APPROACHES TO EUROPEAN ALDER IMPROVEMENT

Terry L. Robison and Richard B. Hall 1/

Abstract.--European alder (*Alnus glutinosa* L. Gaertn.) is an increasingly important species in the Eastern United States for use in soil reclamation, biomass plantations, and as a nitrogen-fixing nurse crop. Information from provenance and progeny tests is beginning to identify sources of superior genetic quality. The next stage in alder improvement will be developing efficient means of putting the superior selections into widescale use. Alder is somewhat unusual among tree species because all three standard tree improvement techniques: 1) seedling seed orchards, 2) clonal seed orchards, and 3) vegetative propagation are potentially useful approaches. Available data on flowering, seed production, grafting, and rooting are summarized, and additional data needs are identified as a means of assessing the relative value of the three approaches. Seedling seed orchards seem to be the best approach at present. Whichever approach is used, the expected returns are high because of alder's early reproductive potential and the short rotations required to benefit from improved alder yields.

INTRODUCTION

We have previously reviewed the potential importance of European black alder, *Alnus glutinosa* (L.) Gaertn., in soil reclamation, biomass production, and as a nitrogen-fixing component of mixed species tree plantations (Robison et al. 1979). Interest in the species continues to increase. In the last three years we have supplied seed for more than 25 field evaluation trials in all parts of the eastern United States. All available nursery stock was sold out this spring, and more nurseries are beginning production. And the State of Kentucky established a seed orchard for the species in 1978 (Oak and Dorset 1981). As data and selections become available from the field trials and as nursery production increases, many more organizations are likely to face the questions: How can the improved materials be produced on a large scale? What are the alternatives? The difficulties? The benefits? In this paper, we review the key considerations, the available data, and the future research needs in answering these questions for applied tree improvement programs. A more theoretical review of the considerations in the genetic improvement of alder has been published previously (Hall and Maynard 1979).

1/ Research Assistant and Associate Professor, Forestry Department, Iowa State University. (Journal Paper No. J-10381 of the Iowa Agriculture and Home Economics Experiment Station, Ames, Iowa. The work was supported by Station Project 2210 (a contributing project to North Central Regional Project NC-99 Regional Tree Improvement) and Cooperative Aid Agreement 13-721 with the U.S. Forest Service Intensive Fiber Yield Project.)

SOURCE SELECTION

Because European alder is an exotic species to the United States, all our improvement efforts will have to start with selecting a source or base population that is adapted to the local conditions. Introduction of the species to North America began in colonial times (Harlow and Harrar 1969). Furlow (1979) shows a range map for some of these naturalized populations in the United States. In these existing stands, natural selection has had time to develop some land races for us. These stands can serve as an initial source' of selections for tree improvement. However, because the original germplasm sources (geographic and population size) for these stands are unknown, they are not suited as a sole source of germplasm for a long-range improvement program.

Testing of known sources of European alder began in 1962 with Funk's seed source study in Ohio (Funk 1979). On the basis of his 16-year results, European alder sources from southeastern West Germany (Bavaria) perform best in Ohio. Since 1979, new seed source trials have been started in seven additional states in the North Central Region (Illinois, Indiana, Iowa, Kentucky, Michigan, Minnesota, and Wisconsin). Early results from plantations in northern Wisconsin, southern Illinois, and central Iowa confirm that alder germplasm from southern Germany is well adapted to our conditions. On the basis of survival and growth over the first 3 years, it seems that sources from Wales, Denmark, Poland, Hungary, northern Italy, and the north shore of the Black Sea also are promising (Maynard and Hall 1980. Unpublished data on file at Iowa State University, Clausen, U.S. For. Serv., Carbondale, Illinois, personal communication). Over the next 10 to 20-year period, all these provenance studies should serve as valuable sources of selected material to initiate tree improvement efforts. An updated list of provenance test locations will be maintained on file at Iowa State University so that we can direct parties to the plantations that could be used in their localities for selection work or breeding. However, these provenance tests do have their limitations as a source of selections. In contrast to the thousands or millions of trees that we have to select among when we start improvement work with native populations, the provenance tests usually will have only 16 to 40 trees per provenance planted at one location. Hence, within-population selection intensities will be very low. Therefore, it may become necessary to conduct selection work in the European stands themselves or to establish large block plantings of selected seed sources in this country.

