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Near rotation-length performance of selected hybrid larch in Central Maine, U.S.A.

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Abstract

Twenty-two year measurements of a test of inter- and intraspecific larch hybrids among European (E), Japanese (J) and tamarack (T) parents growing in central Maine reveal significant hybrid vigor, especially among crosses involving J and E parents. The mean heights and diameters of all the interspecific crosses between J and E parents exceeded those of intraspecific crosses among either of the parents. The mean height after 22 years for all 17 Jx E and Ex J crosses was 19.2 m (63 feet), which compares favorably with heights of loblolly pine plantations at age 25 growing in the southeastern USA, where site index ranged from 12.2 m to 24.4 m (40 and 80 feet respectively). In addition the mean height of these larch crosses was 30% greater than that of a control hybrid seed lot of German origin. Crosses between E and T parents also performed well, but exhibited relatively poor form, and seed set was very low. Seed set and viability for crosses between J and E were as good as

intraspecific parental crosses. Therefore propagation of hybrid larch crosses via controlled pollination and rooted cuttings is feasible, and the potential benefits of larch plantations for Maine's forest economy are briefly discussed.

Key Words: Hybrid larch, hybrid vigor, heterobeltiosis, Japanese larch, European larch, tamarack

Introduction

Reports of naturally occurring larch hybrids between European (*Larix decidua* Mill.) and Japanese larch (*L. kaempferi* (Lamb) Carriere) exhibiting exceptional growth followed the introduction of Japanese larch into European arboretums in 1861 (SANDER and LAANELAID, 2007). Since then, there has been considerable interest in realizing the potential of larch hybrids in France, Sweden, Quebec, the People's Republic of China and throughout US as a rapidly growing plantation species (PAQUES, 1989; PERRON, 2008; ECO et al., 2004). Over the last 30 years, plantations of an open-pollinated half-sib E × J family from a German seed orchard (LANGNER and SCHNECK, 1998) have been established in Maine, Nova Scotia, the Lake States and the state of Oregon. In Maine

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over 10,000 acres of the hybrid were planted, in part to fill the gap in the wood supply following the spruce budworm outbreak in the 1970's and 80's and also as a hedge against another spruce budworm epidemic³⁾. In the Lake States about 100,000 trees per year of the hybrid are being planted, in Nova Scotia about 125 acres per year, and its resistance to the Swiss Needle Cast fungus makes it a desirable replacement for Douglas fir on susceptible sites in Oregon⁴⁾. In Quebec there has been increased demand for the hybrid and a breeding program to produce further genetic improvement is underway (PERRON, 2008).

In Maine, intensive forest management practices including plantation establishment have declined over the last 25 years due to a divestiture of timberlands by integrated wood products companies caused by changes in tax laws and globalization of markets (KELLISON, 2014). In Maine, this has resulted in a drastic shift from industrial forest land ownership to corporate investors with little interest in long-term investment in silviculture. In addition, exaggerated past projections about the demand for soft wood fiber (e.g. EINSPAHR et al., 1984) were confounded by dramatic increases in the proportion hardwood used in pulp, as well as decreased demand for paper due to the replacement of print media with electronic media. Nonetheless the volume of timber harvested in Maine is not declining (MAINE FOREST SERVICE ACTIVITIES REPORT, 2014) and there is no reason to expect that the demand for good quality structural lumber will decline in the future. Also, given that spruce budworm outbreaks are increasing in Eastern Canada and Northern Maine, there are justifications for establishment of plantations of fast-growing species that may also be resistant to the spruce budworm³⁾.

In Maine, recent measurements of a 27 year-old species trial, which included hybrid larch, revealed that the hybrid of German origin was growing at a rate of about 12 m³/ha/y and produced 35% more total volume than the next best species (red pine). 86% of this volume was of potential sawlog size (unpublished data,

³⁾ There is some anecdotal evidence that the spruce budworm had little impact on Eastern larch (*Larix laricina* (duRoi)K. Koch) during the last budworm outbreak, but its effects on hybrid larch are at present unknown.

⁴⁾ Personal communication 2015 by Carl Haag, Larix consulting, 274 S. Reynolds Road, Winslow, ME 04901 USA.

2014). A potential rotation age that is less than half that of natural stands (which is 50 to 70 years for natural stands in Maine) could be realized with hybrid larch. In addition, partial harvesting has increased dramatically since 1989, and in order to maintain a constant wood supply, the area harvested in Maine has nearly doubled. The increased harvest footprint is due to the fact that the volume of wood harvested per acre has decreased by about half since 1989 (MAINE FOREST SERVICE SILVICULTURAL ACTIVITIES REPORTS, 2014).

