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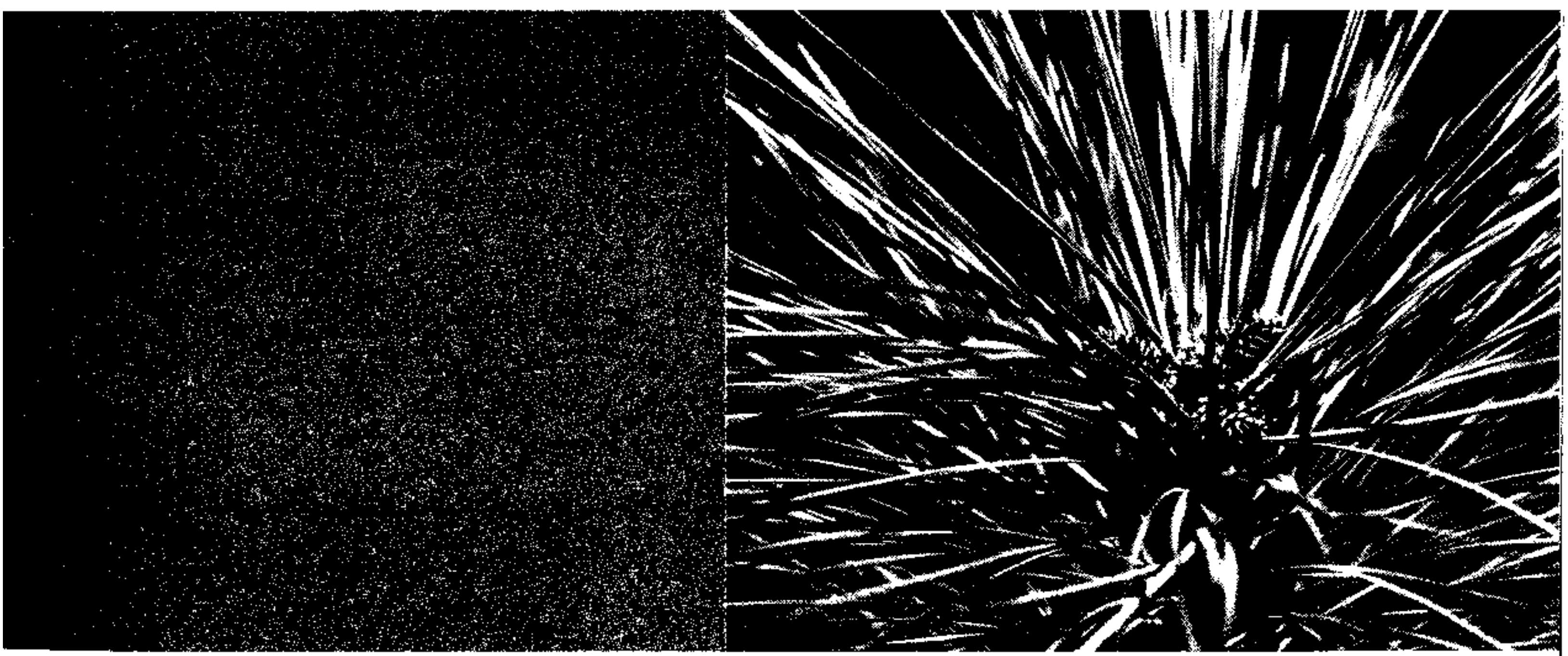
INTRODUCTION to PRACTICAL FOREST TREE IMPROVEMENT



Forest Genetics Laboratory

TEXAS FOREST SERVICE

INTRODUCTION
to
PRACTICAL FOREST TREE IMPROVEMENT

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Chapter 1

PRINCIPLES OF GENETICS

Genetics is the study of heredity. To understand the principles of tree improvement, it is necessary to understand the principles of genetics. Heredity is the process by which all living things produce offspring that resemble their parents. While the inheritance of desirable traits of plants or animals has been used by man for several thousand years, the method by which hereditary properties were passed on from parent to offspring was not fully understood until quite recently. However, by about 1860 the means by which hereditary characteristics were passed on from parents to offspring were identified as the sperm which carried the male contribution and the egg which carried the female portion of the heritable properties. Subsequent studies identified the chromosomes within the sperm and egg as carrying the heritable characteristics.

With the realization that the sperm and egg cells carried heritable units on their chromosomes it became possible to understand and fully appreciate the experimental work done by Gregor Mendel and published in 1865. These experiments were conducted over a period of years using garden peas in which differences were observed through several generations. Exact records provided Mendel with proof that inheritance of visible differences followed a regular and predictable pattern. The same results could be obtained each time the same types of peas were mated.

The laws discovered by Mendel apply equally well to forestry. Every forest nurseryman is probably familiar with the occasional white or albino seedlings which occur in the nursery beds immediately after the seeds germinate. They die very quickly since they lack the green pigment, chlorophyll, which is essential for the life of the tree. Mendel's laws not only explain how we can continue to find these variations within species, or mutants, but they also enable us to predict the proportion of mutants to expect.

An individual tree may appear normal, but in fact may be the carrier of a mutation. The appearance of the individual is. called its phenotype; its true genetic nature is called its genotype.

Mendel and subsequent investigators proved that since each parent contributes at least one factor for each trait, each individual possesses a minimum of two factors called genes for controlling such a trait. Figure 1 illustrates the phenotypes and genotypes in the case of albino pine seedlings. Since a plant is normal whenever it contains at least one "green" gene, the "green" gene is dominant over the "albino" gene because it suppresses the effect of the "albino" gene. The "albino" gene is recessive. When "green - green" individuals are crossed among themselves all their offspring will he the same. This is called true breeding. When two "green-albino" genotypes are crossed with each other, the genes segregate and recombine in all combinations producing all three possible genotypes. This is known as the principle of segregation. or Menders First Law.

Menders work was rediscovered in 1900 after the basic biological research needed to understand the functions of the sperm and egg had been completed. By this time the chromosome was known to be the carrier of the genes. Therefore, the

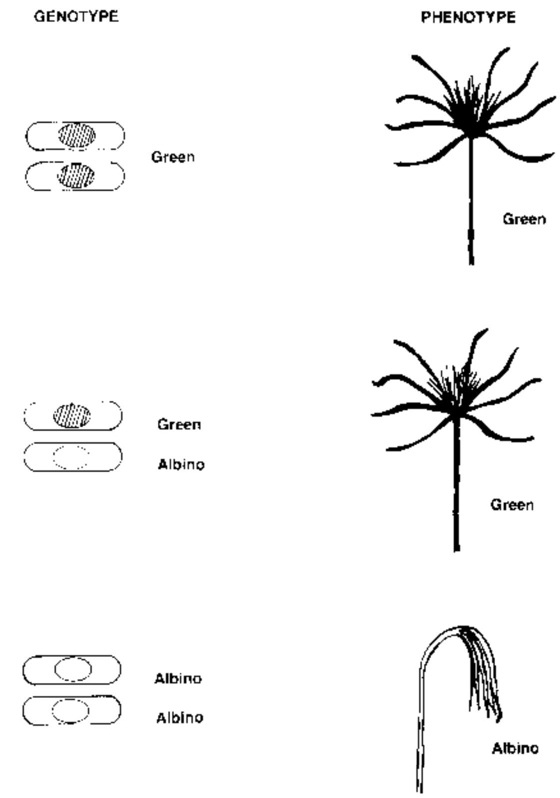


Figure 1. Albino Pine Seedlings.

next major question evolved around the functions of different parts of the chromosome and identification of the gene.

The genes were found to be contained in a long strand of deoxyribonucleic acid (DNA) supported in a protein framework. Each offspring usually will have a different phenotype than either parent as well as a different genotype. The offspring will have one set of chromosomes from each parent, and thus any offspring will have a new and unique combination of genes which will produce an individual that is similar to both parents genotypically but may vary considerably in its phenotype. This occurs because the physical appearance of the individual depends on the genes received from each parent and the environment in which the individual lives.

Requirements of the Genetic Material (DNA)

There are three requirements of the genetic material: first, it must reproduce itself; second, it must act as a blueprint for the synthesis of all proteins; and third, it must make occasional mistakes when reproducing itself, i.e. it must be mutable.

The first requirement for precise reproducibility is important because cell growth and division are continuous processes throughout the life of any organism. With cell division comes the necessity for reproduction of DNA for each daughter cell. Since DNA carries the information needed for protein synthesis, reproduction has to be exact.

