

Unclassified

ENV/JM/MONO(2006)16



Organisation de Coopération et de Développement Economiques
Organisation for Economic Co-operation and Development

27-Apr-2006

English - Or. English

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

ENV/JM/MONO(2006)16
Unclassified

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)**

JT03208122

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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 2006

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 Pacific, 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 subsidiary 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 subsidiary 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, consensus documents are being published on the biology of certain plant species, on selected traits that may be introduced into plant species, and on biosafety issues arising from certain general types of modifications made to plants.

This consensus document addresses the biology of Western White Pine (*Pinus Monticola* Dougl. ex D. Don). It contains information on forestry practices related to Western White Pine, as well as more specific information on taxonomy, natural distribution, reproductive biology, genetics, hybridisation and ecology of this species.

Canada served as the lead country in the preparation of this document. The document has been revised on a number of occasions based on the input from other member countries. The Joint Meeting of OECD's Chemicals Committee and Working Party on Chemicals, Pesticides and Biotechnology recommended that this document be made available to the public.

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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, 24 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 a *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. FORESTRY PRACTICES

A. Deployment of reforestation materials

1. 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 after 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 and clearcutting are used for establishing conifer mixtures 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 reproduction cutting methods (Boyd, 1969). Individual-tree selection cuts cannot be used to regenerate western white pine successfully because more shade-tolerant species, such as western redcedar and western hemlock, are favoured. Group selection cuts may have limited application.

2. Propagation by seed is the major contemporary method for regenerating western white pine. Techniques for collection, processing, testing, and storage of seed are given in Krugman and Jenkinson (1974). Western white pine seedlings are well suited for planting. Both bare-root and container-grown seedlings have excellent survival and growth when properly planted on the appropriate sites. Bare-root stock has better survival with spring planting, but containerised stock appears to have excellent survival when planted during either season (Graham, 1990).

3. The introduced pathogen *Cronartium ribicola*, which causes white pine blister rust, has driven reforestation decisions for western white pine. 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).

4. Western white pine was introduced to Europe after 1825, where it was planted in arboretums 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

5. 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, 1979b; 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 in 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.

6. 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 (B.C. Ministry of Forests, 1995).

C. Breeding programmes

7. 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 seedlings 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).

8. 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 (Sniezko, 1996; Hunt, 1990). 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).

9. 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 program 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 sublines to manage coancestry. The types of resistance recognised in the Oregon and British Columbia breeding programs are similar to the Idaho program (Sniezko, 1996; Meagher *et al.*, 1990). The Oregon program also plans to combine mechanisms of resistance into breeding lines.

10. 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).

11. 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).

12. Biochemical and morphological differences between white pine blister rust resistant and susceptible phenotypes have been investigated. Bark proteins 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).

13. 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 achieved, more emphasis will be placed on increasing growth rate as a secondary objective.

D. Conservation of genetic resources

14. 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). Gene 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 gene 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.

15. *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 II. TAXONOMY

16. Western white pine is one of about 95 tree and shrub species in the family Pinaceae, and one of 35 species native to North America. It belongs to the 'soft pines' (also called white pines or 5-needle pines) in genus *Pinus*, subgenus *Strobus*. *P. monticola* was classified by Critchfield and Little (1966) as one of 14 white pines in section *Strobus*, subsection *Strobi*. Earlier classifications have varied in the number of species assigned to subsection *Strobi*, but *Pinus monticola* has consistently been grouped with *P. ayacahuite*, *P. lambertiana*, *P. strobus*, *P. griffithii* and *P. peuce* (Critchfield, 1986).

17. A recent molecular phylogeny of the genus *Pinus* based on the nuclear ribosomal DNA internal transcribed spacer (ITS) does not support the separation of subsection *Strobi* from subsection *Cembrae* or subsection *Krempfianae* (Liston *et al.*, 1999). While this study did not include *P. monticola*, it did include close relatives including *P. strobus*. The lack of clear differentiation between *Cembrae* and *Strobi* is also evident in the ability of *P. monticola* to hybridise with some, but not all, species in subsection *Strobi*, and some, but not all, species in *Cembrae*. The two subsections have previously been separated primarily by wingless seeds or seed retention in cones, but these traits appear to be polyphyletic rather than monophyletic (Critchfield, 1986).

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

SECTION III. NATURAL DISTRIBUTION

19. 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, to 51°30' N near Bute Inlet in southern British Columbia.

20. 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.

