Practices Code of British Columbia. Victoria, B.C. 57 pp.

Brockley, R.P. 1989. Response of thinned, immature lodgepole to nitrogen fertilization: Three-year growth response. FRDA Report 036, British Columbia Ministry of Forests, Victoria, B.C. 37 pp.

Brockley, R.P. 1990. Response of thinned immature lodgepole pine to nitrogen and boron fertilization. Canadian Journal of Forest Research 20: 579-585.

Brockley, R.P. 1996. Lodgepole nutrition and fertilization: A summary of British Columbia Ministry of Forests research results. FRDA Report 266, British Columbia Ministry of Forests, Victoria, B.C. 43 pp.

Brockley, R.P. 2001. Foliar sampling guidelines and nutrient interpretive criteria for lodgepole pine. Extension Note, British Columbia Ministry of Forests, Victoria, B.C. 8 pp.

Brown, J.K. 1975. Fire cycles and community dynamics in lodgepole pine forests. Pp. 429-456 *in* Proceedings of Symposium on Theory and Practice of Mountain Pine Beetle Management in Lodgepole Pine Forests, Washington State University, Pullman, Washington.

Burdon, R.D. 2002. An introduction to pines. Pp. x-xxi *in* CABI Forestry Compendium (ed.), Pines of silvicultural importance. CABI Publishing. Wallingford, U.K.

Burns, R.M. (technical compiler). 1983. Silvicultural systems for the major forest types of the United States. USDA Agriculture Handbook No. 445, Washington, D.C. 191 pp.

Cannell, M.G.R. and S.C. Willett. 1975. Rates and times at which needles are initiated in buds on different provenances of *Pinus contorta* and *Picea sitchensis*. Canadian Journal of Forest Research 5: 367-380.

Chuine, I., S.N. Aitken and C. Ying. 2001. Temperature-dependent growth in provenances of *Pinus contorta*. Canadian Journal of Forest Research 31: 1444-1455.

Cochran, P.H. 1975. Response of pole-size lodgepole pine to fertilization. USDA Forest Service Research Note PNW-247, Pacific Northwest Forest and Range Experiment Station, Portland, Oregon. 10 pp.

Cochran, P.H. and C.M. Berntsen. 1973. Tolerance of lodgepole pine and ponderosa pine seedlings to low night temperatures. Forest Science 19: 272-280.

Cochran, P.H., W. Lopushinsky, E.C. Steinbrenner and S.R. Webster. 1979. Response of ponderosa pine and lodgepole pine to fertilization. Pp. 89-94 *in* S.P. Gessel, R.M. Kenady and W.A. Atkinson (eds.), Proceedings, Forest Fertilization Conference, Contribution No. 40, College of Forest Resources, University of Washington, Seattle, Washington.

Cole, D.M. 1975. Culture of immature lodgepole stands for timber objectives. Pp. 536-555 *in* Proceedings of Symposium on Management of Lodgepole Pine Ecosystems. Washington State University, Pullman, Washington.

Cole, D.M. 1978. Feasibility of silvicultural practices for reducing losses to the mountain pine beetle in lodgepole pine forests. Pp. 140-147 *in* Proceedings of Symposium on Theory and Practice of Mountain Pine Beetle Management in Lodgepole Pine Forests, Washington State University, Pullman, Washington.

Critchfield, W.G. 1957. Geographic variation in *Pinus contorta*. Maria Moors Cabot Foundation Publication No. 3. Harvard University, Cambridge, Massachusetts. 118 pp.

Critchfield, W.B. 1980. Genetics of lodgepole pine. USDA Forest Service, Research Paper WO-37, Washington, D.C. 57 pp.

Critchfield, W.B. 1984. Impact of the Pleistocene on the genetic structure of North American conifers. Pp. 70-114 *in* R.M. Lanner (ed.), Proceedings of the 8th North American Forest Biology Workshop. Department of Forest Resources, Utah State University, Logan, Utah.

Critchfield, W.B. 1985. The late Quaternary history of lodgepole and jack pines. Canadian Journal of Forest Research 15: 749-772.

Cwynar, L.C. and G.M. MacDonald. 1987. Geographical variation of lodgepole pine in relation to population history. American Naturalist 129: 463-469.

