JUVENILE PERFORMANCE IN THREE BLACK ALDER PROVENANCE PLANTATIONS IN THE NORTHEAST[1]

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ABSTRACT.--One- and two-year heights of 48 black alder provenances were evaluated at three locations. Growth was consistently superior in several provenances from central Europe, and growth was consistently inferior in most provenances from Scotland, Norway, and the eastern Baltic region. Provenance x plantation interactions were strong but followed discernable patterns. Southern European provenances grew relatively faster on the driest site (a Pennsylvania mine spoil) than they did elsewhere; provenances from an inverted U-shaped region in northern and eastern Europe grew relatively faster at the coldest location (in New Brunswick); and provenances from a central European region grew relatively faster at the third location (a Pennsylvania agricultural site). Two measures of form were evaluated after the second growing season in one of the Pennsylvania plantations. Apical dominance varied considerably among provenances and appeared to be the most important characteristic contributing to visual differences in growth habit. Most provenances with relatively strong apical dominance originated north of about latitude 47°. Provenances also differed significantly in branch angle, but only within a range of about 11 degrees.

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INTRODUCTION

Black alder [*Alnus glutinosa* (L.) Gaertn.) is one of the few large trees in a genus noted for an ability to fix atmospheric nitrogen and its usual occurrence in moist habitats. Black alder is most frequently used in the United States for revegetating coal mine spoils. However, the species is also potentially useful as a nurse crop for interplanted pines or hardwoods (Plass 1977), and its wood is suitable for a number of commercial processes (L. H. Phalt cited in Goncalves and Kellison 1980, Phares *et al*. 1975). In Europe, where black alder is native, the species is a commercially important source of wood for pulp, plywood, chipboard, and fiberboard. Considerably more silvicultural and economic information is needed before black alder can be employed to significant extent in U.S. forestry, but its rapid juvenile growth and nitrogen-fixing capability suggest a useful role for the species. Among native trees in the eastern U.S., only black locust also possesses both of these characteristics.

One of the important needs at present is to identify provenances of black alder suitable for different regions of the country and for various silvicultural strategies. In 1976, plans were initiated at Penn State for a range-wide provenance test of the species because many Pennsylvania plantings from local seed sources were experiencing problems with dieback. Our efforts were soon combined with those of Richard B. Hall at Iowa State University, who had a similar interest. Following personal letters of request in fall 1976, European colleagues sent seed to Iowa State from a total of 48 native populations of black alder. Portions of these collections have since been distributed to cooperators in several states for the establishment of experimental plantations. This report summarizes first- and second-year performance in the three plantations of that experiment in the Northeast.

MATERIALS AND METHODS

A map of the provenance origins, with their accession numbers, is shown in Figure 1. A list of the exact locations of these provenances can be found in Maynard and Hall (1981), and some further details on the origin of the study were provided by Robison *et al* (1979). The three plantations evaluated here were propagated from seed sent to The Pennsylvania State University and the University of Maine. Each was planted and propagated as an individual experiment with distinctive objectives. Each plantation follows a slightly different

Figure 1. Natural distribution of Alnus glutinosa and locations of the populations studied (from Boratynski 1980, Robison et al. 1979).

variation of the randomized complete block design, but they can be compared in combined analyses of variance. All 48 provenances are represented in one Pennsylvania plantation ("Bathgate Farm"), 28 of the 48 in a second Pennsylvania plantation ("Pine Glen"), and 47 in a plantation located in New Brunswick, Canada ("Nackawic").

Plantation Establishment and Measurement

Bathgate Farm. The seeds for this plantation were sown in a greenhouse from January 9-11, 1980, in two-quart milk cartons containing a 1:1:1 mixture of peat: vermiculite: "oil dry" (granulated kaolinite clay). Following germination; the seedlings were thinned to one per milk carton, and about three weeks after emergence the seedlings were treated with an inoculum containing the nitrogen-fixing organism (supplied by Dr. Maurice LaLonde, Laval University, Quebec). The arrangement of seedlings consisted of a randomized complete block design, with a "contiguous" plot of four seedlings representing each provenance in each of four blocks. The seedlings were cultured until outplanting under a 16-hour photoperiod with daily waterings and a nitrogen-free fertilizer applied at two-week intervals.

