Genetic Research and Development of Five-Needle Pines (*Pinus* subgenus *Strobus*) in Europe: An Overview

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Abstract—An overview of genetic research on native and exotic five-needle pines (*Pinus* subgenus *Strobus*) in Europe, including the impact of white pine blister rust (*Cronartium ribicola*), is presented. The natural populations of *Pinus cembra* from the Alps and Carpathians are free from blister rust; even though the rust occurs throughout Europe on other five-needle pines and *Ribes* species. *Pinus strobus* was once considered to be an important exotic species for timber production in Europe, but plantations have been abandoned due to the high susceptibility to blister rust. Blister rust resistance has now been transferred to *P. strobus* through hybridization with Eurasian five-needle pines, and the potential for successful utilization of the species in Europe now exists. Other five-needle pine species are not of major interest for European forestry operations.

Key words: five-needle pines, Europe, genetics, *Cronartium ribicola*, genetic resistance, provenance, breeding, hybrid, heritability, genetic gain

Introduction

Only two species of five-needle pines (*Pinus* L. subgenus *Strobus* Lemm.) grow naturally in Europe: Cembran pine (*Pinus cembra* L.) and Balkan pine (*P. peuce* Gris.) (Critchfield and Little 1966). Exotic five-needle pine species have been used to enrich European forests due to the relatively low number of native species and have been the subject of much research and development. For this paper, we prepared a survey on genetic research and use of five-needle pine species in European countries (table 1). We used the responses of the survey in conjunction with published literature and personal communications to compile the following overview on five-needle research and development in Europe.

Cembran pine is distributed in the high-altitude forests in the Alps and the Carpathian region, including the Tatra Mts. (Georgescu and Ionescu-Barlad 1932, Critchfield and Little 1966, Holzer 1975, Contini and Lavarelo 1982). It is naturally distributed in the following countries: Austria, France, Germany, Italy, Poland, Romania, Slovakia, Switzerland, and Ukraine. Cembran pine is important for reforestation of subalpine forests, including restoration of forests near timberline to stabilize watersheds and reduce the risk of avalanches and flash floods (Holzer 1975). The species is used to create mixed Norway spruce (*Picea abies* (L.) Karst) – European larch (*Larix decidua* Mill)-Cembran pine stands at high elevations for increased wind resistance (Blada 1996). Cembran pine also contains high genetic resistance to white pine blister rust caused by *Cronartium ribicola* J.C. Fisch in Rabenh. (Bingham 1972a,b, Soegaard 1972, Holzer 1975, Hoff and others 1980, Blada 1987, 1994a) Cembran pine produces a dense-brown-reddish wood useful for handicrafts (Contini and Lavarelo 1982), and is an excellent landscaping tree due to the crown color, density, and a conical-oval shape (Blada 1997b).

Balkan pine naturally occurs in Albania, Bulgaria, Greece, and Macedonia and is confined to higher elevations in the Balkan and Macedonian regions (Nedjalkov 1963, Fukarek 1970, Mitruchi 1955, Popnikola and others 1978). Balkan pine is important for planting in severe mountain climates to prevent soil erosion, as well as timber production for furniture, barrels, and other purposes (Figala 1927, Nedjalkov and Krastanov 1962, Nedjalkov 1963, Popnikola and others 1978). The species has good tolerance to SO_2 pollution (Enderlein and Vogl 1966) and has shown high blister rust resistance in genetic tests containing both European and North American species (Delatour and Birot 1982, Blada 1987, 2000a, 2000b, Heimburger 1972, Hoff and others 1980). Balkan pine has been used in crossing with other white pines and is considered a good bridging species (Righter and Duffield 1951, Kriebel 1963, Patton 1966, Nikota and others 1970, Heimburger 1972, Blada 1987).

The Cembran and Balkan pines have and are still planted most countries where they naturally occur (table 1, columns 9, 10, 12, and 13). Cembran pine, however, has been less used in France, Germany, and Italy. These species are relatively slow growing and as more five-needle pine species from around the world became known to Europeans, foresters began to experiment with plantations of exotic species.

Exotic five-needle pine species have had a long history in Europe. The following five-needle pine species have been more frequently planted: *P. strobus* L., *P. monticola* Dougl., *P wallichiana* A. B. Jacks., *P. sibirica* Du Tour, *P. koraiensis* Sieb & Zucc., *P. armandii* Franch., *P. flexilis* James, and *P. lambertiana* Dougl. (Schmitt 1972, Soegaard 1972). Eastern white pine (*P. strobus*) was one of the first five-needle pines to be introduced to Europe. With minor exceptions,

In: Sniezko, Richard A.; Samman, Safiya; Schlarbaum, Scott E.; Kriebel, Howard B., eds. 2004. Breeding and genetic resources of five-needle pines: growth, adaptability and pest resistance; 2001 July 23–27; Medford, OR, USA. IUFRO Working Party 2.02.15. Proceedings RMRS-P-32. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

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Table 1—Survey results for native white pine and *Pinus strobus* presence, past or present occurrence of white pine blister rust, past planting or breeding work, and current planting or breeding work in European countries. (Y= yes; N=no; ?=unknown)