Dahms, W.G. 1963. Dispersal of lodgepole pine seed into clearcut patches. USDA Forest Service Research Note PNW-3, Pacific Northwest Forest and Range Experiment Station, Portland, Oregon. 7 pp.

Dahms, W.G. and J.W. Barrett. 1975. Seed production of central Oregon ponderosa and lodgepole pines. USDA Forest Service Research Paper PNW-19, Pacific Northwest Forest and Range Experiment Station, Portland, Oregon. 13 pp.

Dancik, B.P. and F.C. Yeh. 1983. Allozyme variability and evolution of lodgepole pine (*Pinus contorta* var. *latifolia*) and jack pine (*Pinus banksiana*) in Alberta. Canadian Journal of Genetics and Cytology 25: 57-64.

Delcourt, H.R. and P.A. Delcourt. 1991. Quaternary ecology: A paleoecological perspective. Chapman & Hall, London, U.K.

De Vries, S.M.G. 1993. IUFRO provenances of *Pinus contorta* in The Netherlands. *In* D. Lindgren (ed.), Proceedings of Pinus contorta – From untamed forest to domesticated crop. Meeting of IUFRO WP 2.02.06 and Frans Kempe Symposium, Umeå, August 24-28, 1992. Swedish University of Agricultural Sciences, Report 11: 209-210.

Dhir, N.K. and L.K. Barnhardt. 1993. Genetic improvement of lodgepole pine in Alberta. *In* D.Lindgren (ed.), Proceedings of Pinus contorta – From untamed forest to domesticated crop. Meeting of IUFRO WP 2.02.06 and Frans Kempe Symposium, Umeå, August 24-28, 1992. Swedish University of Agricultural Sciences, Report 11: 279-288.

Dong, J. and D.B. Wagner. 1993. Taxonomic and population differentiation of mitochondrial diversity in *Pinus banksiana* and *Pinus contorta*. Theoretical and Applied Genetics 86: 573-578.

Dong, J. and D.B. Wagner. 1994. Paternally inherited chloroplast polymorphism in *Pinus*: Estimation of diversity and population subdivision, and tests of disequilibrium with a maternally inherited mitochondrial population. Genetics 136: 1187-1194.

Dong, J., D.B. Wagner, A.D. Yanchuk, M.R. Carlson, S. Magnussen, X.-R. Wang and A.E. Szmidt. 1992. Paternal chloroplast DNA inheritance in *Pinus contorta* and *Pinus banksiana*: independence of parental species or cross direction. Journal of Heredity 83: 419-422.

Duffield, J.W. 1951/1952. Relationships and species hybridization in the genus *Pinus*. Zeitschrift für Forstgenetik und Forstpflanzenzüchtung 1: 93-100.

Epperson, B.K. and R.W. Allard. 1984. Allozyme analysis of the mating system in lodgepole pine. Journal of Heredity 75: 212-214.

Ericsson, T. 1993. Provenance qualities of the *Pinus contorta* breeding base in Sweden. SkogForsk (The Foresty Research Institute of Sweden) Report No. 4. 33 pp.

Ericsson, T. and O. Danell. 1995. Genetic evaluation, multiple-trait selection criteria and genetic thinning of *Pinus contorta* var. *latifolia* seed orchards in Sweden. Scandinavian Journal of Forest Research 10: 313-325.

Ericsson, T. and B. Andersson. 1997. Can field mortality of lodgepole pine (*Pinus contorta* var. *latifolia*) families be predicted based on early freezing test results? Forest Genetics 4: 61-67.

Ericsson, T., O. Danell and B. Andersson. 1994. Genetic variation of *Pinus contorta* var. *latifolia* breeding material in Sweden. Canadian Journal of Forest Research 24: 723-729.

Eyre, F.H. (ed.) 1980. Forest types of the United States and Canada. Society of American Foresters, Washington, DC. 148 pp.

Fazekas, A.J. and F.C. Yeh. 2001. Random amplified polymorphic DNA diversity of marginal and central populations in *Pinus contorta* ssp. *latifolia*. Genome 44: 13-22.

Forest Genetics Council of British Columbia. 2001. Business Plan 2001/2002. Forest Genetics Council of British Columbia, Victoria, B.C. 19 pp. plus appendices.

Fowells, H.A. (compiler) 1965. Silvics of forest trees of the United States. USDA Agriculture Handbook No. 271, Washington, D.C. 762 pp.

