Economic Importance, Breeding Objectives and Achievements

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Economic Importance, Breeding Objectives and Achievements

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ABSTRACT

This chapter reviews the historical context, economic importance, objectives and achievements to-date for many of the more important conifers undergoing domestication through genetic improvement programs around the world. These provide examples of the context in which genomic technologies will have an impact in forestry. Unlike many other crop plants and livestock animals, forest trees have only been exposed to a few cycles of breeding and selection, and most retain very large amounts of genetic variation in natural populations. These factors present both opportunities and hurdles in the effective application of genomic technologies to existing operational breeding programs.

Keywords: operational tree breeding, plantation programs, breeding, selection, genetic testing, genomic technologies, molecular markers, quatitative trait loci, *Pinus, Picea, Pseudotsuga, Larix*, *Cryptomeria, Chamaecyparis, Cupressus, Thuja, Cunninghamia, Sequoia*

2.1 Introduction

Although conifers are generally regarded as undomesticated trees, genetic improvement through breeding, selection and testing has had a significant impact on the productivity and quality of plantations established in a wide variety of species worldwide. Many conifers have been the target

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For affiliations see at the end of this chapter on page 127.

of tree improvement efforts over the last 50 years, and many of these are now well into their second, third or even fourth cycle of breeding. In the context of these well-established programs, emerging genomic tools offer the greatest potential for immediate impact and deployment of benefits to production forests.

The purpose of this chapter is to describe the context in which genomics can have an impact on current breeding and reforestation of conifers. Descriptions are given for each species or group of species covering historical perspectives, economic importance, breeding objectives, and achievements to-date. In addition, some brief notes are given on the application of genomics technologies, particularly with respect to their current use, or lack thereof, in breeding and selection. While a wide range of species and programs are discussed (see Table 2-1), the list is not exhaustive, although we have attempted to capture some of the most important.

2.2 Pines—*Pinus* L.

The genus *Pinus* is the largest genus in the family Pinaceae and is widely distributed throughout the Northern Hemisphere, with as many as 100 recognized species (Richardson 1998). Many of these are of great economic importance for wood production and are the targets of intensive tree improvement programs, some of the more important of which are discussed here, organized as regional groups.

2.2.1 Northeastern North American Pines (Pinus strobus, P. resinosa, P. banksiana, and P. rigida)

2.2.1.1 Historical Perspective

Four pines grow in the northeast of North America, and all of them have played a major role in the development of this region. Eastern white pine (*Pinus strobus* L.) and red pine (*Pinus resinosa* Ait.) are both characteristic of the Great Lakes and St. Lawrence Forest Regions, where fire plays a role in the establishment of extensive stands (Whitney 1986). While jack pine (*Pinus banksiana* Lamb.) also occurs in the same region, it is primarily a boreal species that is also well adapted to forest fire. It bears serotinous cones, which allow the dispersion of quantities of viable seed following fire (Rudolph and Laidly 1990; Farrar 1995). Pitch pine (*Pinus rigida* Mill.) mainly grows in the Appalachians but in the northeast it can be seen on sandy soils of Pennsylvania, New Jersey, New York and Maine states. It can also be seen in isolated stands up to southern Quebec.

Eastern white pine and red pine were over harvested for many decades, owing to the huge size of the mature trees and their prized wood qualities.

Table 2-1 Species and programs discussed in this chapter.

Family/genus Species/group	Country programs discussed
Pines (*Pinus*)	
Northeastern North American pines (*Pinus strobus, P. resinosa, P. banksiana*, and *P. rigida*)	Canada, United States
Lodgepole Pine (*Pinus contorta*)	Canada, Sweden
Western White Pine (*Pinus monticola*)	Canada, Unites States
Southern Pines (*Pinus taeda, P. elliottii, P. palustris,* and *P. echinata*)	United States, Brazil, Argentina, China, South Africa, Swaziland, Zimbabwe, Australia
Maritime pine (*Pinus pinaster*)	France
Scots pine (*Pinus sylvestris*)	Sweden, Finland, Germany, France, Lithuania, Latvia, Poland, Spain
Radiata Pine (*Pinus radiata*)	New Zealand, Chile, Australia, Spain, South Africa
Spruces (*Picea*)	
Black spruce (*Picea mariana*)	Canada, United States
White spruce (*Picea glauca*)	Canada, United States
Red spruce (*Picea rubens*)	Canada
Sitka spruce (*Picea sitchensis*)	Canada, Great Britain
Norway spruce (*Picea abies*)	Norway, Sweden, Finland, Germany
Other Pinaceae	
Douglas-fir (*Pseudotsuga menziesii*)	Canada, United States, Germany, Belgium, Fance, Italy, Spain, United Kingdom, New Zealand, Argentina, Chile
Larches in Europe (*Larix* spp.)	France
Cypresses (Cupressaceae)	
Sugi (*Cryptomeria japonica*)	Japan
Other Cupressaceae including the whitecedars (*Chamaecyparis lawsoniana, C. nootkatensis, C. obtusa, C. pisifera*), the cypresses (*Cupressus lusitanica, C. macrocarpa, C, sempervirens*), the arborvitae (*Thuja plicata*), Chinese fir (*Cunninghamia lanceolata*), Coastal redwood (*Sequoia sempervirens*)	China, Japan, Korea, New Zealand, Greece, Italy, France, Canada, United States, Columbia, Mexico, El Salvador, Guatemala, Honduras, Kenya, Rwanda, Uganda, Tanzania, South Africa

They were especially suitable for ship masts. By the end of the 19th century, their extensive resources had been decimated, especially in eastern Canada (Daoust and Beaulieu 2004), where they were extensively used in shipbuilding for the British navy. The introduction of an exotic pathogen, the white pine blister rust (*Cronartium ribicola* J.C. Fisher) in the early 20th century decimated remaining eastern white pine stands and caused major losses to advance regeneration. As a result, there are today only scattered remnants of the magnificent natural stands that once covered eastern Canada. Reforestation efforts were engaged for many years to rebuild the pine reserves. Red pine has been one of the most extensively planted species in the northern United States and Canada for many decades. However, the virulence of pests such as blister rust, the white pine weevil (*Pissodes strobi* Peck) and scleroderris canker (*Gremmeniella abietina* Lagerberg Morelet) in large part explains the failures and the cutbacks in the reforestation programs of those two species as well as their reduced presence in the landscape.

The extensive commercial harvest of jack pine forests is more recent, due to poor access to remote stands. The smaller dimension of trees, relative to that of the eastern white and the red pines, made it less attractive to the first settlers. However, as settlement expanded in the 19th century, the need of lumber for house building increased and the utilization of jack pine consequently increased.

Pitch pine, which is a medium-sized tree, was also important during the days of wooden ships (Little and Garrett 1990) due to the large amount of resin its wood contains, which allows it to resist decay. However, it has not been as heavily harvested as the other pines.

2.2.1.2 Economic Importance

Eastern white pine wood is generally pale yellow/white and has medium strength so it can be easily machined. Much of the high grades are now reserved for lumber, while lower-grade material goes into pulp and paper. Its wood is excellent for doors, windows, panelling, moldings and cabinet work (Farrar 1995). Red pine is used primarily for the production of lumber, piling, poles, cabin logs, railway ties, posts, mine timbers, box boards, pulpwood, and fuel. While both species are still a significant resource for industry, their relative economic importance has decreased considerably over the years mainly due to the drastic reduction in supply and quality.

Eastern white pine was formerly one of the favored species for reforestation with annual production up to 40 million seedlings for fiber production and Christmas trees (Eckert and Kuser 1988). However, damage to plantations caused by white pine weevil and blister rust has considerably reduced the interest in this species by public and private landowners. Nevertheless, some reforestation continues with 5 million seedlings still planted annually in eastern Canada. In comparison, reduced demand from industry has caused annual shipments of red pine seedlings to fall to about 1 million, despite that damage from pests is not as serious as for eastern white pine.

Jack pine is now one of the most important commercial tree species in Canada and the Lake States. Its wood is moderately hard and heavy, and relative to other softwoods, of intermediate strength (Hosie, 1979). It is used in building construction as framing, sheathing, scaffolding and interior woodwork. Moreover, it has other commercial applications such as power poles, railroad ties, pilings, mine timbers (Cayford and McRae 1983), and boxes and crates. It is also a good source of wood chips for pulping and commercially important in the manufacture of newsprint in eastern Canada (Law and Valade 1994). Jack pine is extensively planted in Canada with annual shipments of about 80 million seedlings. The vast majority of these seedlings are planted in Ontario and Quebec in the boreal forest where most of the harvesting of jack pine forests occurs.

Pitch pine has a coarse-grained wood that is moderately strong. Southern sources have denser and higher strength and are extensively used in construction of factories, warehouses, bridges, docks, roof trusses, beams, posts, joists and piles. Other uses include interior finish, sheathing, subflooring, fencing, mine timbers, and railroad ties.

2.2.1.3 Breeding Objectives

Over the past 50 years, a number of private- and public-sector organizations have carried out research on the genetics of these pine species. This research demonstrated relatively little morphological variation for red pine in provenance trials (Fowler and Lester 1970). As the presence of moderate to large phenotypic variation is necessary to make good progress through breeding, no applied breeding program was initiated for red pine, such a program being not justifiable based on the extent of reforestation activity. For pitch pine, despite the presence of variation in phenotypic traits and its capacity to hybridize with shortleaf and loblolly pines, reforestation programs were not large enough to justify an investment in the development operational breeding activities. In contrast, research on the genetics of eastern white and jack pine showed extensive variation in various adaptive traits and reforestation programs were large enough to support applied breeding programs.

As for most of forest tree species, breeders' objectives for eastern white pine are to develop improved varieties that are adapted to ecological conditions where they are planted. This is made by delineating breeding zones and selecting and hybridizing superior genotypes for height growth, volume, stem straightness and crown shape for these zones. Moreover, due to its high susceptibility to white pine blister rust and white pine weevil, breeders aim to develop resistance to these pests in their varieties. As eastern white pine has not co-evolved with blister rust, gene variants conferring resistance to those harboring these variants are rare. This has prompted the development of hybrids with other white pine species to transfer resistance genes to the eastern white pine gene pool.

Jack pine breeders aim at developing, for each breeding, zone varieties that are improved for height growth and volume, cold hardiness and reduced branching. Jack pine is known to develop undesirable branch and form characteristics, especially on poor sites and when stand density is not sufficiently high. Variation in branch and form traits has been shown to be partially under genetic control and this can be exploited to improve the species. Jack pine is also sensitive to pests such as scleroderris canker and western gall rust (*Endocronartium harknessii* [J.P. Moore] Y. Hirat.) in the western part of its natural range. However, studies have reported resistance to various pests in the species (Yeatman and Teich 1969). More recently, tree breeders have also focussed on wood traits in order to maintain fiber attributes that give a competitive advantage to the industry using jack pine.

2.2.1.4 Breeding Achievements

2.2.1.4.1 Eastern White Pine

In eastern Canada, the first breeding program for eastern white pine was initiated in Ontario by Carl Heimburger in 1946 with the aim of developing blister rust resistant varieties. Plus-trees in natural stands, which were free of disease symptoms were propagated and used in the production of interspecific hybrids from rust-resistant species such as Himalayan white pine (Pinus wallichiana A.B. Jackson). The program was successful, resulting in the development of rust-resistant interspecific hybrids (Zsuffa 1981), although selected hybrids were not included in operational eastern white pine seed orchards in Ontario (Cherry et al. 2000).

In the late 1970s, an intensive plus-tree selection program in natural populations was launched by the Ontario Ministry of Natural Resources. By the late 1980s, the province had developed eight breeding populations and a network of 18 seed orchards covering over 130 ha. In the mid-1990s, new breeding activities were carried out with the initiation of a genecological study of eastern white pine seed sources from Ontario east of Lake Superior (Joyce et al. 2002).

In Quebec, the eastern white pine breeding program was initiated in the mid-1970s (Corriveau and Lamontagne 1977). From 1976 to 1986, about 150 plus-tree selections were made in natural stands and established by grafting to set up the first-generation breeding population. Production of full-sib families through controlled crosses was initiated in the early 1990s. Several experimental designs were established to evaluate the general- and specific-combining ability for a variety of traits. Six seed orchards were also established in the 1980s to produce seeds for the reforestation program.

Seeds were also collected in more than 100 natural stands in Quebec and others were obtained from collaborators of neighboring provinces and states to set up genecological tests including over 550 open-pollinated progenies from over 225 seed sources. Early growth and phenological trait assessments made it possible to study the genetic structure and patterns of genetic variation in these white pine populations (Beaulieu et al. 1996; Li et al. 1997a). Breeding values were also estimated for height, 12 years after plantation; 14% gain was expected through selection of the best 50 progenies (Daoust and Beaulieu 2004). A new breeding population was set up, grafting three plus-trees from each of the 50 selected families. Several series of new progeny tests were also established in the 1990s and 2000s including half- and full-sib families collected into the breeding orchards.

Recent efforts have focussed on the development of interspecific hybrids resistant to blister rust. The most promising material developed in Ontario for this purpose by Carl Heimburger and Louis Zsuffa was grafted and put in a breeding orchard in Quebec to facilitate controlled crosses. Since the early 2000s, over 130 control crosses have been made to create new hybrids. Seedlings were inoculated with blister rust, and after two inoculation phases, some of the hybrids appeared promising (G Daoust pers. comm. 2009). Somatic embryogenesis techniques are being used to propagate them (Klimaszewska et al. 2001). For the short-term, these hybrid somatic seedlings are being deployed to clonal trials, further testing resistance to blister rust.

There are also some seed orchard facilities established in the Atlantic region in Canada, by JD Irving Ltd in New Brunswick, the Department of Natural Resources in Nova Scotia, the Department of Environment, Energy and Forestry in Prince Edward Island. These seed orchards are now producing the genetically improved seed required for their reforestation programs.

Research on the genetics of eastern white pine in the eastern United States began in the early 1950s with interspecific hybridization experiments and early tests for resistance to the white pine weevil and the white pine blister rust (Kriebel 2004). From the 1950s to the 1980s, extensive cooperative tree improvement activities took place with range-wide and regional provenance trials providing information on geographical variation in adaptability and growth (Wright 1970; Kriebel 1982). Progeny testing was also carried out which allowed estimating inheritance of growth traits and the potential for genetic gain (Adams and Joly 1977; Kriebel 1978, 1983). Some of the progeny tests have been converted into seed orchards. Results of hybridization experiments demonstrated that the two most promising hybrids exhibiting desirable fiber attributes were *P. strobus* x *Pinus wallichiana* A.B. Jackson and *P. strobus* x *Pinus monticola* Douglas ex D. Don and their reciprocal crosses (Wright 1959; Kriebel 1972). Efforts to develop weevil and blister rust resistance in this species have not yet been successful but continue with application of genetic engineering technologies (Kriebel 2004). Ongoing genomics research at the CFS should lead to better understanding of the interaction between the host and disease, and to the development of efficient tools to select eastern white pine tolerant to blister in the future. Eastern white pine is also highly sensitive to sulfur dioxide and ozone, and genetic variation in tolerance to these air pollutants has been investigated (Karnosky and Houston 1979).

2.2.1.4.2 Jack Pine

Early studies of jack pine demonstrated considerable genetic variation in growth traits and insect and disease resistance (Jeffers and Nienstaedt 1972; Polk 1974; Canavera 1975; Yeatman 1975; Rudolph and Yeatman 1982), and breeding programs have since been established throughout much of its natural range in Canada and in the Lake States. Breeding programs were first based on selection of superior provenances, followed by selection of plus-trees within the best provenances to set up the first breeding and seed orchards.

In Atlantic Canada, the New Brunswick Tree Improvement Council initiated its jack pine breeding activities in the mid-1970s based on a seedling seed orchard strategy. About 850 plus-trees were selected in natural stands or provenance tests, and seed collected to establish open-pollinated family tests and seedling seed orchards (Simpson and Tosh 1997). Selected trees were superior for height, stem straightness and crown shape. About 43 ha of first-generation seed orchards were established from 1978 to 1986, with seed production starting in 1984. Prolific seed production allowed roguing of 50% of the families based on height and stem straightness while still meeting needs of the reforestation program. Selection of top-performing families and best phenotypes within these families for straightness and crown and branching traits was completed in 1997 in order to form the 400-parent second-generation breeding population (Tosh and McInnis 2000). Early results of realized gain tests established with seeds collected in the rogued first-generation seed orchards indicates that a 18 to 20% gain in volume (Weng et al. 2006) and a 25% gain in stem straightness could be achieved (Simpson and Tosh 1997).

In Quebec, the Ministry of Natural Resources and Wildlife has conducted a jack pine breeding program since the 1970s. Twelve seed orchards were established with plus-trees selected in both natural stands and provenance trials established in the 1950s, in collaboration with the Canadian Forest Service. Progeny tests were also associated with each of these seed orchards. In 2002, roguing of all first-generation seed orchards was completed based on family breeding values for height, stem straightness and tolerance to scleroderris canker. The gain in merchantable volume was estimated to 2.6 to 8.8 m^3/ha at 40 years (Beaudoin et al. 2004). Three hundred second-generation selections have since been made in the best families of the first-generation progeny tests across two breeding zones (M Desponts pers. comm.).

In Ontario, basic research on the genetics of jack pine was conducted primarily by the Petawawa National Forest Institute with collaborators between the 1950s and the 1970s (Yeatman 1974). The first breeding zones were delineated largely by administrative boundaries in the 1970s and 1980s and tree improvement activities were implemented at the regional level. More than 15 first-generation seed orchards were set up in the various regions, with about 50 family tests accompanying these seed orchards. Since then, all orchards have been rogued at least once. An advanced-generation breeding strategy was developed in 1994 and one of the jack pine programs was selected as a pilot for second-generation breeding. Since then, both an elite and an infusion population were assembled. Controlled crosses were carried out in the elite population and open-pollinated seedlots were collected from the trees making up the infusion population, with new progeny tests now in place to estimate breeding values of these second-generation selections (Ford et al. 2006).

Breeding activities conducted in Manitoba, Saskatchewan and Alberta have been on a smaller scale than those in the eastern Canadian provinces, although seed orchards provide most of the seed needed for the reforestation programs (Falk et al. 2004; Hansen et al. 2006). Some orchards have been rogued based on results of progeny tests. Selections for the establishment of second-generation seed orchards were made in the mid 2000s in Saskatchewan (Corriveau 2004), where the establishment of a new series of progeny trials is underway (Hansen et al. 2006).

In the United States, jack pine has been the subject of breeding programs in Minnesota, Michigan, Wisconsin and Maine. Seed orchards were established in each of those states and second-generation seed orchards in some cases (Stine et al. 1995).

Jack pine is an important commercial species, and there is no doubt that intensive breeding activities will be maintained for this species in the future. In Canada, the breeding plans of various agencies include wood properties among the selection criteria for advanced-generation breeding and consideration of marker-aided selection (MAS) for wood traits to help shorten breeding cycles. Accordingly, it is anticipated that genomic resources will be developed extensively for this species in the coming years.