Rank	Country	Native		Introd.	PPBRO[a]			PP[b]			PPBW[c]		
		P.c	P.p	P.s	P.c	P.p	P.s	P.c	P.p	P.s	P.c	P.p	P.s
1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	Albania	N	Y	?	?	?	?	?	?	?	?	?	?
2	Austria	Y	N	Y	N	N	Y	Y	N	Y	Y	N	N
3	Belarus	N	N	Y	N	N	Y	N	N	Y	N	N	N
4	Belgium	N	N	Y	N	N	Y	N	N	Y	N	N	N
5	Bulgaria	N	Y	Y	N	N	Y	N	Y	Y	N	Y	N
6	Croatia	N	Y?	Y	N	N	Y	N	N	Y	N	?	Y
7	Czech Republic	N	N	Y	N	N	Y	N	N	Y	?	N	N
8	Denmark	N	N	Y	N	N	Y	N	Y	Y	N	N	N
9	England	N	N	Y	N	N	Y	N	N	Y	N	N	N
10	Estonia	N	N	Y	N	N	Y	N	N	Y	N	N	N
11	Finland	N	N	Y	N	N	Y	N	N	Y	N	N	N
12	France	Y	N	Y	N	N	Y	N?	N	Y	N?	N	N
13	Germany	Y	N	Y	N	N	Y	N?	N	Y	N?	N	Y
14	Greece	N	Y	Y	N	N	N	N	N	N	N	N	N
15	Hungary	N	N	N	N	N	Y	N	N	Y	N	N	N
16	Ireland	N	N	Y	N	N	Y	N	N	Y	N	N	N
17	Italy	Y	N	Y	N	N	Y	Y?	N	Y	Y	N	N
18	Latvia	N	N	Y	N	N	Y	N	N	Y	N	N	N
19	Lithuania	N	N	Y	N	N	Y	N	N	Y	N	N	N
20	Luxembourg	N	N	?	N	N	?	?	N	?	N	N	?
21	Macedonia	N	Y	Y	N	N	Y	N	Y	Y	N	Y	N
22	Moldova	N	N	N	N	N	N	N	N	N	N	N	N
23	Netherlands	N	N	Y	N	N	Y	N	N	Y	N	N	N
24	Norway	N	N	Y	N	N	Y	N	N	N	N	N	N
25	Poland	Y	N	Y	N	N	Y	Y	N	Y	Y	?	N
26	Portugal	N	N	N	N	N	?	N	N	N	N	N	?
27	Romania	Y	N	Y	N	N	Y	Y	Y	Y	Y	Y	Y
28	Slovakia	Y	N	Y	N	N	Y	Y	N	Y	Y	N	N
29	Slovenia	N	N	Y	N	N	Y	N	N	Y	N	?	N
30	Spain	N	N	?	N	N	?	?	?	Y?	N	N	?
31	Sweden	N	N	N	N	N	Y	N	N	N	N	N	N
32	Switzerland	Y	N	Y	N	N	Y	Y	N	Y	Y	N	N
33	Ukraine	Y	N	Y	N	N	Y	Y	N	Y	Y	N	N
34	Yugoslavia	N	Y?	Y	N	N	Y	N	Y	Y	N	Y?	N

[a]PPBRO = past and present blister rust occurrence.
[b]PP = past planting or breeding work.
[c]PPBW = present planting or breeding work; P.c, P.p, P.s = *P. cembra, P. peuce, P.strobus*.

eastern white pine was introduced in all European countries (table 1, column 5) and planted for economic reasons (table 1, column 11) (Radu 1974). The species has demonstrated good qualities for timber production, is well adapted to the European climate (Schmitt 1972, Kriebel 1983) and has proven to be resistant to SO_2 pollution (Enderlein and Vogl 1966). The other exotic five-needle pine species have shown to be of minor importance, being used primarily for landscaping and in arboretums. Some Asiatic species have been introduced as genetic sources for blister rust resistance. However, the vast majority of research and development efforts on exotic five-needle pines in Europe have been conducted on eastern white pine

In Europe, eastern white pine was first recorded in 1553, in the Royal Gardens of Fontainebleau, France (Lanier 1961), followed by introduction at Badminton, Great Britain (MacDonald and others 1957) and in Germany in 1770 (Schenck 1949). The first records of the eastern white pine in other European countries were: Switzerland 1850 (Litscher 1908), Poland 1876 (Bialobok 1960), Slovakia 1773 (Musil 1969), Austria 1886 (Cieslar 1901), Romania 1894 (Davidescu 1894) and Bulgaria 1903 (Rusakoff 1936).

Small plantations of eastern white pine were established at intervals through the late 18th and 19th centuries, as the species exhibited good growth. This was especially true in Germany during the great reforestation period that took place through the 18th and 19th centuries (Borchers 1952, Schmitt 1972). Initially, it appeared that eastern white pine would become one of the most important trees of the European forests. In west central Germany, eastern white pine could outgrow all European coniferous species and keep a dominant position in stands for more than 80 years (Schmitt 1972). The species' growth performance also was remarkable under various site conditions in other countries such as Poland, Czechoslovakia, Romania, and Russia (Radu 1974). However, white pine blister rust has seriously impacted the survival and growth of this species. Blister rust attack has halted planting of eastern white pine for wood production in all countries in the last two decades (see table 2, column 14).

