MANAGING GENETIC RESOURCES FOR THE FUTURE
A PLAN FOR THE N. C. STATE INDUSTRY
COOPERATIVE TREE IMPROVEMENT PROGRAM

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Abstract.--Plans have been developed to manage the genetic resources of the N. C. State Cooperative Program for future generations of improvement. The program will be developed with three major phases: (1) Breeding good general combiners, (2) a continuation of the main line program through breeding of second-generation selections, and (3) selection and breeding of trees from unimproved plantations. A regional program concept will be used in the development of the three phases. Within each broadly defined region, five to 10 member organizations will pool genetic resources and share in the breeding and testing work.

Additional keywords: Pinus taeda, tree breeding, selection intensity, coancestry, genetic base, genetic gain.

INTRODUCTION

The North Carolina State University-Industry Cooperative Pine Tree Improvement Program is extensive, with emphasis on improvement through applied genetics. feed orchards of loblolly pine (*Pinus taeda* L.) developed from the first cycle of mss selection are currently producing seed for 150 million plantation seedlings many. Within the next few years these orchards will yield sufficient seed to regenerate more than 400,000 acres per year with 10-20 percent gain in volume Ner unimproved stock. Improvements in tree and wood quality and disease resistnce will be at least of equal magnitude and value. The N. C. State program has aptured only a portion of the improvement possible; ample genetic variation reains for additional cycles of improvement.

Ideally, choices among alternative breeding and testing strategies should be based on long-range (many generations) economic comparisons of net returns with respect to breeding and production costs and returns. However, information is)nly now becoming available to allow meaningful economic evaluations of first generation improvement efforts (Porterfield, 1973). Detailed economic comparisons)f future alternatives would be very speculative. It seems more appropriate to consider within the current program an improvement schedule which maximizes ;enetic gain in the near future with appropriate opportunities for subsequent ycles of improvement. The improvement strategy proposed is rather specific to he biological and economic resources within the N. C. State Cooperative Program. therefore only certain aspects of the plans discussed here will have general pplication to other programs.

A REGIONAL PROGRAM CONCEPT

The North Carolina State Tree Improvement Program was developed as a cooperative. The 26 industrial and three state members have worked as a team freely exchanging

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research results and plant resources. The area of operation includes the range of loblolly pine east of the Mississippi River. Within this area over 45 individual improvement programs with 170 seed orchards have been developed for loblolly pine alone.

Breeding and testing programs have been developed for each member, while the production phase (commercial seed orchards) includes a concerted effort to pool the best of the available plant material within any given geographic area. Good examples of such resource pooling are the 1.5 or improved first-generation production seed orchards. If satisfactory gains are to be obtained in the future it will be necessary to work regionally in the breeding, testing and production programs. No organization has the plant resources available to undertake recurrent selection and improvement independently for advanced generations. Now, as never before, the reliance of each member organization on the regional resource base provided within the cooperative is apparent. Within each broadly defined region from 5 to 10 distinct loblolly pine improvement programs exist that will contribute plant resources to a given regional pool.

Regions are broadly defined by physiographic and environmental conditions. Specific genotypes will generally be utilized only within the region from which they originate, but tests are now underway (wide testing of good general combiner that will reveal their performance outside their region of origin. The concern over movement of trees into differing environments is that genotype - environment interaction may reduce genetic gain.

It can be seen from figure 1 that regions as defined are not entirely distinct. Overlapping is encountered as a direct consequence of gradations in environmental influences and suitable genotypes will be judiciously moved across regional boundaries. Until research results indicate otherwise such movement will be done only when shortages of plant resources within a region make it mandatory for a broadening of the genetic base; extreme caution will be used when any major moves are to be made.

