

CHANGES IN LOBLOLLY PINE SEEDLING ROOT
GROWTH POTENTIAL OVER TIME, DURING COLD
STORAGE, AND AMONG HALF-SIB FAMILIES

by

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(ABSTRACT)

Root growth potential (RGP), the ability of a transplanted seedling to rapidly elongate existing roots and initiate new roots, is used as an indicator of seedling physiological quality. Three separate experiments were conducted on loblolly pine RGP during 1983-84 and 1984-85 using 1-0 nursery-grown seedlings. In the first study, seedlings were hand-lifted from September to April at 17-day intervals in 1983-84 and 7-day intervals in 1984-85. The RGP variation over time was related to environmental and seedling phenological changes. In addition, the new root systems were morphologically described. In the second study, changes in loblolly pine seedlings following different lift-date X cold storage duration treatments were described. These changes were compared to the RGP, shoot activity, and new root system morphology of fresh-lifted

seedlings. Genetic variation in RGP on different lift-dates was quantified in the third study. Variation patterns over time among 14 half-sib loblolly pine families hand-lifted at one-month intervals were examined.

Root growth potential was low in the autumn until the cessation of shoot activity. Seedlings stored poorly if put in cold storage during this time, or prior to the accumulation of at least 400 chilling hours. Seedling RGP increased in the early-winter to a late-February peak, and then decreased when spring shoot elongation occurred during the RGP tests. Similar trends over time were noted with seedlings removed from cold storage during these times. The RGP pattern over time was consistent among years and among the half-sib families, although there were some minor differences among half-sib families in the rate of increase to, and decrease from, the late-winter peak.

Most new roots resulted from elongation of existing roots rather than initiation of new roots regardless of lift-date; however, when seedling metabolism was high (early autumn and late-winter) both root initiation and elongation of existing roots contributed to the new root system. In addition, the morphology of root systems of cold-stored seedlings was similar to fresh-lifted seedlings. Differences in numbers and lengths of new roots among half-sib families were due to

the differential ability to produce new roots through both
root initiation and elongation.

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INTRODUCTION AND OBJECTIVES

Declining southern pine plantation survival has been a growing concern of foresters for the past several years. In a survey of pine plantation survival for the years 1960 to 1978, Weaver et al. (1980; 1981) reported annual survival rates decreased while the total acreage planted annually nearly doubled. Venator (1981) estimated that nearly one-third of the mortality of outplanted seedlings is due to poor stock quality and improper handling procedures. Since approximately 1.3 billion bareroot seedlings are produced annually in the South (Boyer and South 1984, Johnson et al. 1982), this loss in yield is quite substantial.

Nursery-grown seedlings are generally well supplied with nutrients and water, and the size of their root systems may not be critical for their growth in the nursery (Nambiar 1980). However, when seedlings are lifted for bare-root transplanting most of their elongated lateral roots, primary roots, and many lateral roots are broken off (Stone and Schubert 1959a and c). Consequently, the length of the root system transplanted is unlikely to exceed 25 percent of the original (Nambiar 1980). The initial survival of

transplanted seedlings, therefore, depends to a large extent on the ability of the injured root systems to rapidly grow and re-establish contact with the soil. In addition, as survival potential increases due to the greater ability of a seedling to produce new roots, first-year height performance also increases (DeWald et al. 1985b, Feret and Kreh 1985, Feret et al. 1985a and b; 1984). This gain in first-year height affects the ability of seedlings to dominate competing vegetation (Burdett et al. 1983) and conversely, Armson (1958) and Mullin (1963) reported spruce seedlings which grew poorly following transplanting continued to grow poorly for a number of years.

Stone (1955) was the first to report that tree seedlings vary widely in the ability to regenerate roots. It was subsequently reported that the capacity for root regeneration depends on the physiological status of the seedlings, which in part is controlled by nursery growing conditions and handling procedures (Smith 1962). Many aspects of a seedling's ability to regenerate new roots have been studied. A direct relationship of new root growth with field survival and performance following outplanting has been reported for many species in the Coniferae genera Pinus (Feret and Kreh 1985, Feret et al. 1985a and b; 1984, Sutton 1980a, Burdett 1979, Jenkinson 1978, Rhea 1977, Stone 1955),

Abies (Stone and Norberg 1979, Stone 1955), Picea (Sutton 1980a), and Pseudotsuga (Ritchie 1984a and b, Jenkinson 1978, Jenkinson and Nelson 1978, Stone et al. 1962, Stone 1955). This relationship is in sharp contrast to the poor, or lack of correlation with traditional morphological measures used in grading seedlings (Feret and Kreh 1985, Feret et al. 1985a; 1984, Lavender and Wareing 1972, Wakeley 1954).