According to our survey (table 1 column 11), eastern white pine was planted over almost all Europe. Germany contains the largest planted area, approximately. 25,000 ha, of eastern white pine (Stephan, personal communication). In France, plantations with eastern white pine were established during the 19th century. The first plantations for wood production in Romania were established at the beginning of the 20th century, but much larger areas (about 1,360 ha) were established after 1960 (Radu 1974). Based on the initial results of provenance trials, Croatia planted approximately 1,500 ha (Gracan, personal communication).

White pine blister rust began to cause severe problems as early as 1865, when the rust was first noticed by H. A. Dietrich in Estonia (Leppik 1934). The rust spread throughout Europe by 1900 via the alternate host *Ribes nigrum* L. and susceptible *P. strobus* genotypes (Georgerscu and others 1957, Bingham and Gremmen 1971). It was not until 1926, however, that Germany recognized high mortality in eastern white pine due to the disease (compare Schmitt 1972). Correspondingly, planting eastern white pine in Germany was prohibited (Tubeuf 1927). Unfortunately, the species began to be planted again in Germany after 1935 (Wappes 1935). Other European countries followed the German lead (Radu 1974), and suffered serious economic losses due to blister rust. For example, the rust invaded almost all young stands in Romania after 1970, promoted by the simultaneous culture of eastern white pine and *Ribes nigrum* (Blada 1982). Blister rust attacks eastern white pine in all countries where the species has been planted (table 1, column 8). The rust does not attack *P. cembra* nor *P. peuce* in their natural habitats, however, in spite of concurrence with susceptible *P. strobus* and *Ribes* species (table 1, columns 6 and 7).

Research Studies

Provenance Trials

Once widespread planting with eastern white pine stopped, genetic research activities began to slow. Despite the problem of blister rust, Germany and Croatia still continue to make measurements in their provenance trials (table 1, column 14).

Provenance testing of eastern white pine has been conducted in Germany, where two trials with 69 provenances were established in 1966 and 1967, respectively (Stephan 1974). All provenances were originated from the natural range of the species. Growth rate, mortality, and infections by blister rust were assessed at age 11. (Stephan 1974). Height at age 11 was negatively correlated with provenance latitude ($r = -0.40$ to $r = -0.51$). Provenances from southern Appalachian mountain States of North Carolina, South Carolina, and Virginia (south of the 39th degree of latitude) showed better growth than the average in these trials. Provenances from areas north of the 45th degree of latitude (Manitoba, Quebec, Ontario, New Brunswick, Minnesota, and Wisconsin) had poor growth. Significant (p less than 0.5) and highly significant (p less than 0.1) height-height correlations among provenances at different ages were found. The correlations were not strong when the differences in age were great, but particularly strong between heights from the age of five onward. A high number of dwarfed trees from one provenance from Illinois were noticed. Under natural conditions, differences among provenances could be observed for mortality and infection by blister rust. *Pinus monticola* (one provenance) and *P. wallichiana* (two provenances), tested in the same German trial, showed only 85 percent and 40 percent, respectively, of the average height of *P. strobus.* In addition, high mortality could be observed in *P. wallichiana.*

The Croatian research program included 10 eastern white pine provenances, of which six from North America and four from established plantations in Croatia. The tests were established in 1970 and were measured at age 18 (Orlic 1993). For American provenances, the average values for survival, height, and diameter were 70.7 percent, 12.8 m and 20.7 cm, respectively. Similarly, the survival and growth estimates for local provenances were 73.2 percent, 13.7 m and 22.2 cm, respectively, which were higher (3.5, 7.0, and 7.2 percent, respectively) than the American provenances. In term of survival, the local source Hrvatska ranked first and the American provenance New Hampshire ranked second. The New York (USA) and the other two local sources exhibited the poorest survival. The average of total height ranged from 11.9 m to 14.0 m, with an average of 13.3 m, whereas the diameter from 17.7 cm to 23.2 cm with an average of 21.5 cm. The best and the poorest provenance in diameter were Georgia and Wisconsin, respectively. No information was given about blister rust resistance.

Croatia also conducted a species comparison test with eastern white pine, Scots pine (*P. sylvestris* L.), black pine (*P. nigra* Arnold), European larch, and Douglas-fir (*Pseudotsuga menziesii* (Mirb). Franco) was established in Tocak area. After 23 years of testing, eastern white pine was found to have produced the greatest about of volume per hectare (479 cu. m), in comparison to 214, 209, and 164 cu. m/ha produce by Scots pine, European larch and Douglas-fir, respectively (Orlic and Ocvirek 1993). In a 26 year-old trial at Slatki Potok, eastern white pine generated 549.1 cu. m/ha in comparison to only 270 cu. m/ha produced by black pine (Orlic and others 1997). These results demonstrate the superior performance in wood production of eastern white pine in European site conditions.

In Romania, a nursery provenance test of eastern white pine was planted with 45 provenances: 19 from North America and 26 of unknown origin taken from old stands planted across Europe. The weight of 1,000 seeds per provenance was assessed before sowing (Radu 1974). Seed weight means ranged from 11.4 g to 23.2 g, with a mean of 16.9 g. The North American provenances averaged 15.9 g, whereas European provenances weighted 8.8 percent more (17.3 g). Twelve traits including dry matter were measured at age 2. The total height ranged from 8.9 cm to 15.9 cm, with Romanian local seed sources surpassing the other groups of provenances. Significant differences were found among provenances for dry matter content. The provenances from northern Minnesota (USA) had the lowest average height, but the highest proportion of dry matter. In contrast, the fastest growing provenances (North Carolina, Kentucky and Ohio, all from the USA) had the lowest dry matter content even though their height was greater.