Franklin, J.F. and C.T. Dyrness. 1973. Natural vegetation of Oregon and Washington. USDA Forest Service General Technical Report PNW-8, Pacific Northwest Forest and Range Experiment Station, Portland, Oregon. 416 pp.

Fries, A. 1989. Genetic parameters of 2-year-old full-sib families of Pinus contorta and correlation with field test data. Scandinavian Journal of Forest Research 4: 137-147.

Fries, A. 1991. Nursery growth and dry weight of plus tree progenies of *Pinus contorta*. Scandinavian Journal of Forest Research 6: 161-176.

Fries, A. and Z. Kaya. 1997a. Genetic control of rooting ability of lodgepole pine cuttings. Forest Science 43: 582-588.

Fries, A. and Z. Kaya. 1997b. Parameters affecting shoot production and rooting of cuttings from lodgepole pine hedges. New Forests 12: 101-111.

Govindaraju, D.R., D.B. Wagner, G.P. Smith and B.P. Dancik. 1988. Chloroplast DNA variation within individual trees of a *Pinus banksiana – Pinus contorta* sympatric region. Canadian Journal of Forest Research 18: 1347-1350.

Griffin, J.R. and W.B. Critchfield. 1976. The distribution of forest trees in California. USDA Forest Service Research Paper PSW-82 (reprint with supplement), Pacific Southwest Forest and Range Experiment Station, Berkeley, California. 118 pp.

Hamrick, J.L., M.J.W. Godt and S.L. Sherman-Boyles. 1992. Factors influencing levels of genetic diversity in woody plant species. New Forests 6: 95-124.

Hawksworth, F.G. 1975. Dwarf mistletoe and its role in lodgepole pine ecosystems. Pp. 342-358 *in* Proceedings, Symposium on Theory and Practice of Mountain Pine Beetle Management in Lodgepole Pine Forests*,* Washington State University, Pullman, Washington.

Hicks, M., D. Adams, S. O'Keefe, E. Macdonald and R. Hodgetts. 1998. The development of RAPD and microsatellite markers in lodgepole pine (*Pinus contorta* var. *latifolia*). Genome 41: 797-805.

Karlman, M. 1993. The *Gremmeniella* disease situation on lodgepole pine in northern Sweden. *In* D.Lindgren (ed.), Proceedings of Pinus contorta – From untamed forest to domesticated crop. Meeting of IUFRO WP 2.02.06 and Frans Kempe Symposium, Umeå, August 24-28, 1992. Swedish University of Agricultural Sciences, Report 11: 335-349.

Kayahara, G.J., K. Klinka and I. Moss. 1995. Site index−site quality relationships for lodgepole pine, interior spruce, and subalpine fir in the Sub-boreal Spruce zone of British Columbia. Contract Report to Northwood Pulp and Timber Ltd., Prince George, B.C. 24 pp.

Keng, H. and E.L. Little Jr. 1961. Needle characteristics of hybrid pines. Silvae Genetica 10: 131-146.

Klinka, K., Q. Wang and G.J. Kayahara. 1994. Quantitative characterization of nutrient regimes in some boreal forest soils. Canadian Journal of Soil Science 74: 29-38.

Klinka K., J. Worrall, L. Skoda and P. Varga. 2000. The distribution and synopsis of ecological and silvical characteristics of tree species of British Columbia's forests. Canadian Cartographics Ltd., Coquitlam, B.C. 180 pp.

Knowles, P. 1984. Genetic variability among and within closely spaced populations of lodgepole pine. Canadian Journal of Genetics and Cytology 26: 177-184.

Krajina, V.J. 1969. Ecology of forest trees in British Columbia. Ecol. West. North Am. 2: 1-146.

Kral, R. 1993. *Pinus* Linnaeus. Pp. 373-398 *in* Flora of North America Editorial Committee (ed.), Flora of North America North of Mexico, Vol. 2: Pteridophytes and Gymnosperms. Oxford University Press, New York.

Krebill, R.G. 1975. Lodgepole pine's fungus-caused diseases and decays. Pp. 377-405 *in* Proceedings of Symposium on Management of Lodgepole Pine Ecosystems, Washington State University, Pullman, Washington.