Wakeley (1948) suggested morphological grades applied to nursery stock are useful only so far as they distinguish seedlings with a high capacity for survival and growth after transplanting from those with a low capacity. The degree to which a seedling possesses the ability to regenerate roots cannot, however, be visually determined. Two groups of seedlings may be nearly identical but differ so much in root regenerating ability that when outplanted side by side, one group would give total success and the other group complete failure (Sutton 1980b).

In order to determine the ability of a seedling to regenerate new roots, Stone (1955) developed what has now become a standard method of measurement. This measurement involves taking a sample of seedlings, removing any new white root tips, pruning the roots to a specified length, and planting the seedlings in an environment optimum for

root growth. After a given time period (usually 20 to 30 days) the seedlings are excavated and their new root growth is quantified.

Extensive research has been conducted on the root regeneration measured in Stone's (1955) test, including the physiological processes involved, effects of soil temperature and moisture, and the impact of nursery operations such as time of lifting, root pruning, top pruning, fertilization, and cold storage. This research has recently been reviewed by Ritchie and Dunlap (1980) and indicates physiological changes in seedling root systems in the autumn are influenced by genetic factors as well as by soil and environmental conditions. These changes, determining the ability of the root system to withstand lifting and cold storage, have a direct impact on the survival and growth of a seedling when transplanted.

The ability of a seedling to regenerate new roots following physiological changes in the autumn has been measured in the standard root regeneration test, but origins of the regenerated roots, and characteristics of the root system that result in a particular root growth potential have not been described. More information is also needed on the effect of late summer and autumn weather conditions on root growth potential. This area of research is

particularly important because the period seedlings can regenerate the greatest amounts of new roots is also the time they are most tolerant to desiccation and physical damage (Lavender and Wareing 1972, Hermann 1967; 1964; 1962) and, therefore, have the best chance to survive lifting, handling, storage, and outplanting (Ritchie and Dunlap 1980). Kramer and Rose (1985) note a systematic evaluation of seasonal and genetic variation in Southern pine root growth potential is needed, and conclude one of the most important contributions to improving or standardizing seedling quality will be through the understanding of how seasonal root growth potential variation is related to shoot dormancy.

Kramer and Rose (1985) reiterate Ritchie and Dunlap's (1980) statement of an immediate need for a faster method than the standard test for determining root growth potential. Ritchie and Dunlap (1980) proposed the usefulness of the test for evaluating quality could be greatly enhanced if it could be related to an easily and rapidly measurable variable (such as chilling hour accumulation). A better understanding of root regeneration would result in more efficient management of seedling physiological quality.

With these considerations in mind, the purpose of this study was to improve the understanding of root regeneration in loblolly pine (Pinus taeda L.) seedlings. The specific objectives were to:

1. describe the morphological origin(s) of regenerated roots on loblolly pine seedlings;
2. describe the association between changes in the natural environment and regenerated root systems of loblolly pine seedlings;
3. examine genetic influences on root regeneration in loblolly pine seedlings;
4. quantify changes in loblolly pine seedling root regeneration during cold storage.

LITERATURE REVIEW

Organization of Gymnosperm Root Tissues

Primary Growth

A germinating gymnosperm seed develops a radicle from the root apical meristem of the embryo which subsequently emerges and develops into the primary or taproot; the first root of a gymnosperm seedling (Fahn 1982, Esau 1977). This primary root is composed of four groups of cells; those in the root cap, the meristematic region, the zone of elongation, and cells in the region of maturation and differentiation (Fahn 1982, Esau 1977, Kozlowski 1971).

The root cap, as described by Esau (1977), consists primarily of living parenchyma cells derived from cell divisions in the apical meristem. Root cap functions include protection, a source of geotropic responses, assistance in root penetration, and excretion of the mucigel layer (Barlow 1975).

