SELECTION AND BREEDING STRATEGY FOR AN EXOTIC SPECIES: *ALNUS GLUTINOSA* IN NORTH AMERICA

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Abstract. --Initial improvement can be based on land races and existing provenance tests. If cloning techniques improve, selections can be used directly. Otherwise, seed orchards can be established by tree spading selections, cloning, or progeny test conversion. Hybridization can be done on grafted plants in the greenhouse. Both interprovenance and interspecies hybrids should be evaluated. Large populations of the most promising provenances and progenies should be planted at close spacings to provide selections for long-term breeding programs. Because *Alnus glutinosa* can be evaluated and bred over shorter cycles than most tree species, it can serve as a useful model system.

Additional keywords: Alnus spp., seed orchards, cloning, breeding technique, seed production, hybridization.

INTRODUCTION

The selection and breeding of *Alnus glutinosa* (L.) Gaertn. in North America is aimed at providing a fast-growing, tree-form, nitrogen-fixing species for our silvicultural systems. In eastern North America *Robinia pseudoacacia* is the only native tree species that fits these three important requirements, and insect pests limit its usefulness. *Alnus rubra* of western North America is not climatically suited to most of the eastern part of the continent. Potential uses of A. *glutinosa* include mine-land reclamation (Funk 1973, 1979); mixed culture with other species such as *Populus* spp., *Juglans nigra, Platanus occidentalis, Acer saccharinum,* and *Larix* spp. (Plass 1977, Hansen and Dawson 1982); and pure culture of alder for lumber (Phares et al. 1975), fuel (Hall 1982), and windbreaks.

Another important value in discussing an *Alnus glutinosa* improvement program for North America is that it can serve as a model system for two important questions many other tree breeders are faced with: 1) the

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introduction and use of an exotic species and 2) the potential for clonal plantations in the future. Use of an exotic means that there are special requirements for a beginning germplasm base and a different set of challenges and opportunities for matching genotypes with environments. Alnus glutinosa can be cloned for research purposes, but the commercial feasibility of large-scale clonal plantations is still in doubt. As vegetative propagation techniques improve and economics will allow, we may want to shift emphasis in our improvement programs from seed orchards to the production of a genetically superior, but diverse, set of clones.

Alnus glutinosa provides a particularly good model system because its rapid growth rate and potential uses lead to short rotations and, therefore, short evaluation times for selections and progeny tests. Our results to date suggest that evaluation periods as short as 4 years are feasible (Hall et al. 1983). Alnus glutinosa begins producing seed as early as 3-4 years of age (Funk 1965), thus further reducing the breeding/evaluation cycles. These two features mean that tree improvement stages can be completed more quickly in A. glutinosa than in most other tree species. We have the opportunity to try some approaches, evaluate their success, and put the lessons we learn into practice for other tree improvement programs.

Alnus glutinosa tree improvement work has been undertaken by a number of organizations in the United States and Canada (e.g., Funk 1979, Kellison and White 1979, DeWald et al. 1983, Hall et al. 1983). These programs are similar in many respects, and there has been sharing of plant materials among programs. However, this paper will be primarily focused on our approach at Iowa State University and on a more generalized strategy that we are developing for the International Energy Agency's project in breeding for biomass production. Our program was initiated in 1976 (Robison et al. 1978), and the first major field plots were started in 1979 (Maynard and Hall 1980).

DISCUSSION

Figure 1 is a diagram of how we are approaching the genetic improvement of Alnus glutinosa. The stages will be discussed in the order of the circled numbers on the figure.

<u>Organization by breeding zone</u> ①

It is anticipated that there will be considerable genotype X environment interaction in the performance of black alder across the many different areas where it might be used. Therefore, different programs have been undertaken in the different climatic regions of North America. We have supplied starting materials to more than 20 states and Canadian provinces. The rankings of most central European seed sources change little between tests in Iowa, Illinois, Wisconsin, Pennsylvania, and New Brunswick, but some important differences show up when seed sources outside of central Europe are considered (DeWald et al. 1983, Hall et al. 1983). For example, German and some Polish provenances have performed above average in all locations, whereas the value of Scottish, Danish, and Italian provenances depends on where they are grown (table 1). Efforts are under way to refine our knowledge of the genotype X environment