Ledgard, N.J. 1993. A review of research and management of natural regeneration of introduced lodgepole pine (*Pinus contorta* Dougl.) with particular emphasis on its unwanted spread in New Zealand. *In* D. Lindgren, (ed.), Proceedings of *Pinus contorta* – From untamed forest to domesticated crop. Meeting of IUFRO WP 2.02.06 and Frans Kempe Symposium, Umeå, August 24-28, 1992. Swedish University of Agricultural Sciences, Report 11: 388-406.

Lester, D.T. and A.D. Yanchuk. 1996. A survey of the protected status of conifers in British Columbia: *In situ* gene conservation. Province of British Columbia, Ministry of Forests Research, Program Research Report 04. 34 pp.

Lindgren, D. 1993. Breeding *Pinus contorta* in different countries. *In* D. Lindgren (ed.), Proceedings of *Pinus contorta* – From untamed forest to domesticated crop. Meeting of IUFRO WP 2.02.06 and Frans Kempe Symposium, Umeå, August 24-28, 1992. Swedish University of Agricultural Sciences, Report 11: 264-270.

Lindgren, D., K. Lindgren and P. Krutzsch. 1993. Use of lodgepole pine and its provenances in Sweden. *In* D. Lindgren (ed.), Proceedings of *Pinus contorta* – From untamed forest to domesticated crop. Meeting of IUFRO WP 2.02.06 and Frans Kempe Symposium, Umeå, August 24-28, 1992, Swedish University of Agricultural Science, Report 11: 238-263.

Lindgren, K. 1993. IUFRO *Pinus contorta* seed collections: Distribution and publications. In D. Lindgren (ed.), *Proceedings of Pinus contorta* – From untamed forest to domesticated crop. Meeting of IUFRO WP 2.02.06 and Frans Kempe Symposium, Umeå, August 24-28, 1992. Swedish University of Agricultural Sciences, Report 11: 232-237.

Lindgren, K. and J.-E. Nilsson. 1992. Cold acclimation of *Pinus sylvestris* and *Pinus contorta* provenances as measured by freezing tolerance of detached needles. Scandinavian Journal of Forest Research 7: 309-315.

Little Jr., E.L. 1979. Checklist of United States trees (native and naturalized). USDA Agriculture Handbook No. 541, Washington, D.C. 375 pp.

Little Jr., E.L. and W.B. Critchfield. 1969. Subdivisions of the genus *Pinus* (pines). USDA Forest Service Miscellaneous Publication No. 1144. 51 pp.

Lotan, J.E. 1964. Initial germination and survival of lodgepole pine on prepared seedbeds. USDA Forest Service Research Note INT-29, Intermountain Forest and Range Experiment Station, Ogden, Utah. 8 pp.

Lotan, J.E. 1975. The role of cone serotiny in lodgepole pine forests. Pp. 471-495 *in* Proceedings of Symposium on Management of Lodgepole Pine Ecosystems. Washington State University, Pullman, Washington.

Lotan, J.E. 1976. Cone serotiny - fire relationships in lodgepole pine. Pp. 267-278 *in* Proceedings, 14th Annual Tall Timbers Fire Ecology Conference, Tall Timbers Research Station, Tallahassee, Florida.

Lotan, J.E. and D.A. Perry. 1983. Ecology and regeneration of lodgepole pine. USDA Agriculture Handbook No. 606, Washington, D.C. 51 pp.

Lotan, J.E. and W.B. Critchfield. 1990. *Pinus contorta* Dougl. *ex* Loud. Pp. 302-315 i*n* R.M. Burns and B.H. Honkala (technical coordinators). Silvics of North America, Vol. 1. USDA Agriculture Handbook No. 654, Washington, D.C.

MacDonald, G.M. and L.C. Cwynar. 1985. A fossil pollen based reconstruction of the late Quaternary history of lodgepole pine (*Pinus contorta* ssp. *latifolia*) in the western interior of Canada. Canadian Journal of Forest Research 15: 1039-1044.

Meidinger, D.V. and J. Pojar (compilers and eds.). 1991. Ecosystems of British Columbia. Special Report Series 6, British Columbia Ministry of Forests, Victoria, B.C. 330 pp.

Mitchell, R.G., R.H. Waring and G.B. Pitman. 1981. Thinning lodgepole in Oregon to increase tree vigour and reduce mountain pine beetle damage. Unpublished report, Oregon State University, Corvallis, Oregon.