Therefore we explored the possibility of realizing even greater growth gains from interspecific full-sib hybrid families by selecting parents with good growth and form from locally grown plantations. A test including crosses among three larch species was established in 1992 (BALUNIS et al., 1998). Our breeding design closely resembled one recently proposed by PERRON (2008) in order to demonstrate hybrid vigor among full-sib families of hybrids between J and E parents (*L. x marschlinsii* Coaz) in Quebec. Perron proposed a complete diallel between 6 J and 6 E parents, which included reciprocal crosses between J and E parents. Here we report the results of measurements of a 22 year-old progeny test consisting of full-sib intra- and interspecific hybrids among tamarack (*Larix laricina*, (du Roi) K. Koch)), Japanese and European larch.

This report describes:

1. Hybrid vigor exhibited by interspecific hybrids among 3 larch species. Hybrid vigor can occur as heterosis (when the hybrid mean for a given trait exceeds the combined mean of both parents) or heterobeltiosis (when the hybrid mean exceeds the mean of the best parent).
2. Stability of family performance over time.
3. The advantages and feasibility of mass producing and planting hybrids.

Materials and Methods

Plant material, test design

An indoor demonstration breeding orchard consisting of six parents each of J (Japanese larch, six clones), E (European larch, 5 clones) and T (Tamarack or Eastern larch, six clones), all selected for good growth and form, was established in 1987 in order to create interspecific and intraspecific crosses among all three

species. Each cross is identified by 2 letters, the first indicating the species of the female parent, the second the male parent, followed by two numbers, the first representing the female clone, the second the male clone. For clonal origins of the clones for each species, see BALTUNIS et al., 1998. The E parents were selected from Polish provenances planted in 28–37 year-old tests in Iowa and New Hampshire, while J parents were cloned from provenances that exhibited superior growth in 10 year-old tests located in Maine (EYSTEINSSON et al., 1993).

E and J hybridized readily, and as female parents produced similar numbers of seed per cone (89 and 87 respectively) with seed viabilities of 58% and 48% for E and J respectively (EYSTEINSSON, 1992). Seventeen full-sib crosses were available for testing, 9 with J as female and 8 with E as female. There were 5 pairs of reciprocal crosses. Seed numbers per cone and seed viability was comparable to the intraspecific crosses for both parents. Seed set for interspecific crosses involving T was relatively poor, resulting in only 6 T×E crosses with enough seed to be included in the test. Seed set and viability for E×T was extremely poor, so seed from the latter cross were pooled into a single half-sib family. T×J crosses resulted in very low seed viability, while J×T were almost completely unsuccessful. Intraspecific crosses with J, E and T as parents yielded 7, 7 and 9 crosses respectively.

A replicated field test consisting of a total of 51 families, including 7 hybrid groups of inter- and intraspecific hybrids, plus 3 check lots was established in May 1992 in west central Maine (Figure 1). The 3 check lots consisted of: 1) an open pollinated European larch family (XLD-4-89), 2) an ExJ hybrid from a single female parent (XLD-LL-7-89, which originated in Germany from a single cloned E parent which was mass pollinated with pollen collected from a nearby Japanese larch provenance trial (LANGNER and SCHNECK, 1998) and 3) a controlled cross of a pollen mix from two male parents on a single *L. laricina* female parent. The test consisted of 10 complete blocks with randomly located 3 tree row plots for each family, and the perimeter of the test was surrounded by a border row of extra trees. Spacing between trees was 2.3 m. For further details on parental origin, breeding and test design, as well as site preparation and release see EYSTEINSSON (1992) and BALTUNIS et al. (1998).