21. 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 in 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 Inland Empire, 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 IV. REPRODUCTIVE BIOLOGY

A. Reproductive development

22. Western white pine is monoecious. Strobilus buds are differentiated during July and August of the growing season before their appearance in June the following spring. The staminate strobili are about 10 cm long, borne in clusters of 15 to 25 on branches of the middle crown. Pollen dissemination in northern Idaho usually begins during the last week of June and can continue to the middle of July but usually average 8 days (Wellner, 1965).

23. The greenish-yellow to bright pink ovulate strobili are borne on stalks at the tips of the upper branches. The erect conelets are 1.5 cm to 4.0 cm long at the time of pollen dissemination, and grow to 2.5 cm to 5.0 cm by the end of the first growing season. Three growing seasons are required for seed maturation (Wellner, 1965).

24. Time of anthesis may vary over a period of 20 days, and is controlled by temperature during the weeks immediately preceding anthesis. 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 strobilus crops occur every 3 to 4 years, the major cycle being 4 years (Wellner, 1965). Warm, dry stress periods, during the early summer two years before strobilus emergence, favour strobilus production. In contrast, stresses in the late summer of the preceding year or during the period of emergence depress strobilus production. Within individual trees and within localities, maximal pollen shedding and ovulate anthesis practically coincide.

25. 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.

B. Mating system and gene flow

26. Western white pine is a predominantly outcrossing species, typical of most conifers. Single and multi-locus estimates of outcrossing over three 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).

27. 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

28. Cones of western white pine become ripe during August and September of the second year after the strobilus buds are initiated. The colour of ripe cones ranges from yellowish or beige-brown through reddish brown and dark brown (Krugman and Jenkinson, 1974). The cones are about 20 cm to 25 cm long; cones as short as 5 cm and as long as 36 cm have been reported (Graham, 1990). Over 18 years, 380 western white pines from 25 to 70 years old in northern Idaho produced from 2 to more than 300 seeds per cone, with a mean production of 226 seeds (Bingham and Rehfeldt, 1970).

29. Cone production begins as early as age 7 and becomes more prolific with age. Not until trees are about 70 years old does cone production become both frequent and abundant. It continues to increase with age until trees are about 50 cm in diameter. After that, seed production depends on individual tree vigour, crown characteristics, and genetic propensity for cone production (Wellner, 1965).

30. Seed yields for western white pine range from 30,900 to 70,500 seeds per kg, with an average of 59,000 (Krugman and Jenkinson, 1974). In northern Idaho, seed production varies from 41,000 to 457,000 seeds per ha, with average annual seed yields for a 75 year-old stand and an old-growth stand of 8,600 and 99,000, respectively (Graham, 1990).

31. Seed dissemination of western white pine begins in early fall; 15% of the current crop reaches the ground before September 1, about 85% by the end of October, and 15% during the late fall and winter. Seeds are usually disseminated by wind, but squirrels, mice, and various birds also contribute to seed dissemination. Most seeds fall within 120 m of the parent tree, but some have been known to travel over 800 m from the parent tree (Wellner, 1965).

32. Western white pine seeds remain viable after over-winter storage in the forest floor. Seeds have shown 40 % viability after one winter, 25% viability after two winters, and less than 1% after 3 and 4 years of storage in the forest floor. When properly stored, western white pine seeds can remain viable for 20 years (Krugman and Jenkinson, 1974).

33. Cone and seed insects and rodents can cause partial to almost complete failure of cone crops in otherwise poor to fair crop years. The cones beetles (*Conophthorus monticolae* and *C. labertianae*) and cone moths (*Dioryctria abietivorella* and *Eucosma rescissoriana*) can cause serious seed losses (Furniss and Carolin, 1977). Western white pine seeds are also a favourite food of red squirrels and the deer mouse.

D. Natural regeneration

34. Both fresh and stored seed require cold stratification temperatures of 1° to 5°C to break dormancy, and 30 to 120 days of cold, moist conditions before germination commences (Krugman and Jenkinson, 1974). Seed dormancy appears to be controlled by the seed coat, papery layer, and physiological elements of the embryo-gametophyte (Hoff, 1986). Germination is epigeal. There is a strong genetic component to seed germination with high family heritability (Graham, 1990). The papery layer and

seed coat may limit water entry or gas exchange (Dumroese, 2000). Clipping of a portion of the seed coat and papery layer can increase germination rate or reduce the necessary stratification time (Hoff, 1986a).