THE COOPERATIVES FUTURE STRATEGY - A SCHEDULE

A balanced breeding and production program for advanced generation loblolly pi improvement can be realized through the development of three distinct resource base They are: (1) good general combiners, (2) second-generation selections from the main line program, and (3) new plantation selections. These three avenues of current and/or future emphasis are justified on the basis of expected genetic gain, ti liness of the anticipated gain and the operational feasability of development. An important additional consideration is the maintenance of a broad genetic base for future cycles of improvement.

Each of the three avenues of improvement are to be developed within each of th regions described. Scheduling in the western regions of the Cooperative will vary from the others because of later initial program development. However, if the bree ing, selection and orchard establishment is expedited without delay the planned prc duction orchard establishment schedule (see table 1) can be followed.

Figure 1. Generalized Regional Program Boundaries - broken lines designate boundaries with major overlap.

1. Northern Coastal Region - Encompassing Virginia and much of North Carolina.

. Mid-Coastal Region - Encompassing southern N. Carolina and northern S. Carolina.

South Coastal Region - Encompassing Coastal areas of southern South Carolina, Georgia and northern Florida.

C Gulf Coastal Region - Ranging from the southern Georgia Coastal Plain West along the gulf to the Mississippi River.

L Upper Coastal - Western Piedmont Region - Encompassing the upper Coastal and central Piedmont regions of Mississippi, Alabama and Georgia.

6, Eastern Piedmont Region - Ranging Northeast through the Piedmont from Georgia to Virginia.

1, High Piedmont Region - Including Tennessee, northern Mississippi, Alabama and Georgia.

8. Outlier Areas in Florida and the Eastern Shore - It is expected that test results will confirm these areas can be combined with adjacent regions,

Table 1. A schedule of production seed orchard establishment through successive generations of improvement.

Production Orchards	Establishment Period
1st generation	1960[1/] - 1970
1.5 generation (improved first)	1969 - 1978
2nd generation	1976 - 1984
Improved 2nd generation	1986 - 1990
3rd generation	1990 - 1998

With the exception of 1.5 generation orchards, which are established with test clones, all orchards will be subject to upgrading by roguing following testing. It is evident that establishment and production phases of the different stage orchards will be overlapping. An organization may have at any given time as many as three orchards under management or development, e. a first-generation rogued orchard in full production, a 1.5-generation orchard starting to produce and a second-generation orchard under initial establishment. As newer and genetically better orchards begin production older orchards will be phased out.

The three lines of development will serve as the foundation for ongoing production orchard programs. The breeding schedule is schematically outlined in figur 2.

Phase One - Good General Combiners

Good general combiners are first-generation parents that have consistently produced outstanding progeny, as determined from progeny tests. In any given orcha of 25 to 35 clones, as many as 3 to 5 good general combiners have been identified. Improved first-generation seed orchards (1.5 generation) are developed by establishing the good general combiners from each of five to 10 programs within a region int a single orchard. Generally the 1.5-generation orchard clones are selected on the basis of multiple trait superiority. On occasion, specialty orchards have been developed with major emphasis on a single trait such as disease resistance.

At age 8, it appears the progeny from 1.5-generation orchards will produce greater volume than unimproved plantations. This improvement will be 15% greater than gain commonly observed from unrogued first-generation orchards, primarily as a result of increased selection intensity and selection on family performance. Additional breeding and subsequent selection among the progeny of these outstanding clones is expected to result in "super" second-generation orchards with gains on the order of 50% increased volume over unimproved stock. To attain this goal the following program development schedule is planned:

Breeding the general combiners and testing their progeny	1975 - 1983
Improved second-generation orchard establishment	1985 - 1990

The improvement to be derived from developing the good general combiner population is considerable while the additional investment required is minimal.

1/ The initial date in any given period indicates when the first significant orchar acreage has been, or will be established.