A nursery provenance test of Cembran pine was established in Romania. The test consisted of 12 provenances including seven from the Carpathian Mountains and five from the Alps. Blada (1997a) found significant differences among provenances for total height growth, annual height growth and root collar diameter. The top four provenances were Pietrele, Gemenele and Calimani from the Carpathians and Blunbach Grunalpe from the Austrian Alps, which exhibited faster height, height incremental growth, and root collar diameter than other provenances at age 6. Duncan multiple range tests (1955) for these traits suggested that major gaps separated provenances within the natural range of the species; that is, genetically distinct populations could be found in both the Alps and Carpathian Mountains. The same data suggested a discontinuous pattern of distribution suggesting the absence of a gene flow among populations. There were highly significant positive correlations between all traits, suggesting that indirect selection can be applicable. No significant correlations were found between any growth trait and geographic coordinates.

Provenance tests of Balkan pine were investigated in Bulgaria. Thirteen provenances, originating from 1,700 m – 2,100 m in the Pirin and Rila Mountains, were represented in each of the two tests. At age 3, it was found that the Balkan pine provenances from high elevations initiated growth earlier than the provenances from middle elevations (Dobrev 1997a). Approximately 90 percent of the seedlings had lammas shoots at the end of the August of the third growing season. Significant correlations were found between seed size with provenance latitude and elevation. Also, a significant positive correlation was found between height growth and needle length. No significant correlations were found between height growth and latitude or with elevation of provenances.

Dobrev (1997b) investigated the concentration of macro- and microelements in the needles of the 3-year-old seedlings from different Balkan pine provenances. Variation of concentration in macro- and microelements of needles was discontinuous among provenances. Provenances from the northern Pirin Mountains greatly differed in their relative concentration of nitrogen and calcium and copper as compared with provenances from southern Pirin and Rila and Central Balkan Mountains. A geographic differentiation in magnesium concentration of the needles was found. The Pirin Mountains provenances had a higher concentration of magnesium than provenances from Rila and Central Balkan Mountains. A significant positive correlation was found between phosphorus concentration and seedling height.

About three decades ago, various provenance trials were established in Ukraine (Yatsyk and Volosyanchuk, personal communication). A *P. cembra* trial with six provenances originating from Ukrainian Carpathian Mountains was established on 0.5 ha. At age 28, the mean height growth, diameter and volume were 5.0 m, 9.3 cm and 31 cu m/ha were achieved. Two tests of *P. koraiensis* comprising 19 provenances of unknown origin were planted on 2.4 ha. The latest measurement took place at age 22 and 30. The mean height growth, diameter, and volume in the first and second tests were 6.7 m, 11.8 cm, and 8.1 cu m/ha, and 3.9 m, 7.3 cm, and 8.5 cu m/ha, respectively. A trial with four *P. pumila* Regel provenances of Russian origin was established on 0.25 ha. The mean height growth and diameter at the ground level at age 30 were 11.3 m and 3.6 cm, respectively. A 2.5 ha test of *P. sibirica* with 36 provenances of Russian origin was planted. The height growth, diameter and volume at age 23 were 5.4 m, 10.9 cm and 2.4 cubic meters per hectare, respectively. A second trial with 31 provenances, of the same origin, was established on 13 ha. Until now, no other measurements were made. Two *P. peuce* provenances of unknown origin were planted on 0.1 ha. Height, diameter and volume at 22 years of age, measured 7.0 m, 12.5 cm and 13.2 cubic meters per ha, respectively. All provenances of the above species proved to be resistant to blister rust.

The Ukrainians also planted tests of North American species. A 0.1 ha *P. flexilis* plantation with one provenance of unknown origin was made about 33 years ago. The height growth and diameter at age 21 were 6.3 m and 10.8 cm, respectively. All provenances exhibited high susceptibility to blister rust and only 10 percent of trees survived after 21 years of testing. In the same timeframe, a *P. strobus* trial with three provenances of unknown origin was planted on 0.1 ha. After 23 years of testing, the height growth, diameter and volume were 9.7 m, 23.4 cm and 56.3 cu m/ha, respectively. Heavy blister rust attack occurred and only 1.5 percent of the trees survived.

Open-Pollinated (Half-Sibling) Progeny Tests

Blue pine—In 1971 an international program for testing white pines of known origin for resistance against blister rust was proposed (Bingham and Gremmen 1971). Another program dealt with seed collection and exchange (Kriebel 1976). As part of this program, Romania received 36 open-pollinated families of blue pine (*P. wallichiana*) from 16 provenances originated from Pakistani Himalayan Mountains. This material was tested for growth and blister rust resistance by artificial inoculation. Eight traits, including blister rust resistance and height growth were measured at age 11, and the results reported by Blada (1994b). Highly significant differences were observed among families for blister rust resistance (BR1), percentage of trees free of blister rust (BR2), tree survivors (BR3), total height growth (HT), and stem volume (V). BR1, BR2, BR3, HT, and V averaged 3.2 points (10 = the highest resistance), 9.7 percent, 49 percent, 10.4 dm, and 0.458 dm^3 respectively.

