EXAMINATION OF SEVERAL DROUGHT RESISTANCE PARAMETERS IN LOBLOLLY AND VIRGINIA PINE

By

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This study is concerned with the drought resistance of two pine species currently being planted in Oklahoma. The primary objective is to identify families with superior genetic and physiologic traits which allow them to control water loss during periods of moisture stress.

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CHAPTER I

INTRODUCTION

Water as a limiting factor has been a major selective force in plant evolution. A plant's ability to cope with water deficits is an important determinant of its natural distribution (Hanson and Hitz, 1982). The effects of water deficits on tree growth have been an active area of forest research since the early 1950s. Water deficits not only reduce the growth potential of a species, but the responses generated by the deficit largely determine whether a species survives when planted on marginal sites. Cannell and others (1976) have hypothesized that small differences in tree water stress tolerance, avoidance, or recovery might give rise to substantial differences in volume growth. In fact, internal water stress was judged to be the most critical factor limiting height and volume growth of loblolly pine during the growing season, even on wet sites.

Seedlings are particularly vulnerable to desiccation caused by internal water deficits the first two years after establishment. After two years, sufficient root systems have developed to draw on the soil moisture reserves of the deeper soil strata. Research began in the late 1960s to increase seedling survival under drought conditions through an investigation into the morphological and physiological features responsible for, or active in, seedling drought tolerance. An understanding of the plant mechanisms that bring about adaptation to dry environments holds much theoretical and practical value.

The improved survival of planted seedlings on marginal sites, such as the "Cross Timbers" region of Oklahoma would be of practical value. This region, encompassing some 6,214,000 acres, is characterized by low rainfall, high temperatures and low humidities. Low quality hardwoods dominate as the main forest type. Developing this and other marginal sites is becoming more urgent since the forested land base is constantly being reduced by expansion of population centers, construction of highways and dams, and conversion of forest land to agriculture. Since the natural vegetation of these sites has little commercial value, forest type conversion would be a primary way to improve the productivity of these areas and increase timber supplies. Development of drought resistant seedlings would not only allow the conversion of the Cross Timbers region of Oklahoma, but an additional 25,000,000 acres of low quality hardwood sites throughout the South could also be examined for potential conversion. Due to the poor site quality of many of these areas, production of short rotation crops such as posts or pulpwood would be most feasible (Osterhaus, 1973).

Success of forest plantings on marginal sites was noted by Meuli and Shirley (1937) to be dependent upon the use of drought resistant trees. The use of planting stock genetically improved for both growth traits and drought resistance would increase the chances for successful conversion of marginal sites to species of commercial importance. A knowledge of seedling behavior is part of the information needed to judge the suitability of a site for the species in question (Wenger, 1952). The Weyerhaeuser Company currently uses such knowledge in their strategy to match planting sites with the different sources of loblolly pine (*Pinus taeda* L.) used in their Oklahoma plantings (Lambeth and others, 1984).

Numerous plant characters influence tree water relations and not all are desirable in situations where the trees are likely to suffer water stress. Cannell and others (1976) have discussed three characters they deemed valuable in seedling ability to survive transplanting and to survival in very dry areas. These characters included rapid production of large numbers of new roots after transplanting, the presence of leaf waxes, and sensitive stomata. van Buijtenen and others (1976) reported that drought-hardy loblolly pines owed their drought hardiness largely to various avoidance mechanisms, including stomatal control, root and needle morphology, and number of stomata per square millimeter of needle surface. Further research has been called for by the Weyerhaeuser Company to help determine if the differences in survivability seen between the local Oklahoma/Arkansas seed source and the North Carolina seed source during drought is genetic in nature or the result of morphological differences in size between the two seed sources (Burns and others, 1982). Basic understanding and characterization of these mechanisms as they pertain to the drought resistance of families of the Oklahoma/Arkansas provenance of loblolly pine and to several families of Virginia pine will be the major purpose of this study. The scope will be limited to quantifying stomatal and physiological behavior of both species under imposed drought stress, accompanied by examining the morphological changes in root and shoot growth resulting from such stress.

It should be advantageous to seek plants with stomata that close before severe internal stress develops and soil water reserves become depleted. Breeding for particular patterns of stomatal behavior may provide one of the most effective means of maintaining growth in situations where there are periods of moderate water stress. Cannell and others (1976) have recommended that differences in stomatal behavior be surveyed among species, provenances and progenies, and selections with known stomatal responses be tested in different environments. Characterization of family stomatal behavior for both Virginia and loblolly pine will be one objective in this study, resulting in the identification of families that restrict internal water deficits through regulation of stomatal behavior. Regulation of stomatal behavior would allow rapid transpiration when water is available, but conservative water use (through reduced transpiration) under stress. Such behavior would reduce the risks of severe internal desiccation and possible death during severe stress and promote rapid growth when conditions are most favorable.

It is also possible to develop plants which avoid water stress by selecting for patterns of root growth and morphology which enable them to access the largest possible soil water reserves. Rapid production of new and extensive root systems after transplanting allows seedlings to obtain water from larger and deeper volumes of soil. This would allow growth to continue until the soil moisture of those levels becomes limiting and would provide an advantage for survival under droughty conditions. Root morphology is not only valuable for survival during drought, but is a highly valuable growth component. There is some evidence which indicates that seedlings which produce extensive root systems as seedlings as a result of drought stress also produce superior volumes of growth at a later age (Cannell and others, 1978). The ability of drought-hardy seedlings to rapidly produce extensive root systems following planting may be under some genetic control, and therefore, can be exploited (Ksontini, 1983).

The phenotype of drought tolerant seedlings can be described using the environmental and genetic components that compose it. The environmental component is typically expressed through some environmental modification of seedling morphology and is generally understood. The genetic component is more complex, typically physiologic in nature, and less well understood. Some morphological modifications valuable in drought resistance can be induced through nursery practices such as water-stressing, undercutting or lateral root pruning, which require additional time and expense for producers. Understanding the genetic components active in drought tolerance would allow for the breeding of drought tolerant seedlings, and may reduce the additional investments presently made to develop nursery seedlings predisposed to droughty conditions.

Seedling behavior will be examined in this study at the genetic level through the use of loblolly and Virginia pine stock of known genetic background. Drought stress will be imposed under controlled conditions. Differences in performance while under stress, therefore, should result from the genetically inherent differences in the seedling stock under evaluation. Internal water stress will be monitored at the physiologic level using stomatal resistance and xylem pressure potential measurements. Mean individual family performance for each of these physiologic parameters will be determined and tested for statistically significant treatment and family differences. Derivation of an equation to predict the threshold value of xylem pressure potential at stomatal closure will be attempted for each family. The effects of the imposed drought on the seedling growth parameters height, stem caliper, and root-shoot ratio will also be evaluated. The basic intention of these analyses will be the identification of drought tolerant families of loblolly and Virginia pine that can be used in later field evaluation and eventually perhaps developed for production on marginal sites in Oklahoma.

CHAPTER II

LITERATURE REVIEW

Drought is an environmental stress of sufficient duration to produce a plant water deficit, which in turn causes disturbances in physiological processes and ultimately damage to plants (Turner and Kramer, 1980). Plant water deficits result from the depletion of soil moisture caused by the absence of rainfall over long periods of time. The length of time without rain that is necessary to cause injury depends on the kind of plant, the water-holding characteristics of the soil in which it is growing, and the atmospheric conditions that affect the rates of evaporation and transpiration. Drought may be permanent, as in desert areas; seasonal, as in areas with well-defined wet and dry seasons; or unpredictable, as in many humid climates.

The critical feature in plant-water relations is the plant's internal water balance, because that is what controls those physiological processes and conditions which in turn determine the quantity and quality of growth. In order to understand why water deficits reduce plant growth it is necessary to understand how water affects plant processes.

Kramer (1963, p. 31) lists the following four general functions of water in plants:

1. It is the major constituent of physiologically active tissue.
2. It is a reagent in photosynthesis and in hydrolytic processes such as starch digestion.
3. It is the solvent in which salts, sugars and other solutes move from cell to cell and organ to organ.
4. It is essential for the maintenance of turgidity necessary for cell enlargement and growth.

Born in the water, the plant kingdom developed a wayward migration to the land as a kind of offshoot of the original marine environment. Entirely new adaptations were developed for land survival following this migration (Parker, 1968). Adaptations can be defined as heritable modifications in structures or functions, or both, that increase the probability of an organism surviving and reproducing in a particular environment (Turner and Kramer, 1980). The mere survival of protoplasm under severe desiccation appears to be a primitive adaptation, whereas the ability to continue metabolism during drought is a somewhat advanced characteristic. All land plants must endure a certain amount of dryness. Even mangroves growing in the mud of a tidal river or cypress trees flourishing in the quiet waters of a southern swamp put their topmost branches into air that is frequently subjected to drying winds. Drought mechanisms can be found in most or all land plants (Parker, 1968).

During the evolution of the plant kingdom, innumerable modifications in structures and functions have occurred as a result of random mutations and recombinations. Most of these were deleterious and disappeared, but a few were beneficial because they enabled the plants possessing them to survive and reproduce more successfully, and these were preserved by natural selection. As a result, plants growing in increasingly dry habitats accumulated various modifications of characters with adaptive values, such as thick cuticle, extensive root systems, low osmotic potential, and tolerance of dehydration, which increased the probability of their survival (Clarke, 1981).

Drought resistance of trees may reflect desiccation avoidance or desiccation tolerance, with the former much more important. Drought avoidance is of superior adaptive significance to the plant in that it allows the plant to continue growth in all but very severe droughts. Drought tolerators, on the other hand, do not grow during stress periods but merely survive until moisture conditions become more favorable. Drought avoiders will have closed stomata and high osmotic potential during drought stress, while drought tolerators will have open stomates and low osmotic potential (Clarke, 1981). Desiccation avoidance is the result of one or more adaptations in leaves, stems or roots. The various drought-avoidance mechanisms work in conjunction with each other and not necessarily at the same time. van Buijtenen and others (1976, p. 358) have suggested that drought-hardy loblolly pines owe their drought hardiness largely to a combination of avoidance mechanisms. Following extensive testing of drought-hardy and non-hardy sources of loblolly pine, they have determined the following mechanisms to be most important in drought avoidance:

1. Stomatal control: Drought-hardy seedlings appeared to transpire rapidly when water was available, but conserved water under stress.
2. Root morphology: Drought-hardy seedlings seemed to have deeper root systems and wider ranging laterals.
3. Needle morphology: The needles of drought-hardy seedlings were somewhat smaller, with deeper stomatal pits than needles on drought-susceptible seedlings.
4. Number of stomata per square millimeter: Drought-hardy seedlings had fewer stomata per square millimeter because the rows of stomata were somewhat further apart.

The earliest studies on the effects of drought were conducted in the 1950s and examined the direct effects of low soil moisture on the growth of adult trees (Wenger, 1952; Copeland, 1955; Zahner, 1962; Lotan and Zahner, 1963: Bassett, 1964; Buckingham, 1966; Moehring, 1966). Emphasis shifted to the effects of drought on seedling morphology and survival by the mid-1960s (Stransky, 1963; McClurkin, 1966; Stransky and Wilson, 1967; Kaufmann, 1968; Ledig and others, 1970). An interest in the effects of drought on the physiological aspects of seedling and tree behavior also developed during this time. With the increasing understanding of the physiological responses to drought came studies designed to explain the relationship between the morphological and physiological changes that occurred in trees and seedlings resulting from drought stress (Rosas, 1970; Gresham, 1975; Heth and Kramer, 1975; van Buijtenen and others, 1976; Knauf, 1977; Pereira and Kozlowski, 1977; Bilan and others, 1984).

The earliest drought studies reported examined mature trees in stands and seedlings growing in seedbeds or shadehouses under field conditions. Obtaining an evaluation of drought resistance under field conditions is rather difficult since soil moisture control is not possible. Attempts have since been made to evaluate seedlings under man-made shelters built to keep off the rain. These were fairly successful, but still not without problems (Copeland, 1955). The use of growth chambers became widespread in the 1970s. Chambers allow drought to be imposed under reproduceable conditions. Modern advances in molecular technology now allow for the evaluation of drought resistance at the cellular level through the examination of cells from callus grown in tissue culture media (Newton and van Buijtenen, 1984). Correlation between results obtained through tissue culture evaluation and actual field performance are still pending.

This study will examine the external morphological and internal physiological factors active in drought resistance. The following discussion will contain a summary of much of the work done in these areas and the results and implications derived from this work.

The general effects of drought on loblolly pine have been well documented from studies of the 1950s and 1960s. Because past interest in Virginia pine was limited, little information exists concerning the effects of drought on the growth of this species or on its variation in drought resistance. However, information related to the hardiness of the species will be presented later in this discussion.

Vegetative growth is particularly sensitive to water deficits because loss of turgidity retards cell division and enlargement and results in smaller plants (Kramer, 1963). This was observed in green ash (*Fraxinus pennsylvanica* Marsh.) by Meuli and Shirley (1937), shortleaf pine (*Pinus echinata* Mill.) by Copeland (1955), and western larch (*Larix occidentalis* Nutt.) by Vance and Running (1984).

In a study of four geographic seed sources of loblolly pine planted on a droughty site in Mississippi, Thames (1963) found significant height differences at age five between sources of differing drought hardiness. The more drought-hardy seedlings from the Lost Pines region of central Texas were significantly taller than less drought-hardy seedlings from Crossett, Arkansas. Thames suggested that the superior growth exhibited by the Lost Pines source was a result of anatomical differences in needle morphology which resulted in improved water economy over the Arkansas source.

