Section 3.
Native north american larches: subalpine larch (*Larix lyallii*), western larch (*L. occidentalis*), and tamarack (*L. laricina*)

Preamble:

Each of the three North American larch species is usually discussed separately in each section and subsection of this Consensus Document in the following order: subalpine larch (*Larix lyallii*), western larch (*Larix occidentalis*), and tamarack (*Larix laricina*).

1. Taxonomy

Larch forests essentially encircle the colder temperate Northern Hemisphere. Within this area, the larch genus (*Larix*) is represented by 10-15 species and some subspecies or varieties as well as natural hybrids (Schmidt, 1995; Semerikov and Lascoux 2003; Semerikov *et al*, 2003). Ten species usually recognised are the North Eurasian *Larix decidua*, *L. sibirica* (synonym *L. russica*), *L. gmelinii* (including *L. cajanderi*, *L. dahurica*, and possibly *L. olgensis*), and *L. kaempferi* (synonym *L. leptolepis*); the South Asian *L. griffithiana*, *L. mastersiana*, and *L. potaninii*; and the North American *L. laricina*, *L. lyallii*, and *L. occidentalis*. All true larches are in the genus *Larix* Mill., a deciduous needle-leaf lineage in the gymnosperm family Pinaceae. Larch taxonomy has had limited overall attention. This is reflected in a lack of consensus about what constitutes a larch species or subspecies (or botanical variety), and about the phylogenetic relationships among species (Semerikov *et al*, 2003). The proposed division of *Larix* into two sections based largely on cone morphology (Vidakovic, 1991) is not supported by studies of chloroplast DNA variation (Qian *et al*, 1995), nuclear internal transcribed spacer (ITS) region (Gernandt and Liston, 1999), amplified fragment length polymorphisms (AFLPs) (Semerikov *et al*, 2003), or allozyme variation (Semerikov and Lascoux, 1999; Semerikov *et al*, 1999). An early phylogenetic separation (perhaps in the late Tertiary) occurred between the North American and the Eurasian species (Gernandt and Liston, 1999; Semerikov and Lascoux, 1999; Semerikov *et al*, 2003). The native range of each of the three North American larches – *Larix lyallii* Parl. (subalpine larch), *L occidentalis* Nutt. (western larch), and *L. laricina* (Du Roi) K. Koch (tamarack or North American larch) – is well defined with nearly no overlap between them. The disjunct western portion of the range of *L. laricina* (Figure 3) was recognised as the separate species *L. alaskensis* W. Wight (*e.g.* Hosie, 1979), or as the variety *L. laricina* var. *alaskensis* (W. Wight) Raup (Stipanicic, 1975) based on cone and needle morphology. This distinction was not recognised by Viereck and Little (1972), and species or varietal status is not supported by the degree of morphological and anatomical differentiation of the Alaskan tamarack populations (Parker and Dickinson, 1990; Parker, 1993).

The three North American species of *Larix* can be morphologically differentiated as follows: subalpine larch has 4-angled rather than somewhat 3-angled needles in cross section, and its new-growth twigs are densely covered with white cottony hairs. Compared to the other two larches, tamarack has smaller seed cones (1-2 cm long) with fewer (10-30) scales and bracts shorter than the scales; western larch (which has reddish-brown bark) has cones about 2.5-4.5 cm long and the bracts are extended, whereas subalpine larch (which has grayish bark) has cones often still larger (about 4-5 cm long) that appear bristly because the bracts extend farther beyond the scales.

2. Natural distribution

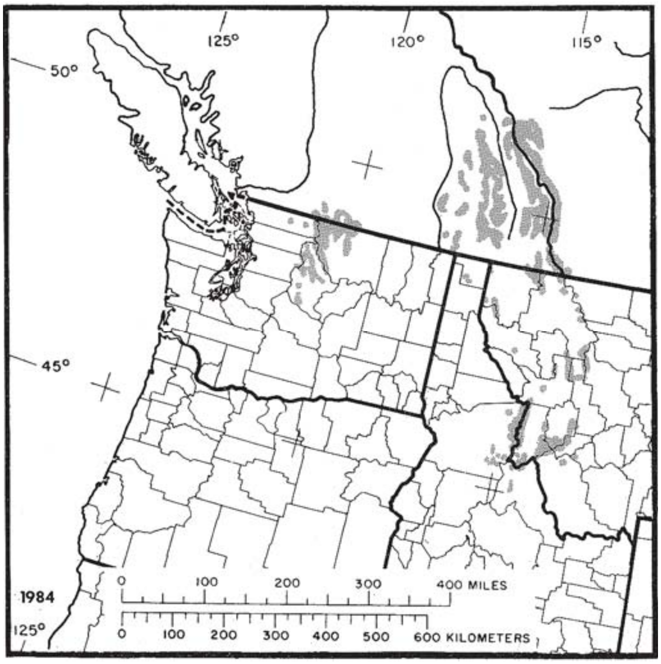
For about 200 years, attempts have been made to identify superior non-native species of larch for reforestation. As a result, plantation of exotic larches can be observed at many locations in the world, particularly in Europe and eastern North America (Krüssmann, 1985). The Japanese larch (*L. kaempferi*) is cultivated in many European plantations because of its more rapid growth than the native larches. Although introduced to Europe and Asia for testing, western larch has not been grown as a timber crop species outside its native range; it is grown ornamentally in arboreta and parks. Sometimes *L. decidua* (European larch) spreads locally from plantings in northeastern North America.

2.1 Subalpine larch

Subalpine larch is a continental, subalpine to boreal, western North American (prevailingly Cordilleran) species (Klinka *et al*, 2000) (Figure 1). It occupies a remote and rigorous environment, growing in and near the treeline. Although occurring in both the Rocky Mountains and the Cascade Range farther to the west (Little, 1979), the two distributions are separated by 200 km at their closest points, in Canada in southern British Columbia (Arno, 1990).

In British Columbia and Alberta, subalpine larch is common along the Continental Divide and adjacent ranges, and in the Purcell Range and southern Selkirk Range (Klinka *et al*, 2000). In the Rocky Mountains, subalpine larch extends from the Salmon River Mountains of central Idaho (latitude 45°30' N) northward to Lake Louise in Banff National Park, Alberta (latitude 51°30' N). Within this distribution, subalpine larch is common in the highest areas of the Bitterroot, Anaconda-Pintler, Whitefish, and Cabinet ranges of western Montana (Arno and Habeck, 1972). In the Cascades, subalpine larch is found principally east of the Cascade Divide and extends from the Wenatchee Mountains in central Washington northward to British Columbia. It spans an elevational range of 1520 to 3020 m (Arno, 1990).

Figure 1. The native range of subalpine larch

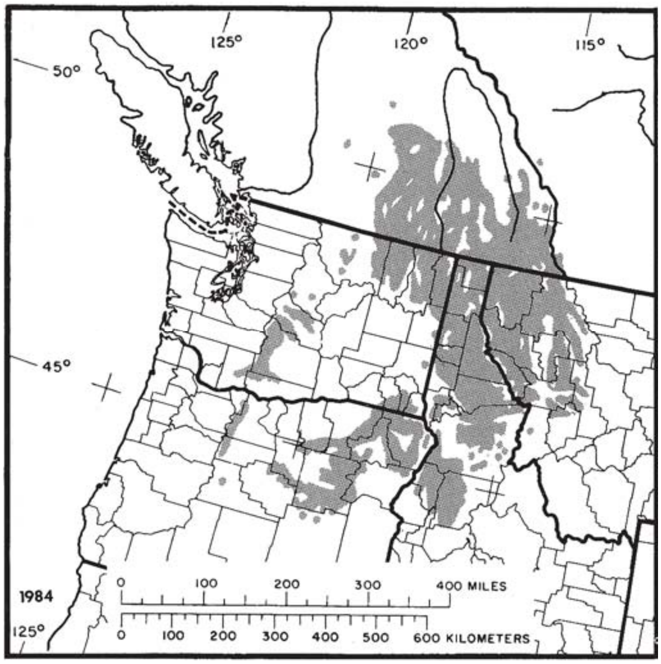


Source: Arno, 1990

2.2 Western larch

Western larch, a western North American (predominantly Cordilleran) species (Klinka *et al*, 2000), has a relatively moderate native range (Figure 2). It grows in southeastern British Columbia, northeastern Washington, the Upper Columbia River Basin of northwestern Montana and across northern and west-central Idaho; and farther westward in the Wallowa and Blue Mountains of southeastern Washington and northeastern Oregon, to the eastern slopes of the Cascade Mountains in north-central Oregon and central Washington (Schmidt and Shearer, 1990). Western larch has an elevational range of around 1500 m, from approximately 500 to 2000 m (Rehfeldt, 1995b).