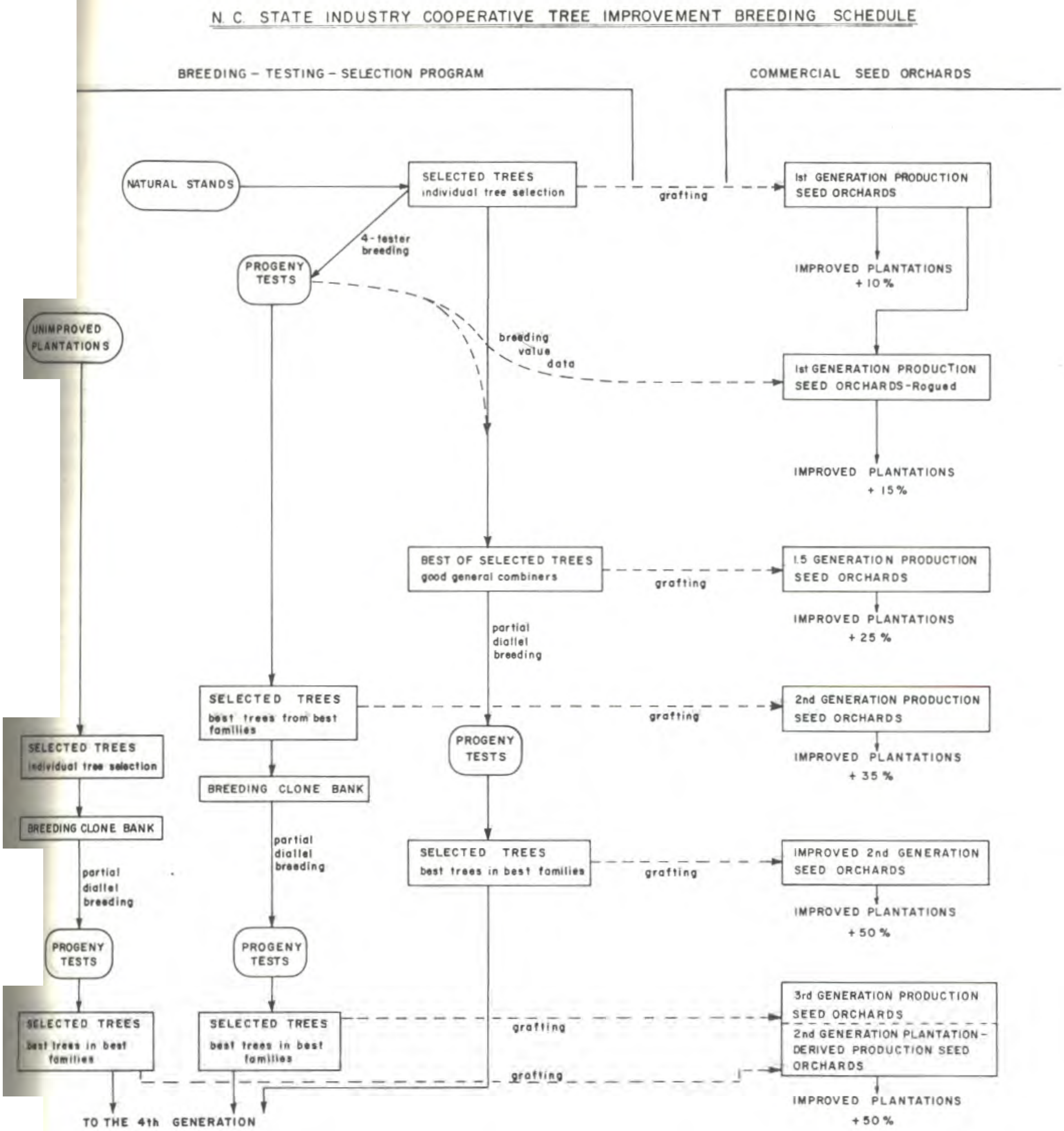

Fig. 2. Flow chart showing some short-term and long-term activities for the Cooperative; these consist of two basic activities:

1. Maximum, immediate utilization of the best plant material already developed
2. Development of a sound, broad genetic base through a long-term selection and breeding program

Good general combiners will be mated in a partial diallel scheme with each clo mated to at least 8 others. Because of the varied number of clones pooled from different programs within each region, it will be impossible to maintain balance in the partial diallel. The objective is to quickly generate a population from known good genotypes in which to select. Crossing will usually be among clones f iom different orchards, the pollen to be provided from the N. C. State pollen bank-1J The number of crosses required from each member will vary from 8 to 12 for each orchard.