Water deficits often reduce leaf area while causing an increase in leaf thickness (Kramer, 1963). Drought was found to be one of the contributing factors in needle length reduction in field studies of Scots pine (*Pinus sylvestris* L.) and red pine (*P. resinosa* Ait.)(Zelawski and others, 1969; Garrett, 1973, respectively). In a comparison of needle characteristics from mesic (East Texas) and xeric (Bastrop County, central Texas) loblolly pine seed sources, Knauf and Bilan (1977) found that with primary needles, length of needles, area of needle cross section, needle surface area, and volume of mesophyll were all significantly different between the two sources. It was suggested that the significantly smaller surface to volume ratio, thicker cuticle and cutinized epidermis of the needles of the Bastrop source indicate the ability to conserve moisture under stress. Evidence also suggests that the needle characteristics of loblolly pine which confer drought resistance are present only at seedling stages when differences in drought hardiness are reflected most by seedling survival (Knauf and Bilan, 1974).

Control of transpirational water loss is another mechanism used by plants to tolerate drought stress. Various physical changes in transpiring plant parts bring about control of water loss. Increased leaf waxes limit water loss from transpiring surfaces. Reduction in the total transpiring surface area also controls water loss, as does control of the opening of stomata (Clarke, 1981).

Plants under water stress close their stomata earlier during the day than unstressed plants. This reduces water loss, but also reduces the intake of carbon dioxide through the stomatal opening, and hence, reduces photosynthesis (Kramer and Kozlowski, 1960; Kramer, 1963; Paleg and Aspinall, 1981).

Dehydration of trees is controlled in part by earlier closure of stomata during each day of a developing drought. However, closing stomata during a drought may not prevent death of those trees that continue to lose water directly through the leaf epidermis after stomatal closure occurs (Kozlowski, 1976). Closure may be beneficial to plants in dry habitats because it postpones development of injurious or fatal water deficits (Kramer and Kozlowski, 1960). When during the day the stomata are open for carbon dioxide supply, the plant may lose too much water by transpiration and cannot maintain a hydration level necessary for metabolic activity. Brix (1962) found a correlation between the decrease in the rates of transpiration and photosynthesis with increasing water stress in loblolly pine seedlings in their second growing season. He concluded that water stress affects photosynthesis chiefly by increasing the diffusion resistance of the stomates and possibly of the mesophyll cells. Stomatal movements, achieved by highly sensitive regulatory mechanisms controlled directly or indirectly by plant water stress, temperature, and ambient air humidity, must therefore be carefully balanced to allow the plant a carbon dioxide supply without endangering the maintainance of a hydration level necessary for metabolic activity (Evaneri and others, 1975).

There is considerable evidence for a genetic component in control of stomatal aperture. Rapid wilting, tip scorching and premature leaf fall in abnormal diploid potato (Solanum tuberosum L.) plants were associated with an inability of the plants to close their stomata. Wilting of Flacca, a wilty mutant of tomato (Lycopersicon esculentum Mill.), resulted from very high transpirational loss. The wilting tendency of the mutants reflected high stomatal frequency, wide stomatal opening, and resistance to stomatal closure even in the dark. The differences in stomatal response of normal plants and wilty mutants were associated with a deficiency of abscisic acid (ABA) in the mutants. When the wilty mutants were sprayed with ABA, stomatal closure was readily induced.

The capacity of early stomatal closure during drought varies markedly both between and within species. Stomata closed sooner and at a lower water deficit in *Ilex cornuta* L. than in *Rhododendron poukhanensis* L. when subjected to drought. As a species, *Ilex* appeared to be more drought resistant than *Rhododendron* because it controlled transpiration more efficiently through earlier stomatal closure, and had a higher resistance to cuticular transpiration. *Eucalyptus rostrata* Schlecht. seedlings were injured more during drought than were seedlings of *E. polyanthemos* Schau. or *E. sideroxylon* A. Cunn. ex Woolls. Transpiration decline curves demonstrated that *E. rostrata* closed its stomata much later than *E. sideroxylon*, and *E. polyanthemos* was intermediate (Kozlowski, 1976).

Much interest has been shown by tree breeders in the role of stomata in desiccation avoidance because genetic variation occurs in stomatal size and control of stomatal aperture under stress. Stomatal size and frequency are usually negatively correlated with each other. Siwecki and Kozlowski (1973) examined the relation of internal leaf anatomy, stomatal size, stomatal frequency, and control of stomatal aperture on transpiration rates of six Populus clones (two clones of P. maximowiczii Henry; one clone from each of the species P. deltoides Bartr. ex Marsh., P. nigra L., and P. trichocarpa Torr. and Gray and one hybrid, P. maximowiczii x P. nigra). Water loss of excised leaves varied widely among clones, as did internal leaf anatomy, stomatal size, stomatal frequency and control of stomatal aperture. Transpiration rates were more closely related to stomatal size, frequency and control than to internal leaf anatomy. No consistent pattern was shown over all clones in the correlation of transpiration rate with any individual feature of internal leaf anatomy examined. The very high transpiration capacity of P. trichocarpa was correlated with low stomatal resistance and large stomata (but low stomatal frequency). The high rate of water loss of P. maximowiczii x P. nigra was correlated with high stomatal frequency. In both of these clones the capacity to keep stomata open for long periods also contributed to their high transpiration rates. Although P. deltoides and P. nigra leaves had relatively large stomata, their low rates of transpiration were attributed to early stomatal closure.

Hogan (1974), in a comparison of wet-zone and dry-zone seed sources of loblolly pine in Texas, studied the effect of various soil watering regimes on percentage of open stomata, transpiration rate and needle water content in four 12-month-old seedlings. He concluded that: (1) the percentage of open stomata was positively related to the rate of transpiration; (2) stomatal transpiration ceased at lower needle water contents in younger than in older seedlings, but long before the lethal range was reached; (3) under favorable conditions Bastrop (dry-zone) seedlings transpired more and had more stomata open than the Polk County (wet-zone) seedlings; (4) under water stress Bastrop seedlings had fewer open stomata and transpired less; (5) Bastrop seedlings conserved water better than Polk County seedlings; and (6) considerable variability existed within each seed source.

Water deficits invariably change the pattern of growth. Besides altering needle morphology, water deficits increase the root to shoot ratio (Kramer, 1963). This may be due to accelerated root development relative to top growth, or to an excessive loss in shoot mass without a corresponding loss in root mass (Marshall, 1931; Paleg and Aspinall, 1981). A high root to shoot ratio, however, does not in itself indicate a greater ability to absorb water. Though plant-part weights and ratios are determined mainly by heredity and age, their modification by the environment is of silvicultural importance, especially during the seedling stage when plants are particularly sensitive to site characteristics (Stransky and Wilson, 1967). Rapid root development after transplanting is important for survival and early growth of southern pines (Cannell and others, 1978).

Although the drought resistance of Virginia pine has not been studied, its ability to grow on dry, sterile, eroded sites and the variability in site type over its natural range suggests some inherent drought tolerance. Snow (1960) observed that Virginia pine seedlings were more tolerant of low soil moisture than most pines, and remained active and grew under quite dry conditions, although the growth rate was slow.

In the 1920s Virginia pine was often described as a scrub tree usually 30-40 feet tall (occasionally 100 feet) inhabiting poor soils. The species was occasionally manufactured into lumber or used for firewood. At that time it was of little economic importance. Then and for many years afterward any Virginia pine planting was done primarily to obtain a ground cover on eroded, sterile soils. But in recent years Virginia pine has been recognized as an important pulpwood species north of the loblolly pine range. The species is capable of producing good yields on sites which may be marginal for loblolly pine because of excessive drainage or because loblolly pine is susceptible to ice and snow damage (Talbert, 1980). Virginia pine can grow rapidly, especially in youth, on infertile sites and produces good pulpwood if grown in closed stands. Hence, several paper companies are now interested in development of better strains for commercial use (Genys and others, 1974). Interest in the species for Christmas tree production is also considable.

Provenance studies of Virginia pine have shown that genetic differences exist in growth rate and survival among sources. A seed source study of 17 origins from ten states showed that southern sources fared poorly when planted in Pennsylvania. When the same sources were planted in Maryland and Tennessee, southern sources did better, but the Alabama source was generally inferior to local material (Genys, 1966). In a geographic variation study in Kentucky and Tennessee, collections from the Great Valley of Tennessee were taller after two years than were northern and western sources.

Several studies have attempted to grow Virginia pine in areas outside its natural range. Virginia pine was used by Clark (1954) as one of 14 different forest species planted to reclaim strip-mined land from Missouri to Oklahoma. The study was established in a dry year and mortality for all species averaged 51.9 percent. Drought accompanied by high temperatures was the major cause of low survival, with most mortality occurring during the first growing season after planting of the 1-0 seedlings. The Virginia pine exhibited a 25 percent survival rate for all planting areas after six years, with a 16 percent survival rate on the Oklahoma site after five years.

Hansen and McComb (1958) observed that many planted pine species, including Virginia pine, outperformed many broadleaf species when planted on old field sites in southern Iowa. The growth of Virginia pine was better than that of five other pine species planted on the same site.

Virginia pine also did well on some sites in Illinois. However, plantations in Missouri, Kansas and Oklahoma were severely infested by Nantucket pine tip moth and survival and growth were poor (Snow, 1960).

Osterhaus and Lantz (1978) recommended Virginia and loblolly pine for planting on the Cross Timbers region of Oklahoma. The recommendation was based on the higher survival and better growth of the two species compared to three other pine species tested. The greatest concern expressed by Osterhaus and Lantz was that of adequate moisture for seedling survival and establishment following planting. Osterhaus (1973) noted that June, July and August are the most critical months for young seedling survival in Oklahoma, due to high temperatures, low humidities and low rainfall prevalent during this period. Once pines were established, it appeared that a succeeding year of poor moisture conditions would not severely affect survival or growth of the trees, but success here demanded a drought resistant seedling.

Kellison and Zobel (1974) have noted through genetic, silvicultural and management studies, large tree-to-tree and stand-to-stand differences in Virginia pine. Clinal variation was only weakly indicated, however. Exploiting the variation expressed in survivability observed in seed source tests may allow the development of Virginia pine seedlings suitable for planting and production in Oklahoma.

Early provenance studies of loblolly pine have shown that sources west of the Mississippi River are inherently slower growing, more drought resistant and more rust resistant than sources east of the River. Results at age 25 in a loblolly pine provenance test in southern Arkansas showed that trees from some eastern seed sources averaged eight feet taller than local Arkansas trees, with the shortest trees being from Oklahoma. However, trees from most of the range appeared well adapted to the climate of southern Arkansas (Wells and Lambeth, 1983).

The Weyerhaeuser Company currently plants North Carolina loblolly pine seed sources on selected sites in Oklahoma. The superior growth rate of the North Carolina sources favors their use over local Oklahoma/Arkansas sources (Lambeth and others, 1984). The Oklahoma/Arkansas provenance, which evolved in a more xeric climate, has obviously responded to natural selection for drought resistance. Therefore, there is some concern that the North Carolina sources may not be able to survive and grow well under the variable climatic conditions of the Oklahoma/Arkansas region. Characterization of the drought potential of the Oklahoma/Arkansas planting sites and comparisons of survival rates between the local and North Carolina seed sources on these sites have resulted in limited planting of the North Carolina seed sources to those sites with soil series that develop no more than 31 centimeters of soil moisture deficit in an extremely dry year. This limitation allows the use of the North Carolina seed source on 60 percent of the Oklahoma/Arkansas area in question, while the remainder of the area is planted with improved sources of Oklahoma/Arkansas loblolly pine.

The identification of superior loblolly and Virginia pine families for planting in Oklahoma is still at an early stage. Both species exhibit considerable variation in drought tolerance. Tree breeders have to select genotypes suitable adapted to exploit the available growing season between damaging frosts and droughts while able to survive these limiting site conditions. Trees in general appear to have adapted conservative strategies for growth, sacrificing rapid rates of dry matter gain for stress tolerance. This conservatism can be exploited (Cannell and others, 1976).

The exploitation of seed source variation exhibited by both pine species examined in this study could allow the identification and development of drought resistant pines for planting in Oklahoma. Development of loblolly and/or Virginia pine improved for both growth and resistance traits could increase survival and growth on forest industry lands and could possible enable the conversion of all or part of the Cross Timbers region in Oklahoma. Further evaluation of the drought resistance of Virginia pine could lead to the development of the Christmas tree industry as an alternative land-use on marginal sites across Oklahoma.

CHAPTER III

METHODS AND MATERIALS

The loblolly and Virginia pine seedlings used in this study were grown from seed sown during the spring of 1984 in prepared seedbeds at the Kiamichi Forestry Research Station located near Idabel, Oklahoma. The loblolly pine seedlings were available full-sib material produced from controlled pollinations of parent trees grafted in the Kiamichi Forestry Research Station seed orchard. These trees represent the current State effort in improvement of Oklahoma/Arkansas loblolly pine. The Virginia pine seedlings were produced from seed collected from open-pollinated stands throughout the natural range of the species and represent part of an on-going provenance study to identify suitable Christmas tree stock for production in Oklahoma. The Virginia pine families were assumed to consist of half-sibs. Figure 1 illustrates the origins of the parent trees used to produce the full-sib loblolly pine progeny used in this study. Figure 2 illustrates the origins of the six open-pollinated families of Virginia pine used in this study.

While in the seedbed, the seedlings were fertilized with Osmocote slow-release fertilizer and drip irrigated during periods of low moisture. Periodic herbicide treatments were applied to control weed competition.