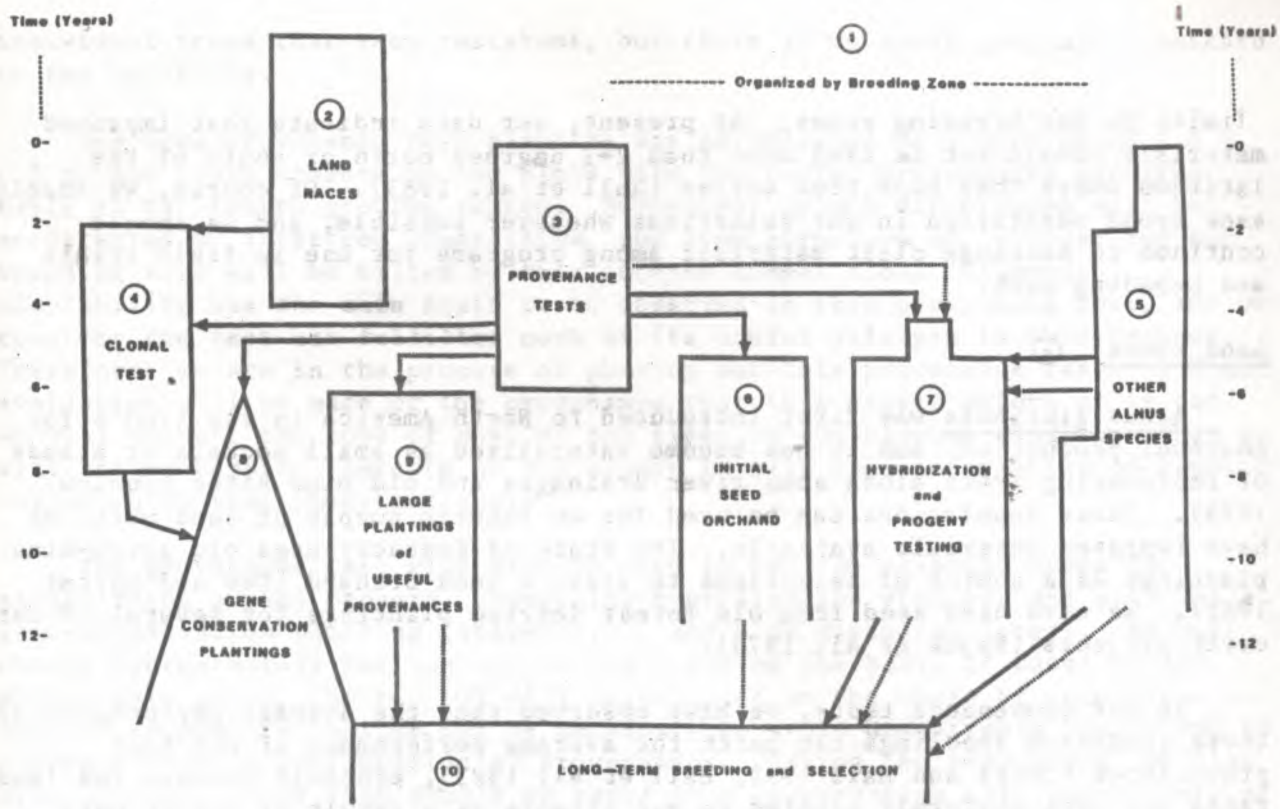

Figure 1.--Flow diagram of the initial stages of our genetic improvement program for Alnus glutinosa. ⟶ represents the flow of plant materials and ⟶ represents the flow of information.

Table 1.-- Relative performance of six Alnus glutinosa provenances grown at five locations

Provenance Number	Geographic Origin	Latitude (North)	Performance in Percent of Plantation Mean Height in: IA	WI	IL	PA	NB
131	Golspie, Scotland	58° 15'	78	96	56	65	82
222	Sakskobing, Denmark	54° 45'	98	103	76	104	105
481	Ingolstadt, W. Germany	49° 0'	126	118	122	142	109
511	Naklo, Poland	53° 8'	124	129	113	108	112
962	Pordenone, Italy	46° 2'	123	76	131	121	120
975	Villa Basilica, Italy	43° 48'	96	69	80	119	110

IA = Rhodes, Iowa WI = Harshaw, Wisconsin IL = Humm Wye, Illinois PA = State College, Pennsylvania NB = Nackawic, New Brunswick. (DeWald et al. 1983, Hall et al. 1983) limits to our breeding zones. At present, our data indicate that improved materials should not be used more than 2-3 degrees north or south of the latitude where they have been tested (Hall et al. 1983). Of course, we should seek broad adaptation in our selections whenever possible, and we should continue to exchange plant materials among programs for use in field trials and breeding work.

