BREEDING STRATEGIES FOR *LARIX DECIDUA*, *L. LEPTOLEPIS* AND THEIR HYBRIDS IN THE UNITED STATES

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ABSTRACT

European larch (*Larix decidua* MILLER), Japanese larch (*Larix leptolepis* (SIEB. *et* ZUCC.) GORD.) and their hybrids (*L.* x *eurolepis* HENRY) are fast-growing coniferous species in eastern North America. European larch usually outperforms Japanese larch under harsh winter conditions in the Lake States and northeastern United States; Japanese larch shows superior performance under milder winter conditions in Northeast and Maritime region of Canada; larch hybrids often outperform both parent species on most sites. Based on variation in growth, frost tolerance, and insect and disease incidents within and between species, larch species and sources are being recommended for commercial planting in the Lake States and Northeast. Breeding strategies are proposed for long-term improvement of larch species in the United States. Simple recurrent selections for general combining ability are proposed to improve pure species of European and Japanese larch. European larch selections will be grouped by source origins to maintain genetic variation. Japanese larch breeding will be less intensive with a single breeding population. Based on reviews of various hybrid breeding strategies, a recurrent selection program based on a F_1 hybrid population is proposed for hybrid larch improvement. The strategy is to use mainly additive genetic effects and combine favorable traits of the two species, i. e., relative canker resistance, straightness, and fast juvenile growth of Japanese larch with cold hardiness and growth vigor of European larch.

Key words: *Larix decidua*, *L. leptolepis*, *L.* x *eurolepis*, breeding strategy, hybridization.

INTRODUCTION

European larch (*Larix decidua* MILLER), Japanese larch (*Larix leptolepis* (SIEB. et ZUCC.) GORD.) and their hybrids (*L.* x *eurolepis* HENRY) have been planted in the United States and Canada since 1850 (NYLAND 1965; COOK 1969; MACGILLIVRAY 1969). These exotic larches are the most rapid-growing coniferous species in northern climates showing superior performance over native larch (*Larix laricina* (DU ROI) K. KOCH), pine, spruce and fir when planted on upland sites in North America (MCCOMB 1955; JEFFERS and ISEBRANDS 1974; HALL 1983; PARK and FOWLER 1983; EINSPAHR *et al.* 1984; FOWLER *et al.* 1988; WYCKOFF *et al.* 1992). Pulpwood rotation ages of 25 - 35 years can be expected when larches are planted on the better forest soils (EINSPAHR *et al.* 1984; LOO-DINKENS *et al.* 1992).

In addition to superior growth rates, larch has wood and fiber characteristics suitable for kraft pulping, with young trees exhibiting pulp strength and yields comparable to mature jack pine and other conifers (EINSPAHR *et al.* 1982, 1983; HATTON 1986). The use of larch for solidwood products has also attracted attention (BALATINECZ 1986). Studies by OLSON *et al.* (1947) indicate strength properties may be suitable for structural lumber; FOWLER *et al.* (1988) also indicate Japanese larch may be suitable for lumber. British tests of European, Japanese and hybrid larch lumber all exceeded target values (BENHAM 1986).

The planting of fast-growing larch species and hybrids offers great potential to increase future softwood supplies (EINSPAHR 1984) in response to softwood consumption increases in the Lake States and Northeast (HACKETT 1990; WIDMANN 1992) and timberland continues to decrease (HAYNES 1990). With its large genetic variation and few major pests, larch can also provide needed diversity in the Lake States' planting programs where red pine currently accounts for about 90 percent of the planting stock. Early larch plantings and field trials in the United States and Canada have shown considerable variation in adaptability and growth among species and geographic seed sources within species (MCCOMB 1955; FARNSWORTH *et al.* 1972; GIERTYCH 1979; BOYLE *et* *al.* 1989). The large genetic variation in a wide range of characteristics, including form, growth, disease resistance, adaptability and wood properties, provides opportunities for genetic improvement for larch species and hybrids in the United States.