Figure 2. The native range of western larch



Source: Schmidt and Schearer, 1990

2.3 Tamarack

Tamarack is a transcontinental North American species with one of the widest ranges of all North American conifers (Klinka *et al*, 2000) (Figure 3). Its northern range limit extends in Canada from Newfoundland and Labrador westward along the northern treeline and across the Continental Divide in northern Yukon Territory to the Mackenzie River drainage. The southern limit is from Maine through northern Connecticut, New Jersey, Pennsylvania, and Ohio, across the lake states, then from Manitoba through central Alberta to northern British Columbia (Johnston, 1990). Its farthest south populations occur locally in the mountains of northern West Virginia and adjacent western Maryland. A major disjunct portion of the western range of tamarack is found in the interior of Alaska, in the Yukon and Kuskokwim river basins between the Brooks Range and the Alaska Range to the south; and three small areas are near or on the Alaska-Yukon border (Viereck and Little, 1972). In the eastern portion of its range, it grows from sea level to 1220 m elevation, while in the western portion of the range it is found between 180 and 520 m (Johnston, 1990).

Figure 3. The native range of tamarack

Source: Johnston, 1990

3. Reproductive biology

3.1. Reproductive development

3.1.1. Subalpine larch

Like all members of the genus *Larix*, subalpine larch is monoecious, with male and female strobili borne separately on spur shoots scattered among leaf-bearing spur shoots. Buds containing male and female strobili begin to swell in late May. Pollen is released from the small, yellowish male strobili and wind dispersed in June, when there is often still snow on the ground (Arno, 1970; Richards, 1981). Female strobili mature by September into 4-5 cm purplish cones. Strobili can be damaged by frost, and this may be a cause of low seed production in most years. The reproductive cycle of subalpine larch has not been studied in detail, and factors limiting pollination, fertilisation, and seed development are not well understood (Schopmeyer, 1974).

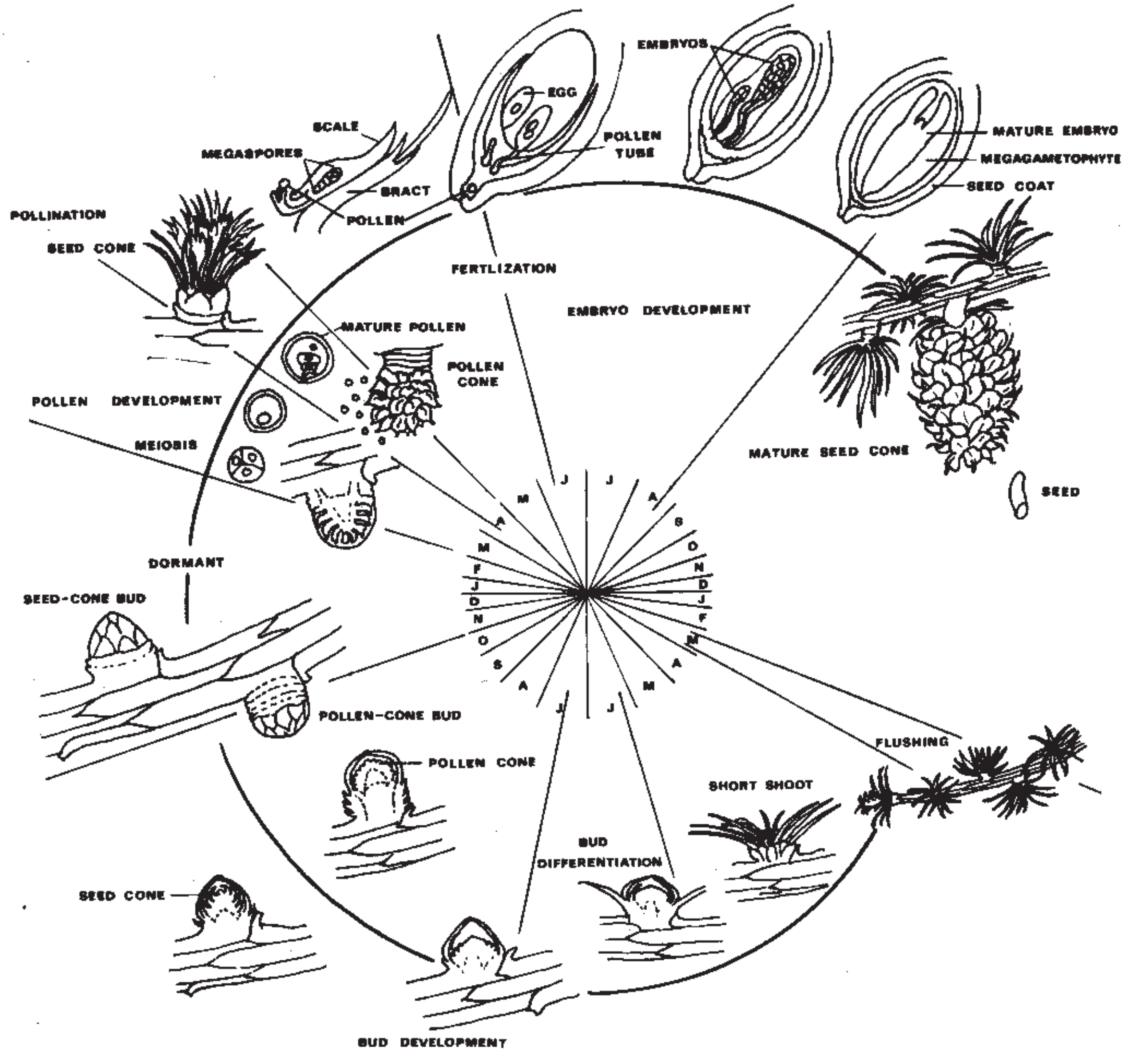
3.1.2. Western larch

Western larch is also monoecious; male and female strobili develop throughout the crown. Reproductive buds are found at the end of short spur shoots. Buds differentiate in June and July, and reproductive and vegetative buds can be distinguished early in the fall, about a year before subsequent cone crops mature (Schmidt and Shearer, 1990). Reproductive buds are larger than vegetative buds. Staminate buds are usually about one and one-half to two times longer than wide, whereas ovulate buds are globose (Figure 4). Buds and strobili can be sampled in fall to predict larch seed crops (Roe, 1966).

Pollen and seed strobili appear several days before vegetative buds open, which typically occurs between mid-April and mid-May (Schopmeyer, 1974; Owens and Molder, 1979b; Owens, 1995). Red or green female strobili are generally conspicuous. Pollination occurs in late May and early June. Following fertilisation, cones complete their development in that same season and mature by mid- to late-August of the same year, reaching 2.5 to 4.5 cm in length (Owens and Molder, 1979a, b; Schmidt and Lotan, 1980).

Stem injection of gibberellin $A_{4/7}$ in May or June increases both pollen and seed cone production (Ross, 1991; Eysteinsson and Greenwood, 1995; Shearer *et al*, 1999). Protocols for *in vitro* germination of western larch pollen have been developed (Dumont-BéBoux *et al*, 2000). The detailed documentation of the reproductive cycle of western larch by Owens and Molder (1979a, b) – illustrated in Figure 4 – is thought to hold for other species of *Larix* as well, albeit with some differences in timing (Owens, 1995).

Figure 4. The 2-year reproductive cycle of western larch



Source: Owens, 1995

3.1.3. Tamarack

Like other members of this genus, tamarack is monoecious with small, solitary male and female strobili interspersed with needles. Yellow male strobili are borne mainly on 1- or 2-year-old spur shoots. The reddish female strobili are borne most commonly on 2- to 4-year-old shoots. On open-grown trees, cones are borne on all parts of the crown. Ripe cones are brown, oblong to ovoid, and 1.3 to 1.9 cm long (Johnston, 1990). Reproductive buds on tamarack generally flush in Ontario and the Lake States from April to May, and in the interior of Alaska from mid- to late May. Seed cones generally ripen in Ontario and the Lake States in August and September (Schopmeyer, 1974).

3.2. Mating system and gene flow

3.2.1. Subalpine larch

Gene flow is likely less in this species than in more widespread conifers, including western larch, due to subalpine larch's relatively narrow and discontinuous distribution, but it has not been estimated. The relatively high level of population differentiation revealed by microsatellite markers for this species supports this supposition (D. Khasa, Université Laval, pers. comm.). A small but significant deficiency of heterozygotes detected for one allozyme locus compared to Hardy-Weinberg expectations may be indicative of some self-pollination or biparental inbreeding in the species (Semerikov and Lascoux, 1999), but outcrossing rates have not been estimated.

3.2.2. Western larch

Western larch has a mixed mating system, with average estimated multilocus outcrossing rates based on seven allozyme loci of 0.85 (El-Kassaby and Jaquish, 1996). This species has an active pollination mechanism, whereby the female strobilus directs pollen to the nucellus, and this mechanism does not discriminate among self, related or unrelated pollen, which may increase selfing (El-Kassaby and Jaquish, 1996). The relationship between stand density and outcrossing rate is unclear (Fins and Seeb, 1986). The degree of population differentiation for this species is typical of western conifers (Fins and Seeb, 1986; Hamrick *et al*, 1992; Semerikov and Lascoux, 1999), indicating relatively high levels of gene flow.

