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JOINT MEETING OF THE CHEMICALS COMMITTEE AND
THE WORKING PARTY ON CHEMICALS, PESTICIDES AND BIOTECHNOLOGY**

Series on the Harmonisation of Regulatory Oversight in Biotechnology No. 38

**CONSENSUS DOCUMENT ON THE BIOLOGY OF WESTERN WHITE PINE
(*Pinus monticola* Dougl. ex D. Don)**

This document replaces ENV/JM/MONO(2006)16 with the identical title that was published in 2006. This latest text includes some revisions.

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OECD Environment, Health and Safety Publications

Series on Harmonisation of Regulatory Oversight in Biotechnology

No. 38

Consensus Document on the Biology of Western White Pine (*Pinus monticola* Dougl. ex D. Don)

Environment Directorate

Organisation for Economic Co-operation and Development

Paris 2008

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 western white pine (*Pinus monticola* Dougl. ex D. Don). 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, 25 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.

SECTION I. TAXONOMY

1. The largest genus in the family Pinaceae, *Pinus* L., which consists of about 110 pine species, occurs naturally through much of the Northern Hemisphere, from the far north to the cooler montane tropics (Peterson, 1980; Richardson, 1998). Two subgenera are usually recognised: hard pines (generally with much resin, wood close-grained, leaf fascicle sheath persistent, two fibrovascular bundles per needle — the diploxylon pines); and soft, or white pines (generally little resin, wood coarse-grained, sheath sheds early, one fibrovascular bundle in a needle — the haploxylon pines). These subgenera are called respectively subgenus *Pinus* and subgenus *Strobis* (Little and Critchfield, 1969; Price *et al.*, 1998; Gernandt *et al.*, 2005). Occasionally, one to about half the species (20 spp.) in subgenus *Strobis* have been classified instead in a variable subgenus *Ducampopinus*.

2. Western white pine (*Pinus monticola* Dougl. ex D. Don) belongs to subgenus *Strobis* (Syring *et al.*, 2007). *Pinus monticola* was classified by Critchfield and Little (1966) as one of 14 white pines in section *Strobis*, subsection *Strobi*, now call section *Quinquefoliae* and subsection *Strobis*, respectively. Earlier classifications have varied in the number of species assigned to subsection *Strobis*, but *P. monticola* has consistently been grouped with the New World species *P. ayacahuite*, *P. lambertiana*, and *P. strobus* and the Old World species *P. wallichiana* (synonym *P. griffithii*) and *P. peuce* (Critchfield, 1986).

3. A molecular phylogeny of the genus *Pinus*, based on the nuclear ribosomal DNA internal transcribed spacer (nrITS), did not support separation of subsection *Strobis* from either subsection *Cembrae* or subsection *Krempfianae* (Liston *et al.*, 1999). While this study did not include *P. monticola*, it included close relatives such as *P. strobus*. Recent research based on chloroplast DNA sequences recognises an enlarged subsection *Strobis* (*sensu lato*) that absorbs subsection *Cembrae*, while retaining the Asian subsection *Krempfianae* (Gernandt *et al.*, 2005). The lack of clear differentiation between subsections *Cembrae* and *Strobis* (*sensu stricto*) is also evident in the ability of *P. monticola* to hybridise with some, but not all species in subsection *Strobis*, and some, but not all species in subsection *Cembrae* (see Section V below). These two subsections had been separated primarily by the nearly wingless seeds and their retention in cones in subsection *Cembrae*, but these bird-dispersal traits appear to have evolved several times rather than once (Critchfield, 1986).

4. No subspecies or varieties are recognized for western white pine. Nonetheless, populations in the Sierra Nevada, Klamath and Warner mountains in the southern portion of its range have been observed to differ substantially from those farther north (Steinhoff *et al.*, 1983).

SECTION II. NATURAL DISTRIBUTION

5. Western white pine is a commonly occurring Western North American species. It is distributed mainly in the central and southern portion of the Cordilleran region and in the central portion of the Pacific region (Klinka *et al.*, 2000) (Figure 1). Western white pine grows along the west coast from latitude 36°N in southern Tulare County, California, USA to 51°30' N near Bute Inlet in southern British Columbia, Canada.

6. Along the west coast of North America the species grows on Vancouver Island, on the adjacent mainland, southward through Washington and Oregon, and in the Cascade Mountains (Critchfield and Little, 1966). It is also found in the Siskiyou Mountains of southern Oregon and northern California, in the Sierra Nevada of California, and near Lake Tahoe, Nevada.

7. In the interior, western white pine grows from 52°30' N near Quesnel, British Columbia, southward through the Selkirk Mountains of eastern Washington and northern Idaho, and into the Bitterroot Mountains of western Montana. Its southernmost interior limit is in the Blue Mountains of northeastern Oregon (latitude 44°14' N). Isolated populations are found as far east as Glacier National Park, Montana. It attains its greatest size in the interior portion of the range, which includes northern Idaho and the adjacent sections of Montana, Washington, and British Columbia (Wellner, 1965).