The seedlings were outplanted on June 12, 1980, on former agricultural land located adjacent to the Pennsylvania State University campus (latitude 40°38', longitude 77°52'). The soil is a silty clay loam, grading into a local alluvium of silt loam in one corner of the plantation. It has an average pH of about 7.0. Prior to planting, the site was sprayed with glyphosate herbicide, and plowed and disked to remove and control existing vegetation. The greenhouse experimental design was carried directly into the field, with the seedlings planted at a 2.1 by 2.1 meter spacing in four-tree row plots. The plantation was mechanically cultivated at about three-week intervals during the first two growing seasons.

Survival by provenance and plot mean height to the nearest 0.5 cm were measured near the end of October 1980 and 1981, after the first and second growing seasons were completed. In addition, two measures of form were made during the second growing season in order to quantify what appeared to be rather striking differences among the provenances. Branch angle was measured on July 21, 1981, as the upper angle between a lateral branch and the main stem axis at a point 8 cm up from the point of insertion. The angles of the upper two dominant branches on the previous year's growth were recorded to the nearest 5 degrees and averaged over the four trees in each plot. Apical dominance was measured on October 5-8, 1981, as the ratio of the length of the 1981 height increment to the length of the lowest lateral branch on that year's shoot growth. The ratio was calculated separately for each tree and averaged for the four trees in each plot.

Pine Glen. The material for the Pine Glen plantation was cultured identically to that of the Bathgate Farm plantation except that the seedlings were grown in #8 Styroblocks instead of milk cartons. The arrangement of seedlings in the greenhouse consisted of five randomized blocks, with each provenance represented in a block by four "non-contiguous" plots of two trees each.

The plantation was established May 29-30, 1980, near the top of a large hill located 3.6 km west of Pine Glen, Pennsylvania (latitude 41°06', longitude 78°06'). The site was former coal spoil reclaimed about one month previously with 8-10 cm of stoney "topsoil" with additions of lime and fertilizer. It had been planted with a mixture of oats, fescue, birdsfoot trefoil, and a clover, and had an average pH of about 5.0 following reclamation. Again, the greenhouse design was carried directly into the field, with the seedlings planted at a spacing of 1.5

m within rows containing two-tree plots and 3.0 m between rows. Immediately following planting and on three additional occasions during the first summer, the seedlings were hand-watered because of very dry soil conditions. Competing weeds were removed by hand from around each tree once during both the first and second summers.

Survival of provenances and plot mean height to the nearest centimeter were measured in mid-October following the first and second growing seasons. However, because of heavy deer browsing and other injury, plantation mean height actually decreased from the first to the second year, and the second-year data were ignored in our analyses for this study.

Nackawic. The seeds for the New Brunswick site were sown in a greenhouse during February 1979 in Spencer-Lemaire "Tinus" containers, using Promix BX as the potting medium. Following germination, the potting medium was treated with an inoculum containing the nitrogen-fixing organism (supplied by Dr. R. B. Hall, Iowa State University).

The seedlings were planted in June of the same year on former agricultural land near Nackawic, New Brunswick (latitude 46°00', longitude 67°15'). The site was plowed and harrowed in the autumn prior to planting. Seedlings were planted in a randomized complete block design, with eight seedlings from each provenance arranged as two adjacent four-tree rows within each of four replications. Spacing between trees is 1.5 x 1.5 m. No cultural treatments were applied after planting. Height to the nearest 0.25 cm and survival were measured in October 1980, following the second growing season.