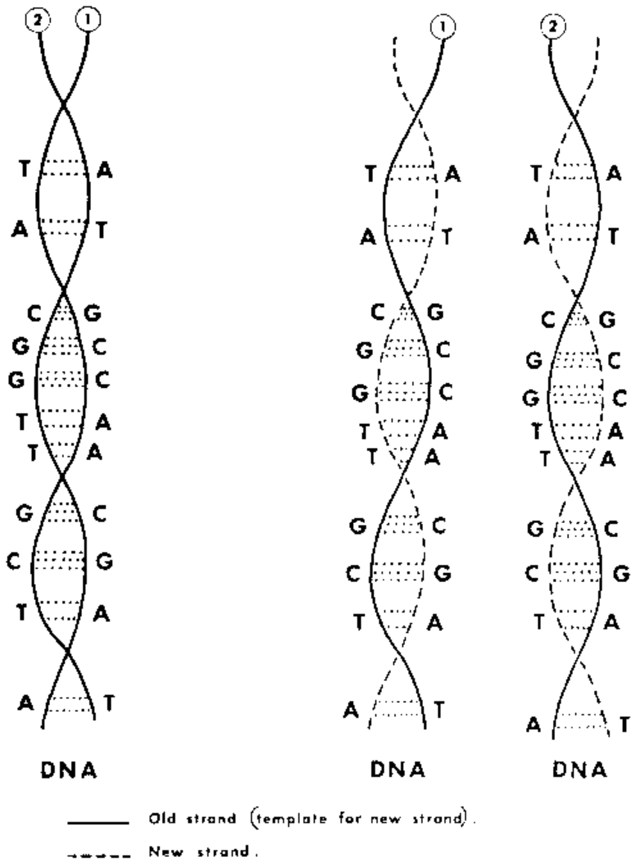


Figure 2. Schematic diagram of DNA replication (duplication).

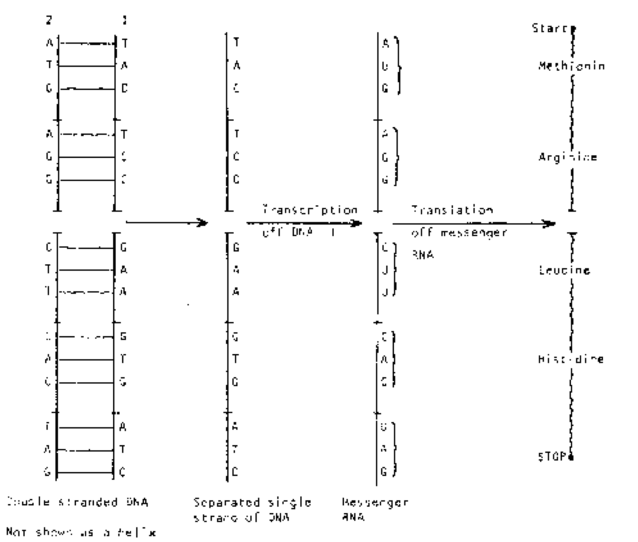


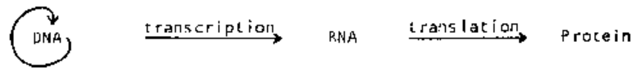
Figure 3. Involvement of DNA and RNA *in polypeptide chain formation (protein synthesis). Please note the start (Mon* AUG *and the stop colon UAG. Note also that only a short sequence of DNA, RNA and protein chains are shown.*

The second requirement is for the genetic material to function as a blueprint for all the proteins necessary for the cell to function. This blueprint was found to be controlled by the sequence of the four organic compounds making up DNA. These four compounds called nucleotides are arranged in groups of 3, and each group (codon) codes for one amino acid.

The third requirement is for the genetic material to be mutable. DNA must be stable from generation to generation, yet it must be capable of change under certain conditions to afford natural selection an opportunity to work. This is a critical requirement in an ever-changing environment.

Transcription and Translation

There is an intermediate step in protein synthesis involving ribonucleic acid (RNA), which is very similar to DNA. DNA is first copied (transcribed) on a single strand of RNA, which then *translates* the coded message into protein:



Translation of the messenger RNA into a protein is a complex process. The RNA strand specifies which amino acids will be included in the final protein, but to do this a highly specialized group of cellular structures called ribosomes take an active part.

The ribosome acts as a tiny machine translating the genetic information on the messenger RNA strand into the appropriate amino acid sequence for a protein. The ribosome binds tightly to the RNA strand, holds the amino acid specified by the RNA strand at its current position and attaches this amino acid to the part of the amino acid chain already assembled. As the ribosome moves along the RNA strand, new amino acids are specified by the RNA strand along its length. Thus the amino acids grow into a long strand of protein (polypeptide) as the ribosome moves along the RNA strand.

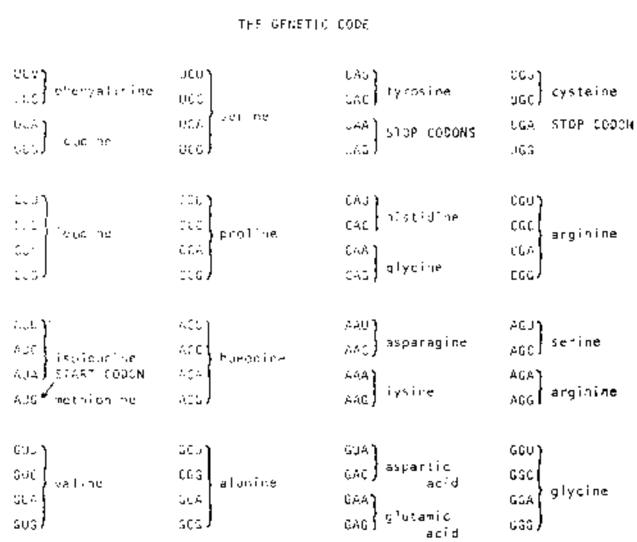


Figure 4. The messenger RNA Codons for amino acids. You will observe that the code is degenerate, which means that there are more than one codon for each amino acid.

DNA and Genes

DNA is the means by which genetic information from one generation passes to the next generation. Before the discovery of DNA, the gene was defined as the smallest genetic unit, but this is no longer a good definition. It is probably easier to look at what a gene does than to define the term.

Groups of nucleotides along a strand of DNA function as genes. Genes have no fixed size but are made up of relatively large numbers of nucleotides, say 600-1800. The number of nucleotides which an individual gene contains has been calculated from the number of amino acids in the protein it produces.

The important point is that DNA possess enormous number of possible combinations for ordering amino acids and thus for determining protein structures.

Mutations

Any change in the base arrangement along the DNA strand may cause a change in the amino acid sequence — and therefore the final product. The changed protein, or enzyme, may he better or worse than the original one. Such a change in the base sequence of DNA within the 600-1800 base pairs in a gene is called a mutation. When a mutation occurs, the gene becomes slightly different from the gene it matches on the other paired chromosome. This modified gene is called an allele. The amino acid chain produced by such an allele may be slightly different from the chain produced by the unmutated gene and cause no real difficulty. Conversely, a radical difference may produce a defective amino acid chain and cause death.

As an example of how a single base change can affect the health of humans, we will look at hemoglobin, an essential part of blood. Asa result of the substitution of a single base at position six of the DNA, the amino acid valise is substituted for glutamine.

NORMAL HEMOGLOBIN- Hb^A

		1	2	3	4	5	6	7	8
Hb^A:	DNA:	CAA	GTA	GAA	TGA	GGA	CTC	CTC	TTT
	mRNA:	GUU	CAU	CUU	ACU	CCU	GAG	GAG	AAA
Sequence of Amino Acids:		val	his	Leu	Thr	pro	glu	glu	lys

SICKLE CELL ANEMIA- Hb^S

Hb^S:	DNA:	CAA	GTA	GAA	TGA	GGA	CAC	CTC	TTT
	mRNA:	GUU	CAU	CUU	ACU	CCU	GUG	GAG	AAA
Sequence of Amino Acids:		val	his	Leu	Thr	pro	val	glu	lys

Figure 5. First 8 colons of the gene coding for normal hemoglobin and the gene coding for the form of hemoglobin found in people suffering from sickle-cell anemia.

This is a change of only one amino acid in a long sequence of amino acids, yet the defective hemoglobin molecule produced by this change causes people with only this hemoglobin to suffer from sickle-cell anemia, a severe disease which causes death. Persons who have one normal gene and a mutant allele are said to have sickle-cell trait, a far less serious disease.

Selection

When Charles Darwin shook the English-speaking world by publishing his observations on evolution and selection, he challenged the doctrine that species were fixed and unchanging. He wrote that new species continuously arose from previous species by selection. The mechanics of the process were not understood then, but with the modern understanding of DNA structure it is much easier to grasp.

As we saw in the sickle-cell anemia mutation, a single base-pair change in DNA produces a different ype of hemoglobin. This mutant gene is recessive. If genes on both chromosomes are of the mutant type, an individual will die prior to reproduction. If a mutant gene plus a normal gene is present, the individual is less fit than persons having unmutated genes on both chromosomes but can usually live normally and reproduce.

With selection acting against the sickle-cell trait, it is puzzling that a large part of the population in certain areas of the world has both mutant and normal forms of this gene. This condition exists because people with the sickle-cell trait are more resistant to malaria, and it is precisely in those areas in Africa and near the Mediterranean where malaria is a major health hazard that sickle-cell anemia is most common.

A buildup of phenotypes with the sickle-cell trait has occurred. Genotypes with two genes (homozygous) for the mutant allele were eliminated from the population before reproduction. Genotypes with two normal genes were susceptible to malaria and were often killed by the disease, but many individuals with one normal and one mutant gene survived. The normal gene produced enough good hemoglobin for survival, while the mutant gene produced enough defective hemoglobin to reduce susceptibility to malaria.

Selection works continuously in nature, but for natural selection to operate there must be some difference between genotypes. Mutation provides this difference, and most mutant forms are promptly selected against and disappear from the population. A mutation occurs very rarely which allows individuals to more efficiently compete within a population. Such individuals will have a selective advantage and over long periods of time will tend to predominate in a population.

