Genetic Improvement and Deployment of western hemlock in Oregon and Washington: Review and Future Prospects

By K. J. S. JAYAWICKRAMA

Department of Forest Science, Oregon State University, Corvallis, OR 97331-5752

(Received 7th October 2002)

Abstract

The genetic improvement of western hemlock in the USA, an important part of its natural range, started around 1972. Since then, 2,283 parent trees have been selected, of which 2,102 have been progeny tested as wind-pollinated families (using seed collected from the parent trees in the wild). Landowners have shown more support for western hemlock improvement as a result of the growing concern about Swiss Needle Cast disease on Douglas-fir in coastal Oregon (OR) and Washington (WA). A cooperative second-generation program got underway in 1992, using crosses between parents from five first-generation programs from OR, WA and British Columbia (BC). The best 30 parents from each program were chosen for a Main population, and the best six of each program for an Elite population. All selections were made on age-10, age-14 or age-15 height growth. The second-generation program resulted in 342 Local Diallel crosses planted on four sites and 166 Elite crosses planted on five sites; test establishment was completed in spring 2001. Three partial tests had been planted in OR and WA in 1998-99, and a full set of sites were also planted in BC.

First-generation western hemlock orchards were established with grafts or rooted cuttings, starting in 1979. Graft compatibility is usually high, and cuttings have also been used with good success. Mature orchards have proven very productive – an intensively managed 18-year-old orchard can produce enough seed for over 4.7 million plantable seedlings per orchard hectare per year. High-gain 1.5-generation orchards are being established, and early selections from second-generation tests can be made starting in 2003. Current annual planting (2001) in OR and WA is estimated at about 9.3 million western hemlock seedlings, of which about 52% originated from orchard seed. There is real potential to improve the ratio of improved to unimproved stock, and to shift production from a broad group of lower-gain parents to a top group of high-gain parents, by the use of rooted cuttings. Rooted cuttings are only needed till the new orchards produce enough high-gain seed. A second-generation orchard with 60 selections was predicted to give 22.4% gain at age-15 (compared to the unimproved base population). Gains can probably be made for wood properties such as density, stiffness and strength, just as for growth rate, by exploiting between-provenance and within-provenance genetic variation. The growing interest in planting the species, the wealth of provenances and families tested, the potential for early and heavy seed production and for using rooted cuttings, demonstrated gains in growth rate and the untapped potential for gains in wood properties, are incentives for working with western hemlock.

Key words: Western hemlock, breeding, seed orchard, cooperative, second-generation.

Introduction

Distribution and abundance of western hemlock

The Pacific coastal forests of North America have given rise to some of the most productive temperate forests and timber species in the world. Douglas-fir (*Pseudotsuga menziesii* (Mirb) Franco) is the most important species west of the Cascade range, but western hemlock (*Tsuga heterophylla* (Raf.) Sarg) also occupies large acreages of the coastal humid zone of Oregon (OR), Washington (WA), British Columbia (BC) and Alaska (PACKEE, 1990). Western hemlock is a dominant or common species, i.e. with potential for more than 10 stems/hectare (4 stems/acre) under climax conditions, on about 8.7 million hectares (20.9 million acres) west of the Cascade crest in the states of OR and WA (unpublished data from Sara Lipow and Ken Vance-Borland, Department of Forest Science, Oregon State University; Brad St. Clair, USDA Forest Service PNW Research Station; J. A. HENDERSON and C. MCCAIN, USDA Forest Service). A prolific seeder, western hemlock is an extremely competitive species on moist sites. It needs an organic horizon to get established, and a moderately acidic pH (PACKEE, 1990), Western hemlock is categorized as the most shade-tolerant conifer of the region for poor soils, and as much more resistant to floods than Douglas-fir (KRAJINA *et al.*, 1982).

Western hemlock can live over 500 years and reach a maximum diameter of 260cm, and a 110 year old hemlock-spruce stand near the OR coast was estimated to hold a stem volume of 1,987 m^3/ha (WARING and FRANKLIN, 1979). The same report mentioned Douglas-fir reaching an age of 1,200 years and a diameter 434 cm, and 1,405 m^3/ha for a 100 year-old Douglas-fir/western hemlock stand in the OR Cascades.

Importance of western hemlock as a timber species

Western hemlock was not even counted as a commercial species in timber cruises done in western WA in the early 1900s (BOLSINGER *et al.,* 1997), partly due to its low market value. In the most recent summary of timber harvest, however, 12 million m^3 western hemlock lumber was cut in western WA in 1991, almost half the total softwood volume of 25 million m^3 (BOLSINGER *et al.,* 1997). Lumber production in the Hem-Fir category (the six-species group in which western hemlock lumber is sold) in 1999 was estimated at 4.01 million m^3 (1,153 million board feet (BF)) in western OR and 5.19 million m^3 (1,490 million BF) in western WA; the comparable figures for Douglas-fir were 12.96 and 5.3 million m^3 (3,724 and 1,522 million BF) respectively (WWPA, 1999a). To put the Hem-Fir lumber production of 9.2 million m^3 for western OR and western WA in perspective, the total lumber production for New Zealand for all species in 2001 was estimated at 3.8 million m^3 (NZFOA, 2001).

The Hem-Fir category is described as being light and bright in color. At the top end of the scale, Hem-Fir clear and nearly clear products are used in high-value appearance-grade products such as wood paneling, cabinets, fascia, molding, millwork and trim. Hem-Fir is also used as the following categories of framing products: structural light framing, light framing, structural joists and planks, and special dimension lumber (including Machine Stress-Rated lumber). It is also used in outdoor structures such as decking after treatment with preservative (WWPA, 1997). Lower-grade hem-fir is used in engineered wood products. Western hemlock has excellent pulping characteristics for groundwood, thermomechanical, kraft and sulfite pulps (PACKEE, 1990).

There is a perception is that western hemlock is less dense, stiff and strong than coastal Douglas-fir. For example, GREEN *et al.* (1999) list western hemlock to have a specific gravity of 0.42, modulus of elasticity of 9 GPa and modulus of rupture of 46 MPa; the figures for coastal Douglas-fir are 0.45, 10.8 and 53 respectively (all values for green lumber). The Hem-Fir category is described as slightly less strong than the Douglas-Fir-Larch species group (WWPA, 1997). Design specifications assume that Hem-Fir to be about 15–20 % less stiff than Douglas-fir Larch (e.g. bending strength ratios for Select Structural grades are 1400: 1500 for Hem-Fir: Douglas-fir Larch), and therefore assign Hem-Fir a lower load-bearing capacity (AF&PA 1997a; WWPA, 1999b). We should note, however, that these design specifications, in the case of the Hem-Fir species group, were derived on tests run between 1977 and 1987 on random lots of lumber sampled in mills (AF&PA 1997b; EVANS and GREEN, 1987). We can therefore infer that these values are based on old-growth forests, or on unmanaged second-growth forests naturally regenerated no later than 1920. We can also infer they are averaged across lumber from different parts of the tree.

Status of western hemlock in reforestation

The proportion of western hemlock in coastal forests has fluctuated during recent times. When old-growth stands were logged in the Pacific Northwest (in the 19th and 20th centuries) Douglas-fir was often preferentially removed , leaving a higher proportion of western hemlock in the coastal areas. These trees, combined with prolific natural seeding, then resulted in a preponderance of western hemlock in second-growth stands in some coastal areas. When planting and thinning became more routine, the low priority given to western hemlock resulted in reverting harvested hemlock-dominated stands to Douglas-fir plantations. For example, the Oregon Department of Forestry reviewed 76,970 hectares of Douglas-fir plantations 10 to 30 years old growing within 29 km of the coast. They concluded that about 31 % of this total had been established on sites where western hemlock and Sitka spruce had dominated the previous stand (HANSEN *et al.,* 2000). Douglas-fir was also preferentially planted in high-elevation sites in the OR and WA.

Lumber prices are still lower for western hemlock and Hem-Fir than for Douglas-fir; for example, figures in November 2000 for dry Douglas-fir clears were US$ 656/thousand board feet (MBF), in contrast to US$ 498/MBF for dry Hem-Fir clears (WWPA, 2000). Transport costs are similar for both species, and can be as high as $200/MBF. Logging costs for western hemlock can be higher than for Douglas-fir, in cases where the hemlock volume is distributed on a larger number of smaller stems. The price differential in the forest can therefore be as high as 2 : 1 in favor of Douglas-fir, giving growers and sellers of logs a clear financial incentive to prefer Douglas-fir over hemlock.

Western hemlock has nevertheless recently gained more importance in both western OR and western WA for four reasons. The first reason is the growing concern about Swiss Needle Cast disease, caused by *Phaeocryptopus gaeumannii,* on Douglas fir plantations in this region (HANSEN *et al.,* 2000). At its worst, seen in some stands in the Tillamook (OR) area, this disease can reduce Douglas-fir to one year's complement of needles (from a normal three to four years); losing this much needles naturally impacts growth rate. Although hemlock lumber fetches a lower price, some growers have come to feel that a healthy hemlock stand is likely to earn more per acre than a diseased Douglas-fir stand in the Swiss Needle Cast zone. It is fair to point out adaptability and disease problems encountered by western hemlock include defoliation by the western hemlock looper (*Lambdina fiscellaria lugubrosa*), infestation by dwarf mistletoe (*Arcethobium tsugense*), root rot caused by several pathogens, and susceptibility to fire (PACKEE, 1990); however the potential pests and pathogens have not prevented the planting of western hemlock in recent years.