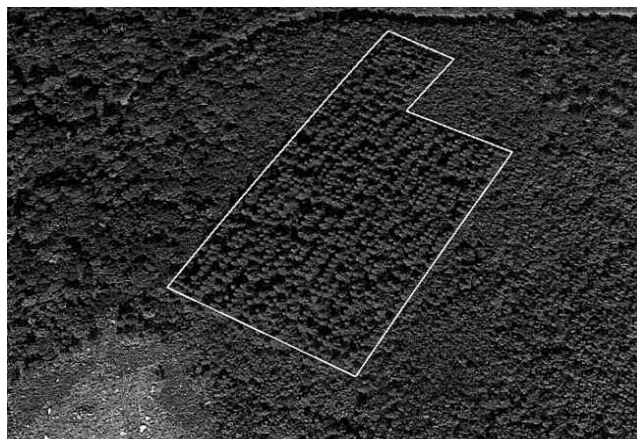


Figure 1. – Aerial photo of the test site taken in 1997. It is located in west-central Maine on an upland site (about 600 m above sea level) on a drumlinoid ridge underlain by a well-drained deep sandy loam soil. Precipitation ranges from 64–107cm and frost-free days from 80-145 days (USDA Natural Resources Conservation Services). There are 10 blocks, each with randomly located 3 tree plots representing each of the 51 families. The whole test is surrounded by a double border row of extra trees.

The test was re-measured after 4, 9 and 22 growing seasons. Tree height in 2013 was measured using a Hagl of vertexIV hypsometer, and diameter was measured at 1.37 m (DBH). Estimates of stem straightness, stem defect, and branch morphology were done within a subset of two blocks due to time constraints, on a scale of 1 to 5, with 1 being best and 5 worst. Stem defect was defined as stem height to where the main stem broke off or formed a double stem. Branch morphology was rough estimate of branch density and diameter, with 5 indicating a relatively high branch density of large diameter branches. No statistical analysis was done on estimates of stem quality.

Statistical analysis

Tree volumes were calculated using equations published for larch in Li et al. (2012). Analyses of variance (ANOVA) were performed at the hybrid group (equation 1) and family (equation 2) levels using PROC MIXED in SAS according to:

$$\text{Eq 1: } Y_{ijk} = \mu + H_i + B_j + (HB)_{ij} + w_{ijk}$$

where Y_{ijk} is the response variables of DBH, HT (height) and VOL (volume) of the k th tree of the i th hybrid group in the j th block ($j=1, 2, \dots, 10$; $i=1, 2, \dots, 7$), μ is the overall mean; H_i is the fixed main effect of hybrid group, B_j is the random

main effect of block, $(HB)_{ij}$ is the their interaction and w_{ijk} is the random error. Main effect of hybrid group was tested using $(HB)_{ij}$ interaction as the error term. Least squares means were generated for significant variables and separation of means were tested using Bonferroni protected tests at the 5% level of significance.

Equation 2 was used to test for differences among families:

$$\text{Eq 2: } Y_{ij} = \mu + F_i + B_j + w_{ij}$$

where Y_{ij} is the response variables of DBH, HT (height) and VOL (volume) of the k th tree of the i th family in the j th block ($j=1,2,\dots,10$; $i=1,2,\dots,51$), μ is the overall mean; F_i is the fixed main effect of family, B_j is the random main effect of block, and w_{ij} is the random error. Family effect was tested using the $(FB)_{ij}$ interaction as the random error term. Least squares means were generated for significant variables and separation of means were tested using Bonferroni protected tests at the 5% level of significance.

Results

Hybrid groups, hybrid vigor

Means for survival, height, DBH and stem volume for all hybrid groups are shown in *Table 1*. Survival across all hybrid groups was 64%, down from 81% 1 year after planting in 1992. The best survival among the 7 hybrid groups

was exhibited by the EJ and JE crosses (76 and 70% respectively, down from 83 and 77%). Survival of TT, the half-sib check lot, was the worst at 48%, down 43%. Most of the crosses with T as a parent suffered greater mortality than the test average. Survival of the XLD-4-89 and XLD-LL-89 check lots was 67 and 61%, down 10 and 16% respectively.

The main effects of 2013 height, DBH and Volume were highly significant among the hybrid groups ($p < 0.0001$), but they did not significantly interact with block. Mean separation shows that the interspecific hybrid groups means for both JE and EJ crosses are consistently better than the intraspecific hybrids for all three parameters, as is shown in *figure 2* and *table 1*. There was no evidence favoring either J or E as female parents despite the larger seed size of Japanese larch ($p < 0.0001$). Therefore all the JE and EJ crosses showed both heterosis and heterobeltiosis. Heterobeltiosis for the hybrid has been previously reported by FERRAND and BASTIEN (1985).

The ET cross, resulting from a mixture of seed from several parents also performed very well. The XLD-4-89 (European) check lot, resulting from open pollinated European larch in Poland, performed somewhat less well than the full-sib EE crosses made from US grown *L. decidua* parents, but the differences were not statistically significant (*Table 1*). The performance of the XLD-LL-7-89 hybrid was significantly lower than that of either JE or EJ crosses.