3.2.3. Tamarack

Tamarack also has a mixed mating system, with a somewhat lower outcrossing rate than most conifers. Using allozyme markers, Knowles *et al.* (1987) estimated the mean multilocus outcrossing rate in five populations as 0.73. Higher stand densities appeared to be related to higher outcrossing estimates. Tamarack likely has fairly high levels of gene flow like most conifers, as indicated by a relatively low degree of population differentation (Cheliak *et al*, 1988), but available methods for indirectly estimating this parameter are poor (Whitlock and McCauley, 1999).

3.3 Seed production

3.3.1. Subalpine larch

Subalpine larch only produces large seed crops about 1 year out of 10, and smaller crops are also relatively rare. Substantial seed is not produced until trees are at least 80 years old, with large, dominant older trees producing the largest crops (Arno, 1990; Arno et al, 1995). Most seeds are released from cones in September. The winged seeds are wind dispersed. There are between 230,000 and 360,500 cleaned seeds per kg (Schopmeyer, 1974). Subalpine larch seed germinates well after a 30-day stratification on a slightly acidic medium or after a treatment with 1% hydrogen peroxide for up to

24 hours (Shearer and Carlson, 1993; Carlson, 1994). Seed collection and handling guidelines for Larix species are available in Schopmeyer (1974).

3.3.2. Western larch

Western larch seed production is usually good, but cone crops vary substantially by year and location. Trees as young at 8 years old can produce seed cones, but they are only start being produced abundantly on trees 40 to 50 years of age. Trees continue to bear large crops for several centuries (Schmidt *et al*, 1976). Long-term records of western larch seed production in Montana show that abundant seed crops are produced at about 5-year intervals. Trees originating from grafted, mature scion produce approximately twice as many cones as those of seedling origin, and five times as many as rooted cuttings (Fins and Reedy, 1995). Cones usually begin to open by early September, but in cool moist summers cone opening may be delayed a month or longer. More than 80% of the seeds usually are dispersed by mid-October. A relatively small proportion of total seed are usually filled, due to a variety of pre- and post-zygotic factors (Owens *et al*, 1994) including lack of pollination (Owens and Molder, 1979b) and frost damage to developing cones (Webber and Ross, 1995). Cones usually fall from the tree during the subsequent winter, but many may stay attached through the next summer. Western larch seeds are relatively small, averaging 200,000 per kg (Schopmeyer, 1974). A cone can contain up to 80 seeds, but on average cones only have half this number. Successfully western larch seed pretreatments include 12 to 24 hours of 3% hydrogen peroxide, or soaking seeds for 18 days at 1^{o}C (Schmidt, 1962; Shearer and Halvorson, 1967).

3.3.3. Tamarack

Tamaracks as young as 5 or 6 years of age can produce both pollen and seed cones (Fowler *et al*, 1995); however, seed production in large quantities does not usually occur until about 75 years of age (Johnston, 1990). Vigorous, open-grown trees 50 to 150 years old produce the best cone crops. In a good year, a single tree may produce up to 20,000 cones with more than 300,000 full seeds. Good seed crops occur at 3 to 6 year intervals, with some seed produced in intervening years. Empty cones remain on trees for 2 to 5 years (Johnston, 1990). The wind-dispersed seeds are approximately 3 mm long, with a 6 mm long chestnut-brown wing. There are between 550,000 and 710,000 cleaned seeds per kg, on average (Schopmeyer, 1974). Tamarack can reproduce well as far as 60 m from the seed-bearing trees if favourable seedbeds are present (Johnston, 1975). Unstratified tamarack seeds germinate well in light at warmer temperatures, but stratified seeds can germinate in the dark at cooler temperatures as well (Farmer and Reinholt, 1986).

3.4. Natural regeneration

3.4.1. Subalpine larch

Subalpine seems to require full light but low temperatures for regeneration (Arno, 1990). It is difficult to regenerate or cultivate even in the relatively cool climates at lower elevations in the Pacific Northwest. Daytime high temperatures and surface drought apparently are lethal. Seed germination is been poor but improves with a 24 hour treatment with a 3% hydrogen peroxide solution (Schopmeyer, 1974). Subalpine larch can have four to six cotyledons, but most individuals have five. All larches have epigeal germination. First-year germinants are seldom found in natural stands. Germination is most successful on northern exposures not fully exposed to afternoon sun on mineral soil. Canopy gaps often contain dense, even-aged cohorts of seedlings or saplings referred to as reproduction glades (Arno, 1990). This typical age distribution suggests that successful reproduction occurs only rarely when conditions are favorable (Arno, 1990). Seedlings grow very slowly above ground the first 20-25 years (Richards, 1981) while seedlings develop extensive root systems while being protected by the snowpack from winter and spring desiccation.

3.4.2. Western larch

Natural regeneration of western larch can be successful provided a reliable seed source, a suitable seedbed, and adequate light are available. Western larch seed disperses up to 240 m from seed trees at the forest margin into open areas (Shearer, 1959). If bare soil is exposed near a seed source, overstocking can result. Dispersal is less uniform in clearcuts than in seed tree and shelterwood silvicultural treatments (Schmidt and Shearer, 1990). Rodent and bird predation reduce seed germination significantly (Stoehr, 2000).

Western larch seeds germinate epigeally about the time of snowmelt, from late April to early June, usually 1 to 2 weeks before associated tree species (Shearer, 1967). Germination is usually rapid and complete after natural stratification during winter. Air temperatures of about 27°C are optimal for germination, but seeds can still germinate at temperatures that are 10° to 15°C cooler (Schopmeyer, 1974).

Western larch is well adapted to mineral soil seedbeds exposed by burning (DeByle, 1981) or mechanical scarification (Schmidt *et al*, 1976; Shearer, 1980). Undisturbed seedbeds of organic matter and areas with heavy root competition have inferior seedling survival. Most mortality occurs during the first growing season; after 3 years seedling losses are minor (Schmidt *et al*, 1976). Seedling survival is primarily impacted by biotic factors early in the growing season and by abiotic factors later. Seedlings established on mineral soil seedbeds are far less susceptible to fungi than those growing on organic substrates. Insolation is the most important abiotic factor impacting seedling survival (Shearer, 1967). Organic substrates result in lethal temperatures earlier and more frequently during the growing season than mineral soils. Drought is the major factor affecting seedling survival later in the growing season, and its effects are greatest in full shade because of competition for moisture by trees and understory vegetation (Schmidt and Shearer, 1990).

Western larch seedlings grow about 5 cm on average the first growing season. Root growth in the first year depends on the conditions. In the shade, roots may average only 2.5 cm the first year, whereas in full light, roots may be over 20 cm long. Subsequent annual height growth averages about 30 cm is typical of the first 4 years (Schopmeyer, 1974; Schmidt and Shearer, 1990).

3.4.3. Tamarack

Tamarack seeds normally germinate between late May and mid-June, and germination peaks at temperatures of 18° to 21°C. Seeds have little or no internal dormancy (Schopmeyer, 1974). Under natural conditions, any existing dormancy is broken during the first winter after seeds are shed (Johnston, 1990). Up to half the seeds that fall may be eaten by rodents, and much of the remaining seed is often damaged by fungi or bacteria. As a result, only 4 to 5% of the seeds may reach germination (Fowells, 1965).

Optimal seedbeds for tamarack are warm, moist, burned mineral or organic soil with no brush but a light herbaceous cover. Slow-growing sphagnum mounds often make a good seedbed, but the moss can provide too much competition under some circumstances. Seedlings in low-light conditions usually grow only 2 to 3 cm the first year and do not usually survive beyond the sixth year; while in full light, they may be as tall as 23 cm the first year and 64 cm the third year. Subsequent growth is generally even more rapid if light is adequate and drainage is good (Fowells, 1965).

3.5. Vegetative reproduction

3.5.1. Subalpine larch

While layering occurs in some larch species and is common in subalpine larch's ecological associate subalpine fir, subalpine larch only rarely spreads by layering (Arno and Habeck, 1972; Arno *et al*, 1995).

Subalpine larch scions have been successfully grafted onto western larch rootstock (B. Jaquish, British Columbia Ministry of Forests, pers. comm.). Given the success of somatic embryogenesis using immature embryo explants in other *Larix* species, it is likely that this technique would be successful for subalpine larch, but it is unlikely to be developed due to the low economic value and lack of need for reforestation with this species. Likewise, methods of organogenesis developed for *Larix gmelinii* (Lin *et al*, 2004) would likely be transferable to all three species of larch discussed here.

3.5.2. Western larch

Western larch does not layer or sprout from stumps or roots in nature. Parent trees are established in seed orchards through grafting (Staubach and Fins, 1988). Juvenile cuttings of western larch root easily, but initially exhibit a high degree of plagiotropism, although most plagiotropic stecklings recover orthotropic growth within 2 years (Edson *et al*, 1995, 1996). Semi-hardwood cuttings collected from July through September yielded higher rooting percentages than softwood cuttings collected in June (Edson *et al*, 1995). Micropropagation methods for multiplying plants using axillary buds have also been developed (Edson *et al*, 1995). Rooted cuttings are not currently used for reforestation due to the poor stock quality. Somatic embryogenesis has been achieved for western larch (Thompson and von Aderkas, 1992; Benkrima and von Aderkas, 1995) but is not being used for operational reforestation. Given the relatively small size of breeding programs for this species, it is unlikely that these programs will adopt a clonal forestry strategy requiring vegetative propagation, but these technologies could be used to overcome seed shortages by bulking seedlots or family seed collections.