The terms "struggle for existence" or "survival of the fittest- have a different meaning in evolution than in describing a death struggle between individuals. More significant than the ability simply to survive is the ability to reproduce. In cut-over native stands of loblolly pine, large-crowned trees may produce several thousand more seed each year than adjacent small-crowned trees. The latter are desirable for industrial use, but the former will, by the sheer numbers of seed produced, leave more offspring and thus contribute more genes to the next generation.

Speciation

The formation of new species requires both mutations and natural selection. Mutations provide raw material for natural selection to act upon. Many different mutants and a long period of time may be required before a substantial difference exists between a population and the parent species. Then some form of separation of the population from the species is required — this could be physical separation, climatic change, migration, or any number of similar events. Once the population is reproductively separated from the parent species, continuous action of mutation and selection will eventually change the genetic constitution of the isolated population until it is a different phenotype and genotype.

When the population has changed enough to appear different from the parent species, and when it can no longer breed with the original population a new species exists.

Chapter II

GENETICS OF NATURAL FOREST STANDS

Why It Is Important to Understand The Genetics of Natural Stands

Forest trees are different from agricultural crops in many ways. For example, they are still occurring in their natural state with, genetically speaking, rather limited human interference. Some of the best trees have been eliminated by high-grading, but the genetic effect is probably rather limited. This means that, in contrast with agricultural crops, which have been cultivated for thousands of years, forest stands still are a tremendous source of natural variation, which we can use and also need to protect. This fact has two consequences: 1) We need to preserve these reservoirs of genetic variation as a source of future breeding stock. 2) We need to know the genetic mechanisms operating in natural stands to effectively utilize these trees in a breeding program.

Some of the Virtues of Diploidy and Sex

Most of the trees we are concerned with are diploid organisms and have two instead of one copy of each chromosome. There are two advantages to this:

1. Having a second chromosome is like having an extra copy of a letter. If one gets mutilated, you still have all the information in the other. Similarly, a mutation (a mistake in copying) in a single chromosome might knock out a particular gene and completely disable the organism, but if the organism has another copy of the chromosome, it still has all the information to produce the enzyme and survive.

2. Because of the second set of chromosomes, the plant is able to tolerate many of these copying mistakes. The sexual process causes the chromosomes to be separated and re-united in all kinds of combinations, some of which may be useful. Thus, in a haploid organism, any unfavorable mutation is immediately penalized, while in a diploid organism it can be preserved and a lot of variation can accumulate in a population.

Major Evolutionary Processes

There are four major evolutionary processes operating in natural forest stands: 1) Mutation, leading to variation; 2) Migration, such as movement of seed and pollen , 3) Hybridization; and 4) Natural selection.

Let us look at some of these individually. The first three processes are concerned with creating variation. Mutation is the basic creative force, and the other two serve to move and mix this variation. Selection, on the other hand, is the force that molds this variation into the existing shapes. There are different kinds of genetic variation, and the distinction is very important for breeding work. One type is called additive. This simply means that the seedlings resemble the average of their two parents. Another kind is called dominance variation. This means that the seedlings resemble one parent more than the other. Additive variation can be used readily in a seed orchard relying on random pollination, while dominance variation can only be used by making controlled crosses between specific parents.

Mutations. The following are the most significant facts about mutations:

1. Mutations occur at specific rates. In other words, the probability that a particular gene will mutate is normally constant.

2. Most of these mutations are harmful.

3. Most mutations are recessive. One reason for this is that the second gene will produce enough enzyme for the tree to survive. Dominant mutations are eliminated rapidly by natural selection.

4. An equilibrium will be established in a forest stand, keeping each mutant present in the forest at a steady level. The number of carriers of the recessive gene will increase, until so many mutant seedlings occur that the mutant genes will be eliminated at the same rate they are formed.

5. This equilibrium depends on the environment. If a change in the environment occurs, a new equilibrium will be established.

Migration. The most important means of migration in forest trees are pollen dispersal by wind or insects, and seed dispersal by wind, water, or animals. Since movement is limited, a forest tree population has an effective size depending on the number of individuals that can breed with each other and the limited distance a seed can move. In pine trees, it is estimated that the effective population size might be around 200 trees. Such an interbreeding population is sometimes called a "neighborhood."

Neighborhood sizes and shapes vary for different species. For instance, cottonwood, or other hardwoods that grow along streams, have neighborhoods which are long and narrow because their seed float down the river, causing a considerable flow of genes downstreams. This can have important practical consequences. It is, for instance, quite possible that in such a case seed sources may perform better upstream than at their native location, because genes, making the trees suited for the region upstream, are moving downstream faster than natural selection can eliminate them.

Hybridization. Normally, there are certain harriers to crossing between tree species. Such barriers may be incompatibility of pollen of one species with the female flowers of another, sterility of the hybrids, or differences in date of flowering. (This last factor is especially important in the southern pines.) These crossing barriers are only partial, and occasionally hybrids do occur. The genes from one species may enter a population of another species. This gene flow may be both ways or may he predominantly one-directional. The process of genes flowing from one species to another is called introgression. One often finds the formation of hybrid swarms and gene flow from one species to another.

Introgression is more likely to occur if there is a favorable environment for the hybrids. Disturbed environments are often favorable for the establishment of hybrids. Because of man-made disturbances, such environments are quite common. Similarly, introgression often occurs at the edge of a species range. There is a so-called tension zone at the limits of the species range. Again, this is an environment that may be favorable for hybrids. It is no coincidence that hybrids between loblolly and shortleaf pines are so common in East Texas.

Natural Selection. Natural selection is the force that molds all the variation and gives it shape. Darwin expressed this idea in the concepts of "The Struggle for Life" and "Survival of the Fittest." The last phrase does not mean survival of the fittest in the sense of the strongest individual, but survival of the most prolific. The tree that leaves the most seedlings contributes most to the next generation. This determines the course of evolution. Natural selection does not necessarily produce the type of tree most desirable from man's point of view. If a tree is scrawny looking, forked, and crooked, but has its many limbs full of cones, and is a prolific seed producer it will be favored by natural selection. Yet it is not the kind of tree any wood producer considers desirable.

The concept of the "Struggle for Life" is not one of a physical struggle in any real sense. As foresters, we are familiar with the concept of competition, and this is what is meant by "The Struggle for Life": Competition for resources such as light, water, nutrients and growing space. I recently saw a good example. We have just rogued an orchard in which every limb of one clone reached up into the canopy. About 30% of the dry weight of this clone was in stemwood and about 50% was in limbs, clearly a pretty bad arrangement from the point of view of wood production. On the other hand, the tree was competing very effectively for light, having all its needles in the upper part of the canopy.

Results of Evolutionary Forces

The final result of these forces is the creation of genetically different populations, adapted to different environments. This is the origin of geographic races. These races may vary gradually or there may be very sudden changes. When there is a sudden change or a marked contrast they are called ecotypes. Gradual changes are referred to as dines. Both can be extremely useful in a breeding program. The "Lost Pines" in Bastrop, e.g., are adapted to a very droughty environment. Here is a ready-made selection that is useful for human purposes.

Summary

Four major evolutionary processes are operating in forest-tree populations: mutation, hybridization, migration and natural selection.

Most mutations are harmful, most are recessive. An equilibrium is established that depends on the environment. If the environment changes, the equilibrium is affected, changing the genetic make-up of the population. This results in the formation of geographic races.

Migration is caused by pollen dispersal by wind and insects, and seed dispersal by wind, water and animals. A population can be thought of as subdivided into smaller breeding units or neighborhoods of rather limited effective population size. The size and shape of these neighborhoods depends on the species.

There are very few barriers to crossing between species that are perfect, and often a certain amount of hybridization takes place. This occurs particularly in disturbed environments and leads to introgression, or a flow of genes from one species to another.

Natural selection is the force that gives shape to the highly variable population. The most prolific individuals will contribute most to the following generation. Success often depends on effective competition for resources, such as light, water and nutrients. As a result of selection, geographic races develop adapted to different environments.

Chapter III

GEOGRAPHIC VARIATION IN LOBLOLLY, SHORTLEAF AND SLASH PINE

Geographic variation exists in trees just as it exists in other plants and animals. The reasons for geographic variation are complex because of the many factors which have worked to gether to produce the geographic differences in trees which can be detected.

The development of differences within species has taken a long time, perhaps hundreds of thousands of years, and has occurred over a great many different types of climate. During this time period many types of mutations have occurred in trees and have formed the genetic basis for geographic variation. Crossing among mutants results in turn in new genetic combinations slightly different from the parent stock. Selection has favored some genetic types (genotypes) in certain parts of the species range while trees with a slightly different genetic composition were selected against and gradually disappeared in that part of the species range. This is illustrated by the drought resistance found in the western extreme of the loblolly pine range. Over a long period of time trees in different geographic areas have become genetically different from trees in other geographic areas. Within any geographic area there remains a lot of genetic variability or genetic differences among the trees occupying the area but these trees have more genes and mutations in common than do trees from different geographic areas.

As already indicated "survival of the fittest" means survival of the most reproductively fit. Those trees which successfully produce large numbers of offspring will eventually predominate in a population over trees which produce few offspring if all other factors are equal. Trees which can best reproduce under specific environmental conditions in one part of the species range have such a reproductive advantage. Each different geographic area within the range will tend to have a population of such trees but the distinction between adjacent geographic areas will be smaller than the differences between tree populations from distant geographic areas.