Genetic variance estimates for BR1, BR2, BR3, HT, and V accounted for 91, 99, 96, 79, and 38 percent, respectively, of phenotypic variance. Therefore, this high amount of genetic variance could be used in a blue pine breeding program. Narrow-sense heritability estimates at the family level for BR1, BR2, BR3, and HT were high: 0.909, 0.998, 0.960, and 0.974, respectively. Heritability for V was much lower (0.380). These estimates, coupled with the large amount of variation observed within blue pine population suggest a two-way selection program for rust resistance and growth would be rewarding. If the best 5, 10, or 15 families were selected and planted on sites more or less similar to that used in this trial, a genetic gain of 67, 51, and 40 percent in BR1 and 18, 14, and 11 percent in V, respectively, could be achieved.

A highly significant positive phenotypic correlation was found between blister rust resistance and latitude. All families that originated from above 35° N latitude exhibited a higher resistance to rust than families from lower latitudes. No significant phenotypic correlations were found among growth traits and latitude or between growth traits and blister rust resistance. Therefore, growth and blister rust resistances are independent traits, indicating that improvement using indirect selection is not possible.

Cembran pine—As part of the Romanian five-needle pine breeding program, a nursery test with 136 open pollinated families of *P. cembra* was established. Highly significant differences among families were found for height, root collar diameter (RCD), and total number of branches (TNB) (Blada in preparation). The genetic coefficient of variation for height, RCD, and TNB were 22, 14.6, and 26.3 percent, respectively, and the narrow-sense heritability estimates for height, RCD and TNB were 0.968, 0.938, and 0.966, respectively. Consequently, an improvement program with stone pine would be yield positive results.

Genetic correlations among height with TNB, RCD, and TNB were high: 0.881, 0.571 and 0.713, respectively. Selection in height or in RCD should lead to an indirect increasing of the TNB. However, an increased number of branches is a negative characteristic, as it lowers the quality of wood. Therefore, the number of branches in the next generation should be minimized by selecting fast growing trees with small number of branches.

If selecting the best 30, 35, 40, or 45 of the 136 families, genetic gains in height of 28.8, 26.8, 25.1, and 23.4 percent, and in RCD of 18.8, 17.6, 16.4, and 15.3 percent, respectively, could be expected. By using these early test results to guide an operational improvement program, two types of production seed orchards were planned: a seedling seed orchard using the fastest growing seedlings in the best 45 families and a clonal seed orchard using ortets from the best 45 trees.

Breeding and Seed Orchards

A few countries reported clonal seed orchards, such as: Cembran in Austria, Slovakia Romania and Ukraine; Balkan pine in Romania; and eastern white pine in Croatia and Romania.

A genetic improvement program was started in Romania in 1977 due to the potential importance of eastern white pine in consideration of blister rust. This program included both intra- and interspecific hybridization and has a final objective of establishing seed orchards composed of selections with high general combining ability for resistance to blister rust (Blada 1982). Due to the lack of official interest in five-needle pines, the scope of the initial program was restricted to continuing the measurements in the already established trials. These hybrid trials perform well, and additional details will be given elsewhere in these proceedings.

Another Romanian breeding program under way is concerned with *P. cembra*. The program was initiated in 1989 with the following objectives: (a) phenotypic selection of parents in natural populations; (b) provenance and half-sibling family testing; (c) full-sibling family (both from intra- and inter-specific crossing) testing and genetic parameters estimation; and (d) seed orchards establishment with the best combiners for both improved mass seed production and as a base population for advanced-breeding population (Blada 1990).

Full-Sibling Progeny Tests

Romaina was the only country that reported full sibling progeny tests in response to the survey. A 10 x 10 full diallel crossing experiment was conducted in Gemenele on native populations of *P. cembra* from Romanian Carpathian Mountains. The experiment was conducted to provide information on the genetic variation and inheritance of important breeding traits. Cotyledon number, total height, annual height increment, RCD, TNB, and lammas shoots formation were measured from age 2 to 6 (Blada 1999). The most prominent result from this experiment was that significant general combining ability (GCA), specific combining ability (SCA), and reciprocal effects for all traits were found. Also significant maternal effects occurred in number of traits, suggesting control by nuclear and extranuclear genes and by nuclear x extranuclear gene interactions.

Growth measurements indicated a progressive increase with age of the GCA variance within phenotypic variance. The GCA variance of the total height growth, increased from 2 percent at age 2 to 25 percent at age 6, while the GCA variance of the root collar diameter increased from 8 percent at age 4 to 14 percent at age 6. Similarly, the SCA variance of the total height growth ranged from 15 percent at age 2 to 27 percent at age 6. The diallel analysis showed that both GCA and SCA variances were important sources of variation. Dominance variance exerted a greater influence on 10 out of 17 traits as evidenced by SCA / GCA variance ratios. However, the magnitude of these ratios suggested that additive effects might be almost as important as nonadditive effects in the study. Consequently, the breeding strategy can employ both additive as well as nonadditive variations, indicating that considerable progress under direct selection is possible. If two out of 10 randomly selected parent trees exhibited significant GCA effects for total height, then it can be estimated that 20 percent of trees within the basic natural population could be selected as good combiners.