Statistical Analyses

Analyses of variance for provenance differences in each of the metric characteristics were calculated for each plantation on the basis of plot means. Where appropriate, plot means were weighted in the analysis according to the number of surviving trees contributing to each. "Plots" at Pine Glen were considered to be the eight-tree non-contiguous plots rather than the two-tree contiguous plots because of moderately heavy mortality. Thus, block by provenance interaction was not tested in any of the analyses, although the experimental design would have permitted it for the Pine Glen plantation. Provenances 2160, 2810, and 8030 were omitted from the analysis of variance for branch angle because of insufficient data. In addition, the reciprocals of those data

were used in the analysis in order to meet the assumption of homogeneity of error variances.

Combined analyses of variance were performed to compare one-year heights at Bathgate Farm vs. Pine Glen,two-year heights at Bathgate Farm vs. Nackawic, and one-year heights vs. two-year height increments at Bathgate Farm.

RESULTS AND DISCUSSION

Survival

Survival after two growing seasons was 93 percent at Bathgate Farm, 76 percent at Nackawic, and 48 percent at Pine Glen (Table 1). The heavy mortality at Pine Glen was probably caused by a combination of browsing, drought stress, and weed competition. In general, the provenances with the heaviest mortality at a plantation were also among the slowest growing. Exceptions to this were an Iranian provenance (8030) and an Italian provenance (9810), which exhibited fast growth but rather poor survival in the Pennsylvania plantations.

Height Growth

Provenance and plantation mean heights are presented in Table 1. In general, growth was best at Bathgate Farm, where the tallest provenances grew in excess of 1.8 m during their first two growing seasons. Growth was poorest on the mine spoil at Pine Glen, where no provenance grew more than 0.3 m the first year and virtually all provenances suffered a net loss in height during the following year. At all locations, provenance differences in height were statistically significant. Height data for both the first and the second growing season and for all 48 provenances are available only for Bathgate Farm, so it is most convenient to describe the results at that plantation and then compare the others to it.

At the end of the first growing season at Bathgate Farm, provenances differed so strongly in growth that the tallest was more than ten times as tall as the shortest. This ratio decreased to approximately 5:1 after the second growing season because of accelerated growth in several of the short northern provenances. Although the provenance X year interaction for mean annual height increment was statistically significant, very few provenances changed drastically in relative growth from one year to the next (Table 1). The interaction was due largely to the Iranian provenances (8010, 8030), which sustained considerable injury over the first winter.

TABLE 1. - Provenance means tor relative height, survival, and form characteristics at the three plantations.