Second, some growers feel that it would be prudent to partially reverse the trend of converting high-elevation stands to Douglas-fir, and plant a reasonably high proportion of western hemlock and Noble fir (*Abies procera* Rehd.) in these areas. Third, there is evidence that western hemlock out-competes Douglas-fir in terms of volume growth on some moist coastal and high-elevation sites, even without Needle Cast influence. For example, western hemlock advanced-regeneration sometimes competes aggressively with planted Douglas-fir. There are reports of 33–101 % greater mean annual increment (MAI) compared to Douglas-fir (STEINBRENNER, 1976). It is estimated that western hemlock attains significantly higher yields than Douglas-fir when compared at the same site index, carrying more trees per acre for a given dbh, and more volume in trees of the same dbh and height (WILEY, 1976). It should be noted, however, that stands of higher site index can be found for Douglas-fir than for western hemlock (WILEY, 1976). For example, a Douglas-fir site index of 42.4 m equates to a western hemlock site index between 33.9 and 38.5 m (WILEY, 1976). Douglas-fir was taller than western hemlock at 28 years in a replicated trial on Vancouver Island (OMULE, 1987). Fourth, the stem deformation caused by the white pine weevil has made landowners less willing to plant Sitka spruce (*Picea sitchensis*), the other naturally dominant species in the coastal humid zone.

Objective of this paper

Genetic improvement is recognized as a cost-effective way to boost the productivity of forest tree plantations. Forest growers in the Pacific Northwest of the United States have made a massive investment in testing and breeding several important species. Some background and results on Douglas-fir improvement have been published, but western hemlock genetic improvement in OR and WA has had very little coverage after some early papers (PIESCH, 1976; KUSER and CHING, 1980; FOSTER and LESTER, 1983; FOSTER *et al.,* 1985). This paper therefore reviews and documents 30 years of genetic improvement in western hemlock in western OR and WA, an important part of its natural range, and discusses short-term prospects. There is also a longstanding, active and comprehensive western hemlock genetic improvement program in BC.

Geographic Variation

Rangewide provenance trials are an important step in the genetic improvement of a forest species. Small provenance tests were planted early in the twentieth century, e.g. Douglas-fir trials in 1910 and 1912 in USA and Germany (SILEN, 1964; KLEINSCHMIT and BASTIEN, 1992) and southern pines (WAKELY and BERCAW, 1965). More comprehensive trials have been planted since the 1950s, such as for the southern pines in the southeastern USA (WELLS and WAKELY, 1966), and a Douglas-fir study planted from California to BC (WHITE and CHING, 1985). A western hemlock provenance test was planted in BC in 1968 with 15 populations spanning 2° in latitude and 550 meters in elevation. These were planted on four sites which themselves ranged from 60–100 to 520–580 meters elevation (POLLARD and PORTLOCK, 1986). More tests were planted in BC 1993-96 (KING *et al.,* 1998) based on extensive seed collections in the late 1980s.

Comprehensive long-term provenance trials have yet to be planted in OR or WA for western hemlock, although there were plans for such a study in the mid-1970s (PIESCH, 1976). Local adaptation and small breeding zones were emphasized in the first generation of testing as for Douglas-fir (SILEN and WHEAT, 1979). This left the option of wide testing a much smaller proportion of high-ranked first-generation parents after recombining them in a second cycle of breeding and testing. This was a cost-effective strategy, but meant that there is little information to date on which to base wide-transfer decisions. In general foresters in western Oregon and Washington have been reluctant to move tree seed (for western hemlock and other species) long distances, fearing damage due to spring or fall frosts, cold, drought, disease and general lack of adaptation.

There have been some studies, of limited scope, on adaptation and genotype x environment interaction and including OR and WA sources. In the first, after seedling adaptation/cold-hardiness studies, KUSER and CHING (1980) recommended not moving seedlings more than 2° north of their genetic origin and more than 400 meters above elevation of origin. They noted a strong north-south cline among coastal provenances. The following has to be considered, however: the north-south range examined in this study was more than 20°, which is far greater than the extent in OR and WA. As pointed out by KING (1990) there is no a significant regression in the KUSER and CHING (1990) data for a more limited north-south extent.

In the second study, FOSTER and LESTER (1983) examined progeny test results for the parent trees selected by Crown Zellerbach Corp. They found no significant site x family interaction for fifth-year height growth. The test sites ranged from 110 to 44° m. elevation and went from Cathlamet (46° 15') to Tillamook (45° 30'). In the third, OR sources appeared to show greater height growth, earlier bud flush and less autumn and spring frost hardiness than sources from BC, when grown in BC (HANNERZ *et al.,* 1999).

First-Generation Selection and Testing

Strategies and Procedures

The "progressive tree improvement" model, promoted by ROY SILEN and JOE WHEAT and emphasizing testing lots of selections through wind-pollinated seed (SILEN, 1966; SILEN and WHEAT, 1979), was adopted for western hemlock as well as for Douglas-fir. Recognizing the economy of sharing costs through co-operative tree improvement, three of the programs were set up as co-operatives.

Typical "progressive" tests had several sets with about 30 families in each set. The families within a set were tested together on as many as 12 sites, with four to five replicates per site and four to six trees planted in a replicate in a non-contiguous design. This design meant that families were well-ranked, with over 100 seedlings planted per family, and within-set comparisons could be made with confidence.

Coastal western hemlock

Although western hemlock grows on much of western OR and WA (the main exception being the Willamette Valley in OR), most selection and testing has been done at low-elevation within a few miles of the ocean (from Newport in OR to the western part of the Olympic peninsula in WA). The Western Hemlock Tree Improvement Committee was formed in 1972. The first program to start was in the Forks region on the Olympic peninsula. While western hemlock was a clear second to Douglas-fir as a commercial timber species, it was too prevalent and competitive in the area to ignore. By 1978 five programs were underway. Credit is due to the far-sighted pioneers who got this work started, despite the low priority given to this species and the argument that prolific natural hemlock regeneration made planting programs (let alone genetic improvement) unnecessary.

Crown Zellerbach Corp. was an early leader in the genetic improvement of western hemlock, starting their program in 1975. In addition to progeny testing, the company's researchers and foresters worked on seedling and rooted cutting production, clonal testing, and seed production research. Weyerhaeuser Co. has selected and tested western hemlock from three coastal areas: 106, 277 and 111 parents from the Longview, Vail and Twin Harbors areas respectively (LIPOW *et al.,* in press). The company took an intensive plus-tree selection approach choosing the best phenotype from selected 100-tree plots (PIESCH, 1976).

In all there were eight coastal first-generation programs. Some details on six of these programs are given in *Table 1*.

Table 1. – Summary of first-generation selection and testing programs for western hemlock in Oregon and Washington.

Name	Location	Elevation (m)	Started	Number of parents
Tillamook	NW Oregon	242-364	1975	270
Tillamook Addition	NW Oregon	150-300	1980	80
Crown Zellerbach	NW Oregon and SW Washington	15-364	1975	213
Forks	Forks vicinity on Olympic Peninsula	30-400	1973	278
Grays Harbor	Grays Harbor vicinity on Olympic Peninsula	0-150	1978	432
Siletz	Siletz river valley in Oregon Coast range	NA	1978	50
Skagit	Snohomish, Skagit and Whatcom counties in North Washington Cascades	150-760	Ca. 1980	175[1]
Bureau of Land Management	North Oregon Cascades	300- 760	1980	180

[1]Untested.

Cascade western hemlock

Three programs were started. One was begun in the northern part of the WA Cascades by Scott Paper and Georgia-Pacific Corp.; 175 parents were selected and grafted in orchard on Whidbey island and near Bellingham, but were never tested. This program has had a low priority after a promising start, since little western hemlock is planted in the area. Another set of tests was established in the northern extent of the OR Cascades by the Bureau of Land Management; in this case the 180 parents were all progeny tested (*Table 1*). Weyerhaeuser Company has tested 111 parents from the WA Cascades (LIPOW *et al.,* in press).

Lessons learned

Douglas-fir being the dominant species in the region both in operational forestry and in genetic improvement, it was only logical that practices used for Douglas-fir influenced those for western hemlock. In some cases, first-generation tests were harmed by over-preparing the sites. In some cases stumps were removed, and most of the slash as well; this had the effect of scraping off topsoil and organic matter. We now know that a

Table 2. – Examples of heritabilities estimated from open-pollinated western hemlock trials planted in Oregon and Washington.

Program	Number of Parents	Number of sites	Age of Measurement	Narrow-sense Heritability	Family-Mean Heritability	Source
Crown Zellerbach	87	4	5	-	0.57	Foster and Lester (1983)
Grays Harbor	448	3-5	10	0.06	0.48	Unpublished NWTIC analyses
Tillamook	270	10	15	0.06	0.45	Unpublished NWTIC analyses
Tillamook Addition	95	5	10	0.07	0.38	Unpublished NWTIC analyses

high organic content and plenty of woody debris are needed for good establishment of western hemlock (PACKEE, 1990). Herbicides were used with less success than for Douglas-fir. In other cases, greenhouse-grown seedlings sometimes lost their needles when exposed to full sun.

Early hemlock improvers made great efforts and investments (such as fencing) in their tests. Individual heritabilities even for height growth were nevertheless typically low. Family-mean heritabilities were fortunately quite high due to generous numbers of progeny planted per parent, allowing for good ranking of the parents. For example, narrow-sense heritabilities were usually less than 0.1, but family-mean heritabilities reached 0.57 (*Table 2*). These figures tend to be lower than comparable figures for Douglas-fir in the region (e.g. YANCHUK, 1996; STONECYPHER *et al.,* 1996; JOHNSON *et al.,* 1997) and for other temperate conifers (e.g. HODGE and WHITE, 1992; ADAMS *et al.,* 1994; JAYAWICKRAMA, 2001a). Little has been published on specific combining ability since almost all the mature data available are from open-pollinated tests; however, a great deal of information will soon be available from the second-generation program described below.