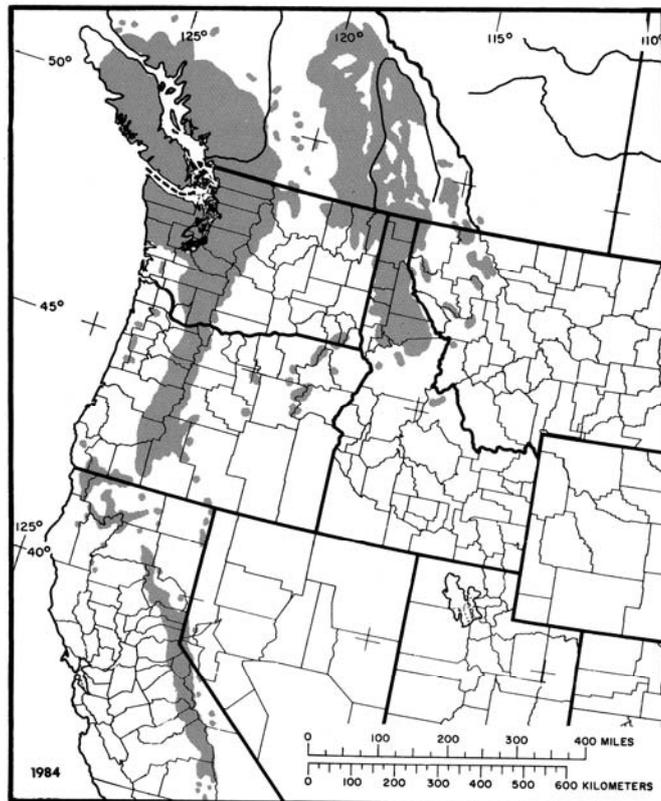


Figure 1. The native range of western white pine (from Graham, 1990)

SECTION III. REPRODUCTIVE BIOLOGY

A. Reproductive development

8. Western white pine is monoecious. Reproductive buds differentiate during July and August; then buds open and strobili appear in June of the following year. Male strobili are about 10 cm long, borne in clusters of 15 to 25 on branches in the middle of the crown. Pollen is shed starting in late June, and can continue until mid-July, but usually averages 8 days (Wellner, 1965). Female strobili are borne on stalks in the upper crown. The erect seed cones are 1.5 cm to 4.0 cm long at the time of pollination, and grow to 2.5 cm to 5.0 cm by the end of the first growing season.

9. After wind dispersal, the saccate pollen grains initially adhere to lipid microdrops of the micropylar arms of female strobili. A pollination drop is then secreted from the ovule, as in other pines, and it accumulates pollen. The pollination drop can be enhanced through artificial misting. Pollen lands on the drop and is withdrawn into the micropyle (Owens *et al.*, 2001). After pollination, germination occurs and pollen tubes penetrate approximately one third of the way through the nucellus. The generative cell and tube nucleus move into the pollen tube, and the megagametophyte initiates free division. The cones and pollen tubes then enter a dormant state around mid-July. Growth does not resume until the following April, when pollen tubes complete growth, the generative cell divides mitotically to produce two sperm nuclei, and fertilisation occurs by the end of May. Each ovule has three to five archegonia (Owens and Bruns, 2000). Multiple fertilisation events can produce multiple proembryos, but mature seeds typically contain only one embryo.

10. The timing of anthesis can vary up to 3 weeks, and is controlled by temperature during the previous weeks. Anthesis is delayed about 5 days per 300 m increase in elevation, and by about 11 days per degree Celsius below normal temperatures for May and June. In northern Idaho, good cone crops occur every 3 to 4 years (Wellner, 1965). Warm, dry stress periods, during the early summer 2 years before strobili emerge favour the differentiation of reproductive buds. In contrast, stresses in the late summer when reproductive buds are forming or during the period of emergence depresses production of reproductive buds.

B. Mating system and gene flow

11. Western white pine is a predominantly outcrossing species, typical of most conifers. Single and multi-locus estimates of outcrossing over 3 years were all over 0.92 (El-Kassaby *et al.*, 1993). Relatively high rates of inbreeding depression, polyembryony and spatial separation of male and female strobili all likely play a role in reducing effective self-pollination, although no phenological barriers to selfing appear to exist (Bingham *et al.*, 1972).

12. The strong differentiation between populations in the Sierra Nevada of California and the mountains of southern Oregon and those in the remainder of the range indicates little gene flow occurs between these regions (Steinhoff *et al.*, 1983). The lack of strong differentiation among central and northern populations might suggest high levels of gene flow, but may just reflect a common origin of these populations from a single Pleistocene refugium (Critchfield, 1984).

C. Seed production

13. Cones of western white pine become mature during August and September of the second year after reproductive buds differentiate. Ripe cones range from yellowish- to reddish-brown (Krugman and Jenkinson, 1974). Mature cones are usually 20 to 25 cm long, although they can vary from 5 to 36 cm (Graham, 1990).

14. Trees as young as 7 years of age can produce seed cones, and trees become more productive with age. Cone production does not become frequent and abundant until trees are about 70 years. Seed production increases with age and size until trees are about 50 cm in diameter. After that, seed production depends on individual tree vigour, crown shape, and genetics (Wellner, 1965; Owens and Fernando, 2007).

15. Individual cones can contain more than 300 seeds, but averaged 226 in an 18-year study (Bingham and Rehfeldt, 1970). Western white pine seeds are relatively large for a temperate conifer, averaging 59,000 seeds per kg and ranging from 30,900 to 70,500 seeds per kg (Krugman and Jenkinson, 1974). The seed rain per hectare can be high but variable. In northern Idaho, stand-level seed production varied from 41,000 to 457,000 seeds per ha (Graham, 1990).

16. Seeds are released by the flexing of cone scales from early fall through winter, with 15% shed before September, 70% shed during September and October, and 15% shed during the late fall and winter. The winged seeds are usually dispersed by wind, but squirrels, mice, and various birds also transport seed. Most seeds fall within 120 m of the seed parent tree, but some have been known to travel over 800 m (Wellner, 1965).

17. Western white pine seeds can remain viable for a few years in the forest floor. Seeds have shown 40% viability after one winter, 25% viability after two winters, and less than 1% after 3 or 4 years in the forest floor (Graham, 1990). When properly dried and cold stored, western white pine seeds can remain viable for at least 20 years (Krugman and Jenkinson, 1974).