2.2.2 Lodgepole Pine (Pinus contorta)

2.2.2.1 Historical Perspective

Lodgepole pine (*Pinus contorta* Dougl.) is one of the most important ecological and commercial hard pine species in western North America. With its large geographic range and economic importance, it has amassed a substantial utilization and management history as well as a very large body of research. The largest portion of its commercial range and management exists in the Canadian provinces of British Columbia and Alberta. It is also locally important in several of the northwest United States, but typically the volumes harvested are relatively small compared to British Columbia and Alberta.

In the 1970s and 80s, it became one of the most utilized species for reforestation in Sweden, and still is considered locally important in the northern latitudes of that country largely due to its superior growth rates over the native *Pinus sylvestris* L. (Elfving et al. 2001). It was also introduced to dozens of other countries, such as New Zealand, Argentina, and Great Britain, as its potential as a productive exotic conifer was explored around the world; however, the results have varied from important successes as an exotic to dramatic failures, e.g., becoming invasive (Ledgard 2001).

The first summary of the genetics of lodgepole pine was in the important "The Genetics Of" series, authored by William Critchfield (1980). Another large body of work on lodgepole pine was published by Koch (1987), which examined phenotypic variation for dozens of characteristics across the natural range of the species. Many other studies followed, ranging from mating systems in natural populations (e.g., Epperson and Allard 1984), biogeography of the species with molecular and quantitative studies (Wheeler and Guries 1982a, 1982b; Wheeler and Critchfield 1985; Yang et al. 1996; Godbout et al. 2008), leaf chemistry (von Rudloff and Lapp 1987), variation in quantitative traits of interest in genetic improvement programs (Xie et al. 2007), disease and pest resistance (Yanchuk et al. 1988; Wu et al. 2005), and more recently examination of the impacts of climate change on the potential adaptation and optimization of populations (Rehfeldt et al. 1999; Wang et al. 2006).

Although there are four subspecies recognized in the *Pinus contorta* complex, the largest and most important is var. *latifolia*, commonly referred to as "interior" pine. Shore pine, var. *contorta*, is the second largest component in terms of range, followed by var. *bolandaria* and the small outlier var. *murrayana* (tamarack pine), both of which are restricted to the southern part of the distribution in the United States. One unique biological characteristic of "*latifolia*" pine particularly is the serotinous "closed" seed cone, which is thought to have evolved as a regeneration strategy in response to fire. Lodgepole pine's basic adaptive strategy can be described as a genetic "specialist" (Rehfeldt 1988) as it typically has strong genetic clines, although these clines vary greatly across its natural range. All varieties exhibit special ecological distributions or "niches", which is not surprising considering the large range of lodgepole pine. Below, we focus on the most common of the three subspecies, var. *latifolia*.

2.2.2.2 Economic Importance

Harvest volumes for lodgepole pine in managed stands are in the order 350 m^3/ha, at a rotation age of 50–80 years. In the 1960s, lodgepole pine was not treated as a serious economic crop due to relatively small log diameters, but expansive natural monocultures (resulting mainly from regeneration after fire) and new processing technology in the '70s moved lodgepole to the forefront of economic importance in western Canada. Furthermore, rapid early growth and ease of establishment made lodgepole pine a favorite species for reforestation, with annual planting numbers in British Columbia in the order of 70–80 million trees.

The recent annual harvest of lodgepole pine in British Columbia (2006-2007) was over 35 million cubic meters, which represent approximately one-half of the annual allowable harvest in the province. These particularly high harvest levels have been due in part to increased salvage logging, as an attempt to obtain some remaining value of the millions of cubic meters pine being killed in an epidemic outbreak of *Dentroctonus ponderosae* (mountain pine beetle, MPB). It is expected that by the end of the MPB outbreak, approximately 80% of the mature lodgepole in British Columbia would have been killed. The devastating loss of a majority of the mature as well as young lodgepole stands from MPB attack represents a massive economic and social challenge to British Columbia, and is a sobering reminder of the drastic changes that climate, insect and diseases, combined with forest management practices can have on forests dominated by a single species. Spread of MPB into the neighboring province of Alberta may impact the species there as well.

In Sweden, reforestation with the introduced lodgepole pine peaked during the 1980s, with up to 40,000 ha planted annually (ca 20% of total reforestation). Planted area decreased during the early 1990s, levelling out at approximately 3,000 ha per year since then (Swedish Forest Agency, *http://www.svo.se*). In total, lodgepole pine now covers ca 600,000 ha (3% of commercial forest land). Harvest of lodgepole pine is still negligible, and mainly from thinnings, since planted stands have not yet reached rotation age for final cut.

2.2.2.3 Breeding Objectives and Achievements

In British Columbia, interest in breeding of lodgepole pine followed forest industry expansion into the interior, and provenance and progeny testing commenced in the late 1960s and early '70s. In 1969, one of the largest provenance tests for any conifer species in the world was established by Keith Illingworth, representing 153 seed sources planted across 60 sites in British Columbia and the Yukon (Ying et al. 1985). This network of trials has provided an enormously rich database for many questions related to breeding zone development, selection of superior provenances, and research on the effects of climate on adaptability and productivity. Data at age 32 years were the last that could be collected, as many of the test sites have been damaged extensively by MPB.

In the 1970s, significant breeding efforts were developed in Sweden, with the majority of the breeding population originating from the very high latitude natural populations in Canada (Ericsson 1994). Breeding commenced to develop 11 advanced-generation breeding groups that cover climatic differences in the country (Wilhelmsson and Andersson 1993), although the majority of investment is on nine of these.

Currently in British Columbia, eight breeding zones are recognized, and five of these now have second-generation tests in place, varying in age from 3–5 years. The initial population development for these breeding zones utilized provenance test data and incorporated local and superior non-local open-pollinated families, with 300–400 families per zone. Traits under selection have primarily been height at age 10, height growth with restrictions on wood density loss (due to small adverse genetic correlations) and disease traits such as western gall rust. Genetic gains in volume growth at rotation are currently predicted to be between 7 and 12% among the various breeding zones. Future breeding objectives may shift emphasis to a few other diseases and pests, and to attempt to address new concerns over climate change, adaptation and forest health. Genomic studies are underway to help elucidate gene expression in the mountain pine beetle system. The TRIA project (*www.thetriaproject.ca*) is hoping to utilize genomic tools to better understand the interactions between the genomes of bark beetles, fungal pathogens and host pine trees.

Lodgepole pine in British Columbia and Alberta will undoubtedly remain among the top two species in reforestation and forest management over the next rotation. Its ecological suitability and relatively fast growth rates, across many interior sites in its native range, will make it difficult for other species, native and non-native to substantially replace it on the landscape.

2.2.3 Western White Pine (Pinus monticola)

2.2.3.1 Historical Perspective

Western white pine (*P. monticola* Dougl. ex D. Don) is a member of the five-needle pines, which have long been an important part of the landscape of western North America, not just for their commercial and historic importance, but also for their aesthetic and ecological values. Other five-needle pines such as whitebark pine (*Pinus albicaulis* Engelm.) and limber pine (*Pinus flexilis* James) provide valuable tree cover for wildlife in exposed alpine country, food for birds and mammals and act as stabilizing elements for snow packs and soils in these steep and fragile environments. Sugar pine (*P. lambertiana* Dougl.) has also been a major commercial timber species.

The western five-needle pines have suffered from several serious problems, first with over-harvesting and then with issues arising from fire control removing the regeneration environment, browsing of young regeneration by ungulates, and mountain pine beetle (*Dendroctonus ponderosae* Hopkins). The most serious problem has been white pine blister rust caused by the exotic rust *Cronartium ribicola* J.C. Fischer, accidentally introduced to North America in the early part of the 1900s. All breeding efforts on North American white pines have targeted resistance to this pathogen. Arguably the largest effort has been made with western white pine, particularly in the "Inland Empire" program in Idaho.

2.2.3.2 Breeding Objectives

Richard Bingham initiated resistance breeding programs in Idaho as early as 1946 (Bingham 1983). McDonald et al. (2004) reviewed this and the other western regional programs (USDA Forest Service Regions 1, 5 and 6). Strongly influenced by Bingham's work in Region 1, the Region 6 program (Oregon and Washington) was started a decade later at the Dorena Tree Improvement Center near Cottage Grove, Oregon. Both Regions 1 and 6 started by rigorously selecting healthy survivors, then producing full-sib crosses, often in standing ortets (Bingham 1983). A Phase II program in both regions had less exacting candidate tree selection but followed up with inoculation and screening of open-pollinated progeny. Region 1 introduced this Phase II program in 1965 and has screened over 3,000 candidate trees (McDonald et al. 2004). This open-pollinated testing phase started in Region 6 in 1971 and Dorena has since screened over 4,900 western white pine and 4,500 sugar pine candidate parent trees (R Sniezko pers. comm.).

An early program in British Columbia screened ramets (grafted cuttings) from canker-free field selections following the protocols developed for eastern white pine in Wisconsin and Minnesota (King and Hunt 2004).

This early effort was abandoned, but in 1983 a program based on the USDA western regional Phase II programs of inoculation was initiated. Open-pollinated seedlots were screened from 300 widely distributed candidate parent trees from the coast and 300 from the interior regions of British Columbia (Hunt 2004).

All three of these western white pine programs were influenced by that initiated by Bingham, but were regionally adjusted. For example, in British Columbia, where the rust severity is generally less than in the United States, canker-free parents with intact lower branches were selected as candidate trees. In the Inland Empire, stand infections could average more than 150 cankers per tree so while most selected candidates had fewer than three cankers, canker-free trees were so rare that disease-free status could not used as a criterion (McDonald et al. 2004).

2.2.3.3 Breeding Achievements

Although white pine blister rust is an exotic pathosystem in North America, two important inheritable forms of resistance have been noted: major gene (R-gene) and multigenic "partial resistance" (Kinloch 2003). Although these may not always be distinguishable in the observed phenotypic distribution of resistance, progress has still been made by selecting the phenotype based on early field survival and slow canker growth. More information on the underlying genetic mechanisms will ultimately have implications for the effectiveness, practicality and durability of resistance. Breeding program activities are shifting from open-pollinated screening to controlled (full-sib and backcross) breeding to gain a more thorough understanding of what controls the phenotypic expression and durability of resistance.

As for eastern white pine, genomics resources and tools are expected to be developed in order to select western white pines tolerant to blister rust. A suite of candidate genes is already available in white pine to test for associations with "partial resistance", and a further association study, utilizing a diallel population composed of selected Oregon and British Columbia selections, is expected to be initiated later in 2010.

2.2.4 Southern Pines (Pinus taeda, P. elliottii, P. palustris, and P. echinata)

2.2.4.1 Historical Perspective and Economic Importance

In the southern United States, the "South", 10 species of southern yellow pines (*Pinus* sp.) are common across many forest ecosystems. In the late 1800s and early 1900s when commercial forestry started, longleaf pine (*P. palustris* Mill.) and shortleaf pine (*P. echinata* Mill.) were the most important commercial species in the South. When plantation forestry developed in the middle of the 20th century, loblolly pine (*P. taeda* L.) and slash pine (*P. elliottii* Engelm.) were the species of choice for planting and continue to be the most commercially important timber species today both in the United States (Wear and Greis 2002; McKeand et al. 2003; Sampson 2004) and in other countries (Zobel et al. 1987; Bridgwater et al. 1997). Both loblolly and slash pines have also been used extensively as exotic species in plantation forestry programs in Australia, China, southern Africa, and southern South America (Zobel et al. 1987; Bridgwater et al. 1997).

The silvical characteristics of loblolly and slash pine have some important distinctions. Loblolly pine is broadly adapted to a wide range of sites and is limited primarily by winter cold and drought. When the best genetic material is planted and given the necessary resources to grow, mean annual increments for loblolly pine of 20 m^3 ha^{-1} yr^{-1} are readily achieved (Allen et al. 2005). Slash pine typically does best on wet, poorly drained soils in the lower coastal plains of the Southeast (Baker and Langdon 1990; Lohrey and Kossuth 1990).

In 2007, 1.1 billion trees were planted in the South, with loblolly pine (840 million) accounting for 77.4%, and slash pine (126 million) 11.6% of the planting (McNabb 2007). On average, for each of the past five years, approximately 500,000 ha of loblolly pine and 80,000 ha of slash pine were planted in the region, all with genetically improved seedlings (McKeand et al. 2003).

There are more than 5 million ha of loblolly and slash pines planted outside of the United States. The majority of these are found in Brazil and China, with lesser amounts in Argentina, Australia, South Africa (and surrounding countries), and Uruguay. The first plantings of the southern pines in China were in the 1920s (Bridgwater et al. 1997). Through the early 1990s, slash pine dominated, because of its ability to survive on poor sites. Since the 1990s, large plantation areas of loblolly and slash pines have been established in southern and eastern China, with commercial quantities of seeds coming from seed stands and orchards in the United States and Zimbabwe.

The first introductions and commercial plantings of the southern pines occurred in northern Argentina, southern Brazil in the 1940s and '50s (Bridgwater et al. 1997; C Peirano pers. comm.). Brazil has the largest plantation area of southern pines in Latin America with 1.6 million ha established, 1.2 million ha of loblolly and 360,000 ha of slash pine (D Chaves pers. comm.). The current planting rate is approximately 30,000 ha per year. Argentina has approximately 400,000 and 270,000 ha of loblolly and slash pine established, respectively, primarily in the subtropical northern provinces of Missiones and Corrientes. Slash pine and the hybrid, *P. elliottii x P. caribaea* var. *hondurensis* is especially preferred in Corrientes where lowlying areas have a tendency to be wet during the year. Improved silviculture practices, like bedding, might make *P. taeda* more attractive as a species on these sites in the future. The forestry plantation programs in Uruguay are relatively new. Currently, 144,500 ha of loblolly pine have been established with the prospect of much greater expansion (J Posse pers. comm. 2008).

The southern pines have been grown in South Africa since the 1890s with expansion into other countries in southern and eastern Africa since the late 1920s (Poynton 1977). In general, loblolly pine has always been a secondary species to *P. patula* in most highland areas of the region. Its main disadvantages are its relatively poor stem form (Poynton 1977), its propensity to produce reaction wood at the base in some environments (van der Sijde et al. 1985), and its adaptability to a limited number of sites in the southern African environment. Recently, however, it has gained more attention as an alternate to *P. patula* on some sites because of its resistance to Pitch canker (*Fusarium circinatum*) and as sawmillers learn how to identify and handle the reaction-wood problem.

Slash pine remains the most widely planted of the southern pines in southern Africa, especially in South Africa, Swaziland and Zimbabwe, on the drier and/or colder sites, for both pulpwood and sawtimber (Bridgwater et al. 1997). In South Africa and Swaziland, 192,000 and 10,000 ha of slash pine and 27,500 and 2,000 ha of loblolly pine have been established, respectively (DWAF 2006). Lesser amounts occur in southern and eastern Africa as far north as the equator (Bridgwater et al. 1997; Poynton 1977).

Loblolly pine and slash pine were introduced into Queensland, Australia in 1917 and 1925, respectively (Bridgwater et al. 1997). Loblolly pine was eventually found to be poorly adapted to the region but slash pine did well on the excessively wet sites. On sites that are better drained, the *P. elliottii* x *P. caribaea* var. *hondurensis* hybrid and pure *Pinus caribaea* are now preferred with 62,120 and 50,345 ha established, respectively (I Last pers. comm. 2008). The seeds for the pure species and hybrids all come from advanced generation breeding orchards.

2.2.4.2 Breeding Objectives

In the southern United States, deployment practices such as planting only the best open-pollinated families to the best sites are resulting in dramatic increases in productivity. Increased resistance to fusiform rust disease, caused by the fungus *Cronartium quercuum* (Berk) Miyabe ex Shirai f. sp. *fusiforme*, especially in slash pine, has also had major impacts on plantation yields (Vergara et al. 2004). In the early 2000s, 59% of the loblolly and 43% of the slash were annually deployed as open-pollinated families by companies and small landowners (McKeand et al. 2003). In the last 10 years, seed orchard managers have had great success in developing methods to mass produce full-sib families for operational planting. The gains from improved quality and yield are very impressive when both the female and male parents are selected (e.g., Bramlett 1997; Bridgwater et al. 1998; Jansson and Li 2004; McKeand et al. 2008). From 2000 to 2007, over 94 million full-sib family seedlings were planted in the South (McKeand et al. 2008), and annual deployment of mass control-pollinated seedlings has grown to 35–40 million (4–5% of the total planting). Propagation of selected clones has also become a reality via somatic embryogenesis (e.g., Pait 2005), with over 10 million somatic seedlings planted to-date, and the numbers increasing annually.

From the beginning of tree improvement programs in the region (see Schmidtling et al. 2004 for a summary of tree breeding in the southern United States), the focus has been on selecting, breeding, testing, and planting trees that provide landowners with the greatest return on their investments (e.g., Zobel 2005). Historically, the greatest emphasis for both loblolly pine and slash pine was on volume production; more wood production for both pulp and solid wood products. For slash pine, a critical trait for volume production is resistance to fusiform rust disease. Slash pine is extremely susceptible to rust, and gains in rust resistance have been a major success (Vergara et al. 2004). Stem form traits (straightness, forking, and small, flat-angle branches) were also important criteria. In fact, the most dramatic improvement made in loblolly pine was the improvement in straightness.

Outside of the United States, tree breeding programs for the southern pines have been in existence in some countries since the late 1950s and early '60s (Poynton 1977; Mullin et al. 1978). The breeding objectives in these exotic environments are similar to those in the United States. Breeding for volume has been important in most countries, but stem straightness and branch characteristics have received very high priority in tree improvement programs especially in southern and eastern Africa to maximize recovery rates at local sawmills. The gains from selection for form traits are apparent when African bred loblolly pine is grown in compartments adjacent to genetic material from other countries. In the last 10 years especially, breeding programs have also concentrated on improving wood quality traits.

Most breeding programs for exotic southern pine plantations are one to two cycles behind the most advanced programs in the United States. There is still general usage of open-pollinated seeds from clonal orchards for operational planting, but this is gradually giving way to more use of seeds from control crosses with seedlings multiplied by vegetative propagation. Cutting programs of several million seedlings per year are common in industrial nurseries at some localities. The more advanced programs in southern Latin America are also actively involved in testing genetic material produced from somatic embryogenesis.

2.2.4.3 Breeding Achievements

For loblolly pine originating from the largest improvement program, second-generation seed orchards currently produce 77% of the seed while third-cycle orchards produce 12% (NCSUCTIP 2008). Estimated gains in volume production for open-pollinated families at rotation age from the second-generation improvement program pine vary from 13 to 21% over non-improved checks depending on the region in the southern United States. From rogued second-generation orchards, gain estimates vary from 26 to 35% (Li et al. 1999). Third-cycle orchards are expected to produce volume gains of 30 to 40% over non-improved.

If only the best family is planted in a region, the gains could be as high as 50–60%. With mass controlled pollination (Bramlett 1997), gains in stem form and sawtimber potential can be as much as 100% over the non-improved check which is twice as great as that from open-pollinated families (McKeand et al. 2008). Resistance to fusiform rust resistance has also been greatly improved in loblolly pine. There are individual families that have less than 10% infection when non-improved checks have 50% infection (Isik et al. 2008).