Accession number	Location of origin	Height as percentage of plantation mean: Pine Glen age one	Bathgate Farm age one	Bathgate Farm age two	Hackawic age two	% survival after second season: Pine Glen	Bathgate Farm	Hackawic	Branch angle (degrees)[a]	Apical dominance[b]
1180	Ireland	—	116	111	111	—	94	75	50.5	1.41
1270	Ireland	—	110	121	103	—	100	75	52.2	1.54
1310	Scotland	62	39	65	82	32	94	59	54.2	1.72
1510	Scotland	—	78	92	100	—	87	69	52.9	1.54
1720	Wales	—	85	95	103	—	87	56	53.5	1.52
2110	Norway	—	66	68	87	—	81	75	54.1	1.82
2130	Norway	43	28	52	74	50	87	78	47.5	1.52
2160	Norway	—	14	27	62	—	50	78	—	1.20
2210	Denmark	111	148	138	125	67	100	78	51.6	1.69
2220	Denmark	81	113	104	105	52	100	66	51.4	1.27
2610	Finland	48	32	49	72	12	100	75	48.9	1.52
2810	Estonia	94	50	59	96	35	69	53	52.0	1.79
2910	Latvia	—	75	75	101	—	94	72	51.0	1.33
4310	West Germany	100	125	121	112	52	100	72	55.2	1.56
4510	West Germany	115	136	118	95	47	100	47	51.7	1.41
4720	West Germany	—	113	127	81	—	100	31	51.1	1.61
4810	West Germany	95	129	142	109	40	94	53	55.5	1.69
5110	Poland	90	131	108	112	40	94	84	55.0	1.52
5410	Poland	—	99	97	101	—	94	66	54.0	1.35
5420	Poland	88	88	95	110	55	87	69	53.2	1.39
5610	Poland	—	116	104	115	—	100	97	50.8	1.26
5620	Poland	—	96	108	104	—	94	91	50.8	1.35
5710	Czechoslovakia	—	82	82	102	—	94	97	49.4	1.47
5820	Czechoslovakia	—	105	104	106	—	100	84	51.7	1.32
5910	Hungary	—	124	125	127	—	100	84	54.4	1.67
5920	Hungary	127	121	132	117	52	100	94	55.3	1.75
6140	Netherlands	93	108	115	112	47	94	75	54.3	1.54
6330	Switzerland	100	97	98	114	57	100	87	52.5	1.37
6380	Switzerland	86	108	107	107	37	87	87	54.6	1.47
6530	France	93	108	123	114	52	100	69	54.7	1.43
6820	France	126	108	106	113	45	100	94	52.0	1.54
7040	Bulgaria	103	110	102	97	42	94	66	54.8	1.39
7220	Yugoslavia	106	106	110	105	57	94	72	52.7	1.43
7240	Yugoslavia	—	99	116	98	—	100	77	52.7	1.52
7920	Bulgaria	—	109	103	117	—	87	77	50.7	1.52
7950	Bulgaria	108	105	104	103	65	100	78	51.1	1.37
8010	Iran	—	126	83	80	—	100	69	44.1	1.35
8030	Iran	121	135	75	56	25	75	81	49.6	1.27
8410	Russia	—	104	111	82	—	87	84	45.8	1.35
8430	Ukraine	112	110	113	105	55	94	81	49.3	1.28
9010	Greece	—	103	89	—	—	100	—	49.4	1.27
9110	Spain	102	87	82	67	70	87	78	52.0	1.30
9120	Spain	101	98	82	63	42	94	78	52.9	1.25
9620	Italy	—	108	121	120	—	87	97	54.3	1.52
9730	Italy	117	96	105	105	52	100	69	49.7	1.22
9750	Italy	109	120	119	110	67	94	84	48.2	1.43
9810	Italy	139	129	118	88	37	81	72	51.5	1.37
9850	Italy	130	115	98	121	57	100	97	48.5	1.15
Plantation mean:		21.6cm	58.9cm	134.2cm	97.7cm	48	93	76	51.8	1.22
Standard Error:		1.93	3.89	8.02	2.70	—	—	—	3.86	.150

Measured during the second growing season at Bathgate Farm

'Ratio of 1981 terminal growth increment to the length of the lowest lateral branch on 1981 growth (black alder has sylleptic growth).

Without these two provenances, the interaction variance component is negligible.

With the exception of a tall Danish provenance (2210), the fastest growing trees at the end of the second year at Bathgate Farm originated from a small region extending from western Hungary through southern West Germany to northeastern France (Table 1, Figure 1). Other provenances in West Germany and The Netherlands to the north of this region, and in northern Yugoslavia and northern Italy to the south, were also relatively fast growing. Within this broader region of central Europe, only the Czechoslovakian provenance 5710 and the two

Swiss provenances (6330, 6380) had intermediate or slow growth rates. Nearly all the provenances surrounding this region had intermediate or slow growth. Exceptions to this, which could signify small areas of fast-growing populations outside of central Europe, were both of the Irish provenances (1180, 1270), and both provenances from the southern U.S.S.R. (8410, 8430).

The tallest provenance at Pine Glen after one year was 9810 from southern Italy. This provenance was over three times as tall as the shortest and 39 percent taller than the plantation mean. In contrast to Bathgate Farm, most provenances with above-average height at Pine Glen were from southern Europe (south of latitude 45°) (Table 1). The only exceptions to this were three provenances from West Germany (4510), Denmark (2210), and Hungary (5920), all of which grew considerably faster than others from northern Europe. The shortest provenances in the plantation were the most northerly in origin (2130, 2610); this was true at Bathgate Farm, also.