3.5.3. Tamarack

Along the northern limit of trees in Canada and Alaska, layering is the dominant type of reproduction for tamarack (Elliott, 1979). Further south, layering is uncommon but may occur when branches are covered by sphagnum moss or drifting sand. Roots are also known to produce adventitious shoots (Fowells, 1965). While tamarack roots easily from juvenile cuttings (Park and Fowler, 1987), the rooting ability of cuttings from 3 to 10 year old donors varied widely among clones, setting dates and donor age (Morgenstern *et al*, 1984). Methods have been developed for somatic embryogenesis in tamarack using excised, immature embryos but these techniques are not yet being used operationally for reforestation. Somatic embryogenesis for *Larix* species provides a system for regeneration following genetic transformation (Klimaszewska *et al*, 1997).

4. Genetics

4.1 Cytology

Subalpine larch, western larch, and tamarack

All species of *Larix*, like most other genera in the Pinaceae, have a haploid number of 12 chromosomes (Wright, 1962). Polyploidy and aneuploidy are rare in conifers. A cross between *L. occidentalis* and *L. decidua* (European larch) produced a single triploid hybrid (Larsen and Westergaard, 1938).

The cytology of reproduction in western larch has been documented by Owens and Molder (1979a, b). The inheritance of plastids appears to be paternal, whereas mitochondrial inheritance is largely but not exclusively maternal, which is typical of other members of the Pinaceae (Neale and Sederoff, 1989; Owens, 1995) and other *Larix* species (DeVerno *et al*, 1993).

4.2. Genetic variation

4.2.1. Population variability

4.2.1.1. Subalpine larch

There are no published estimates of among-population variation in subalpine larch. The isolation and characterisation of 14 microsatellite loci in this species has facilitated ongoing studies of this subject (Khasa *et al*, 2000). Preliminary results of population genetic surveys using these markers indicate much greater population differentiation in subalpine larch than in western larch, as expected given the discontinous distribution of subalpine larch, with estimates of F_{st} of 0.133 for subalpine larch and 0.047 for western larch (D. Khasa, Université Laval, pers. comm.).

4.2.1.2. Western larch

Provenance variation in western larch is significant but clines are considerably flatter than those of some other western conifers with sympatric distributions (Rehfeldt, 1995a, b). Populations separated by 500 m in elevation differ significantly (Rehfeldt, 1995b). Weak but significant clinal variation corresponding to climatic variables, including mean annual temperature and number of frost-free days, has been observed for height growth, phenology, lammas growth, and resistance to *Meria* needle cast (Rehfeldt, 1982, 1992, 1995b). Natural populations in environments differing by 40 frost-free days annually are significantly genetically different, whereas for interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) and Rocky Mountain lodgepole pine (*Pinus contorta* subsp. *latifolia*) in the same region, populations differing by around 20 frost-free days differ significantly (Rehfeldt, 1995a, b). Clinal variation has also been observed for components of shoot growth (Joyce, 1985; Zhang and Fins, 1993).

Population genetics studies of western larch using allozyme analysis have yielded G_{st} estimates ranging from 0.086 to 0.100 (Fins and Seeb, 1986; Semerikov and Lascoux, 1999), indicating that the vast majority of genetic variation is found within rather than among populations. These estimates are similar to the average G_{st} for gymnosperms of 0.073 (Hamrick *et al*, 1992).

4.2.1.3. Tamarack

Provenance testing for this species has not been extensive, probably because of the North American interest in provenances of much faster growing exotic larches such as *L. kaempferi* (Japanese larch), which can grow up to three times as much volume on some sites in eastern Canada (Fowler *et al*, 1988). Tamarack has been infrequently included in the provenance trials of exotic larches, and then only as a control (Boyle *et al*, 1989). Thus, comprehensive provenance trials of tamarack are young relative to those of many other species.

Six-year height growth in a rangewide provenance trial was strongly and negatively correlated with latitude of origin ($r = -0.78$), and moderately correlated with longitude ($r = -0.58$), whereas interaction of provenance by test-site location was significant but weak (Fowler *et al*, 1995). On a smaller geographic scale, Rehfeldt (1970) found significant variation among provenances within Wisconsin (USA) for height, and a positive correlation between date of bud set and parent-tree location frost-free period. Canadian populations in Ontario did not vary significantly for stem form or survival in one study (Boyle *et al*, 1989), but this trial was not designed as a classic provenance trial and included only three populations. In contrast, a study of variation in cold hardiness among 66 Ontario tamarack populations found genetic differentiation over relatively short geographic distances and steep genetic clines, indicating allowable seed transfer distances should be short for this species (Joyce, 1988). In an investigation of the potential to use tamarack as a plantation species on waterlogged sites in France, significant variation was found for growth and form traits among eight provenances from the southeastern portion of its range. There was an unfavourable correlation between growth rate and stem-form quality (Pâques and Périnot, 1994).

In population genetics studies, the degree of differentiation among populations for allozymes appears to be comparable to that of other conifers, with G_{st} estimated at 0.05 based on 15 loci (Cheliak *et al*, 1988). Although this indicates that most of the genetic variation exists within rather than among populations, in the same study Nei's genetic distance (D) averaged 0.032 among populations, a relatively high estimate for a widespread conifer. On a regional scale, in a study of 44 populations of tamarack from northern Ontario, among-population variation accounted for just 2% of total allozyme variation (Liu and Knowles, 1991). Populations of tamarack in Alaska differ somewhat from those in other areas of the range in cone and needle morphology, supporting the hypothesis of descent from a different Pleistocene refugium than the eastern populations, but the differentiation is not sufficient to warrant recognition of Alaskan tamarack as a separate taxonomic variety (Parker and Dickinson, 1990).

4.2.2. Individual-level variability

4.2.2.1. Subalpine larch

In a comparative allozyme study of both North American and Eurasian larch species, subalpine larch had relatively low levels of heterozygosity in the single population studied (expected heterozygosity of 0.082), lower than all the other species studied except *L. gmelinii* var. *olgensis* (or *L. olgensis*), another larch with a narrow ecological niche (Semerikov and Lascoux, 1999).

4.2.2.2. Western larch

Estimates of expected heterozygosity within populations from allozyme analysis range from 0.082 (Fins and Seeb, 1986) to 0.15 (Semerikov and Lascoux, 1999). The first estimate is somewhat low for a gymnosperm, whereas the second is more typical (Hamrick *et al*, 1992).

Estimated individual heritabilities for growth traits in western larch are higher than for many conifers, averaging 0.25 for height growth (Rehfeldt, 1992). Daily growth rate during the linear portion of the height growth curve has a similar heritability to total height growth but is weakly correlated with shoot phenology, unlike total height growth, and thus may be a better trait for breeding selection (Rehfeldt, 1992).

4.2.2.3. Tamarack

Tamarack has relatively high levels of genetic diversity within stands for both quantitative traits (Rehfeldt, 1970; Jeffers, 1975) and genetic markers. Estimates of expected heterozygosity based on allozyme loci range from 0.10 to 0.22, depending on the populations and allozme loci analyzed (Cheliak *et al*, 1988; Liu and Knowles, 1991; Semerikov and Lascoux, 1999).

Analysis of 16-year height in tamarack progeny trials in Ontario revealed little to no genetic variation among families (Boyle *et al*, 1989), whereas Park and Fowler (1982, 1987) found significant genetic variation for height growth. Narrow-sense heritability for 5-year height over three sites was relatively low, however, with estimates ranging from 0.01 to 0.14 (Park and Fowler, 1987). Clone mean heritabilities are relatively high (0.44 to 0.80), suggesting there may be opportunities to exploit non-additive genetic variation in future breeding programs (Park and Fowler, 1987; Fowler *et al*, 1995).

4.3. Inbreeeding depression and genetic load

4.3.1. Subalpine larch

There are no estimates available of inbreeding depression and genetic load in subalpine larch.

4.3.2. Western larch

There have been no direct studies of inbreeding depression reported for this species. As outcrossing rates for western larch are estimated to be significantly lower than 1, this may indicate that inbreeding depression is less pronounced than in some other conifers (El-Kassaby and Jaquish, 1996).

4.3.3. Tamarack

Tamarack has below-average self-fertility and a high genetic load in terms of lethal equivalents (Fowler *et al*, 1995). Genetically the trees in natural stands are not randomly distributed, and those growing in close proximity are often related (Park and Fowler, 1982). Unlike seeds and seedlings, which have deficiencies of heterozygotes, populations of mature trees approach Hardy-Weinberg expectations for heterozygosity, indicating that there is natural selection against inbred seedlings (Knowles *et al*, 1987; Cheliak *et al*, 1988).