Mirov, N.T. 1956. Composition of turpentine of lodgepole x jack pine hybrids. Canadian Journal of Botany 34: 443-457.

Mirov, N.T. and J. Hasbrouck. 1976. The story of pines. Indiana University Press, Bloomington, Indiana. 148 pp.

Moss, E.H. 1949. Natural pine hybrids in Alberta. Canadian Journal of Research, Section C, Botanical Science 27: 218-229.

Newman, K.W. and R.C. Jancey. 1983. Character selection and data structure in geographic variation in *Pinus contorta*. Silvae Genetica 32: 137-141.

O'Reilly, C. and J.N. Owens. 1989. Shoot, needle, and cambial growth phenology and branch tracheid dimensions in provenances of lodgepole pine. Canadian Journal of Forest Research 19: 599-605.

Owens, J.N. and M. Molder. 1994. The reproductive cycle of lodgepole pine. British Columbia Ministry of Forests, Victoria, B.C. 35 pp.

Perry, D.A. and J.E. Lotan. 1977. Opening temperatures in serotinous cones of lodgepole pine. USDA Forest Service Research Note INT-228, Intermountain Forest and Range Experiment Station, Ogden, Utah. 6 pp.

Perry, D.A. and J.E. Lotan. 1979. A model of fire selection for serotiny in lodgepole pine. Evolution 33: 958-968.

Pfister, R.D. and J.R. Daubenmire. 1975. Ecology of lodgepole pine (*Pinus contorta* Douglas). Pp. 27-46 *in* Proceedings of Symposium on Management of Lodgepole Pine Ecosystems, Washington State University, Pullman, Washington.

Rehfeldt, G.E. 1985. Genetic variances and covariances in *Pinus contorta*: estimates of genetic gains from index selection. Silvae Genetica 34: 26-33.

Rehfeldt, G.E. 1987. Components of adaptive variation in Pinus contorta from the Inland Northwest. USDA Forest Service Intermountain Research Station Research Paper INT-375. Moscow, Idaho. 11 pp.

Rehfeldt, G.E. 1988. Ecological genetics of *Pinus contorta* from the Rocky Mountains (USA) - a synthesis. Silvae Genetica 37:131-135.

Rehfeldt, G.E. 1989. Genetic variances and covariances in freezing tolerance of lodgepole pine during early winter acclimation. Silvae Genetica 38: 133-137.

Rehfeldt, G.E., C.C. Ying, D.L. Spittlehouse and D.A. Hamilton Jr. 1999. Genetic responses to climate in *Pinus contorta*: Niche breadth, climate change and reforestation. Ecological Monographs 69: 375-407.

Richardson, D.M. and S.I. Higgins. 1998. Pines as invaders in the Southern Hemisphere. Pp. 450-473 *in* D.M. Richardson (ed.), Ecology and biogeography of *Pinus*. Cambridge University Press, Cambridge, U.K.

Satterlund, D.R. 1975. Climatic factors and lodgepole pine. Pp. 297-309 *in* Proceedings of Symposium on Management of Lodgepole Pine Ecosystems, Washington State University, Pullman, Washington.

Schopmeyer, C.S. 1974. Seeds of woody plants in the United States. USDA Agriculture Handbook No. 450, Washington, D.C. 883 pp.

Smithers, L.A. 1961. Lodgepole pine in Alberta. Canadian Department of Forestry Bulletin 127, Ottawa, Ontario. 153 pp.

Sorensen, F.C. and W.T. Adams. 1993. Self fertility and natural selfing in three Oregon Cascade populations of lodgepole pine. *In* D. Lindgren (ed.), Proceedings of Pinus contorta – From untamed forest to domesticated crop. Meeting of IUFRO WP 2.02.06 and Frans Kempe Symposium, Umeå, August 24-28, 1992, Swedish University of Agricultural Sciences, Report 11: 358-374.

Stephan B.R. 1980. Diseases, insect pests and other damage in *Pinus contorta* as an exotic species. Pp. 221-230 *in* Proc. IUFRO w.p. meeting 1980 on *Pinus contorta* provenances (S2-02-06) in Norway and Sweden. Rapp. och upps. 30, Sveriges Lantbruksuniversitet, Garpenberg.