A cooperative larch improvement program was initiated in 1980 at the Institute of Paper Chemistry (Appleton, Wisconsin) with support from several pulp and paper companies and state agencies in the Lake States and northeastern United States. The larch breeding program is now part of the Aspen & Larch Genetics Cooperative at the University of Minnesota. Early emphasis of the program was on evaluation of wood, pulp, growth and adaptability of larch species and provenances. Based on that information, larch species and sources are being recommended for commercial planting in the Lake States and Northeast. Phenotypical selections have been made from field trials and plantations across the eastern North America. Two European larch and one hybrid seed orchard consisting of European and Japanese larch parents have been established in the program. The main focus of the program is now shifting to breeding and testing for advanced generation improvement. This paper reviews larch performance in eastern North America and outlines the breeding strategies for improving larch species and hybrids in the northcentral and northeastern United States.

LARCH PERFORMANCE AND PLANTING IN NORTH AMERICA

Considerable variation has been found for growth habit, frost tolerance and insect and disease resistance within provenance and between Japanese and European larch species (FARNSWORTH *et al.* 1972; GIERTYCH 1979; BOYLE *et al.* 1989). European larch usually outperforms Japanese larch under harsh winter conditions (PAULEY *et al.* 1965; LEE & SCHABEL 1989; WYCKOFF *et al.* 1992), while Japanese larch shows superior performance under milder winter conditions (HOLST 1974; PARK & FOWLER 1983; FOWLER *et al.* 1988). Hybrids between European and Japanese larch (*Larix* x *eurolepis*) often outperform both parent species (DALLIMORE *et al.* 1967; HOLST 1974; BOYLE *et al.* 1989; WYCKOFF *et al.* 1992). European larch and hybrids are being planted on upland sites throughout the Lake States and Northeast. Japanese larch is being planted in the southern areas of the Lake States, Northeast and Maritime region of Canada.

The key elements for establishing European larch in eastern North America are depth of free rooting (AIRD & STONE 1955), available soil moisture (well-aerated, good moisture holding capacity), avoiding sites with solums ≤ 62 cm (GILMORE 1990), avoidance of frost (late spring frosts are more damaging than early fall), and control of competing vegetation. Resistance to needlecast disease (*Mycosphaerella laricina*) is also an important factor.

Among the four major sources of European larch, Sudeten origins (Sudeten Mountain and northern Czechoslovakia) and Polish sources (central and southern Poland) are often superior in growth than Tatra and Alpine sources (GENYS 1960; JEFFERS & ISEBRANDS 1974; BARNES 1977; GIERTYCH 1979). Provenance differences in growth and stem form are similar to those found in Europe (WEISGERBER & ŠINDELÁŘ 1992). The primary Sudeten and Polish sources (from original natural stands) generally have an average stem form and sometimes poor form, while the Tatra and Alpine sources usually exhibit good stem form (BOYLE *et al.* 1989). Most of the secondary sources of Sudeten and Polish (from non-native stands) show good stem form possibly due to artificial selections. Sudeten larch has shown more tolerance to late spring frost and better recovery than other larch sources in Wisconsin (WYCKOFF *et al.* 1992). Sudeten larch also showed better resistance to a needlecast disease in the Lake States than other sources (OSTRY *et al.* 1991). Seed sources currently recommended in the Lake States and Northeast are from Sudeten Mountain origins in the northern part of the Czech Republic and origins in central and southern Poland.

Japanese larch has site requirements similar to those of European larch, but requires greater care in selecting locations that minimize freeze damage. In the Lake States, those areas tend to be in the southern portion and in narrow belts where climate is moderated by the Great Lakes. Late spring frost is the major cause for planting failure in the Lake States (PAULEY *et al.* 1965; FARNSWORTH *et al.* 1972), but it is not as a serious problem under oceanic conditions in the Maritime region of Canada (PARK & FOWLER 1983; FOWLER *et al.* 1988). Fairly large location differences in growth are found but the pattern is not associated with geographic origins (PAULEY *et al.* 1965; GENYS 1971; FARNSWORTH *et al.* 1972; BOYLE *et al.* 1989; FOWLER *et al.* 1988). Seed sources that have performed well in the northern areas of Wisconsin are from Mt. Nantai and Akaishi Mts. (unpublished data).