* Kiamichi Forestry Research Station

Figure 1. Geographic origins of parent trees used to produce the full-sib loblolly pine progeny

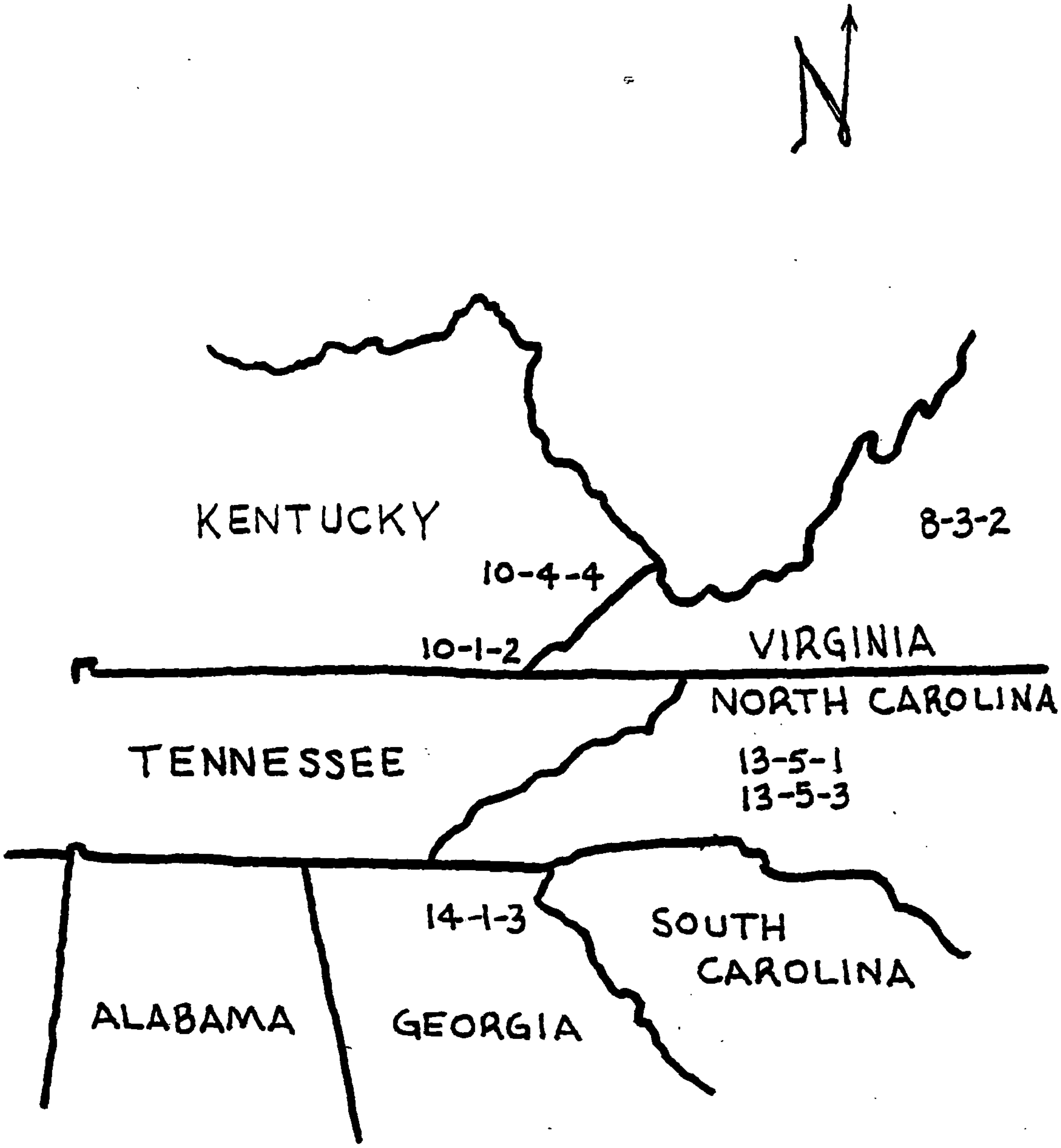

Figure 2. Geographic origins of the six open-pollinated families of Virginia pine used in this study

In January 1985, the loblolly and Virginia pine seedlings were lifted from the seedbed, bundled by family, and transported to Stillwater in seedling bags containing wet sphagnum moss to prevent the seedlings from drying out en route. Once in Stillwater the seedlings were promptly stored in refrigeration for three days until potted. The 1-0 seedlings were potted in quart milk cartons containing a 1:3 soil mix of clay:Redi-Earth potting soil mix. Ten grams of 19-6-12 Osmocote slow-release fertilizer was added to each container and the seedlings were placed in the greenhouse where they were to remain until sufficient top growth had developed to allow proper sampling material for the study.

Selection of the healthiest, most uniform individuals representing the eight full-sib families of loblolly pine and six half-sib families of Virginia pine was made in mid-April. The seedlings were placed in a growth chamber at this time. To allow seedling acclimitization to the new growth chamber environment, temperature and day length were set to closely resemble greenhouse conditions (70°F day, 60°F night, 12-hour day length). These were gradually changed over a two-week period until the predetermined experimental conditions, based on the recommendations of previous researchers, were met. These conditions were designed to maximize growth and not be the stressing factor in this study.

The growth chamber thermostat was set at 75°F (24°C) day and 55°F (13°C) night for the study period. This allowed the daytime temperature to reach the summer optimum reported by Bormann (1956) with a wide spread between day and night temperatures to promote maximum growth as observed and recommended by Kramer (1957). It was also intended to maximize growth by raising the initial day length of 12 hours to 16 hours as recommended by MacGregor and others (1961). Average light intensity was 619.9 ± 64.8 micro-Einsteins per second per square meter of photosynthetically active radiation measured in the 400 to 700 nm band. Fluctuations in chamber humidity, which might cause some bias in measurement of stomatal resistance, were monitored with a portable hygrothermograph. No direct control of humidity was available within the chamber itself.

One week prior to the beginning of data collection, twelve of the healthiest, most uniform individuals within each family were chosen for study. These twelve were divided into four groups of three, with each group of three individuals being as uniform in height and size as possible. Each three-tree group was then randomly assigned a treatment level. There were three treatment levels and four replicates requiring twelve seedlings per family. Seedlings were grouped within each replicate by treatment with both the position of the individual family member within treatment and the placement of the treatment group within each replicate being random. Not all families represented in this study had the required twelve seedlings needed to complete the study design. Missing individuals within each family were replaced with filler trees which were not measured during the study period. Filler trees always replaced control seedlings allowing family representatives to fill the more important stress treatment groups.

The two species were kept separate within the chamber with the 72 Virginia pine seedlings occupying the left half of the chamber and the 96 loblolly pine seedlings occupying the right half. A diagram of the chamber layout is presented in Figure 3.

The three treatment levels chosen and applied on an individual-seedling basis were determined from actual water use calculations made during the first five days of the experiment. Seedlings were watered, weighed, and their cartons placed in plastic bags to prevent water loss from evaporation from the soil surface. The seedlings were reweighed after five days. Loss in weight was assumed to be due to seedling water use. The amount of water used by each seedling over the five-day period was calculated and extrapolated to estimate the amount of water used in ten days, the length of each measurement period. Treatment 1 was the control, in which seedlings received 100 percent of their water requirement each period and were assumed to be under little or no stress during the study. Treatment 2 was termed moderate stress. Seedlings under this treatment level were to receive one-third of their calculated water requirement during the second period. Treatment 3 was termed severe stress and seedlings allotted to this treatment were only

REP 4 TRT 3 LOBLOLLY	REP 4 TRT 2 LOBLOLLY	REP 4 TRT 1 LOBLOLLY
REP 3 TRT 3 LOBLOLLY	REP 3 TRT 2 LOBLOLLY	REP 3 TRT 1 LOBLOLLY
REP 2 TRT 1 LOBLOLLY	REP 2 TRT 3 LOBLOLLY	REP 2 TRT 2 LOBLOLLY
REP 1 TRT 2 LOBLOLLY	REP 1 TRT 3 LOBLOLLY	REP 1 TRT 1 LOBLOLLY

REP 4 TRT 1 VIRGINIA	REP 4 TRT 2 VIRGINIA	REP 4 TRT 3 VIRGINIA
REP 3 TRT 3 VIRGINIA	REP 3 TRT 2 VIRGINIA	REP 3 TRT 1 VIRGINIA
REP 2 TRT 2 VIRGINIA	REP 2 TRT 3 VIRGINIA	REP 2 TRT 1 VIRGINIA
REP 1 TRT 1 VIRGINIA	REP 1 TRT 3 VIRGINIA	REP 1 TRT 2 VIRGINIA

Figure 3. Growth Chamber Layout

given one-sixth of their calculated water requirement (one-half of the amount received by seedlings under Treatment 2) during the second period. These treatment levels were chosen based on the results of a preliminary study conducted in 1984.

The study was conducted in four consecutive ten-day periods. Seedlings were watered at the end of each period. Within each treatment level, the amount of water received during the third and fourth periods was halved from the amounts received from previous periods. Controls were maintained at a fully-watered status. During the last period, Treatment 3 seedlings received no water, rather than one-half of the amount received by this treatment level in period three. The amount of water received by treatment and period is shown in Table I.

TABLE I

AMOUNT OF WATER RECEIVED BY STRESS TREATMENT AND 10-DAY PERIOD AS A PERCENT OF TOTAL CALCULATED WATER REQUIREMENT

	Period			
	1	2	3	4
Treatment				
Control	100	100	100	100
Moderate Stress	100	33.3	16.7	8.3
Severe Stress	100	16.7	8.3	0

Measurements

Prior to potting, the green weight of each seedling was recorded to the nearest one-hundredth (0.01) gram. Seedling height (HT1) and stem caliper (CAL1) were measured after potting. HT1 was taken as the distance from the surface of the potting soil to the tallest growing point, measured to the nearest one-eighth (0.125) inch (3.175 mm). CAL1 was measured with a caliper to the nearest one-thousandth (0.001) inch (0.025 mm) at a point on the stem corresponding to the top of the carton.

The following data were collected during the 40-day stress period:

1. Stomatal resistance (SR). Measured on days 1, 4, 7 and 10 of each period for Virginia pine and on days 1, 4, 8 and 10 of each period for loblolly pine.

2. Predawn xylem pressure potential (XPP1). Measured on days 1 and 10 of each period for both species.

3. Midday xylem pressure potential (XPP2). Measured on days 1 and 10 of each period for both species. Midday was defined as the midpoint in the 16-hour growth chamber day length.

Stomatal resistance (SR) was measured at midday with a LI-COR 1600 steady-state porometer fitted with a four cm^2 head. Measurements were taken midway along the length of one three-needle fascicle in loblolly pine and midway along the length of a two-needle fascicle in Virginia pine.

Measurements were confined to new growth in all but two families of Virginia pine in which all the new growth had been removed during the fourth period for xylem pressure potential determination. Differences in SR values from foliage from differing age classes did not appear evident. Because the portion of foliage measured did not cover the entire four square centimeters of the attachment head, calibration for total surface area was required. Following the method of Johnson (1984), total surface area measured on loblolly pine was estimated to be 1.7 square centimeters and 1.0 square centimeter for Virginia pine. These respective values were entered into the porometer by species and were used by the porometer to adjust the final reading to the total surface area actually involved in the measurement.

Stomatal resistance values often appeared on the digital porometer display within ten seconds. The values for severely stressed seedlings often exceeded 100 seconds per centimeter and required more than ten seconds for the digital display to stabilize. Any seedling recording such a value was assumed to have closed stomates and a value of 100 was recorded for analysis purposes. One hundred (100) seconds per centimeter was chosen as the point of stomatal closure in pine based on reports of values at stomatal closure for other conifer and broadleaf species in the literature.

Prior to the start of each stomatal resistance measurement period, temperature and humidity were checked using sensors contained on the porometer head. This was done to insure proper porometer function. Highly erroneous readings can result when the porometer is used outside a recommended humidity range (LI-COR, Inc., 1984).

Predawn xylem pressure potential (XPP1) was measured using a Scholander pressure bomb. One needle fascicle was used for each observation with each species. Research has shown measurement using one fascicle to be as reliable an indication of moisture stress as measurement of pressure using whole branchlets, thereby reducing the amount of needed sampling material (Johnson and Nielson, 1969; Kelliher, 1983). Pressure was applied to the needle fascicle until xylem sap appeared at the cut surface viewed through a 10X magnifying glass. The pressure value at this point, measured in negative bars, was recorded. These measurements were conducted before the lights came on inside the chamber and are an indicator of the nightly rehydration that had occurred within the seedlings' xylem systems.

Midday xylem pressure potential (XPP2) was measured in the same manner as XPP1, only during the middle of the 16-hour chamber day, and is an indicator of the internal level of desiccation being reached in response to the imposed water stress.

Stomatal resistance and xylem pressure potential adjust either in response to one another or in response to some environmental stimuli. To gain some understanding of the diurnal changes that occur in seedlings, corresponding measurements of SR and xylem pressure potential were taken on the fifth day of each period starting with the predawn measurement of xylem pressure potential. The corresponding value of SR at this time was assumed to be at or near zero. Corresponding values of SR and xylem pressure potential were recorded at consecutive two-hour periods following the initial measurement until such time when the seedlings appeared to have closed stomates (SR=100), or no other measurements could be taken before the lights went out in the chamber. Only seedlings that received Treatment 2 were measured in this particular part of the study because it was felt that they would be more likely to exhibit stronger diurnal changes than either non-stressed seedlings or severely stressed seedlings. The information gained from these diurnal measures of SR and xylem pressure potential should allow determination of the threshold values of xylem pressure potential at which stomatal closure occurs.

The following data were collected at the close of this study: final height (HT2), final caliper (CAL2), and root-shoot ratio (RSRATIO). HT2 and CAL2 were measured using the same method used to measure HT1 and CAL1 at the start of the study. Height growth was calculated as the difference between HT1 and HT2. Stem caliper growth was calculated as the difference between CAL1 and CAL2.