In the southern United States, breeding programs have put much more emphasis on improving traits that are important to solid wood products. Volume production is still the most important trait, but selection against stem defects such as excessive sweep, forking, ramicorn branching, and large, steep branches has become more prevalent. With the development of rapid screening techniques for wood quality traits such as bending strength (e.g., Jones et al. 2005; Roth et al. 2007) and wood density (Isik and Li 2003), breeders are now incorporating these traits into selection indices to improve value.

For slash pine, realized gain in stand yield for first-generation averaged about 10%, or an extra inside-bark volume of 25 m^3/ha at age 25 years (Vergara et al. 2004). For fusiform rust resistance, which is critical for productivity in slash pine stands, the 25% realized gain for rust resistant material compared to rust susceptible material obtained at age 16 was conservatively extrapolated to a 25-year-old rotation-age gain of 51.4 m^3/ha in inside-bark volume (Vergara et al. 2007).

Gain estimates from programs outside the United States are not readily available. The average productivity of first-generation loblolly pine in southern Latin America is approximately 28–30 m^3/ha/year. Estimates for growth of third-generation material on the best locations (deep fertile soils) in southern Latin America are 55 m^3/ha/year (over bark). Growth rates of this magnitude are already being seen in some operational plantings of second-generation material established on good sites in Santa Catarina, Brazil and measured at 16 years of age. Serious diseases have not yet affected the southern pines in Latin America or in southern and eastern Africa, but insect attacks are becoming more problematic in Southeast Asia (H Wang pers. comm. 2008).

The southern pines, and in particular loblolly pine, have long been the subject of marker studies, particularly for wood quality traits and disease resistance. Most recently, the breeding programs for loblolly and slash pine have entered a collaboration with the Conifer Translational Genomics Network (CTGN), in the hopes of making genomics-assisted selection an operational reality (*http://www.pinegenome.org/ctgn/*). Led by UC Davis, with additional funding from the USDA and the US Forest Service, the CTGN will genotype up 7,500 trees and analyze genetic variation at about 7,000 loci previously identified as single nucleotide polymorphisms (SNPs). Phenotypic information will be associated with SNP variation, focussing on stem volume, fusiform rust resistance, wood quality, and stem form, with the goal to develop selection tools.

2.2.5 Maritime Pine (Pinus pinaster)

A dozen pine species are native to Europe, and several of them are cultivated to more or less a large extent, such as European black pine (*Pinus nigra* Arn.) and Scots pine (*P. sylvestris* L.) as well as the Mediterranean pines of southern Europe: Turkish pine (*P. brutia* Ten.), Canary Island pine (*P. canariensis* C. Sim.), Aleppo pine (*P. halepensis* Mill.), Maritime pine (*P. pinaster* Ait.), and stone pine (*P. pinea* L.). These species have long been used for wood production and in some cases for resin production (Maritime pine), or even edible seed production (stone pine). Some are the subject of breeding and plantation in different countries, usually where they are also present in natural stands: for example European black pine and sub-species in Spain, France, Greece, and Turkey, Scots pine in many countries corresponding to its natural area (the largest of the genus *Pinus*), Turkish pine in Turkey, Aleppo pine in Greece and Israel, stone pine in Spain, and Maritime pine in France, Portugal and Spain. Of these Mediterranean pines, Maritime pine has been the most extensively planted and has also been introduced as an exotic outside Europe, in areas such as southwestern Australia. Breeding of Maritime pine in southwestern France started in the 1960s, after several species and provenances trials had shown that the local "pin des Landes" was the best adapted and the fastest growing tree in the Aquitaine soil and climatic conditions.

2.2.5.1 Historical Perspective

Between the end of the 18th century and today, the Maritime pine stands in southwestern France (Aquitaine region) expanded from a natural forest of

250,000 ha, located along rivers and the Atlantic coast, to a cultivated area of one million ha. Such a progression was the result of the determination of the local land owners and public authorities to stabilize coastal dunes, drain 700,000 ha of marshes, and plant a new forest. Once the forest was settled, the challenges of nature and of a changing economic background had to be addressed repeatedly (Riou-Nivert 2002). Between 1939 and 1950, fire destroyed 400,000 ha. In the 1950s, the resin market collapsed, due to international competition and the emergence of oil by-products. Production objectives were reoriented towards timber, supported by the progress in silviculture and the breeding of improved varieties, marketed in the early 1980s. During the winter of 1985, an intense cold wave in southwestern France destroyed 30,000 ha of Maritime pine plantations from Spain and Portugal provenances, which had been established during the major reforestation effort following the fires of the 1940s. The genetic origin of seed source stands is now systematically verified by a terpene test, and seed harvest from non-local stands is forbidden. A hurricane in December 1999 felled more than 100,000 ha in Aquitaine: 28 million cubic meters were levelled (*http://agreste.agriculture.gouv.fr/*). Once more, the Maritime pine forest resource had to be reconstituted. Reforested areas increased, reaching 23,000 ha/year, while 100% of plantations have been established with seedlings from second-generation seed orchards (GPMF 2002).

Should this be--Spanish and Portugese provenances?

Yes, it should be.

2.2.5.2 Economical Importance

Maritime pine is by far the most planted tree species in France where it represents 10% of the forest area and 24% of wood harvest (French Ministry of Agriculture, *http://agreste.agriculture.gouv.fr/*). Average productivity is about 10 m^3/ha/y, but can reach 20–25 m^3/ha/y on the best sites. The rotation age is typically 45 years and is decreasing with improved varieties. Today, some 8.5 million m^3 are harvested annually, most of which is processed locally, 60% as saw-timber, and 40% as industrial round wood. Forest management and primary wood processing represents 40,000 jobs in Aquitaine and are an essential economic activity in this region, bringing a turnover that is greater than that of Bordeaux wines.

2.2.5.3 Breeding Objectives and Strategies

2.2.5.3.1 Provenance Choice and Plus-tree Selection

The breeding program started in the 1960s, when early provenance trials had already shown the superiority of the local Landes provenance for growth and cold resistance (Illy 1966). Aquitaine is the most northern region of the species' natural distribution, which is otherwise localized on the

Atlantic coast of Spain and Portugal and around the Mediterranean basin (Spain, southeastern France, Italy, Tunisia, Algeria, and Morocco). Cold resistance was identified as an important issue, especially when lowest night temperatures in Aquitaine can reach –10°C or –15°C every few winters (-20°C in February 1985). The local provenances were thus chosen to build up a breeding population, despite their form defects: trunk flexuosity and poor branching. A total of 380 plus-trees were selected phenotypically on the coastal sand dunes of Aquitaine, based on height and diameter, and visual scoring of stem form. This first phenotypic selection proved to be efficient for improving growth and stem straightness, as shown by a progeny test comparing plus-trees progeny with their non-selected neighbor-tree progenies on two locations after 10 years old (Danjon 1995). In addition, genetic variation among provenances and performance of crosses between provenances were explored (Harfouche and Kremer 2000; Harfouche et al. 2000). Among all tested combinations, Landes x Corsica families proved to be the best material for growth and form in Aquitaine conditions. A few hundred clones from the Corsica provenance were selected in provenance trials located in Aquitaine, based on growth, stem straightness, branch quality, *pyralis* resistance (*Dioryctria sylvestrella*), and cold resistance. The objective of this second population is to produce improved Landes x Corsica varieties for better stem straightness and branch quality.

2.2.5.3.2 Breeding Strategy and Selection Criteria

Development of the breeding program followed a classical recurrent-selection approach, with a main population composed of the Landes plus-trees. In the first two cycles of selection, factorial mating designs with four to six crosses per parent, or hierarchical (nested) mating designs with two crosses per parent were used to produce the next generation. Forward selection was based on an individual-family index, with total height, diameter at breast height and stem deviation from vertical at 10 years as selection criteria (Baradat and Pastuszka 1992; Durel 1992). For these three traits, narrow-sense heritability in the base population was moderate to low (0.19, 0.14 and 0.16, respectively) (Bouffier et al. 2008b), and an adverse genetic correlation exists between growth and stem straightness (-0.2 between diameter and straightness). Following this strategy, the main population has cycled through three generations, with more than 4,500 individuals selected, and 5,000 families tested over 500 ha of trials (GPMF 2002).

The changes in genetic variance accompanying selection and breeding has been studied in this material, using an individual genetic model to estimate heritability and additive coefficient of variation over three generations for traits under selection (Bouffier et al. 2008b). For growth traits, the results showed a clear decrease (30 to 40%) in genetic variation from the Aquitaine natural resource to the selected plus-tree founder breeding population, and stabilization of variance from founder breeding population to the next-generation breeding population. The pattern was different for stem straightness, and difficult to interpret due to different measurement methods over time. It was concluded that the recurrent selection strategy based on one main population could sustain several generations of breeding and selection, considering the level of additive coefficients of variation for the selected traits and a status number of the breeding population (population effective size, Lindgren et al. 1996) close to 100.

For the next generation of the breeding population, the focus is on a reduction of population census size and better management of pedigrees, to optimize selection efficiency while producing regularly renewed varieties with increasing genetic gains. Eight unrelated sublines were assembled within the breeding population based on pedigrees and breeding values, allowing the deployment of unrelated selections to clonal seed orchards. Status number is used as an indicator of genetic diversity. Double-pair mating designs are used to produce material for progeny tests and the base of the next generation, while polycross testing is performed for parental ranking. Trials are replicated on several contrasting sites, usually with single-tree plots and a large number of replications per site.

Including new selection criteria is also a focus: studies on pests and diseases resistance (Jactel et al. 1996; Kleinhentz et al. 1998; Burban et al. 1999; Lung-Escarmant and Guyon 2004), wood quality (Pot et al. 2002; Bouffier et al. 2008c, 2009), and drought tolerance (Dubos et al. 2003; Dubos and Plomion 2003; Nguyen-Queyrens and Boucher-Lannat 2003; Eveno et al. 2008) are ongoing. Some new criteria have already been included in the selection process: rust resistance (*Melampsora pinitorca*) is tested on future seed orchard parents through a cut-shoot assessment (Desprez-Loustau 1990), wood density is evaluated at the family level in progeny trials with an IML-Resi tool (Bouffier et al. 2008a), and branch quality is scored visually in progeny tests (GPMF 2002).

Breeding forest tree varieties in the context of changing climate is another challenge. Models predicting the evolution of climate in southwestern France during the next decades show an elevation of air temperature and a seasonal shift in precipitation distribution from spring and summer to winter, which will likely result in decreased forest productivity (Loustau et al. 2005). Although these are hypotheses, interest to improve drought resistance has been increasing. Current varieties of Maritime pine in Aquitaine were selected, tested and used in one breeding zone. Selection is aimed at producing multipurpose varieties adapted to the different soil types of Aquitaine, including dry, semi-humid and humid podzol soils. In the near future, seed orchards could be rogued to favor clones that are better adapted to the drier sites as and when their progeny tests are assessed in a changing climate. As for future varieties, different strategies are considered: locating progeny trials in more southern and drier sites as an anticipation of future climate, infusing new diversity into the breeding population either by selecting better adapted trees in the local provenance, using the national network for Maritime pine natural genetic resources conservation, either by selecting adapted inter-provenance combinations (Landes x Portugal and Landes x Morocco progenies are already being tested), as well as introducing new selection criteria for drought resistance, e.g., water-use efficiency (Brendel et al. 2002), resistance to cavitation (Lopez et al. 2005), and molecular markers for these traits.

2.2.5.4 Breeding Achievements

Three generations of seed orchards have been produced. For economic and technical reasons, the deployment strategy for Maritime pine varieties in Aquitaine is based mainly on open-pollinated orchards.

The first-generation orchards were seedling seed orchards based on a very large number of full-sib families, corresponding to the progeny tests of plus trees, and were rogued after genetic assessment. These orchards demonstrated genetic gains of 10–15 % in volume and stem straightness at about age 15 years (GPMF 2002).

Second-generation orchards were characterized by a reduced genetic base and greater genetic gain, compared to those in the first generation. They were based on a few tens (usually around 30) of backward-selected clones, either as classical grafted clonal orchard or as a randomized plantation of polycross families obtained by controlled pollination between selected clones (Baradat et al. 1992). The polycross family seed orchards were planted over 180 ha and are open-pollinated. The expected genetic gain was estimated from progeny trials at age 13 years to be 30% for both criteria over unimproved material. Since the hurricane of 1999, when annual reforested areas of Maritime pine in Aquitaine increased from 15,000 to 23,000 ha, 70% have originated from second-generation orchards.

Third-generation seed orchards have been established over 180 ha, and should enter in production by 2010–2015. They are either clonal or polycross family seed orchards. This third generation also includes a Landes x Corsica variety, to be produced by controlled pollination.

In the future, seed orchards will have to be renewed more rapidly, to better respond to likely climate change and developments in the marketplace. Recent adaptations in the Maritime pine breeding program, such as the optimization of population management through sublining and of selection efficiency with BLUP evaluations, are expected to be augmented with marker-assisted selection for complex traits such as wood quality and drought resistance.

2.2.6 Scots Pine (*Pinus sylvestris*)

2.2.6.1 Historical Perspective

Scots pine (*Pinus sylvestris* L.) has a wide natural geographic distribution, the most extensive in the genus *Pinus* and in the family Pinaceae (e.g., Boratyńsky 1991). The species ranges from Scotland and Spain in the west to the far east of Russia (Siberia), and from Spanish Sierra Nevada mountains in south to the northernmost part of Scandinavia. It occurs on a variety of soils in very diverse climates, in pure as well as in mixed forest stands. In northern Europe and Asia, Scots pine is a dominant species of the boreal forest (Willis et al. 1998). It has also been introduced to North America as an exotic species, initially both for ornamentals, Christmas trees, and timber production, but now grown primarily for Christmas trees.

Scots pine is the most intensively studied tree species from the standpoint of provenance variation. Provenance studies had already started by the end of the 19th century (reviewed by Langlet 1971). In 1907, an international provenance study with pine from different climatic regions was established by IUFRO members, and this was followed by several others (e.g., Giertych 1991). The aim of early provenance research was to reveal the possible use of seed from different origins with respect to germination, survival, and growth. Langlet (1936) undertook an extensive study of physiological variation in Scots pine from 582 localities in Sweden in the 1930s. He demonstrated a genetically controlled clinal variation in physiological traits related to cold hardiness. Eiche (1966) established a large provenance series in the early 1950s, from which much valuable information has been extracted, elucidating genetic parameters for many traits. Eiche (1966) demonstrated hereditary adaptation of provenances and the possibility to improve survival in plantations suffering from cold damage by transferring provenances from north to south. This pioneering work has been followed by numerous population genetic studies in the same or new field experiments in Sweden (e.g., Remröd 1976; Eriksson et al. 1980; Persson 1994) and in other countries (e.g., Giertych and Mátyás 1991).

2.2.6.2 Economic Importance

Scots pine is one of the most commercially important Eurasian forest trees and widely used in plantation programs in temperate zones (Volosyanchuk 2002). It has major economic significance throughout its natural range (Mikola 1991), both for high-quality sawn products and for pulp and paper, with Russia, Finland, and Sweden comprising the largest areas for timber production. In addition, Scots pine has also been widely planted for timber production beyond its natural distribution in western Europe, Eurasia, and North America, and to a small extent even in Mexico and New Zealand (Boratyńsky 1991).

In Sweden, commercial Scots pine forests occupy 12 million ha of productive forest land (ca 50%), with a total stocking of about 1,100 million m^3, an annual cut of 30 million m^3, and annual planting of 120 million seedlings (ca 32% of total seedling production). According to the Swedish Forest Agency (*http://www.svo.se*), the value of forest product exports in 2007 totalled 127,000 million SEK (ca US$18 billion), or 11 % of total exports and 4 % of GNP. More than 100,000 people are employed in the forestry sector (2.2 % of all workers). Based on its share of total harvest volume, Scots pine contributes roughly 30–40% to these figures.

In Finland, there are 13.6 million ha of Scots pine dominated forest, representing 65% of the forest area and 50% of the standing volume (FFRI 2008). About 55,000 ha annually are artificially regenerated with pine, where direct seeding is used on more than half of the area (requiring 20-times as much seed as planting).

According to Russian Federal Agency of Forestry (A. Fedorkov, pers. comm.), Scots pine in Russia covers 117 million ha (42 million in Europe and 75 million in Asia). It is the second most dominant species with a standing inventory of 15,000 million m^3, or 20% of total standing volume.

In other European countries, areas dominated with Scots pine are considerably smaller, but still contribute significantly to total production and are considered economically important.

2.2.6.3 Breeding Objectives

Much information on genetic parameters for many traits is available from a large number of investigations carried out over many years (e.g., reviewed by Giertych and Mátyás 1991; Eriksson 2008). Significant genetic variation and heritability has been shown for both growth traits (e.g., Haapanen 2001), stem quality and wood properties (e.g., Ståhl and Ericson 1991; Persson et. al 1995) and adaptive traits (e.g., Persson and Andersson 2003), demonstrating good potential for improvement through breeding. Hannrup (1999) grouped Scots pine traits, where phenology traits generally show high values for both additive genetic variation and heritability, growth traits show large genetic variation but low heritability, and morphological traits such as wood density and tracheid length show little variation but high heritability. Further, genetic correlations between height at different sites within climatic regions are usually high (Haapanen 1996; Zhelev et al. 2003; Persson et al. 2006), indicating limited genotype-environment interaction.

Although Scots pine is considered a cold-hardy species, withstanding short vegetative growth periods and very low winter temperatures, regeneration at high latitudes and altitudes is at risk of mortality due to cold damage. Because of its large natural range, Scots pine is host to many different pests (Stephan 1991). Genetic variation in resistance to fungi (e.g., *Melampsora pinitorqua, Cronartium ssp., Phacidium infestans, Gremmeniella abietina*) has been shown (e.g., Quencez and Bastien 2001), while similar results are lacking for insect resistance.

Overall breeding objectives for Scots pine in Sweden are to improve value production, while maintaining sufficient genetic diversity and preparedness for climatic change, through a multiple-population breeding strategy (Danell 1993; Wilhelmsson and Andersson 1993). Target traits are grouped in selection traits for improved (i) adaptation/survival, (ii) yield, and (iii) stem and wood quality. Selection indices based on genetic variation, correlation between assessed traits and goal-traits, and economic weights are used to identify predictors of highest economic yield in different geographic areas (populations). The sustainability of such programs over 10 generations, with spruce as the model species, has been validated in simulation studies by Rosvall et al. (1998).

Finland has a breeding program of similar size and structure as that in Sweden (Haapanen and Mikola 2008), with the main objectives to improve growth and branching (branch size and angle). Parallel objectives can be found in other programs, for example: in Russia, where yield and stem quality are targeted (A Fedorkov pers. comm.); height, survival and stem shape in the Czech Republic (O Ivanek pers. comm.); growth traits, stem straightness, and branch quality in Latvia (Jansons et al. 2008); height growth, stem quality, and frost resistance in Turkey (Bilir and Ulusan 2008).