Thomas, B.R., S.E. Macdonald, M. Hicks, D.L. Adams and R.B. Hodgetts. 1999. Effects of reforestation methods on genetic diversity of lodgepole pine: An assessment using microsatellite and randomly amplified polymorphic DNA markers. Theoretical and Applied Genetics 98: 793-801.

U.S. Soil Conservation Service. 1975. Soil taxonomy (a basic system of soil classification for making interpreting soil surveys). USDA Agriculture Handbook No. 436, Washington, D.C. 754 pp.

Wagner, D.B., G.R. Furnier, M.A. Saghai-Maroof, S.M. Williams, B.P. Dancik and R.W. Allard. 1987. Chloroplast DNA polymorphisms in lodgepole and jack pines and their hybrids. Proceedings of the National Academy of Sciences (USA) 84: 2097-2100.

Wagner, D.B., J. Dong, M.R. Carlson and A.D. Yanchuk. 1991a. Paternal leakage of mitochondrial DNA in *Pinus*. Theoretical and Applied Genetics 82: 510-514.

Wagner, D.B., Z.-X. Sun, D.R. Govindaraju and B.P. Dancik. 1991b. Spatial patterns of chloroplast DNA and cone morphology variation within populations of a *Pinus banksiana – Pinus contorta* sympatric region. American Naturalist 138: 156-170.

Wang Q., G.G. Wang, K.D. Coates and K. Klinka. 1994. Use of site factors to predict lodgepole pine and interior spruce site index in the Sub-boreal Spruce zone. Research Note No. 114, British Columbia Ministry of Forests, Victoria, B.C. 26 pp.

Wang, T., S.N. Aitken, P. Rozenberg and M.R. Carlson. 1999. Selection for height growth and Pilodyn pin penetration in lodgepole pine: Effects on growth traits, wood properties, and their relationships. Canadian Journal of Forest Research 29: 434-445.

Wang, T.L., S.N. Aitken, P. Rozenberg and F. Millier. 2000. Selection for improved growth and wood density in lodgepole pine: effects on radial patterns of wood formation. Wood and Fiber Science 32: 391-403.

Wheeler, N.C. and R.P. Guries. 1982a. Biogeography of lodgepole pine. Canadian Journal of Botany 60: 1805-1814.

Wheeler, N.C. and R.P. Guries. 1982b. Population structure, genetic diversity, and morphological variation in *Pinus contorta* Dougl. Canadian Journal of Forest Research 12: 595-606.

Wheeler, N.C. and R.P. Guries. 1987. A quantitative measure of introgression between lodgepole and jack pines. Canadian Journal of Botany 65: 1876-1885.

White, E.E., E.A. Allen, C.C. Ying and B.M. Foord. 2000. Seedling inoculation distinguishes lodgepole pine families most and least susceptible to gall rust. Canadian Journal of Forest Research 30: 841-843.

Witzell, J. and M. Karlman. 2000. Importance of site type and tree species on disease incidence of *Gremmeniella abietina* in areas with a harsh climate in northern Sweden. Scandinavian Journal of Forest Research 15: 202-209.

Wright, J.W. 1962. Genetics of forest tree improvement. Food and Agriculture Organization of the United Nations, Rome. 399 pp.

Wu, H.X. and C.C. Ying. 1997. Genetic parameters and selection efficiencies in resistance to western gall rust, stalactiform blister rust, needle cast and Sequoia pitch moth in lodgepole pine. Forest Science 43: 571-581.

Wu, H.X. and C.C. Ying. 1998. Stability of resistance to western gall rust and needle cast in lodgepole pine provenances. Canadian Journal of Forest Research 28: 439-449.

Wu, H.X., F.C. Yeh, R.P. Pharis, B.P. Dancik, I.B. Jiang, I. Dymock and N.K. Dhir. 1995. Genetic parameters of greenhouse growth and performance of 2-year *Pinus contorta* ssp. *latifolia*. Scandinavian Journal of Forest Research 10: 12-21.

Wu, H.X., C.C. Ying and J.A. Muir. 1996. Effect of geographic variation and jack pine introgression on disease and insect resistance in lodgepole pine. Canadian Journal of Forest Research 26: 711-726.

Wu, H.X., F.C. Yeh, N.K. Dhir, R.P. Pharis and B.P. Dancik. 1997. Genotype by environment interaction and genetic correlation of greenhouse and field performance in *Pinus contorta*. Silvae Genetica 46: 170-175.