Second-Generation Breeding and Testing

Merging First-Generation Programs

An important shift took place after the first cycle of selection and testing. Breeders and cooperators alike were prepared to go beyond the small first-generation breeding zones, in search of higher selection intensities and economies of scale. First-generation programs from coastal OR, WA and BC were merged in 1992 to form the Hemlock Tree Improvement Cooperative (HEMTIC).

Breeding Goals and Selection Criteria

While the importance to a genetic improvement program of having a breeding objective has been stressed (e.g. PONZONI and NEWMAN, 1989; WOOLASTON and JARVIS, 1995) this step has rarely been taken for conifer breeding programs (JAYAWICKRAMA and CARSON, 2000) including western hemlock. In the case of western hemlock in OR and WA, families have been ranked and selected for use in the second-generation program almost exclusively on age-10, age-14 or age-15 height growth. Western hemlock normally has good stem straightness, so this trait needed relatively low emphasis in the testing program. The implicit breeding goal was to find well-adapted families that gave the most stem volume at harvest.

The Breeding Strategy

Procedures adopted for cooperative second-generation breeding and testing of western hemlock include many similarities and some important differences to that for Douglas-fir. Many details of the second-generation western hemlock program are outlined in two unpublished HEMTIC internal reports (KING, J. N. and D. W. CRESS, 1991. Breeding plan proposal for western hemlock cooperative tree improvement; KING, J. N., C. CARTWRIGHT and D. W. CRESS, 1998. Western Hemlock tree improvement: Selection of P-1 parents. These documents are proprietary to HEMTIC members.)

The second-generation population was formed by recombining the top 150 first-generation parents, 30 each from five first-generation programs. This equated to roughly 1 in 10 tested parents. The top 30 of these 150 parents were designated as Elite parents (six parents from each first-generation program). In all cases "backwards selections" (tested first-generation parents) were used. The underlying principle was Recurrent Selection for General Combining Ability.

The Mating Design and Controlled Pollination

The breeding strategy had two structures. In the first, ("Local Diallels") the selected parents were each crossed with five other parents drawn from the same first-generation program, in six-parent disconnected partial diallels. In the second, ("Elite Crosses") the 30 Elite parents were crossed within and across first-generation programs in partial diallels. Each Elite parent was used up to 10 times in such Elite crosses. This two-pronged approach was taken to balance the possibility that local adaptation might prove important, as well as the potential of boosting gain by crossing the fastest growing parents across programs. Disconnected six-parent partial diallels were used in the North Carolina State University – Industry Cooperative's (NCSU-ICTIP) second-cycle loblolly pine breeding population (TALBERT, 1979) and both the BC and the Weyerhaeuser Douglas-fir programs (STONECYPHER *et al.,* 1996; YANCHUK, 1996).

Western hemlock has proven to be easier to breed than Douglas-fir, especially on mature ramets growing on good orchard sites. Crossing has also been expedited from the active research in Canada on using gibberellic acid (GA 4/7) to promote cone production (summarized in WEBBER, 2000). Cone crops occur yearly, cones contain an average of 25 filled seed each (WEBBER, 2000) and a single isolation bag can result in as many as 500 seed (unpublished data from RICK QUAM, OR Department of Forestry). This allowed completing the controlled-crosses much faster than has been the case for second-generation Douglas-fir programs.

The Testing Program

HEMTIC adopted the following types of tests: family-ranking/selection tests; family blocks; and adaptability-screening tests.

Family-Ranking/Selection Tests

These tests were designed to give precise estimates of family means and family-site interactions (genotype x environment interactions = GxE). A "Sets-in-Replicates" design (SCHULZ and COCKERHAM, 1966) was adopted for the Local Diallels, with families within a local diallel grouped together in a set. Two controls were used in every set-rep combination in every test : a mix of several controlled-crosses between Grays Harbor parents (referred to as the Grays Harbor standard), and a local woods-run (unimproved) control. The unimproved controls were operational bulk lots collected from many local wild trees; a BC lot was used at the BC sites, a Grays Harbor lot used at the WA sites, and a Clatsop lot used at the OR sites. The Elite Partial Diallels were planted according to a completely randomized design. Only one control was used (the Grays Harbor standard).

Partial tests were planted on two sites in 1998 (one each in OR and WA) and a third was planted in 1999. The major (complete) planting in OR and WA was in winter 2000-1, with four

Local Diallel sites (about 39,400 trees planted representing 342 crosses) and five Elite Partial Diallel sites (about 26,400 trees planted representing 166 crosses). This set of tests is also fully replicated in BC as part of the HEMTIC testing program.

For the 2001 HEMTIC planting in WA and OR, 80 test trees were planted per family in a Local Diallel (20 trees in each of four test sites) and 125 test trees were planted for each family in an Elite Diallel (25 trees in each of five test sites). Single-tree plots were used in each case. These tests were planted at 2.4 m x 2.4 m spacing, or 1.8 m x 1.8 m spacing in cases where it was difficult to find a uniform site big enough to fit the trial at the wider spacing. Tests will be thinned by a factor of 50% (or thereabouts) at some point following the final assessment (e.g. at age 15).

All OR and WA HEMTIC tests have been planted in areas in which western hemlock is dominant or common, in areas with a strong maritime influence (within a few miles of the Pacific Ocean, or close to the Columbia river in one case), with high to adequate precipitation, and below 600 meters in elevation.

Two landowners have alos taken HEMTIC seedlings and planted tests in the Cascade range, one in northern WA and one in OR.

Family Blocks

100-tree full-sib family blocks were used in the HEMTIC program. These would increase the total number of trees planted per family in OR and WA to 180 or 205, and allow even more intense within-family selection. Blocks were planted in 2001 for 155 families, with about 22,500 trees planted in total. Full-sib selection blocks were adopted first by the radiata pine program in New Zealand (SHELBOURNE *et al.,* 1986; JAYAWICKRAMA and CARSON, 2000) and later by the loblolly pine and slash pine programs in the southeastern USA (WHITE *et al.,* 1992; MCKEAND and BRIDGWATER, 1998).

Adaptability-Screening Tests

Adaptability has been given a high priority in forest tree improvement programs in the Pacific Northwest. Cold-hardiness is considered important for western hemlock for movement to higher latitudues and altitude. This trait has been shown to be strongly inherited in coastal Douglas-fir (AITKEN and ADAMS, 1997; O'NEILL *et al.,* 2001), and testing protocols have been developed for Douglas-fir (ANEKONDA *et al.,* 2000) and for western hemlock (HANNERZ *et al.,* 1999). Variation in budburst, budset and cold-hardiness within sources can be larger than variation among sources (WHEELER *et al.,* 1990). Preliminary work on western hemlock has shown a moderate genetic component to spring frost injury and that some fast-growing families had a low incidence of injury (HANNERZ *et al.,* 1999). A weak, statistically significant and adverse family-mean correlation (0.22) was shown between age-four height growth and spring frost injury (HANNERZ *et al.,* 1999).

We do not yet have estimates how well traits such as budburst and frost injury correlate with rotation-age volume or rotation-age value. The main benefit would therefore be in predicting adaptability in the establishment and early- juvenile phases (i.e. to age 10 or so), on sites at higher elevation than those sampled in the first- and second-generation tests. An appropriate strategy for adaptability testing is to be formulated shortly.

Selection Age and Selection Procedure

First-generation NWTIC tests were usually measured five, 10 and 15 years from sowing. The optimum age for selecting western hemlock has not be studied intensively. Based on studies in other temperate conifers (e.g. JOHNSON *et al.,* 1997; HAAPANEN, 2001; LAMBETH and DILL, 2001) we could expect that final measurement and selection at around 1/4 to 1/3 rotation (i.e. around 12 years from planting) would be efficient.

Gain Expectations and Projections

The large number of first-generation parents tested allowed a high selection intensity (in the order of 1 in 10 for the Main program, 1 in 60 for the Elite population). It was estimated that an orchard population of 60 trees drawn from the second-generation tests could yield about 22.4% gain in age-15 height when compared to the base population (KING, J. N. and D. W. CRESS, 1991). Breeding plan proposal for western hemlock cooperative tree improvement. Unpublished HEMTIC Report). Age-8 results from genetic gain trials in BC indicate that elite crosses have in the order of 30% height gain (unpublished data from CHARLIE CARTWRIGHT, BC Ministry of Forests, Cowichan Lake Research Station, Mesachie Lake, BC; WOODS *et al.* 1995).

Third, the gain prediction listed above assumes that all provenances have the same growth potential. In reality it is more likely that one or more of the provenances will prove highly productive. The use of a fast-growing non-local provenance has been known to add a boost of gain comparable to a full generation of breeding and testing. As stated by ZOBEL and TALBERT (1984), "the largest, cheapest and fastest gains in most forest tree improvement programs can be made by assuring the use of the proper species and seed sources within species". Early age-4 results from a trial in Vancouver Island showed open-pollinated families from Grays Harbor, with a selection intensity of 1:10 and expected average gain of 8%, to be taller than full-sib crosses from southeastern BC with selection intensity of 1:30 and expected average gain of 18%; this could be an early indication of superior growth of the Grays Harbor provenance (HANNERZ *et al.,* 1999).