PROPAGATION ALTERNATIVES

European black alder is somewhat unusual among tree species because all three standard tree improvement techniques: 1) seedling seed orchards, 2) clonal seed orchards, and 3) vegetative propagation are potentially useful approaches for production of improved materials for outplanting. The first production orchards (Zobel and McEllwee 1964) can be established from selections known to perform well in specific regions as based on the data becoming available from provenance and progeny studies. The present task is to analyze the biology of black alder to choose the appropriate production method.

Seedling Production

The standard approach to producing black alder planting stock has been to grow 1-0 bare root nursery stock (U.S.D.A. 1974). A number of nurseries in the eastern United States have experience (or are developing it) in the production of black alder. On a smaller scale, we have found it more desirable to produce containerized planting stock (Maynard and Hall 1980) to conserve seed and control actinorhizae development.

Seed Orchards

Black alder flowers relatively early. The flowers start appearing at 3 to 4 years of age, and substantial flowering occurs in 6 to 8 years (Funk 1965). Several trees from Hungarian and Danish seed sources in our provenance study (Hall and Maynard 1979) began flowering in the second year after planting, and many more trees have begun flowering in the third year. It has been postulated, however, that early flowering can adversely affect vegetative growth (Matthews 1963) and, possibly, nitrogen fixation (Hall and Maynard 1979), so it may be necessary to avoid early-flowering trees in seed orchard establishment (Heybroek 1978, Hall and Maynard 1979). Selection against early-flowering trees would delay seed production and lead to higher costs unless inexpensive methods to culturally promote early flowering are developed. Because of the important trade-offs involved in early flowering, we have been closely monitoring our provenance test in this regard. We recently analyzed the growth rates for the first two and one-half seasons for 98 trees from five of our better provenances. Of these trees, 51 had begun to produce flowers, and 47 had not. At this stage, the flowering trees have exhibited significantly faster growth over each of the first three growing seasons of their existance. This may be only a reflection of the concept that good vegetative vigor is conducive to flowering. It will be next growing season at least before we can observe the influence that heavy seed crops may have on vegetative growth.

If genotypes can be used that naturally flower at 4 years of age or less, then it is doubtful that grafting would offer much advantage. On the other hand, if it proves necessary to select against early flowering to develop superior vegetative growth, then clonal orchards could be more important. The years to flowering after grafting of scions from mature trees onto established rootstocks is not known for black alder. If grafting significantly reduces the time to flowering, as has been found with other species (Wright 1976), then clonal seed orchards may be justified. The greatest problem confronting the use of clonal seed orchards is the grafting process itself. Limited grafting work has been done with alder (Chiba 1966, Robison et al. 1979, Robison 1980). One apparent problem is that high levels of phenolics present in alder tissue may inhibit grafting success. And the potential problems of graft incompatibility and topophysis also should be studied. However, observations on a 14-year-old clonal seed orchard in Bavaria have indicated that these are not problems with black alder (Clausen, U.S. For. Serv., Carbondale, Illinois, personal communication 1981). Flowering scions have been grafted successfully onto rootstocks to concentrate breeding stock in one area (Robison et al. 1979, Robison 1980), but it is not known whether these scions will maintain their flowering status. Should grafting prove an unacceptable method of clonally propagating black alder, rooted stem cuttings might be used. We regularly use softwood cuttings to produce clonal material for research needs. Cuttings could be produced in quantities sufficient for the establishment of clonal seed orchards. Whether these cuttings flower at an age comparable to seedlings is not known. We have established a clonal test plantation to determine this and other characteristics of rooted cuttings.

Once flowering is established, good seed crops usually occur regularly (Funk 1965, Stettler 1978), although a 1977 drought caused production of mostly empty seed in a black alder stand in Iowa (Hall and Maynard 1979). To ensure the production of filled seed, research is needed on the process of seed development and maturation. The critical stages during seed production must be delineated and correlated with environmental conditions. The delayed fertilization that is characteristic of black alder (McVean 1955) may be one such stage. Irrigation during this period before fertilization in June and July may be necessary to ensure the production of filled seed.