Wu, H.X., F.C. Yeh, R.P. Pharis, N.K. Dhir and B.P. Dancik. 2000. Study of early selection in tree breeding. Silvae Genetica 49: 152-157.

Xie, C.-Y. and C.C. Ying. 1995. Genetic architecture and adaptive landscape of interior lodgepole pine (*Pinus contorta* ssp. *latifolia*) in Canada. Canadian Journal of Forest Research 25: 2010-2021.

Xie, C.-Y. and C.C. Ying. 1996. Heritabilities, age-age correlations, and early selection in lodgepole pine (*Pinus contorta* ssp. *latifolia*). Silvae Genetica 45: 101-107.

Yanchuk, A.D., F.C. Yeh and B.P. Dancik. 1988. Variation of stem rust resistance in a lodgepole pine provenance-family plantation. Forest Science 34: 1067-1075.

Yang, R.C. 1985. Effect of fertilization on growth of 30-year-old lodgepole pine in west-central Alberta. Information Report NOR-X-268, Northern Forest Research Centre, Canadian Forestry Service, Edmonton, Alberta. 11 pp.

Yang, R.-C. and F.C. Yeh. 1993. Multilocus structure in *Pinus contorta* Dougl. Theoretical and Applied Genetics 87: 568-576.

Yang, R.-C. and F.C. Yeh. 1995. Patterns of gene flow and geographic structure in *Pinus contorta* Dougl. Forest Genetics 2: 65-75.

Yang, R.-C., F.C. Yeh and A.D. Yanchuk. 1996. A comparison of isozyme and quantitative genetic variation in *Pinus contorta* var. *latifolia* by F_{st}. Genetics 142: 1045-1052.

Yang, R.-C., N.K. Dhir, F.C. Yeh and Y. Hiratsuka. 1997. Geographic variation in susceptibility of Alberta lodgepole pine to western gall rust. Canadian Journal of Forest Research 27: 1398-1405.

Yang, R.-C., N.K. Dhir and L.K. Barnhardt. 1998. Comparative assessment of genetic variation of young high-elevation lodgepole pine for height and western gall rust resistance across two sites in Alberta. Canadian Journal of Forest Research 28: 478-484.

Yang, R.-C., Z. Ye and Y. Hiratsuka. 1999. Susceptibility of *Pinus contorta—Pinus banksiana* complex to *Endocronartium harknessii*: host-pathogen interactions. Canadian Journal of Botany 77: 1035-1043.

Ye, T.Z., R.-C. Yang and F.C. Yeh. 2002. Population structure of a lodgepole pine (*Pinus contorta*) and jack pine (*Pinus banksiana*) complex as revealed by random amplified polymorphic DNA. Genome 45: 530-540.

Yeh, F.C. and C. Layton. 1979. The organization of genetic variability in central and marginal populations of lodgepole pine *Pinus contorta* ssp. *latifolia*. Canadian Journal of Genetics and Cytology 21: 487-503.

Ying, C.C. and R.S. Hunt. 1987. Stability of resistance among *Pinus contorta* provenances to *Lophodermella concolor* needle cast. Canadian Journal of Forest Research 17: 1596-1601.

Ying, C.C. and Q. Liang. 1994. Geographic patterns of adaptive variation of lodgepole pine (*Pinus contorta* Dougl.) within the species' coastal range: field performance at age 20 years. Forest Ecology and Management 67: 281-298.

Ying, C.C., K. Illingworth and M. Carlson. 1985. Geographic variation in lodgepole pine and its implications for tree improvement in British Columbia. Pp. 45-53 *in* D.M. Baumgartner, R.G. Krebill, J.T. Arnott and G.F. Weetman, (eds.) Lodgepole pine: the species and its management. Cooperative Extension Services, Washington State University, Pullman, Washington.

Ying, C.C., C. Thompson and L. Herring. 1989. Geographic variation, nursery effects and early selection in lodgepole pine. Canadian Journal of Forest Research 19: 832-841.

Zavarin, E., W.B. Critchfield and K. Snajberk. 1969. Turpentine composition of *Pinus contorta × Pinus banksiana* hybrids and hybrid derivatives. Canadian Journal of Botany 47: 1443-1453.

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