Deployment

Seed Movement and Transfer

Seed Zones and Adaptability

There has been much debate and concern in western OR and WA about seed transfer of forest tree species, and the consequences of establishing plantations using "off-site" seed. This led to such developments as the generic 1966 Seed Zone Map (WESTERN TREE SEED COUNCIL, 1966), and more recently to species-specific seed zones (RANDALL, 1996). In the revised system, eight seed zones are specified for western hemlock in OR and six in WA. The zones are further subdivided into 1,000 ft elevation bands. Overall, the revised zones tend to be much larger than the 1966 zones, and are long in the north/south direction, and narrower in the east/west direction. The zones for western hemlock are larger than for Douglas-fir in the same area. It should be pointed out, however, that this zone delineation was not based on comprehensive provenance tests (although there were some short-term common-garden studies). Growers in WA and OR are also unable to capitalize on gains from using fast-growing non-local sources, such as has been practiced for loblolly pine in the southeastern USA (ZOBEL and TALBERT, 1984); current data do not allow such choices.

The Ministry of Forests developed seed zones for BC to meet the same need as the seed zones in OR and WA. Most genetic variation is attributable to elevation, longitude, and latitude. Guidelines on seed transfer for western hemlock rest on open-pollinated trial series planted in 1979; in this series 29 parent trees originating from 10 to 850 m elevation were planted out on sites ranging from 150 to 1100 m. Breeders looked at rank changes for height and dbh (age 10 and age 15 data) and concluded that 0-600 m to be one zone (thus growers could move seed from a parent originating at 50 m to 550 m etc.) but a sharp change seemed to occur around 600 m. The Ministry of Forests therefore allows transfer limits of 0 to 600 m, within a latitude band of up to 6o 30' for a given set of orchards (ANONYMOUS, 1995).

There is now evidence from age-6 data that full-sib crosses from Gray Harbor can outgrow local BC hemlock at 700 m in the counterpart of the Cascades Mountains in BC, while showing good survival (unpublished data, Charlie Cartwright, BC Ministry of Forests, Cowichan Lake Research Station, Mesachie Lake, BC). This is encouraging for HEMTIC members wishing to deploy HEMTIC seedlings in the OR Cascades, and for those contemplating broader transfers along the OR/WA coast.

Operational Experience on Seed Transfer

Western hemlock has been deployed slightly further east than the origin of the parent trees in OR for a couple of decades. Crown Zellerbach Corp. was the pioneer in this respect, and later purchasers of their landbase have continued this work. Prior to 1990 this was with unimproved seed, since then, the seed source in the last ten years has been tested first-generation orchard seed. So far, there has been no evidence of maladaptation. More recently, coastal sources (< 300 m in origin) have been moved up to 500 m on occasion; the author is not aware of resultant plantation failures attributed to frost. Western hemlock has been grown successfully as an exotic as far away as the United Kingdom and Germany, which suggests it can adapt to distinct environments.

The transfer limit of 0 to 600 m in BC should be seen in the perspective when compared to OR and WA; 600 m in the BC Cascades gets persistent snow in the winter, which is unlikely at that elevation in OR and WA. Use of non-local western hemlock would probably be less risky in cases where the species occurs naturally in the area, whereas reforestation with western hemlock should proceed with caution on dry sites with little naturally occurring hemlock.

Options for future deployment and future testing

The second-generation (HEMTIC) population includes parents originating from 45° to 51° N, from sea level to 582 m elevation. This population should therefore have enough genetic variability to cope with a wide range of site conditions. Data from these tests will allow the following (i) establishment of second-generation seed orchards (ii) ability to use non-local first-generation parents in high-gain 1.5 generation orchards (by identifying widely adapted first-generation parents) and (iii) inferences on north-south transfer in the coastal zone. The main HEMTIC tests are located in a relatively narrow zone in the east-west direction, however, and will not allow inference on transfers far inland in the OR Coast Range or to the Cascades.

Seed Orchards, Seed Production and Producing Genetically Improved Planting Stock

First-Generation Orchard Establishment

Tree improvers in OR and WA had painful experiences with graft incompatibility in Douglas-fir (SILEN and COPES, 1972; SILEN and WHEAT, 1979). They were understandably reluctant to embrace grafted orchards for western hemlock. The first orchards were established in the period 1979–1983 by the Quinault Indian Nation, OR Department of Forestry, Crown Zellerbach Corp. and Georgia Pacific Corp.

First-generation orchards were eventually established by nine companies and agencies. Practitioners were relieved to find that either grafts or rooted cuttings were equally viable. Incompatibility did not prove to be an issue, even relatively mature trees (over 40 years) rooted well enough to establish orchards, and plagiotropic growth was not a problem. There has been no need to develop graft-compatible rootstock families, although it appears prudent to use fast-growing stock as rootstock. Potted orchards are an option in western hemlock (EASTHAM and ROSS, 1988; WEBBER, 2000) and have been used to a limited extent in OR and WA.

Seed Production

Orchard seed production was slow to get underway. The first orchard to produce significant quantities of seed being OR Department of Forestry's Schroeder orchard, which produced 14.5 kg in 1993. The buildup of seed production over time is illustrated in *Figure 1*, in which seed per ha. per year is plotted for four first-generation orchards. There was little or no seed produced during the first 10 years, followed by a very rapid increase. Part of this increase can be attributed to the gradual maturation and development of orchards, and part to techniques to stimulate seed production, applied widely starting in the 1990s. One reason for stimulating seed production was the increased demand due to the growing incidence of Swiss Needle Cast disease.

It now appears that a mature hemlock orchard can produce over 30 kg/ha/year. A combination of stem girdling (a single, complete circumferential cut on the stem made with a knife) and gibberellic acid (GA 4/7) injected to the stem is used to stimulate seed production. Seed counts vary from 440,000 to 550,000 per kg. This is much higher than for Douglas-fir; so while a Douglas-fir orchard may produce comparable amounts of kg/ha, the amount of hemlock seed / ha can be five or six times as high. At a conservative average of 312,000 plantable stock per kg. of seed, a mature well-managed orchard can produce the equivalent of 4.7 million improved stock per hectare per year. This assumes 15 kg seed/orchard ha/yr and a seed to plantable stock ratio of 3:2. Western hemlock ramets can be top-pruned and kept at a workable height, making orchard management less expensive without hurting seed production.

Western hemlock orchards on a variety of sites have produced seed, even in relatively wet locations in the OR coast range and on the moist west coast of the Olympic peninsula. However, *Figure 1* probably shows that orchards vary in their productive capacity: Orchard B is on a fertile valley site prone to summer drought while Orchard D is on a moist coastal site with relatively infertile soil. In general, sites prone to summer drought, such as the Willamette valley in OR, and the eastern fringe of the Olympic peninsula (Sequim and Whidbey Island) have been very productive. Irrigation is needed on such sites, letting ramets grow fast early on, and keeping them alive in very dry years. The Willamette Valley and the Sequim area have the added advantage of having little naturally occurring or planted hemlock, thereby reducing the contamination by low-gain wild pollen. Another factor for the differene in orchard production could be the intensity and timing of stimulation.

Producing and Deploying Genetically Improved Planting Stock

No figures are published on how many western hemlock seedlings are planted per year in western OR and WA. I asked 18 companies and public agencies for their planting estimates, and found that about 9.3 million western hemlock seedlings were planted in these two states in 2001, of which about 52 % originated from orchard seed, and the rest from unimproved seed (wild collections). Some companies can now use orchard

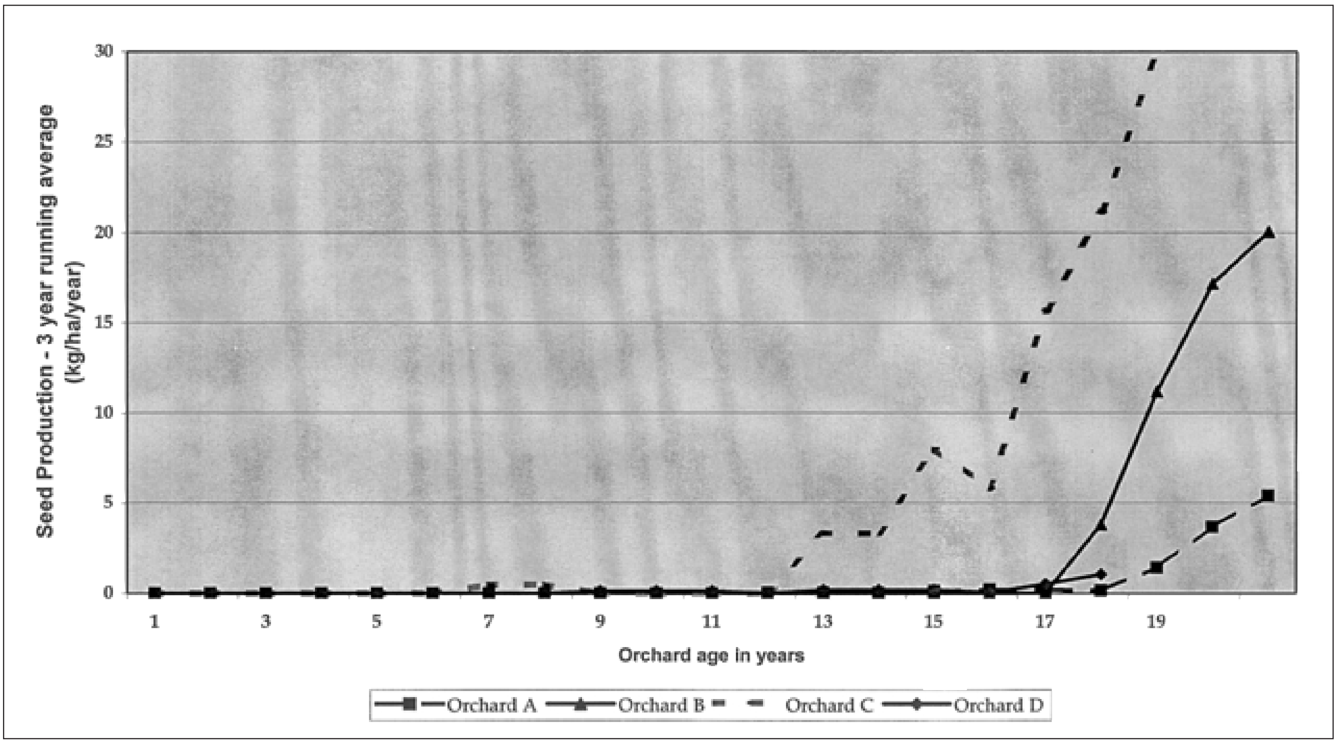

Figure 1. – Seed production as a function of orchard age for four first-generation western hemlock seed orchards from Oregon and Washington.