Historically, there has been an extensive Scots pine breeding program for the northeastern part of Germany, focussed on preservation of genetic variability, adaptation to site conditions and climate changes, resistance to biotic and abiotic hazards, yield and quality, and transfer of valuable genetic material into practice (Kohlstock and Schneck 1992). The program included progeny-tested orchards as well as plans for cross breeding (two-clone orchards) to utilize specific combining ability. However, interest in tested regeneration material of Scots pine has declined, and the future of Scots pine breeding in Germany is uncertain (V Schneck pers. comm.).

In some other countries, breeding objectives reflect concern about the impacts of biotic stress. Although productivity and stem quality are important, particular emphasis is put on resistance to pathogens in France (C Bastien pers. comm.), and tree health in Lithuania (D Danusevicius pers. comm.), while genetic conservation and genetic variability are stressed in Spain (R Alia pers. comm.) and in Poland (J Kowalczyk pers. comm.).

2.2.6.4 Breeding Achievements

Generally for Scots pine, genetic gain from breeding programs are realized through crops from clonal or seedling seed orchards. Deployment of Scots pine to plantations is entirely from seed, as vegetative propagation is currently difficult and costly on a large scale. A worldwide review in 1991 showed that there were ca 10,000 ha of Scots pine orchards established (Mátyás 1991), indicating high expectations of improved regeneration stock through breeding. The former Soviet Union contributed half of the total orchard area, with Finland, Sweden, China, and Poland as other major contributors.

The level of genetic gain obtained depends on both testing accuracy and selection intensity, both of which vary among countries and programs. In addition, estimates of genetic gains are usually available only from a restricted number of trials, which usually introduces an upward bias due to unaccounted G x E variance, etc. This makes it difficult to generalize on breeding achievements; however, some rather comprehensive results and estimates of breeding accomplishments are available.

In Sweden, the first round of improved regeneration stock from phenotypically selected trees in clonal orchards started to accumulate in the 1980s. Gains, as predicted from large series of progeny trials with unselected control lots as comparison, showed superiority in height (9.2%), breast height diameter (5.4%), and volume (18.9%) at age 27 (Andersson et al. 2007). Calculations based on growth and site-index functions indicated that the height superiority corresponds to a 10% difference in volume production at full rotation (80–100 years). There were minor changes in survival (–1.4%), ramicorn frequency (–1.0%), and stem break frequency (1.3%). Jansson (2007) found 11.7% superiority in volume per ha at age 30 for progenies from phenotypically selected trees in south Sweden, estimated from five trials with block-plots. Based on genetic parameters from numerous Scots pine trials and realized selection intensities, Rosvall et al. (2002) estimated genetic gains for the third round (1.5 generation) of Scots pine orchards currently under establishment in Sweden. Figures varied between 23 to 27 % predicted gain at rotation-age volume production per ha, and included both initial phenotypic selection gains and gains from selection of genetically tested material. In addition to gain in growth, a gain of 5–13% in survival was estimated for those orchards intended for climatically harsh sites. Since selection indices include also pest resistance, stem and branching characters, etc., improvements are also expected here, but no precise estimates are available.

In Finland, Haapanen (M Happanen pers. comm.) reports 15–20% predicted gain in stem volume at age 12–20 years for bulked open-pollinated first-generation orchard seed lots, in comparison with local wild seed lots. In addition, improved branch quality (smaller branch diameter) was observed. Establishment of tested 1.5-generation orchards started in 1997 with expected gains of 25–30 % in early stem volume.

The genetic quality (breeding value) for height and stem form of seed orchards in Britain have been predicted (Lee 1999). Existing, first-generation seed orchards with phenotypically selected trees, were 8–12% superior in height and 0–3% superior in stem form compared to unimproved seed from registered stands, at age 10 years. New orchards with top-performing progeny-tested clones are predicted to give genetic gains of 14–20% in height and 5–19% in stem form, depending on how the traits are weighted.

In Latvia, Scots pine breeding is at the beginning of the second cycle. Orchard seed (almost 100%) from both the first-generation and 1.5-generation orchards is used in operational forestry. Genetic gains from open-pollinated 1.5-generation mother trees are predicted to be 10–14% in height and diameter at age 21–36 years (Jansons et al. 2008).

In summary, many programs still utilize improved stock from first-generation orchards with phenotypically selected trees. The superiority of this stock is around 10% in early height (20% in early volume), which corresponds roughly to 10% in full-rotation volume (Andersson et al. 2007). In addition, some improvement in stem and branch quality is achieved. These gains should be rather accurate for first-generation untested orchards over various countries and programs, as the plus-tree selection was carried out in similar ways (Pihelgas 1991). Depending on pollen contamination rates, predictions should be somewhat reduced to give realized gains.

Orchards with tested clones (1.5-generation) are also coming into production. Depending on the size of the breeding program, and thereby the selection intensity, and the weighting of traits, the superiority generally varies between 15–30% for early height or full-rotation volume, although realized gains would be somewhat reduced by outside-orchard pollen contamination. Adaptive traits (survival), stem and branch quality, and resistance to fungus were also targeted, are expected to yield additional gains.

Marker-aided or genomic selection approaches are not used in operational Scots pine breeding. However, microsattelites are used for paternity identification in applied research projects, e.g., investigations on mating patterns and contamination rates in seed orchards (Torimaru et al. 2010). Although numerous research projects on MAS using simple sequence repeats (SSRs) and SNPs are in progress, large-scale genome-wide association or evaluation using dense SNP maps are considered to have the best potential for assisting Scots pine breeding in the future.

2.2.7 *Radiata Pine* (Pinus radiata)

Within its native California, radiata pine (*Pinus radiata* D. Don) is a comparatively obscure species, prized much more for its amenity value and producing Christmas trees than as a timber species. Elsewhere, it has become an extremely important commercial species (Scott 1960; Burdon ~~2001, ~~2002). Plantations occupy over 4 million ha, roughly 500 times the present natural distribution of the species. Its very rapid growth, ease of collecting and storing seed, easy handling in the nursery, amenability to transplanting, modest edaphic requirements (typical of true pines), and the versatility of its wood, make it the utility softwood of choice almost wherever it will grow satisfactorily. Climatic conditions that exceed its tolerances include severe winter cold, heavy snowfalls, damp heat, and severe drought especially combined with high temperatures, such that a mild oceanic climate suits it best. Also, it demands higher soil fertility than many pines. The site tolerances reflect a natural habitat that is a highly localized variant of a Mediterranean climate, with summer sea fogs caused by a cold ocean current. The limitations mean that the successful plantings are very predominantly within the Southern Hemisphere, New Zealand, Chile and Australia being the largest growers, and Spain being the only Northern Hemisphere country with major plantings.

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Delete "2001, "

2.2.7.1 Historical Perspective

While known to the Spanish who colonized Mexico and California, radiata pine only became known to mainstream European plant collectors and botanists with the collection of herbarium specimens and seed by David Douglas in 1833, although the species was named from herbarium specimens collected separately by John Coulter. This was during a fashion for collecting and exchanging the many newly discovered conifer species from North America and northern India. Material from the Douglas collection was distributed in Britain and later to British colonies (Shepherd 1990). Early introductions were on a specimen-tree scale.

In New Zealand, the first confirmed introduction was in 1859, via Australia. Its good growth, over the length of the country, soon led to fresh seed importations, and larger-scale plantings. The country evidently became self-sufficient for seed by the early 1880s. Later on, New Zealand became a major seed exporter, notably to South Africa and parts of Australia. Only after 1921 did New Zealand make a massive commitment to the species for timber, to make good depletion of the native timbers. This led to a planting boom during 1925–1935. After World War II major processing industries were established with pulp and paper mills as well as sawmills. From around 1960, the plantations were seen as the base for major exports, leading to a second planting boom beginning in the 1960s and peaking during the 1970s and ’80s.

The first introduction to Australia was slightly earlier than in New Zealand. Local shortages of softwoods led to establishment of plantations, in addition to plantings for shelter and amenity. Commercial plantings began in South Australia in 1885; Victoria and New South Wales followed suit in the 1920s and 1930s, with major expansion after World War II. While there are pulp mills and reconstituted wood plants, Australia continues to place a major emphasis on producing light structural timber from the species. Radiata pine, despite some early problems with micronutrient deficiencies, has become by far the pre-eminent softwood plantation species in southeastern Australia, and with significant plantings in western Australia.

The first introduction to Chile was much later, in 1887, near Concepción. It soon became popular in that locality, but it was only towards 1940 that it was used for large-scale afforestation. Rapid expansion of processing plants occurred in the 1960s and 1970s, with considerable emphasis on pulping. Major planting began again in the 1970s, with strong financial encouragement from the government.

Introduction to Spain reportedly occurred in the 1860s. Plantings are close to the north coast, predominantly near the western end of the Pyrenees, in the Basque Autonomous Region. The plantings are almost all dispersed among large numbers of very small owners.

In South Africa, seed importations began earlier than in New Zealand and Australia, but the species is confined to the climate of a coastal strip in western Cape Province, where it is favored for light structural timber. The species has also been tried in many other countries, with many failures. Initial success was often published enthusiastically, unlike the subsequent failures. Even so, there are various countries where some plantings have performed acceptably, although good statistics are elusive.

2.2.7.2 Economic Importance

The area over which the species is managed is not huge compared with some other species. Few forest tree species, however, are grown more intensively as plantation crops. Worldwide, it is thought there are over 4.1 million ha planted to radiata pine, with around 1.6 million and 1.4 million ha in New Zealand and Chile, respectively (MAF 2007; INFOR 2007). A total of 730,000 ha are established in Australia (ABARE 2007) and close to 300,000 ha in Spain (DGB 2005; cited by Crecente-Campo 2009).

The versatility of the radiata pine wood rates highly, even among pine timbers, despite shortcomings of its corewood. It can be used for solid-wood products, and both chemical and mechanical pulps. The solid-wood products cover both light structural and appearance-grade lumber, and the latter can be quite high-value. While at present its long-fiber kraft pulp rates as a commodity, it now tends to be a by-product rather than a primary one. The mechanical pulps are now valued for magazine papers.

In New Zealand, radiata pine has since around 1925 been the mainstay for replacing dwindling supplies of native timber species that are not readily domesticated. It has since become the basis of major export industries, with a total annual roundwood harvest of nearly 20 million m^3, making the country the 12th largest producer of coniferous roundwood and the third largest exporter of coniferous logs. The contribution of the forestry sector, including derived industries, which is around 95% based on radiata pine, is estimated at around 3.5% of the GDP (over US$2.5 billion), and 10% of the country's total export receipts, based on 7% of the land area (MAF 2007). This has been despite a depressed state of the sector, due to a strong New Zealand dollar, an historical focus of the corporates on producing commodity products and on log exports, and some correction of over-harvesting, factors that obscure the species' full contribution to wealth. In addition to producing wood, *P. radiata* makes important contributions to soil conservation and provision of shelter, the shelter plantings containing an additional timber resource.

In Chile, radiata pine is also the mainstay of a large forestry sector, albeit less pre-eminent than in New Zealand. Annual roundwood harvest is some 25 million m^3 (INFOR 2007), the country being the ninth largest producer of coniferous roundwood. Contributions to GDP of primary production from the species are estimated at around US$ 2.3 billion, ca 2% GDP (G Ortiz pers. comm.). The species also greatly dominates forestry exports (ca. US$3.9 billion) (loc cit). The contribution has been helped by very active government encouragement to reduce the economy's extreme exposure to the world market for copper. Many of the plantings have also rehabilitated severely degraded land.

In Australia, radiata pine is also less pre-eminent in the forestry sector than in New Zealand, being 73% of total softwood plantation area (Wu et al. 2007), and it is oriented very much towards local markets. The species probably contributes around 11 million m^3 to the annual roundwood harvest. In the solid-wood area, conifers comprise around three-quarters of the sawtimber production (ABARE 2007), and are widely favored for light construction, for which locally grown radiata pine is generally well suited.

2.2.7.3 Breeding Objectives

Given the general attractiveness of the species for domestication, and strong indications of great genetic variation, it was a logical subject for breeding (Burdon 2004). Research on its genetic variation began in Australia in the late 1930s. Active breeding work, however, began there only in the 1950s, and the effort was long fragmented among the states. In New Zealand, an intensive breeding program was mounted in the early 1950s, from the Forest Service's Forest Research Institute in a large, centralized operation. South Africa began breeding work at the same time, but with the comparative small area that suits the species, the breeding program has remained relatively minor. In Chile, an abortive start was made on breeding in the early 1970s, but was started afresh, adapting the United States Industry/ University Cooperative model, in 1976. In the Basque Autonomous Region of Spain a breeding program began around 1990.

Among breeding objectives the basic, common features have been general health and vigor. Beyond these, breeding objectives have varied among the programs. This largely reflects the phenotypic plasticity of the species, whereby environmental effects mean that different traits are prime candidates for genetic improvement on different sites.

In New Zealand, early breeding largely addressed improving tree form on the fertile pumice-land sites that carried a major portion of the plantation estate. Apart from dominant crown status and general health, trees were selected very intensively for stem straightness, and light, wide-angled branching. The specification for branching generally led to choice of trees with a "multimodal" or "short-internode" branching habit. Favorable genetic correlations between this habit, growth rate, and general tree form, led in 1968 to explicit choice of a short-internode "ideotype", by way of indirect selection to help improve growth and form and to control branch size. In this context, pruning butt logs was done to produce high-quality appearance-grade timber. Selection of an alternative, "long-internode" ideotype was pursued in a side program (Shelbourne et al. 1986), for assuring clear-cuttings of timber without having to prune, albeit at a cost of potential genetic gain in growth and form. Early market acceptance, however, was almost nil. An offshoot of the main, short-internode breeding program was selecting for resistance to *Dothistroma pini*, which is now become an almost universal selection trait, along with resistance to needle cast associated with *Cyclaneusma minus*. A portfolio of different breeds, representing different breeding goals (Jayawickrama and Carson 2000), has become a distinctive feature of New Zealand's radiata pine breeding program. This largely finesses the question of assigning explicit economic weights to different traits, and reflects the combination of the species' environmental plasticity, the diversity of end products in New Zealand creating a complex production system, and the associated difficulty of assigning economic weights. Shorter rotations and more aggressive thinning regimes have exposed shortcomings in wood quality, leading to a recent focus on genetic improvement of stiffness and stability in service.

In Australia and South Africa, where tree form was often better because of lower soil fertility, selection tended to focus less on tree form and more on vigor. In recent years, the selection in Australia has shifted more to wood density and stiffness, reflecting the importance of structural timber combined with how the widespread use of fertilizer tended to compromise timber stiffness. The emphasis on structural timber means a simpler production system than in New Zealand, which has encouraged efforts to derive explicit economic weights for breeding-goal traits (e.g., Ivković et al. 2006a, b). However, complex patterns of pronounced genotype-site interaction in Australia (e.g., Wu and Matheson 2005) pose a continuing challenge in breeding for good local adaptation.

Chile followed New Zealand in pursuing the short-internode ideotype, despite good prospects of growing satisfactory trees of a long-internode ideotype (Burdon 1978). As with other main growers of the species, there is now an increasing focus on genetic improvement of wood properties. The structure of the breeding program, being originally company-based, produced a built-in regionalization.

2.2.7.4 Breeding Achievements

Breeding achievements have depended not only on efficient selection and testing for appropriate breeding objectives, but also on early and efficient delivery of genetic gain in planting stock. Open-pollinated clonal seed orchards were initially used for delivering genetic gain. In New Zealand, the first orchard planting was in 1958 and the first orchard seed was produced in 1968. Despite a difficult learning experience, the country was self-sufficient for seed-orchard seed by 1986. In Australia, there were mixed fortunes with early seed orchards, and major losses of orchards from fire in 1983. Chile benefited from the New Zealand experience on how to site and manage the orchards, most of the orchards coming into full production faster than their early New Zealand counterparts.

From around 1980, delivery systems for genetic gain have been changing. Use of controlled pollination, to capture more genetic gain, has become possible through vegetative multiplication of top-ranked controlled crosses, or through large-scale controlled pollination in orchards that produce seed close to the ground. More recently, clonal forestry, i.e., mass-propagation of well-characterized clones, has been commercialized, to capture non-additive in addition to the additive gene effects and achieve greater crop uniformity, although technical challenges remain.

Despite good combinations of variability and heritability, the important task of demonstrating and quantifying genetic gain accurately is not straightforward. Available growth data come mainly from quite young trees, whose performance needs to be projected into harvest-age production and quality and value of the logs and their end-products. However, special genetic-gain trials, and growth modelling (e.g., Carson et al. 1999), have allowed projection of stem volume gains at different crop ages. For tree-form traits, available data often involve subjective scores, which pose their own problems of quantification.

Notwithstanding these difficulties, major genetic gains have been achieved (Wu et al. 2007; Burdon et al. 2008; F Drppelmann pers. comm.), even in the first generation of breeding. In New Zealand, considerable gains have been achieved in growth rate and, on many sites, massive improvements in tree form. This has allowed large reductions in initial stocking and tending costs, and will mean better wood recovery through reduced logging waste. However, the major genetic shift towards a short-internode habit brings an increased dependence on pruning to improve clearwood yield.

In keeping with the intensive breeding programs, radiata pine has in recent years become the subject of considerable genomic research (see references in Plomion et al. 2007; Wilcox et al. 2007; Burdon and Wilcox 2011), although many of the findings remain unpublished. The species has been involved in several comparative genomics studies (op cit), which have all indicated close synteny and colinearity among various pines. Searches for quantitative trait loci (QTL) (e.g., Carson et al. 1997; Devey et al. 2004; Cato et al. 2006) have suggested a general paucity of large-effect QTL. This, combined with generally minimal population-wide linkage disequilibrium (e.g., Kumar et al. 2003), has led to a shift in emphasis towards association genetics for pursuing the option of genome-based selection. Also, at least one genomic study (Kuang et al. 1998) has endorsed the hypothesis that very imperfect and variable effective self-fertility is due to genetic load in the form of deleterious recessive genes.

2.3 Spruces (*Picea* A. Dietr.)

The genus *Picea* is a member of the family Pinaceae, with about 40 species distributed throughout the cooler parts of the Northern Hemisphere. Within their natural ranges, some of these are extremely important economically and have been the focus of reforestation and breeding efforts. A few have also become important far outside their natural range.

2.3.1 Black Spruce (*Picea mariana*)

2.3.1.1 Historical Perspective

Black spruce (*Picea mariana* [Mill.] B.S.P.) is one of the most widely distributed and hardiest of boreal forest conifers in North America (Farrar 1995). It ranges from northern Massachusetts to northern Labrador on the Atlantic coast, and west across Canada to the west coast of Alaska (Viereck and Johnston 1990). It is also one of the most planted tree species in Canada. It harbors large amounts of genetic variation in quantitative traits, which is an indication of the adaptive capacity of its populations (Khalil 1984). Various patterns of clinal variation have been reported for germination rate, survival rate, phenology, juvenile growth and hardiness (e.g., Dietrichson 1969; Morgenstern 1969; Corriveau 1981; Park and Fowler 1988; Beaulieu et al. 1989a; Morgenstern and Mullin 1990; Parker et al. 1994; Beaulieu et al. 2004).