RSRATIO was measured following the careful removal of each seedling from its container. The extracted seedlings were severed at the root collar, their respective roots and shoots labeled, placed in paper bags, and oven-dried for 48 hours at 70°C. Once dry, the root and shoot weights were recorded to the nearest one-hundredth (0.01) gram. Shoot dry weight was divided into root dry weight to obtain the root-shoot ratio.

Prior to RSRATIO determination, five seedlings from each family were rewatered and used to calculate pressure-volume (P-V) curves. P-V curves allow the determination of several valuable physiological water relations parameters. Because P-V curves shift for stressed seedlings when compared to curves of non-stressed seedlings, control seedlings were used in this determination. For those families containing filler trees in control positions, healthy seedlings from Treatment 2 were used. No family ever required the use of more than three seedlings from this treatment, however.

The selected seedlings were placed in a bucket of water after extraction, placed in total darkness and allowed to rehydrate 12 hours overnight. Once fully-hydrated, the seedlings were severed at the root collar. The roots were labeled, placed in a paper bag, and used for RSRATIO determination. The shoots were weighed immediately, placed in a perforated plastic bag to reduce evaporative moisture loss, and placed in the Scholander pressure bomb. Pressure was applied until xylem sap could be seen on the cut surface, and that pressure value was recorded. The seedling shoot was then removed from the pressure bomb and immediately reweighed. The difference in initial weight and weight after the application of pressure is an indirect measure of the weight of the sap forced from the xylem at that pressure. The seedlings were then taken outside and placed in direct sunlight to dry for one hour.

After one hour's time, the seedlings were brought inside, pressure was reapplied with the value of the balancing pressure being recorded, and the seedlings were then weighed. This process was repeated until such time when the seedlings had dried to a point that the balancing pressure required to cause exudation of sap from the xylem exceeded the highest value measurable by the pressure bomb (40 bars). Once the seedlings had reached this point, they were placed in paper bags and oven-dried at 70°C for 48 hours. The oven-dry weight of the shoots was then recorded and used in both P-V determination and RSRATIO calculation.

In the variation of P-V determination used here, the inverse of the balancing pressure required for sap exudation after each drying period is plotted against the cumulative weight loss measured in the seedling up to that point. The volume of sap expressed at each balancing pressure is estimated in this variation by the corresponding loss in seedling weight experienced after the application of pressure (Jones and Higgs, 1979; Ritchie and Roder, 1985).

Statistical Analysis

The statistical analyses of the data collected in this study used the GLM procedure of SAS (SAS Institute Inc., 1982). The GLM procedure uses the method of least squares to fit general linear models and is used with most unbalanced designs. The GLM procedure was used to calculate Type II sums of squares and F-statistics to determine family and treatment significance of the drought resistance parameters SR, XPP1 and XPP2, height and stem caliper growth and root-shoot ratio. The GLM procedure was also used to produce the Type II sums of squares, mean squares and variance coefficients used to calculate the heritabilities and corresponding standard errors for the drought resistance parameters. Finally, the GLM procedure was used to derive the predicted regression equations from the diurnal data to estimate family threshold values of xylem pressure potential at stomatal closure, and was used to produce the regression line best fit to the P-V data allowing the determination of three physiological water relations parameters for each family in this analysis.

The GLM procedure calculates least square means for each effect listed in the model statement of the SAS program. This allowed treatment and family comparisons and rankings to be made. When significant, family and treatment means were ranked and compared for developing trends.

In analyzing the drought resistance and growth parameters of interest, a split-plot design incorporating a randomized block design was used allowing for greater precision in family comparisons than treatment comparisons. The following model was employed:

$$Y_{ijk} = u + R_i + T_j + a_{ij} + f_k + (tf)_{jk} + b_{ijk}$$

where,

Y_{ijk} = mean of family k receiving treatment j in replicate i

u = true family mean

R_i = effect of replicate i

T_j = effect of treatment j

a_{ij} = replicate by treatment interaction effect

f_k = effect of family k

$(tf)_{jk}$ = treatment by family interaction effect; assumed to be equal to zero in this model when summed over all treatment levels

b_{ijk} = residual error

The analysis of variance (Anova) table and F-tests used in this analysis appear in Table II.

The data collected on the three drought resistance parameters (SR, XPP1 and XPP2) were analyzed by respective measurement day for significance due to treatment and/or family effects. Height and stem caliper growth differences were tested for significance due to treatment and family effect. Family, replicate by family and treatment by replicate effects were all considered to be random effects. Replicate was fixed as a check to guage whether measurements would become biased during the lengthy measurement period because of the large sample size involved in the data collection. (No such bias was indicated.) Calculated F-values were declared statistically significant if the probability of obtaining a larger F-value by chance was five percent

TABLE II

ANOVA TABLE AND F-TESTS USED TO DETERMINE SIGNIFICANCE OF STOMATAL RESISTANCE (SR), PREDAWN XYLEM PRESSURE POTENTIAL (XPP1), MIDDAY XYLEM PRESSURE POTENTIAL (XPP2), HEIGHT GROWTH, STEM CALIPER GROWTH AND ROOT-SHOOT RATIO

Source of Variation	Degrees of Freedom	Mean Square	Expected Mean Square
REP	3	MS6	$\sigma_e^2 + c_1\sigma_{r*t}^2 + q_1R$
TRT	2	MS5	$\sigma_e^2 + c_2\sigma_{t*f}^2 + c_3\sigma_{r*t}^2 + q_2T$
REP * TRT	6	MS4	$\sigma_e^2 + c_4\sigma_{r*t}^2$
FAM	5 or 7[!]	MS3	$\sigma_e^2 + c_5\sigma_f^2$
TRT * FAM	10 or 14[@]	MS2	$\sigma_e^2 + c_6\sigma_{t*f}^2$
ERROR	#	MS1	σ_e^2

F-tests:

$F_{TRT} = \frac{MS5}{MS4}$ with 2 and 6 degrees of freedom

$F_{FAM} = \frac{MS3}{MS1}$ with 5 or 7 and error degrees of freedom[!][#]

$F_{TRT*FAM} = \frac{MS2}{MS1}$ with 10 or 14 and error degrees of freedom[@][#]

Note:

σ_e^2 = residual error variance component

σ_{t*f}^2 = treatment by family interaction component

σ_f^2 = family variance component

σ_{r*t}^2 = replicate by treatment variance component

T = average of the squares of treatment effect

TABLE II (Continued)

Note (Continued):

R = average of the squares of replicate effect

c_1-c_6 = coefficients of random effects

q_1-q_2 = coefficients of fixed effects

! The Virginia pine family component has 5 degrees of freedom. The loblolly pine family component has 7 degrees of freedom.

@ The Virginia pine treatment by family interaction component has 10 degrees of freedom. The loblolly pine treatment by family interaction component has 14 degrees of freedom.

The error degrees of freedom varied by species and measurement day.

(.05) or less.

Table III contains the analysis of variance used to produce the mean squares and variance coefficients for the calculation of heritability (h^2) for the drought resistance parameters. Because drought resistance is a threshold trait with expression occurring after development of water stress, it was decided to calculate heritabilities at the time of greatest stress when higher h^2 estimates would be expected. Therefore, h^2 for SR, XPP1 and XPP2 was calculated by treatment for both Virginia and loblolly pine from data collected on each parameter on the tenth day of each period. The following formula was used to calculate h^2 (Falconer, 1981):

$$h^2 = \frac{\sigma_f^2}{\sigma_f^2 + \sigma_e^2}$$

where,

σ_f^2 = family variance component
σ_e^2 = error variance component

The error variance component was estimated from the family by replicate interaction variance component. No residual error variance existed.

Standard errors were also approximated for each h^2 estimate. The following formula was used (Kendall and Stuart, 1958):

$$\text{standard error } (\hat{h^2}) = \frac{\text{MfMe}}{(\text{Mf} + 3\text{Me})^2}\sqrt{8\left(\frac{1}{\text{d.f.}_F} + \frac{1}{\text{d.f.}_E}\right)}$$

where,

Mf = family mean square

TABLE III

ANALYSIS OF VARIANCE CALCULATING HERITABILITIES OF STOMATAL RESISTANCE, PREDAWN XYLEM PRESSURE POTENTIAL AND MIDDAY XYLEM PRESSURE POTENTIAL FOR LOBLOLLY AND VIRGINIA PINE BY TREATMENT FOR DAY 10 OF EACH PERIOD

Source of Variation!	Degrees of Freedom	Mean Square	Expected Mean Square
REP	3	MS3	$\sigma_e^2 + q_1R + q_2R*F$
FAM	5 or 7@	MS2	$\sigma_e^2 + c_1\sigma_f^2 + q_3R*F$
REP * FAM	#	MS1	$\sigma_e^2 + q_4R*F$
ERROR	0	-	σ_e^2

Note:

σ_e^2 = residual error variance component

R = average of the squares of the replicate effect

R*F = average of the squares of the replicate by family interaction effect

σ_f^2 = family variance component

q_1-q_4 = coefficients for fixed effects

c_1 = coefficient for family variance component

! Family effects considered random.

@ The Virginia pine family component has 5 degrees of freedom. The loblolly pine family component has 7 degrees of freedom.

The degrees of freedom for the replicate by family interaction component varied by species and measurement day.

Me = error mean square

$d.f._F$ = degrees of freedom associated with the family term

$d.f._E$ = degrees of freedom associated with the error term

CHAPTER IV

RESULTS AND DISCUSSION

Growth Parameters

Height

Mean height growth for loblolly pine was 0.376 inches (9.550 mm). Mean height growth for Virginia pine was 0.569 inches (14.453 mm). Although no significant treatment differences in height growth appeared in either species, growth under control conditions was approximately double that under stressed conditions. Under control conditions loblolly pine height growth averaged 0.534 inches (13.564 mm) while Virginia pine averaged 0.869 inches (22.073 mm). Further study into the lesser growth rates under stress and non-stress conditions seen for loblolly pine compared to Virginia pine would be of interest.

Stem Caliper

Mean stem caliper growth for loblolly pine was 0.005 inches (0.127 mm) while that for Virginia pine was 0.011 inches (0.279 mm). Under control conditions, the average increase in loblolly pine stem caliper was 0.017 inches (0.432 mm) and in Virginia pine 0.027 inches (0.686 mm).

Virginia pine increased stem caliper more than loblolly pine under both stress and non-stress conditions. These results are similar to those for height growth, suggesting an overall ability for Virginia pine seedlings to grow faster under stress or non-stress than loblolly pine. These findings are supported by reports of superior Virginia pine seedling growth compared to other pine species under similar conditions (Hansen and McComb, 1958; Osterhaus and Lantz, 1978).

Treatment differences in stem caliper growth between stressed and non-stressed Virginia pine seedlings were significant. Differences between the two stress treatments were not significant. Stem caliper growth differences occurred in loblolly pine, and may be real, but were only significant at the 10% level. The loblolly pine differences were interesting, however, as severely stressed seedlings actually had negative stem caliper growth (shrinkage). Stem caliper growth of Virginia pine remained positive over all treatment levels. Mean treatment stem caliper growth for Virginia and loblolly pine is presented in Table IV. Loblolly pine appears to be more sensitive to water deficits than Virginia pine, as indicated by the shrinkage in stem caliper under severe stress.

Family differences in mean stem caliper growth summed over treatments were not significant in either species. Mean family stem caliper growth for loblolly pine families is presented in Table V and for Virginia pine families in

TABLE IV

MEAN STEM CALIPER GROWTH FOR VIRGINIA AND LOBLOLLY PINE BY TREATMENT

TRT	$\bar{x}$ caliper growth (in.) ± std error	
	SPECIES	
	Virginia pine[!]	Loblolly pine[@]
1	0.027 ± 0.004 a	0.017 ± 0.004 a
2	0.004 ± 0.003 b	0.002 ± 0.004 b
3	0.006 ± 0.003 b	-0.001 ± 0.004 b

Note: ! treatment means followed by same letter not significantly different

@ loblolly pine stem caliper treatment differences significant at the 10% level

TABLE V

MEAN STEM CALIPER GROWTH SUMMED OVER TREATMENTS FOR LOBLOLLY PINE FAMILIES

Family	$\bar{x}$ caliper growth (in.) ± std error@	
87 x 81	0.013 ± 0.006	a
80 x 91	0.011 ± 0.007	ab
75 x 84	0.011 ± 0.007	ab
80 x 81	0.009 ± 0.006	ab
73 x 86	0.008 ± 0.006	ab
74 x 75	0.004 ± 0.006	ab
89 x 71	-0.004 ± 0.008	ab
76 x 81	-0.005 ± 0.006	b

Note: @ family means followed by same letter not significantly different

Table VI. It is interesting that several loblolly pine families (76 x 81 and 89 x 71) showed no growth and even slight shrinkage in stem caliper. (Family 76 x 81 also had the lowest mean height growth.) All Virginia pine families showed positive stem caliper growth.

In Virginia pine, family 14-1-3 and family 8-3-2 showed the greatest stem caliper growth. Families 14-1-3 and 8-3-2 also had the largest average growth in height. These greater growth rates remained consistent over all treatment levels, suggesting an ability within these families to maintain positive turgor during periods of stress, a highly desirable trait for continued growth during periods of moderate water stress. The physiological control of internal water balance for these families will be considered with the examination of the drought resistance parameters later in this presentation.

Root-Shoot Ratio (RSRATIO)

No significant treatment differences in the loblolly pine root-shoot ratios were found. However, family differences were significant (Table VII).