Table 1. – Least Square Means (LSMean) for percent survival, total height, DBH, and individual tree stem volume by hybrid group at age 22. Commercial check means (XLD-4-89 & XLD-LL-7-89) are listed for comparison. Values within a column followed by the same letter are not significantly different at $\alpha=0.05$ using Bonferroni's protected LSD. Numbers in parentheses in the stem volume column represent age 22 rank versus age 5 rank.

Hybrid Group	Survival (%)		Height (m)		DBH (cm)		Stem Volume (dm ³)	
	LS Mean	SE	LS Mean	SE	LS Mean	SE	LS Mean	SE
ET	72 ab	8.7	20.2 a	0.6	25.1 ab	0.9	435.8 (1-1) a	27.9
JE	70 ab	4.1	19.2 a	0.3	25.4 a	0.4	429.8 (2-4) a	13.1
EJ	76 a	4.2	19.2 a	0.3	25.1 a	0.4	428.7 (3-5) a	13.2
TE	60 ab	4.5	18.3 ab	0.4	22.2 bc	0.5	322.2 (4-3) b	15.3
EE	76 a	4.3	17.7 b	0.3	20.7 c	0.5	273.5 (5-7) c	13.7
TJ	51 b	6.7	16.4 bc	0.5	19.9 cd	0.8	263.6 (6-2) cd	25.2
XLD-4-89	67 ab	8.6	17 bc	0.6	20.4 cd	1.0	248.3 (7-9) cd	28.4
XLD-LL-7-89	61 ab	9.1	16.4 bc	0.7	18.6 cd	1.1	231.3 (8-10) cd	31.2
JJ	58 b	4.5	15.8 c	0.4	17.7 d	0.5	182.9 (9-8) d	15.4
TT	48 b	4.0	13.1 d	0.4	14.2 e	0.5	106.2 (10-6) e	14.5

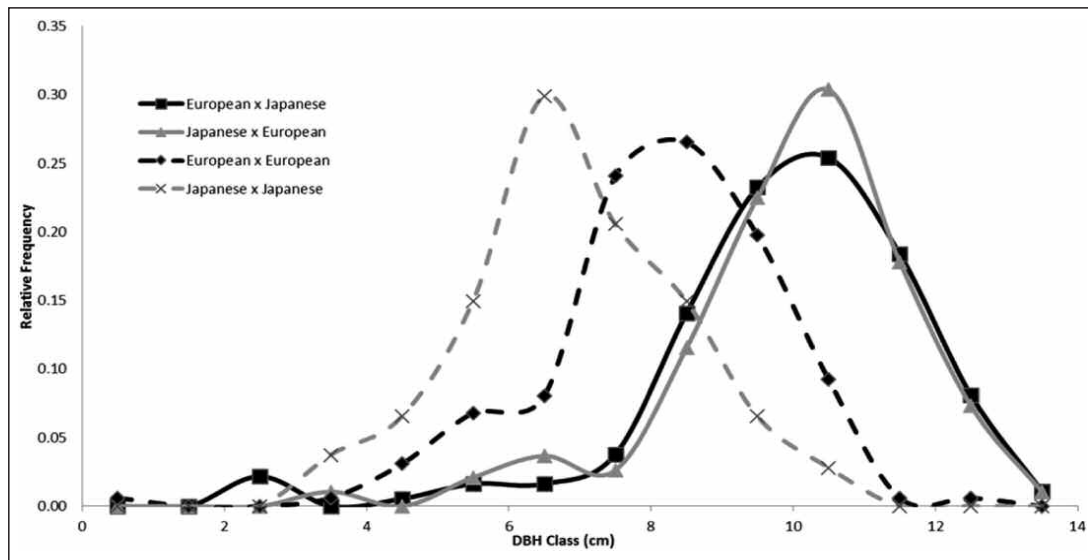


Figure 2. – Relative frequency of trees in one inch DBH classes for E × J, J × E, E × E and J × J families. The data are normalized for visual effect, so that the area under the curves for each hybrid group is similar in order to compensate for differences in sample size between groups.

Crosses involving J and E parents not only exhibited hybrid vigor in terms of growth but also the least defect (in terms of broken or forked tops) of any of the families in the test. Overall the test mean was about 17%, while EJ and JE means were about 5%. Defect for EE and JJ crosses was 15 and 17% respectively. TT crosses showed the most defect at 54%, while ET and TE crosses showed 13 and 11% respectively. The check lots XLD-489 and XLD-LL-7-89 showed 27 and 6% defect respectively. Estimates of branch morphology and stem straightness were crude and did not show consistent patterns of variation among hybrid groups; crosses with T as a parent tended to score above the test average, especially TT.