Considering one-year heights of the two Pennsylvania plantations together, some provenances were consistently below average (especially 1310 2130, and 2610) while others wore consistently above average (especially 4510, 8030, and 9810). However, the combined analysis of variance of the 28 provenances common to both sites revealed a significant provenance by site interaction. All provenances in north-central Europe, in the region bounded by Denmark, Poland, northern Switzerland, eastern France, and The Netherlands, grew relatively better at Bathgate Farm than at Pine Glen. All provenances in Europe south of that region, with the exceptions of 7040 and 9750, grew moderately to considerably better at Pine Glen. The provenances involved in this regional comparison accounted for 83 percent of the total contributions to the interaction sum-of-squares in the entire plantation. The Estonian provenance 2810, which performed below-average at both plantations but relatively better at Pine Glen, accounted for practically all of the remainder.

It is interesting to speculate on the origin of this difference in geographic performance between planting sites. Bathgate Farm and Pine Glen differ most strongly in their edaphic characteristics. The locations are within 40 km of one another and experience reasonably comparable regimes of temperature and precipitation; but the soil at Pine Glen has a relatively lower pH, is considerably less fertile, and is more droughty because of the drainage pattern of the site and the coarse texture of the soil. Moisture was especially critical at

Pine Glen during the first growing season, and the trees would probably not have survived had they not been hand-watered on four occasions.

We unfortunately know little about the soils on which these black alder provenances evolved, but precipitation data from nearby weather stations (Wernstedt 1972) suggest that there may be habitat differences in available moisture during the growing season. Considering all provenances in the geographic comparison described above, those that performed relatively better at Pine Glen originated in habitats with less precipitation in July and August ($\bar{x}$ = 36 mm) than those that performed relatively better at Bathgate Farm ($\bar{x}$ = 84 mm). June and especially May precipitation data are more similar for the two regions, but the difference in July and August precipitation is consistent for every provenance. Therefore, it is possible that these southern European provenances have evolved a greater tolerance to summer drought and that this accounts for their relatively better performance at Pine Glen.

Two-year heights at Nackawic ranged up to 1.2 m, with the fastest growing provenance 27 percent taller than the plantation mean and over two times taller than the shortest. In contrast to the results of the two Pennsylvania plantations, there was no distinct geographic pattern to the variation in height at Nackawic. The fastest growing provenances were inconsistently scattered throughout Ireland, The Netherlands, Denmark, France, Switzerland, Italy, Bulgaria, Poland, and Hungary (Table 1). The shortest provenances were generally more concentrated in the north in Scandinavia, and in southern Europe in Spain, southern Italy, and Iran.

The combined analysis of variance of two-year heights from the Nackawic and Bathgate Farm plantations showed significant provenance main effects. Trees from Hungary (5910, 5920), Denmark (2210), France (6530), and Italy (9620, 9050) had above-average heights at both sites. Those from Spain, Iran, and Scandinavia were consistently below average.

However, the provenance by site interaction term in this analysis was also significant. As in the Bathgate Farm/Pine Glen contrast, there was a remarkably distinct geographic pattern to the differences in provenance performance at Bathgate Farm versus Nackawic. Practically all of the provenances from the inverted U-shaped region defined by Wales, Scotland, Scandinavia, and eastern Europe south to latitude 47°00' (provenance 5920, Figure

1) performed relatively better in the more northern plantation. In contrast, most of the provenances in central Europe from Denmark southward, and across southern Europe and Asia south of latitude 47°00', performed relatively better at Bathgate Farm. The only provenances that deviated appreciably from this pattern were 6330 (Switzerland), 6820 (France), 7920 (Bulgaria), and 9850 (Italy), all of which grew relatively better at Nackawic. Even with these discrepancies, the provenances that followed the pattern accounted for 87 percent of the total contributions to the interaction sum-of-squares. Many of the provenances that performed relatively better at Nackawic were among the most cold hardy in measurements taken by DeWald (1982) at Bathgate Farm, and perhaps this cold hardiness gave them a growth advantage at the more northerly site.