Family 80 x 81 possessed the largest RSRATIO. It was significantly larger than that of any other loblolly pine family. No other significant differences were observed in RSRATIO among families. The significantly larger RSRATIO found in family 80 x 81 is probably genetic and probably existed prior to the study. Family 80 x 81 showed moderate

TABLE VI

MEAN STEM CALIPER GROWTH SUMMED OVER TREATMENTS FOR VIRGINIA PINE FAMILIES

Family	$\bar{x}$ caliper growth (in.) ± std error@	
14-1-3	0.017 ± 0.005	a
8-3-2	0.016 ± 0.007	a
10-1-2	0.014 ± 0.005	a
13-5-3	0.012 ± 0.005	a
13-5-1	0.011 ± 0.005	a
10-4-4	0.006 ± 0.004	a

Note: @ family means followed by same letter not significantly different

TABLE VII

MEAN ROOT-SHOOT RATIOS SUMMED OVER TREATMENTS FOR LOBLOLLY PINE FAMILIES

Family	x root-shoot ratio ± std error@	
80 x 81	0.72 ± 0.04	a
75 x 84	0.55 ± 0.05	b
74 x 75	0.54 ± 0.05	b
87 x 81	0.53 ± 0.04	b
89 x 71	0.50 ± 0.05	b
73 x 86	0.50 ± 0.05	b
76 x 81	0.49 ± 0.04	b
80 x 91	0.40 ± 0.05	b

Note: @ family means followed by same letter not significantly different

growth in stem caliper and below average height growth compared to the other families of loblolly pine.

Inherently larger root-shoot ratios resulting from smaller shoot mass relative to root mass would be an advantage in seedling survival under drought conditions. High root-shoot ratios provide the tree greater access to larger and possibly deeper volumes of soil. Family 80 x 81 apparently possesses such an advantage for survival during drought. However, there appears to be a corresponding loss in volume growth.

In Virginia pine, apparent differences in RSRATIO occurred due to treatment, but were only significant at the 10% level. As expected, the stressed treatments produced larger root-shoot ratios than the control treatment.

There were significant family differences in RSRATIO for Virginia pine (Table VIII). Families 8-3-2, 10-1-2 and 10-4-4 possessed the highest mean root-shoot ratios, significantly higher than families 13-5-1 and 14-1-3. Although Virginia pine seedlings appear to be able to produce larger root-shoot ratios in response to soil moisture deficits, the family differences in RSRATIO found here appear due at least in part to the inherent differences in family seedling size. Differences in RSRATIO under control conditions suggest that families 10-4-4 and 14-1-3 may have possessed inherently different root-shoot ratios at the beginning of the study, while the remaining family differences in RSRATIO developed in response to the stress treatments.

TABLE VIII

MEAN ROOT-SHOOT RATIOS SUMMED OVER TREATMENTS FOR VIRGINIA PINE FAMILIES

Family	$\bar{x}$ root-shoot ratio ± std error@	
10-4-4	0.66 ± 0.07	a
8-3-2	0.66 ± 0.09	ab
10-1-2	0.61 ± 0.07	abc
13-5-3	0.45 ± 0.07	bc
13-5-1	0.41 ± 0.07	c
14-1-3	0.41 ± 0.08	c

Note: @ family means followed by same lettet not significantly different

Drought Resistance Parameters

Stomatal Resistance (SR)

Significant treatment differences in mean SR were found in loblolly pine, particularly during the latter half of the study (Table IX). Severely stressed seedlings would be expected to maintain the highest mean SR, however, this was not always observed. Control seedlings exhibited the lowest mean SR, often significantly lower than moderately and severely stressed seedlings. Significant differences between moderately-and severely stressed seedlings occurred infrequently, but may have been observed had the study been continued.

No significant differences among family mean SR values were found on any measurement day in loblolly pine. The loblolly pine families used in this study represent a small sample of a population known to exhibit high drought tolerance. Little family variation might be expected due to the small sample size but may have become evident had the study been continued longer than it was. This could easily explain the similar responses found in loblolly pine compared to the varied responses found in Virginia pine.

Significant treatment differences in mean SR occurred on only one measurement day during the entire study in Virginia pine. The trend exhibited on this day was not expected. Moderately stressed seedlings were found to exhibit significantly lower mean SR than either control

TABLE IX

STOMATAL RESISTANCE (SR) TREATMENT MEANS AND STANDARD ERRORS FOR LOBLOLLY PINE FOR DAYS SIGNIFICANT TREATMENT DIFFERENCES OCCURRED

Period	Day	Trt	$\bar{x}$ SR (sec cm^{-1}) ± std error@	
1	8	1	40.24 ± 7.01	a
1	8	2	60.15 ± 6.85	b
1	8	3	42.31 ± 7.01	a
2	8	1	44.00 ± 5.91	a
2	8	2	76.41 ± 5.77	b
2	8	3	67.15 ± 5.91	b
3	1	1	41.39 ± 6.04	a
3	1	2	59.29 ± 5.88	b
3	1	3	72.20 ± 5.88	b
3	8	1	51.72 ± 5.32	a
3	8	2	87.24 ± 5.28	b
3	8	3	83.56 ± 5.28	b
4	1	1	48.59 ± 5.15	a
4	1	2	78.43 ± 5.27	b
4	1	3	77.79 ± 5.28	b
4	4	1	46.96 ± 5.18	a
4	4	2	82.50 ± 5.30	b
4	4	3	91.16 ± 5.18	b
4	8	1	46.54 ± 5.73	a
4	8	2	83.29 ± 5.86	b
4	8	3	79.30 ± 5.73	b
4	10	1	48.21 ± 5.07	a
4	10	2	79.44 ± 4.75	b
4	10	3	89.00 ± 4.77	b

Note: @ treatment means within each group (period) followed by same letter not significantly different seedlings or severely stressed seedlings. The mean SR of the control seedlings was not significantly different from that of severely stressed seedlings, indicating possible waterlogging of the control seedlings due to poor container aeration and drainage. This condition could raise the mean SR of control seedlings to a value near that expected from severely stressed seedlings. Measures were taken to alleviate this problem through less frequent watering of the control seedlings, resulting in lower, more reasonable SR values in the control seedlings.

More readily apparent for Virginia pine were significant differences in family mean SR, particularly during the latter half of the study (Table X). Several families exhibited behavior patterns that remained unchanged through much of the study. Families 8-3-2 and 10-4-4 consistently displayed significantly lower mean SR values than all other families, while family 13-5-3 almost always exhibited the highest mean SR.

Family 13-5-1, from the same origin as family 13-5-3, registered more moderate values of mean SR over time, indicating an ability to continue gas exchange with the environment and hence photosynthesize longer under stress than family 13-5-3. Although selections for families that continue photosynthesis and growth longer during droughts is desirable, it is important that the internal water deficits created by prolonged gas exchange with the environment not become too severe. These implications will be examined in

TABLE X

STOMATAL RESISTANCE (SR) FAMILY MEANS AND STANDARD ERRORS FOR VIRGINIA PINE FOR DAYS SIGNIFICANT FAMILY DIFFERENCES OCCURRED

Family	Period	Day	$\bar{x}$ SR (sec cm^{-1}) ± std error@	
10-1-2	3	1	4.96 ± 10.10	a
8-3-2	3	1	7.17 ± 11.23	a
13-5-1	3	1	30.47 ± 9.46	a
10-4-4	3	1	42.80 ± 10.10	b
14-1-3	3	1	45.18 ± 10.07	b
13-5-3	3	1	47.36 ± 9.80	b
10-4-4	3	10	20.11 ± 10.49	ab
8-3-2	3	10	31.92 ± 14.61	ab
10-1-2	3	10	51.95 ± 9.83	b
13-5-1	3	10	53.33 ± 9.83	b
14-1-3	3	10	71.69 ± 11.09	c
13-5-3	3	10	76.69 ± 9.83	c
10-4-4	4	7	18.94 ± 9.52	a
8-3-2	4	7	59.03 ± 13.30	b
13-5-1	4	7	67.28 ± 8.95	b
14-1-3	4	7	69.59 ± 10.10	b
10-1-2	4	7	69.83 ± 8.68	b
13-5-3	4	7	73.05 ± 8.95	b
8-3-2	4	10	32.22 ± 15.47	a
10-4-4	4	10	36.98 ± 10.42	ab
13-5-1	4	10	65.15 ± 10.42	abc
10-1-2	4	10	65.60 ± 10.42	abc
14-1-3	4	10	70.43 ± 11.75	ac
13-5-3	4	10	92.09 ± 10.42	c

Note: @ family means within each group (family) followed by same letter not significantly different

the following sections.

Mean SR values for Virginia pine seldom reached the magnitude of those observed for loblolly pine. The differences were most dramatic under control conditions, suggesting an ability within Virginia pine to more closely regulate stomatal opening. Virginia pine stomata remained open during non-stress conditions, more so than did the stomata of loblolly pine. Stomata closed in both species as stress increased, but Virginia pine stomata remained open longer than loblolly pine stomata, allowing photosynthesis and growth to continue further into the stress treatment. This behavior would explain the larger growth rates for Virginia pine height and stem caliper over loblolly pine.

Predawn Xylem Pressure Potential (XPP1)

Significant differences in mean XPP1 due to treatment appeared evident on every measurement day following the first ten-day stress period in loblolly pine (Table XI). These differences tended to be strongest at the end of each period. As expected, the control seedlings exhibited the lowest mean XPP1 while the severely stressed seedlings had the highest mean XPP1. Only on the tenth day of the third and fourth periods were treatment means significantly different across all levels.

Predawn xylem pressure potential estimates nightly plant xylem rehydration. As stress increases, internal plant water deficits increase. As soil moisture levels

TABLE XI

PREDAWN XYLEM PRESSURE POTENTIAL (XPP1) TREATMENT MEANS AND STANDARD ERRORS FOR LOBLOLLY PINE FOR DAYS SIGNIFICANT TREATMENT DIFFERENCES OCCURRED

Period	Day	Trt	$\bar{x}$ XPP1 (-bars) ± std error@	
2	10	1	9.4 ± 0.6	a
2	10	2	12.9 ± 0.6	b
2	10	3	12.8 ± 0.6	b
3	1	1	7.7 ± 0.5	a
3	1	2	9.2 ± 0.5	b
3	1	3	10.3 ± 0.5	b
3	10	1	9.7 ± 0.6	a
3	10	2	12.3 ± 0.6	b
3	10	3	14.6 ± 0.6	c
4	1	1	9.8 ± 0.9	a
4	1	2	12.3 ± 1.0.	ab
4	1	3	14.7 ± 1.0	b
4	10	1	10.9 ± 0.8	a
4	10	2	15.3 ± 0.7	b
4	10	3	18.1 ± 0.7	c

Note: @ treatment means within each group (period) followed by same letter not significantly different decrease, the amount of soil water available for plant xylem rehydration decreases. With insufficient soil moisture available to meet the increasing demand in xylem rehydration by stressed seedlings, internal plant water deficits increase. The significant treatment differences in XPP1 reached during the latter half of the study suggest that the study should have continued longer.

Significant loblolly pine family differences in mean XPP1 occurred on only one day (period 2 day 10) in this study. The results do not provide enough evidence from which to make any sound conclusions. One explanation for the lack of further family differences in mean XPP1 might be that the seedlings osmotically adjust. Osmotic adjustment is the lowering of cell osmotic potential in response to internal water loss. This ability is currently viewed as an important adaptation to drought. Osmotic adjustment may have been triggered early during this study as a mechanism to avoid further water deficits in this drought-hardy provenance. Significant family differences in mean XPP1 may have been observed had the study continued.

In Virginia pine, significant differences in mean XPP1 due to treatment occurred on the two measurement days of the fourth period. In both cases the trends were as expected with the control seedlings exhibiting the lowest mean XPP1 while severely stressed seedlings exhibited the highest mean XPP1. No significant treatment differences occurred between moderately and severely stressed seedlings.

Significant family differences in mean XPP1 were more prevalent in Virginia pine, beginning on the tenth day of the second period (Table XII). Families 8-3-2 and 10-4-4 tended to have the lowest mean predawn xylem pressure potentials, often times significantly lower than that of several other families. Family 13-5-3 always had the highest mean XPP1, often significantly higher than that of any other family. Family mean values of XPP1 were rather consistent over time.

These trends in mean family XPP1 follow those observed for mean SR. Families 8-3-2 and 10-4-4 had the most open stomata (lowest mean SR) and still maintained the lowest mean values of XPP1, indicating an ability to continue gas exchange with the environment without severely dehydrating their xylem systems. Their metabolic activity continues, as does photosynthesis and growth. These families would be valuable in screening tests due to their desirable behavior.