Germination of black alder seed generally is good, with seed from open pollinations yielding from 40 to 80 percent germination (Robison 1980). Seed from controlled pollinations germinate at rates of 20 to 60% for outcrosses and from 0 to 8% for selfs (Hagman 1970, Robison 1980). A pollen tube incompatibility system is thought to be the cause of the depressed self fertility in black alder (Hagman 1970, 1975, Stettler 1978). Nursery germination rates can be expected to be much less than those under ideal conditions because of the small size of alder seed and its sensitivity to moisture stress during germination.

The amount of genetic gain achieved in a clonal versus seedling seed orchard has been used often as a criterion for determining which seed orchard design is better (e.g., Wright 1964, Goddard and Brown 1961, Johnsson 1964, Zobel and McElwee 1964). The clonal seed orchard method often is shown to produce higher gains because of the reliance on progeny tests to rogue the initial planting. Seedling seed orchards, which are derived from progeny tests themselves, are shown to give almost as much gain in most cases. However, because the trees making up the final seedling seed orchard may not have been progeny tested themselves, the actual combining abilities of the trees are not known, and the offspring produced from such an orchard may not be supeior (Zobel and McElwee 1964). Conversely, proponents of seedling seed orchards state that additional gains are possible with this method through controlled breeding and testing because of the broader workable genetic base available in seedling seed orchards compared with clonal seed orchards (Goddard and Brown 1961).

Genetic gain considerations are not that important in the choice of seed orchard design if three points are considered. First, trees selected (or retained) for inclusion in seed orchards, whether of clonal or seedling origin, should be progeny tested (Toda 1964, Barber and Dorman 1964). Data on combining abilities of the parents will be needed to thin the seed orchards to the combination of trees most likely to produce superior offspring. Progeny tests are also a necessary step in seed certification (Barber 1975) and will be needed in each region and under the various management systems that the trees are to be grown if significant genotype x environment interactions exist (Libby 1964).

Second, seed orchards should not be equated with breeding orchards. Seed orchards are for the primary purpose of producing genetically superior seed. Additional plantings containing a much broader genetic base than possible in a seed orchard should be established for breeding and gene conservation purposes (Weir and Zobel 1975, van Buijtenen 1975). These plantations, often termed gene or tree banks (Zobel and McElwee 1964, Libby 1973), are the source of new genes and gene combinations that may prove beneficial in the future when management practices, product requirements, or environmental concerns require a change in the genetic makeup of the trees (Zobel and McElwee 1964).

Third, first-generation production orchards are not the end of the line for genetic improvement of a species. Additional breeding and testing will be needed to provide a source of material for advanced generation seed orchards (Zobel and McElwee 1964, Libby 1973, Weir and Zobel 1975). The first production orchards are established only as a means of providing the best possible improvement in the shortest possible time (Zobel and McElwee 1964). Because of these three considerations--1) the requirement for progeny testing, 2) the requirement for additional breeding orchards, and 3) the requirement for advanced generation orchards--the first seed orchards established for black alder will depend on technical considerations more than gain optimization.

Inbreeding often is cited as a problem in seedling seed orchards because related individuals often are retained in close proximity after roguing (Zobel and McElwee 1964). Inbreeding should not be a problem if care is taken when the progeny test is thinned to seed orchard specifications (Goddard 1964) and if alder's incompatibility system reduces matings between relatives (Goddard and Brown 1961) or if inbred seedlings are sufficiently weak that they can easily be culled before field planting. Unfortunately, the effectiveness of the incompatibility system has not been adequately tested for sibling matings and other types of mating between related trees that might occur in a seed orchard. Another possible remedy is to move related trees apart by using a tree spade. This technique also could solve the problem of nonuniform spacing after roguing. Five years ago a group of young alder trees at the Iowa State Nursery was moved with a tree spade. Because of initial top dieback, all trees were cut back to the stump. All trees sprouted, and most began producing seed crops again in the third year after they were moved. This year, they are producing a commercially significant amount of strobili. This raises the possibility that alder seed orchards could be managed on a coppice basis, a portion of the orchard being cut back periodically to keep the production of seed closer to the ground for ease in collection.

Early thinning to promote flowering and wide crowns is needed when converting progeny tests to seedling seed orchards. This early thinning cuts the evaluation period in progeny tests. Therefore, juvenile-mature correlations are needed to improve selection of superior trees. We are conducting one such study to determine age-age correlations for growth and wood characteristics in 15- to 18-year-old black alder. Should shorter rotations be employed to grow black alder, the progeny tests could be grown for most or all of the rotation before thinning.