With this in mind it is somewhat easier to understand some of the differences in the major Southern pines which have been observed when trees from one area have been moved to a different area as in geographic seed source studies.

Briefly, it appears that local sources tend to become adapted to the worst possible climatic conditions that can be encountered in an area: specifically southern seed sources moved into a northern area are less conservative than local seed sources: they start to grow sooner and grow longer because in their native area it is safe to do so. This lack of conservatism may lead to increased growth in most of the species range but at the northern edge the climatic differences are great and may approach the maximum cold limits the species can endure in its native habitat. Under these conditions increased frost damage in both late spring and early fall reduce the growth advantage the species gains by starting early and growing later than local species. Reduced survival will result when the maximum low temperature to which the species is adapted is surpassed. Under these conditions local seed are better suited for planting and will probably grow better than more southern seed sources.

Loblolly Pine

Movement of seed from one geographic area to another area should be done only within rather carefully prescribed limits. Data accumulated over the past twenty years by Wakeley and Wells in the Southwide Pine Seed Source Study indicates that survival, growth, and disease resistance of loblolly pine is directly related to the source of the seed and the geographic planting area.

In general, loblolly can be moved safely from south to north for fairly long distances (up to 200 miles) and trees can be moved from west to east. Movement from east to west is less successful due to fusiform rust and drought. Natural hybridization between loblolly and shortleaf pine on the western extreme of the loblolly pine range has been suggested as the reason for increased drought and disease resistance.

In more specific instances, loblolly pine from Southeast Texas can be safely planted in all of East Texas, all of Louisiana west of the Mississippi river, and the non-mountainous areas of the southern half of Arkansas. Loblolly from southeastern Louisiana, especially Livingston Parish, can be planted eastward to the Atlantic Ocean and in the southern % of Mississippi, Alabama and Georgia. In the northern part of the natural range of loblolly pine local seed sources are a safe source of seed. Based on these studies it seems probable that definite growth increase could be obtained by moving trees within these boundaries but not to the extreme limits of the species range.

Shortleaf Pine

Shortleaf pine has shown a different survival pattern in these test plantings in the Western Gulf Region: there have been no marked differences in survival in the various seed sources. In northern tests northern trees exhibited better survival than southern seed sources.

The best growth was obtained when southern sources were planted up to 250 miles north of the point of seed origin.

Two important points should be made about the performance of shortleaf pine in these tests (1) actual gain in production may be obtained by moving the southernmost sources up to 250 miles north and (2) near the northern edge of the shortleaf range the best survival and growth can be obtained by using local sources.

Slash Pine

While differences in shortleaf and loblolly pine are relatively clearcut and easy to describe, differences in slash pine performance in geographic tests is much more difficult to define. This may be due to the much smaller geographic range of the species which is possibly more uniform than the range of the other major Southern pines. The species may not be subject to the diverse temperature and geographic extremes encountered by loblolly and shortleaf pine.

In the Southwide Seed Source study one important fact seems clear: slash pine seed from southern Florida performed poorly in field plantings. Differences in growth and survival for other sources were not readily identifiable. Other studies now underway confirm the poor showing of the Florida slash and indicate a difference in height growth among other sources. Also, Squillace (1966) was able to detect stand variation in both total height and stem diameter in slash pine, and has recently reported different patterns of resin production in different parts of Florida.

Until more information is available general comments on the advantages of moving slash pine progeny within its natural range are of little value.

In test plantings west of the natural range of slash pine, seed sources from southeastern Louisiana and western Mississippi have performed better than sources from the eastern part of the species range.

Chapter IV

ALTERNATIVE METHODS OF OBTAINING TREE IMPROVEMENT

When initiating a tree improvement program there are several alternative methods one might follow. Those that are currently being used are (1) mutation breeding, (2) use of exotics, (3) hybridization between species, and (4) selection of the best individuals from native species. Each method is ideally suited to certain conditions because of the biology of the organism and the use to which the crop is to be put.

Mutation Breeding

Although mutation breeding has been used successfully in some plant breeding programs, it is not yet a very useful tool in forest tree improvement. There are many reasons for this. The most important of these are covered below.

a. Most mutations are harmful.

A long-recognized problem is that the majority of mutations either decrease the vigor of the organism or kill it. Occasionally one does get a useful mutation, but it takes a tremendous amount of work, much, much more work than is justifiable in forest-tree improvement.

b. One-gene traits.

Mutation breeding has been most successful for trees with traits controlled by only one gene. Thus, a single mutation of only one gene resulted in changing the performance of the organism in the desired direction. In forest trees we are faced with the situation where we have many genes controlling each trait. Each gene then has only partial control of the performance of the organism. A mutation of only one or several of these multiple genes, even if it is in the desired direction would not help much in a practical breeding program.

c. Vegetatively reproduced crops.

Mutations are successful with a crop that can be vegetatively reproduced. If a good mutation is produced in one individual, the breeder creates exact reproductions of that plant by grafting or rooting. The southern pines can not presently be vegetatively reproduced on a mass scale. Introducing a single desirable mutation into your breeding stock by sexual means is a long, hard and probably impractical job.

Use of Exotics

Exotics have been successfully introduced into a forest economy when rather special conditions existed in regard to the native species. The native species were (a) limited in type, (b) lacking genetic variability and (c) of poor quality.

a. Limitation in type.

The ideal example of this is found in Australia and New Zealand. They need softwoods since the native species are essentially all hardwoods. Thus, slash, loblolly and Monterey pine were introduced to satisfy the demand for this type of wood.

b. Lack of genetic variability.

In the northeast, workers interested in tree improvement of red pine found that the genetic variability is very limited. There is little hope then that much genetic improvement can be obtained. Thus, they introduced scotch pine, it species having a great deal of variability.

c. Poor quality.

This situation exists in South Korea. The native Japanese red pine is very poor in form and growth rate. The Koreans are successfully using the loblolly-pitch hybrid to fill their needs.

Many exotics have been unsuccessfully introduced into the southeast. The reason for their failure is clear. The conditions needed for successful introduction do not exist in the southeast at the present time since our native pines fulfill most of our needs. Our species (1) produce the desired product, (2) have plenty of genetic variability and (3) produce a greater volume of wood of the desired quality than anything introduced.

Species Hybrids

When you choose a hybridization program, you are hoping either to obtain hybrid vigor or to combine in the hybrid desirable traits from the parents. Present research results indicate little hybrid vigor is to be obtained by species crosses in the southern pines. Desirable species traits may however be combined in a hybrid. Loblolly x shortleaf or slash x shortleaf hybrids may have potential in droughty and rust-hazard areas. Likewise, crosses within species among geographic races can yield new, useful genetic combinations.

Either within or between species hybridization to combine desirable traits can be useful in certain areas of the southern pine region. It is not nearly so pertinent to needs in the southwest because (1) rust is not nearly so bad a problem, (2) western loblolly is relatively rust resistant, and (3) western loblolly sources are drought hardy. However, you must remember that before you can be successful in a hybridization program, a very careful selection within each parental population must be made. Only the best parents will produce the best hybrids. This leads to the fourth alternative.

Selection of the Best Individuals from Native Species

This tree improvement method is best in situations where native species are of the desired type and quality and possess utilizable genetic variability in economically important characteristics. Our native southern pines are variable. There is utilizable variability at three levels. Geographic variability forms the highest level. There is also variability among stands and among trees within stands. The trees vary in form, growth rate, wood and fiber properties, survival ability, disease and insect resistance.

The native southern pines also are of the desired type and quality to produce the wood products needed by our wood-using industries. They produce a greater volume of wood than any non-native species. For these reasons, then, we feel that the mass selection approach of using the best individuals from our native species will yield the greatest gains in the first selection cycle.

This mass selection entails (1) selection of the best geographic source, (2) selection of the best individual trees within the best source, and (3) progeny testing of the trees established in seed orchards.

Figure 6. Geneticist checks straightness on an 18-year-old loblolly pine second generation selection. Its family has produced an average of 41 percent more volume than unimproved parents.

Chapter V

THE SEED ORCHARD APPROACH TO TREE IMPROVEMENT

The seed orchard approach to tree improvement is not the only possible way to produce better trees. Many other approaches have been quite successful, such as, for instance, the introduction of exotics, (Monterey pine in Australia), clonal line breeding (cottonwood), the establishment of seed production areas, or mass hybridization (the pitch pine-loblolly pine hybrid in Korea).

The seed orchard approach is most suitable for current needs in the South for the following reasons:

1. The nature of the species we are working with makes selection in natural stands and plantations the most promising.

2. We need large amounts of seed to fill our projected planting needs.

3. The need for seed is extremely urgent.

The Seed Orchard Concept

The seed orchard concept provides a solution for the immediate problems in the South. It involves the following steps.

1. Mass selection of desirable trees in natural stands and plantations.

2. Setting up seed orchards, using these selected trees as parents or as a source of grafts.

3. Progeny testing the seed orchards.

4. Roguing the seed orchards on the basis of the results of the progeny tests.

A number of studies of the genetics of southern pines have shown that, on the average, selection is a more promising approach to tree improvement of the southern pines than hybridization. Hybridization may be useful in some cases but would have to be preceded by selection anyway. Mass selection in existing forest tree stands is therefore obviously the first step in any tree improvement program.