Because of the rapid increase of relatedness among families (coancestry) the good general combiner breeding program is expected to terminate as a breeding line with the completion of improved second-generation orchards. Only a few outstanding lines will be carried forward as a part of the continuing recurrent selection program. Some crossing among good general combiners from widely separated regions will be done, but their uncertain potential dictates minimal emphasis until the value of the wide crosses is known. Results from wide testing of good general combiner progeny and a wide crossing program will be available within a few years.

Phase Two - The Main Line Program

Each member organization selected from 25 to 35 first-generation parent trees from natural stands. These were progeny tested using a 4-tester (or 5-tester) factorial mating scheme which provided information necessary to rogue the seed orchards and to identify the best general combiners. The progeny tests also serve as a population base for second-generation selection. The very best of the second-generation selections are established in production seed orchards while all are included in clone banks to be subsequently mated to create a base population for a third cycle of selection. The schedule for this main-line phase is as follows:

a.	First-generation seed orchards	1960 - 1970
b.	Breeding and testing first generation-selections	1967 - 1977
c.	Second-generation orchard establishment	1974 - 1980
d.	Breeding and testing second-generation selections	1980 - 1988
e.	Third-generation orchard establishment	1990 - 1998

The second-generation production orchard is comprised of the best of the total second-generation select population. Since maximum genetic gain is the objective, the trees established in the orchard are selected as intensively as possible. An additional constraint on the use of second-generation selections in the production orchard is that many are related, being half-sibs or full-sibs, thus the chance of inbreeding is introduced. To use second-generation selections with no regard for the likelihood of related matings would jeopardize the genetic improvement, thus related selections are used only when they can be spatially separated in the orchard. A 90' spacial separation is minimal according to studies by McEllwee (1970).

Diversity must be retained in the breeding population because it is the base of genetic variation for the third generation. Each member organization will obtain approximately 100 second-generation trees per orchard program for inclusion in their breeding clone bank. Therefore, 500 to 1000 second-generation selections will be retained within each regional program. Although such a large number of selections seems impressive, the utility of this population as a breeding base is deceiving

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1/ The pollen bank provides for long-term storage of pollen from good general combiners in a central location. Pollens will be distributed as needed in the breeding program because of extensive coancestry. The amount of relatedness results directly from the use of the tester mating design; a maximum of only 4 or 5 unrelated selections per orchard or 20 to 50 unrelated selections per region are available, depending on the number of programs within the region. With complete outcrossing the third-generation base population for any given region can have no more than 10 to 25 completely unrelated families.

With the above limitation, two conclusions are: (1) The base populations to be developed for third-generation regional programs, even though large in numbers, will provide limited utility by themselves because of the coancestry. A broadening of genetic base is essential. (2) A very large investment in this phase of the breeding program does not appear justified.

The base populations can be enlarged in a number of ways: (1) If the wide testing of good general combiners indicates good adaptability the operational region size will be increased with the number of useable selections within any region becoming greater. (2) If inbreeding tests show only a moderate depression from low levels of inbreeding, the breeding population could then be enlarged in proportion to the number of related matings allowable in the production seed orchards. The genetic base would be broadened by making available more genotypes per region. (3) If "heterotic" effects result from wide crossing with little concurrent reduction of additive genetic variance, breeding and selection with widely separate genotypes would be justifiable. Such a wide cross program could be useful with good general combiners and second-generation selections. (4) A direct procedure for broadening the base involves selection and breeding of new genotypes with the subsequent incorporation of useful individuals into the third-generation base population. Such a program to expand genotypes is to be implemented by selection and breeding plantation trees. (see following section - phase three).