As previously mentioned, progeny tests should be conducted to test parent trees in both seedling and clonal seed orchards. These secondary progeny tests are a potentially valuable source of additional seed orchards if greater quantities of seed are needed or if significant genotype x environment interactions exist. The progeny tests then could be thinned to the trees performing best in a particular region.

Expected Returns from Genetically Improved Seed

Because of certain biological characteristics of black alder and the potential use of short rotations, the expected monetary returns from using improved seed are high. Marquis (1973) discussed several factors that were the most important influences affecting profits with tree improvement. First was the amount of seed produced per tree. Species that produce large amounts of seed are more profitable than species producing small amounts. This is because less seed orchard acreage is needed to produce sufficient quantities of seed. Second, fast-growing species with short rotations are more profitable than slow-growing, long-rotation species, if the value of the species are comparable. Interest charges on initial costs have less time to accumulate. Third, the value of the final product affects profits. The higher the value of the product, the more profitable is the investment in seed orchards. Last, genetic gain influences profits. Gains in growth rates increase the profits realized from tree improvement efforts, assuming constant value of yield and costs. Moreover, gains can be made in wood quality as well as physical yield, thus increasing the value as well as the volume of the final product.

Black alder has the potential to capitalize on at least three of these factors. This species produces abundant sees. A female black alder catkin produces approximately 60 seeds, and one mature tree produces about 4000 catkins (McVean 1953), yielding 240,000 seed par tree per year on the average. The growth rate of black alder rivals that of sycamore (Kellison and White 1979), and black alder has the potential to be intensively cultured on short rotations (Dickman 1975). The species presently is relatively unimproved. Therefore, because of its inherent wide variability and the availability of other Alnus species for interspecific hybridization (Hall and Maynard 1979), black alder provides excellent opportunities for rapid genetic gain through selection and breeding. The only unfavorable factor is the product value. Black alder is used in Europe for pulp and other wood products, but a commercial market has not yet been established in this country. This situation could change quickly once selections are available that perform well in specific regions. Black alder has too many added benefits such as nitrogen fixation, coppice regeneration, and good fiber and fuel characteristics to be ignored much longer for commercial planting.

The following discussion illustrates the amount of increased gross revenues expected, given several levels of genetic gain in volume of black alder on a 6-year rotation and at a discount rate of 20%. (This discussion is modeled after a paper by Perry and Wang (1958). The following conservative assumptions were made to carry out this evaluation:

1) The land is owned, and all costs and prices remain constant over time. 2) One pound of seed will produce 10,000 plantable seedlings (USDA 1974) (with 340,000 seeds per pound this is a very conservative assumption and may increase with improved nursery practices or containerization). 3) Trees are planted on an 8 x 8 foot spacing, or 680 trees per acre. 4) Eighty percent of the trees will survive until final harvest at 6 years. 5) Specific gravity of green, barky black alder chips is 0.40, yielding 1.25 tons/100 ft^3 (a conservative estimate based on estimates from Vurdu (1977) and Gonclaves and Kellison (1980). 6) A price of $12.50 per ton or $15.50 per 100 ft^3 of delivered barky chips (Coder and Wray 1981). 7) Growth data for unimproved black alder grown in southern Illinois will be used as a basis of analysis (Table 1) .

Given these assumptions, one pound of seed would produce enough seedlings to stock 14 acres, and each acre of seed orchard (15 x 15 foot spacing in the seed orchard) could support annual planting operations on approximately 2000 acres of forest land. These figures compare very favorably with southern pine seed orchards, which require 3-7 acres of seed orchard to produce sufficient stock to plant 2000 acres of land (USDA 1974).

The values in Table 1 were used to calculate the increased gross revenue per acre and per pound of seed under various levels of genetic improvement (Table 2). This analysis indicates the monetary gains possible with modest increases in volume production through genetic improvement. A 5% gain, for example, results in an added gross revenue after discounting of $1.74 per acre and $24.31 per pound of seed. This means that an extra $1.74 per acre can be spent on cultural practices or that an extra $24.31 can be spent on seed for each pound bought and still realize a 20% profit.