Heritability estimates were high enough to ensure genetic progress in improving growth and other traits. For height growth, heritabilities for both family and single tree level increased from age 2 (0.065 and 0.021 respectively) to age 6 (0.453 and 0.366 respectively). In the same manner, heritabilities for root collar diameter, for both family and individual level, increased from 0.228 to 0.321 and from 0.126 to 0.157, respectively.

Interspecific Hybridization

***P. strobus x P. peuce* hybrids**—In Romania a 7 x 4 factorial crossing was conducted between eastern white pine (female) and Balkan pine (male) to combine the rapid growth of eastern white pine with high resistance to blister rust of Balkan pine (Blada 2000a). The resulting families were artificially inoculated at age 2 and planted in the field at age 6. Blister rust resistance (BRR), trees free of blister rust (TFBR), tree survival (TS), tree height (H), diameter at 1.30 m (D), basal area (BA), stem volume (V), stem straightness (SS), and branch thickness (BT) were measured at age 17. Highly significant differences among hybrid families were found for all traits except stem straightness. Selection at family level, therefore, can be carried out for the most economically important traits, including BRR and V.

There was large genetic variation among the parents for all traits examined. The effects of eastern white pine female parents were significant not only for growth traits but for BRR, TFBR, and TS as well. This suggests that there were (1) additive genetic control for all traits and (2) parents with high GCA could be selected for breeding. The existence of resistance to the blister rust within eastern white pine (as a female parent) agreed with results found by Riker and others (1943), Riker and Patton (1954), Patton and Riker (1958), and Patton (1966) and were contrary to Heimburger (1972). Balkan pine (as a male parent) had significant effects on growth traits but no significant effects on BRR, TFBR, and TS. Therefore, all male Balkan pine parents exhibited the same level of resistance to blister rust in this study, as found by Blada (1989) at an earlier age of the study. This was contrary to Patton's study (1966), which found differences in blister rust resistance among his *P. peuce* selected parents. Male x female interaction effects were significant and highly significant for all traits except for stem straightness, suggesting a nonadditive gene action on most traits.

Significant, positive phenotypic correlations were found among growth traits. Such correlations imply significant genetic gains in these traits even if selection was practiced on only one trait. However, correlations between stem straightness and growth traits were low, ranging from 0.30 to 0.32. Low phenotypic correlations (0.01 to 0.33) were obtained between blister rust resistance and growth traits, thereby suggesting that the two traits were inherited independently and tandem selection cannot be applied.

Mid- and high-parent heterosis was calculated (MacKey 1976, Halauer and Miranda 1981). Balkan pine was found to be the best parental species for blister rust resistance and stem straightness, whereas eastern white pine was the best parent species for all growth traits. Mid-parent heterosis was positive for all but one trait and accounted for 34 percent for BBR, 55 percent for TFBR, and 53 percent for TS. Substantial mid-parent heterosis was also found in most growth traits, such as 26 percent in volume growth. The total height growth had the lowest (13 percent) positive mid-parent heterosis, while the stem straightness was the only trait displaying a negative mid-parent heterosis. High-parent heterosis was negative for all traits. For example, at age 17, this heterosis accounted for -5 percent for blister rust resistance, -8 percent for trees free from blister rust, and -9 percent for total height growth. Generally, hybrids were intermediate between the two parental species over all characteristics and incorporated desired characteristics from both parent species.

Genetic gain using the average of breeding values of the best parents was calculated. Selecting the best three eastern white pines (females) for blister rust resistance (average breeding value was 0.833) would result an increase of 9.5 percent for blister rust resistance. Similarly, using the best five Balkan pines (males - average breeding value was 21.6 dm^3) to cross with the above females for volume growth rate would result in a genetic gain of 18.3 percent in the overall mean (118.0 dm^3).

***P. strobus x P. wallichiana* hybrids**—In Romania, a factorial crossing was conducted among seven female trees of eastern white pine and four male trees of blue pine to combine the rapid growth of former species with high resistance to blister rust of the latter species (Blada 2000c). The hybrid families were artificially inoculated at age 2 and planted at age 6. Blister rust resistance (BRR), TS, H, annual height growth, D, BA, V, SS, and BT were the measured traits at age 17.

Factorial analysis indicated significant differences among hybrid families for all traits except branch thickness. The effects of eastern white pine (female) were significant not only for the growth traits, but for BRR and TS, again suggesting an additive genetic control in all growth traits and blister rust resistance and that high GCA parents could be selected for breeding. Blue pine (male) had significant effects on TS, H, tree survivors, annual height growth, BA, and SS, but no significant effects on BRR, D, V, and BT. It is important to note that blue pine male parents exhibited the same level of blister rust resistance. Male x female interaction effects were significant except for TS and SS, suggesting that nonadditive gene action had an influence on all economically important traits.