Hybrid group and family rank changes

Hybrid group rank changes in height from 1994 to 2013 are shown in *table 1*. While the ET hybrid group rankings did not change much, the JE and EJ groups advanced from 4th to 2nd and 5th to 3rd respectively. The JJ, TJ and TT group ranks declined by four, four and two places respectively. The EE group advanced 2 places and in general all groups with E as a parent increased in rank, which included the check lots XLD-489 and XLD-LL-7-89.

Full-sib family rank changes for the 17 families involving J and E parents are shown in *Table 2*. The average ranks of these families

decreased from 18 to 7 from age 4 to 22. Some individual families, like JE33, showed dramatic increases in rank. Although there were considerable changes in rank over time, most of the families increased in rank over time; e.g. 15 of the 17 families increased in rank from 1999 to 2013. With the exception of one ET family, 11 of the best families in the test involved J and E parents. All the crosses between J and E parents ranked better than any of the intraspecific crosses among either parent, and as a hybrid group decreased in rank more than any of the other groups.

Clonal bias

Clonal bias favoring the best crosses could include: 1) dominant clonal gender, and 2) dominant clones. Four of the 11 parental clones contributed to the majority of the crosses made; Clones J2, J6, E1 and E3 were parents in all but 1 of the 17 families. Considering only the 17 families shown in *table 2*, female parental gender of the top 10 families are evenly divided between Japanese and European larch. Thus there does not seem to be a dominant parental gender. J2 and J6 were parents in 13 of the families, 5 of which were included in the top 8 crosses, while 7 were in the bottom 8. E1 and E3 were parents in 10 families, 7 in the top 8 and 4 in the bottom 8. Clone E3 was represented in the top 3 families. Although only a

few clones were involved in most of the crosses, the European clones may be favored in the best families. The intraspecific crosses among E parents exhibited significantly better height growth than those among J parents (*Table 1*).

Discussion

Most reports of hybrid vigor by crosses between J and E parents resulted from a small number of crosses involving only one or a few parental sources (PÂQUES 1989, 2004). In addition, tests which compare hybrid performance with that of intraspecific crosses among their parents are rare. Hybrid larch has been identified as the most productive variety in Quebec's commercial forests, and a hybrid breeding strategy is underway (PERRON, 2008). PERRON has proposed a second generation breeding strategy where progeny from intra- and interspecific diallels of selected Japanese and European parents will be evaluated simultaneously.

Our study represents a small scale test of this approach, presenting data from a 22 year-old test containing 7 intraspecific crosses for each set of J and E parents and 17 interspecific hybrids between J and E. We have demonstrated substantial heterosis and heterobeltiosis for hybrids between J and E parents, since all the interspecific hybrid means exceed the means for the best intraspecific parental crosses. There were no apparent differences between reciprocal crosses with either J or E as

female parent (*Table 2*). An exception is the control operational E×J hybrid XLD-LL-7-89 of German origin, whose mean was less than that of the E×E crosses (*Table 1*). The superior performance of the hybrids we made is probably because their parents represented locally adapted selections that were chosen on the basis of relatively good height growth. Nonetheless, the control hybrid greatly improved in rank from 50 at year 4 (next to last) to 33 in year 22. Overall, the rank of hybrid families with J and E as parents increased over time, with 14 of the 17 families improving in rank over time (*Table 2*).

In addition we have shown that hybrids between T×E and T×J exhibited hybrid vigor, although seed set for these crosses was relatively low (18% and 1% respectively). E×T crosses resulted in very low seed viability (about 3%), but the pooled mean for height of seedlings from several crosses was the best in the test (*Table 1*). PÂQUES (1992) was unable to make T×E crosses because T flowered before E pollen was available. His attempts at a T×J cross resulted in poor seed set, and the height growth of this hybrid was less than that of either parent. Although our estimates of stem quality were crude and done on only 2 blocks, T parentage was associated with relatively high levels of stem defect, and to a lesser extent with stem straightness and branch morphology. PÂQUES (2004) demonstrated significant parental effects on stem morphology in J×E hybrids.

Table 2. – Height rank changes for the 17 full-sib families with J and E parents from 1996 to 2013.