Generally, provenance differences at both Bathgate Farm and Nackawic are similar to the results of other studies in the United States. Results from Bathgate Farm support Funk's (1979) conclusion that the best north-central European provenances are to be found in southern West Germany. Although several provenances grew well at Bathgate Farm, the tallest after two years was 4810 from southern West Germany. Results from Nackawic are similar to those of Funk in that the most northern provenances had below-average heights in both tests. However, the Nackawic results differ in the relatively poor performance of the West German trees at this site.

Maynard and Hall (1981) reported the first-year results of a study of 48 black alder provenances growing in two Midwestern plantations. Since these were the identical provenances as are planted at Bathgate Farm, a direct comparison with our first-year data for that plantation is possible. The correlations between provenance means at Bathgate Farm and at Maynard and Hall's two locations are positive and statistically significant ($r = 0.83$ and 0.47 for Iowa and Wisconsin plantations, respectively). Several northern European provenances (especially 1310, 2130, 2160, 2610, and 2910) were below average in height at all locations, and other provenances (notably all those from West Germany and several of those from Italy) were consistently above average. However, there were major interactions across the three plantations. Several provenances grew well or very well at two plantations and poorly at the third: 9810 (Italy) and 6820 (France) grew considerably below-average only in Wisconsin, and 5710 (Czechoslovakia) and 1720 (Wales) only in Pennsylvania. There is no apparent geographic pattern to these interactions, and it is possible that

some of them will disappear or change as the plantations become older.

Form

Provenance variation in branch angle was slight, between 44.1 degrees and 55.5 degrees (Table 1), and only the extremes of provenance means are significantly different from one another. Branch angle was not significantly correlated with either latitude or longitude, and the only evident pattern to the variation was that most of the trees with smaller branch angles were native to the southeastern portion of the species' range (Iran, Russia, Greece, and Italy). Those with larger angles were generally native to the central portion of the range. Provenances in other regions were either intermediate or variable.

Apical dominance varied considerably more among provenances than did branch angle, and it appeared to be the most important characteristic contributing to visual differences among trees in growth habit. Provenance means for the apical dominance ratio varied from 1.15 to 1.82 (Table 1), the former indicating a tree whose seasonal apical growth was only marginally faster than seasonal branch growth. This ratio was correlated weakly but significantly with latitude of origin. All provenances with relatively strong apical dominance (arbitrarily, ratios of 1.67 or greater) originated north of approximately latitude 47 . Most southern provenances, as well as some of the northern provenances, had relatively weak apical dominance. Since apical dominance was measured by comparing shoots that had arisen from the same bud through sylleptic growth, it is doubtful that the results were affected in any way by cold injury.

CONCLUSIONS

These results from the first and second year of plantation growth indicate large differences among black alder provenances and considerable opportunity for selection. The majority of provenances with above-average height growth were native to central Europe and northern Italy. However, provenance rankings varied considerably among plantation locations. Of the 28 provenances common to all three plantations, only one (5920, Hungary) was consistently taller than the plantation mean by one standard deviation. Two additional provenances (5910, Hungary, and 2210, Denmark) excelled by one standard deviation at Bathgate Farm and Nackawic, where 47 provenances were represented in common.

There were definite geographic patterns to provenance by plantation interactions, and these patterns appear to make sense in light of presumed selection pressures. In general, southern European provenances performed relatively better on the driest site, and northern and northeastern European provenances performed relatively better at the coldest location. If these interactions do indeed reflect differences in climatic adaptation, they will probably persist as the plantations get older and could provide the basis for regional guidelines to provenance selection in this species.

Branch angle and apical dominance affect the quality and quantity of wood produced in the trunk, and the manner in which a group of trees occupies the site by intercepting light. Thus, they are potentially important selection criteria in genetic improvement. In our study, the range of provenance means in branch angle was narrow, and provenance variation was small relative to within-provenance ("error") variation. Based on age-two results, this characteristic will probably not be an important factor in provenance selection. In contrast, degree of apical dominance differed considerably among provenances. If the differences persist with age, the crown forms of older trees will almost certainly vary enough to be an important consideration in improving black alder for different cultural systems such as conventional monocultures and mixed-species plantings.

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