The contribution of GCA variance to the phenotypic variance was 87 percent for H, 53 percent for D, and 77 percent for V; whereas the contribution of SCA variance to the same traits was lower, that is, 10, 41, and 22 percent, respectively. Both additive and dominance variances could be used for improvement in wood production. The contribution of GCA variance to the phenotypic variance was 73 percent for BRR and 53 percent for TS, while the contribution of the SCA variance for the same traits was only 9 percent for the former and 0 percent for the latter trait. The GCA / SCA variance ratios demonstrated that there was additive genetic variation for all traits. The GCA-F / GCA-M variance ratios revealed that estimates of GCA variance of females were much greater than estimates of males for all traits, except BT. These results suggested that the greatest amount of additive variance associated with both blister rust resistance and growth traits was found within eastern white pine parent population. The blue pine male parent contribution to the additive variance was insignificant for blister rust resistance but significant for some growth traits.

The narrow-sense heritability estimates at the family level were high for all traits. For example, the estimates of 0.828 and 0.885 and 0.777 for BRR, H, and V, respectively, were obtained. The magnitude of heritability estimates was due to the high level of additive variance attributable to the female parents. In general, the individual-tree narrow sense heritabilities appeared to be high for blister rust resistance (h^2_w = 0.421), moderately high for total height growth (h^2_w= 0.327), low for diameter (h^2_w= 0.122), and very low for branch thickness (h^2_w= 0.085). In conclusion, heritability estimates were high enough to ensure progress in improving genetic blister rust resistance and growth traits by using *P. strobus x P. wallichiana* F_1 hybrids.

Both positive and negative GCA effects, which significantly ($p<0.05$) differed from zero, were generally found for both male and female parents for most traits. None of the blue pine male parents had significant GCA effects on BRR as these parents exhibited the same level of resistance. The range of estimated GCA effects among parents suggested that it may be possible to select parents with superior breeding values for BRR and growth traits.

Genetic and phenotypic correlations between SS and growth traits were relatively low, ranging between 0.143 and 0.288. Both types of correlations between BT and total height were high and negative (-0.543 and -0.533), indicating that larger trees produced thinner branches. High, positive genetic and phenotypic correlations were obtained between these two traits with BRR, $r_G = 0.928$ and $r_p = 0.916$ respectively. In addition, high, positive genetic correlations were obtained between BBR and D ($r_G = 0.680$), BA ($r_G = 0.655$), and V ($r_G =. 608$), suggesting that tandem selection can be applied.

Estimates of high-parent heterosis were positive only for TS and height and negative for all other traits. From these estimates, it is evident that hybrids combined their parental genes for both rapid growth and blister-rust resistance. These results may justify the use of F_1 *P. strobus* x *P. wallichiana* hybrid production. Genetic gains could be realized in increasing in both blister-rust resistance and timber production. Even smaller increases in resistance and volume growth would give appreciable improvement in yield, especially when considered in relation to large-scale plantation programs.

Host-Parasite Investigations

In order to investigate the pathogenic variation of *C. ribicola* a German-Korean joint inoculation experiment was conducted (Stephan and Hyun 1983, also in Stephan, these proceedings). *Cronartium ribicola* strains used in the German experiment were able to infect only *Ribes nigrum*, but not *Pedicularis resupinata* L., the alternate host species in Korea. Therefore, this host plant species cannot be considered as a host for the German fungus material. *Cronartium ribicola* strains used in the Korean experiment could infect only *P. resupinata*, thereby confirming pathogenic variation in *C. ribicola*.

The same joint experiment corroborated other reports, such as La and Yi (1976), that demonstrated a wider pathogenic variation of *C. ribicola* in eastern Asia. There is an increase of blister rust strains with a stronger virulence than had been observed in Korea since 1963 (La and Yi 1976)) and Japan since 1972 (Yokota and others 1975). Apparently, only the *Ribes* host-strain of *C. ribicola* had invaded Europe in the last century, and from Europe was subsequently introduced to North America. Introduction of the *Pedicularis*-host strain of *C. ribicola* into North America would be a potential disaster for endemic five-needle species (Stephan and Hyun 1983), as this strain is very virulent.

In 1971, the International Union of Forest Research Organizations (IUFRO) proposed an international program for testing white pine blister rust resistance. Parallel trials were carried out in the Western and Eastern United States, in France, South Korea, Japan and Germany (Bingham and Gremmeen 1971, Stephan 1986). In Germany, 14 species with a total of 63 provenances/progenies have been tested by artificial inoculation. After 10 years, Stephan (1986) found significant differences among the species investigated. Asian five-needle pines are generally more resistant to the blister rust than North American species. No or relatively weak symptoms were observed in *P. pumila, P. parviflora* Zieb. & Zucc., *P. sibirica*, and *P. koraiensis*. Surprisingly, a few provenances of *P. wallichiana* showed high infection rates. Most of native North American white pines showed a very high infection rate of more than 90 percent. *Pinus albicaulis* Engelm., *P. flexilis, P. lambertiana* and *P. monticola* were severely damage, although *P. aristata* Engelm. was relatively less infected. The fungus infected nearly 100 percent of the tested *P. strobus* provenances. This partially can be explained by the theory that the gene center of blister rust and blister rust resistance is in north central Asia (Bingham and others 1971).