seed for all their reforestation. Western hemlock planting is still a relatively small proportion of the planting of forest tree species in OR and WA, given that an estimated 160 million seedlings were distributed from nurseries in these two states in 1997 (OKHOLM, 1997). For comparison, seedling use in neighboring BC for 2001 is estimated at 3.8 million, down from 5.7 million in 1995 (Forest Genetics Council of British Columbia, 2001).

Seedlings from these orchards are deployed as mixed-family lots (sometimes segregated to elite-1, elite-2, non-elite etc) for the most part, although at least one landowner is planting large single-family blocks. Orchard stock is being deployed up to 900 m elevation in the OR coast range. Western hemlock is planted both as a pure species and in species mixtures. In the past 1+1 (ROSE and MORGAN, 2000) and other types of bareroot seedlings were the norm for western hemlock, but landowners are increasingly turning to containerized planting stock.

Current Developments and Short-Term Prospects

New Orchards and Rooted Cuttings

Several members of HEMTIC have established high-gain 1.5 generation orchards, including the best parents from adjacent first-generation programs. These orchards are expected to start producing seed in the near future. Cone and seed production is reported to begin as early as one year after rooting cuttings from mature trees (PIESCH, 1972; 1976); it remains to be seen if we can repeat this success. There is the option of making early selections from the first US-based HEMTIC tests, and the BC-based HEMTIC tests, starting probably around 2003. The merits and potential gains from different selection scenarios (ratios of first-generation parents: second-generation progeny in orchards, age of selection etc) are to be evaluated shortly.

There is real potential to improve the ratio of improved to unimproved stock with the use of rooted cuttings. It has been apparent for years that western hemlock is easier to root than Douglas-fir (e.g. PIESCH, 1976; FOSTER *et al.,* 1985; PACKEE, 1990; WIGMORE and WOODS, 2000). Even for landowners who own orchards, this technique can be used to shift production from a broader group of lower average gain to a top group of high-gain parents. Rooted cuttings can also be used to bulk-up seed from the new, high-gain 1.5 generation orchards until these enter heavy production.

Controlled mass pollination (CMP) also needs to be strongly considered as an option, either as a means to produce high-gain seed for bulking up via rooted cuttings, or as a means to produce seed for seedlings. Even with the top group of orchard parents, further gains could be obtained by crossing the very best for use on the most productive sites. Based on the estimate mentioned earlier of 500 seed per pollination bag on a productive orchard site, and assuming 50 bags for a large ramet, we could produce as much as 25,000 high-gain controlled pollinated seed from a single large ramet in one year. The seed cost per seedling for CMP may be as low as 0.06 Canadian $ (unpublished data, P. BROWN, Canadian Forest Products Ltd, Sechelt, BC, Canada).

I modelled the production of genetically improved stock over time for four scenarios. In the first, I used the average seed production of the four orchards shown in *Figure 1*, and a conversion ratio of 312,000 plantable stock per kg. seed. In the second, I assumed that all seed were grown to produce stoolbeds, and 25 plantable stock were produced from each stoolbed a year later. A yield of 25 plantable stock per stoolbed is conservative, given that results in WIGMORE and WOODS (2000) from eight crosses suggest an average yield of 50 per stoolbed. In the third, I assumed that the entire seed production curve could be brought forward three years compared to the old orchards, based on aggressive orchard management and modern stimulation techniques. In the fourth, I combined the rolling forward with the use of rooted cuttings. These scenarios are presented in *Figure 2*, and underscore the potential to dramatically reduce the time delay between orchard establishment and delivery of genetically-improved stock to plantations. For example, the number of plantable stock grows very slowly in scenario one till age 12, steps up till age 16 and then leaps up after age 17. Under scenario four, it would be possible to reach 300,000 plantable stock per orchard hectare five years from orchard establishment, compared with 13 years for scenario one.

The potential is enormous: taken to an extreme in which all the seed from a mature orchard producing 15 kg/ha/ year were put into stoolbeds, one orchard hectare could produce 118 million genetically improved cuttings per year, enough to meet all planting needs in western OR and WA several times over! The labor needed for harvesting and setting cuttings on such a huge scale will naturally prove prohibitive. It is far more likely that a company may use cuttings to reach a goal of 250,000 to 500,000 trees per year, until the orchard is old enough to produce the required amount of seed. It should be noted that cuttings are likely to be more expensive to grow than seedlings (WIGMORE and WOODS, 2000).

There is need for a new thinking and a clear strategy on future orchard establishment. On the one hand, large orchards will eventually produce far more seed than are needed. On the other hand, small orchards will take longer to meet the planting needs, and will be more susceptible to low-gain pollen contamination. Small orchards, combined with controlled mass pollination and multiplication via rooted cuttings, may be the most logical approach.

Improving Wood Quality

Wood density, average fiber length and fiber coarseness appear to be strongly inherited (KING *et al.,* 1998), so that it is safe to say that wood and fiber properties could be improved by genetic selection with the right approach. KING *et al.* (1997; 1998) advocated improving the fiber properties of western hemlock to improve pulpwood value, and also give some early information on stiffness and strength testing.

It is time to review some paradigms on wood quality and wood quality improvement, in light of current realities and knowledge. First, as pointed out earlier, many perceptions on the relative merits of Douglas-fir vs. western hemlock are based on old-growth and unmanaged second-growth forests. It is always relevant to question how much of those perceptions apply to intensively managed plantations. Second, there may be incentives to look beyond wood density alone. It is being recognized that stiffness in juvenile wood may be as much controlled by microfibril angle as by density (CAVE and WALKER, 1994; COWN *et al.,* 2000), with some arguing that the case for wood density as the single controlling factor has been overstated. Relative density was shown to drop from 0.44 at the pith to 0.38 at ring 15 in one study on second-growth western hemlock; however, MOE increased from 7.2 to 11.5 GPa over the same range of rings (KENNEDY, 1995). Microfibril angle was shown to decrease from about 30° to about 22° over the same range in a different study on second-growth western hemlock FABRIS (2000). Mean relative density observed by FABRIS (2000) was actually higher for western hemlock than for Douglas-fir for the first eight rings from the pith. Third, technologies for measuring wood properties and wood quality are changing rapidly. For example, there are new and faster methods to measure microfibril angle and even traits (such as stiffness and strength) which are closer to the end-product. Preliminary results indicate that microfibril angle is heritable in western hemlock (unpublished data from CHARLIE CARTWRIGHT, BC Ministry of Forests, Cowichan Lake Research Station, Mesachie Lake, BC). This preceding discussion does not imply that all existing perceptions on hemlock wood quality are invalid, but rather that critical review is indicated.

Very large differences for stiffness, sometimes larger than for density, have been shown between genetic entries. SHELBOURNE *et al.* (1997) reported radiata pine clone means to vary from 7.1 to 13.8 GPa for Modulus of Elasticity, compared to 354 to 438 kg/m^3 for whole-tree basic density. Similarly MOE clone means for Douglas-fir ranged from 9 to 13 GPa in one study in France (LAUNAY *et al.,* 2000) and MOE clone means for sugi (*Cryptomeria japonica*) were shown to vary from 2.8 to 7.2 GPa