Because of the great urgency of the need for improved seed the next step is immediate establishment of seed orchards. The genetic value of the selections, however, is still unproven, since the selected trees owe their desirable qualities in part to what they inherited from their parents and in part to the environment in which they grew up. It is therefore necessary to follow up the establishment of the orchard by testing the progeny of the selected trees. A number of trees thus will be carried in the seed orchard which will turn out to be undesirable from a genetic point of view. This is the price we pay to have seed available 15 to 20 years sooner than would be the case if the progeny testing were done before the orchard was established, as is the common procedure in agricultural and horticultural breeding.

Grafted Versus Seedlings Seed Orchards

The advantages of grafted seed orchards are:

1. They can be established in a short period of time.

2. Rapid genetic gain is obtained.

3. Grafts tend to flower early.

The disadvantages are:

1. The high cost of grafting.

2. The problems some clones experience with incompatibility.

The advantages of seedling seed orchards set up from wind pollinated seed are:

1. It is fast.

2. It is cheap.

The disadvantages are:

1. Only a small genetic gain is obtained.

2. They are slower to flower than grafted orchards.

The advantages of setting up a seedling seed orchard from controlled pollinated seed is that a high genetic gain is obtainable, possibly somewhat higher than a grafted orchard.

The disadvantages are:

1. They are slow to set up.

2. They are slow to flower.

3. It is fully as costly as setting up a grafted orchard if not more so.

4. More selections are needed to minimize inbreeding.

5. The orchards are considerably more complex than grafted seed orchards and therefore more difficult to handle.

Combined Progeny Testing and Seed Orchards

A number of researchers have advocated to combine progeny tests and seed orchards to reduce cost and obtain greater genetic gains. There are very serious objections to this procedure, however, because basically the two ideas are incompatible. Progeny testing should be done under the circumstances under which one expects to grow the seedlings commercially. In other words progeny tests should be grown at fairly close spacings and should not be babied. On the other hand seed orchards require wide spacing for early seed production, fertilization and irrigation. Under these circumstances growth, form and susceptibility to diseases and insects would be seriously altered, making a satisfactory evaluation of the progenies impossible.

Figure 7. Recently primed slash pine seed orchard of Texas Forest Service.

Chapter VI

SELECTION, GENETIC GAIN, AND GRADING SYSTEMS

To predict the gain from selecting certain trees as parents for the next generation, it is necessary to describe the group of trees (referred to as the population) from which these parents were selected and the method used to select them. In this chapter the theory of selection and prediction of genetic gain will be discussed. The fundamentals behind the grading system will also be examined, and these will be tied in with the gains from selection.

Selection Theory

To predict gains from selection, certain descriptive measurements are needed of the population from which the parents are selected. These measurements serve to characterize a particular tree population, just as body measurements describe a person. Knowledge of the population characteristics allows you to predict selection gains, just as chest and sleeve measurements allow a store clerk to provide you with a proper size shirt.

Whenever all the trees of a population are measured and these measurements are plotted on a graph according to their frequency of occurrence, a predictable curve may be drawn around the points. It is the well-known bell-shaped curve.

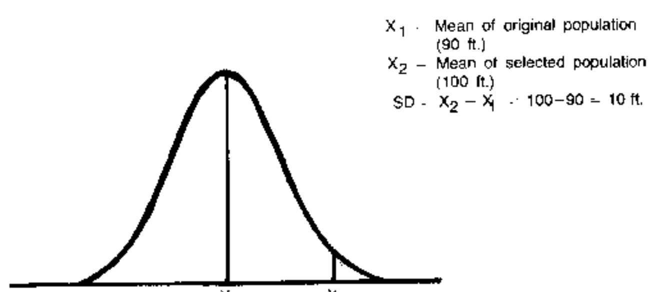


Figure 8. Distribution of tree heights in a forest stand.

Assume that Figure 8 was obtained from measurements of tree heights. We see that there are a large number of height measurements near the center of the bell (the population mean), with smaller and smaller numbers of such measurements either above or below the mean. For illustrative purposes, we can assume that this curve describes the distribution of heights within a stand of loblolly pine where you are going to make superior tree selections. Since you are interested in obtaining taller trees, you would select as parents of the next generation only individuals from the upper end of the distribution. You can easily calculate the average height of the selected trees, and the average height of all the trees in the stand. Assume that the average stand height (Xi) equals 90 feet, and the average height of the selected trees (X2) 100 feet. The difference between these two measurements 100-90 or 10 feet is known as the selection differential (SD). The selection differential is one of the two characteristics needed to describe the tree population in order to make predictions of genetic gain.

The second characteristic needed is the heritability (h^2). Simply said, a heritability measurement describes what portion of the superiority of the parents is inherited. Expressing the same thing another way, the heritability is the genetic portion of the differences between trees. The remaining portion is caused by differences in the environment. If the height of the offspring exactly equals the parental height at an equivalent age, then the heritability for that characteristic is one. The less the offspring resemble the parents the closer the heritability approaches zero. Generally in forestry our heritabilities are less than 0.5.

Knowing these two population characteristics, you can calculate how much gain in total tree height you should realize if you mate the selected individuals among themselves and then measure the height of their offspring. Gain is calculated by multiplying the selection differential (SD) by the heritability (h^2).

$$\text{Gain} = \text{SD} \times h2$$

Assume that we have a heritability for total height of 0.5 and a selection differential of 10 feet. Gain would then be (.5) (10) or 5 feet. Therefore, the new population obtained from matings among our selected trees should have an average height of 90 + 5 or 95 feet.

You might naturally ask, how can we get a greater gain? This can be accomplished in one of two ways, one way is to raise the selection differential. Say for instance, that we had not picked the tallest trees for the parents of our next generation. We now find that by more diligently searching our stand we can find trees that average 110 feet in total height rather than 100 feet. Our selection differential is then 20 feet instead of 10, and the corresponding gain would he (.5) (20) or 10 feet.

The second way of obtaining greater gain is to somehow raise the heritability value. This may be accomplished by including more genetic differences or making the environment more uniform. In the case of superior tree selection this is done by making selections in well-stocked, even-aged, non-highgraded stands.

Grading Systems

Most breeding programs attempt to obtain improvement in more than one trait. However, some traits are more strongly inherited than others. Likewise, improvement in some traits brings more economic return than equal improvement in others. Some method must be used to combine the several traits, their inheritance values, and their economic values into a single expression, one which weights each factor according to its merit. This is done by the grading system.

Generally, a tree is given a total score which is the sum of various points for height, diameter and form characteristics. The higher the score the better the tree. Put in equation form: total score = height score + diameter score + form score. In most grading systems more possible points are obtainable in some traits than others. Typically, growth characteristics are weighted more heavily than form characteristics. This differential weighting arises because of differences in economic importance and inheritance values.

An examination of the mechanics of the grading system is helpful. The individual point values assigned to each characteristic are arrived at by taking into account the probable gain for a characteristic weighted by the economic worth of this gain. Total tree score equals GiEi + G2E2 + G3E3 where:

GI = expected gain in height growth

El = economic worth of this gain

G2 = expected gain in diameter growth

E2 = economic worth of this gain

G3 = expected gain in form characteristics

E3 = economic worth of this gain

This equation could easily be extended to include more characteristics. However, the more characteristics are being selected for, the less gain is made in each individual characteristic.

Remember from the previous discussion that expected gain in each characteristic is determined by the selection differential and the heritability. We see then that the point score for one characteristic is arrived at by taking into account three factors: (1) the amount of superiority of a trait, (2) the strength of inheritance of the trait, (3) the economic worth of this superiority. Thus a characteristic with a very high expected gain but little economic value would be assigned only a few possible points in the grading system no matter how large the selection differential attainable. A characteristic with a medium amount of expected gain but high economic worth would be assigned a large number of possible points.

It is important to note that the values in the equation will remain the same from organization to organization for a given selection differential. However, the economic worth may vary from organization to organization. Thus a tree could score quite high for one organization but be barely acceptable for another.

An example is given below. We have a grading system set up with the maximum possible points as follows: height = 50, diameter = 30, and form = 20. The maximum score is 100, with less than 80 being a non-acceptable tree. Let's examine the weights given by two different organizations.

Economic weights for various characteristics

	Company 1	Company 2
Height	1	1.5
Diameter	1	.8
Form	1	.05

Company one weights all traits equally hut company two puts more emphasis on volume than on form. Suppose we have a tree scoring 85 points distributed as height = 35, diameter = 30, form = 20. Let's apply the weights for each company. The score for company one is still 85; therefore the tree is acceptable. The score for company two is 77.5; the tree is not acceptable. It is very important to keep this in mind when contemplating obtaining trees from other organizations to use in your own program.

Characteristics Being Sought in Superior Trees

Not all organizations are selecting for or attach equal importance to the traits listed. However, the majority of those listed are included in most of the grading systems. Many of the grading systems in use today, at least in the southeastern U.S., are quite similar in stressing volume superiority and form. Individual organizations differ widely in their requirements for wood properties. In all cases the exact procedure followed should be adapted to the biology of the species. One cannot select a black cherry following a procedure developed for loblolly pine.

Characteristics

Superior height growth rate.
Superior diameter growth rate.
Good pruning ability.
Straight, no crook or spiral bole.
Flat branch angle.
Narrow, compact, well formed crown.
Disease resistance.
Insect resistance.
Drought hardiness.
Wood characteristics.
Cold hardiness.