Land races (2)

Alnus glutinosa was first introduced to North America in the 1700's for charcoal production, and it has become naturalized as small pockets or stands of reproducing trees along some river drainages and old mine sites (Furlow 1979). These populations can be used for an interim supply of seed until we have improved materials available. The state of Kentucky used old strip-mine plantings as a source of selections to start a seed orchard (Oak and Dorset 1981). We have used seed from old Forest Service plantings for several of our early projects (Bajuk et al. 1978).

In our provenance tests, we have observed that the average performance of these land-race seedlings can match the average performance of our best provenances (Genys and Hall 1983, Hall et al. 1983), probably because the land races are more uniformly adapted to our climate as a result of one or more cycles of natural selection. However, we suspect the land races represent a rather small sample of the germplasm diversity available in A. glutinosa's natural range. Also, their geographic origins are almost completely unknown, and they do not match some of the outstanding individual trees that are present in our introductions. Therefore, we should go back to original sources for most of the germplasm that we will need in building a long-range improvement program.

Provenance tests (3)

Many tree improvement programs start with provenance tests, but this need is particularly critical for exotics. Through the very helpful cooperation of many European scientists and foresters, we began assembling a collection of more than 650 seed lots that represented most of the range of the species. For our field tests, this was pared to 48 provenances from across,Europe and into Asia minor (see fig. 1 in DeWald et al. 1983). We planted one of these trials in central Iowa and one in northern Wisconsin in 1979 (Maynard and Hall 1980). Companion studies using the same 48 sources were planted in southern Illinois (Forest Service), central Pennsylvania (The Pennsylvania State University), and western New Brunswick (University of Maine) (DeWald et al. 1983, Hall et al. 1983).

Our observations indicate that trees of Scandanavian origin cease growth in mid-season (probably due to photoperiod response) and are usually stunted. Trees from near the Mediterranean, Black, and Caspian Seas have some of the best one-year growth rates, but they suffer winter damage (Maynard and Hall 1980, Hall et al. 1983). The provenance tests also are providing our first opportunity to screen for resistance to a canker dieback that has been attributed to Phomopsis (Oak and Dorset 1981). There are a number of individual trees that seem resistant, but there is no clear geographic pattern to the variation.

Our Iowa provenance test planting was established on a spacing of 1.5 x 1.5 m, and crown closure on the plots with the better provenances occurred early in the fourth growing season. Subsequent growth differences will be accentuated by intertree competition, and some germplasm of interest for our breeding work will be killed by this intense competition. Climatic adaptability was the main trait to be observed in this provenance test, and we consider the test has fulfilled much of its useful lifespan in this respect. Therefore, we are in the process of phasing out this provenance test. A final evaluation will be made of the provenance test this winter before it is cut. We will harvest the tops of most of the trees to run biomass studies. Then we will follow coppice regrowth on the stumps to gain some information on genetic variation in that important trait.

The provenance test will also be used to provide selected trees for establishing a seed orchard, conducting hybridization studies, and starting a gene-conservation planting (stages 6, 7, and 8 as discussed later). We will choose approximately the top 10% of the trees on the basis of total height. Within this group, the top 10% will be selected on the basis of stem diameter. Some adjustment in choices may be necessary to avoid undesirable traits and to insure a broad representation of provenances. During the evaluation, we also will note any trees that should be saved in a conservation planting because of special traits that they carry.