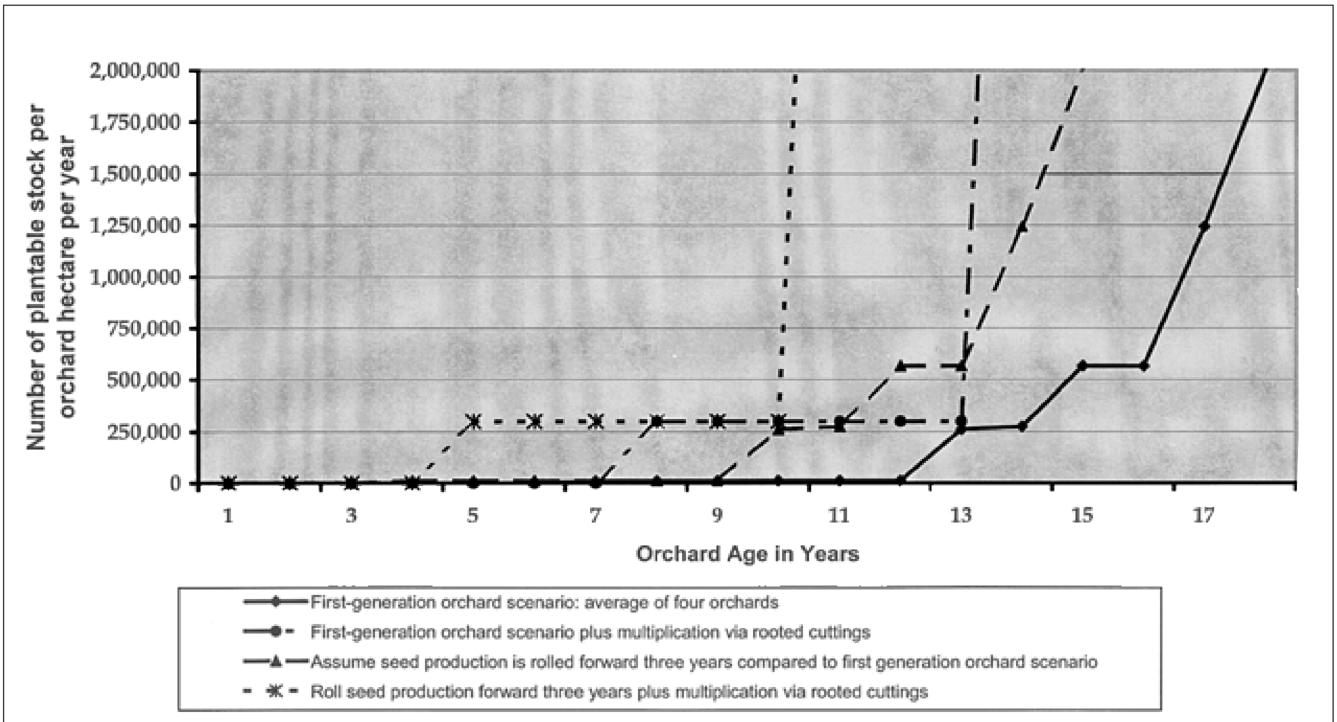

Figure 2. – Rate of delivery of genetically improved western hemlock planting stock to plantations for four scenarios.

(OHTA and FUJISAWA, 1997). In another study on 12 sugi clones grown on six common sites, 65 % of the variation in modulus of elasticity could be attributed to clones while only 4.7 % could be attributed to sites (FUJISAWA *et al.,* 1994). A number of direct and indirect tests for stiffness and strength are being developed, some suitable on standing trees for ranking genetic entries (e.g. LAUNAY *et al.,* 2000; JAYAWICKRAMA, 2001b). Given that western hemlock is penalized for being considered less stiff and strong than Douglas-fir, and given that Swiss Needle Cast disease makes Douglas-fir less competitive on moist coastal sites, there may be a real opportunity to progress a high-wood-stiffness breed of western hemlock.

We could exploit provenance variation in wood properties, if it occurs in western hemlock as reported for Douglas-fir (LOO-DINKINS *et al.,* 1991) and loblolly pine (BYRAM and LOWE, 1988; TAUER and LOO-DINKINS, 1990), in addition to within-provenance variation. The logical place to look for such variation, for wood density and other properties, would be in the second-generation test population. Provenance and within-provenance variation in wood properties could be exploited by the use of parental and forwards selection. The fastest way to get gain for wood properties would be to re-rank first-generation orchard parents (eg. for wood density, stiffness and strength), and to make controlled crosses or collect seed preferentially based on wood quality rankings. We could follow the precedent set by the New Zealand radiata pine program. That program has ranked top production parents for wood density and grain spirality and is now ranking them for wood stiffness (VINCENT, 1997; NZFRI 1997; JAYAWICKRAMA, 2001b). Forwards selections could also be selected and used in breeding and production populations as appropriate.

Hemlock millers, growers and tree improvers alike have some marketing opportunities. Hemlock lumber seems to be penalized too heavily in price compared to Douglas-fir, if the only issue is lower strength and stiffness. For example, it can be inferred from span tables in WWPA (1999b) that using only 5–10 % more Hem-Fir lumber (than would be needed if the same building was made using Douglas-fir Larch lumber) for a given building would meet design specifications, yet the lumber value of hemlock (removing log transport costs) can be as low as 60 % that of Douglas-fir. Lumping together all western hemlock grown in OR and WA with five true fir species, as now practiced in grading (AF&PA, 1997b), penalizes western hemlock which has better strength properties than others in the species group (RICHEN, 1976). Visual grading according to species groups, which is the main way Western lumber is graded, is inefficient compared to Mechanical Stress Rating (MSR) in which each piece of timber is treated on its own merits and tested individually. MSR would, for example, pick up differences between species, between lumber from different regions, and between lumber from different parts of the tree. Thus hemlock growers would appear to benefit (by better returns) from updated grading rules, segregation by species, and quantitative measures of stiffness and strength.

Cascade western hemlock

As mentioned earlier, work is underway (although on a smaller scale) to test second-generation coastal hemlock in the Cascades. At present the Bureau of Land Management has no plans to take its Cascade hemlock program into a second-generation of breeding and testing.

Getting Genetic Gain in western hemlock

Despite its "step-child" status compared to Douglas-fir, it may paradoxically be possible to get higher levels of genetic gain in this species. First, there has been less concern about merging breeding zones, and to date it appears that long north-south transfers are feasible. This could allow a large boost of gain by using fast-growing non-local sources. Second, orchardists and breeders have not had to fight graft incompatibility. This resulted in the use of parental clones in the orchards, in contrast to the widespread use of full-sib seedling orchards as in the case of Douglas-fir in the 1970s (SILEN and WHEAT, 1979). Third, some of the premier seed orchard locations have little naturally occurring or planted western hemlock nearby, resulting in less low-gain pollen contamination. Fourth, western hemlock is a prolific seeder allowing for lots of seed per controlled cross; this can be exploited in easier and faster breeding, and the use of cost-effective, high-gain control-pollinated seed. Fifth, the rootability of western hemlock cuttings can be exploited to shift production to higher-gain seedlots (including controlled crosses between elite parents) and to reduce the time delay in getting stock from new, elite genotypes into operational plantations (as outlined in the previous section). Prolific seeding combined with rootability also translates to a higher productivity in terms of genetically improved stock per orchard acre, perhaps 125 times as high as for Douglas-fir. The fact that hemlock orchards can be top-pruned with less effect on seed production is also a factor in reducing the cost of orchard management.

Clonal forestry as a method for deployment and / or clonal testing of the breeding population may become options for western hemlock, as they may for any major temperate conifer. The reliability and cost of propagation technologies, confidence on gains addeds as a result, and public perceptions will all play a part in applying these techniques for western hemlock in OR and WA.

Acknowledgments

Crown Zellerbach Corp, OR Department of Forestry, Quinault Indian Nation, Rayonier Co., Simpson Timber Co., USDA Forest Service, and USDI Bureau of Land Management were the first organizations to undertake western hemlock genetic improvement in OR and WA. R. SILEN (USDA Forest Service – PNW Research station) and J. WHEAT (Industrial Forestry Association) were promoters and leaders of co-operative tree improvement in the region, for western hemlock and other species, between 1966 and 1985. US-based HEMTIC members are Boise Cascade Corp., USDI Bureau of Land Management, Crown Pacific Ltd., Hampton Tree Farms, Inc., OR Department of Forestry, Quinault Indian Nation, Rayonier Timberlands Operating Co., Simpson Timber Co., Plum Creek Timber Co., The Campbell Group and Willamette Industries Inc. J. KING, D. CRESS, M. BORDELON (OR Department of Forestry) and J. HARGROVE (Quinault Indian Nation) played key roles in forming HEMTIC. J. KING and C. CARTWRIGHT (BC Ministry of Forests) and D. CRESS (NWTIC) have provided technical direction for HEMTIC, which operates within the Northwest Tree Improvement Cooperative (NWTIC). D. CRESS and J. KING ran the unpublished NWTIC analyses quoted in this paper. J. HARGROVE has served as HEMTIC Chair for many years, and T. WILLIAMS played a major role in establishing the tests planted in 2001 in OR and WA. I thank J. HARGROVE, R. QUAM (OR Department of Forestry), W. SCHLATTER (Willamette Industries, Inc.) and J. SMITH (Plum Creek Timber Company) for insights on seed production. I also thank C. CARTWRIGHT, D. HAMLIN (The Campbell Group), G. R. JOHNSON (USFS-PNW station), R. GUPTA, S. LIPOW, M. NEWTON, two journal reviewers and most particularly D. CRESS (OR State University), for helpful comments on this paper, and M. MURK for formatting the manuscript for publication.