Natural introgressive hybridization between black spruce and red spruce has been documented in the sympatric zone that mainly takes place in southern Quebec, New Brunswick, Nova Scotia and New England (e.g., Perron and Bousquet 1997). As both are close species, they are known to introgress, but introgressed populations are generally found on disturbed sites (Morgenstern 1996).

Due to this phenomenon, more attention must be paid to seed source transfer in order to make sure that they are well adapted to the environmental conditions of the recipient site.

Knowledge of patterns of genetic variation as well as of the strength of genetic control on characters is of fundamental importance if a breeding program and reforestation efforts are to succeed. While selection and breeding were begun in some Canadian provinces in the 1960s, large-scale tree improvement programs have been initiated in most of the provinces since the mid-1970s (Park et al. 1993).

2.3.1.2 Economic Importance

Black spruce is a medium-size tree that can reach on poor-drained sites average heights of about 20 m and diameters of 30 cm whereas on well-drained sites, it can reach up to 30 m high and 60 cm in diameter (Farrar 1995). It is one of the most important species in Canada and northern United States for manufacturing high quality pulp and paper and solid wood products, including framing material, millwork, crating and piano sounding boards (Alden 1997). Historically, it has also provided specialized products such as healing salves from spruce gum, beverages, aromatics and binding material (Viereck and Johnston 1990).

2.3.1.3 Breeding Objectives

As for many other commercial species, selection is primarily based upon stem growth, wood quality traits and tolerance to biotic and abiotic adverse factors. Contrary to other spruces and pines, the stem is generally straight and the crown form is fairly uniform in black spruce. Consequently, less emphasis was put on selection criteria for these traits.

2.3.1.4 Breeding Achievements

While black spruce programs have been established in most jurisdictions where the species grows naturally, their importance and progress varies among them. New Brunswick, for instance, is now in a position to initiate a third breeding cycle. Tree improvement activities are carried out by the New Brunswick Tree Improvement Council, formed by the New Brunswick Department of Natural Resources, the Canadian Forest Service and six large industrial companies (Tosh and Fullarton 2006). Since the first breeding activities in the mid-1970s, two generations of seed orchards were set up by the Council. The first-generation was established as seedling seed orchards between 1980 and 1987, with open-pollinated seed collected from plus-trees selected in natural stands. Progeny tests accompanied the seed orchards and data collected in these tests allowed improvement of the orchards by roguing. A second-generation series was established between 1989 and 1997 by grafting selections into orchards. Since then, all polycross and controlled crosses needed to evaluate the general combining and specific combining abilities of the selected trees were made and all the tests are now in place (Tosh and Fullarton 2006) and third-generation selection in the older full-sib tests will begin in the near future. A portion of the annual reforestation stock requirement is now produced using somatic embryogenesis techniques from elite crosses.

Nova Scotia, Prince Edward Island and Newfoundland and Labrador have also established first-generation seed orchards that now supply the current seed demand for reforestation. A second-generation program is currently conducted by the industrial partners of the Nova Scotia Tree Improvement Working Group (Frame and Steeves 2006). First-generation seed orchards in this province as well as in Prince Edward Island have been rogued to increase expected gain (MacKinnon et al. 1997).

In Quebec, breeding activities also began in the 1970s. Five breeding zones were delineated using 16-year data collected on a range-wide provenance trial replicated on four sites (Beaulieu et al. 1989a). First-generation breeding populations were assembled by selecting superior phenotypes in the best performing provenances. Controlled crosses were carried out and full-sib families were vegetatively multiplied to establish progeny tests. In the 1980s, a network of 24 seedling seed orchards and 42 open-pollinated progeny tests were established using plus-tree selections made in natural stands. Roguing of first-generation seed orchards is now complete, as well as the establishment of the five second-generation clonal seed orchards with elite trees selected from progeny tests accompanying first-generation seed orchards and those established with full-sib families from controlled crosses in the first-generation breeding population. About 3 million rooted cuttings are also produced annually for the reforestation program using seeds form tested full-sib families. Breeding activities for the development of the third-generation program are now underway (Beaudoin et al. 2004).

In Ontario, first-generation breeding zones were created in the early 1970s, and as for most provinces, largely delineated by administrative boundaries (Ford et al. 2006). First-generation seed orchards were set up and they have now been rogued. The installation of genecological trials in the 1990s allowed including information on variation in adaptive traits in the delineation of biologically-sound second-generation breeding zones. The northeastern region has been selected to develop a pilot second-generation breeding program. Selection of superior genotypes was done in first-generation open-pollinated progeny tests and controlled crosses were made. Second-generation progeny tests were set up in accordance with a nucleus breeding system, with the breeding population substructured into elite and infusion populations (Cherry and Joyce 1998).

In Manitoba, breeding zones have been delineated and breeding work is achieved in a collaborative mode by Manitoba Conservation and three forest companies. First-generation seed orchards and open-pollinated progeny tests were established in the 1990s and the early 2000s, and some of the seed orchards have been rogued (Falk et al. 2006). Alberta is also breeding black spruce and has first-generation seed orchards in place.

In the United States, first-generation seedling seed orchards have also been set up in Maine and Vermont (Carter and Simpson 1985; Carter et al. 1988) to produce the genetically improved seed for their reforestation programs.

The development of genomic resources for black spruce is a focus of research at the CFS and Genome Canada's "Arborea" project, with the aim to develop MAS for adaptive traits such as growth and phenology as well as for wood quality traits in the context of shorter rotations. The objective is to more rapidly develop varieties that can better sustain climate-change conditions with faster generation turnover, and to optimize the forest products value chain.

2.3.2 White Spruce (Picea glauca)

2.3.2.1 Historical Perspective

White spruce (*Picea glauca* (Moench) Voss.) has a transcontinental range, from Newfoundland and Labrador west across Canada along the northern tree limit to Hudson Bay, the Northwest Territories, Yukon and Alaska, and is adapted to a wide range of soil and climatic conditions (Nienstaedt and Zasada 1990). It is a medium-sized tree that can reach up to 25 m in height and 60 cm in diameter (Farrar 1995). Research on the genetic variation of white spruce began in the 1930s in both Canada and the United States where it has demonstrated great potential for genetic improvement (Niensteadt and Teich 1971). Results from provenance trials have clearly indicated the superiority of white spruce populations originating from the Lower Ottawa Valley and adjacent areas in most of the regions where they were tested. This has had a great influence on the composition of the breeding populations. In some regions of British Columbia, white spruce grows with Sitka spruce (*Picea sitchensis* [Bong.] Carr.). It also grows with Engelmann spruce (*Picea engelmannii* Parry ex Engel.) in the same province, as well as in Alberta, the Northwest Territories and Yukon, and natural hybrids occur (Farrar 1995). White and Engelmann spruce have been shown to be the extreme forms of a clinal pattern of variation associated with altitude (Roche 1969) and hybrids are known as the “interior spruce complex”. Hence, interior and white spruces from eastern regions of Canada have been considered to be sufficiently different to warrant separate breeding programs.

2.3.2.2 Economic Importance

White spruce is one of the most important commercial species in the boreal forest of North America. It is used extensively for manufacturing of pulpwood and solid-wood products. It is used for framing material, general millwork, boxes and crates and piano sounding boards (Farrar 1995; Alden 1997). Historically, its wood was used for fuel, its bark to cover summer dwellings, its branches for bedding and its resin for medicinal purposes by aboriginal people (Nienstaedt and Zasada 1990). Due to its high survival rate, capacity to adapt to various ecological conditions and fast growth rate, it is one of the most planted species in Canada, especially in British Columbia, Alberta and Quebec.

2.3.2.3 Breeding Objectives

In white spruce, selection has focussed primarily on increasing economic value by improving stem growth and straightness, volume, as well as crown form and branch size, while maintaining a broad genetic base for adaptability and pest resistance, especially to the white pine weevil (*Pissodes strobi* [Peck]) in western Canada. More recently, emphasis has been put on wood physical properties.

2.3.2.4 Breeding Achievements

White spruce breeding programs started in most jurisdictions in the 1970s and are now well established. Breeding strategies vary from region to region, but generally use progeny testing and recurrent selection combined with clonal seed orchards to produce seed for reforestation programs.

In New Brunswick and Nova Scotia, two distinctly different programs have been implemented for the first generation: (1) seedling seed orchards to capture genetic variation at the provenance level, and (2) clonal seed orchards to capture within provenance variation (Fowler 1986). The former were established between 1978 and 1982 on 8.6 ha using open-pollinated seed from the Lower Ottawa Valley to develop improved varieties adapted to the Maritimes (Carter and Simpson 1985). For the clonal seed orchards, plus-trees were selected in natural stands in each province. They were established between 1985 and 1987 and covered 9 ha. Polycrosses and pair mating were used to generate the seed for progeny tests to estimate both the general and specific combining abilities of selected parent trees, as well as selection plantations in which candidates were selected for the second-generation. Roguing of first-generation seed orchards has been completed and forward selection to establish second-generation clonal seed orchards is underway, with 4.1 ha established to-date (Tosh et al. 2009).

In Newfoundland and Labrador, clonal seed orchards were established in the early 1990s. Since then, polycrosses have been performed and selection plantations established in the early 2000s (English and Linehan 2000).

White spruce breeding activities in Quebec began in the early 1970s to support a major reforestation program. Between 1972 and 1990, over 360 million seedlings were planted (Beaulieu 1994). In the mid-1990s, about 70 million seedlings were planted annually on both private and public lands, but this has now declined to about 25 million. As in the Maritimes, breeding populations in Quebec were developed using various sources of superior material. First, analysis of data collected in genecological tests established in the late 1970s and early '80s allowed delineation of two large breeding zones based on patterns of genetic variation observed and existing ecological classification (Li et al. 1993; Beaulieu 1996; Li et al. 1997). Provenance trials set up in the 1950s and '60s provided a first pool of tested material for the selection of superior genotypes to build the first-

In ref.--1997a and b

Citation should be "Li et al. 1997b"

generation breeding populations and seed orchards. The volume production of the best provenances at age 25 years was 20–50% better than local seed sources. About 100 plus-trees were selected from these provenances and grafted in the early 1980s, together with additional selections made in the genecological tests. Polycross and pair matings were made and progeny tests established in the mid 1990s. Controlled crosses were completed and a new series of progeny tests was established in the early 2000s. Second-generation orchards have already begun to provide seed for reforestation programs, with some material vegetatively bulked up as rooted cuttings.

In Manitoba, three breeding zones were delineated and open-pollinated family tests as well as first-generation clonal seed orchards were established (Falk et al. 2004), some of which have been rogued (Falk et al. 2006). In Alberta, first-generation clonal seed orchards were established between 1982 and 1989 for each of three breeding zones, with accompanying open-pollinated progeny trials. These orchards have been rogued several times since their inception (Hansen et al. 2009).

In British Columbia, the interior spruce breeding program was structured in two phases. The first began in the mid-1960s and addressed the needs of three regions. The second began in the mid-1970s and focussed on other regions where interior spruce was important. First-generation seed orchards established at this time have now been rogued and provide much of the planting stock. Controlled crosses have also been made and full-sib second-generation tests are in place. Selection of superior genotypes has begun and the establishment of a breeding orchard has been initiated (Carlson et al. 2009).

In Maine, private forest companies have established small first-generation clonal seed orchards in the 1970s whereas 10 ha of clonal and seedling seed orchards were set up in the 1960s in the State of New York (Carter and Simpson 1985). Breeding programs have also been undertaken by the USDA Forest Service in Minnesota, Wisconsin and Michigan in the 1970s (Nienstaedt and Teich 1971).

Major research efforts have been underway in Canada through several projects in recent years, to develop genomic resources and implement molecular breeding for adaptive and wood quality traits in both eastern and western white spruces. Various schemes are being deployed to identify informative gene SNPs including QTL/gene co-localization studies, association genetic approaches and genomic selection. Association studies are also underway to evaluate the possibility of using candidate genes for early selection in the spruce terminal weevil resistance programs (also involving Sitka spruce) in the British Columbia Forest Service breeding programs.

2.3.3 Red Spruce (Picea rubens)

2.3.3.1 Historical perspective

Red spruce (*Picea rubens* Sarg.) is a common spruce in the Maritime provinces of Canada and southward into the Appalachian Mountains of the United States (Farrar 1995). It is also present in Quebec and Ontario but only in the southern regions. While it is an important forest species, it is not widely planted. As introgressed hybrids contribute substantially to observed variation in phenotypic traits and adaptation (Morgenstern et al. 1981), seed-source transfer has been carefully monitored. Research on the genetics of red spruce began in the early 1950s with the involvement of the Canadian Forest Service and the collaboration of the eastern Canadian provinces and the federal and state research organizations of the United States (Holst 1955). The aim was to identify superior populations that could be used directly in reforestation programs.

2.3.3.2 Economic Importance

When utilized for structural products, red spruce is not distinguished from other spruces and is processed in a group called SPF (Spruce, Pine and Fir). Its wood physical properties are in the range of those of white and black spruces (Jessome 1977) and its wood is mainly used for lumber, flakeboard, plywood, and pulpwood. Other marginal uses are for poles piling, boatbuilding and cooperage stocks, as well as sounding boards for a variety of musical instruments (Blum 1990).

2.3.3.3 Breeding Objectives

Selection in red spruce, has focussed on improving stem growth and straightness, volume as well as crown form and branch size while maintaining a broad genetic base for adaptability and pest resistance, especially to the spruce budworm (*Choristoneura fumiferana* [Clem.]) and the yellow-headed spruce sawfly (*Pikonema alaskensis* [Roh.]).

2.3.3.4 Breeding Achievements

Nova Scotia initiated its red spruce breeding program in 1976 and the selection of plus-trees was completed in 1985 (Fowler 1986). Clonal seed orchards were established to provide the genetically improved stock for the reforestation program. In Quebec, first-generation clonal seed orchards were also established in the 1980s using plus-trees selected in natural stands as well as in range-wide provenance trials established in the late 1950s by the Canadian Forest Service (Morgenstern et al. 1981). Reforestation of red spruce in Quebec has not been extensive, due to low productivity when planted on open sites and its susceptibility to winter drying and frost damage (Morgenstern et al. 1981; Beaulieu et al. 1989b), so advanced-generation breeding had not been continued. On the other hand, New Brunswick responded to an increased interest in planting red spruce by reviving its program in 2004. Second-generation red spruce clonal seed orchards had been established in 1999, and by 2007 they occupied 3.6 ha (Tosh and Fullarton 2008).

In ref. 2006

Citation should be: "Tosh and Fullarton 2009" -- new reference added to list

As red spruce is highly susceptible to winter dessication and given the relative paucity of breeding resources for this species, red spruce breeders in the future may resort to genomic approaches to identify adaptive polymorphisms and select trees that are more tolerant to winter drying and frost damage. The current development of gene catalogs and SNP directories for white spruce and black spruce should help accelerate the application of MAS in red spruce.

2.3.4 Sitka Spruce (Picea sitchensis)

2.3.4.1 Historical Perspective

In its native range, Sitka spruce (*Picea sitchensis* (Bong.) Carr.) occupies a narrow strip on the north Pacific coast of North America, extending for 2,900 km from 61°N latitude in south-central Alaska to 39°N in northern California. Throughout this tremendous north-south range, Sitka spruce is a coastal species, occupying islands of the Alexander Archipelago in Alaska and the Queen Charlotte Islands (QCI) in British Columbia, and, with the exception of river valleys, rarely reaching more than a few kilometres from the coast along a narrow strip on the mainland (Harris 1990).

While its natural range is not extensive and the species' economic importance ranks far below that of other western conifers, Sitka spruce is a keystone species in some of the most productive ecosystems of North America, particularly in the QCI (Peterson et al. 1997). Nevertheless, in the Pacific Northwest United States, British Columbia and Alaska, Sitka spruce is not a preferred species for reforestation and in fact is often considered unacceptable. This is because it is attacked by the white pine or terminal weevil (*Pissodes strobi* Peck), which repeatedly kills the emerging leader of young plantation trees. The weevil is a native insect that occurs across Canada and the northern United States. Sitka spruce is particularly susceptible to this pest; damage is so severe that young plantation trees often become stunted and bushy as terminal leaders are repeatedly killed and young trees fail to achieve apical dominance. This has reduced planting to offshore islands such as the QCI and Alaska.

Outside its natural range, Sitka spruce has played an important role in plantation forestry, particularly in northern Europe (Hermann 1987). In Great Britain, Sitka spruce is the most widely planted conifer, accounting for nearly 700,000 ha of forest or 30% of the total forest estate (Forestry Commission 2003). The species is well suited to areas of high rainfall and lower quality agricultural soils that predominate in the north and west of Britain. It is planted from Cornwall in the southwest England (latitude 51° N), through Wales and northwestern England, across northeastern England and southern Scotland and up into the Scottish Highlands (latitude 58°N).

Although the species was originally described by Archibald Menzies in 1792, it was not introduced into Britain until 1831 by David Douglas. By the time the British Forestry Commission (the State Forestry Service) was formed in 1919, experience from sample trees planted in arboreta and on large estates had established the species as fast-growing, hardy in exposed conditions and capable of growing on site types which at the time were mainly planted with Norway spruce (*Picea abies* [L.] Karst.). The superior growth of Sitka ultimately led to an increase in its popularity through the 1930s and beyond as the forest estate expanded under the then-government policy of afforestation.

2.3.4.2 Economic Importance

Wood from Sitka spruce offers unique qualities for manufacture of the highest quality sounding boards for many musical instruments, and its outstanding strength-to-weight ratio made it strategically important during both World Wars for construction of aircrafts (Brazier 1987). Although a relatively minor species in its native range, Sitka spruce is now hugely important to British forestry and wood utilization industries. The main objective of growing Sitka is to generate construction-grade timber that will displace material imported mainly from Scandinavia and the Baltic states, although smaller material also feeds the pulp and particle board industries which have become well established in Britain.

Annual growth in Britain averages 12 to 26 m^3/ha/yr, translating to rotation lengths of 50 years down to 35 years, depending on the site. Around 32 million plants are sold annually within Britain to plant over 12,000 ha, predominately for restock harvested forest land. Sitka spruce is also a primary plantation species in Brittany (France) and Ireland, where productivity of stands is similar to or greater than that in Britain (Vaudelet 1982; Serrière-Chadoeuf 1986; Guyon 1995; Thompson et al. 2005).

2.3.4.3 Breeding Objectives

Within its native range, breeding has focussed on developing robust resistance to the white pine weevil. This program is based on investigations of the extent and nature of genetic resistance to the pest, with the goal of restoring the Sitka spruce component of the regenerated coastal forests. The mechanisms for resistance are very likely complex, with the density of sclereid cells and resin canals thought to be important. In some genotypes, a strong resistance factor, almost a "total resistance", was also observed, but its mechanism is unknown (Alfaro et al. 2002). The evidence is that this resistance is stable, viable over a wide area and appears durable.

In Britain, the main objective is to increase the end-of-rotation value to the construction grade industry, relative to that achieved using unimproved seed imported from the Pacific Northwest. Trees are selected which combine good growth rate, with improved stem straightness and branching qualities, and better wood stiffness. Wood stiffness is a complex trait involving wood density, microfibril angle and other internal characteristics such as proportion of compression wood. Under current practice, only wood density is screened as a surrogate for wood stiffness.