Where to Look

Dense even-aged stands on good timber sites offer the best chance for finding select tree candidates. A good site will allow a tree to express any genetic superiority it may have, and a dense even-aged stand offers competition among trees.

This does not mean that genetically desirable trees do not occur in uneven-aged or open stands. It simply means that it is difficult to evaluate trees in such stands as some trees will have an unfair competitive advantage due to age or growing space. A select tree must he judged on how well it will do in a competitive situation against trees its own age.

For some purposes it may not be possible or desirable to select from dense even-aged stands. For example, trees selected for their adaptability to marginal sites would normally be selected from such marginal sites. Similarly, some hardwood species are rarely found in even-aged stands.

Stands can be natural or planted. Caution must be exercised before selecting from plantations because their geographic origin is often not known. Certainly the available knowledge on desirability of geographic sources should be exploited whenever tree selections are made (See Chapter III).

Stand age is also important. The performance of a tree in a very young or very old stand is not necessarily a good indication of its potential at rotation age. Performance at one-half the rotation age is probably a good index, but superiority at rotation age is what counts.

Maintaining a Broad Genetic Base

Forest trees have an extremely long cycle compared to other agricultural crops. From seed collection to harvest may require 20 years or more. Even in intensive plantation culture of southern pines a substantial time factor is involved. The production cost and the value of the final crop make it important to use the most productive seed sources to maximize production from each acre.

Through forest genetics it is possible to greatly increase wood production and at the same time improve wood quality. Yet there are some inherent dangers in any artificial selection and breeding system which does not make adequate provisions for the ever changing populations of forest disease organisms and insect pests. This point has been repeatedly emphasized by disasters which have occurred in narrow-genetic-based agricultural crops. In forestry it is imperative that we build safeguards into our selected population to prevent such catastrophies. The long lead time required to develop improved trees does not allow us the same margin for error that annual crop breeders have.

Chapter VII

SEED ORCHARD ESTABLISHMENT

Seed orchard establishment includes the following major steps: site selection, site preparation, design of the orchard, and establishment of the grafts.

Site Selection

The first and most critical step is the selection of the seed orchard site. It will have to support the orchard for as much as 40 years and can make or break the program. We now know a little about what constitutes a good site for a seed orchard.

1. The site should be intermediate in fertility. Very poor and extremely good sites have caused difficulties. If anything, a low fertility level is preferable since it can be readily corrected by fertilization.

2. It is extremely important to have good drainage in the orchard for several reasons:

a. Survival of grafts or understock for field grafting is better.

b. The area should be accessible for heavy equipment at all times.

3. The orchard should be located away from ice belts.

4. The orchard should not be too close to the coast, where there is danger of hurricanes.

5. The orchard should not be in an area where flooding by future man-made lakes can occur.

6. Accessability under all weather conditions.

Site Preparation

The next important step is site preparation. Since the expected life of an orchard is about 40 years, it is worth while to do a thorough job of site preparation, including stump removal and leveling if the site has a stand of trees on it. If ditch or flood irrigation is to be used, this should be taken into account.

Spacing

There are several common spacings in use and one of the most common is an initial 30 x 30 feet. Some orchards are being established on a 40 x 40 initial spacing while others are planted on a 30 x 15 spacing. Close spacing of 15 x 15 or even 20 x 20 will require roguing before 10 years and will present difficulties because at such an early age little information on progeny performance will be available. Close initial spacing will result in somewhat greater cone production after thinning because good seed producers will be favored.

A uniform and fairly wide spacing is highly desirable because of the nature of seed orchard establishment and management. Irregular spacing and poor design can cause problems in management for the entire life of the orchard.

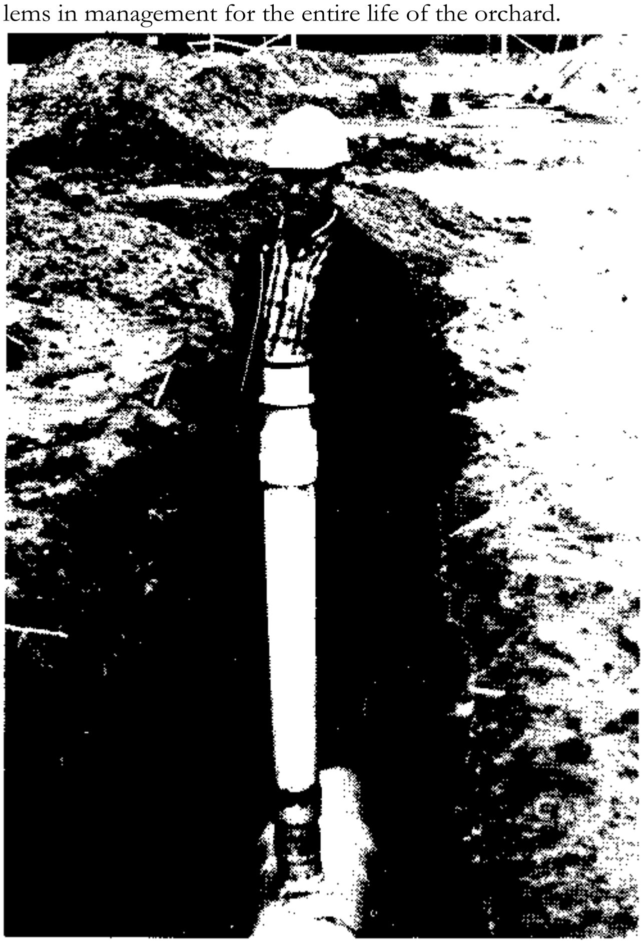


Figure 9. A permanent underground irrigation system is best installed prior to graft establishment. This main irrigation line supplied one of Weyerhaeuser's nurseries and the adjacent seed orchard.

Design

The main objectives in designing a seed orchard are:

1. Provide a sufficient number of clones to:

a. Reduce the risk of failure due to graft scion incompatibility or lack of cone production in some clones.

b. Provide for an opportunity to rogue.

c. Provide an adequate amount of material for future breeding. This objective is met by including 20 or more clones in the orchard.

2. Optimize cross pollination among clones. This can be accomplished by making sure that each tree in the orchard is surrounded by at least two rings of unrelated individuals.

3. Provide an adequate supply of improved pollen throughout the orchard. In first generation orchards this cannot be influenced by the design. In more advanced orchards special pollinator clones can he distributed through the orchard.

4. Minimize the proportion of contaminating pollen. For this reason the orchard is usually surrounded by a 400 foot wide isolation strip.

5. Minimize the amount of inbreeding in the orchard. In first generation orchards one can help the problem by not planting relatives or members of the same clone in close proximity. In more advanced orchards one can favor clones which are highly self-sterile or whose selfed progeny is as good as the crosses.

Establishment of Grafts

Since so far no practical method of rooting cuttings of the Southern pines has been developed, it is necessary to propagate selected pines by grafting. Some of the hardwoods by contrast can be successfully propagated by both methods.

Figure 10. The side graft is one of the most common types used for pines. The cleft graft, made by cutting off the top of the seedling and splitting the stem is also very poplar.

Three methods of grafting are in common use: pot grafting, nursery bed grafting and field grafting.

Pot grafting is fast and convenient, but will often result in pot binding. This in turn may lead to a poorly developed root system and produce trees susceptible to windthrow.

Grafting in the nursery bed avoids the problem of pot binding but necessitates transplanting the grafts. Grafts up to two feet can be successfully transplanted bare-root during the dormant season if they have been undercut early enough to provide an abundant lateral root system. They can also be transplanted with a ball of soil as soon as the graft union has firmly healed.

Field grafting involves planting several seedlings at each desired location and grafting on some of the best ones the following season. It is often the most successful of the three methods, but can result in several successful grafts at one location and none at another. A limited amount of transplanting is therefore necessary in conjunction with this method.

Chapter VIII

SEED ORCHARD MANAGEMENT

Most seed orchard practices are designed directly or indirectly to keep seed orchard trees healthy and to produce the maximum amount of seed. Management principles aimed at protection and the stimulation of seed production have been developed and applied with varying degrees of success.

Increased Flower Production

A combination of subsoiling, irrigation, and fertilization has been reported to substantially increase seed production in some orchards.

Disking. Although it has been shown that disking can promote flowering in orchards, especially the production of male flowers, a stable ground cover is usually desirable to prevent erosion and disking is a suitable treatment only under special conditions.

Subsoiling. Subsoiling is used to stimulate growth and seed production in orchard trees. It also prevents formation of above ground root surfaces which would be subject to injury and would provide infection points for disease.

Irrigation. Irrigation is a must during the establishment phase of a seed orchard. The season of irrigation in an established orchard is important. Irrigation during the first half of the summer and then subjecting the orchard to drought the second half has resulted in increased cone production.

Fertilization. It is difficult to generalize about fertilization because soil and climatic conditions influence the response of trees to fertilizer. In addition clones differ in their ability to respond to fertilizer with increased cone production.

Phosphorus has been shown to stimulate the production of both male and female flowers. The effect of nitrogen varies: at low levels it increases flowering and at high levels it decreases flowering.

A desired fertility level should be predetermined and a balanced commercial fertilizer applied, on the basis of soil tests, in amounts sufficient to attain the desired fertility level.