18. A number of cone and seed insects can cause partial to almost complete failure of cone crops in years with poor or moderate crops. Substantial seed losses result from cone beetles (*Conophthorus monticolae* and *C. labertianae*) and cone moths (*Dioryctria abietivorella* and *Eucosma rescissoriana*) (Furniss and Carolin, 1977). Western white pine seeds are also eaten by both red squirrels (*Tamiasciurus hudsonicus*) and deer mice (*Peromyscus maniculatus*).

D. Natural regeneration

19. Both fresh and stored seed require 30 to 120 days of cold stratification at temperatures of 1° to 5°C to break dormancy and obtain good germination rates (Krugman and Jenkinson, 1974). Seed dormancy appears to be controlled by the seed coat or nucellus as well as embryo or gametophyte physiology (Hoff, 1986a). Germination is epigeal, as in all pines. There is a strong genetic component to seed germination (Graham, 1990). The nucellus and seed coat may limit water entry or gas exchange (Dumroese, 2000). Clipping of a portion of the seed coat and nucellus can increase germination rate or reduce the stratification requirement (Hoff, 1986a).

20. The seeds of western white pine usually germinate in the spring when soil is wet from melting snow. Exposed mineral soil is a better seedbed than organic matter even though the forest floor may contain many more stored seeds (Graham, 1990). Germination starts in April at lower elevations, and can continue on exposed sites until July and on protected sites until August (Graham, 1990). Germination begins and ends much earlier in full sunlight than in shade. Soil temperature appears to control the initiation of germination, and dry mineral or organic soil can inhibit germination (Wellner, 1965).

21. During the first growing season, seedling mortality is high due primarily due to disease, but insects, rodents, and birds can also cause mortality. *Fusarium*, the cause of a damping-off disease, and *Neopeckia coulteri*, a snow mold, are major agents of mortality (Hepting, 1971). *Rhizina undulate* can kill seedlings up to 5 years old. Abiotic stresses cause most seedling mortality late in the first growing season, primarily to temperature and drought. For the most part, western white pine seedlings have low drought tolerance (Minore, 1979). High surface temperatures result in seedling mortality on exposed sites, and drought is sometimes problematic under shady conditions where root penetration is slow, and therefore inadequate to capture adequate soil moisture.

22. On severe sites, partial shade promotes seedling establishment while on northern aspects and more sheltered sites, full sun is preferable. Due to its relative shade intolerance, western white pine grows best in full light on all sites once established (Wellner, 1965).

23. Early growth of western white pine seedlings, both above and below ground, is usually moderate. In the first summer, the primary root grows from 5 to 50 cm, depending on light, nutrients and moisture. Growth in height is much less than roots, with seedlings averaging 3 to 5 cm by the end of the first growing season. In northern Idaho, open-grown western white pine seedlings reach a height of about 1.4 m in about 8 years (Graham, 1990).

24. In northern Idaho, western white pine initiates both height and diameter growth in early May. In British Columbia, shoot elongation usually ends by early August and buds are usually set by mid-August (Schmidt and Lotan, 1980).

25. Western white pine is usually managed under even-aged silvicultural systems (Burns, 1983). Clearcutting can be followed by natural regeneration, planting of seedlings, or a combination of both. Although success of natural regeneration is high, the advantage of planting is in providing an excellent opportunity for planting of genetically improved, rust-resistant stock and initial stocking control (Fins *et al.*, 2001). Successful natural regeneration requires adequate seed source, appropriate seedbed, and suitable microsites.

E. Vegetative reproduction

26. Western white pine does not layer or sprout naturally. Stem cuttings from trees more than 4 to 5 years old root with poor success (Bingham *et al.*, 1972). Auxin promotes rooting of stem cuttings, and this effect can be further enhanced with sucrose. Needle fascicles from 2-year-old seedlings have produced roots and some have produced shoots successfully (Graham, 1990) but fascicles lose the ability to root with maturation of seedling donors (Andrews, 1980).

27. Western white pine grafts relatively easily with scions from trees of all ages collected from all parts of the crown. Early spring grafting before flushing has the highest success rate. The majority of grafts are compatible, although some incompatibility has been reported (Hoff, 1977). Grafting is generally more successfully when conducted under greenhouse conditions than in the field. Interspecific grafting has been accomplished on other five-needle pine rootstocks, such as eastern white pine (*Pinus strobus*), sugar pine (*P. lambertiana*), and blue pine (*P. wallichiana*) (Bingham *et al.*, 1972).

28. Western white pine has been cloned through tissue culture, both from bud slice explants and via somatic embryogenesis. Bud explants have resulted in a relatively low multiplication rate due to the production of relatively few shoots per explant (Lapp *et al.*, 1996). Somatic embryogenesis holds more promise. While relatively few lines that are initiated from single embryos become embryogenic, methods have been developed that yielded at least one successful line per family. The multiplication rate for the successful lines will be large (Percy *et al.*, 2000).

SECTION IV. GENETICS

A. Cytology

29. Like other members of the genus *Pinus*, the haploid number of chromosomes is 12 in western white pine (Saylor and Smith, 1966). Chloroplasts are inherited predominantly paternally, while mitochondria are primarily inherited maternally, although some biparental inheritance of organelles can occur (White, 1990; Owens and Bruns, 2000). At the time of fertilisation, maternal plastids are excluded from the neocyttoplasm but maternal mitochondria remain. Paternal chloroplasts and a small number of paternal mitochondria are released into the egg from the pollen tube with cytoplasm from the tube cell and generative cell. Maternal mitochondria migrate to and aggregate in the perinuclear zone at the time of fertilisation (Bruns and Owens, 2000).