Six years probably is not the optimal rotation age for black alder; 13 to 14 years may be more realistic (Glavav 1962). But by using shorter rotations, the costs incurred during the rotation have less time to accumulate added interest charges. Also, the cost of subsequent rotations could be reduced with the use of coppice management that would negate the need for establishing new stands after every harvest.

Vegetative Production

The major alternative to seed orchards is the use of vegetative propagules for field planting. This method is advantageous because intact genotypes of superior selections can be captured (Schreiner 1966, Libby 1973, Hall and Maynard 1979), and rapid genetic gain can be made (Kleinschmit 1977). Clonal production would be beneficial if nonadditive genetic variance proves important in black alder as it has in the southern pines (Dorman and Zobel 1973, Dorman and Squillace 1974). This is likely because black alder is a polyploid and would have the potential for much dominance and epistatic variance (Hall and Maynard 1979). Potential pest problems created by low genetic diversity can be surmounted by the use of multiclonal lines (Schreiner 1966).

Table 1.--Yield and value of European black alder grown in Illinois. Adapted from Kellison and White (1979).

Age	Height (feet)	DBH	Vol./Tree (cubic feet)	Vol./Acre (cubic feet)	Value/Acre (dollars)	Value/pound of seed (dollars)
2	8.0	--	--	--	--	--
3	13.3	--	--	--	--	--
4	21.6	2.4	0.32	174.8	27.94	391.16
5	25.9	3.3	0.70	380.8	59.02	826.28
6	32.8	3.9	1.23	669.1	103.71	1451.94

Table 2.--Effect of genetic improvement for volume in Alnus glutinosa on gross revenue per acre and per pound of seed.

Genetic gain (percent)	Gross Revenue		Discounted Gross Revenue			
	per acre	per pound of seed	per acre		per pound of seed	
0	103.71	1451.94	34.73		486.25	
1	104.75	1466.46	35.08	(0.35)[a]	491.11	(4.86)
5	108.90	1524.54	36.47	(1.74)	510.56	(24.31)
10	114.08	1597.13	38.20	(3.47)	534.88	(48.03)
15	119.27	1669.73	39.94	(5.21)	559.19	(72.94)

a/ Numbers in parentheses indicate the increase in revenue with a given level of genetic gain for volume.

A mixture of several genotypes indeed may have better defense against environmental and pest catastrophes than a continuum of seedling genotypes (Libby 1973)

Stem cuttings are now the best approach for cloning black alder, although tissue culture techniques may be developed (Hall and Maynard 1979). We routinely achieve more than 50% success in rooting softwood cuttings in our greenhouse. Similar rates have been achieved with dormant hardwood cuttings, but the success of this method is more variable. Alders sprout prolifically from cut stumps, therefore, it should be easy to establish and maintain cutting orchards. Several unknown factors concerning the rooting and growth of black alder cuttings must be delineated, however.

As with other species, our observations indicate that cuttings from mature trees may be more difficult to root than juvenile cuttings. Coppicing may restore rooting ability, or small numbers of cuttings could be established from older trees with these ramets utilized as stock plants for subsequent multiplication. Clonal tests must be initiated in several locations to determine genotype x environment interactions, juvenile-mature correlations, and performance of cuttings taken from young material compared with those taken from older material (Libby 1973, Heybroek 1978). Most of all, however, a reliable, inexpensive method of propagating stem cuttings must be found. A method of establishing unrooted cuttings directly in the field would be desirable, but this looks unpromising at present (Hall and Maynard 1979). For difficult-to-root species, Hartmann and Kester (1975) have suggested pretreatment of hardwood cuttings with auxin, followed by a cold-storage period to initiate root formation and allow more rapid root growth once outplanted. This technique may have potential for alder and should be evaluated.

Clonal production has many advantages, and plantations to test the growth of cuttings through maturity are warranted. But until consistently reliable methods are developed for rooting alder, cutting orchards are the least desirable method of production.

CONCLUSIONS AND SUMMARY

Provenance test data and materials are becoming increasingly available to support alder selection and breeding programs. The south-central part of the native range of the species seems to offer the best germplasm for use in the north-central United States.

Seedling seed orchards seem to be the best method for producing improved material for outplanting. More is known about seedling production and growth than the production and growth of cuttings and grafts. Initially, at least, seedling seed orchards offer the simplest approach.