35. The seeds of western white pine usually germinate in the spring in soil at full field moisture capacity from melting snow. Germination can continue on exposed sites until July and on protected sites until August. Under open-area climate, germination begins and ends much earlier than in low light conditions. Soil temperature probably controls germination initiation, and forest floor and upper mineral soil layer seasonal moisture limitation probably stop germination (Wellner, 1965). Exposed mineral soil is a better seedbed than organic materials even though the forest floor may contain more many stored seeds (Graham, 1990).

36. During the first growing season, a high percentage of seedlings die, primarily due to disease, but insects, rodents, and birds can also cause serious seedling losses. *Fusarium*, cause of a damping-off disease, and *Neopeckia coulteri*, a snow mold, can cause extensive seedling mortality during the first year (Hepting, 1971). Seedlings up to 5 years old are often killed by *Rhizina undulata*. Seedling mortality late in the first growing season is due primarily to temperature and drought. High surface temperature is the most important cause of mortality on exposed sites, and drought is a factor in low light environments where root penetration is slow and unable to keep pace with receding soil moisture.

37. For the most part, western white pine seedlings have low drought tolerance (Minore, 1979). Western white pine seedling establishment is favoured by partial shade on severe sites. On more sheltered sites, such as north slopes, little or no shade is best for seedling establishment. Once established, western white pine grows best in full sunlight on all sites (Wellner, 1965).

38. Early root and shoot growth in seedlings is usually moderate. In the first summer, the primary root grows about 15 to 30 cm in full light and only 5 to 8 cm in low light. Seedlings planted in well-aerated, nitrogen-rich soil can have a first-year root elongation up to 50 cm. Seedlings usually average between 3 and 5 cm in height by the end of the first growing season. In northern Idaho, open-grown western white pine seedlings require about 8 years to reach a height of 1.4 m (Graham, 1990).

39. Both height and diameter growth of western white pine in northern Idaho usually begin about the first week of May. In British Columbia, shoot growth usually ends by early August and winter buds are typically set by mid-August (Schmidt and Lotan, 1980).

40. Western white pine has been maintained using a silvicultural system that regenerates even-aged stands (Burns, 1983). This is most practically accomplished by clearcutting and using natural regeneration, planting, or both methods. 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

41. Western white pine does not naturally reproduce by sprouting or layering. Cuttings from trees more than 4 to 5 years old are difficult to root (Bingham *et al.*, 1972), although cuttings from 3-year-old seedlings have been rooted successfully using rooting hormones. IBA (auxin) promotes rooting of stem cuttings, and this effect can be enhanced with sucrose. Needle fascicles from 2-year-old seedlings have produced roots and some have produced shoots successfully (Graham, 1990) but fascicles from older seedlings lose the ability to root (Andrews, 1980).

42. Western white pine is relatively easy to propagate by grafting at all ages. Several types of grafts have been used but early spring grafting before flushing has been most successful. Scions taken from various locations in the tree crown grafted with equal success. Some graft incompatibility has been reported, although the majority of grafts are compatible (Hoff, 1977). Grafting conducted under greenhouse conditions is more successful than field grafting. Interspecific grafting on other five-needle pine rootstocks, such as eastern white pine (*Pinus strobus*), sugar pine (*P. lambertiana*), and blue pine (*P. griffithii*), has also been successful (Bingham *et al.*, 1972).

43. 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 initiated from single embryos become embryogenic, methods have been developed that have yielded at least one successful line per family. The multiplication rate for the successful lines will be large (Percy *et al.*, 2000).

SECTION V. GENETICS

A. Cytology

44. 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

45. Populations of western white pine from the Sierra Nevada, southern Cascade and Warner Mountains differ from those farther norths in morphology, growth rate and allozyme frequencies. Variation among populations within these groups is typical for conifers for molecular markers, 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).

46. 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, 1979; Rehfeldt *et al.*, 1984; Campbell and Sugano, 1989). 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, typically 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*).

B.2 Variation among individuals within populations

47. 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).

48. Within-population genetic variation is high for polygenic traits as well. Heritabilities have been estimated for a variety of traits including blister rust resistance and growth rate. Heritabilities 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 h_f^2 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 (Bower and Yeh, 1988; Rehfeldt *et al.*, 1991).

C. Inbreeding depression and genetic load

49. 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).