B. Genetic variation

B.1 Population-level variability

30. Populations of western white pine from the Sierra Nevada, southern Cascade and Warner Mountains differ from populations farther north in morphology, growth rate and allozyme frequencies. Variation among populations within these groups for molecular markers is typical for conifers, but surprisingly low for quantitative traits. Genetic distances and G_{st} values among populations for allozymes are relatively small among populations and regions except for those populations in southern Oregon and California (Steinhoff *et al.* 1983). Genetic distances among populations excluding those in southern Oregon and California were all less than 0.025, whereas the genetic distance between southern and northern populations was 0.075. A subsequent principal component analysis of these data supported the lack of genetic differentiation among regions for all but the southern populations (Guries, 1984), as does variation in terpene composition (Zavarin *et al.*, 1990). The lack of strong differentiation among more northern populations for genetic markers may support the hypothesis that this species recolonised the northern portion of its current range from a single glacial refugium in southern Oregon during the last glacial period (Critchfield, 1984).

31. While the relatively low levels of variation among northern populations for selectively near-neutral genetic markers may not be surprising given the glacial history of this species, the lack of differentiation for quantitative, adaptive traits including cold hardiness, growth rate and phenology is unexpected for a widespread conifer. The high levels of within-population variation argue against the lack of among-population variation over most of the range generated by a demographic event, such as a bottleneck, resulting in a lack of genetic variation to allow population differentiation. Numerous studies have found little variation associated with provenance (Rehfeldt, 1979; Steinhoff, 1979a, 1979b; Rehfeldt *et al.*, 1984; Campbell and Sugano, 1989; Chuine *et al.*, 2006). Trees originating from environments as different as northern Idaho and Vancouver Island or the Olympic Peninsula show similar growth and survival in reciprocal transplant studies and other genetic tests (Steinhoff *et al.*, 1983). Populations from the coastal and interior portions of the range differ only slightly for cold hardiness and growth, and populations within these regions do not differ substantially for these traits (Thomas and Lester, 1992). The late initiation of primary growth in spring, often not until June, and the very rapid predetermined elongation after initiation may alleviate the need for adaptation of populations for traits relating to phenology and cold hardiness to local climatic factors as is typical of conifers such as Douglas-fir (*Pseudotsuga menziesii*) and lodgepole pine (*Pinus contorta*) (Chuine *et al.*, 2006).

B.2 Variation among individuals within populations

32. While variation among populations of western white pine is surprisingly low, within-population variation is high for both genetic markers and for quantitative traits. Within-population variation for allozymes revealed an average of 65% polymorphic loci, 1.7 alleles per locus, and expected heterozygosity of 0.18 within populations (Steinhoff *et al.*, 1983).

33. Within-population genetic variation is high for polygenic traits as well. Heritabilities have been estimated for a variety of traits including white pine blister rust resistance and growth rate. Heritability estimates for resistance based on the bark reaction mechanism are relatively low, with individual heritability (h_i^2) estimated as 0.04, and family heritability (h_f^2) as 0.33 (Hoff, 1986b). The resistance mechanism associated with a low number of needle lesions is under stronger genetic control, with h_i^2 estimated as 0.37 in Idaho (Hoff, 1986b) and as 0.77 in British Columbia (Meagher and Hunt, 1996). Individual heritabilities for growth traits for seedlings growing in raised nursery beds in Oregon were also moderate, ranging from 0.31 to 0.48 for height, and 0.44 to 0.46 for diameter (Campbell and Sugano, 1989). Sapling-aged trees in field tests in British Columbia had an individual heritability of 0.36 for height, while 25-year-old trees in Idaho had much lower estimates for height and diameter of 0.11 and 0.14 respectively (Rehfeldt *et al.*, 1991; Bower and Yeh, 1988).

C. Inbreeding depression and genetic load

34. Like most conifers, western white pine has a fairly high genetic load. Self-pollination results in an average of 47 seeds per cone, while control-pollinated outcrossing averages 88 seeds per cone (Bingham and Rehfeldt, 1970). Western white pine exhibits relatively strong inbreeding depression for growth traits. Progeny resulting from self-pollination grow at 60 to 70% of the rate of progeny of unrelated parents (Bingham *et al.*, 1972).

SECTION V. HYBRIDIZATION

35. *Pinus monticola* has been successfully hybridised experimentally with four species in the subsection *Strobis* (as narrowly circumscribed by Critchfield and Little, 1966): *P. parviflora*, *P. peuce*, *P. strobis*, and *P. griffithii*. Hybridisation has not been limited to within subsection *Strobis* (*sensu stricto*). Filled seed have been produced in artificial crosses with three species in the sometimes-recognised subsection *Cembrae*: *Pinus albicaulis*, *P. cembra* and *P. korainensis* (Bingham *et al.*, 1972). Seedlings have been grown from *P. monticola* x *P. cembra* and *P. monticola* x *P. korainensis* crosses, but died before the crosses could be verified (Bingham *et al.*, 1972). Hybrids have been verified between *P. monticola* and both *P. flexilis* and *P. strobiformis*, species sometimes classified in subsection *Strobis* and sometimes in subsection *Flexiles* (Critchfield, 1986). Natural hybrids between *P. flexilis* and *P. strobiformis* have been reported where their native ranges overlap (Kral, 1993). Crosses with *P. armandii*, the white pine least susceptible to blister rust and thus a potential source of genes conferring resistance, have failed, as have crosses with *P. parviflora* (Bingham *et al.*, 1972). Crosses to *P. aristata* and *P. balfouriana* in section *Parrya*, subsection *Balfourianae*, have yielded little seed and no seedlings (Bingham *et al.*, 1972). Crosses with *P. lambertiana* as the female parent yielded no seed, but the reciprocal cross did produce seed. However, the seedlings from the latter crosses did not exhibit phenotypes intermediate to the parental species (Critchfield, 1986), and they are no longer considered to have been interspecific hybrids (Fernando *et al.*, 2005).