Family 13-5-3 had high values of mean SR, but still suffered larger internal water deficits than other families, suggesting poor control in water loss or in xylem rehydration after stomatal closure. Family 13-5-1, from the same origin as family 13-5-3, also had high mean values of XPP1, but lower mean values of SR compared to family 13-5-3. Family 10-4-4 had relatively low values of mean XPP1, while family 10-1-2, of the same origin, had higher mean values of XPP1. These among family within origin differences, as well as among origin differences, suggest various types of mechanisms exist in local as well as regional populations,

TABLE XII

PREDAWN XYLEM PRESSURE POTENTIAL (XPP1) FAMILY MEANS AND STANDARD ERRORS FOR VIRGINIA PINE FOR DAYS SIGNIFICANT FAMILY DIFFERENCES OCCURRED

Family	Period	Day	$\bar{x}$ XPP1 (-bars) ± std error@	
8-3-2	2	10	6.1 ± 0.8	a
10-4-4	2	10	6.5 ± 0.8	a
10-1-2	2	10	7.1 ± 0.7	a
14-1-3	2	10	7.4 ± 0.8	a
13-5-1	2	10	8.1 ± 0.7	a
13-5-3	2	10	10.3 ± 0.8	b
8-3-2	3	1	5.0 ± 0.7	a
10-4-4	3	1	5.4 ± 0.7	ab
10-1-2	3	1	6.5 ± 0.7	ab
14-1-3	3	1	6.7 ± 0.7	abc
13-5-1	3	1	7.2 ± 0.6	bc
13-5-3	3	1	8.5 ± 0.6	c
10-4-4	3	10	6.9 ± 0.9	a
8-3-2	3	10	7.3 ± 1.2	ab
14-1-3	3	10	9.8 ± 0.9	bc
13-5-1	3	10	10.2 ± 0.8	bc
10-1-2	3	10	10.5 ± 0.8	c
13-5-3	3	10	13.3 ± 0.9	d
8-3-2	4	1	7.7 ± 1.3	a
10-4-4	4	1	8.4 ± 0.9	a
14-1-3	4	1	9.2 ± 1.0	a
10-1-2	4	1	9.6 ± 0.9	a
13-5-1	4	1	9.8 ± 0.9	a
13-5-3	4	1	12.8 ± 0.9	b
8-3-2	4	10	9.6 ± 1.7	a
10-4-4	4	10	10.5 ± 1.1	a
13-5-1	4	10	12.5 ± 1.1	a
14-1-3	4	10	12.6 ± 1.3	a
10-1-2	4	10	13.2 ± 1.1	a
13-5-3	4	10	17.9 ± 1.1	b

Note: @ family means within each group (family) followed by same letter not significantly different

and genetic selection could be used to develop a drought tolerant population.

Significant within-family among treatment differences in mean XPP1 were observed in Virginia pine on the tenth day of the second period and during both measurement days of the fourth period. These differences appeared in families 10-4-4 and 13-5-3 and consisted of change in mean XPP1 values from those expected under the stress treatments used in this study. For example, under severe stress mean XPP1 values in family 13-5-3 were not the highest, as would be expected. The highest mean XPP1 value for this family in this example was observed under moderate stress. Significant differences in response to stress, as measured by XPP1, indicate higher sensitivity to stress within certain families plus an inability to moderate levels of XPP1 during stress. Further study into the variation in sensitivity within certain families would be of interest.

Family rankings remain consistent on the tenth day of the fourth period, with families 8-3-2 and 10-4-4 showing lower mean values of XPP1 under all treatment levels and with family 13-5-3 showing the highest mean values of XPP1 under moderate- and severe-stress levels. This would suggest the possibility for increasing control of internal water deficits in Virginia pine by selecting for increased ability to rehydrate xylem overnight during stress, as demonstrated in families 8-3-2 and 10-4-4. Introduction of these families into breeding programs could increase the drought tolerance of a population.

Midday Xylem Pressure Potential (XPP2)

Significant treatment differences in mean XPP2 in loblolly pine occurred on only three measurement days, while significant family differences appeared on only one measurement day. On the tenth day of the first period, mean treatment values of XPP2 were significantly lower in control seedlings than in moderately stressed seedlings, with the differences between controls and severely stressed and between moderately and severely stressed seedlings not being significant. On the first day of the third period, mean values of XPP2 in the controls were significantly lower than in either the moderately or severely stressed seedlings, with no significant differences in mean XPP2 occurring between moderately and severely stressed seedlings. On the tenth day of the fourth period, mean values of XPP2 were significantly different across all treatment levels, with controls having the lowest mean value of XPP2. The development of significant treatment differences in mean XPP2 between moderately and severely stressed seedlings on the last day of the study suggest that extension of the study stress period may have allowed distinct trends to develop among treatment means.

Significant loblolly pine family differences in mean XPP2 occurred on the tenth day of the first period (Table XIII). Family ranking on this day was similar to that noted

TABLE XIII

MIDDAY XYLEM PRESSURE POTENTIAL (XPP2) FAMILY MEANS AND STANDARD ERRORS FOR LOBLOLLY PINE ON THE TENTH DAY OF THE FIRST PERIOD

Family	$\bar{x}$ XPP2 (-bars) ± std error@	
75 x 84	9.5 ± 1.2	a
89 x 71	11.5 ± 1.3	b
80 x 81	12.3 ± 1.0	b
87 x 81	12.9 ± 1.0	b
80 x 91	13.2 ± 1.0	b
76 x 81	13.2 ± 1.1	b
74 x 75	14.2 ± 1.0	b
73 x 86	15.0 ± 1.0	b

Note: @ family means followed by same letter not significantly different

on measurement days when family differences in mean XPP1 were significant. As with the lack of further significant family differences observed in mean XPP1, the lack of significant family differences in mean XPP2 beyond the first period might be due to osmotic adjustment. These inherently drought resistant sources of loblolly pine may have reached some threshold during the first period which triggered osmotic adjustment. If so, family differences might not appear until another stress threshold is reached. The relatively short duration of this study may have precluded the identification of significant family differences within the Oklahoma/Arkansas provenance of loblolly pine, or all of these families may share similar reaction behavior in response to stress.

Significant treatment differences in mean XPP2 occurred on only two measurement days in Virginia pine. On the first day of the second period, control seedlings exhibited the highest mean XPP2. This may have been the result of waterlogging caused by poor aeration and drainage within the planting containers. On the first day of the fourth period, control seedlings exhibited the lowest mean XPP2 while moderately stressed seedlings exhibited the highest mean XPP2. No significant differences in mean XPP2 occurred between moderately and severely stressed seedlings on either measurement day.

Significant differences in mean XPP2 were much more prevalent among Virginia pine families than among loblolly pine families, particularly during the last two periods of the study. Mean Virginia pine family XPP2 and standard errors are presented in Table XIV for each significant measurement day.

Obvious family trends appear for mean XPP2 in Virginia pine. Families 8-3-2 and 10-4-4 most often exhibited the lowest mean XPP2 while family 13-5-3 always possessed the highest mean XPP2. These differences are significant and closely resemble the differences observed for SR and XPP1, indicating that families 8-3-2 and 10-4-4 were under less stress due to an inherent ability to control internal water deficits during the middle of the day. The large root-shoot ratios of these families may also assist them in control of internal water deficits during the middle of the day by allowing access to larger volumes of soil. Family 13-5-3, on the other hand, could not control internal water loss during the middle of the day which in turn resulted in the highest mean value of XPP2 compared to the other families of Virginia pine.

Drought Resistance Parameter Correlation

When summed over families for both species, the strongest correlations between the drought resistance parameters were between mean XPP1 and mean XPP2 for both loblolly pine (Table XV) and Virginia pine (Table XVI). In loblolly pine, mean XPP1 and mean XPP2 appeared to remain strongly, positively and significantly correlated, both among treatments

TABLE XIV

MIDDAY XYLEM PRESSURE POTENTIAL (XPP2) FAMILY MEANS AND STANDARD ERRORS FOR VIRGINIA PINE FOR DAYS SIGNIFICANT FAMILY DIFFERENCES OCCURRED

Family	Period	Day	$\overline{x}$ XPP2 (-bars) ± std error@	
10-4-4	2	10	8.6 ± 1.0	a
8-3-2	2	10	8.7 ± 1.0	a
10-1-2	2	10	9.8 ± 0.9	a
13-5-1	2	10	10.9 ± 0.9	ab
14-1-3	2	10	11.0 ± 1.0	ab
13-5-3	2	10	13.1 ± 0.9	b
10-4-4	3	1	8.0 ± 0.9	a
13-5-1	3	1	8.3 ± 0.9	a
8-3-2	3	1	9.3 ± 1.1	a
14-1-3	3	1	9.4 ± 1.0	a
10-1-2	3	1	9.8 ± 1.0	ab
13-5-3	3	1	12.4 ± 1.0	b
10-4-4	3	10	10.4 ± 1.0	a
8-3-2	3	10	11.1 ± 1.4	ab
10-1-2	3	10	13.1 ± 1.0	ab
14-1-3	3	10	13.7 ± 1.1	b
13-5-1	3	10	13.8 ± 1.0	b
13-5-3	3	10	19.4 ± 1.0	c
8-3-2	4	1	9.1 ± 1.7	a
10-4-4	4	1	9.1 ± 1.2	ab
10-1-2	4	1	12.0 ± 1.2	abc
13-5-1	4	1	12.6 ± 1.2	ac
14-1-3	4	1	13.6 ± 1.3	cd
13-5-3	4	1	16.6 ± 1.2	d
10-4-4	4	10	12.2 ± 1.5	a
8-3-2	4	10	13.2 ± 2.2	ab
10-1-2	4	10	16.6 ± 1.5	bc
13-5-1	4	10	18.0 ± 1.5	bc
14-1-3	4	10	20.1 ± 1.7	cd
13-5-3	4	10	23.4 ± 1.5	d

Note: @ family means within each group (family) followed by same letter not significantly different

TABLE XV

CORRELATION COEFFICIENTS SUMMED OVER FAMILIES FOR DROUGHT RESISTANCE PARAMETERS IN LOBLOLLY PINE

	Period 1	Period 2	Period 3	Period 4
Trt 1				
SR[!] x XPP1[@]	.33*	.31*	.57*	.49*
SR x XPP2[#]	.39*	.29*	.53*	.40*
XPP1 x XPP2	.89*	.73*	.79*	.86*
Trt 2				
SR x XPP1	.24	.38*	.46*	.32*
SR x XPP2	.34*	.43*	.43*	.34*
XPP1 x XPP2	.87*	.68*	.59*	.44*
Trt 3				
SR x XPP1	.22	.60*	.27*	.24
SR x XPP2	.24	.42*	.26	.32*
XPP1 x XPP2	.76*	.65*	.75*	.55*

Note: ! SR = stomatal resistance

@ XPP1 = predawn xylem pressure potential

* correlation coefficient (r) significant at the 5% level

XPP2 = midday xylem pressure potential

TABLE XVI

CORRELATION COEFFICIENTS SUMMED OVER FAMILIES FOR DROUGHT RESISTANCE PARAMETERS IN VIRGINIA PINE

	Period 1	Period 2	Period 3	Period 4
Trt 1				
SR[!] x XPP1[@]	-.05	.19	.12	.21
SR x XPP2[#]	-.01	.22	.30	.45*
XPP1 x XPP2	.46*	.47*	.45*	.35*
Trt 2				
SR x XPP1	.13	.08	.64*	.57*
SR x XPP2	.20	.18	.57*	.38*
XPP1 x XPP2	.57*	.19	.86*	.63*
Trt 3				
SR x XPP1	.29	.31*	.47*	.50*
SR x XPP2	.04	.25	.43*	.45*
XPP1 x XPP2	.69*	.68*	.79*	.73*

Note: ! SR =stomatal resistance

@ XPP1 = predawn xylem pressure potential

XPP2 = midday xylem pressure potential

* correlation coefficient (r) significant at the 5% level

within each period and from period to period. In Virginia pine, this correlation was not quite as strong or consistent.

Correlations between mean SR and either mean XPP1 or mean XPP2 were also smaller and less consistently significant in Virginia pine, but became more strongly correlated with time. No significant correlations between mean SR and mean XPP1 or between mean SR and mean XPP2 existed for Virginia pine during the first half of the study. These correlations became significant and fairly consistent, however, during the latter half of the study.

These results suggest that values of XPP2 probably closely follow XPP1 values, with SR being most influenced by the XPP2 parameter, particularly in loblolly pine. Because the mean SR and xylem pressure potential parameters are more often significantly correlated in loblolly pine, it would appear that the stomatal resistance mechanism and the xylem pressure potential mechanism may be more closely linked in this species. This relationship appears less evident in Virginia pine, suggesting that the level of stomatal opening is less influenced by the xylem pressure potential level. If stomatal opening is influenced less by xylem pressure potential levels, then as a species, Virginia pine may be more drought tolerant than loblolly pine, because it can continue stomatal gas exchange with the environment longer under periods of stress and still maintain a favorable balance in xylem pressure potential. This turgor maintenance capacity evident in Virginia pine may result from osmotic adjustment, although reports indicating the possible existence of osmotic adjustment in Virginia pine are limited.