2.3.4.4 Breeding Achievements

Breeding efforts in British Columbia have focussed on quantifying resistance to weevil, based on statistically testable data (King et al. 2004), and development of methodology for rapid screening (five years) using artificial infestations (Alfaro et al. 2008). Many populations, families and individuals have now been screened to ascertain which have resistance that is durable and useable in the breeding program (King et al. 2008). The best individuals and families have been established into seed orchards which are now producing seeds with a high degree of resistance (King and Alfaro 2004). New guidelines for the deployment of resistant Sitka spruce have been proposed, which include recommending Sitka spruce as not only an acceptable but even the preferred species for many coastal sites (Heppner and Turner 2006).

Not listed in ref.

Change citation to "King and Alfaro 2009" -- added to references

The breeding of Sitka spruce in Britain has followed the classical breeding theory: selection of the best origin, selection of plus trees from stands in forests, followed by testing of selected plus trees through comparative half-sib progeny tests, subsequent measurement of trials and then re-selection of a breeding and production populations based on multi-trait index selection. Samuel et al. (2007) summarized the processes involved in identifying provenances best suited for planting in Britain. The general conclusion was that material from around the QCI (54° N) was most suitable for the bulk of Britain although in the milder areas of southwest England and Wales, Washington sources (48° N) or even Oregon material (45° N) were well adapted.

Plus-tree selection in Britain commenced during the early 1960s (Fletcher and Faulkner 1972) and progressed through into the early 1980s. Over 1,800 candidate trees of predominately QCI origin were selected. Progeny tests were established with open-pollinated seeds, with each candidate evaluated in replicated trials established on an average of three sites, and compared against standard controls of unimproved QCI and Washington origin (Lee 2001). The trials were measured regularly for height and later stem diameter, stem straightness and wood density. The best 340 plus tress were identified, based on a multi-trait index combining 15-year stem diameter, straightness and wood density, and these used as first-generation breeding parents. In the second generation, the program expects to stratify the breeding population into six sublines of equal mean genetic value, and to apply positive assortative mating within sublines (Lee 2001).

Improved planting stock has been available from the Sitka spruce breeding program since the early 1990s. Improved stock can be derived either from seedlings raised from seed collected in progeny-tested clonal seed orchards, or as rooted cuttings derived from stock plants originating from controlled pollinations. The controlled pollination of selected seed parents uses a polymix of 20 or so unrelated pollens, again from selected trees. Predictions of genetic gain have been impressive, up to around 20% for both stem diameter and stem straightness with minimal loss in wood density. More recently, these half-sibling family mixtures used in the production of stock plants and ultimately rooted cuttings, have given way to full-sibling families (Lee 2006). Sawmill studies involving trees from some of the earlier half-sib progeny tests have suggested end-of-rotation gains for volume of around 25% relative to unimproved QCI material (Lee and Matthews 2004), and an increase of high-end value sawlogs of up to 130% (Mochan et al. 2008). Improved material is in high-demand and this is now entirely satisfied from home-produced improved sources.

Despite having contrasting breeding objectives, groups in Canada and Britain are collaborating to develop geneomic resources and identify markers associated with a range of economically important traits, including disease and insect resistance and wood density. In particular, the British effort has invested in MAS, with an initial objective to identify a suite of DNA-based markers, which could be used in the laboratory as surrogates for direct field selection. Three large clonal trials were planted in 2004 on climatically contrasting sites across Britain. Each trial contains the same material; 1,500 clones from each of three full-sib families, along with the usual QCI control (used also in the Canadian program). It is hoped that the tests will enable the identification of QTLs contributing to wood density, stem and branch quality (Lee et al. 2007).

Research also continues to develop somatic embryogenesis and cryopreservation of Sitka spruce. If successful, this will prove instrumental in harnessing the material identified in the British MAS program for quick deployment to the field (Lee et al. 2004), and for confirmation and delivery of stable weevil resistance (El-Kassaby et al. 2001).

2.3.5 Norway Spruce (Picea abies)

2.3.5.1 Historical Perspective

Norway spruce (*Picea abies* [L.] Karst.) is one of the most abundant and economically most important forest tree species in Europe. Its natural geographic range covers 31 degrees of latitude from the Balkan Peninsula to its northernmost extension near Khatanga River, Siberia. Longitudinal range is from the French Alps to the Sea of Okhotsk in eastern Siberia. The vertical distribution is from sea level to altitudes above 2,300 m in the Italian Alps. Its natural range in Europe is to a large extent in the boreal and in the mountainous region of the temperate zone. The species is, however, widespread outside this range, particularly in western and central Europe. This is due to the fact that the proportion of Norway spruce has been substantially increased in Europe by reforestation and afforestation in order to establish forests for timber production. This process started in particular at the beginning of the 19th century when many forests in Europe had been affected by forest devastation due to overexploitation and soil degradation. The species can easily be established artificially outside its natural range, in particular in the rather oceanic climate in western Europe that seems to provide a physiological optimum for Norway spruce. It has been regenerated artificially in areas naturally occupied by European beech, oak and other broadleaved tree species. To some extent, Norway spruce has also been planted in North America, especially in eastern Canada. Due to the wide distribution of Norway spruce and considerable differentiation in provenances, it is not possible to define very distinct site requirements for the species.

The first provenance trials with Norway spruce were established in the late 1800s in Austria and were followed by several series of national and international experiments (König 2005). The most important of these are the two IUFRO series of 1938 and 1964, which together comprise more than 1,100 provenances and were planted at more than 40 locations. The field experiments have revealed certain genetic-geographic variation patterns with regard to growth and have clearly demonstrated that the local provenance as a rule is not the best (König 2005). A considerable increase in growth rate can therefore be obtained by judicious transfer of provenances. In the case of extreme environmental conditions, like in northern Scandinavia and at high altitudes in the Alps, large losses can result as a consequence of inappropriate provenance transfers.

2.3.5.2 Economic Importance

The most extensive coverage of Norway spruce is found in Sweden and Austria, where the species covers more than 25% of the total land area and more than 40% of the forest area (Spiecker 2000). A large coverage of Norway spruce, with 15–25% of the total land area and more than 25% of the forest land, can also be found in Finland, Norway, Czech Republic, and Slovakia. In Switzerland and Germany, the species covers 10–15% of the total land and more than 30% of the forest land. All these countries are in the natural range of the species, but with plantations also outside the areas where it occurs naturally. This is also the case in the western part of Europe; in Belgium, the Netherlands, Denmark, Great Britain, Ireland and most parts of France.

The highest volume production of Norway spruce is found in pure plantations and often outside its natural range (Schmidt-Vogt 1977; von Teuffel et al. 2004). On average, the annual increment of Norway spruce in Europe during the last 20-year period has been about 7.3 m^3/ha (von Teuffel et al. 2004), but growth rates are much higher in several countries where Norway spruce is planted as an exotic. Norway spruce accounts for 40% of the total increment in Nordic forests, making it a very important commercial tree species in this region. There has been a considerable increase in the growth rate of Norway spruce in Europe during the last 40–50 years, which could be due to several factors such as changes in land use, forest management, natural disturbances, climate changes and nitrogen deposition (Spiecker 2000). However, in recent decades, some problems have been exposed due to its susceptibility to air pollution, wind, snow, ice and storms, and also to certain fungi and weevils. The use of maladapted provenances has resulted in damage and reduced yield in plantations. These negative factors have made Norway spruce less popular in reforestation, in particular outside its natural range.

Norway spruce produces large volumes per unit area of straight timber that is suitable for structural applications, panelling and furniture. Its relatively fine branching and long, lean and straight fibers makes it particularly attractive as raw material for the pulp and paper industry. It is therefore a widely used and valuable tree species for the forest industry in Europe.

2.3.5.3 Breeding and Breeding Objectives

The genetic variability in Norway spruce has been studied in provenance and progeny trials, often planted at several sites, and by genetic markers such as isozymes and DNA markers. The most pronounced patterns of variation demonstrated in provenance trials relate to the populations' responses to climatic conditions. In northern Europe, these patterns of variability often relate to latitude and longitude, and to the degree of continentality, and will sometimes vary clinally. They are expressed as variation in budflush and duration of the annual growth period in spring, and the corresponding cessation of growth and development of frost-hardiness in autumn. These annual growth patterns have implications for frost-hardiness, growth potential and wood-quality traits, and are important for proper choice of reforestation materials. At the same time, there is large variability for the same traits within natural populations. In central Europe, the regional variation patterns are less clear, owing to a long history of planting and provenance transfers.

Breeding of Norway spruce was initiated in several European countries in the late 1940s (Danell 1991; Mikola 1993). The work typically started with the selection of phenotypically superior "plus trees" in natural stands (Skrøppa 1982; Gabrilavicius and Pliura 1993; Mikola 1993). Mature trees were selected that had superior height and diameter growth and stem and branch quality, compared to neighboring trees in the stand. These were established by grafting onto rootstocks in clonal archives and seed orchards. Each grafted seed orchard was composed of a rather large number of selected clones (50–500), with the intention of seed production for one geographic region. The seed orchards generally start to flower 10–15 years after grafting, although the periodicity and amount of flowering are very much dependent on climatic conditions at the orchard site. To promote flowering, orchards have often been located on warmer sites, relative to those from where the parents originated and where the orchard seed is intended for use.

It was soon realized that the selection of plus trees in natural Norway spruce stands is not an efficient method to identify superior genotypes. It is necessary to test the genetic value of each parent, based on an evaluation of their offspring. In the Nordic countries, this is done in progeny tests planted at several sites where assessments are made of survival, height and diameter growth and quality traits. The progeny tests are sometimes supplemented with tests where seedlings are grown under controlled conditions in growth chambers and measurements made of physiological traits. On the basis of several traits, a subset of the original parents is selected for further breeding. Seeds for operational planting can be collected selectively in the orchard, the orchard thinned or a new orchard established with the best progeny-tested parents.

In other countries, breeding programs were based on materials selected from populations with high adaptive potential exhibited in comparative provenance trials. The best individuals from families of the best provenances were selected to produce seeds in orchards, or to create a breeding population through controlled crosses. Some of these programs also targeted mass production of rooted cuttings of tested clones (Birot 1982; van de Sype and Roman-Amat 1989; Kleinschmit 1993). Of major concern in the breeding strategies have been the breeding objectives; the sizes of breeding and production populations required to maintain genetic diversity; test design and efficiency; and identification of suitable regions where the orchard seed should be recommended for use.

The principal breeding objectives in most programs are to improve the value of production in future spruce stands and to mitigate risk under variable environmental conditions. The selection criteria needed to achieve these goals will vary among different breeding populations, based on the varying regional conditions. Under the severe conditions in the northern boreal forest, adaptation to the climatic conditions is crucial. Frost hardiness in artificial freezing tests, the timing of flushing in spring and survival, vitality and lack of injuries in field tests are therefore important target traits. Spring frost events may also occur at more southern latitudes, and selection for late bud flushing may also be important here. Selection for yield is mostly based on height or diameter growth. Some programs aim to keep stem and wood quality at the present level, while others also want to select for improvement of quality traits. Another important target for breeding has been resistance to root rot (*Heterobasidion annosum*), but research efforts have not yet succeeded in developing reliable techniques for selection of resistant materials. In the last decade, adaptation to changing climate conditions has been an increasing concern. In Sweden, this objective has been addressed by establishing a system of multiple breeding populations, which are bred for adaptation to different combinations photoperiod and temperature conditions, including combinations that lie outside of what is normal under the present climatic conditions (Andersson 2002).

2.3.5.4 Breeding Achievements

The regeneration of Norway spruce forests is based both on natural regeneration and planting, with the former often preferred where it is feasible. While seed orchards are common in many countries, the bulk of Norway spruce seeds are still collected in natural or planted stands. Each seed lot should be identified by the geographic origin of the stand, and in several countries it is required that the seed stand should be selected for superior performance. The relative amounts of seeds from forest stands and from genetically improved seed harvested in seed orchards vary considerably among countries and regions within countries. In the Nordic region, there has been a considerable increase in the use of seed orchard seed during the last five-year period. In Norway, 77% of the 300 kg Norway spruce seeds sold in 2007 in the southeastern region originated from seed orchards. The nearly 12 tons of Norway spruce seeds that were produced in Swedish seed orchards in 2006 will be produce 1.2 billion plants, sufficient to regenerate 450,000 ha (Almqvist et al. 2008).

Genetic tests have shown that the productivity of Norway spruce stands established with seedlings originating from untested first-generation seed orchards is about 10% higher than those from unselected material of the same provenance (Andersson 2002). The difference in quality is less, but even here there has been some improvement. Genetic thinning of these orchards could increase the gain further. In Sweden, a second round of seed orchards was established using a mix of untested and tested parent trees. The gain in volume production from these orchards is estimated to be in the range of 12–25% (Rosvall 2001). In a third round of seed orchards, based on a new generation of tested parents from the breeding populations, a gain of some 35% is anticipated (Rosvall 2001).

A comparison of production and economics of Norway spruce stands in southern Sweden established with genetically improved and unimproved seedlings showed that the increased gain in volume production resulted from earlier thinnings and shorter rotation age (Rosvall et al. 2004). A 68% increase in the present value of improved planting stock could be expected, based on the realistic assumption of a 22% increase in volume growth and a 10-year reduction in rotation age.

The use of clonal forestry based on rooted cuttings was popular in the 1970s in Germany, Denmark and Sweden, but now occurs only on a small scale. The same is true for bulk propagation of rooted cuttings from selected full-sib families. Clonal forestry based on somatic embryogenesis has potential to become a valuable tool for intensive wood production, and methods for somatic embryogenesis in Norway spruce are now to a point where operational testing and deployment programs can be launched (Devillard and Högberg 2004).

Marker-aided or genomic selection has not yet been applied to breeding of Norway spruce. A list of "recommended" nuclear microsatellites has been established for the species, and research is underway using SNPs to identify candidate genes for the terminal bud set (M Lascoux pers. comm. 2009). Meanwhile, a project in Sweden is sequencing the Norway spruce genome; its results will facilitate the development of genetic markers and dissection of complex traits, and likely lead to applications in breeding (PK Ingvarsson pers. comm. 2009).

2.4 Other Important Pinaceae

2.4.1 Douglas-fir (Pseudotsuga menziesii)

Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) is an important timber species in western North America, where it is valued for its high wood and timber quality, fast growth and broad resistance to diseases and insects. Along the Pacific coast, the coastal variety *P. menziesii* var. *menziesii* extends in a continuous fashion from latitude 37° to 53°, while the interior variety *P. menziesii* var. *glauca* (Beissn.) Franco ranges from the 19° (from the mountains of central Mexico along the Rocky Mountains) to latitude 55° (Hermann and Lavender 1990). In the southern part of its interior range, Douglas-fir distribution is non-continuous. In the western United States, Douglas-fir grows on roughly 17 million ha (Smith et al. 2001), while in Canada it grows on 4.5 million ha (Hermann and Lavender 1999). It can grow from sea level up to 3,000 m on the slopes of the Rockies (Howe et al. 2006). Due to its desirable economic characteristics and its wide ecological niche, this highly adaptable and plastic species has been introduced to Europe and several countries of the southern hemisphere (New Zealand, Argentina and Chile), where it is a major commercial conifer species.

2.4.1.1 Historical Perspective

Douglas-fir has been a major species in North America since the mid-Pleistocene, establishing itself as a keystone species over large parts of its range (Lipow et al. 2003). During the last 200 years through to the early 1900s, forests in the Pacific Northwest of the United States and in British Columbia were mainly clearcut followed by slash burning and natural regeneration. This mode of reforestation favored the establishment of Douglas-fir on the dry soils of clearcuts, often replacing other species such as western hemlock (*Tsuga heterophylla* [Raf.] Sarg.) and western redcedar. In the 1950s, planting following clear cutting and slash burning reduced rotation ages and became the reforestation method of choice (Curtis et al. 2004). Only small relics of old-growth Douglas-fir are still present throughout its natural range.

Douglas-fir was introduced in Europe in 1827 by the Scottish botanist David Douglas. Initially planted as an ornamental, it was utilized for forest plantations by the end of the 19th century. Its position, compared to other forest species, remained modest until the middle of the 20th century when it became a major reforestation species in western Europe, mainly with the support of post-war national or regional forest grants. Today's plantations in western Europe exceed 700,000 ha, representing the largest area of Douglas-fir outside its natural range.

Douglas-fir was first introduced to New Zealand in 1859 (Miller and Knowles 1994). It has been used in plantations since the early 1900s and is economically the second-most planted species. The use of Douglas-fir in New Zealand initially declined in the mid 1960s after the fungal disease Swiss needle cast (*Phaeocrytopus gaumanii*) became established in the North Island. Interest and enthusiasm for Douglas-fir is now keenest in the South Island where growing conditions are more favorable, and wherever Swiss needle blight has not had a significant impact on stand health and productivity. In the South Island, there are large areas where Douglas-fir has distinct advantages as the primary commercial species due to its good growth and tolerance of winter climatic extremes.

Unknown Douglas-fir provenances were introduced to Argentina in the early 20th century on Victoria Island in Nahuel Huapi Lake in northwest Patagonia. Growth pattern studies associate this land race with Californian origins (Rehfeldt and Gallo 2001). However, only in 1940 was the first plantation made by the State Forests Institute, and it was not until the 1970s that the provincial government began programs with the objective to identify appropriate areas for intensive forest plantations (Buamscha 2002). The current area of Douglas-fir in Argentina ranges from Neuquen province (latitude 40° 15′ S) to Chubut province (latitude 43° 13′S).

The introduction of Douglas-fir to Chile was similar to that in Argentina. While first introduced early in the 20th century, it is only in 1940 that the first plantations were made, principally in the Cautín province (IX Region). Site conditions in the south of Chile, from Cautín (latitude 38° S) to Llanquihue (latitude 41° S) are favorable for the growing of Douglas-fir (Siebert et al. 2003).

2.4.1.2 Economic Importance

Douglas-fir is one of the most valuable and productive timber species. In the western United States alone, over 27.8 million m^3 of Douglas-fir lumber was produced in 2002 (Howe et al. 2006) while in British Columbia in 2006/07 Douglas-fir contributed roughly 12% of the provincial allowable annual cut (10.2 million m^3 of a total of 83.6 million m^3). In addition, in 1999, Douglas-fir accounted for one third of all log exports in the United States (Howard 2001) and 60% of all log exports in British Columbia in 2003/04.

France and Germany represent more than half and nearly one fourth of the European Douglas-fir area (400,000 ha and 160,000 ha, respectively). Other European countries where Douglas-fir is important are: United Kingdom (50,000 ha), Spain (35,000 ha), Belgium (20,000 ha) and Italy (12,000 ha). As a result of its plasticity and its high volume yield, Douglas-fir tends presently to replace Norway spruce in middle-elevation regions.