5. Hybridisation

5.1. Subalpine larch and western larch

Subalpine larch and western larch are separated by 400 m or more of elevation in most parts of their ranges. The opportunities for natural hybridisation are limited to the Bitterroot Range in western Montana, where they are sympatric. In this area, *Larix lyallii* hybridises naturally with *L. occidentalis* (Carlson and Blake, 1969; Carlson *et al*, 1990, 1991; Arno *et al*, 1995); however, a usual difference of nearly 2 months in reproductive phenology likely limits their hybridisation (Carlson, 1994). Controlled cross-pollinations between *L. lyallii* females and *L. occidentalis* males result in high seed set, but the reciprocal cross produces few viable seeds (Carlson, 1994). The hybrid offspring are less vigorous than *L. occidentalis* but faster growing than *L. lyallii*, and the stems are (on average) thicker than those of either parent species. Climatic warming may favour these hybrids in sympatric regions. Both subalpine larch and western larch can be artificially hybridised with *L. laricina* (Fowler *et al*, 1995).

A cross between western larch and *L. decidua* (European larch) produced a single hybrid (Larsen and Westergaard, 1938). Western larch can be hybridised with *L. kaempferi* (Japanese larch), and while seed set is low, the seedling offspring can grow approximately twice as fast as intraspecific *L. occidentalis* crosses (Wang, 1971). These interspecific hybrids are not used for operational reforestation in North America (B. Jaquish, British Columbia Ministry of Forests, pers. comm.), and current forest policy on public land discourages use of exotics, including hybrids. Dunkeld larch, *L.* × *marschlinsii* (synonym *L.* × *eurolepis*) (*L. decidua* × *L. kaempferi*), is planted extensively in Europe because of its larch canker resistance (Baltunis and Greenwood, 1998; Mabberley, 1998). In western North America, if either *L. kaempferi* × *L. occidentalis* hybrids or the species *L. kaempferi* were planted on a broad scale, they could have a significant impact on the gene pool of natural western larch populations, given the somewhat weak reproductive barrier between these species and the rapid growth of the hybrids (Wang, 1971). It is not known whether *L. kaempferi* or its hybrids with *L. occidentalis* can also hybridise with subalpine larch. *Larix kaempferi* originates from lower latitudes (in Japan) than North American larches and is less frost hardy than *L. occidentalis* (Wang, 1971); although it can grow as high as 2800 m in its native environment so may have some tolerance for colder environments. The intensive silviculture necessary for production and establishment of hybrid plantations in North America would likely be directed towards lower elevation, high-productivity sites. If planting of *L. kaempferi* or its hybrids became common, it seems likely that they would be likely be used in areas with substantial elevational separation, thus providing both physical distance and phenological barriers to hybridisation between the plantations and natural populations of subalpine larch.

Attempts at intergeneric *in vitro* hybridisation resulted in western larch pollen germinating and penetrating archegonia of *Pinus monticola* (western white pine). However, successful fertilisation did not occur (Dumont-BéBoux *et al*, 1998).

5.2. Tamarack

Larix laricina has relatively low crossability with other *Larix* species. It has experimentally been crossed most readily with the two other North American larches. Tamarack has also been hybridised with *L. decidua*, *L. sibirica* (Siberian larch), and *L. kaempferi*, but the crossability with these three species was extremely low (Fowler *et al*, 1995). Hybrids between *L. decidua* females with tamarack as the pollen parents were the most vigorous of several *Larix* hybrids evaluated in a trial in Maine (USA) (Baltunis and Greenwood, 1998). Crosses between tamarack and *L. kaempferi* produced little viable seed, but the resulting offspring were relatively vigorous (Baltunis and Greenwood, 1998; Baltunis *et al*, 1998).

6. Ecology

6.1. Climate

6.1.1. Subalpine larch

Subalpine larch is well adapted to a very cold, snowy and generally moist continental subalpine-boreal climate. The extreme lower and upper altitudinal limits of subalpine larch over its entire geographic range are 1520 and 3020 m (Arno, 1990). For more than half of the year, mean temperatures are below freezing. The growing season is defined by mean temperatures above 6°C (Baker, 1944), only lasts about 90 days and is punctuated by occasional frosts and snowfall. July mean temperatures range from approximately 9° to 14°C, but minimum temperatures during the growing season are as low as -5°C and maximums as high as 27°C. January mean temperatures range from -7°C in the northern Cascades to -14°C in Alberta, and long-term record minimum temperatures are likely as low as -50°C near the Continental Divide in Alberta and Montana (Arno, 1990).

Mean annual precipitation for most subalpine larch sites is between 800 and 1,900 mm, the greater amount being more prevalent near the crest of the Cascades. Most stands in Montana's Bitterroot Range receive 1,000 to 1,500 mm. Approximately 75% of this precipitation is snow and sleet. Typically, the snowpack begins to accumulate by late October. By mid-April, it reaches a maximum depth averaging about 2 m in stands near the Continental Divide and about 3 m farther west. The snowpack does not melt away in most stands until early July. The average snowfall is about 10 m in most stands west of the Continental Divide (Arno, 1990).

6.1.2. Western larch

Western larch grows predominantly in continental cool-temperate climates, and marginally in subalpine-boreal climates (Klinka *et al*, 2000). Mean annual temperature within its native range is about 7°C; ranging from an average annual maximum of 29°C to an average annual minimum of -9°C (Schmidt and Shearer, 1990). Average growing season temperatures from May to August are approximately 16°C, with July the warmest month. The frost-free season varies from 60 to 160 days, usually from early June through early September; however, frosts can occur in any month of the year (Schmidt *et al*, 1976).

Annual precipitation ranges from an average around 710 mm in the northern part of the larch's range to 810 mm in the south, with extremes of 460 mm and 1,270 mm. Snow accounts for over half of the total precipitation on montane and subalpine sites. About one-fifth of the annual precipitation occurs during the growing season, mostly in May and June. July and August are usually dry, with clear sunny days, low humidity, and high evaporation rates (Fowells, 1965).

6.1.3. Tamarack

Tamarack grows under a wide range of climatic conditions across its large range, but predominantly within a montane boreal climate. Across its range, average January temperatures vary from -30° to -1°C, and average July temperatures are 13° to 24°C. The minimum temperatures recorded within the species range vary from -29° to -62°C; the maximum from 29° to 43°C. Tamarack grows with less than a 75 day frost-free period over much of its range, with 120 frost free days in interior Alaska and 180 days along its southern limits. Longer daylength during the growing season generally compensates for the shorter growing season at northern latitudes (Fowells, 1965). Annual precipitation within the range of tamarack is also highly variable, ranging from 180 mm at Fort Yukon, Alaska, to 1,400 mm in eastern Canada. Of this precipitation, 75 to 355 mm is during the growing season. Annual snowfall has a similarly wide variation, from around 100 cm in the District of Mackenzie in northwestern Canada to over five meters near the coasts of Labrador and Quebec (Johnston, 1990).

6.2. Soils

6.2.1. Subalpine larch

The sites occupied by subalpine larch underwent intense glaciation during the Pleistocene and have been deglaciated for less than 12,000 years. As a result, most soils occupied by subalpine larch stands are immature and weakly developed. Short, cool summer temperatures retard chemical weathering. Microbial activity including nitrogen fixation that might enrich the soil is also apparently restricted by low soil temperatures as well as high acidity (Arno, 1990).

Subalpine larch commonly grows on previously unvegetated talus slopes covered with granite or quartzite rock, but the species is absent or scarce on limestone and dolomite (Arno and Habeck, 1972). It can also root in bedrock cracks. This substrate preference is in constrast to several other cold-climate conifers, including *L. sibirica* and tamarack, which often grow on calcium-rich, basic soils (Ritchie, 1957; Hustich, 1966).

Subalpine larch achieves its best growth where soils are kept moist throughout summer by aerated seeps such as in high-elevation basins and near the base of talus slopes. It can also tolerate acidic, organic soils on boggy meadow sites. It is most abundant on cool, north-facing slopes and in high montane basin, but can also grow on south-facing slopes if soils are relatively moist (Arno, 1990).

6.2.2. Western larch

Western larch can tolerate very dry to very moist soil moisture conditions and very poor to very rich soil nutrient conditions, but the most productive growth occurs on fresh to moist, rich to very rich sites. Although this species has a relatively wide climatic and edaphic amplitude, it is infrequent on very moist sites and absent on wet sites. Compared to other tree species, it tolerates water-deficient soils well (Krajina, 1969; Klinka *et al*, 2000).

Relationships between potential site index of western larch and categorical measures of site quality were quantified by New (1999) in the major portion of its British Columbia range. The larch site index values (1) increased with greater soil water supply from water-deficient to fresh and moist sites, and then decreased with greater water surpluses; and (2) increased from very poor through very rich sites, with the rate of increase diminishing with higher availabilities of nitrogen. The increase in site index values along the soil nutrient gradient was consistently steeper than along the soil moisture gradient (Table 1).

Western larch grows on a wide variety of soils, most commonly on soils that have developed from calcium and magnesium-rich glacial till or colluvium. Most soils supporting the growth of western larch are Inceptisols and Alfisols (Soil Conservation Service, 1975), and infrequently Spodosols which generally occur close to the upper elevation limits of the species (Fowells, 1965).