Heritabilities of Drought Resistance Parameters

Heritabilities for the three drought resistance parameters were low, with fairly large standard errors, particularly for loblolly pine (Tables XVII to XIX). Virginia pine estimates were somewhat larger and suggest that the parameters XPP1 and XPP2 might be under moderate genetic control. Drought tolerance possesses certain qualities which liken it to a threshold trait (Falconer, 1981). The mechanisms required for survival under drought conditions become activated after passing some threshold level of stress. The clue to understanding the inheritance of such characters lies in the idea that the character has an underlying continuity with a threshold which imposes a discontinuity on the visible expression. When the underlying variable is below this threshold level the individual has one form of phenotypic expression, e.g., it is "normal"; when it is beyond the threshold the individual has the other phenotypic expression, e.g., it is "affected." The underlying continuous variable has been called the liability, is both genetic and environmental in origin, and may be thought of as the rate of change undergone by seedlings in response to drought. Under the threshold, the rate is negligible, but it is much larger above the threshold. Heritability (h^2) estimates for water stress parameters of trees under stress would be

TABLE XVII

STOMATAL RESISTANCE HERITABILITY (h^2) ESTIMATES AND STANDARD ERRORS FOR VIRGINIA AND LOBLOLLY PINE BY TREATMENT ON DAY 10 OF EACH PERIOD

			h^2 ± std error	
Period	Day	Trt	Virginia pine	Loblolly pine
1	10	1	-0.05 ± 0.11	-0.03 ± 0.10
1	10	2	0.16 ± 0.15	0.14 ± 0.13
1	10	3	0.05 ± 0.13	0.34 ± 0.14
2	10	1	-0.17 ± 0.08	-0.15 ± 0.07
2	10	2	0.23 ± 0.16	-0.04 ± 0.10
2	10	3	-0.00 ± 0.12	-0.23 ± 0.05
3	10	1	0.31 ± 0.18	0.37 ± 0.14
3	10	2	0.05 ± 0.13	-0.27 ± 0.04
3	10	3	0.14 ± 0.15	0.03 ± 0.11
4	10	1	0.25 ± 0.17	0.15 ± 0.13
4	10	2	-0.10 ± 0.09	0.12 ± 0.13
4	10	3	0.54 ± 0.15	0.08 ± 0.12

TABLE XVIII

PREDAWN XYLEM PRESSURE POTENTIAL HERITABILITY (h^2) ESTIMATES AND STANDARD ERRORS FOR VIRGINIA AND LOBLOLLY PINE BY TREATMENT ON DAY 10 OF EACH PERIOD

			h^2 ± std error	
Period	Day	Trt	Virginia pine	Loblolly pine
1	10	1	0.08 ± 0.14	-0.21 ± 0.06
1	10	2	-0.05 ± 0.11	-0.05 ± 0.09
1	10	3	-0.01 ± 0.12	0.12 ± 0.12
2	10	1	-0.13 ± 0.09	0.01 ± 0.11
2	10	2	0.55 ± 0.15	0.20 ± 0.13
2	10	3	0.06 ± 0.14	0.18 ± 0.13
3	10	1	0.55 ± 0.17	0.06 ± 0.12
3	10	2	0.29 ± 0.16	0.28 ± 0.14
3	10	3	0.57 ± 0.15	-0.10 ± 0.09
4	10	1	0.42 ± 0.18	0.08 ± 0.12
4	10	2	0.01 ± 0.12	0.22 ± 0.14
4	10	3	0.70 ± 0.12	0.31 ± 0.14

TABLE XIX

MIDDAY XYLEM PRESSURE POTENTIAL HERITABILITY (h^2) ESTIMATES AND STANDARD ERRORS FOR VIRGINIA AND LOBLOLLY PINE BY TREATMENT ON DAY 10 OF EACH PERIOD

			h^2 ± std error	
Period	Day	Trt	Virginia pine	Loblolly pine
1	10	1	0.05 ± 0.13	-0.07 ± 0.09
1	10	2	0.27 ± 0.17	0.12 ± 0.12
1	10	3	0.15 ± 0.15	0.18 ± 0.13
2	10	1	-0.04 ± 0.12	0.28 ± 0.14
2	10	2	0.18 ± 0.16	0.07 ± 0.12
2	10	3	0.26 ± 0.16	0.35 ± 0.14
3	10	1	0.48 ± 0.18	0.22 ± 0.14
3	10	2	0.57 ± 0.14	-0.02 ± 0.10
3	10	3	0.64 ± 0.13	-0.19 ± 0.06
4	10	1	0.10 ± 0.15	-0.16 ± 0.08
4	10	2	0.60 ± 0.14	-0.19 ± 0.06
4	10	3	0.62 ± 0.14	0.34 ± 0.14

expected to be larger than for trees not under stress.

Heritabilities for SR calculated by period (Table XVII) were low for both species and contained large standard errors. As expected, h^2 for SR increased by period with the increase in stress. Heritability estimates appeared to be larger in Virginia pine than in loblolly pine.

When calculated by treatment (Table XVII), h^2 estimates for SR were still low with large standard errors. Heritability estimates increased slightly with increasing stress treatment in Virginia pine, but were erratic and showed little change in loblolly pine. It would appear that SR is under little genetic control, especially in loblolly pine and for the material and treatments in this study. This suggests breeding for specific patterns of stomatal behavior would be difficult in loblolly pine. However, some breeding for specific patterns of stomatal behavior may be possible in Virginia pine. Further testing with larger sample size is recommended to increase our understanding of stomatal behavior in these species.

Heritability for XPP1 (Table XVIII) was somewhat higher than h^2 for SR. This was observed for both species. Heritability estimates increased over time and with treatment stress level in both species. Breeding for favorable activity in nightly xylem pressure potential recovery may be possible in both species, with the greatest results to be expected in Virginia pine. Predawn xylem pressure potential appears to be under moderate genetic control in this species.

Heritabilities calculated for XPP2 (Table XIX) were moderate in Virginia pine, but tended toward zero in loblolly pine. Standard errors were fairly large in both species. More gains in control of midday xylem pressure potential would be expected from Virginia pine than from loblolly pine.

The larger h^2 estimates for the drought resistance parameters in Virginia pine may be the result of the larger genetic diversity in the sample population used in this study compared to the limited diversity in the loblolly pine families. More study with longer stress periods and larger sample sizes is recommended to verify these h^2 estimates.

Diurnal Regressions

The data collected during the diurnal measures of SR and xylem pressure potential were plotted and predictive equations derived for each family for each period. When separate analyses showed no significant changes in SR due to period, the data were pooled to create a single regression equation for each family. This provided an average estimate of the level of xylem pressure potential reached at stomatal closure (SR=100). The results are presented in Table XX for loblolly pine and Table XXI for Virginia pine. Results from the regression equations support the results from the analysis of the drought resistance parameters. The values of xylem pressure potential at stomatal closure obtained here for loblolly pine are similar to those reported in the

TABLE XX

FAMILY REGRESSION EQUATIONS TO PREDICT XYLEM PRESSURE POTENTIAL (XPP) AT STOMATAL CLOSURE (SR=100) FOR LOBLOLLY PINE

Family	Predicted Equation
75 x 84	$\hat{Y} = 10.2 + 0.020(SR)$ @SR=100, XPP=12.2!
80 x 81	$\hat{Y} = 11.3 + 0.024(SR)$ @SR=100, XPP=13.7
74 x 75	$\hat{Y} = 11.9 + 0.020(SR)$ @SR=100, XPP=13.9
80 x 91	$\hat{Y} = 12.0 + 0.028(SR)$ @SR=100, XPP=14.8
89 x 71	$\hat{Y} = 13.6 + 0.012(SR)$ @SR=100, XPP=14.8
87 x 81	$\hat{Y} = 14.0 + 0.018(SR)$ @SR=100, XPP=15.8
76 x 81	$\hat{Y} = 14.8 + 0.012(SR)$ @SR=100, XPP=16.0
73 x 86	$\hat{Y} = 12.4 + 0.038(SR)$ @SR=100, XPP=16.2

Note: ! units for XPP are -bars

TABLE XXI

FAMILY REGRESSION EQUATIONS TO PREDICT XYLEM PRESSURE POTENTIAL (XPP) AT STOMATAL CLOSURE (SR=100) FOR VIRGINIA PINE

Family	Predicted Equation
8-3-2	$\hat{Y} = 7.5 + 0.023(SR)$ @SR=100, XPP=9.8!
10-1-2	$\hat{Y} = 9.1 + 0.022(SR)$ @SR=100, XPP=11.3
13-5-1	$\hat{Y} = 8.8 + 0.033(SR)$ @SR=100, XPP=12.2
10-4-4	$\hat{Y} = 12.0 + 0.006(SR)$ @SR=100, XPP=12.6
13-5-3	$\hat{Y} = 9.9 + 0.038(SR)$ @SR=100, XPP=13.7
14-1-3	$\hat{Y} = 9.7 + 0.042(SR)$ @SR=100, XPP=13.9

Note: ! units for XPP are -bars

literature (Teskey and Hinckley, 1985). As a species Virginia pine appears to be more drought tolerant than loblolly pine because it maintains less negative values of xylem pressure potential at stomatal closure than does loblolly pine, thus maintaining positive turgor allowing for continued growth during moderate stress.

Results of the regression analysis indicate that those families that maintained lower mean values of XPP1 and XPP2 also had the least negative xylem pressure potentials at stomatal closure. These results correspond favorably with results from the analysis of XPP1 and XPP2 in loblolly pine. Families 74 x 75, 75 x 84 and 80 x 81 had lower mean values of XPP1 and XPP2 under stress than other families of loblolly pine. From the diurnal analysis, the lower values of XPP1 and XPP2 in these families might be due to stomatal closure at less negative xylem pressure potentials which enables the seedlings to avoid severe internal desiccation. This is a desirable trait allowing seedling survival longer during extended droughts and permitting growth to resume more quickly when conditions become favorable.

The diurnal analysis results also correspond favorably with the results of the analysis of SR, XPP1 and XPP2 in Virginia pine. Family 8-3-2 most often had the lowest mean values of SR, XPP1 and XPP2, indicating the ability to continue water exchange with the environment and not suffer severe internal water deficits. Family 8-3-2 also had the smallest water deficit at stomatal closure. This might be due to stomatal behavior which enhanced the control of internal plant water losses, or be the result of a larger root-shoot ratio which would allow for greater uptake of soil water under stress.

Virginia pine family 10-4-4 which had low mean values of SR, XPP1 and XPP2 similar to those of family 8-3-2, closed stomata at more negative values of xylem pressure potential. Families 10-1-2 and 13-5-1 closed stomata at less negative values of xylem pressure potential than family 10-4-4, but had high mean values of XPP1 and XPP2. These unexpected results might be explained by the fact that these families had smaller root-shoot ratios than family 10-4-4. Smaller root-shoot ratios would result in less uptake of soil water under stress. Under moderate stress families 10-1-2 and 13-5-1 always had lower mean values of XPP1 and XPP2 than family 10-4-4. But under severe stress, family 10-4-4 always had the lowest mean values of XPP1 and XPP2. Change in rank among these families due to their inherent differences in internal water balance indicate the importance of large root-shoot ratios during periods of water stress.

Virginia pine family 13-5-3 consistently had the highest mean values of SR, XPP1 and XPP2 compared to other families of Virginia pine. This family also had the second most negative value of xylem pressure potential at stomatal closure. This would suggest that poor stomatal control, low root-shoot ratio and high water loss combined to cause family 13-5-3 to reach more severe levels of internal desiccation under stress. This family would be undesirable in selection to improve the drought tolerance of Virginia pine.

P-V Analysis

Certain valuable water relations parameters can be estimated directly from a P-V curve. The most important of these is the osmotic potential at full turgor ($\psi_{\pi o}$) as it sets the upper limit to which turgor forces can develop at full hydration--the lower the initial osmotic potential the greater the initial turgor pressure. Because this value is an estimate of the amount of osmotically active solutes per unit volume of symplastic water, it strongly influences the rate of change in osmotic potential per unit of water loss.

The magnitude of osmotic potential at incipient plasmolysis (ψ_{ip})--the theoretical wilting point--is also very important because it establishes the lower limit to the water potential at which positive turgor can exist. In other words, a low value of osmotic potential at incipient plasmolysis would enable the plant to maintain positive turgor while under high water stress.

Another parameter often noted on P-V curves is the percent of tissue water at full turgor which is held in the symplasm (denoted SV). This can be obtained from the x-intercept of the osmotic potential regression line. (For reference, a hypothetical P-V curve is drawn in Figure 4.) Literature values of SV of leaf and stem tissue vary from

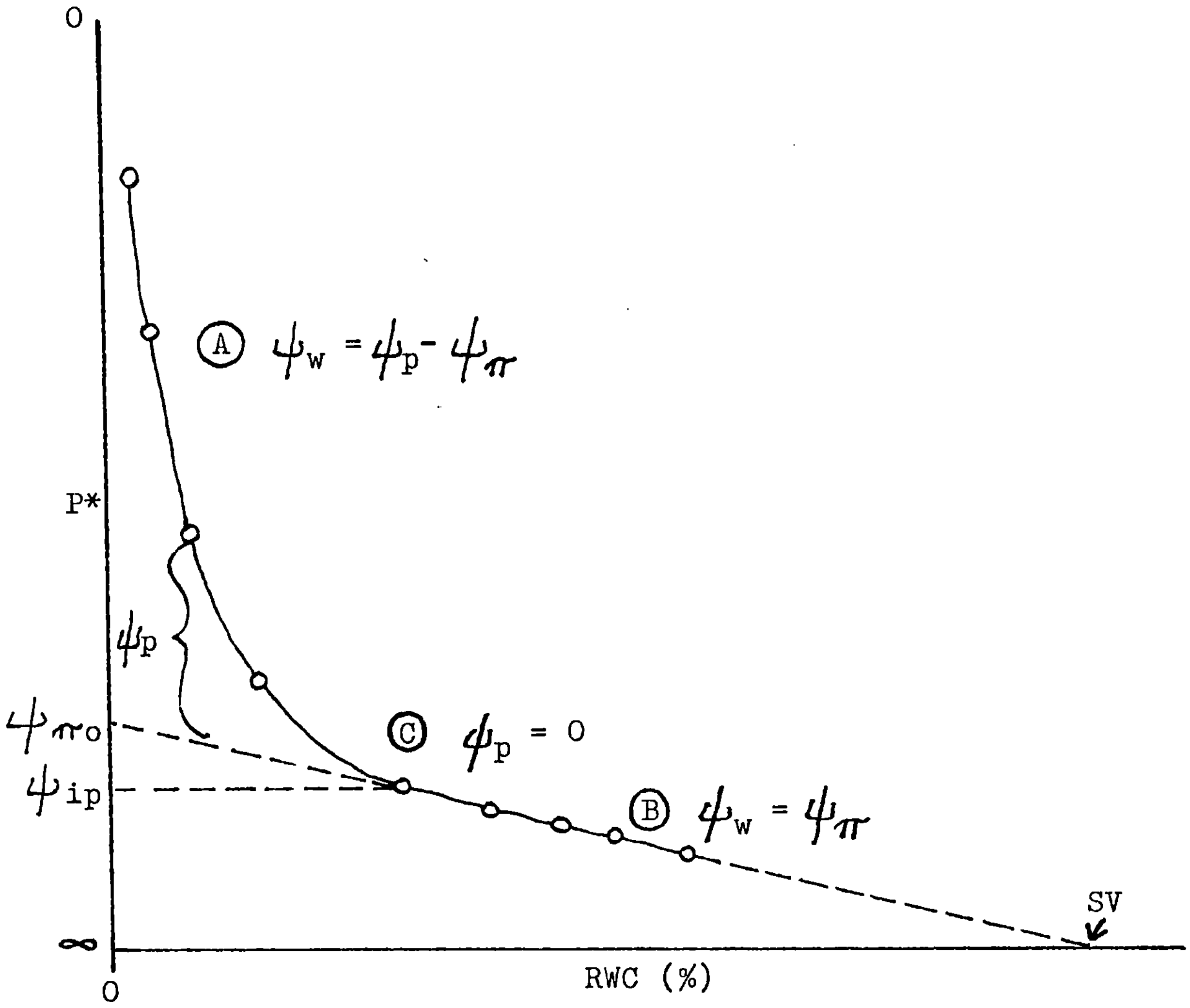

Figure 4. A hypothetical P-V curve. In curvilinear region "A", chamber pressure (P*) balances both the osmotic (ψ_π) and turgor forces (ψ_p) in the sample tissue. At point "C", turgor pressure falls to zero, thus in region "B" chamber pressure balances only osmotic potential. Extrapolation of region "B" to the abscissa gives an estimate of the symplasm volume (SV) and to the ordinate gives an estimate of the osmotic potential at full turgor ($\psi_{\pi o}$). The osmotic potential at incipient plasmolysis (ψ_{ip}) can be estimated from point "C".

about 50 to 75 percent (Ritchie and Dunham, 1979).