36. *Pinus monticola* x *P. strobis* seedlings are vigorous, and grow much more rapidly than *P. monticola*, although the relative growth advantage is less for sapling-aged hybrids. Hybrids with *P. griffithii*, *P. flexilis* and *P. strobiformis* have also grown well at Placerville, California (Bingham *et al.*, 1972).

SECTION VI. ECOLOGY

A. Climate

37. Western white pine grows in a variety of wetter climates, both maritime and continental, ranging from subalpine boreal (less frequent) to temperate (frequent) to mesothermal (frequent) (Klinka *et al.*, 2000). There are three major regions within the species range, differing in climate: 1) Vancouver Island and the Cascade and Siskiyou Mountains; 2) the interior portion of the range, comprising northern Idaho, northern Montana, northeastern Washington and southwestern British Columbia; and 3) the Sierra Nevada of California.

38. Vancouver Island, the Cascade Mountains, and the Siskiyou Mountains have cool maritime climates, with wet winters and dry summers. Precipitation varies considerably across this region with elevation and the orientation of the mountain ranges. Latitudinal variation from Oregon through British Columbia is relatively small (Shumway, 1979). Precipitation ranges from 1500 to 2010 mm on Vancouver Island and in the Cascade Mountains to 510 to 1520 mm per year in the Siskiyou Mountains. Deep, heavy snowpacks develop over 600 m in elevation. Temperatures range from a low of -18°C to a maximum of 38°C (Graham, 1990).

39. In the parts of the Sierra Nevada where western white pine grows, mean annual precipitation ranges from 760 to 1500 mm, and most of this falls as snow. The temperature averages -9°C in February and 27°C in July and August, with maximum temperatures near 37°C.

40. Despite being 400 km from the Pacific Ocean, the climate of the interior portion of the range is still under a maritime influence. Annual precipitation is between 710 and 1520 mm, with little of this during the summer. Snowfall averages 262 cm and ranges from 122 cm to 620 cm. Mean annual temperature in the interior ranges from 4°C to 10°C with extremes from -40°C to 40°C (Wellner, 1965).

B. Soils

41. Western white pine, a calciphytic species, tolerates a relatively wide range of soil moisture conditions, ranging from moderately dry to wet, and a somewhat narrower range of soil nutrient conditions, ranging from medium to very rich soils. The most productive growth occurs on fresh to moist, nitrogen-rich soils. Compared to other Pacific Northwest tree species, it does not tolerate water- and nutrient-deficient soils, but can tolerate water-surplus and inundated soils (Krajina, 1969; Klinka *et al.*, 2000).

42. Many young western white pine trees suffer mortality in strongly leached, calcium-poor soils in wet climates. When trees are already showing signs of calcium deficiency, their roots are readily killed by summer drought. Plants experimentally subjected to calcium deficiency frequently wilt, even when water is available. In other cases of calcium deficiency, western white pines die more slowly, from the top down, exhibiting chlorosis and later necrosis (Krajina, 1969).

43. A variety of soils support western white pine along the Pacific Coast. The species grows best on deep, well-aerated soils but is most common on coarse-textured soils. The soils are derived from a variety of parent materials and are generally shallow to moderately deep with medium acidity. Organic matter

content is usually low to intermediate, and textures range from sandy loam to clay loam. The majority of the soils in which western white pine grow are Spodosols.

44. The soils on which western pine grows in the interior portion of the range are also diverse and predominantly Spodosols that have developed from weathered granite, schist, quartzite, argillite, sandstone, and shale. Soil depths range from 25 to over 230 cm. The upper soil layer is often composed of loess or loess-like material (Cooper *et al.*, 1987). In British Columbia, soils have developed from base-rich glacial materials (till, fluvial, or lacustrine deposits) (Wellner, 1965).

45. Western white pine grows from sea level to subalpine elevations, and on a variety of slopes and aspects. It is most common on lower slopes, along creeks, northerly aspects and alluvial terraces (Graham, 1990).

C. Synecology

46. Depending on site and disturbance history, western white pine grows predominantly as a minor (infrequently as a major) species in even-aged, mixed-species stands, and is present in all stages of secondary succession. Occasionally, it is a minor component in transition old-growth stands on calcium-rich soils in cool temperate and cool mesothermal climates. As a moderately shade-tolerant species, it is considered a persistent seral species which attains a dominant position in the stand only following wildfires, using even-aged silviculture systems, or through stand treatments favouring the species (Graham, 1990).

47. Associates of western white pine include *Abies amabilis* (amabilis fir), *A. concolor* (white fir), *A. grandis* (grand fir), *A. lasiocarpa* (subalpine fir), *A. magnifica* (red fir), *A. procera* (noble fir), *Acer macrophyllum* (bigleaf maple), *Alnus rubra* (red alder), *Arbutus menziesii* (Pacific madrone), *Betula papyrifera* (white birch), *Chamaecyparis lawsoniana* (yellow-cedar), *Larix occidentalis* (western larch), *Libocedrus decurrens* (incense cedar), *Picea engelmannii* (Engelmann spruce), *P. sitchensis* (Sitka spruce), *Pinus balfouriana* (foxtail pine), *P. contorta* (lodgepole pine), *P. flexilis* (limber pine), *P. jeffreyi* (Jeffrey pine), *P. lambertiana* (sugar pine), *P. ponderosa* (ponderosa pine), *Pseudotsuga menziesii* (Douglas-fir), *Thuja plicata* (western redcedar), *Tsuga heterophylla* (western hemlock), and *T. mertensiana* (mountain hemlock) (Franklin and Dyrness, 1973; Eyre, 1980; Graham, 1990; Klinka *et al.*, 2000).