Clonal Tests

Most uses of Alnus glutinosa are of a short-rotation, intensive culture nature where clonal planting stock would be desirable if it could be economically produced (Hall and Maynard 1979). Alnus glutinosa is now cloned primarily by rooting of softwood cuttings from greenhouse stock plants (Robison and Hall 1981). In contrast to some Populus species and other easy-to-root trees, the Alnus cuttings root slowly and take. several months to establish a growth pattern similar to a seedling. Unless substantial improvements are found in this technique, it could not support large-scale commercial propagation of alder. Recently, a group at the University of Minnesota has been successful in producing Alnus glutinosa clones by in vitro shoot-tip culture (Garton et al. 1981), and we have begun using the system. They calculated that at least 10 million plantlets could be produced in 1 year by their method. If these plantlets can be economically produced in a condition ready for field planting, then the barrier to commercial plantations of clones will be removed.

If phenotypic selection is not highly reliable, clonal evaluations might offer a more precise method of verifying a selection's genetic qualities. We have begun testing the value of this method by cloning phenotypically selected trees from two older plantings in Ohio and Illinois along with some of our own selections (Hall et al. 1983). At 2 years of age, broad sense heritability was 0.32 for height and 0.59 for basal diameter. Basal diameter also showed a better rank correlation with ortet performance. More testing of the clonal evaluation method will be pursued with selections made in the provenance test.

If the clonal evaluations improve selection efficiency, then all subsequent phenotypic selections should pass through this stage of testing. This stage would also serve to measure the relative ease of cloning the different genotypes, a critical selection criterion if vegetative propogation will be the mode of putting improved trees into commercial planting operations.

Other Alnus species for breeding use

Alnus glutinosa does not have all of the traits that we desire, most notably drought tolerance. A variety of tree forms, habitat preferences, regeneration characteristics, and other useful traits is present in the genus Alnus. So there are opportunities to use other species directly or in hybridization programs should the need arise (Hall and Maynard 1979). European research has shown the potential for hybrid vigor by breeding A. glutinosa with some of its close relatives. At this time A. incana, A. cordata, A. rubra, and A. accuminata are of the most interest. In the only test in which we have a direct comparison, the best A. incana trees outgrew the best A. glutinosa trees in height (Hall et al. 1983). Verweij (1977) made similar observations in The Netherlands.

Although it would be nice to have a full scheme of provenance, individual tree, and clonal selection to support the use of these species, this probably would not be feasible. We are gradually acquiring seed from locations that should be reasonably well adapted to our conditions and establishing field plots to support our future breeding efforts. We also plan to exchange pollen with other researchers to obtain a wider spectrum of parents for our hybridization work.

Initial seed orchard

Some trees in our Iowa provenance test produced seed in their third growing season. At the end of the fourth growing season, we collected more than 560 g of seed from 83 trees that were flowering. At an 80% germination rate and 700 seeds/g this would be enough to produce more than 300,000 seedlings. However, the average germination rate on this seed collection was only 7.5%. We have observed wide year—to—year fluctuations in seed quality in older stands, evidently due to weather conditions. Alder flowers. early (March in Iowa) when frost and wind damage are common. Fertilization is delayed 2 to 3 months (McVean 1955) and may be adversely affected by early summer droughts. Seed coat development takes place regardless of what has happened to pollen development. Therefore, we do not yet know whether our poor seed quality last year was due to insufficient cross—pollination in the young stand or poor weather conditions. An even larger crop of seed seems, to be developing this year, the fifth growing season, so we will continue studying the problems involved.

Although there are arguments against converting provenance tests to seedling seed orchards (Robison and Hall 1981), we believe that this may be feasible with this species. Alnus glutinosa has a self—incompatability system (Hagman 1975) that should limit serious inbreeding. Our experience so far is that only the best—growing trees are flowering (Hall et al. 1983). By the time poorer phenotypes would reach a flowering size, we probably could afford to eliminate them from the planting. With closely spaced trials like ours, most of the poorer trees would be overtopped, and their flowering reduced or eliminated anyway, if the stand were left to develop as a seed orchard.