Family	# of trees	Rank , 22y	Rank, 7y	Rank, 4y
EJ31	19	2	25	16
JE33	13	3	14	38
JE63	22	4	9	27
JE21	27	5	12	34
EJ42	29	6	2	1
EJ46	22	7	11	31
EJ11	30	8	1	6
EJ36	26	9	17	25
JE65	16	10	6	14
JE11	29	11	4	15
JE64	23	12	5	17
EJ16	21	14	26	43
JE62	21	15	3	26
EJ26	24	16	23	29
JE25	26	17	21	13
JE23	18	19	15	24
EJ12	23	24	28	36

Production of hybrids between J and E parents for plantation establishment should be considered for several reasons: 1) they exhibit considerable hybrid vigor with growth rates comparable to Southern pine, 2) have very good survival in the field, 3) have good stem form, 4) the crosses can be made with good seed set comparable to that of intraspecific crosses of either parent, and 5) Hybrid larch cuttings root well (PÁQUES, 1992; PEER and GREENWOOD, 2001). PÁQUES (1992) reports that 80 and 62% of cuttings rooted from 2 year-old seedling donor ortets of E×J and J×E crosses respectively. PEER and GREENWOOD (2001) found that cuttings from 1-2 year-old ortets rooted 85–100% of the time. In addition, hybrid larch plantations represent an opportunity to enhance the economic value of timber output and at the same time increase the rate and amount of carbon sequestered in the Maine woods.

The average height at age 22 of all 17 hybrid families with J and E parents was 19.1 m (63 feet). Site index values for loblolly pine plantations at age 25 range from 12.2 m (40 feet) to 24.4 m (80 feet), so hybrid larch plantations exhibit growth that is quite comparable to southern pine on average sites (HARRISON and BORDEERS, 1996). In the South, even though loblolly pine plantations are only 11% of the forested area, they provide 40% of the total timber volume (CARTER and FOSTER, 2006). Therefore incentives for limited establishment of hybrid larch plantations could increase the economic value of Maine's forests in this time of uncertain economic and climatic change. The demand for newsprint and coated paper is steadily declining because digital media are replacing magazines and newspapers. This is reflected in a recent wave of mill closures. However the softwood lumber market has excellent prospects as the nation's housing sector slowly rebounds from the worst downturn since the Great Depression. Maine's prospects in softwood lumber are improved by harvest cutbacks in Eastern Canada and the surplus of beetle-killed wood from British Columbia (L.C. Irland, personal communication 2015).

In the current wood products market, the wood properties of larches are competitive with native species. The mechanical properties of JxE larch hybrids rank higher than either of the parents in France (PÁQUES, 1989). Larch wood in general is more dense and stronger

than white pine, red spruce or balsam fir (KRETSCHMANN, 2010). Japanese, European and Eastern larch all share similar wood properties with Douglas fir, which is considered one of the best domestic sources of dimension lumber because of its high strength, density and rot resistance (Western Wood PRODUCTS ASSOCIATION, 2002). J and E are both moderately rot resistant (CURNEL et al., 2008), and GIERLINGER et al. (2004) report that the J parent confers greater rot resistance to the E×J hybrids than the E parent.

Also larch plantations can potentially alleviate the estimated social cost of carbon, which has increased almost 5 fold since 2008 (PIZER et al., 2014). Hybrid larch with its rapid growth and relatively dense wood can sequester carbon faster than any other northeastern conifer. Measures to alleviate the effects of atmospheric carbon dioxide will become more urgent as the climate continues to warm. Hybrid larch presents the state of Maine with an opportunity to proactively address this issue.

Conclusions

1. Crosses between J and E parents outperform either of their parents (heterobeltiosis), and the locally produced hybrids described in this paper were more than 30% taller than the XLD-LL-89 hybrid check lot (LANGNER and SCHNECK, 1998) that has been extensively planted in Maine and elsewhere with excellent results.
2. Family rankings were unstable, but hybrids between J and E parents improved steadily in rank over time.
3. Hybrid families from J and E parents set seed as well as their parents and hybrid families can be multiplied via vegetative propagation.

This study demonstrates that high potential exists for introduction of these hybrids into commercial forestry practice in the north and central US. Growth performance substantially exceeds that for species now being planted. We are preparing a further comparison and economic analysis of hybrid performance relative to other species. We predict that by the time new plantations of hybrids are harvested, markets for larches as solid wood products, pulpwood, and biomass energy will exist.

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