Table 1. Edatopic grid for western larch showing predicted site index values (m at 50-yr bh), using New's soil moisture and soil nutrient model (n+315, m+/-95% confidence interval), and mean measured site index values according to actual moisture and nutrient regimes

Indicated sample sizes refer only to the predicted and measured site index values

Actual soil moisture regime	Number of plots (n); site index	Actual soil nutrient regime Site index values				
		Very poor	Poor	Medium	Rich	Very rich
Excessively dry	n	3	0	0	0	0
	Predicted	8.6±1.7	9.2	11.5	12.7	13.0
	Measured	8.6	nd	nd	nd	nd
Very dry	n	6	14	8	2	0
	Predicted	13.2±0.6	13.8±0.8	16.1±0.9	17.3±0.7	17.5
	Measured	13.2	14.3	15.4	16.6	nd
Moderately dry	n	0	45	44	6	0
	Predicted	16.7	17.4±0.5	19.6±0.5	20.8±0.5	21.1
	Measured	nd	17.2	19.9	20.8	nd
Slightly dry	n	0	52	58	28	0
	Predicted	19.2	19.9±0.3	22.2±0.5	23.3±0.7	23.6
	Measured	nd	19.9	21.9	23.7	nd
Fresh	n	0	0	18	11	5
	Predicted	20.9	21.5	23.8±0.5	25.0±0.6	25.2±1.1
	Measured	nd	nd	21.9	23.7	25.6
Moist	n	0	0	1	2	5
	Predicted	22.5	23.1	25.4±1.3	26.6±1.3	26.8±1.1
	Measured	nd	nd	26.5	26.2	26.8
Very moist	n	0	0	0	4	1
	Predicted	16.1	16.7	19.0	20.2±1.3	20.4±2.9
	Measured	nd	nd	nd	20.6	18.7
Wet	n	0	0	0	1	0
	Predicted	16.3	17.0	19.2	20.4±1.6	20.7
	Measured	nd	nd	nd	20.4	nd

nd – no data were obtained due to absence or sporadic occurrence of western larch under some edaphic conditions.

6.2.3. *Tamarack*

Tamarack grows in a wide range of conditions, from moderately dry to wet soil moisture and poor to very rich soil nutrients, although the most productive growth occurs on fresh to moist and nutrient rich to very rich sites (Krajina, 1969; Johnston, 1990; Klinka *et al*, 2000). Compared to many other tree species, it tolerates water-surplus soils well; thus, it grows most commonly on wet organic soils (Histosols - Soil Conservation Service, 1975) developed from sphagnum and woody peats. Woody peat is usually better decomposed, has more nitrogen and mineral nutrients, and is less acidic than sphagnum moss peat. On upland sites the species is associated with mineral soils (especially Inceptisols and Entisols) that range from coarse sand to heavy clay, and with calcareous soils (Johnston, 1990). Tamarack is more abundant on peatland than upland sites due to its tolerance of high soil moisture, high acidity and low soil temperature. It grows best, however, on moist but well-drained loamy soils in riparian zones and on seep areas, and on mineral soils with a shallow surface layer of organic matter (Fowells, 1965).

6.3. Synecology

6.3.1. Subalpine larch

Subalpine larch is more frequent in pure stands and scattered clumps than in mixed-species stands. It typically forms scattered, open, park-like groves <0.1 ha in size. It is a pioneer species on avalanche slopes, colluvium, and rock outcrops, but can form edaphic climax communities near the upper treeline in association with other subalpine species such as whitebark pine (*Pinus albicaulis*), subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*) and mountain hemlock (*Tsuga mertensiana*) (Eyre, 1980; Klinka *et al*, 2000). Subalpine larch stands are a variant of forest cover type Whitebark Pine (Type 208) but also occur in Engelmann Spruce-Subalpine Fir (Type 206). In British Columbia, subalpine larch is a minor component in the transition between continental high-elevation forest and alpine tundra zones, between 1,800 and 2,300 m (Krajina, 1969; Klinka *et al*, 2000). In the western United States, subalpine larch is a component in the *Tsuga mertensiana* (west of the Cascades) and *Abies lasiocarpa* zones (Franklin and Dyrness, 1973). The understory of most subalpine larch stands throughout the Pacific Northwest is dominated by grouse whortleberry (*Vaccinium scoparium*), smooth woodrush (*Luzula hitchcockii*), mountain arnica (*Arnica latifolia*), and red mountain heather (*Phyllodoce empetriformis*), but on some relatively cold, exposed sites, krumholz subalpine fir and whitebark pine form an understory (Arno, 1970).

6.3.2. Western larch

Western larch may grow in pure stands but is more frequent in mixed-species stands. Old-growth western larch stands are now rare. Despite being a long-lived species, in the absence of fire it is replaced by shade-tolerant species. It is present in all stages of fire-driven, secondary succession. Depending on climate and soil moisture, its most common associates are (1) in the drier temperate climates: interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) and ponderosa pine (*Pinus ponderosa*); (2) in the wetter temperate climates: grand fir (*Abies grandis*), western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*) and western white pine (*Pinus monticola*); and (3) in subalpine-boreal climates: Engelmann spruce, subalpine fir and mountain hemlock; as well as (4) across its whole range: lodgepole pine (*Pinus contorta* subsp. *latifolia*) (Fowells, 1965; Eyre, 1980; Klinka *et al*, 2000). Western larch stands typically have a diverse understory with dense herbaceous and less dense shrub layers (Pfister *et al*, 1977).

In the United States, western larch comprises the majority of forest cover type Western Larch (212) but is also found in Mountain Hemlock (205), Engelmann Spruce-Subalpine fir (206), Interior Douglas-fir (210), Grand Fir (214), Western White Pine (215), Lodgepole Pine (218), Rocky Mountain Juniper (220), Western Hemlock (224), Western Redcedar-Western Hemlock (227), Western Redcedar (228) and Interior Ponderosa Pine (237) (Schmidt and Shearer, 1990) (Society of American Foresters, 1980). In British Columbia, western larch is a significant component of a number of forest communities in the continental montane forested zones, and to a limited extent in the continental subalpine forest (Krajina, 1969; Klinka *et al*, 2000).

6.3.3. Tamarack

Tamarack forms extensive pure stands in the Canadian boreal forest and in northern Minnesota (USA). In the rest of its range, the species is found locally in both pure and mixed stands. It is a major component in the forest cover types (Eyre, 1980) Tamarack (Type 38) and Black Spruce-Tamarack (Type 13) and is a minor component in Jack Pine (Type 1), Balsam Fir (Type 5), Black Spruce (Type 12), Red Spruce-Balsam Fir (Type 33), Northern White-Cedar (Type 37), Black Ash-American Elm-Red Maple (Type 39), White Spruce (Type 107), Balsam Poplar (Type 203), Black Spruce (Type 204), Black Spruce-White Spruce (Type 253), and Black Spruce-Paper Birch (Type 254).

Black spruce (*Picea mariana*) is usually found with tamarack in mixed-species stands on all sites. Tamarack stands cast relatively light shade and as a result usually have well-developed shrub, herb, or moss layers featuring a high diversity of species (owing to the extensive range of the species). The moss layer is typically composed of sphagnum (*Sphagnum* spp.) and other bryophytes (Eyre, 1980). Herbs include sedges (*Carex* spp.), cottongrass (*Eriophorum* spp.), false Solomon's seal (*Smilacina trifolia*), marsh cinquefoil (*Potentilla palustris*), marsh-marigold (*Caltha palustris*) and bogbean (*Menyanthes trifoliata*). Shrubs include dwarf and swamp birches (*Betula glandulosa* and *B. pumila*), willows (*Salix* spp.), speckled alder (*Alnus rugosa*), and red-osier dogwood (*Cornus stolonifera*), Labrador-tea (*Ledum groenlandicum*), bog-rosemary (*Andromeda glaucophylla*), leatherleaf (*Chamaedaphne calyculata*) and small cranberry (*Vaccinium oxycoccos*) (Fowells, 1965).

6.4. Stand dynamics

6.4.1. Subalpine larch

Subalpine larch is very shade-intolerant (Arno, 1990). Whitebark pine is also shade-intolerant, but is most abundant on warm-aspect slopes and thus tends to complement rather than compete with the larch (Arno and Habeck, 1972). At the highest elevations and coolest sites, subalpine larch forms parkland-like climax communities owing to its superior hardiness to other subalpine conifers. Its hardiness is due to resistance to the winter desiccation stress that occurs during warm periods when soils are still cold or frozen (Richards, 1981; Richards and Bliss, 1986). Subalpine larch has adaptations to winter dessication stress include deciduous leaves and woody protected buds (Arno, 1970). Its deciduous foliage requires a large amount of moisture throughout the summer, however, compared to evergreens and consequently it occupies relatively moist sites.