48. Western white pine is found in eighteen of the forest cover types of western North America (Eyre, 1980). It is the dominant species in the Western White Pine cover type (Type 215). The western white pine component in this type is usually even-aged with an understory containing multi-aged trees of the more shade-tolerant softwoods; occasionally, a minor component of other shade-intolerant softwoods may also be present in the upper canopy. Western white pine is a common but minor component, along with many other tree species, in seventeen other cover types: Mountain Hemlock (205), Engelmann Spruce–Subalpine Fir (206), Red Fir (207), Interior Douglas-Fir (210), Western Larch (212), Grand Fir (213), Lodgepole Pine (218), Western Hemlock (224), Coastal True Fir–Hemlock (226), Western Red Cedar–Western Hemlock (227), Western Red Cedar (228), Pacific Douglas-Fir (229), Douglas-Fir–Western Hemlock (230), Port-Orford-Cedar (231); Interior Ponderosa Pine (237); Jeffrey Pine (247), and California Mixed Subalpine (256) (Eyre, 1980).

49. The cover and composition of understory vegetation in all these cover types will vary depending on site (climate and soil), associated tree species, stand developmental stage, and stand density. Relative to other tree species, light interception by western white pine is low, thus providing favourable light conditions for the development of diverse understory vegetation.

D. Stand dynamics

50. Western white pine is dependent on periodic wildfires. Rapid growth and longevity have enabled western white pine to persist as a widespread element in Pacific Northwest forests. Without major disturbances such as fire or timber harvesting, western white pine would be replaced over time by more shade-tolerant conifers (Franklin and Dyrness, 1973; Graham, 1990). Trees are generally long-lived, with many individuals living 300 to 400 years, and rarely up to 500 years. Old trees are often more than 180 cm in diameter and 60 m tall (Graham, 1990; Klinka *et al.*, 2000).

51. Western white pine can be naturally regenerated using even-aged silviculture such as seed tree or shelterwood systems. Adequate natural regeneration usually develops within 5 to 10 years of harvest. Without a naturally blister rust-resistant seed source on a site, planting should be used to regenerate the stand after harvest. In shelterwoods, growth will be markedly reduced if the overstory is dense and its removal is delayed (Wellner, 1965).

52. The composition of mixed stands containing western white pine is determined during the first 30 years after regeneration (Graham, 1988; Jain *et al.*, 2004). Young lodgepole pine and western larch can grow considerably faster in height than juvenile western white pine. Lodgepole pine's growth superiority usually disappears by age 50, but western larch can usually maintain a height advantage over western white pine. Grand fir can match western white pine's height growth for the first 30 years, and Douglas-fir has similar height growth. On northerly aspects and in shaded conditions, shade-tolerant western hemlock can also equal the height growth of western white pine (Deitschman and Pfister, 1973).

E. Damaging agents

53. Western white pine has relatively thin bark, moderately flammable foliage and highly flammable cones, making it intermediate in fire resistance among its coniferous associates (Minore, 1979), yet it depends on fire or logging to remove competing conifers. As a result of both fire protection and blister rust infection, the proportion of western white pine regeneration (planted and natural) in northern Idaho, eastern Washington, and western Montana decreased from 44% in 1941 to 5% in 1979 (Graham, 1990). Between 1976 and 1996, approximately 100,000 ha in the Inland Northwest were replanted with blister rust resistant stock from the Idaho breeding programme (Fins *et al.*, 2001).

54. Dormant western white pine is, along with lodgepole pine, one of the more cold-hardy western North American conifers. Needle desiccation can result from winds or sun causing excessive moisture loss during times when soil is frozen or cold. Western white pine is quite tolerant of heat compared to most of its shade-tolerant associates. It is relatively wind-firm but snow breakage is common in pole-stage stands (Graham, 1990).

55. The most serious of the diseases infecting western white pine is white pine blister rust, caused by the pathogen *Cronartium ribicola* (Hepting, 1971). In northern Idaho and adjacent regions, a favourable climate and abundant *Ribes* alternate hosts contribute to heavy losses. However, selection and breeding of naturally rust-resistant parent trees for the planting of rust-resistant nursery stock has been successful. Other stem diseases are of little consequence.

56. A physiological disorder called pole blight can result from extended periods of drought (Graham, 1990). Symptoms include yellow foliage, necrotic resinous areas on the trunk, and top or whole tree death. This disease appears to be caused by root deterioration in soils restricting water uptake (Leaphart, 1958; Leaphart and Stage, 1971)

57. The principal root disease of western white pine is caused by *Armillaria* spp., resulting in dieback of foliage, reductions in growth, resin exudates at the root collar, and black rhizomorphs. *Heterobasidion*

annosum and *Phellinus weirii* also cause some mortality. *Phellinus pini*, *Heterobasidion annosum*, and *Phaeolus schweinitzii* are the most damaging butt rot fungi (Hepting, 1971).

58. The bark beetle *Dendroctonus ponderosae* (mountain pine beetle) is the most significant insect pest of western white pine. Bark beetles kill groups of mostly mature trees weakened by blister rust (Furniss and Carolin, 1977).