References

ADAMS, W. T., WHITE, T. L., HODGE, G. R. and POWELL, G. L.: Genetic parameters for bole volume in longleaf pine: large sample estimates and influences of test characteristics. Silvae Genet. **43**: 357–366 (1994). — AF&PA: National design specification for wood construction-supplement American Forest & Paper Association (1997a). — AF&PA: National design specification for wood construction-commentary American Forest & Paper Association (1997b). — AITKEN, S. N. and ADAMS, W. T.: Spring cold hardiness under strong genetic control in Oregon populations of *Pseudotsuga menziesii* var *menziesii.* Can. J. For. Res. **27**: 1773–1780 (1997). — ANEKONDA, T. S. and ADAMS, W. T.: Cold hardiness testing for Douglas-fir tree improvement programs: guidelines for a simple, robust and inexpensive screening method. West. J. Appl. For. **15**: 129–136. (2000). — ANONYMOUS: Forest Practices Code of British Columbia. Seed and Vegetative Material Guidebook, April 1995 (1995). — BOLSINGER, C. L., MCKAY, N., GEDNEY, D. R. and ALERICH, C.: Washington's public and private forests. USDA Forest Serv. Resource Bull. PNW-218 (1997). — BYRAM, T. D. and LOWE, W. J.: Specific gravity variation in a loblolly pine seed source study in the western Gulf region. For. Sci. **34**: 798–803 (1988). — CAVE, I. D. and WALKER, J. C. F.: Stiffness of wood in fast-grown plantation softwoods: the influence of microfibril angle. For. Prod. J. **44**(5): 43–38 (1994). — COWN, D. J., HEBERT, J. and BALL, R.: Modelling *Pinus radiata* lumber characteristics. Part 1: Mechanical properties of small clears. N. Z. J. For. Sci. **29**: 203–213 (2000). — EASTHAM, A. M. and ROSS, S. D.: Comparison of production systems in potted western hemlock orchards. *In:* WORRALL, J., LOO-DINKINS, J. and LESTER, D. P (Ed). "Physiology And Genetics Of Reforestation", Proc. 10th North American Forest Biology Workshop, July 10–22, 1988, Vancouver, British Columbia. University of British Columbia, Vancouver, BC. pp. 141–148 (1988). — EVANS, J. W. and GREEN, D. W.: Mechanical properties of visually graded lumber: Volume 3, Hem-Fir. USDA Forest Service Forest Products Laboratory, One Gifford Pinchot Drive, Madison, WI 53705-2398. (1987). — FABRIS, S.: Influence of cambial ageing, initial spacing, stem taper and growth rate on the wood quality of three coastal conifers. PhD Thesis, Department of Forestry, University of British Columbia. 250 p. (2000). — Forest Genetics Council of British Columbia: Business Plan 2001-2002. (2001). — FOSTER, G. S. and LESTER, D. T.: Fifth-year height variation in western hemlock open-pollinated families growing on four test sites. Can. J. For. Res. **13**: 251–256 (1983). — FOSTER, G. S., CAMPBELL, R. K. and ADAMS, W. T.: Clonal selection prospects in western hemlock combining rooting traits with juvenile height growth. Can. J. For. Res. **15**: 488–493 (1985). — FUJISAWA, Y., OHTA, S., NISHIMURA, K., TODA, T. and TAJIMA, M.: Wood characteristics and genetic variations in Sugi (*Cryptomeria japonica*) III. Estimation of variance components of the variation in dynamic modulus of elasticity with plus-tree clones. Mokuzai Gakkaishi **40**(5): 457–464 (1994). — GREEN, D. W., WINANDY, J. E. and KRETSCHMANN, D. E.: Mechanical properties of wood. Pp. 4-1 to 4-45 *In:* Wood Handbook: Wood as an engineering material. Reprinted from USDA Forest Service General Technical Report FPL-GTR-113. For. Prod. Soc. (1999). — HAAPANEN, M.: Time trends in genetic parameter estimates and selection efficiency for Scots pine in relation to field testing method. For. Gen. **8**: 129–144. (2001). — HANNERZ, M., AITKEN, S. N., KING, J. N. and BUDGE, S.: Effect of genetic selection for growth on frost hardiness in western hemlock. Can. J. For. Res. **29**: 509–516 (1999). — HANSEN, E. M., STONE, J. K., CAPITANO, B. R., ROSSO, P., SUTTON, W., WINTON, L., KANASKIE, A. and MCWILLIAMS, M. G.: Incidence and impact of Swiss needle cast in forest plantations of Douglas-fir in coastal Oregon. Plant Disease **84**: 773–778 (2000). — HODGE, G. R. and WHITE, T. L.: Genetic parameter estimates for growth traits at different ages in slash pine and some implications for breeding. Silvae Genet. **41**: 252–262. (1992). — JAYAWICKRAMA, K. J. S.: Genetic parameter estimates for radiata pine in New Zealand and New South Wales: A synthesis of results. Silvae Genet. **50**: 45–53 (2001a). — JAYAWICKRAMA, K. J. S.: Breeding radiata pine for wood stiffness: review and analysis. Australian Forestry **64**: 51–56 (2001 b). — JAYAWICKRAMA, K. J. S. and CARSON, M. J.: A breeding strategy for the New Zealand Radiata Pine Breeding Cooperative. Silvae Genet. **49**: 82–90 (2000). — JOHNSON, G. R., SNIEZKO, R. A. and MANDEL, N. L.: Age trends in Douglas-fir genetic parameters and implications for optimum selection age. Silvae Genet. **46**: 349–358 (1997). — KENNEDY, R. W.: Coniferous wood quality in the future: concerns and strategies. Wood Sci. Tech. **29**: 321–338 (1995). — KING, J. N.: The significance of geographic variation patterns for western hemlock genetic improvement. Proc. Joint Meeting of Western Forest Genetics Association and IUFRO Working Parties S2.02-05, 06, 12 and 14. Douglas-fir, Contorta Pine, Sitka Spruce and Abies Breeding and Genetic Resources. August 20–24, 1990, Olympia, Washington (1990). — KING, J. N., CARTWRIGHT, C., GEE, W., HATTON, J. and ELLIS, S.: The potential for improving western hemlock pulp, paper and structural wood quality. *In:* ZHANG, S. Y., GOSSELIN, R., and CHAURET, G. (Ed). "Timber Management Toward Wood Quality and End-Product Value". Proc. CTIA/IUFRO International Wood Quality Workshop. August 18–22, 1997, Quebec City, Canada. Pp. IV-101 to IV-104 (1997). — KING, J. N., CARTWRIGHT, C., HATTON, J. and YANCHUK, A. D.: The potential of improving western hemlock pulp and paper quality. I. Genetic control and interrelationships of wood and fibre traits. Can. J. For. Res. **28**: 863–870 (1998). — KLEINSCHMIT, J. and BASTIEN, J. CH.: IUFRO's role in Douglas-fir (*Pseudotsuga Menziesii* (Mirb.) Franco) tree improvement. Silvae Genet. **41**: 161–173 (1992). — KRAJINA, V. J., KLINKA, K. and WORRALL, J.: Distribution and ecological characteristics of trees and shrubs of British Columbia. Faculty of Forestry, The University of British Columbia (1982). — KUSER, J. E. and CHING, K. K.: Provenance variation in phenology and cold hardiness of western hemlock seedlings. For. Sci. **26**: 463–470 (1980). — LAMBETH, C. and DILL, L. A.: Prediction models for juvenile-mature correlations for loblolly pine growth traits with, between and across test sites. For. Gen. **8**: 101–108 (2001). — LAUNAY, J., ROZENBERG, P., PACQUES, L., DEWITTE, J.-M.: A new experimental device for rapid measurement of the trunk equivalent modulus of elasticity on standing trees. Ann. For. Sci. **57**: 351–359 (2000). — LIPOW, S. R., ST. CLAIR, J. B. and JOHNSON, G. R.: Ex situ gene conservation for conifers in the Pacific Northwest. USDA Forest Service General Technical Report (in press). — LOO-DINKINS, J. A., YING, C. C. and HAMM, E. A.: Stem volume and wood relative density of a non-local Douglas-fir provenance in British Columbia. Silvae Genet. **40**: 29–35 (1991). — MCKEAND, S. E. and BRIDGWATER, F. W.: A strategy for the third breeding cycle of loblolly pine in the south-eastern U.S. Silvae Genet. **47**: 223–234 (1998). — NZFOA 2001: NZ Forest Industry Facts & Figures. Published jointly by NZ Forest Owners Assoc., NZ Ministry of Agriculture & Forestry and the NZ Forest Industries Council (2001). — NZFRI: GF Plus, Juvenile wood quality index. NZFRI Research Directions No. 18, December 1997. New Zealand Forest Research Institute Ltd., Rotorua, New Zealand. 15 p. (1997). — OHTA, S. and FUJISAWA, Y.: Wood quality improvement of SUGI (*Cryptomeria japonica*) required by end users. *In:* ZHANG, S. Y., GOSSELIN, R., and CHAURET, G. (Ed): "Timber Management Toward Wood Quality and End-Product Value". Proc. CTIA/IUFRO International Wood Quality Workshop. August 18–22, 1997, Quebec City, Canada. Pp. IV-69 to IV-75 (1997). — OKHOLM, D.: Pacific Northwest Nursery Directory and Report. Pub. No. R6-CP-TP-97. USDA Forest Service, State and Private Forestry. Portland, Oregon. 62p. (1997). — OMULE, S. A. Y.: Comparative height growth to age 28 for seven species in the CWHd subsone. FRDA report 5. Canadian Forestry Service and British Columbia Ministry of Forests and Lands. 9 p. (1987). — O'NEILL, G. A., ADAMS, W. T. and AITKEN, S. N.: Quantitative genetics of spring and fall cold hardiness in seedlings from two Oregon populations of coastal Douglas-fir. For. Ecol. Manage. **149**: 305–318. (2001). — PACKEE, E. C.: *Tsuga heterophylla* (Raf.) Sarg. Western Hemlock. *In:* BURNS, R. M. and HONKALA, B. H., Silvics of North America Volume 1, Conifers. USDA Forest Service Agriculture Handbook 654. pp 613–621 (1990). — PIESCH, R. F.: Cone and seed production of one-year-old rooted cuttings of western hemlock. Can. J. For. Res. **2**: 370–371 (1972). — PIESCH, R. F.: Tree improvement in western hemlock. *In:* ATKINSON, W. A. and ZASOSKI, R. J. (Ed): Proc. Western Hemlock Management Conference, May 1976. College of Forest Resources, University of Washington. Pp. 155–165 (1976). — POLLARD, D. F. W. and PORTLOCK, F. T.: Intraspecific variation in stem growth of western hemlock. Can. J. For. Res. **16**: 149–151 (1986). — PONZONI, R. W. and NEWMAN, S.: Developing breeding objectives for Australian beef cattle production. Anim. Prod. **49**: 35–47 (1989). — RANDALL, W. K.: Forest tree seed zones for western Oregon. State of Oregon Department of Forestry (1996). — RICHEN, C. W.: Attitude of management toward western hemlock. *In:* ATKINSON, W. A. and ZASOSKI, R. J. (Ed). Proc. Western Hemlock Management Conference, May 1976. College of Forest Resources, University of Washington. Pp. 7–9. (1976). — ROSE, R. and MORGAN, P.: Guide to reforestation in western Oregon. Oregon Department of Forestry and College of Forestry, Oregon State University, Corvallis, OR 97331, USA (2000). — SCHULZ, W. M. and COCKERHAM, C. C.: The effects of field blocking on gain from selection. Biometrics **22**(4): 843–863 (1966). — SHELBOURNE, C. J. A.: Genetics of adding value to the end-products of radiata pine. *In:* BURDON, R. D., MOORE, J. M. (Ed): "IUFRO '97 Genetics of Radiata Pine". Proc. NZ FRI-IUFRO Conference 1-4 December and Workshop 5 December, Rotorua, New Zealand. FRI Bulletin No. 203. pp. 129–141 (1997). — SHELBOURNE, C. J. A., BURDON, R. D., CARSON, S. D., FIRTH, A. and VINCENT, T. G.: Development plan for radiata pine breeding. Forest Research Institute, Rotorua, New Zealand (1986). — SILEN, R. R.: Regeneration aspects of the 50-year-old Douglas Fir heredity study. *In:* Proc. 1964 Annual Meeting of Western Reforestation Coordinating Committee, Nov. 30 and Dec. 1 1964, Spokane, Washington. (1964). — SILEN, R. R.: A simple progressive tree improvement program for Douglas-fir. USDA For. Serv. Res. Note PNW-45. 13 p. (1966). — SILEN, R. R. and COPES, D. L.: Douglas-fir seed orchard problems – A progress report. J. For. **70**: 145–147 (1972). — SILEN, R. R. and WHEAT, J. G.: Progressive tree improvement program in Coastal Douglas-fir. J. For. **77**: 78–83 (1979). — STEINBRENNER, E. C.: Soil-site relationships and comparative yields of western hemlock and Douglas-fir. *In:* ATKINSON, W. A. and ZASOSKI, R. J. (Ed): Proc. Western Hemlock Management Conference, May 1976. College of Forest Resources, University of Washington. Pp. 236–238 (1976). — STONECYPHER, R. W., PIESCH, R. F., HELLAND, G. G., CHAPMEN, J. G. and RENO, J.: Results from genetic tests of selected parents of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) in an applied tree improvement program. For. Sci. **42**(2) Monograph 32. (1996). — TAEUR, C. G. and LOO-DINKINS, J. A.: Seed source variation in specific gravity of loblolly pine grown in a common environment in Arkansas. For. Sci. **36**: 1133–1145 (1990). — TALBERT, J. T.: An advanced-generation breeding plan for the N.C. State University – Industry Pine Tree Improvement Cooperative. Silvae Genet. **28**: 72–75. (1979). — VINCENT, T. G.: Radiata pine breeding. New Zealand Tree Grower **18**(2): 21–24 (1997). — WAKELY, P. C. and BERCAW, T. E.: Loblolly pine provenance test at age 35. J. For. **63**: 168–174 (1965). — WARING, R. H. and FRANKLIN, J. F.: Evergreen coniferous forests of the Pacific Northwest. Science **204**: 1380–1386 (1979). — WEBBER, J. E.: Western hemlock: a manual for tree improvement seed production. British Columbia Ministry of Forests Research Program. Working Paper 44/2000. (2000). — WELLS, O. O. and WAKELY, P. C.: Geographic variation in survival, growth and fusiform-rust infection of planted loblolly pine. Forest Science monograph 11. (1966). — WESTERN TREE SEED COUNCIL.: State of Oregon: tree seed zone map. 1:500,000. Lambert conformed conic projection. colored. USDA Forest Service, Portland, Oregon. (1966). — WHEELER, N. C., STONECYPHER, R. W. and JECH, K. S.: Physiological characterization of select families to aid in source movement decisions: supplementing long-term performance trials. *In:* Proc. Joint meeting of Western Forest Genetics Association and IUFRO Working Parties S2.02-05, 06, 12 and 14. Douglas-fir, Contorta pine, Sitka spruce and Abies Breeding and Genetic Resources. August 20–24, 1990. Olympia, Washington, USA. (2000). — WHITE, T. L. and CHING, K. K.: Provenance study of Douglas-Fir in the Pacific Northwest Region IV. Field Performance at Age 25 Years. Silvae Genet. **34**: 84–90 (1985). — WHITE, T. L., HODGE, G. R. and POWELL, G. L.: An advanced-generation tree improvement plan for slash pine in the southeastern United States. Silvae Genet. **42**: 359–371 (1992). — WIGMORE, B. G. and WOODS, J. H.: Cultural procedures for propagation of rooted cuttings of Sitka Spruce, western hemlock and Douglas-fir in British Columbia. Research Branch, BC Ministry of Forests, Victoria, BC. Working Paper 46/2000. (2000). — WILEY, K. N.: Site index and yield of western hemlock. *In:* ATKINSON, W.A. and ZASOSKI, R.J. (Ed). Proc. Western Hemlock Management Conference, May 1976. College of Forest Resources, University of Washington. Pp. 228–235. (1976). — WOODS, J. W., KING, J. and CARTWRIGHT, C.: Early genetic gains verified in realized-gain trials of coastal Douglas-fir and western hemlock. Extension Note 01, British Columbia Ministry of Forests Research Branch, 31 Bastion Square, Victoria, British Columbia. (1995). — WOOLASTON, R. R. and JARVIS, S. F.: The importance of breeding objectives in forest tree improvement. *In:* Proc. CRCTHF-IUFRO Conference on Eucalypt Plantations: Improving Fibre Yield and Quality. Hobart, Australia, 19–24 February 1995. pp. 184–188 (1995). — WWPA: Hem-Fir Species Facts. Western Wood Products Association (1997). — WWPA: 1999 Statistical Yearbook of the Western Lumber Industry. Western Wood Products Association P. 27. (1999a). — WWPA: Western Lumber Product Use Manual. Western Wood Products Association (1999b). — WWPA: Coast F.O.B. Price Summary Nov. 2000. Report #11, Issued December 11, 2000. Western Wood Products Association (2000). — YANCHUK, A.: General and specific combining ability from disconnected partial diallels of coastal Douglas-fir. Silvae Genet. **45**: 37–45 (1996). — ZOBEL, B. and TALBERT, J.: Applied forest tree improvement. John Wiley & Sons, New York. (1984).