Second-generation selections from female parents with outstanding good general combining ability will be bred in the synthesis of the third-generation base population. Progeny from the best three to five general combiners per orchard will constitute the breeding population. By contrast, little if any selection on the male side of the pedigree (selection among the testers) is judged desirable. With few testers from which selection can be made, gains will be minimal, while increased coancestry would be significant. Only selections having extremely poor male parents will be eliminated; it appears that progeny from three of the four or five male testers are good enough to be included in the breeding program. Thus each orchard program will contribute selections from 12 full-sib families to the regional breeding population. A regional breeding population will be comprised of several full-sib selections from each of 60 to 120 full-sib families. Only occasionally will extremely superior individuals from poor families be included in the breeding program. Use of a combined selection index will enchance identification and the likelihood of success from breeding such unusual individuals.

Control of potentially deleterious inbreeding in advanced-generation production orchards can only be achieved if complete pedigree information is available (Zobel et. al. 1972, Weir 1972). Therefore, specific mating will be continued in the breeding program with second-generation selections. However, unlike previous breeding efforts, many sets of full-sib individuals will be included in this breeding population. The individual members of a full-sib set can be pooled without any loss of vital pedigree information. Pooling full-sibs into a single breeding entity will confound the variation among full-sib and cousin progeny in what is commonly referred to as "within family" variation. While this and other similar confounding makes es timation of genetic components of variance and subsequently genetic gain rather co plex, it does not restrict the genetic variation open to selection nor does it contribute to any nonidentifiable increase in coancestry. Pooling full-sibs into a single breeding entity will reduce costs for this phase of the breeding and testing program. Because of the expected limitation on utility of the resulting population such a reduction is appropriate.

Each of 60 to 120 full-sib sets are to be bred to six others in a partial dial scheme. To complete such a program, 180 to 360 total crosses will be required within a region. The five to 10 member organizations of a region will each be required to complete about 36 crosses. This workload is commensurate with the utility of the p ulation to be derived. Because of the difficulty in comparing performance within a population having a mixture of inbred and outbred individuals, all breeding work will be restricted to crossing among unrelated individuals.

For production purposes, third-generation selections from the main-line program are to be combined with second-generation selections derived from the plantation se tion and breeding (to be described in the next section--phase three). Estimates of genetic gain expected from these combination seed orchards do not substantially diff from those for improved second-generation orchards. The fact is these combination orchards may never be established. However, the investment in breeding these resou is required so that improvement beyond the maximum shown (figure 2) can be realized. Without breeding main-line second-generation selections and/or plantation selections, additional genetic gains in the fourth generation will not be possible.

Phase 3 - Plantation Selection and Breeding

Coincidental with development of third-generation production seed orchard progr is the need to broaden the genetic base. In the South many thousands of acres of genetically unimproved loblolly plantations exist that constitute a most valuable ge pool yet to be exploited. An extensive selection and breeding program with planted_ trees will serve to broaden the genetic base and simultaneously utilize available gene tic variation. Plantation selection must be initiated soon if the scheduling objecti of the third-generation production program are to be met. The proposed schedule is as follows:

a. Plantation selection 1975 - 1979
b. Breeding and testing 1980 - 1988
c. Plantation derived second-generation orchard establishment 1990 - 1998

Genotypes derived from selection and breeding of plantation trees will have bee subjected to only two cycles of recurrent selection which will be combined with the third-generation material already available. Thus a "catching-up" effort is required from plantation selections which can be successful only if selection intensity is hig and environmental effects on candidate selections are minimal. Some control of the environment is realized by selection in plantations established at uniform spacing with trees of the same age. Site preparation prior to plantation establishment norma reduces vegetative competition which reduces environmental extremes.

Genetic gains from the second-generation plantation selections are expected to nearly equal third-cycle recurrent selection of the main line improvement program.