Subalpine larch is a long-lived, very slow-growing tree. Height growth is exceedingly slow for the first 20 to 25 years as seedlings become established, but increases rapidly thereafter (Richards, 1981; Richards and Bliss, 1986). Vigorous saplings 1.2 m tall are generally around 30 to 35 years of age. Dominant trees attain small to moderate dimensions, depending upon site conditions, but rare individuals have reached 200 cm in diameter and 30 m in height (Arno, 1990). Leaders grow as short shoots with short internodes in most years, and the annual height increment is substantial in only about 1 in 4 years (Worrall, 1995). Subalpine larch only rarely grows in a shrubby or krummholz form. Although the common life span for dominant trees is 4 to 5 centuries, many individuals attain 700 years, and the oldest trees are estimated to live about 1,000 years (Arno, 1970). Even though subalpine larch frequently forms single-species stands, it can also grow below its usual elevation range in association with subalpine fir, Engelmann spruce and whitebark pine.

6.4.2. Western larch

Western larch is one of the most shade-intolerant conifers in the Pacific Northwest (Klinka *et al*, 2000). Consequently, it grows in even-aged stands. Its primary associates are usually the same age as the larch, but often appear younger due to slower growth. As western larch stands mature, shade-tolerant associates continue to establish and form younger canopy strata (Schmidt and Shearer, 1990). Due to its longevity (often >500 years), western larch is often a persistent seral species, particularly on low-productivity sites.

Fire is essential to the maintenance of western larch in natural populations. High-intensity fires thin stands, reduce fuels, and prepare seedbeds that promote establishment of shade-intolerant conifers, particularly the western larch. Without fire, shade-tolerant associates eventually replace the larch (Schmidt and Shearer, 1990). Even-aged silvicultural systems best fit the ecological requirements of western larch. These systems provide an adequate seed source and the microsite conditions needed for establishment. Site preparation of prescribed burning or scarification to reduce the duff layers and vegetative competition is often necessary for its successful regeneration (Burns, 1983).

6.4.3. Tamarack

Although young seedlings can tolerate some shade, tamarack is very shade-intolerant, and must become dominant to survive, especially in mixed stands (Johnston, 1990). Tamarack is considered a pioneer tree, especially in wetlands. It is generally the first tree to invade filled-lake bogs in primary succession (Fowells, 1965). Tamarack can reproduce successfully on burns (Rowe and Scotter, 1973), so immediately after fire it is one of the early seral tree species on most sites in the boreal forest. Because of its intolerance to shade, tamarack is eventually replaced by black spruce in ombotrophic wetlands, and by northern white-cedar (*Chamaecyparis thyoides*), balsam fir (*Abies balsamea*), and swamp hardwoods in minerotrophic wetlands (Fowells, 1965). Recurring outbreaks of larch sawfly (*Pristiphora erichsonii*) throughout the range of tamarack have probably speeded succession to black spruce or other associates (Eyre, 1980).

In full-light conditions, tamarack is one of the fastest growing conifers on upland sites of the North American boreal forest. On peatlands, tamarack grows faster than any other native conifer. It can reach heights of 24 to 27 m and diameters of 30 to 38 cm. Maximum age is generally 150 to 180 years, but trees 230 to 240 years old are not rare and one individual was documented to have lived to 335 years (Eyre, 1980; Johnston, 1990).

6.5. Damaging agents

6.5.1. Subalpine larch

Violent winds often damage subalpine larch crowns in conjunction with loads of clinging ice or wet snow. If advanced heart rot has so weakened the bole, high winds can break off the trunk causing tree death. The quinine fungus *Fomitopsis officinalis*, which causes brown trunk rot, produces the only conks commonly found on living trunks. Subalpine larch typically suffers little damage from insects or other diseases. Isolated witches' brooms, with dense branch-clusters and branch swelling, are widely scattered in subalpine larch stands, and have been attributed to parasitic dwarf mistletoe (*Arceuthobium laricis*), fungal infection, or perhaps even a genetic abnormality (Arno, 1990).

Avalanches are an important source of damage in high elevation, steep terrain, but the flexibility of younger trees, the strength of trunks larger trees and lack of foliage make subalpine larch less vulnerable to damage than evergreen subalpine trees. Poles up to 13 cm thick and 6 m tall can survive flattening by snowslides, only to straighten again in summer (Arno and Habeck, 1972). Because of their avalanche tolerance, subalpine larch often occupies avalanche paths, forming a disturbance-maintained "disclimax" (Arno, 1990).

6.5.2. Western larch

Mature western larch is a highly fire-resistant tree because of its thick bark, high and open branching habit, and the low flammability of its foliage. Seedlings and saplings have little resistance to fire, but poles are moderately resistant (Fowells, 1965). The species is highly resistant to windthrow because of its extensive root system (Schmidt *et al*, 1976). Immature trees are very sensitive to noxious fumes, but due to their deciduous foliage, the larches accumulate fewer harmful deposits than evergreen conifers (Carlson and Dewey, 1971).

Dwarf mistletoe (*Arceuthobium laricis*) is the most damaging pathological agent affecting western larch. It can infect seedlings as young as 3 to 7 years old, and infection continues throughout the life of the tree (Wicker and Shaw, 1967). Mistletoe decreases height and diameter growth, kills tree tops, reduces seed viability, creates conditions suitable for other diseases and insects, and causes burls, brashness, and some mortality. Infected residual trees left after harvesting or fire can promptly infect other trees, as mistletoe seed can be ejected as far as 14 m (Smith, 1966). The other important disease found in western larch are needle cast caused by *Hypodermella laricis*, quinine fungus caused by *Fomitopsis officinalis*, and rot caused by *Phellinus pini*. The two most serious insect pests are larch casebearer (*Coleophora laricella*) and western spruce budworm (*Choristoneura occidentalis*) (Schmidt *et al*, 1976).

6.5.3. Tamarack

Tamarack has thin bark and as a result is highly susceptible to fire damage. Its roots are shallow on peatlands, resulting in mortality from all but very light fires. In the boreal forest, tamarack stands have a high surface-fire hazard in the spring but a low crown-fire hazard in pure stands (Rowe and Scotter, 1973). Tamarack stands are often killed by abnormally high water levels. High water levels also result in dieback and the development of adventitious roots and shoots (Denyer and Riley, 1964). Strong winds can uproot large trees growing in swamps or other wet sites where rooting is most shallow. Tamarack is fairly windfirm compared with its common associate black spruce (Johnston, 1990).

The most destructive insect pest of tamarack is the larch sawfly (*Pristiphora erichsonii*). Periodic epidemics of this defoliator occur across Canada and the northern United States. Another serious defoliator of tamarack is the larch casebearer (*Coleophora laricella*). Severe outbreaks have caused extensive mortality of trees of all ages (Johnston, 1990).

Tamarack is host to many pathogens, but none cause sufficient disease to have substantial economic impact. Tamarack is essentially free of stem diseases. The parasitic plant eastern dwarf mistletoe (*Arceuthobium pusillum*) is occasionally found where the tree is growing in mixtures of infected black spruce, but the resulting witches' brooms are small (Hepting, 1971). Several root- and butt-rot fungi reported on tamarack include *Armillaria ostoyae*, *Scytinostroma galactinum*, *Phaeolus schweinitzii*, and *Inonotus tomentosus*. The principal heart-rot fungi are *Fomitopsis officinalis* and *Phellinus pini* (Hepting, 1971). Tamarack is very susceptible to the European larch canker (*Lachnellula willkommii*), but this exotic disease is only a problem in maritime areas in eastern Canada and Maine (USA) (Magasi, 1983).

7. Forestry practices

7.1. Deployment of reforestation materials

7.1.1 Subalpine larch

Subalpine larch is a non-timber species and its wood has essentially no commercial value. As no timber harvesting has been done, even in the best-developed stands, nor does any seem likely on the upper subalpine sites in the future, and considering cultivation difficulties, there has not been any need for seedling production for the species. On an experimental basis, seedlings have been successfully grown and outplanted (Arno *et al*, 1995).

7.1.2. Western larch

Western larch is the fastest-growing and largest of the larches in Pacific Northwest forests, and the most important native timber species of the genus. The presence of this species in pure as well as mixed-species stands is valuable where multiple resource use is the major management objective. Depending on the site and management objective, clearcutting, patch-cutting, strip-shelterwood, and seed-tree systems are suitable for growing western larch (Burns, 1983). Considering its shade intolerance and fast growth rate, western larch is a desirable component in mixed-species stands including shade-intolerant trees, such as ponderosa pine or lodgepole pine (*P. contorta* subsp. *latifolia*), or shade-tolerant trees, such as western redcedar or western hemlock. Propagation by seed is the only contemporary method for regenerating western larch. Techniques for collection, processing, testing, and storage of seed are given in Schopmeyer (1974). Small, infrequent cone crops have resulted in intermittent seed shortages for artificial regeneration (Schmidt and Shearer, 1990). Natural regeneration (where applicable) or planting, using a containerised stock, is used for establishment. Burning or scarification is required for successful natural regeneration of western larch (Schmidt *et al*, 1976; Shearer, 1980; DeByle, 1981).