Progeny and clonal tests need to be established to determine combining abilities of selected genotypes for roguing purposes and to determine growth and reproductive characteristics of vegetative propagules. If superior genotypes are found that should be included in the initial seed orchard, the selections could be propagated vegetatively to preserve the intact genotype and then be placed in the orchard.

Further genetic improvement beyond simply choosing the best source of black alder is warranted. Increases in genetic gain are very possible because of the wide intraspecific and interspecific genetic base available for breeding. Even with modest improvements in volume growth, it has been shown that significant monetary gains can be made. Finally, the market for black alder is expected to expand because of its technical properties as a pulp or energy species, its tolerance of poor sites, and its ability to coppice.

LITERATURE CITED

Barber, J. C. 1975. Seed certification. Pages 143-149 in R. Faulkner, ed., Seed Orchards. British Forestry Commission Bulletin 54. Her Magesty's Stationery Office, London.

Barber, J. D., and K. W. Dorman. 1964. Clonal or seedling seed orchards? Silvae Genet. 13:11-17.

Chiba, S. 1966. Studies on the tree improvement by means of artificial hybridization and polyploidy in Alnus and Populus species. Bull. Oji. Inst. For. Tree Improvement No. 1, Aji Paper Co., Ltd., Japan.

Coder, K., and P. H. Wray. 1981. Iowa timber prices. Iowa Coop. Ext. Serv. Pamph. Pm-785 (rev.).

Dickman, D. I. 1975. Plant materials appropriate for intensive culture of wood fiber in the North Central Region. Iowa State J. Res. 49(3):28 1-286.

Dorman, K. W., and A. E. Squillace. 1974. Genetics of slash pine. U.S.D.A. For. Serv. Res. Pap. WO-20. 20 pp.

Dorman, K. W., and B. Zobel. 1973. Genetics of loblolly pine. U.S.D.A. For. Serv. Res. Pap. WO-19 21 pp.

Funk, D. T. 1965. Silvics of European alder. U.S.D.A. For. Serv. Cent. States. For. Exp. Stn. Columbus, Ohio. 21 pp.

Funk, D. T. 1979. Alnus glutinosa provenance trials on Ohio strip mines: Sixteen-year results. Pages 28-32 in R. P. Guries, Ed., Proceedings of the First North Central Tree Improvement Conference, Madison, WI., August 21-23, 1979.

Furlow, J. J. 1979. The systematics of the American species of Alnus (Betulaceae) Parts I and II. Rhodora 81:1-21, 151-248.

Glavav, V. 1962. 0 visinskom rastu crne johe du dobe od 20 godina. Sumarski List. 88(11/12):408-414.

Goddard, R. E., and C. L. Brown. 1961. An examination of seed orchard concepts. J. For. 59:252-256.

Conclaves, P., and R. C. Kellison. 1980. Potential of black alder in the South. North Carolina State Univ. Tech. Rep. 62. 31 pp.

Hagman, M. 1970. Observations on the incompatibility in Alnus. Proc. IUFRO Sect. 22 Working Group meeting on Sexual Reproduction in Forest Trees, Vargaranta, Finland. 1(10):1-19.

Hagman, M. 1975. Incompatibility in forest trees. Proc. R. Soc. Ser. B. 188:313-326.

Hall, R. B., and C. A. Maynard. 1979. Considerations in the genetic improvement of alder. Pages 322-344 in J. C. Gordon, C. T. Wheeler, D. A. Perry, eds., Symbiotic Nitrogen Fixation in the Management of Temperate Forests. Oregon State University, Corvallis, OR.

Harlow, W. M., and E. S. Harrar. 1969. Textbook of Dendrology. McGraw-Hill Book Co., NY.

Hartmann, H. T., and D. E. Kester. 1975. Plant propagation-principles and practices. Third edition. Prentice-Hall, Inc. Englewood Cliffs, NJ.

Heybroek, H. M. 1978. Primary considerations: multiplication and genetic diversity. Unasylva 30 (119/120):27-33.

Johnsson, H. 1964. Forest tree breeding by selection. Silvae Genet. 13:41-49.