Equally rapid improvement with second-generation selections from the wild tree selections was not possible, since environmental variation was high in the forests from which the original parents were chosen. Additionally selection intensity is lower with the third cycle of selection in the main-line program because of the prevalence of relatedness. Lower selection intensity results in less genetic gain.

Each member of the Cooperative will obtain 100 selections from plantations for each operating orchard. Therefore, each regional program will have from 500 to 1000 new plantation selections. The goal of 100 trees per program per member is not based on optimizing selection intensity or genetic gain, but is the maximum number of trees possible under operational constraints. With large plantation acreage, more trees could be selected with little sacrifice in selection intensity, but manpower resources prevent this.

The plantation selections will be mated using a partial diallel scheme requiring six crosses per clone. This number has been determined according to projected optimization of genetic gain as reported by Squillace (1973). This scheme will result in 1500 to 3000 specific crosses per region with each cooperating organization responsible for 300 crosses over a six to eight year period. The task is large, but rewards are considerable. This effort will enable each regional program to carry forward (beyond the third generation) a breeding population varying in size from 250 to 500 unrelated, fully pedigreed lines. More importantly, significant genetic gains in the third and subsequent generations will be attainable.

Plans to combine trees from the plantation selection and breeding phase with the main-line breeding phase of the program require comparison testing. This is essential to insure that plantation derived material resulting from only two cycles of selection will perform on a par with trees of the original program subjected to three cycles of recurrent selection. The testing for comparative purposes is operationally feasible since the two phases of program development are coincidental in time.

The opportunity for expansion of the genetic base through this third phase of the program is considerable, yet it will require a substantial commitment of resources to insure success. If such a commitment is not made soon the opportunity will be lost since most plantations of loblolly pine in the recent past and near future will be from seed orchard derived stock. As the vast acreages of unimproved plantations that now exist are harvested, a genetic resource with tremendous potential will disappear forever. Failure to take the needed action will severely restrict the future potential for genetic gain and its use to enhance forest productivity.

THE COOPERATIVES FUTURE STRATEGY - APPLICATION

The N. C. State Cooperative Tree Improvement Program applies genetic improvement methods to increase the quality and productive potential of forest plantations. The end products of these research and development efforts are improved trees. A regional program concept is to be followed in all future development as a means to increase efficiency and better utilize resources. Within each region, established-production seed orchards provide the "pay off" by producing large quantities of genetically improved seed. Each new orchard in the development sequence will pay greater dividends than the previous one in terms of genetic gain for a complex of economically important traits. Successive seed orchards overlap in time; older orchards will be phased out as newer and better ones commence seed production.

The selection, breeding and testing program provides the foundation of genetic resources on which the future production orchard effort depends. As breeding develops successive generations of better trees, the very best are selected for inclusion in production orchards. Short intervals between successive generations will result in greater gain per unit time; generally applied programs become more profitable as gen eration intervals decrease (Squillace and Gansel, 1972). Selection, breeding and testing strategy must be responsive to the pressure of time as this relates to maximizing profitability, a goal of every applied program.

In the long term, a breeding program must provide for effective base population resynthesis on a recurring schedule. The breeder should strive for control of coancestry in order to retain flexibility while developing production orchards with maximum selection differential to develop the greatest gain. The program must be flexible to accommodate a dynamic population. Breeding populations will be continually built up with new and better selections and purged of trees which fail to maintain the required measure of superiority. Continued emphasis on selection for general combining ability is appropriate since this is the only source of variation that can be effectively utilized with current tree improvement technology.

The proposed management strategy for genetic resources of the N. C. State Coop erative maintains a realistic balance between the short and long-range objectives. Production orchards have been established and many are now producing near expected capacity. New and better orchards are currently being created; others will become reality as trees with higher genetic value become available from the breeding progr Breeding strategy is planned to develop additional genotypes for maximum immediate utilization and to provide for a broad genetic base suitable for long-term recurrent selection and breeding.

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