Hybrid larch often displays superior growth to both pure parental species on most sites (DALLIMORE *et al.* 1967; HOLST 1974; WYCKOFF *et al.* 1992). Its site requirement does not differ from either parent species. Freeze damage is a limiting factor for establishment under harsh winter conditions, but hybrid larches can recover from freeze injury at a rate greater than Japanese larch and less than European larch (WYCKOFF *et al.* 1992).

PROPOSED BREEDING PROGRAM FOR LARCH SPECIES

The cooperative larch breeding program is currently supported by 17 private and public organizations in the northcentral and northeastern United States. Larch plantations are being planted by the cooperative members mainly for pulp and paper products. With different frost injury and site requirements among species, European larch and hybrids are suitable for planting on upland sites in the Lake States and Northeast and Japanese larch for the southern areas of the Lake States and Maritime region of Northeast. Considering the cooperative's sites across a wide geographic area, the larch breeding program is designed to improve both pure species (European larch and Japanese larch) and their hybrids.

European Larch Breeding Program

Major characteristics considered in the cooperative's breeding program for European larch are adaptability (frost tolerance), growth, stem form, disease resistance (needlecast and canker), and wood quality. Large variation among and within populations in those traits suggests that a recurrent breeding program for general combining ability (GCA) would be effective for pure larch species improvement. Genetic gain for volume growth from provenance selection plus progeny testing of selections has been estimated about 15 to 20 percent in Europe (DIETZE 1976).

Most of the phenotypic selections in the current breeding program are from various provenance trials and plantations in eastern North America, which originated from three major geographic races in Europe: Sudeten, Polen, and Alpen seed sources (GIERTYCH 1979; BOYLE *et al.* 1989). Additional selections will be made from Tatra sources to balance the gene pool collection. Selections will be grouped into breeding groups depending on seed source origins to maintain genetic diversity among geographic sources. Control of the ancestral races should help to maintain genetic variation within the breeding population (BURDON & NAMKOONG 1983) and avoid inbreeding in the production population (VAN BUIJTENEN & LOWE 1979). Grouping would also provide opportunities for intraspecific hybridization among races, combining desired characteristics from different larch sources. For example, crossing vigorous Sudeten larch with good form Alpen and Tatra larch has an improvement in form and growth (HERING 1990 viz. WEISGERBER & ŠINDELÁŘ 1992).

A base breeding population of 200 trees is proposed for pure European larch improvement. The population size is considered adequate to maximize short term genetic gain and provide long-term improvement (NAMKOONG *et al.* 1980; Kang 1991). Considering the large geographic variation within species, the 200 selections representing the four major sources will be divided into 20 breeding groups according to their origins with 10 trees in each. There will be 10 groups of Sudeten source, six Polen, two Alpen and two Tatra. A greater representation for Sudeten and Polish sources in the base breeding population is needed as they have shown better adaptation and growth (GIERTYCH 1979; BOYLE *et al.* 1989) and needlecast disease resistance (OSTRY *et al.* 1991) in North America. Including Alpen and Tatra genotypes in the base breeding population is also important because well-shaped and finely-branched east Alpen larch and less canker susceptible Tatra larch could be valuable gene resources in breeding for stem form and canker resistance (WEISGERBER & ŠINDELÁŘ 1992). New selections will be made from provenance tests, plantations and other improvement programs and grafted into clone banks for gene conservation and future generation breeding.