In a number of instances it has been shown that increased cone production resulted when irrigation and fertilization were applied simultaneously, while each one alone had only a small effect.

Girdling. Attempts to initiate distress flowering through girdling a part of the tree trunk has been tried on various size trees in both seed orchards and seed production areas. It has not been satisfactory as a practical method to stimulate cone production.

Pruning. Stimulation of flower production by various levels of pruning compared to unpruned controls has been tried experimentally. Again, no increase in flowering was noted.

Protection of the Seed Orchard

Fire. Because of the expense of establishing and maintaining a seed orchard, considerable effort should be made to remove any possibility of damage by fire. The precautions necessary to prevent fire depend on each individual orchard and should be considered as a part of a comprehensive seed orchard management plan.

Disease. Diseased grafts should be discarded prior to planting or removed as soon as possible after disease is detected in the planted grafts. The stumps of trees removed in roguing should be treated to prevent entry of *Fames annosus.*

Erosion. Orchards located on slopes may require terracing to prevent erosion. Even on relatively gentle slopes erosion can be a problem until a suitable ground cover is established. In choosing a ground cover the possibility of using a vacuum seed collection machine in the future should be considered.

Insects. In many orchards insect control is the number one problem. The problem is made even more serious by stringent laws governing the use of pesticides. Before an insecticide can *be* used in seed orchards, it must be registered for control of a specific insect species on a specific tree species. Registration of pesticides is a slow and costly process. For southern pine seed orchards, Guthion (azinphosmehtyl) has been registered for spray application to control cone worms.

The extent of cone and seed losses in an orchard is difficult to determine and a thorough study may be necessary to obtain an accurate estimate of losses. Some recent studies have shown annual losses of 50% and more of the potential seed crop.

Figure 11. Application of Guthion in Olinkraft's orchard with a hydraulic sprayer. Dioryctria *damage to the treated cone crop was estimated at only one percent.*

Because of the high value of the seed — estimates run from $100-$1,000 per pound — an adequate control program is extremely important even for moderate losses.

Maximum control does not necessarily follow adoption of a control system reported effective in another geographic region on a different tree species or even on the same tree species. Even control methods reported effective in the same general area may not work in a given orchard.

The possibility for developing biological insect control in the future holds some promise. Such controls are highly desirable but at present are not sufficiently developed for orchard use.

Another possibility is the increasing of orchard size to compensate for seed losses. This may be an admission of defeat but some spray programs have been so ineffective in the past that increasing the orchard size may be justified.

Figure 12. "Cherry-picker" used for cone collection. Since rental on this machine is almost $75 *per day, a good cone crop and careful management are required if its use is to he economically feasible.*

Chapter IX

PROGENY TESTING - PURPOSE AND PRINCIPLES

Introduction

The objectives of progeny testing are: (1) to evaluate family lines for the purpose of roguing seed orchards (2) to establish plantings from which to make second generation selections.

Genetic improvement in first generation orchards is obtained in two steps. Step one is the mass selection that is practiced in the original selection. Step two is the progeny testing and roguing of the seed orchards. Squillace[1] points out that the step in which one will get the greatest advance depends on how much of the variation is environmental and how much genetic. If most of the variation is genetic there is little additional gain from progeny testing. If most of the variation is environmental, one can make substantial gains from it. This is the situation for many characters, particularly those related to quantity production.

Second generation selection is the other major objective of progeny testing. In this step progeny test plantations are screened on the basis of characters desired and selections are made on the basis of periodic measurements and data collected on specific individuals or families within the test. Selections made in progeny test plantations are then entered into seed orchards to provide seed for field planting and for further selection.

Types of Progeny Tests

There are any number of progeny testing schemes, some of which are better than others. One can use open-pollinated or wind-pollinated seed. The seed can be obtained from the ortet or from the ramet. One can use controlled pollinated progeny tests, using a pollen mixture, or individual testers, following the four-tester or the five-tester scheme. One can use a scheme where the testers actually change from one clone to the next. Let us discuss briefly some of the advantages and disadvantages of these methods.

The wind-pollinated progeny tests have the advantages of being quick and cheap, as far as being established initially. Of course when it comes to making the measurements there is still a considerable job. They have a definite usefulness. If one can get an open-pollinated progeny test from the original selections one can get some early answers to help make decisions for the first roguing but it will not be an accurate base for the final roguing. Open-pollinated tests of seed collected from ramets in the orchard have a definite usefulness in that this is actually the seed that is coming out of the orchard and will be used for commercial production.

By far the best method is to use control pollinated seed. Different crossing schemes have different advantages. The use of pollen mixtures is rather undesirable. The pollen mix combines the worst features of the open pollinated and controlled pollinated progeny tests. It will give a general indication of the genetic quality of the tree, but open pollinated tests will give this type of information too. On the other hand there still is the expense of making the controlled crosses. The tester schemes are by far the best, both from the point of view of testing and providing material for second generation selections, and they are being generally used throughout the South. They give an exact evaluation of the clones and also may indicate a number of specific crosses which are outstanding. A summary of the advantages and disadvantages of different progeny testing methods is given in Table 1.

[1]Squillace, A. E. 1967. Selection of superior trees. Proceedings of the Ninth Southern Conference on Forest Tree Improvement. P. 7-9.

TABLE I
ADVANTAGES AND DISADVANTAGES OF DIFFERENT METHODS OF PROGENY TESTING

Type of Progeny Tests	Advantages	Disadvantages
Open pollinated.	1. Can be established easily. 2. Cheap.	1. Lack of precision. 2. Limited usefulness as source of second generation selections. 3. No information on specific combining ability.
Controlled crosses using pollen mixture.	1. Slightly cheaper than individual crosses.	1. No information on specific combining ability. 2. Inbreeding will result if used for second generation selections.
Controlled crosses, using male parents. (four tester)	1. High precision. 2. Gives information on specific combining ability.	1. Costly. 2. Gives a narrow genetic base for second generation selections.
Controlled crosses, using small diallels.	1. High precision. 2. Excellent for second generation selections. 3. Gives maximum information on specific combining ability.	1. Costly.

Different tester schemes have been proposed to increase the number of parents acting as male and female parents in progeny tests. One, the four tester scheme, utilizes four male parents on all females in the orchard. This system works well in practice and gives good base line control in progeny tests hut has a serious drawback when future selections (second generation selections) are made from the progeny test material. Many trees in the progeny test will be closely related, leading to a narrow genetic base and considerable inbreeding in future generations.

To avoid this type of inbreeding situation other methods of crossing have been advocated which would reduce the potential for inbreeding and still maintain reasonable control material to act as a base line in progeny tests. One such system is a scheme in which a series of small independent diallels crosses are made (each possible male x female cross within a selected groups of trees) and the progeny from these crosses are planted and used as in the four-tester system.

An alternative is a variable tester scheme in which each successive clone has one new tester added and one of the previous testers dropped.

Progenies from these systems will possess fewer parents in common than in the four-tester system, will provide an adequate base line for comparison of progenies, and will offer more possible unrelated candidates for second generation selection. Information on specific combining ability will also be available.

What Makes a Good Progeny Test

Now let us look at some of the requirements for a good progeny test. First of all, uniformity of site is important. It is not impossible but prohibitively costly to carry out a good progeny test on a highly variable site, since each family would have to be repeated many times to average out the site effects.

Secondly, the test needs to be replicated. Even on the most uniform site there are differences in soil composition, drainage and fertility which make it necessary to repeat the plantings several times. Replication should be done both in space and in time.

The replication in space has a two-fold purpose. First of all, the test should be replicated a number of times on the same site to average out site variations. Secondly, it is quite useful to test the same progenies on more than one site, since they may not perform as well on one soil as they do on another.

It is also important to plant the same test out in different years, since the weather may vary greatly from year to year. Some progenies may stand up much better under a summer drought, for instance, than others, and planting a test in only one year may not give this type of information.

Two kinds of control seed lots should be included in progeny tests. One type is used to determine the progress made and consists of nursery run stock. The other type is used as a common base for comparing partial plantings made in different years at different planting sites. The need for this second type becomes apparent when one considers the time required to obtain all desired crosses in a seed orchard. To avoid this extensive delay partial plantings are made as the seed becomes available and the common base is used to compare test plantations of progeny from different parental combinations separated by both time and distance. An example of such a comparison base is the six crosses available among testers in a four-tester scheme. These crosses are planted in all test plantings.

Next in importance is proper randomization. If the families were always planted in the same order, erroneous results could easily be obtained if there was a gradual change in site from one side of the test area to the other. Errors would also be introduced by the suppression of families which start growth slowly if they were consistently planted next to a very fast growing family.

The conditions under which the test is carried out is also of critical importance. The test should be established on a site which is typical of the sites on which the seedlings will be planted commercially. The spacing should be closely the same to commercial spacing and the thinning regime should also duplicate that to which the seedlings raised from the orchards will be subjected. The golden rule for progeny testing in this respect is "Treat the test seedlings as you expect the commercial seedlings obtained from the seed orchard will be treated."

Finally, the progeny tests will need to be carried out over a sufficiently long period. Early results may be interesting, but fast starters may run out of steam early and slow starters may be good growers at a later age. Ideally a progeny test should be left for the full rotation age. The limited experience available so far indicate that at about half of the rotation age meaningful results can be obtained.