Kellison, R. C., and G. White. 1979. Black alder performance in the southeast. Pages 345-355 in J. C. Gordon, C. T. Wheeler, and D. A. Perry, eds., Symbiotic Nitrogen Fixation in the Management of Temperate Forests. Oregon State University, Corvallis, OR.

Kleinschmit, J. 1977. Problems of vegetative reproduction. No. FO-FTB-77-4/5 In: Proc. IUFRO/FAO Third World Consult. For. Tree Breeding, Canberra, Australia, 21-26 March 1977. CSIRO, Division of Forestry Research, Canberra, A.C.T., Australia.

Libby, W. J. 1964. Clonal selection, and an alternative seed orchard scheme. Silvae Genet. 13:32-40.

Libby, W. J. 1973. Domestication strategies for forest trees. Can. J. For. Res. 3:265-276.

Marquis, D. A. 1973. Factors affecting financial returns from hardwood tree improvement. J. For. 71:79-83.

Matthews, J. D. 1963. Factors affecting the production of seed by forest trees. Forest Abstr. 24(1):I-XIII.

Maynard, C. A., and R. B. Hall. 1980. Early results of a range-wide provenance trial of Alnus glutinosa (L.) Gaertn. Pages 184-201 in Proceedings of the Twenty-seventh Northeast Forest Tree Improvement Conference, Burlington, VT. July 29-31, 1980.

McVean, D. N. 1953. Alnus. J. Ecol. 41:447-466.

McVean, D. N. 1955. Ecology of Alnus glutinosa. I. Fruit formation. J. Ecol. 43:46-60.

Oak, S. W., and R. Dorset. 1981. Evaluation of mortality in a European black alder seed production area. Gilbertsville, KY. 1981. Report #81-1-26, Forest Pest Management, Ashville Field Office.

Perry, T. 0., and Chi-Wu Wang. 1958. The value of genetically superior seed. J. For. 56:843-845.

Robison, T. L. 1980. Controlled pollination, grafting, and vegetative propagation of Alnus glutinosa. Unpublished M.S. Thesis, Iowa State University Library, Ames, IA.

Robison, T. L., C. A. Maynard, J. Thomas, and R. B. Hall. 1979. A germplasm collection and evaluation program for Alnus glutinosa. Pages 73-85 in K. C. Steiner, ed., Proceedings of the Twenty-sixth Northeastern Forest Tree Improvement Conference. University Park, PA. July 25-26, 1978.

Schreiner, E. J. 1966. Maximum genetic improvement of forest trees through synthetic multiclonal hybrid varieties. Pages 7-13 in E. J. Schreiner, ed., Proceedings of the Thirteenth Northeastern Forest Tree Improvement Conference, August 12-13, 1965, Albany, NY.

Stettler, R. F. 1978. Biological aspects of red alder pertinent to potential breeding programs. Pages 209-222 in Utilization and Management of Alder, U.S.D.A. For. Serv. Gen. Tech. Rep. PNW-70.

Toda, R. 1964. A brief review and conclusions of the discussion on seed orchards. Silvae Genet. 13:1-4.

U.S.D.A. 1974. Seeds of Woody Plants in the United States. U.S. Dep. Agric., Agric. Handb. 450.

Van Buijtenen, J. P. 1975. The planning and strategy of seed orchard programmes, including economics. Pages 9-24 in R. Faulkner, ed., Seed orchards, British Forestry Commission Bulletin 54. Her Magesty's Stationery Office, London.

Vurdu, H. 1977. Anatomical characteristics of stem, branch, and root wood in European black alder (Alnus glutinosa L. Gaertn.). Ph.D. dissertation. Iowa State University, Ames, IA (Order No. 78-5976, University Microfilms, Ann Arbor, MI.)

Weir, R. J., and B. Zobel. 1975. Advanced generation seed orchards. Pages 118-127 *In:* R. Faulkner, ed., Seed Orchards. British Forestry Commission Bulletin 54. Her Magesty's Stationery Office, London.

Wright, J. W. 1964. Flowering age of clonal and seedling trees as a factor in choice of breeding system. Silvae Genet. 13:21-27.

Wright, J. W. 1976. Introduction to Forest Genetics. Academic Press, NY.

Zobel, B., and R. L. McElwee. 1964. Seed orchards for the production of genetically improved seed. Silvae Genet. 13:4-11.