50. 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 VI. HYBRIDISATION

51. *Pinus monticola* has been successfully hybridised with four species in the Critchfield and Little (1966) classification of subsection Strobi: *P. parviflora*, *P. peuce*, *P. strobus*, and *P. griffithii*. Hybridisation has not been limited to within subsection strobi. Filled seed have been produced in artificial crosses with three species in subsection Cembrae: *Pinus albicaulis*, *P. cembra* and *P. korainensis* (Bingham *et al.*, 1971). Seedlings have been growth from *P. monticola* x *cembra* and *P. monticola* x *korainensis* crosses, but died before the crosses could be verified (Bingham *et al.*, 1971). Hybrids have been verified between *P. monticola* and both *P. flexilis* and *P. strobiformis*, species sometimes classified in Strobi and sometimes in subsection Flexiles (Critchfield, 1986). 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 intermediate phenotypes to the parental species (Critchfield, 1986).

52. *Pinus monticola* x *strobus* 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.*, 1971).

SECTION VII. ECOLOGY

A. Climate

53. Western white pine grows in a variety of wetter, both maritime and continental climates ranging from subalpine boreal (less frequent) to temperate (frequent) to mesothermal (frequent) (Klinka *et al.*, 2000). The regions of Vancouver Island, the Cascade Mountains, and the Siskiyou Mountains within the species' range have cool maritime climates, with wet winters and dry summers. Precipitation varies considerably throughout the region depending on elevation and the orientation of the mountain ranges. Climatic variation along the latitudinal gradient from northern Oregon through British Columbia is small (Shumway, 1979). In general, precipitation on Vancouver Island and in the Cascade Mountains averages from 1,500 to 2,010 mm per year while precipitation in the Siskiyou Mountains is lower averaging from 510 to 1,520 mm per year. The winter snow line varies with latitude and lies at an average 600 m elevation, with heavy snowpack. Temperatures of the Vancouver Island – Cascade Mountain portion of the western white pine range vary from a low of -18°C to a maximum of 38°C. January is usually the coldest month of the region and July and August the warmest months (Graham, 1990).

54. In the Sierra Nevadas where western white pine grows, the mean annual precipitation varies from 760 to 1,500 mm, with most falling as snow. The temperature averages between -9°C in February to 27°C in July and August, with maximum temperatures near 37°C.

55. The climate of the Inland Empire is influenced by the Pacific Ocean 400 km to the west. Summers are dry, with the majority of precipitation during the fall and winter, averaging between 710 and 1520 mm. Snowfall averages 262 cm but ranges from 122 cm to 620 cm. Annual temperature in the inland range of western white pine averages from 4 to 10°C with extremes from -40°C to 40°C (Wellner, 1965).

B. Soils

56. 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 does tolerate water-surplus and inundated soils (Krajina, 1969; Klinka *et al.*, 2000).

57. Many young western white pine trees are eliminated 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 pine die more slowly, from the top down, exhibiting chlorosis and later necrosis (Krajina, 1969).

58. 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.

59. The soils on which western pine grows in the Inland Empire 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, the soils have developed from base-rich glacial materials (till, fluvial, or lacustrine deposits) (Wellner, 1965).

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

C. Synecology

61. 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).

62. Associates of western white pine include *Abies amabilis*, *A. concolor*, *A. grandis*, *A. lasiocarpa*, *A. magnifica*, *A. procera*, *Acer macrophyllum*, *Alnus rubra*, *Arbutus menziesii*, *Betula papyrifera*, *Chamaecyparis lawsoniana*, *Larix occidentalis*, *Libocedrus decurrens*, *Picea engelmannii*, *P. sitchensis*, *Pinus balfouriana*, *P. contorta*, *P. flexilis*, *P. jeffreyi*, *P. lambertiana*, *P. ponderosa*, *Pseudotsuga menziesii*, *Thuja plicata*, *Tsuga heterophylla*, and *T. mertensiana* (Franklin and Dyrness, 1973; Eyre, 1980; Graham, 1990; Klinka *et al.*, 2000).

63. Western white pine is represented in 18 forest cover types of western North America and Canada (Eyre, 1980). It is the key species in the Western White Pine cover type (Type 215). Most often, the western white pine component in this type is even-aged with an understory containing multi-aged trees of the more shade-tolerant softwoods; occasionally, a minor component of shade-intolerant softwoods may also be present in the upper canopy layer. In the other 17 cover types, western white pine is a common, typically minor component, along with many other species: 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 Redcedar–Western Hemlock (227), Western Redcedar (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).