Within each breeding group, two matings of 5-parent disconnected half diallels will be made. The mating design is to evaluate selected parents for breeding values and produce progenies for the next generation selections (NAMKOONG *et al.* 1988). A complimentary mating with polycross and single-pair mating could not simplify the crossing because of breeding groups involved. A balanced factorial or other diallel designs would be too costly and not efficient for utilizing mainly additive genetic effects. The mating design is chosen also for economical and field design considerations of the cooperative.

All progenies from the diallels will be field tested on major site types anticipated for future larch planting. Field tests will be evaluated at age five for adaptation, growth, form, and resistance to needlecast and insects. Although larch canker is currently not a major problem in the United States, long-term disease evaluation will be part of the evaluation process. Recent advances in early selection research for conifer species (LOWE & VAN BUIJTENEN 1989; CARTER *et al.* 1990; LI *et al.* 1991, 1992) indicate that five-year field test data should be generally reliable for family selection. Average performance of parents (GCA) will be estimated from diallels. The three best families (with high GCA) from 10 full-sib families within each diallel will be selected. The best two individuals from each of these families will be grafted into a breeding orchard for early flower stimulation. A new diallel for second generation breeding will be composed of five individuals from the six selected individuals in a diallel. If inbreeding becomes a problem within each diallel, two diallels from the same breeding group will be combined. The selection intensity is relatively low in the breeding population, but it will not reduce the genetic gain because much higher selection intensity is used in the production population (seed orchard).

The GCA information estimated from field tests will be used to rogue existing European larch seed orchards. A separate production population will consist of only the best parent from each breeding group. New seed orchards will be established with the best individuals in the best families from different breeding groups (10 – 20). Clones from sources with growth and adaptation superiority could have a greater representation in seed orchards. The best clone from each diallel within a breeding group can also be used to increase the clone numbers in a seed orchard and increase seed source representation.

Japanese Larch Breeding Program

Breeding for Japanese larch will not be intensive due to restricted planting sites in the region. Suitable planting sites are mainly in the southern range of the Lake States and Northeast. A simple recurrent selection system for GCA will be used to improve adaptation (frost-resistance) and growth characteristics. Because of the relatively small provenance differences (GENYS 1971; FARNSWORTH *et al.* 1972; PARK & FOWLER 1983; FOWLER *et al.* 1988), a single breeding population will be used for the breeding program. A breeding population size of 150 will be used to accommodate both the intraspecific and the hybrid breeding program with European larch. A polycross will be made with a standard pollen mix of 10 trees for Japanese larch selections to determine their general combining ability. Progenies from the polycrosses will be field tested and evaluated. Seed orchards will be established with the best GCA parents. Supplement mass pollination with a positive assortative mating approach will be used to generate improved materials for planting.

Hybrid Larch Breeding Program

Hybrid larch breeding has, so far, concentrated on crossing individual selections from the two species and then using outstanding crosses for short-term gains. Possible long-term breeding strategies have been discussed (FOWLER 1986; PAQUES 1989), but the lack of basic genetic information has made the selection of a strategy difficult. A reciprocal recurrent selection (RRS) program with two breeding populations (COMSTOCK *et al.* 1949) would be effective if the emphasis is for non-additive genetic effects and differences in gene frequencies between the two species (NAMKOONG *et al.* 1988). A recurrent selection program prior to or after hybridization would be attractive and less expensive than RRS if gene action for hybrid vigor is mainly due to additive genetic effects or if combination and transfer of favorable characteristics are desirable for two species (BRIDGWATER & FRANKLIN 1986; NAMKOONG *et al.* 1988).

Reliable genetic information regarding heterosis in larch hybrids is scarce and contradictory. Based on the generally observed hybrid vigor, KEIDING (1980) and PAQUES (1989) suggest that gene action may be primarily non-additive. NILSSON (1959 viz. PAQUES 1989) suggests that additive genetic effects may be more important. Genetic parameters estimated from a 12 x 12 factorial mating of European and Japanese larch clones showed that additive genetic effect is predominantly important for all traits measured (total height, stem straightness, and branching characters) after the nursery stage (PAQUES 1992). Hybrid progeny performance was accurately predicted by the GCA of both parents at age six. Such strong additive genetic effects for hybrid performance certainly suggest that a simple recurrent selection strategy should be more efficient than a RRS program. When additive genetic effects (and possibly a portion of inseparable epistasis effect in the estimates) are of primary importance, accumulation of favorable alleles or interacting alleles of various loci in the population is of interest, rather than the fraction of heterozygous genotypes.