Some Practical Aspects of Progeny Testing

Handling of progeny test material in nursery. The basic cultural techniques used for commercial planting stock apply to progeny test materials. Standard-size nursery beds and standard bed preparation should be used. Seed preparation is the same with bird repellants and fungicide being used as treatments. The seed are stratified if stratification is required by the species. However, due to the high value of progeny test seed, great care must be used in selecting a nursery bed location which will not be subject to poor drainage or flooding and which will have the most homogeneous soil available in the nursery. Nursery accidents are extremely damaging if progeny test material is destroyed.

Replication within the nursery bed is important. Non-uniform soil in the nursery bed may provide conditions which greatly favor or penalize seedlings grown in a particular nursery location. Non-uniform irrigation, nursery accidents caused by man, insect, or disease can destroy a portion of the seedlings in a nursery bed in a short time. Adequate replication within the nursery bed provides a measure of safety against such events and increases the probability that all seedlings used in field tests are the products of reasonably uniform nursery conditions. Seed sources used as checks should be treated exactly as test seed lots, planted in replications within the same bed and lifted and outplanted at the same time that test seedlings are planted.

Site preparation. Site preparation includes all necessary steps for getting the site ready for planting. This may include land clearing, windrowing and burning. Burning of windrowed material greatly improves the site of the burn therefore windrows should be spaced in such a way as to minimize their influence on the progeny test when it is planted.

The important point to remember about site preparation is that it is essentially the same for routine planting or progeny test planting. The objective is to determine how well the test material will perform in the field and in competition with other seedlings in the progeny test planting.

Field planting. This is one of the most critical steps in progeny testing. A poorly designed or replicated plot on a highly variable site will yield little reliable information. Careless handling of test seedlings may greatly reduce vigor and initial growth or even substantially reduce survival.

The actual planting procedures and spacings are individual matters but it is of critical importance to treat all test material uniformly. Accidentally subjecting a part of the test seedlings to stresses or exceptionally favorable conditions not experienced by the remainder of the progeny in the test will produce an error in analysis of the data obtained from the tests: for analysis of data all seedlings are assumed to have grown under identical conditions.

Silcicultural treatment of the progeny tests. Thinning progeny tests can be a difficult problem. The commercial practice to be followed with the improved seedlings should be the basis for any thinning done in progeny test plantations. Row thinning or silvicultural thinnings will be made depending upon which type thinnings are planned for the improved seedlings. If no thinning is planned prior to rotation age of production plantations then test plantations should not be thinned.

In most instances, progeny tests should be treated as ordinary production plantations. This implies that only routine protective measures should be used to control diseases, insects and animals. There is one exception to this: if an unexpected danger threatens to destroy the entire progeny test, immediate control is justified.

Records. Record keeping is the most critical step in progeny testing.

A mistake in labeling produces results which are erroneous and a lost label can create a useless test planting.

The correct and adequate labeling of test plantings is the first step in record keeping. Any system used must provide for permanence and be accurate in such detail that future workers unfamiliar with the plot can easily identify all sources with a minimum of confusion. An important point is that these are long-term projects and the individual supervising the planting will probably not be the one who makes the first measurement in five years and almost certainly will not make the fifteen-year measurements.

Measurements to be made. A number of measurements will have to be obtained over a period of years. These will include routine height and diameter measurements and later specific gravity and disease resistance evaluations. Great care must be exercised in accurately recording all data; carelessness may require another trip to the field to correct errors found in the original measurements.

Early measurements may give an indication of outstandingly good or poor families. Relative performance is not static, however, and considerable shifting in rank takes place until about half the rotation age is reached. After the mid-point of the rotation is reached more stable relationships usually develop.

Chapter X

WHAT RESULTS CAN WE EXPECT

By the way of conclusion let us look at the things that already have been achieved by a variety of people in the field of tree improvement and the accomplishments we can look forward to in the near future. Let us first look at some of the fringe benefits. There are a number of things one gets out of a tree improvement program besides improved seed. One is the establishment of a stable seed source. Knowing where your seed is coming from and obtaining it from the proper geographic area are substantial achievements. Stopping the erosion of quality that is going on now is another important outcome. Last but not least is the availability of an assured supply of seed for the ever-increasing planting programs.

Information is available from heritability studies and progeny tests which have been carried on in many different places in the South. These tests, some over 20 years old, show that *we* can expect gains in excess of 10 percent in each individual characteristic. The total improvement will be more than 10 percent because trees are selected for many different traits. On the other hand, it is not correct to simply add the progress in each trait. A gain in one trait might cause a slight loss in another. However, gains in traits such as height and diameter will cause a corresponding increase in volume production.

When gain figures are reported, the methods used calculating gains should he clearly understood. far most programs standard reporting procedures present gains in terms of percentages compared to a standard check source. The control approximates the production from unselected or - average - planting stock. This ensures that the gains are due to genetic characteristics and not the environment.

Rather than a percentage gain, this information can be presented in terms of standard deviations from a population mean. In both cases the intent is the same: comparison of growth and yield between progeny from selected and unselected trees.

The ultimate requirement for a progeny test is to provide data as a solid basis for decisions on whether to keep families or individuals for future breeding or whether these individuals or families should be discarded.

In short, we must know how to accurately determine how well a selected tree will grow and yield when planted as a crop tree.

Strangely enough, it seems that no matter how strongly a character is inherited the gain estimated is about 10%. The character that is controlled strongest by genetics is wood specific gravity. Progeny tests show that wood specific gravity is about 50% inherited. This means that if the average specific gravity is .52, as it is in Texas, and one selects trees with a specific gravity of .62, the seedlings from these trees will have a specific gravity of .57 at the same age and under the same growing conditions.

This represents about a 10% gain. A character like height is only about 20 to 25% inherited. The range to select from is much greater, however, and the expected gain is again about 10%. Diameter is tremendously affected by the environment and has a wide response range but quite a low heritability. This is reflected in progeny of loblolly pine from the same parent grown at two different spacings, for instance 6 x 8 and 10 x 10 feet. While the average height of the two tests will be approximately equal, the average diameter of the 10 x 10 spacing can be as much as two inches more than the 6 x 8 spacing. Genetically the two plots are composed of the same material, but the different environment of the added growing space will make a substantial difference in average diameter. The two factors again compensate for each other, and the expected gain is 10%.

In East Texas it seems that volume growth and wood specific gravity are correlated. On the average there is a reduction in specific gravity with increased volume growth. The correlation is not strong however, and some fast growing families have high specific gravity as well. The most important point is that one cannot take either volume growth or wood specific gravity alone and know what the production is in terms of tons of dry wood per acre. It is best to determine both volume growth and wood specific gravity, and calculate the total amount of dry wood produced. This is the production figure that is really meaningful to the pulp and paper industry.

For the lumber and plywood industry the situation is different, since the main concern here is with board-foot volume. Specific gravity still comes into the picture, however, in terms of the quality of the wood; whether it will have the necessary strength, whether it will meet the specifications for plywood, etc. The actual cellulose production is not as important in this case.

Improvement in wood quality is a lot more involved and has been the subject of discussion for a long time, especially in the pulp and paper field. About 15 years ago very little was known about wood quality. Even people in the mill would not commit themselves on the kind of wood they wanted if we could grow it. In the last 15 years a great deal has been learned about the way wood quality does affect pulp and paper-making properties, but it is by no means simple and straightforward. The real crux of the matter is that one cannot give a general definition of good wood. One has to define it in terms of its use. What is good for the Texas Forest Service is not necessarily good for the world. Southland Paper Mills, Inc., for example, is particularly interested in low wood specific gravity, while Southwestern Timber Co. prefers high wood specific gravity. Once the use is known, one can begin to talk about quality. Wood properties such as specific gravity, fiber length and fiber wall thickness can be increased or decreased in any specified direction. This property is especially important in pulps made of Southern pine. Straightness and natural pruning also affect wood quality, since there will be less compression wood and fewer knots. This is of value for both lumber and paper.

There are several good examples of genetic gains by reduction in losses. In East Texas, drought resistance is the outstanding example. By increasing drought resistance, losses due to mortality during the first two years can be considerably reduced. Resistance to fusiform rust is another example. In a high-hazard area the reduction in losses will probably far exceed any gains which can be obtained by selection for volume production. The development of a brownspot resistance longleaf is also a good example. In this respect, hybridization can be particularly useful. The Southern Institute of Forest Genetics, for example, is developing a short leaf-slash pine hybrid resistant to fusiform rust. In Korea, hybridization has been made a spectacular success by the mass production of a hybrid between pitch pine and loblolly pine, a hybrid which is extremely well adapted to their conditions. As one can see, there is a definite role for selection as well as hybridization.

In conclusion, the original estimates of 5 percent to 10 percent improvement in productivity in one generation appear very conservative. Data from 15- and 20-year old Texas Forest Service progeny tests have shown volume gains of 6.9 percent before roguing for trees selected for good growth rate and form. After roguing, these selected trees had a volume gain of 19.7 percent more than nursery-run checks. While this roguing removed only those trees whose progeny were producing less than nursery-run checks, a heavier roguing would produce a substantially larger volume gain. Reports from other tree improvement programs working with southern pine indicate similar volume gains. Volume production gains of this rate are possible for several generations. In addition to an increase in volume improvements in wood quality, grade yield and resistance to pests can be expected to make a substantial economic increase in productivity. These other improvements are not as easily quantified.

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