The regression line from which these parameters can be estimated was predicted from the data obtained from the five seedlings used from each family during the P-V determination. A regression line was predicted for each family to fit the data. The three physiological water relations parameters were calculated for each family and are presented in Table XXII.

The capacity of a plant to maintain positive turgor at decreasing water potentials would be a direct measure of its ability to carry out metabolic and growth processes while under water stress. A difference in turgor maintenance capacity could arise from the effects of three interacting mechanisms. First is the magnitude of the initial turgor pressure (set by $\psi_{\pi 0}$); second is the ability to adjust cell osmotic potential in response to water loss (osmotic adjustment); and third is the comparative elasticity of cell walls. Cell wall elasticity influences the rate of change in positive turgor pressure with respect to change in relative water content. Cells with rigid walls drop their positive turgor pressures more rapidly than cells with less rigid walls in response to a given reduction in relative water content. This would imply that selection for individuals with large differences between $\psi_{\pi 0}$ and ψ_{ip} would lead to the selection of individuals in which positive turgor pressure drops more slowly per unit drop in relative water content. This behavior is desirable because it allows growth and

TABLE XXII

SYMPLAST VOLUME (SV), OSMOTIC POTENTIAL AT INCIPIENT PLASMOLYSIS (ψ_{ip}), AND OSMOTIC POTENTIAL AT FULL TURGOR ($\psi_{\pi o}$) FOR LOBLOLLY AND VIRGINIA PINE FAMILIES

LOBLOLLY PINE

Family	SV(%)	$\psi_{ip}^{@}$	$\psi_{\pi o}^{@}$	$\Delta\psi^{\#}$
89 x 71	62.5	19.7	13.3	6.4
87 x 81	60.0	18.0	13.9	4.1
80 x 91	61.0	18.9	13.4	6.0
80 x 81	56.2	20.1	17.4	2.7
76 x 81	100.0	23.5	23.4	0.1
75 x 84	84.0	21.9	18.9	3.0
74 x 75	41.0	23.8	15.7	8.1
73 x 86	49.5	23.9	21.3	2.6

VIRGINIA PINE

Family	SV(%)	ψ_{ip}	$\psi_{\pi o}$	$\Delta\psi$
14-1-3	66.0	17.4	11.2	6.2
13-5-3	21.0	23.2	21.1	2.1
13-5-1	64.5	24.5	24.4	0.1
10-4-4	70.5	21.5	11.3	10.2
10-1-2	46.0	17.8	13.9	3.9
8-3-2	69.5	16.4	11.8	4.6

Note: @ units for ψ_{ip} and $\psi_{\pi o}$ are -bars

\# $\Delta\psi = \psi_{ip} - \psi_{\pi o}$

metabolic activities to continue under stress, thus maximizing the growth potential of the species.

Large $\psi_{\pi_o}-\psi_{ip}$ gradients indicate that tissue elastic properties more effectively buffer cell volume changes within seedlings during drought, enabling turgor pressure to remain positive over a broad range of water deficits. The largest $\psi_{\pi_o}-\psi_{ip}$ gradients were observed for loblolly pine family 74 x 75 and Virginia pine families 8-3-2, 10-4-4 and 14-1-3. This would suggest some adaptation to droughty conditions in these families. Virginia pine families 8-3-2 and 10-4-4 also had low mean values of SR, indicating an ability to continue photosynthesis and growth under stress.

Low (more negative) values of ψ_{ip} in shoots and high SV may be one sign of adaptation to droughty conditions. Loblolly pine families 75 x 84 and 76 x 81 as well as Virginia pine families 10-4-4 and 14-1-3 had high SV and the most negative values of ψ_{ip} in their respective species. However, only loblolly pine family 75 x 84 and Virginia pine family 14-1-3 exhibited good stem caliper growth. This would suggest that the values of ψ_{ip} shown for families 76 x 81 and 10-4-4 were below that required for good growth to continue. Results from the diurnal analysis support this fact. Values of SV, ψ_{ip} and ψ_{π_o} obtained in this study for loblolly pine are similar to those reported in the literature for loblolly pine and other conifers (Ritchie and Schula, 1981).

Virginia pine family 13-5-3 had the smallest SV and the second smallest $\psi_{\pi o}-\psi_{ip}$ gradient, suggesting high sensitivity to change in internal water level due to drought. High mean values of XPP1 and XPP2 in this family under stress also provide evidence of its poor adaptation to droughty conditions. Inclusion of this family in breeding programs designed to increase drought tolerance in this species would not be suggested; nor would selection for possible production in Oklahoma.

CHAPTER V

SUMMARY AND CONCLUSIONS

Results from this study suggest that considerable variation exists in growth and drought tolerance between and within the two species of pine examined. Evidence suggests that within each species, further testing with several recommended families and further screening could result in considerable gains in survival and growth under droughty conditions.

Virginia pine appears more capable of continuing growth under stress than loblolly pine. Virginia pine increased stem caliper more than loblolly pine under both stress and non-stress conditions. The material sampled in this study suggests an inherently greater growth rate for Virginia pine while loblolly pine appears to be more sensitive to water deficits. Considerable variation was expressed in stem caliper growth by the male and female contributors of the loblolly pine progeny. No significant treatment differences in height growth appeared in either species.

Inherent differences in root-shoot ratio within and between the two species may explain in part the differences in growth and control of internal water balance observed in this study. Root-shoot ratios in Virginia pine were typically larger than those observed for loblolly pine. Inherently larger root-shoot ratios resulting from smaller shoot mass relative to root mass would probably be advantageous for seedling survival during drought conditions. Significant family differences in root-shoot ratio were observed in Virginia pine. Apparent differences in root-shoot ratios resulting from stress treatment were also observed in Virginia pine, but were only significant at the 10% level. No significant differences in root-shoot ratios for loblolly pine resulting from treatment stress were indicated. An ability to increase root-shoot ratio during stress might also be advantageous for continued growth and survival during stress.

Differences in stomatal behavior appeared between and within each species. Mean stomatal resistance values for Virginia pine seldom reached the magnitude of those observed in loblolly pine. This would suggest that Virginia pine continued gas exchange with the environment longer under stress, thus enhancing growth during this period. Family differences in mean stomatal resistance appeared in Virginia pine during the latter half of the study, but were never observed for loblolly pine families. This is best explained by the differences in genetic diversity in the sample populations used in this study. The loblolly pine provenance probably had considerably less genetic variation in its families than in the Virginia pine provenance. The results may also reflect real species differences.

Significant treatment differences in mean stomatal resistance were found in loblolly pine, particularly during the latter half of the study, while significant treatment differences in mean stomatal resistance were found on only one day for Virginia pine. Again, this suggests an ability within Virginia pine to continue gas exchange with the environment while under stress, thus enhancing growth, while loblolly pine stomates closed rapidly under stress. Both behavior patterns may be advantageous during drought, but the behavior in loblolly pine reduces the growth potential, particularly in the families examined in this study.

Similar trends were observed for predawn and midday xylem pressure potentials, measures of nightly xylem rehydration and midday xylem stress, respectively. Significant family differences in both traits were more prevalent in Virginia pine than in loblolly pine. This may again be due to the differences in genetic diversity between the sample populations. Treatment differences in both traits were more prevalent in loblolly pine, suggesting a poor ability within loblolly pine xylem systems to rehydrate during stress compared to Virginia pine, possibly due to the smaller root-shoot ratios of loblolly pine. This inability to rehydrate under stress would result in higher values of midday xylem pressure potentials, stomatal closure and growth cessation.

No genetic differences appeared in the water relations of the loblolly pine families used in this study. This does not mean that differences do not exist, however. The lack of family differences within the Oklahoma/Arkansas region could also prove valuable to local industry looking to reduce operational costs since individual selections of parent material for use in producing drought resistant progeny would be unnecessary. One possible reason for the lack of differences observed among families could be the inherently high drought tolerance of the provenance and the time required before such differences are manifested. Use of a larger sample size within the Oklahoma/Arkansas provenance may have allowed the identification of drought tolerant families. Also, the use of some less tolerant eastern provenance may have allowed better characterization of the relative drought tolerance of the Oklahoma/Arkansas provenance. Differences in inherent drought tolerance might also have become more apparent if the study had been continued for a longer period of time.

The strongest correlation of drought resistance parameters was between mean predawn and mean midday xylem pressure potentials for both species. Correlation between mean stomatal resistance and either mean predawn or mean midday xylem pressure potential was smaller and less consistently significant. These results suggest that mean levels of midday xylem pressure potentials are highly influenced by mean levels of predawn xylem pressure potentials, with stomatal resistance being most influenced by the mean level of midday xylem pressure potential. These trends seem logical and are particularly noticeable in loblolly pine.

The drought resistance traits measured in this study--stomatal resistance, predawn xylem pressure potential and midday xylem pressure potential--appear to be under some genetic influence. Heritability (h^2) estimates for stomatal resistance were quite low in both species and contained large standard errors. This would suggest limited progress in breeding for a particular pattern of stomatal behavior. Heritability estimates for predawn xylem pressure potential and midday xylem pressure potential appear to be somewhat higher for both species, especially Virginia pine. Standard errors for these estimates are still somewhat large. Predawn and midday xylem pressure potentials appear to be under moderate genetic control, which indicates some ability to breed for seedlings more tolerant to or better able to avoid large internal water deficits. Breeding for such traits appears to be much more favorable in Virginia pine than in loblolly pine.

The differences in h^2 estimates expressed for these traits between species may reflect the differences in genetic diversity between the sample populations used in this study. The use of a more diverse sample of Virginia pine families compared to loblolly pine may well explain the higher h^2 estimates obtained for the drought resistance traits in Virginia pine.

Results obtained from the analysis of diurnal stomatal and xylem pressure potential behavior indicate that the families which maintained lower mean values of predawn and midday xylem pressure potentials also had less negative xylem pressure potentials at stomatal closure. Values for loblolly pine xylem pressure potential at stomatal closure, although higher than those for Virginia pine, were similar to values reported in the literature. Stomatal closure at less negative levels of xylem pressure potential is beneficial for growth and survival during drought. Less negative values of xylem pressure potentials increase chances of survival during lengthy droughts and allow growth to resume more quickly when conditions become favorable.

Virginia pine families 8-3-2, 10-4-4 and 14-1-3 could be suggested for field testing and possible production in Oklahoma. These families controlled water use well and exhibited considerable growth under stress. These families also possess high root-shoot ratios which would be advantageous for survival during drought, as large root systems enable seedlings to access larger and deeper volumes of soil for water. Family 14-1-3 is suggested for further study. Osmotic adjustment may play an active role in this family's physiological management of internal water balance. Closer examination of this and other families' needle morphology, root morphology and physiological water relations under stress may be enlightening.

The results for loblolly pine were not conclusive. Little evidence exists to make family selections with any strong degree of certainty. Further examination of families from the Oklahoma/Arkansas provenance and other origins is suggested. Perhaps the biggest factor to consider in the production of several of these families is their sensitivity to water deficits. Growth of the loblolly pine families used in this study was found to be quite sensitive to the levels of imposed stress used during this study.

The use of several families, particularly 76 x 81 and 89 x 71, would not be recommended when volume production is the primary objective in forest tree production. These families were the most sensitive to water deficits. Several families did make good growth and are suggested for further study. They include family 74 x 75, which had a high root-shoot ratio and produced good height growth under stress; family 75 x 84, which had a high root-shoot ratio and produced good caliper growth under stress; and family 80 x 81, which possessed the largest root-shoot ratio for this species. Use of family 80 x 81 would be suggested when survival under stress is the major objective in forest tree planting in Oklahoma.

Because this study was conducted in a growth chamber, further testing should be done with both species to determine if family performance expressed under these controlled conditions is truly indicative of performance under field conditions. Loblolly pine drought studies using the families in this study should be conducted on sites characteristic of those planted to loblolly pine in southeastern Oklahoma.

The Virginia pine families used in this study have already been outplanted at several locations across Oklahoma. Family survival should be determined for these sites. This would allow examination for possible correlations between drought resistance determined under controlled environments and actual field survival and later height growth. The determination of such correlations will substantiate the validity of using controlled environment chambers to determine the drought tolerance of certain species, provenances, and families.

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