64. 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

65. The presence of western white pine has depended nearly entirely on the periodic recurrence of wildfires. Rapid growth and longevity are the main adaptations that have enabled western white pine to remain a widespread element in Pacific Northwest forests. Without fire or timber harvesting, western white pine would gradually be replaced by more shade-tolerant conifers (Franklin and Dyrness, 1973; Graham, 1990). In the absence of white pine blister rust (*Cronartium ribicola*), the species is long lived: trees are commonly 300 to 400 years old (rarely up to 500 years old), and old trees are often more than 180 cm in diameter and 60 m tall (Graham, 1990; Klinka *et al.*, 2000).

66. Western white pine can be regenerated using even-aged, seed-tree, and shelterwood silvicultural systems resulting in adequate and diverse natural regeneration within 5 to 10 years after the cut. If a natural blister rust-resistant seed source is not present on the site, planting can be used to regenerate the stand. In shelterwood cuttings, a high-density overstory and a prolonged time until removal will greatly reduce western white pine growth (Wellner, 1965).

67. The composition of a western white pine stand is determined during the first 30 years following stand initiation (Graham, 1988). Lodgepole pine and western larch can grow 1.5 times faster in height than western white pine during this period. Western larch can usually maintain its superior height growth, but lodgepole pine's growth superiority seldom lasts past age 50. Similarly, grand fir can equal western white pine height growth for the first 30 years. Douglas-fir has similar height growth. On northerly aspects and in shaded conditions, western hemlock height growth can also equal that of western white pine (Deutschman and Pfister, 1973).

E. Damaging agents

68. Western white pine depends on fire or timber harvesting to remove competing conifers and allow it to become established as a persistent early seral species (Wellner, 1965). Its relatively thin bark and moderately flammable foliage make it intermediate in fire resistance among its coniferous associates (Minore, 1979). As a result of fire protection and blister rust infection, the proportion of western white pine regeneration (planted and natural) in northern Idaho, eastern Washington, and western Montana has 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 program (Fins *et al.*, 2001).

69. Dormant western white pine is tolerant of cold and along with lodgepole pine is one of the more frost-tolerant western North American species. Needle desiccation can occur when cold, dry winds cause excessive moisture loss that cannot be replenished due to cold or frozen soil or tree trunks. Western white pine is more tolerant of heat than most of its more shade-tolerant associates. Depending on the site, western white pine is relatively windfirm but snow often causes breakage in pole-stage stands (Graham, 1990).

70. Western white pine is affected by many diseases (Hepting, 1971). The most prominent and serious is white pine blister rust (*Cronartium ribicola*). In northern Idaho and adjacent areas, a combination of climate and abundant alternate host plants (*Ribes* spp.) contribute to heavy losses. However, it is possible to minimise the damage through selection of naturally rust-resistant parent trees for natural regeneration and for the planting of rust-resistant nursery stock. Other stem diseases are of little consequence.

71. In prolonged periods of drought, pole blight, a physiological disorder, can occur in 40 to 100 year old stands, causing yellow foliage and necrotic resinous areas on the trunk. Later the top dies and in a few

years, the entire tree. This disease does not appear to be caused by a primary pathogen but results from rootlet deterioration in soils which restrict water uptake (Leaphart, 1958; Leaphart and Stage, 1971). At present, the disease is not a major cause of mortality in western white pine stands, except on water and nutrient-deficient sites (Graham, 1990).

72. The principal root disease of western white pine is *Armillaria* spp., causing fading foliage, growth reduction, root-collar exudation of resin, root dieback, and black rhizomorphs. *Heterobasidion annosum* and *Phellinus weiri* also cause some mortality. The most important butt-rot fungi are *Phellinus pini*, *Heterobasidion annosum*, and *Phaeolus schweinitzii* (Hepting, 1971).

73. Bark beetles are the most damaging group of insects that attack western white pine. *Dendroctonus ponderosae* kills groups of trees weakened by blister rust, primarily in mature forests (Furniss and Carolin, 1977).

SECTION VIII. SUMMARY

74. Although it is a valuable timber species, western white pine is and will probably remain to be only a minor forest component in western North America. The major hazard limiting its wider application is blister rust. It 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 programs for western white pine have achieved substantial gains in resistance to white pine blister rust. These programs will continue to play a key role in the management of this species. Breeding programs will need to continue to select for a variety of types of disease resistance, and to emphasise those mechanisms under polygenic control. The breeding programs also have a major responsibility for gene 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. Through this deployment, 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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