SECTION VII. FORESTRY PRACTICES

A. Deployment of reforestation materials

59. Western white pine is grown within most of its range using even-aged silvicultural systems. Clearcut, seed-tree, and shelterwood cuts result in adequate and diverse natural regeneration within 5 to 10 years of harvesting (Burns, 1983; Graham, 1990). If a natural white pine blister rust resistant seed source is not present on the site, planting must be used to regenerate the species. When natural regeneration of clearcuts is used for establishing mixed species stands which include western white pine, it is common to regenerate 11,000 trees per hectare, 1,000 of which are western white pine. Similarly, seed-tree cuts can produce 12,000 trees per hectare, 1,500 of which are western white pine. Shelterwood harvesting produces more trees, but the proportion of western white pine is less than for other silvicultural systems that produce higher light levels for regeneration (Boyd, 1969). Western white pine is not sufficiently shade tolerant for individual-tree selection cuts. Group selection cuts may have limited application.

60. The introduced pathogen *Cronartium ribicola*, which causes white pine blister rust, has driven reforestation decisions for western white pine. Propagation and planting of resistant seedlings is the primary method for regenerating western white pine. Techniques for collection, processing, testing, and storage of seed are given in Krugman and Jenkinson (1974). The planting of either bare-root or container-grown seedlings on appropriate sites can result in excellent survival and growth. Bare-root stock appears to have better survival when planted in spring than in fall, but containerized seedlings have high survival when planted during either season (Graham, 1990).

61. The vast majority of seed used for reforestation of western white pine comes from seed orchards containing grafted ramets from white pine blister rust resistant ortets identified in breeding programs in Oregon, Idaho, and to a lesser extent, British Columbia. The frequency of genotypes that are resistant to this disease is very low in the wild, thus the success of plantations originating from wild seed lots is low (Fins *et al.*, 2001).

62. Western white pine was introduced to Europe after 1825, where it was planted in arboreta and parks. In 1880, it was included into a network of experimental plantations by the German Forest Research Institute, but its use as a timber crop species in western and central Europe is very limited (Hermann, 1987).

B. Provenance transfer

63. Western white pine is unusual for a widespread conifer in that it shows little evidence for local adaptation of populations in seedling genecological studies or field provenance trials (Rehfeldt, 1979; Steinhoff, 1979a; Rehfeldt *et al.*, 1984; Campbell and Sugano, 1989; Thomas and Lester, 1992). While populations from the Sierra Nevada, California, and the Klamath and Warner mountains in southern Oregon clearly differ from populations farther north, there is little variation among the northern populations (Steinhoff *et al.*, 1983). This has permitted large provenance transfers both geographically and elevationally when deploying genetically selected blister rust resistant seed. Although separate seed orchards were initially established for low, mid and high-elevation areas in Idaho, there is little evidence to support management of more than one seed zone (Rehfeldt *et al.*, 1984; Mahalovich and Eramian, 1995). Campbell and Sugano (1989) recommended a total of five seed zones for Washington and Oregon.

64. In British Columbia, there are two seed zones, one for the coastal portion of the range, and one for the interior (Hunt, 1994). Seed imported from seed orchards in Idaho is routinely used for reforestation in southern British Columbia up to 52°N latitude and 1450 m elevation. Seed from wild stand collections in British Columbia in the coastal portion of the range have no provenance transfer limits. Collections in the interior of the province can be transferred a maximum from the collection site to the planting site of 2° latitude to the north, 1° latitude south, 3° longitude east or 2° west, and 700 m up or down in elevation (British Columbia Ministry of Forests, 1995).

C. Breeding programmes

65. The oldest continual breeding program for western white pine was initiated in 1950 in eastern Washington State and Idaho. This program was established as a result of the failed efforts to manage white pine blister rust through the eradication of native *Ribes* spp., the alternate hosts of the disease, and the observation that a small percentage of trees were able to survive in severely infected stands. Phenotypically resistant parents were crossed, and the progeny tested for rust resistance. Resistant seedlings were used to establish a breeding orchard at Moscow, Idaho. These selected trees were then crossed to create the F2 generation for testing and selection. The original breeding orchard was then converted to a seed orchard for seed production for reforestation (Fins *et al.*, 2001). A similar program, modelled after the successful Idaho approach, was initiated at Dorena, Oregon, in 1956 (Sniezko, 1996). A very early breeding program was initiated in British Columbia in the late 1940's, but was abandoned from 1960 until 1984, when a joint provincial-federal breeding program was established (Meagher *et al.*, 1990; Hunt, 1994).

66. Breeding programs typically screen for resistance to *Cronartium ribicola* through artificial inoculation of seedlings with telia of the rust on *Ribes* spp. leaves. Infected leaves are either collected in *Ribes* gardens maintained and inoculated for this purpose, or from plants in the wild. Two-year-old seedlings are placed in a chamber with high humidity and temperatures of 12-18°C. *Ribes* leaves are placed on screens above the seedlings, and sporefall is monitored. When spore fall reaches a threshold level after a day or two, usually 6,000 per cm², *Ribes* leaves are removed and the seedlings remain in the chamber for an additional 36 hours to allow for spores to germinate (Mahalovich and Eramian, 1995). Seedlings are then placed outside and monitored for rust resistance over a three to five-year period, depending on the program (Hunt, 1990; Sniezko, 1996). Information is also derived from infection and mortality levels in field genetic tests (Fins *et al.*, 2001). Assessments of growth rate are conducted following screening for blister rust resistance (Mahalovich and Eramian, 1995).