In New Zealand, Douglas-fir is planted on more than 113,000 ha (MAF undated) and is suited primarily as structural and framing timber because of its good stiffness and stability characteristics. Its timber falls within the density range of radiata pine, but has longer fibers and greater strength. A major advantage over radiata pine is that wood density and stiffness does not decrease seriously near the pith, so that framing timber can be sawn from much smaller logs including thinnings.

Currently, Douglas-fir occupies over 8,000 ha in the Argentinean Patagonian region (Jovanovski et al. 2005) and 15,000 ha in Chile (Siebert et al. 2003). This could be considered insignificant compared to the potential that Douglas-fir has in the region, and a shortage of wood supplies is foreseen for the future years. The price of Douglas-fir wood is similar and competes with that of native species such as southern beech (*Nothofagus* spp. Bl.) and Chilean cedar (*Austrocedrus chilensis* [D. Don] Pichi-Serm. & Bizzarri).

2.4.1.3 Breeding Objectives

Within its native range in North America, the main goal of the tree improvement programs is improvement of stem volume in genotypes adapted to their target environment (Howe et al. 2006). In the United States, small breeding zones were identified initially based on the seedling studies of Campbell (1979), who found that adaptive traits were finely shaped by local conditions. This led to the delineation of small breeding zones, 60,000 ha in size and elevational ranges up to 300 m (Silen and Wheat 1979). However, results from provenance studies established by Ching (1965) showed that local populations were rarely the best performers and provenance-site interactions were not important at age 25 years (White and Ching 1985). This led to the formation of much larger breeding zones (Stonecypher at al. 1996).

In British Columbia, early Douglas-fir improvement started with intraspecific (racial) crosses of parents growing in drastically different environments (Orr-Ewing 1966). A contrasting approach was also explored via the recurrent selfing of genotypes to the S_3 generation (Orr-Ewing 1976). However, practical tree improvement started with the diallel program of Chris Heaman, using six-parent partial diallels in 8 series planted on 11 sites per series (Yeh and Heaman 1987).

Early provenance evaluations in Germany indicated strong differentiation of populations in Douglas-fir provenances. To obtain more complete information about Douglas-fir variability, adaptability and physiology, IUFRO started in 1967 a systematic and representative collection of 182 indigenous provenances, covering the whole natural range. These were distributed to 59 institutions in 36 countries. This provenance collection, planted over more than 100 sites, has been the base of a vast number of biosystematics studies and provided several European institutes with genetic resources to start or diversify their breeding activity (Kleinschmit and Bastien 1992).

In 1985, six European countries (Belgium, France, Germany, Italy, Spain, and United Kingdom) agreed to collect a base population from a broad genetic base of superior provenances in previous IUFRO tests to provide accurate genetic parameter estimates for further breeding. This base population, made of 1,000 open-pollinated progenies harvested at low elevation from United States Pacific Northwest has been evaluated in field tests, covering 270 ha in western Europe and straddling over 10 degrees of latitude. Selection criteria were: adaptedness, expressed as survival, bud flush and bud set (frost damage avoidance), stem quality, volume growth, and wood quality (despite adverse genetic correlations with growth) (Rozenberg et al. 2001).

In New Zealand, Douglas-fir improvement started with provenance trials of large numbers of provenances in 1957 and 1959 from the United States Pacific Northwest and northern California (Shelbourne et al. 2007). Before the provenance trial results were known, a breeding population was established based on plus-tree selections from 35–50 year-old stands, probably from Washington provenances planted during the Depression in Kaingaroa Forest in the Central North Island. Parents were selected and grafted, and open-pollinated progeny tests established with little delay in the early 1970s. However, early test results from the 1957 and 1959 tests at age 13 years, showed superior growth of Californian and southern Oregon provenances, causing the breeding program to stall for the following 14 years (Shelbourne et al. 2007).

In 1988, in the wake of high log prices, industry interest revived and a new breeding program was started in New Zealand with 186 selections (superline) composed largely of better coastal fogbelt provenances in the 1959 provenance trials and material of Fort Bragg origin. Plus-trees were grafted in an archive and it was planned to progeny test these clones by polycross and use pair crossing for forward selection. This strategy failed to deliver sufficient seed or crosses, and has recently been revised to rely on an open-pollinated testing strategy in the clonal archive for generation turnover and breeding value estimation. It is intended that relatedness among selections will be assessed by DNA pedigree analysis (Shelbourne et al. 2007).

In Argentina, the growth potential of the land race is high. The principal objectives of the breeding program initialized in 1998 by INTA Bariloche were therefore: (1) to increase growth and improve form by selections from the land race; (2) to supply improved seed from seed production areas; (3) to broaden the genetic base from fast-growing Washington and

Oregon populations; (4) to assess genetic diversity of the land race; and (5) to maintain adaptability

In Chile, the breeding program has objectives similar to those in Argentina, nevertheless the propagation procedures are much more developed; for example, rooting cutting propagation, management of donor plants (hedges), and evaluation of flowering induction techniques.

2.4.1.4 Breeding Achievements

In coastal British Columbia, forward selections from the diallel program were grouped into sublines consisting of 10 to 15 parents in a total of 32 sublines. Each parent is progeny tested using a standard polymix and, at the same time, four to six full-sib families with a common parent are tested in 5 x 5 family blocks on two sites for the purpose of forward selection. This complementary testing is to be carried out in four series. Forward selections from the first series have been grafted for third-generation orchard establishment (Stoehr et al. 2008). The primary selection trait was height growth, while a secondary trait was wood density. For interior Douglas-fir, control crossing for second-generation testing is underway. Rotation-age volume gains in selections from first-generation open-pollinated tests were above 25%.

In the United States Pacific Northwest, realized genetic gains of elite crosses (between selected first-generation parents) in realized gain trials were close to the predicted values based on progeny tests, i.e., 6% for height, 8% for diameter and 28% for tree volume (St. Clair et al. 2004). Crossing and testing for second-generation orchards are underway (Howe et al. 2006).

Until recently, Douglas-fir plantations in Europe were established primarily with seeds collected from North America. As a consequence of the IUFRO provenance experiments, the European Community sponsored four missions to North America to check the status of the original IUFRO seed-collection stands. In order to preserve valuable Douglas-fir genetic resources in Europe, more than 1,000 ha of *ex situ* conservation plantations have been established in France, Germany and Belgium. The outstanding performance of Douglas-fir has justified the establishment of 34 seed orchards (163 ha) ~~seed orchards~~ in seven countries of the European Union~~,~~ 26 (109 ha) in the "Qualified" category and 8 (54 ha) in the "Tested" category). The largest orchard plantings are France and Germany, with 8 orchards (98 ha) and 9 orchards (35 ha), respectively.

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In New Zealand, selections from the two unrelated "superlines" will be grafted into open-pollinated orchards. Recently the economic importance of timber stiffness has been recognized, with stiffness as well as yield and log quality established as objective traits. Wood density or stiffness were not criteria in the selection of parents in the "superlines", and to remedy this a number of selections are now being undertaken for wood stiffness, diameter and stem straightness in both second-generation land-race stands of Fort Bragg, Californian origin and in existing progeny trials (H Dungey pers. comm.). Seedlots from the Fort Bragg land race have proven to be top performers for volume growth in the 1959- and 1996-planted trials.

In South America, first-generation testing and breeding are underway and early results have led to the establishment of seed orchards and seed production areas in Argentina (Gallo et al. 2005).

Detailed marker association studies have been limited to cloned (rooted cuttings) seedlings from a single full-sib family to identify QTLs for several adaptive traits, such as spring bud flush and spring and fall frost hardiness (Jermstad et al. 2001a, b). For spring flushing, there was congruence in QTL presence and linkage group location from year-to-year, but not between test sites, suggesting that different suites of genes are governing growth initiation in different environments. Significant QTLs were also found for spring and fall cold-hardiness, but their locations revealed that different genes are responsible for the two cold-hardiness traits. In a follow-up study, significant QTL x treatment interactions have been detected in the same genetic background (Jermstad et al. 2003), indicating that QTLs as tools for selection is still in a developmental state in Douglas-fir. In a more recent study, again in the same family, Wheeler et al. (2005) showed that, with a larger sample size, several QTLs for adaptive traits can be classified as candidate genes.

2.4.2 Larches in Europe (Larix)

The genus *Larix* Mill. is composed of 10 or so species distributed across the Northern Hemisphere, three in North America, six in Asia and one in Europe, with additional subspecies and natural hybrids often recognized (Schmidt 1995). Important breeding programs are well established for various species, including western larch (*Larix occidentalis* Nutt.) in British Columbia and the United States Pacific Northwest (Jaquish et al. 1995) and for tamarack (*Larix laricina* [Du Roi] K.Koch) in Quebec and the Canadian Maritime Provinces (Fowler et al. 1995). In Europe, the focus of genetic improvement is on European larch (*Larix decidua* Mill.), the exotic Japanese larch (*Larix kaempferi* [Lamb.] Carr.), and their hybrid, Dunkheld larch (*Larix × eurolepis* Henry, syn. *Larix marschlinsii* Coaz.); these European efforts are discussed in greater detail in the following sections.

2.4.2.1 Historical Perspective

Natural European larch forests are limited to mountainous areas, including the Alps, the Sudetan Mountains, the Tatras and hills in central Poland. Some relic populations also exist in the Romanian Carpathian Mountains. The native range of European larch is highly discontinuous and of small size but due to human pressure release on farmland, it has naturally extended upwards and downwards the mountains as in the French Alps since nearly a century. Yet, most of larch planting was outside its native range in northern and western Europe such as in Belgium, Denmark, France, Ireland, Scotland, Germany, Poland, etc.

Due to its fast growth, excellent stem form and durable wood, larch has long attracted attention from European foresters who attempted to move European larch from its native mountain range towards northern-Europe lowlands. These introductions, mostly from alpine seed sources, proved unsuccessful; after one or two decades of satisfactory growth, many plantations suffered dieback caused by larch canker (*Lachnellulla willkommii* Hartig).

Interest then shifted to an exotic species, Japanese larch, but either it proved poorly adapted to more continental sites because of its sensitivity to summer drought or it exhibited poor stem form (crookedness), due probably to a more extended photoperiod. Its popularity was thus short-lived.

Research on geographic variation and the general expansion of conifer tree improvement programs in the 1950s heightened awareness of the importance of genetic variation and the use of well-adapted seed sources. Breeders also resumed work on the hybrid larch, which had been discovered much earlier in 1900 occurring as open-pollinated offspring of Japanese larch growing near European larch on an estate in Dunkeld, Scotland (Larsen 1937).

2.4.2.2 Economic Importance

European larch forests now cover over 1 million ha in Europe with more than half of them established outside the species' native range. As such, while it plays a major economic role at regional levels such as in the Alps, larch appears as a minor species among other European conifers. Other exotic species like Douglas-fir and Sitka spruce have been adopted rapidly, while expansion of larch plantations has been relatively modest. A major reason for this has been a frequent lack of seed, due to highly irregular seed crops.

Planting of larch may yet expand in the future, as it processes exceptional soil and climate adaptability (wind resistance), juvenile growth (probably the fastest-growing conifer in Europe), and desirable wood properties (among the best coniferous wood in terms of not only physical and mechanical properties, but also appearance and natural durability). It can be used either in pure or mixed stands (e.g., with some broadleaf species), in afforestation/reforestation, but also in agro-forestry. Light tolerant, it is appreciated as a nurse species for shade-tolerant species, and being a fast grower, it allows an early economic return before slower-growing species in mixture (mostly broadleaves) come into commercial production. The most valuable use of its wood is as lumber for indoor use (flooring, wall panelling, carpentry), but also for traditional outdoor uses like in carpentry (bridges, towers), wall panelling, roof tiling, etc.

2.4.2.3 Breeding Objectives

Reforestation in the native range of European larch is often based on natural regeneration. Artificial regeneration by planting is also used but, for conservation purposes, only local reproductive material is planted, obtained mostly from selected seed stands and more rarely from seed orchards. In these areas, use of exotic larches is often prohibited. Population conservation is a priority with large protected areas being delimited for *in situ* conservation. Most of these forests established in (high) mountains and steep slopes play a protection role before timber production.

Intensively managed commercial stands are established outside the native range of European larch, in much more favorable environmental conditions (lower elevations, milder climate). Larch forests are in these areas established by planting, with clear-cutting at rotation age; natural regeneration is rarely practiced, and exotics are welcome. Wood production is the main target but management approaches vary; those in France and United Kingdom usually favoring fast growth, short rotations (40–50 years), limited environmental risks and fast economical returns, while elsewhere in central Europe, management is over longer rotations (90–120 years) seeking larger volumes and higher-value wood.

Larch breeding programs expanded rapidly across Europe in the 1940s, and have typically targeted reforestation in these more productive lowland sites. Most of the effort is on pure European larch and its hybrid with Japanese larch; breeding of pure Japanese larch is not pursued. Others like Eurasian larches, such as Siberian larch (*Larix russica* [Endl.] Sab. ex Trautv., syn. *Larix sibirica* Ledeb.), and the North American tamarack are sometimes established in Scandinavian countries (Martinsson and Lesinski 2007), but are not the objects of breeding work.

For both European and hybrid larches, breeding objectives are similar and include growth, stem form (crookedness), branching and resistance to larch canker. Late frost damage is rarely a concern and, even if phenology is currently assessed, it is seldom used as a selection criterion. In more advanced programs, some wood properties like wood density and modulus of elasticity (MOE; an indicator of wood strength) are included. Research is also ongoing for traits such as heartwood formation and quality, and drought tolerance.

As breeding zones are not (yet clearly) defined at national levels for larch, breeding is usually for whole countries, except in the native range and some areas unsuited for the species. Stable varieties across these large areas are required and genotype-environment interaction is used as a selection criterion.

For European larch, short-term, low-input breeding is used with the final aim to release first-generation seed orchard varieties. For hybrid larch as well, with very few exceptions, the strategy is generally restricted to first-generation hybrids, identifying outstanding varieties combining favorable parental traits. The French program for hybrid larch is an exception, where for the last 20 years breeding has been strongly linked to research on sources and prediction of interspecific heterosis, as well as conditions required to benefit from F_2-hybrids.

While abundant flowering and seed crops of European larch are irregular, production of improved varieties from seed orchards works rather well, especially on continental sites. In contrast, production of first-generation hybrids, either by sexual or asexual means, has remained problematic, which seriously impedes rapid expansion of hybrid larch plantations. Over the last two decades, research work has focussed on the improvement of propagation systems.

2.4.2.4 Breeding Achievements

2.4.2.4.1 European Larch

The first significant step towards larch breeding was achieved when results from international IUFRO provenances trials of European larch became available about 30 years ago (Schober 1985). Clearly, populations from Central Europe (*sudetica* and *polonica*) performed well all over Europe and were the least sensitive to canker, while some populations from the Alps were characterized by a better stem form, but having lower vigor and a high sensitivity to canker. Planting programs responded to these results, favoring selected seed stands of Sudetan and central Poland.

Most of European larch breeding populations were established with Sudetan and central Poland selections, with the addition to some landrace origin parents in some programs, and first-generation clonal seed orchards established with these materials. Commercial crops are now available from most and the evaluation of their genetic value is currently in progress, with improvement by roguing (1.5-generation orchards) planned. Recent results from genetic diversity studies and connected progeny trials focussed on best stands of Sudetan/central Poland origins will be exploited to establish second-generation orchards, emphasizing stem straightness of progeny-tested clones.

2.4.2.4.2 Interspecific Hybrids

The interspecific hybridization between European larch and Japanese larch is intended to combine favorable traits of both species: juvenile growth and larch canker resistance of Japanese larch, with stem straightness and fine branching of European larch. Thousands of hybrid combinations have been created in Europe by control crossing or by open-pollination in seed orchards. Overall, hybrids have shown superiority over their pure parental species for phenology, growth, stem form, and branching (Pâques 1989, 2002a); for example, gains in total height compared to the parental controls was from –5 to +140%.

While it might be that hybrids benefit from the canker resistance of Japanese larch, many interspecific hybrids fail to combine expected parental properties in a favorable way. For several traits, it has been shown that levels of heterosis can vary widely and can be either positive or negative (Pâques 2002a). The simple and supposedly low-cost strategy has clearly shown its limits and has finally proven to be costly due to the low rate of successful combinations. The work of C.S. Larsen, who conducted an active larch hybridization program in Denmark in the 1940s, had already shown the importance of the choice of parents and of their improvement prior to interspecific recombination. Many successful hybrid varieties still used in Europe today rely on this early work. A systematic approach has been used in France over the last 20 years to better understand the genetics of heterosis and the role of parental species, and to developing predictors of heterotic combinations (Pâques 2002b). Improvement of parental breeding populations integrates this knowledge. In parallel, composite breeding is explored as an alternative strategy: second-generation hybrids have been created to study levels of heterosis and the impacts of inbreeding depression (Pâques 2007).

Application of MAS has been proposed by Arcade et al. (2002) who found several significant QTLs for ring wood-density traits (effects ranging from 3.4–6.2% of the phenotypic variance). Generally, given its short rotation and early expression of important traits, the motivation to apply MAS as an early selection tool for larches is perhaps less than with other longer-rotation-species. Markers have, however, found a place in assessment of genetic distance in relation to heterosis and of allelic dosage in hybrids.

For more than 60 years, parents from the best hybrid combinations have been established in interspecific hybrid seed orchards with various layout designs (alternating rows of species clones, tree by tree, etc.), number of clones (bi-clonal orchards to multi-clonal orchards in excess of 200 clones), and clone origins. Unfortunately, commercial crops from these open-pollinated seed orchards have remained well below expected yield and quality. In addition to low seed set, the proportion of hybrids in seed lots is highly variable from orchard to orchard and from year to year (< 20% to > 60%) as first revealed by isozyme markers or more recently by cytoplasmic DNA markers (Acheré et al. 2004). Poor climatic conditions during pollination (frost damage, snow, alternating warm and cold days, etc.) and differences in parental phenology are the main causes of these failures.

2.4.2.4.3 Mass Propagation

Several approaches to overcome poor seed production in hybrid orchards have been tested, including the improvement of generative reproduction conditions, as well as the development of better vegetative propagation techniques. Among the various methods developed for generative reproduction, supplemental mass pollination by electrostatic dusting of female clones (kept in a separate orchard) is the most promising (higher seed set with up to 95% hybrid fertilization) and has been put into practice in France (Philippe et al. 2006). While clonal propagation by cuttings was extensively tested with disappointing results due to rapid ageing of donor plants, "bulk" propagation by cuttings of young seedlings from selected families looks more promising (Verger and Pâques 1993; Le Pichon et al. 2001) and is being implemented on a pilot scale. Recent and significant progress in somatic embryogenesis and cryo-conservation of larch (Lelu-Walter and Pâques 2009) offer new opportunities, in combination with cutting propagation and deployment, as maintenance of juvenility of donor materials is possible.

2.5 Cypresses (Cupressaceae)

Cypresses, the Cupressaceae including the former Taxodiaceae and Cunninghamiaceae families (Gadek et al. 2000), comprise a diverse group of species with a worldwide distribution. The family has species on every continent except Antarctica, and occurs across a wide range of climatic and edaphic environments. Many of the up to 30 genera are monotypic and a significant portion of the 140 or so species have localized, relict distributions.