If a recurrent selection system is chosen for hybrid breeding, the question becomes whether selection should occur in the parent populations prior to hybridization or after hybridization in the F_1 generation. Based on available genetic information (NILSSON 1959 viz. PAQUES 1989; PAQUES 1992), a recurrent breeding strategy after hybridization (based on a single hybrid population) is preferred unless it can be proven that intraspecific GCA is a good indicator of interspecific GCA and hybrid performance. This breeding system is especially desirable when the breeding objective is to combine different traits from two species into hybrid individuals (NAMKOONG *et al.* 1988). Breeding should be able to combine these traits present in the hybrid population, e.g. cold-hardiness and fast growth, into individuals by within-population recurrent selection and mating. It is in general agreement that larch hybrid breeding should not be directed toward achieving heterosis only but also generating combinations of favorable characteristics of two species (BOYLE *et al.* 1988; PAQUES 1989). For example, it is desirable to combine the relative canker resistance, straightness, and fast juvenile growth of Japanese larch with the relative cold hardiness and growth vigor of European larch (FOWLER *et al.* 1988; PAQUES 1992).

The evidence from maize breeding, in which strong heterosis has been demonstrated, indicates that the gain from recurrent selection with a single hybrid base population is comparable to the gain from a hybrid breeding system with two parent breeding populations (MOLL *et al.* 1978; MOLL & HANSON 1984). If a hybrid breeding system with two parent populations is not especially advantageous to one with single breeding population in maize, it is uncertain if the heterosis in larch hybrids is sufficient to warrant such a hybrid breeding program. Since hybrid vigor can also be due to additive by additive interaction or other multilocus epistasis of the two parent species, family selection from a single population can be effective for improving hybrids (COTTERILL *et al.* 1987; NAMKOONG *et al.* 1988).

There is little evidence that hybrid superiority diminishes with succeeding generations of larch hybrids; seed collected from hybrids has often been used for plantations (COOK 1971; GIERTYCH 1979). Hybrids of the F_2 and F_3 generations can be more vigorous in growth and stem form than pure species (HOLST 1974; LE CAM 1981). In a larch planting in the Lake States, hybrid F_2 progenies showed slightly larger variation, but still significantly superior over pure parental species (unpublished data). Similarly, HYUN (1973) observed that *Pinus rigida* x *taeda* hybrid F_2 retained similar vigor as the original F_1 with no significant increase in variability. A small percentage of hybrid individuals may be inferior because of gene segregation, but it should be of no practical consequence in plantation management, as they occur at random and are readily eliminated in the nursery or during commercial thinning (COOK 1971). Because thinning is a common practice in commercial forestry, breeding for uniformity may not have the same degree of importance as in crop breeding (PAQUES 1989). In fact, open-pollinated seeds from F_1 plantations have been recommended for commercial planting of *Pinus rigida* x *taeda* hybrids (HYUN 1976).

A recurrent selection system with a single hybrid population is proposed for long-term breeding of hybrid larch in the United States, based on available information, i.e., importance of GCA, combining favorable traits, costs, and flexibility. The proposed breeding strategy can be modified or changed as additional information becomes available. The strategy is flexible because both parental populations are maintained for pure species improvement. If it becomes necessary to restore the heterozygous genotypes in an advanced generation, a new hybrid population can be generated. Alternatively, if intraspecific GCA can indeed be used to predict interspecific GCA and hybrid performance, the hybrid breeding program can be simplified. In addition, a reciprocal recurrent breeding scheme can also be established if it is warranted by new data from well designed experiments.