Quantitative Genetic Structure of Stem Form and Branching traits in Douglas-fir Seedlings and Implications for Early Selection

By J. J. VARGAS-HERNANDEZ[1], W. T. ADAMS and D. G. JOYCE[2]

Department of Forest Science, Oregon State University, Corvallis, OR 97331-7501

(Received 16th October 2002)

Abstract

Open-pollinated (OP) and full-sib (FS) families of coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) were grown in two replicated nursery regimes in order to evaluate the magnitude and repeatability of genetic parameter estimates for stem form (stem sinuosity, forking) and branching (number, length and angle of branches) traits in 2-year-old seedlings, and the relationships of these traits with stem growth. With data from older trees of the OP families growing in the field (ages 12 and 24), genetic control of similar traits was compared at the different ages, and nursery-field correlations (r_{xy}) were estimated. With the exception of forking, estimates of family heritability (h^2_f) were moderate to strong for stem form and branching traits in seedlings ($0.32 \le h^2_f \le 0.94$; mean = 0.73), and similar to growth traits ($0.45 \le h^2_f \le 0.90$; mean = 0.75). Family performance and estimates of genetic parameters were relatively stable across nursery regimes and family type. Genetic relationships among traits in seedlings were similar to those observed in older field-grown trees, indicating that these traits are controlled by similar sets of genes in the two age classes. Nursery-field correlations between comparable traits were consistent across nursery regimes, but r_{xy} was strong enough to be useful for early testing purposes (i.e., $| r_{xy} | \ge 0.30$), only for number of whorls with steep-angled branches (WSAB), branch length, and branch angle in older trees. Predicted gains from early selection for these or correlated traits were at least 40–50% of those expected from selection at older ages. Because of unfavorable genetic correlations, selection for stem growth potential alone at the seedling stage is expected to produce unfavorable impacts on WSAB and stem sinuosity in older trees. To avoid such negative effects on wood quality, both stem form and branching traits should be included as selection criteria in Douglas-fir breeding programs.

Key words: Pseudotsuga menziesii, stem sinuosity, forking, repeatability, wood quality, nursery-field correlations.

Introduction

Stem form and branching traits have important economic impacts on both wood quality and productivity of forest trees. Stem sinuosity, stem forking, and occurrence of branches that

[1] Current Address: Instituto de Recursos Naturales, Colegio de Postgraduados, Montecillo, Edo. de México, México 56230

[2] Current Address: Ontario Ministry of Natural Resources, P.O. Box 1000, Sault Ste. Marie, Ontario P6A 5N5