The Cupressaceae is the most important family in horticulture, with thousands of varieties in existence. Many of these are also used for forestry. Of these, *Cryptomeria japonica* D. Don. (sugi, or Japanese cedar) is by far the most commonly planted and has the longest history of genetic improvement. We discuss this species separately, followed with a more general discussion of the other important members of the Cupressaceae.

2.5.1 Sugi (*Cryptomeria japonica*)

2.5.1.1 Historical Perspective

During a very long history of cultivation, many varieties of sugi have been developed. Miyajima (1983) classified these into two types; those cultivars that have been improved artificially, and those representing unimproved geographic races. The first cultivars were selected in the 16th century, and forest plantations first established in the early 18th century. At this time, the main cultivars were selected by foresters on Kyushu Island. Many cultivars have been developed subsequently, and most have been maintained vegetatively by cuttings. Because these cultivars have been cultivated for a long period of time, various characteristics such as growth performance, wood quality, rooting ability and flowering are well understood.

2.5.1.2 Economic Importance

Sugi is one of the most important timber species in Japan, favored for its straight bole and rapid growth. It has been planted over 4.53 million ha, and comprises 45% of the artificial forest in Japan. Total log production in Japan in 2007 was 29 million m^3, and almost half of this was sugi. Approximately 80% of houses built using the post-and-beam construction method use a pre-cut system. Therefore, there is an increasing need for high quality products, with good performance in terms of dryness, dimensional stability, and strength. For these reasons, the market share of kiln-dried lumber is increasing. Sugi wood is also durable and easily worked, and is typically used for buildings, bridges, ships, and furniture. A recent topic of wood industry is the development of new laminated wood products, using *Pseudotsuga menziesii* for outer-layers and sugi as inner-layers.

2.5.1.3 Breeding Objectives

Initially, the main breeding objective was to improve growth. Later, other breeding objectives, such as resistance to the sugi bark borer, *Semanotus japonicus*, and resistance to snow damage were included. Although sugi grows well, the wood has lower strength than that of imported timbers, and the high moisture content of heartwood prevents efficient kiln-drying. More recent breeding objectives have included improving wood strength and lowering the moisture content of heartwood.

It is said that 16% of Japanese people suffer from allergies due to sugi pollen, and addressing this problem has become an objective for breeders. Two strategies have been proposed to ameliorate this problem; one is to select varieties with lower pollen production, and the other is to select for low-allergenic pollen. The two major allergy proteins in the pollen of sugi have been documented; Cry j 1 and Cry j 2. Efficiency of CO_2 fixation is a further breeding objective to address issues associated with global warming.

2.5.1.4 Breeding Achievements

Systematic breeding of sugi began in the late 1950s. The Forestry Agency of the Japanese Ministry of Agriculture and Forestry has established a network of tree breeding stations throughout the country, so that all climatic conditions are represented. Over 3,600 plus trees have been selected from four breeding regions, excluding the Hokkaido Breeding Region, which is a cool-temperate area. As mentioned above, the main breeding objective initially was to improve growth, and volume production gains of 15% over local varieties were achieved. Based on progeny trials, 50 clones or families showing superior growth were selected, and a further 25 clones or families selected for bole straightness. The second-generation population was established using controlled crosses among these superior trees.

The breeding program also addressed the problem of the sugi bark borer, whose larvae feed on bark and xylem. An inoculation test was established, and 61 resistant clones have been identified and released for deployment. Another problem is that trees can become crooked in regions with heavy snowfall, due to the pressure exerted by snow load. Eight clones and 19 families that grow straight in these regions have been developed.

Research on wood quality using 563 sugi selected clones showed that the coefficient of variation was greater than 30% in heartwood moisture content, and 17.5% in MOE (Hirakawa et al. 2003). Furthermore, broad-sense heritability of MOE and heartwood moisture content was high, 0.597 to 0.857, and 0.53 to 0.57, respectively (Fujisawa et al. 1992, 1995). These results indicate that further improvement of these characters can be achieved by breeding. Fujisawa (1998) discussed quality management of fast-growing material, and recommended clonal forestry to attain high wood quality and to decrease variation of wood quality.

Kuramoto et al. (2000) analyzed QTLs associated with wood strength using a linkage map in the F_1 progeny of two cutting cultivars of sugi. Effective QTLs were associated with MOE and wood density. Several QTLs for MOE were detected in the linkage maps of parent cultivars. Because these QTLs explained approximately 45% of the total phenotypic variances in one parent cultivar, they were deemed appropriate for use in breeding programs.

Evaluation of wood quality is time-consuming and labor-intensive, so simple testing methods for standing trees are required to execute large-scale selection. There was a high correlation between stress-wave propagation velocity in the longitudinal direction and the MOE (Ikeda et al. 2000). Kamaguchi et al. (2000) proposed a non-destructive measurement to estimate heartwood moisture content, where vibration of the tree trunk is measured after lateral impact. Using these two simple methods to evaluate MOE and the heartwood moisture content, forward selection of second-generation candidates has been implemented.

As there is a large variation in production of male strobili, 131 plus trees bearing fewer male strobili were selected as "low pollen", and new seed orchards established with this material. Male sterility is an equivocal answer to the pollen allergy problem. Taira et al. (1993) first reported male-sterile trees, and found that this characteristic is controlled by a single recessive gene (Taira et al. 1999). To date, approximately 20 male-sterile trees have been identified. Genetic modification has been proposed to introduce this character, as it is difficult to introduce it into a population using traditional breeding methods. Goto et al. (1999) found that the major allergenic protein, Cry j 1, varied markedly among trees, and the DNA sequences of the gene encoding the protein have been reported (Griffith et al. 1993). This gene was located on a linkage map (Goto et al. 2003) and some Cry j 1 isoforms with different binding properties to monoclonal antibodies were found (Goto et al. 2004).

Volume, wood density, and carbon content of the wood have been evaluated as components of CO_2 fixation. Using such components high CO_2 fixation variety will be developed.

2.5.2 Other Cupressaceae

2.5.2.1 Historical Perspective

In addition to sugi, several other species in the Cupressaceae are commercially important with associated breeding programs, including some of the highest value timber species. These include: the whitecedars, such as Port Orford-cedar (*Chamaecyparis lawsoniana* [A.Murr.] Parl.) from the Pacific Northwest of the United States, yellow-cedar (*Chamaecyparis nootkatensis* (D. Don) Farjon & D.K. Harder[1]) from western North America, and Hinoki (*Chamaecyparis obtusa* [Sieb. & Zucc.] Endl.) from southern Japan and Taiwan; the cypresses such as Mexican cypress (*Cupressus lusitanica* Mill.) from Mexico, Monterey cypress (*Cupressus macrocarpa* Hartweg ex Gord.) from western California, and Italian cypress (*Cupressus sempervirens* L.)

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[1] taxonomic authorities plan to resolve nomenclature for this species in 2011; current synonyms include *Callitropsis* and *Xanthocyparis* (Little et al. 2004).

from the Mediterranean region; the arborvitae such as western redcedar (*Thuja plicata* Donn ex D. Don.) from western North America; and Chinese fir (*Cunninghamia lanceolata* (Lambert) Hooker) from China and Vietnam. Many Cupressaceae species have had historical ties to indigenous people, both for spiritual value and traditional uses. Western redcedar, known as the "Tree of Life", has had a rich history with aboriginal cultures because of its multitude of traditional practical and aesthetic values.

2.5.2.2 Economic Importance

Many Cupressaceae species are highly prized for their aromatic and durable heartwood, as well as dimensional stability. Logs are typically higher in demand and price than most other commercial conifers. For example, western redcedar in British Columbia accounted for approximately 30% of the volume harvested on the coast and economic value to the provincial government (the primary owner of forest lands) was over 50% greater than coastal Douglas-fir (US$164/m^3 vs. $99/m^3) for 2006 and 2007. The high demand for logs drives enhanced reforestation programs for many Cupressaceae species.

Chinese fir is an important timber species in China with over 400,000 ha of plantations established annually (Minghe and Ritchie 1999a). The highly durable wood is used in construction, bridge and ship building, and coffin making. In Japan, hinoki and sugi together comprise approximately 70% of forest plantations (JFA 2008). Hinoki wood is lemon-scented and rot-resistant, and is uniquely used in palace and temple construction. Coastal redwood (*Sequoia sempervirens* [D. Don] Endl.) is a high-value conifer species endemic to California, with approximately 0.5 million ha of commercial, second-growth forests (Olson et al. 1990). The heartwood is highly valued for its beauty, light weight, and resistance to decay.

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Both Mexican and Monterey cypresses have been widely domesticated away from their native ranges in Central and North America, mostly in warm temperate and subtropical regions including New Zealand, southern Europe, and South America. Mexican cypress is a fast-growing, drought-tolerant tree that is used for saw logs, pulp, wind breaks, and as an ornamental. Following the introduction and spread of exotic canker diseases, Mexican cypress has become the most widely planted member of the Cupressaceae for tree improvement, supplanting the preferred Monterey cypress, whose logs are used for boats and furniture.

Approximately 12 million western redcedar and yellow-cedar trees are planted annually in British Columbia. The heartwood of western redcedar is very resistant to decay and has high dimensional stability. The wood is used for outdoor construction, including posts, decking, shingles, and siding. Yellow-cedar is used in finish carpentry, such as exterior siding, shingles, decking, exposed beams, glue-laminated beams, panelling, cabinetry and boat building. Both species are prized by artisans for carving.

2.5.2.3 Breeding Objectives

Despite the high value and use, only a handful of economically important Cupressaceae species have been the focus of tree improvement activities, although many species have been studied and evaluated for natural levels of population variability for a range of traits.

2.5.2.3.1 Asia-Pacific Region

The oldest tree improvement program in the world is most likely that of Chinese fir in China. Clonal forestry has been practiced for over 800 years (Minghe and Ritchie 1999a, b). More recently, recurrent selection programs have been developed in a number of provinces using both open-pollinated and full-sib crosses, together with wind-pollinated seed orchards (Zhuowen 2003). Selection has focussed on growth and wood density. Breeding programs are well-established for sugi (see previous section above for details) and Hinoki, the two most important conifer species for plantations in Japan. Tree breeding efforts for Hinoki in the first generation have utilized open-pollinated families from over 1,000 seed parents, and selections have been made for growth, bole straightness and heartwood color. Second-generation matings are integrating the different trait selections through a factorial design (T Kondo pers. comm.). Sawara cypress (*Chamaecyparis pisifera* [Sieb. & Zucc.] Endl.) is also the subject of improvement activities and plantation forestry, primarily in temperate montane areas. In Korea, Hinoki has been used in breeding programs since 1965, with selections for growth, form, and insect and disease resistance. The first orchards began producing seed in the 1980s, with advanced-generation orchards being developed (Kang 2007). The introduced species Mexican cypress and Monterey cypresss both have breeding programs in New Zealand using open-pollinated families for both first- and second-generation progeny trials, along with clonal trials in the second generation. The major target traits have been vigor and stem straightness, and, in the case of Monterey cypress, resistance to stem canker disease (*Seiridium* spp.).

2.5.2.3.2 Europe

Italian cypress is the Cupressaceae species with the most intensive tree improvement program in Europe. It has both cultural and economic importance. Since about 1927, the fungal pathogen *Seiridium cardinale*, indigenous to California, has spread rapidly throughout the global range of cypress and related species, including Europe, Asia, Africa, and Australasia, causing widespread and increasing mortality. The main impact of *Seiridium* fungi is death from stem canker, also termed cypress blight. Breeding programs have thus targeted selection and breeding for disease resistance, using clonal and sexual recombination to increase gains. To date, research programs in Greece, Italy, and France have conducted the largest body of work in breeding and improvement for canker resistance (Santini et al. 1997; Papageorgiou et al. 2005; P Raddi pers. comm.).

2.5.2.3.3 North America

Breeding of western redcedar in British Columbia has focussed on growth, heartwood durability, and mammalian damage resistance. Selections from first-generation polycrossed trials are currently being bred for advanced-generation testing. Minimal inbreeding depression and ease of vegetative propagation have facilitated selfing and cloning as tools for testing and deployment of populations. Short generation intervals have allowed for relatively quick advancement. The breeding program for yellow-cedar, also in British Columbia, has tested clones from partial diallels in the first generation. Forward selections based on vigor and stem form are being bred for second-generation testing. Port Orford-cedar, indigenous to California and Oregon, has a breeding program to develop resistance to the introduced pathogen *Phytophthora lateralis*. Both putative dominant single (major) gene and quantitative resistance mechanisms have been identified (Sniezko et al. 2004). Since this species has short generations and is amenable to vegetative and sexual reproduction, improvement has been rapid, yielding several hundred resistant first-generation F_1 selections available for deployment.

2.5.2.3.4 Central and South America

Mexican cypress, indigenous to Mexico, El Salvador, Guatemala, and Honduras, has been introduced throughout Central and South America for timber production (Cornelius et al. 1996), where it has naturalized in some areas. Privately established tree improvement trials began selections in Colombia in the 1970s (Ladrach 1983), with breeding programs starting in 1977. The major traits of interest are volume growth, disease and insect resistance, stem form, crown form, and wood quality. Most progeny trials and deployed seedlings are open-pollinated, but some controlled crossing has been successful.

2.5.2.3.5 Africa

Introduced Cupressaceae, particularly Mexican cypress and Monterey cypress, have been grown in plantation forests of tropical and subtropical countries for decades. Monterey cypress was a preferred species in Kenya for its greater yields, but due to its susceptibility to *Seiridium* canker disease, has widely been replaced by Mexican cypress (Roux et al. 2005). Stem taper, stem form, wood grain angle, stem branches, and susceptibility to key diseases were considered in the selection of trees for the Kenyan tree improvement program. The introduced cypress aphid (*Cinara cupressi*), has been spreading throughout the region since 1986 severely damaging stands, and is now the subject of selection and breeding for resistance, along with cypress canker (Ciesla 1991; Mugasha et al. 1997). Beginning in the late 1960s under individual corporate and government programs, South Africa has reaped considerable economic benefits from a comprehensive tree improvement program, including Mexican cypress. The predominance of the private sector in forest management and research in tree improvement, however, has limited the availability of information on these programs (Denison 2001).

2.5.2.4 Breeding achievements

2.5.2.4.1 Asia-Pacific Region

Improved clones of Chinese fir have been deployed for close to 800 years for reforestation. Prior to the 1950s, reforestation by either stump cuttings or rooted cuttings accounted for 80% of the plantings in Chinese fir (Minghe and Ritchie 1999a). An increased emphasis on seedling-based forestry resulted in only 65 million rooted cuttings planted in 1991, accounting for 5.4% of the total annual planting stock. First- and second-generation orchards have been established with this species as well, and in 1984, 30% of the planting demand was meet through orchard seed (Jusheng 1985), with volume gains from the second-generation orchard predicted to be 40% over unimproved seedlots (Zhuowen 2003). The majority of seed used for reforestation of Hinoki comes from over 334 ha of first-generation open-pollinated orchards (McKeand and Kurinobu 1998). Operational open-pollinated orchards of Hinoki are established on a regional basis, with some in advanced generations. In addition to orchard seed, clones are also available for reforestation throughout the breeding regions of Japan, although supply is limited (McKeand and Kurinobu 1998).

2.5.2.4.2 Europe

In Greece, dozens of canker-resistant clones of *Cupressus lusitanica* are available for deployment, but base levels of resistance in testing populations remain below 5% (Santini et al. 1997).

2.5.2.4.3 North America

All of the approximately 8 million western redcedar plants required annually in the primary breeding zone for this species in British Columbia are from improved first-generation orchard seed with expected volume gains at rotation of 7–10%. Selections from the relatively young breeding program is taking advantage of high breeding values to create operational full-sib family seedlots with 15–20% volume gain when available. Currently, yellow-cedar clonal planting stock is delivering up to 20% volume gain at rotation. For Port Orford-cedar, gains in *Phytophtora* resistance range from double to over 6 times that of wild populations from the same breeding zone (8–29% natural resistance vs. 27–63% selected resistance (Elliott 2006). All three of the above species have short generations, and are amenable to vegetative propagation and sexual reproduction including selfing, resulting in rapid improvement.

2.5.2.4.4 Central and South America

The Colombian program in the first generation of selection yielded early gains (age 3, relative to a rotation of 16 years) of 13% in height and 50% in volume, but effectively no difference in stem or crown form (Ladrach 1983).

2.5.2.4.5 Africa

South Africa, Kenya, Rwanda, Uganda, Tanzania, and other countries have established a network of Mexican cypress plantations for wood production from selected material that have been assessed for variability in growth and yield parameters. Most are from open-pollinated selections but seed production areas are now widely used to produce seed that can be transferred across cooperating countries on suitable sites, based on provenance studies. In Kenya, the Kenya Tree Seed Centre is the central repository and distribution center for forest seed and clone banks, and also manages a network of seed orchards. Since the early 1960s, plus-trees, provenance, and progeny testing have resulted in advanced-generation gains of approximately 30% for Mexican cypress (Bernard 2001) over unimproved yields.

2.5.2.4.6 Summary

The combination of substantial additive variation for economic traits, ease of grafting and cloning, precocious reproduction, and wide range of ecological adaptations make the Cupressaceae an ideal taxonomic group that has demonstrated many successes through tree improvement. Gains can be substantial when selecting for one or several traits, with limited or no trade-offs between growth and disease or insect resistance. Although the wood is generally soft, rapid fiber production supports a diverse range of forest products. The horticultural sector has long sought value in the Cupressaceae, and the emerging non-timber forest products sector is increasing its utilization for distilled oils, phytochemicals, bark, chips, and green foliage. To date, prospects for marker-aided selection are limited, given the lack of correlations identified between traits of interest and molecular markers or QTLs for this taxon; however, short generations and high gains from breeding programs indicate that phenotypic selection for quantitative traits, supported by genetic and biochemical data is a viable system for efficient improvement.

2.6 Concluding Remarks

Conifers are the target of major tree breeding efforts worldwide. While much progress has been made through conventional approaches to breeding, tree breeders face enormous challenges with long generation turnover times, costly field testing, and relatively undomesticated genetic resources. In this chapter, we have attempted to describe the varied circumstances and state of the art for breeding of many of the more important conifers.

Advances in molecular technologies could have an enormous impact on the rate of progress and achievements made by tree breeding programs. To succeed, new technologies must be carefully integrated into the context of existing programs so that they respond to opportunities and build on gains already realized. Markers are already playing an important role in understanding the patterns of variation and genetic basis for some traits, as well as assisting in the positive identification of individuals and their pedigree. However, with a few notable exceptions, markers for individual large-effect QTLs for most economic traits have not been discovered, which dampens somewhat the prospects for marker-assisted evaluation. This is consistent with experience in marker-aided breeding with livestock animals, where effort is now focussing on genome-wide scans and approaches to genomic selection (e.g., Meuwissen et al. 2001). Learning from the animal-breeding experience suggests that forward-looking tree breeding programs will be archiving pedigreed DNA samples with associated phenotypic records, in anticipation of the availablity of affordable chips that will permit scanning of very dense SNP maps in important conifer genomes.

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