Genetically improved seed is produced in seed orchards where selected parents are grafted onto conspecific rootstock. In British Columbia, two first-generation seed orchards produce approximately 50% of the total seed currently needed for reforestation for western larch (Forest Genetics Council of British Columbia, 2001). In approximately 5 years, these orchards should provide all of the seed for reforestation in the two major seed planning zones for this species.

7.1.3. Tamarack

Tamarack is a small to medium-sised tree that is a timber species primarily in eastern North America. Its pronounced shade intolerance requires even-aged silvicultural systems, with adaptation of clearcutting or seed-tree cutting. Regeneration often requires some type of site preparation, such as slash disposal or herbicide spraying (Johnston, 1975). Techniques for collection, processing, testing, and storage of seed are given in Schopmeyer (1974). Tamarack stands can be established either through natural regeneration or through planting, of containerised seedlings. Seedling root:shoot ratio must be balanced, seedlings dormant, and a wide spacing used for successful plantation establishment (Johnston, 1990). All the seed currently used for planting in eastern Canada's Maritime region comes from first-generation grafted seed orchards (Fowler *et al*, 1995).

7.2 Provenance transfer

7.2.1. Subalpine larch

Due to the lack of planting of this species, as well as the difficulties in obtaining viable seed, no provenance trials have been established to provide provenance transfer guidelines. In the absence of additional information, for restoration purposes the use of locally collected seed would be advisable. In British Columbia, seed transfer rules for species lacking provenance trial data, including subalpine larch, are 1° latitude S, 2° latitude N, 3° longitude W, 2° longitude E, and 300 m up or 200 m down in elevation from the collection location, based on provenance trial results for other tree species (British Columbia Ministry of Forests, 1995).

7.2.2. Western larch

Local seed zones and breeding programs provide locally adapted seed. In British Columbia, under the Forest Practices Code, western larch seed collected from natural stands can be used for reforestation on sites up to 1° latitude S, 2° latitude N, 3° longitude W, 2° longitude E, and 300 m up or 200 m down in elevation (British Columbia Ministry of Forests, 1995). In southern British Columbia, there are two local breeding zones for western larch, each with one seed orchard providing improved seed for reforestation in that zone (Forest Genetics Council of British Columbia, 2001). Based on seedling genecological studies, Rehfeldt (1995a, b) concluded that seed should be used within ±225 m of where it is collected. Provenance transfer may offer some gains in growth, but further research on risk of maladaptation is needed to test this hypothesis (Rehfeldt, 1995b).

7.2.3. Tamarack

Based on the limited data available, tamarack shows similar patterns of variation to other widespread conifers, and local seed zones and breeding programs provide locally adapted seed. Local provenances or those from slightly south of local typically appear to be among the best (Jeffers, 1975; Riemenschneider and Jeffers, 1980). In Ontario, seed for all species is managed within 38 seed zones based on a climate model for the province (D. Joyce, Ontario Ministry of Natural Resources, pers. comm.). In British Columbia, seed transfer limits are the same for tamarack as subalpine larch (see above). In Alberta, transfer of seed for all conifers including tamarack is limited to 80 km and 150 m in elevation (N. Dhir, Alberta Forest Service, pers. comm.).

7.3. Breeding programmes

7.3.1. Subalpine larch

There are no breeding programs for subalpine larch, nor are there likely to be, based on the lack of harvesting and artificial reforestation for this species.

7.3.2. Western larch

There are active breeding programs for western larch in both British Columbia and the Inland Northwest region of the United States. Based on the substantial variation within seed and breeding zones for polygenic traits (Joyce, 1985; Fins and Rust, 1989; Rehfeldt, 1992; Zhang and Fins, 1993), potential gains of up to 20% could be achieved in the first generation of selection (Rehfeldt, 1995b). The British Columbia Ministry of Forests breeding program has approximately 600 plus-trees in progeny tests, and grafted seed orchards will be rogued based on the results from these tests, primarily evaluating for growth rate, with wood density as a secondary trait (Forest Genetics Council of British Columbia, 2001). A similar breeding program is underway by the Inland Empire Tree Improvement Cooperative, based at the University of Idaho.

7.3.3. Tamarack

There are active breeding programs for tamarack in Quebec and the Maritime provinces in Canada, although planting is not extensive (Fowler *et al*, 1995). These breeding programs are approaching the second generation. Parent trees are evaluated for general combining ability based on the performance of progeny from polycrosses. Grafted clonal seed orchards are rogued based on the results of these progeny trials. Ontario no longer has an active breeding program for tamarack (D. Joyce, Ontario Ministry of Natural Resources, pers. comm.). In the Maritime region, there are approximately 300 plustrees under evaluation in progeny tests (Fowler *et al*, 1995). First generation clonal seed orchards containing grafted ramets of these parents will be rogued based on the results of these tests for growth and form traits. High clonal heritabilities for economic traits in this species indicate an opportunity to exploit non-additive genetic variation in future breeding programs (Fowler *et al*, 1995).

7.4. Conservation of genetic resources

7.4.1. Subalpine larch

As subalpine larch is neither harvested nor planted, and occurs in high-elevation ecosystems that are relatively well represented in natural parks, wilderness areas, and other conservation areas, gene conservation for this species is accomplished through *in situ* protection in established reserves. In British Columbia, subalpine larch was found to be well protected in existing reserves (Lester and Yanchuk, 1996). The greatest threat to subalpine larch and other high-elevation species in terms of genetic resources is climate change, as the rate of climate change may exceed the maximum migration rate of species, and high-elevation species exist in discontinuous ecosystems (Aitken, 2000).

7.4.2. Western larch

Western larch genetic resources are being maintained both *in situ* in established protected areas such as natural parks and ecological reserves, and *ex situ* in seed and clone banks, breeding arboreta and genetic field tests. A survey of the degree of protection of conifer genetic resources in British Columbia in 1996 concluded that western larch was adequately protected at that time (Lester and Yanchuk, 1996), and reserves have nearly doubled in area since then. Rehfeldt (1995b) suggested that while the controlled, local collection and deployment of seed and localised breeding programs for this species protect the natural genetic structure and diversity, it may be prudent to establish gene pool reserves for western larch in some areas.

7.4.3. Tamarack

Given the broad distribution of tamarack, its presence in many unharvested ecosystems such as bogs, and the use of natural regeneration or local provenances as seed sources for planting, the genetic resources of tamarack likely are being well conserved. A thorough gap-analysis only of the *in situ* protected status of this species for the small portion of its range within British Columbia has been published (Lester and Yanchuk, 1996).

8. Summary

***Subalpine larch**:*

The primary values of subalpine larch are for watershed protection, wildlife habitat, outdoor recreation, and aesthetics. The ability to occupy steep north slopes and snow chutes where other trees can scarcely grow suggests that it helps to stabilise snow loads and reduce the severity of avalanches. The unusual hardiness of this species and its adaptations for survival on environmentally extreme sites make it of special interest for scientific study, and reclamation plantings on subalpine sites. There is a tremendous lack of genetic information on this species, and genetic management is limited to in situ gene conservation. The current degree of protection of genetic resources of subalpine larch in natural parks is adequate. Climate change is the primary threat to this high-elevation species.

***Western larch**:*

Western larch, a species with relatively narrow ecological amplitude, is one of the important and valuable timber crop species in western North America. Across its range it functions predominantly as a long-lived seral and fire-adapted species. Because of its rapid growth rate, western larch produces a higher volume of wood sooner than many of its associates. It is an exposure-requiring species that is easy to regenerate. Although growing typically in even-aged stands, it may associate even in early stages of secondary succession with several shade-tolerant tree species forming stratified uneven-age stands, and be a prominent component in many ecosystems in several climatic zones in the Pacific Northwest. Western larch is not only an important timber species but also a major tree cover in many scenic and recreational areas and critical watersheds. The seasonal change in hue of foliage from light green in the spring and summer, to gold in the fall, enhances the beauty of these montane forests. The genetic base of this species is well-protected in existing natural parks and reserves over most of its range. Despite available technologies for somatic embryogenesis and genetic transformation, and its rapid growth rate and high wood quality, genetic improvement is limited to local selective breeding due to the relatively small numbers of seedlings planted annually, primarily on public lands within its native range. Genetic transformation and tissue culture methods developed for other Larix species could likely be adapted for western larch.

***Tamarack**:*

Tamarack is a major component of the North American boreal forest, with a very wide ecological amplitude. Across its extensive range, tamarack functions predominantly as a pioneer and early seral, relatively short-lived, and fire-adapted species. Local, small breeding programs have been established and will likely continue for this species in the eastern portion of the range. While somatic embryogenesis and genetic transformation technologies are available, it is unlikely these or other biotechnological methods will be applied on a large scale due to the slow growth rates, long rotations and relatively few seedlings planted annually for this species. Genetic transformation and somatic embryogenesis techniques have been developed for tamarack.

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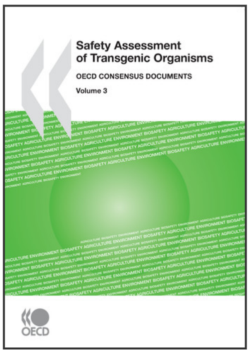

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