A single pair mating design with 150 European larch and 150 Japanese larch is proposed to generate the hybrid base breeding population. The mating would provide a maximum number of unrelated hybrids for selection. Hybrid progeny will be field evaluated for growth, frost incidence and stem form. Following hybrid evaluation at age five, a combined family and within family selection will be used to select superior hybrids as parents for the next generation breeding. Three outstanding individuals from the best 50 hybrid crosses will be selected for a base population of 150 trees for the next generation hybrid breeding. A single-pair positive assortative mating based on performance will be used to generate 75 full-sib families for field testing. Based on field test information, three individuals from the top ranked 50 families will be selected to form the new base population for advanced breeding.

The parents that produce the best hybrids will be identified from hybrid progeny tests for hybrid seed production. Hybrid seed orchards with selected parents from two larch species will be established as those in Denmark (KEIDING 1970) and France (STEINMETZ *et al.* 1987). Controlled crosses through supplemental mass pollination will be used to create specific hybrid combinations for commercial use. Superior hybrids will also be vegetatively propagated for commercial planting.

LARCH SEED PRODUCTION AND PROPAGATION

Seed production for improved European, Japanese and hybrid larch is often restricted by irregular flowering, frost damage, and low seed-set per cone (MITCHELL 1958; KEIDING 1970; PAQUES 1989). Several experiments have shown promise in stimulating larch flowering (precocious and early) through treatments of fertilization, root pruning, girdling, strangulation, mulching and applications of giberellins GA_3 and $GA_{4/7}$ (cf. BONNET-MASIMBERT 1992). Indoor accelerated breeding techniques for flower stimulation and pollination are being developed for larch species (EYSTEINSSON & GREENWOOD 1990; EYSTEINSSON 1992). Under favorable greenhouse conditions, foliar sprays or stem injection of $GA_{4/7}$ can stimulate sufficient flowers on 3-years-old grafts for breeding purposes (EYSTEINSSON *et al.* 1993). Research is under way to apply these indoor approaches in field conditions for commercial seed production. One time stem $GA_{4/7}$ injection has been applied in a hybrid larch orchard to examine the potential for commercial use.

A hybrid seed orchard with 10 European larch clones and six Japanese larch clones has been established for hybrid larch seed production. The design was to collect hybrid seeds only from one species as those in Denmark (KEIDING 1970), but flowering time, low seed set, and low proportion of hybrid seeds are major problems for seed production (PAQUES 1989). Matching clone phenology and flowering patterns of the two species may be useful to improve the seed production. Supplemental mass pollination is being tested to overcome some of these problems (STEINMETZ *et al.* 1987). As hybrid programs move into advanced generations, use of hybrids as parents in a seed orchard (or plantation) would be more effective in producing large quantities of seeds (HYUN 1976; PAQUES 1989). This is especially true for the proposed hybrid breeding strategy with one single hybrid larch population.

Mass vegetative propagation in larch breeding programs will capture greater genetic gains than sexual propagation, particularly in advanced generations where pure parent species are not kept for producing uniform F_1 hybrids. Techniques for *in vitro* propagation of adventitious shoots have been developed for juvenile larch (DINER *et al.* 1986; MULCATHEY & KARNOSKY 1986; KRETZSCHMAR 1993) and for older trees (LALIBERTE & LALONDE 1988), but the high cost and intensive labor associated with these techniques make them impractical for operational use at this time. Although larch is considered one of the easier conifer species for propagation from cutting, success from this technique is often dependent on species, clones, ages and position of the cuttings, and treatment and culture conditions for rooting (CHANDLER 1959; WUNDER 1974; JOHN 1979; CARTER 1984; FARMER *et al.* 1986). It is in general agreement that greenwood cuttings from young seedlings have great potential for large-scale mass propagation. Further work is needed to refine rooted cutting and *in vitro* techniques to develop a cost-effective propagation technique for larch breeding programs.

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