As part of our plan to phase out our provenance test, we want to evaluate another procedure for seed orchard establishment that we first proposed 2 years ago (Robison and Hall 1981). The best trees selected in the provenance test (see step 3) will be moved by tree spade to a nearby location where they can be replanted on a 3 x 3 m spacing as a designed seed orchard. If warranted by seed demand, additional seed orchard trees will be produced by cloning the selected trees. One advantage of working with seed production in Alnus glutinosa is the rapid rate at which coppiced or cloned trees regain a flowering condition. We have observed good seed crops on trees after 2 or 3 years of coppice regrowth. In our clonal test, several selections began flowering in their second year (Hall et al. 1983). Hence, new seed orchard acreage can be brought into production relatively quickly, and seed orchard trees can be periodically pruned to make seed harvests easier and prevent crowding.

Hybrids and progeny testing (7)

Hybrids can be a source of increased vigor and adaptations to new environments. It is important to evaluate both possibilities in Alnus glutinosa. Hybridization between provenances has been tried in other species with beneficial results. As an exotic species, no provenance of Alnus glutinosa in North America is growing in the environment that it was selected for by natural processes. We, in effect, are planting it on "hybrid sites" and we may well improve our production by assembling the right combinations of germplasm to fit these new sites. Using trees for short-rotation biomass production also requires genotypes that are not selected for directly by natural crossing and selection.

Therefore, the opportunities for hybrid vigor and new adaptations are being explored by making crosses between selected provenances and with other alder species. One consideration in making interspecies crosses is that A. glutinosa seems to serve much better as the male parent (Hall and Maynard 1979). Pollen is easily forced by placing cut branches in the greenhouse in late winter or early spring. Pollinations can be efficiently done by using the mini-bag system (Gerhold 1968). Because of the potential for weather conditions that interfere with seed set, we have begun doing our crossing work on flowering scions grafted to greenhouse stock plants. This system has been used successfully for alder by Steenackers in Belgium. The grafted scions often continue to flower in subsequent years.

This spring, we made 182 grafts from selected trees in our provenance test. After 5 months, 61% of the grafts are still living, and most of them are developing normal-appearing strobili. These results are much better than we had previously anticipated (Robison and Hall 1981). Each inflorescence typically has 4 to 8 strobili. On the average, each strobilus can produce 60 seeds (McVean 1955). Hence, a few pollination bags can yield sufficient seed of a particular cross for progeny testing. These characteristics warrant the use of controlled pollinations for most progeny testing.

We believe that it will be important to use different types of progeny test designs, depending on the objective. To most efficiently analyze differences among hybrid families, the single—tree plot approach (Libby and Cockerham 1980) should be used. In some cases small, multitree block or row plots will be more appropriate. For example, poplar breeders in Europe plant out single—family or clone rows of 5 to 10 trees each to simplify their disease—inoculation studies. In other situations, we may be less concerned with selecting the best families than we are with selecting the best trees within each family. For example, we may already know which parents have good combining ability, but we want to develop a set of superior clones with diverse pedigrees. In this situation, each hybrid family should be planted out in its own large block. Assuming that juvenile growth rate is one of the selection criteria, these plantations should be made on a close spacing to utilize natural selection. Because our 1.5 x 1.5 m spacing gave crown closure in the middle of the fourth growing season, spacings of 1 to 2 m should be the most appropriate choices for progeny tests considering short—rotation uses.

Gene—conservation plantings

In any genetic selection program, there are always individuals that don't meet the current selection criteria, but may carry useful germplasm for future needs. Working with tree improvement, we are faced with the dilemma that each tree saved can occupy substantial space; yet long time intervals can be involved in starting over to produce flowering trees carrying desired traits. In alder, we hope this dilemma will be less acute because we can move trees to the edges of our test sites and/or keep them coppiced so that they occupy smaller land areas. Eventually space and/or vigor problems may necessitate new storage techniques for this germplasm. Further developments in tissue culture and cryogenics might provide one useful alternative.

Large plantings of useful provenances

A major problem in the improvement of an exotic is that it may not be convenient to go back to the origin of the best sources identified in the provenance test to select the best individuals for the next round of. improvement. Even if this can be done, there is no assurance that superior individual tree performance in the native habitat will carry over to the new environment, particularly the highly modified one that may be used for intensive culture. Yet, a provenance test usually contains too few tested individuals to use them as the sole *basis* for a long—term breeding program. As with most recent provenance test designs, we planted small row plots (8 trees/plot) and only four replications in our field design so that we could study more provenances (Maynard and Hall 1980). With a maximum of 32 trees per provenance to choose from, our selection intensity is very low, and our genetic base very narrow. Therefore, it seems essential when working with an exotic to go to a special stage where large populations of the most promising sources are planted for future selection work. This need not be delayed long after the start of the provenance test because the provenances with the best climatic suitability should be evident after the first few growing seasons.