67. There have been many, varied descriptions of rust resistant phenotypes (Hunt, 1997). Early selections in the Idaho program are thought to have been resistant due to a few single-gene (vertical) mechanisms. The emphasis in the program is now to select first for combinations of polygenic (horizontal) mechanisms of resistance, and second for vertical resistance. The Idaho programme has identified eight types of rust resistance in western white pine. Four of these are thought to be controlled polygenically, conferring horizontal resistance: 1) low frequency of needle lesions; 2) early exhibition of stem symptoms; 3) cankers that remain alive over a 3-year period following inoculation; and 4) a high proportion of bark reaction in cankered seedlings 3 years after inoculation. The four remaining types of resistance are thought to be vertical, controlled by single genes: 1) apparent immunity, with no needle lesions following inoculation; 2) abscission of needles with lesions during the first summer after infection; 3) retention of infected needles without the development of a canker; and 4) bark reaction resulting in the termination of canker growth following inoculation. The Idaho program is focussing on selecting families with more than one type of vertical resistance, and selecting individuals within those families exhibiting horizontal resistance (Mahalovich and Eramian, 1995; Fins *et al.*, 2001). Families with particular combinations of resistance mechanisms will be grouped into breeding sublimes to manage coancestry. The types of resistance recognized in the Oregon and British Columbia breeding programs are similar to the Idaho

programme (Meagher *et al.*, 1990; Sniezko, 1996). The Oregon programme also plans to combine mechanisms of resistance into breeding lines.

68. Field genetic tests of F2 improved material in Idaho have mortality rates that average 42% lower than controls (unselected seedlots) over sites with a wide range in blister rust severity. Operational trials of F2 versus unimproved stock have yielded similar results, with mortality rates of 7% for improved material and 42% for unimproved stock. Tests have also shown that infection levels vary greatly from one site to another (Fins *et al.*, 2001). In coastal British Columbia, progeny of phenotypically selected and tested trees had infection levels of 13% in field trials, while unselected trees had infection levels of 95% and above (Hunt and Meagher, 1989).

69. The degree of resistance of genetically selected stock varies with site and with races and virulence of *Cronartium ribicola* (Goddard *et al.*, 1985; Hoff and McDonald, 1993). The instability of single-gene resistance has been shown by Kinloch and others (1999). They established the single-gene basis of a resistant phenotype with a hypersensitive bark reaction. This form of resistance has already broken down in both *Pinus monticola* and *P. lambertiana* to a virulent race of blister rust in some limited geographic areas in California and Oregon. Idaho F2 seedlings suffered relatively high levels of infection on some sites in coastal British Columbia (Hunt and Meagher, 1989).

70. Biochemical and morphological differences between white pine blister rust resistant and susceptible phenotypes have been investigated. Bark protein differences have been documented between slow canker growth resistant and susceptible phenotypes (Davidson and Ekramoddoullah, 1997). A protein associated with cold hardiness in western white pine (Pin mIII) has been found to be up-regulated by blister rust infection, possibly reflecting a stress response (Davidson and Ekramoddoullah, 1997; Yu *et al.*, 1997; Ekramoddoullah *et al.*, 1998). Genotypes with the reduced needle lesion frequency form of resistance appear to have smaller, less round stomata than susceptible genotypes (Woo *et al.*, 2001).

71. The primary objective for breeding programs has been disease resistance, and comparatively little attention has been paid to other traits of interest such as growth rate and wood properties. However, considerable gains for increased growth rate are possible with this species (Rehfeldt *et al.*, 1991). As programs advance and high levels of resistance are achieved, more emphasis will be placed on increasing growth rate as a secondary objective.

D. Conservation of genetic resources

72. The level of mortality of young, naturally regenerated trees from wild populations are so high that unlike most tree species in western North America, western white pine genetic resources will not be well-protected *in situ* (Hunt *et al.*, 1985; Mahalovich and Eramian, 1995; Fins *et al.*, 2001). Genetic conservation in this species will best be protected through a combination of the maintenance of breeding orchards, seed orchards, clone banks and seed banks, and through the aggressive planting of genetically improved, resistant genotypes throughout the natural range of this species. The three breeding programs dedicated to this species all provide such *ex situ* protection of genetic diversity in this species. Slight losses of genetic diversity in this species may occur through breeding and deployment. However, any reductions in overall diversity are likely to be small, and much lower than if genetic conservation relies on wild populations slowly evolve higher levels of resistance, suffering large reductions in numbers of trees in the process and likely leading to the extinction of some populations.

73. *In situ* reserves will provide some secondary protection of genetic diversity in western white pine. In British Columbia, a gap analysis of degree of protection of conifers found that this species is fairly well represented in existing parks and ecological reserves, but that outlying populations in a few regions deserved further attention (Lester and Yanchuk, 1996).

SECTION VIII. SUMMARY

74. Although western white pine is a valuable timber species, it is, and will probably remain, only a minor forest component in western North America. The major hazard limiting its wider application is white pine blister rust. Western white pine is, however, a very productive and desirable species considering its rapid growth, clean bole with minimum taper, narrow crown, and non-resinous wood. Across its range, western white pine functions as a long-lived seral species. It is typically a minor component in the upper canopy of mixed-species, softwood dominated stands at all seral stages. Compared to other pines, it does not tolerate water- and nutrient-deficient sites. Western white pine grows in some of the finest western outdoor recreation areas and has considerable aesthetic value.

75. Long-term, aggressive breeding programmes for western white pine have achieved substantial gains in resistance to white pine blister rust. These programmes will continue to play a key role in the management of this species. Breeding programmes will need to continue to select for a variety of types of disease resistance, and to emphasize those mechanisms under polygenic control. The breeding programmes also have a major responsibility for genetic conservation as wild populations in protected areas with a high incidence of blister rust may not maintain high enough population sizes for maintenance of genetic diversity or even population persistence. The lack of strong population differentiation or local adaptation, unusual in a widespread conifer, has facilitated the deployment of genetically improved, blister rust resistant seed. Resistant western white pine can be widely deployed to resume a variety of economic and ecological roles in forests in western North America.

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