There were no differences among provenances within species. The experiment also included a few F_1 and F_2 progenies between *P. lambertiana* and *P. monticola*, which possessed a certain level of improved resistance to blister rust under North American conditions. Only one provenance of *P. lambertiana* showed 20 percent less attack than in unimproved provenances. In *P. monticola*, the F_1 and F_2 progenies selected for rust resistance were severely attacked 7 years after artificial inoculation. The comparison of the German results with those obtained in France (Delatour and Birot 1982), Japan (Yokota 1983), and North American tests were interesting. Three years after inoculation there were significant correlations between the German and French results with respect to the percentage of rust-free trees in the seedlot BR n° 41 (*P. lambertiana*) and seedlot BR n° 43 (*P. monticola*). There were no significant correlations with the American results and the French seedlot BR n° 46 results, nor were there correlations with the Japanese results (Stephan 1986).

A similar IUFRO test was carried out in France. This French test demonstrated that the species from Europe and Asia proved to be less susceptible to rust than the American species. (Delatour and Birot 1982).

A survey on blister rust resistance in native (Cembran pine) and introduced five-needle pine species was conducted in Romania (Blada 1982, 1990). After 1970, blister rust had caused severe attacks to all young stands of eastern white and western white pines. This severe outbreak was promoted by simultaneous culture of the five-needle pine species with *Ribes nigrum*. Mature populations and young seedlings from natural regeneration of *P. cembra* distributed throughout the Carpathian Mountains were free from blister rust. *Ribes alpinum* L. and *R. petraeum* Wulf. Populations coexist at high altitude with Cembran pine and were also free from blister rust, although they have been shown to be susceptible (Georgescu and others 1957, Blada, unpublished data). After approximately two decades of survey, blister rust still could not be found on Cembran pine nor the *Ribes* species (Blada, unpublished data). The absence of the infection on both Cembran pine and natural *Ribes* populations indicates that the Romanian Carpathian Mountains do not represent a gene center for *C. ribicola*, as suggested by Leppik (1967). The rust was recently introduced via eastern white pine seedlings from Germany and *Ribes* sp. collections from elsewhere (Blada, in preparation).

Research at Molecular Level

Studies concerning genetic differentiation and phylogeny of stone pine species based on isozyme loci are summarized in a previous publication and in this volume (Krutovskii and others 1992, Politov and Krutovskii in these proceedings). Another molecular study of a Russian five-needle pine (*P. sibirica*) was conducted by Goncharenko and others (1992). Enzyme systems in the seeds of natural populations from various parts of Siberia were analyzed by starch gel electrophoresis, and 36 alleles at 20 loci were defined. Of the genes controlling these enzyme systems, 55 percent proved to be polymorphic, with an average 17.6 percent of gene/tree being heterozygous. Interpopulation genetic diversity accounted for a little over 4 percent of the total genetic diversity. The Ney distance coefficient ranged from 0.008 to 0.051, with an average of 0.023. The data obtained suggested lack of any marked genetic differences between central and marginal Siberian populations.

Genetic diversity and differentiation among five populations of Cembran pine from the Italian Alps were studied by means of isoenzyme variation at 15 loci and contrasted with five Scots pine populations (Bulletti and Gullace 1999). The two species showed similar values for the mean number of alleles per locus and percentage of polymorphic loci, while the expected heterozygozity for Scots pine was higher than that for Cembran pine (0.332 vs. 0.281). All the populations studied showed an excess of homozygotes; the Allevet population of Cembran pine had the highest value of fixation index (0.206). Furthermore, the latter stand exhibited the lowest allelic richness index value. Only 2.7 and 3.5 percent, respectively, of the observed genetic diversity in Cembran and Scots pines was due to differentiation among populations. Therefore, the populations for each species studied share similar respective gene pools, and there were no barriers hampering gene flow. The results of the study provide useful information for *in situ* conservation of genetic variability. Moreover, the data obtained can also be used for the identification of the most valuable stands for the production of high quality seeds.

A comprehensive study concerning phylogenetic relationship among *P. cembra, P. sibirica* and *P. pumila*, using microsatellites and mitochondrial *nad1 intron 2* sequences was recently completed (Gugerli and others 2001). The three-chloroplast microsatellite loci combined into a total of 18 haplotypes. Fourteen haplotypes were detected in 15 populations of *P. cembra* and one of *P. sibirica*, five of which were shared between the two species, and the two populations of *P. pumila* comprised four species-specific haplotypes. Mitochondrial intron sequences confirmed grouping of the species. Sequences of *P. cembra* and *P. sibirica* were completely identical, but *P. pumila* differed by several mutations and insertions/deletions. A repeat region found in the former two species showed no intraspecific variation. These results indicate a relatively recent evolutionary separation of *P. cembra* and *P sibirica*, despite their presently distinct distributions. The species-specific chloroplast and mitochondrial markers of *P. sibirica* and *P. pumila* should help to trace the hybridization in their overlapping distribution area and to possibly identify fossil remains with respect to the still unresolved postglacial recolonization history of these two species.

Acknowledgments

The authors express their gratitude to all colleagues from several countries who supplied information concerning genetic activities in five needle pines in their own countries. Particularly, our thanks are due to Drs. R. Stephan (Germany), R. Yatsyk and R. Volosyanchuk (Ukraine), J. Gracan (Croatia), A. Nanson (Belgium) and R. Longauer (Slovakia). The thanks are extended to our technician, Cristiana Dinu, for her help during the preparation of this report.

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