Large block plantings of at least 1000 trees from each well-adapted provenance should be set out as joint commercial and scientific ventures. As these "provenance plantations" mature, they will provide the opportunity to make selections with reasonably high intensity. As they flower, they should be producing seed of a new, selected, land-race type that can help support nursery operations temporarily.

We have identified some provenances that grow very vigorously but have insuffient cold hardiness and some with particularly desirable branching characteristics. We would like to use some of this germplasm by crossing selected individual trees with our better trees from adapted sources. To obtain sufficient selection intensities, we plan to plant blocks of 100 or more trees per provenance at close spacing (1 x 1 m) where we can let natural thinning take out all but the best-growing trees. The same approach could be used for Phomopsis canker resistance by letting the disease ado, the thinning work.

Long-term breeding and selection (10)

All trees of potential breeding value should be established in a breeding arboretum or gene—conservation planting. This would include the trees chosen for commercial propagation, those carrying special traits of interest, and trees of other Alnus species that have demonstrated value in producing hybrids. Because *Alnus glutinosa* flowers profusely under the right conditions and the mini—bag technique can be used to produce large progeny populations from a few flowering branches, most advanced generation breeding should be based on controlled pollinations. This means that only a few trees are needed to represent each clone and that the layout of the arboretum will not be restricted by cross—pollination conditions.

To test the relative merits of particular crosses, progeny tests with small numbers of trees per family plot would be used. For crosses of known value, mass plantings similar to step 9 would be established with the goal of choosing outstanding individuals from the populations with a high selection intensity.

Until cloning is practical for a species, the more traditional seed orchard methods must be followed. Even when cloning becomes feasible, there are likely to be less intensive and/or long rotation uses that would be served as well or better by seed orchard progeny. Hence, our improvement program for *Alnus glutinosa* considers both the clonal and seed orchard approaches.

The clonal production of commercial planting stock would be supported by stock plants of the best clones identified at any particular stage of the improvement program. The number of superior clones selected will depend on the number of uses and the specificity of clone performance related to growing sites and cultural practices. At least 7 to 25 clones should be available for each type of plantation grown either in mixture or as small single—clone groupings (Libby 1982). The physical nature of the "cutting orchard" will probably be very much different from the familiar cutting orchards used to support the production of hardwood cuttings in *Populus.* It is most likely to take the form of gieenhouse stock plants and/or continuously subcultured tissues. The availability of cloning does not reduce the need for breeding work. Indeed, breeding efforts are even more relevant in clonal forestry because nonadditive genetic variance can be exploited while we continue development of genetically diverse clones. At the same time, cloning can quickly multiply the results of difficult-to-make crosses.

We have previously considered the relative merits of seedling versus clonal seed orchards for Alnus glutinosa, and both approaches have their own advantages (Robison and Hall 1981). When within-family variation is high, cloning of the parents to use in a seed orchard should be better than converting progeny tests to seed orchards. It may also be desirable to locate certain clones adjacent to one another to capitalize on interprovenance or interspecies hybrid vigor. If needed, biclonal orchards could be established in the same fashion to produce a particular type of hybrid. The self-incompatability system of A. glutinosa (Hagman 1975) should effectively insure the production of predominantly hybrid seed.

An additional level of selection could be gained by doing controlled pollinations among the most promising trees available, including those clones with special traits to contribute. The progeny tests of this material could be converted into a seedling seed orchard by thinning to the best families and the best tree on each family plot that was retained. The ability to move trees by tree spade solves the spacing problem that is often cited as a disadvantage of such a conversion.

CONCLUSION

Many opportunities exist for the genetic improvement of Alnus glutinosa as a component of North American silviculture. Further research results from selection and breeding studies, the rate of development of cloning techniques, and general utilization and economic considerations will govern which of these improvement techniques will be most actively pursued. In addition, the work can serve as an important model system for many other tree species.

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