Directly above the root cap is the meristematic region which can extend a considerable distance from the apex depending on the growth rate of the root. This is the zone of active cell division, giving rise to all the cells and

tissues of the root (Fahn 1982, Esau 1977, Torrey and Feldman 1977, Kozlowski 1971). A unique area within the meristematic region is characterized by slower cell division than the surrounding cells. This group of cells, termed the quiescent center, is located proximal to the junction of the root cap and the rest of the root (Esau 1977, Torrey and Feldman 1977, Clowes 1975, Wilcox 1962a). The specific function of this region is presently unclear. It may determine and define sites and shapes of the meristems (Torrey and Feldman 1977, Clowes 1975) or, as Esau (1977) suggests, it may be responsible for regenerating the root cap following root tip injury and for resuming cell division during the recovery from cold-induced rest.

Directly behind the meristematic zone is the region of elongation in which cells laid down by the meristem increase in size (primarily longitudinally). Hermann (1977) describes the rate of elongation of these cells as highly variable within a given species, being determined by interacting environmental factors such as moisture and temperature. Above the zone of elongation is the region of differentiation and maturation. Differences in the distribution of mitoses and degree of early cell enlargement contribute to the initial differentiation of this region into three major tissue systems: the epidermis, cortex, and

vascular cylinder (Fahn 1982, Esau 1977, Kozlowski 1971). The epidermis is primarily an absorbing tissue in young roots as well as the source of root hairs (Esau 1977). In his description of gymnosperm root anatomy, Wilcox (1954) noted the absence of an epidermis or other specially differentiated dermal layers in mature conifer roots.

The cortex is composed primarily of parenchyma cells and large intercellular spaces. The radial arrangement of cells in this tissue arises from repetitive cell divisions in the same relative plane (Esau 1977). The innermost layer of the cortex further differentiates into the endodermis, which eventually surrounds the vascular stele and contains the suberized cells of the casparian strip (Fahn 1982, Sutton 1980b, Esau 1977, Wilcox 1954).

The vascular cylinder, or stele, develops from procambial tissue and first appears as a column in the center of the young root. It is composed of vascular tissues and the non-vascular pericycle tissue. The pericycle, consisting primarily of parenchyma and some sclerenchyma cells, is the first cell layer in the vascular cylinder that can be identified. This tissue gives rise to lateral roots, part of the vascular cambium, and often, phellogen (Fahn 1982, Esau 1977).

The vascular tissues develop as longitudinal bundles or strands which later grow together to form one xylem strand (Sutton 1980b). Esau (1977) described the primary, or protoxylem as a solid core with ridge-like projections or strands extending toward the pericycle. The number of protoxylem strands in a root varies among species and can vary among roots in the same plant. The number of strands differentiated in a root affects root system morphology because lateral root development normally occurs adjacent to these strands (Fayle 1975). Sutton (1980b) found the diarch condition (two strands) to predominate in species of the genera Pinus, Picea, and Tsuga.

Tracheids of the protoxylem are narrow and occur on the tips of each projection or strand within the xylem. The metaxylem elements commonly have secondary cell walls, bordered pits, mature later than the protoxylem tracheids, occur further inward, and increase in width toward the center of the xylem. These cells often have secondary cell walls and bordered pits. Sieve elements occur at the periphery of the vascular cylinder with the protophloem cells maturing first, followed by cells of the metaphloem further inward. Companion cells are found in the metaphloem but are not always present in the protophloem. The cells between the xylem and phloem are procambial cells and

eventually differentiate into the vascular cambium of seed plants (Fahn 1982, Esau 1977).

Secondary Growth

Secondary root growth initiates with the formation of secondary vascular tissues from the vascular cambium, and development of periderm from phellogen. Cells of the procambium and some from the pericycle outside of the xylem ridges become active to form a cambium that completely surrounds the xylem. This cambium produces phloem and xylem cells through periclinal (parallel with the circumference) cell divisions and increases in circumference by anticlinal divisions. Periderm formation follows the initiation of secondary vascular growth (Fahn 1982, Esau 1977). Cortical cells isolated by phellogen activity die and collapse, temporarily resulting in a diameter smaller than the young tip portions (Sutton 1980b).

Gymnosperm Seedling Lateral Root Development

Lateral root initiation and elongation are different processes, regulated by different factors (Lavender and Hermann 1970). Kozlowski and Scholtes (1948) reported that the relative amounts of lateral root elongation and initiation varied among species but there was also

significant variability within a species. Additionally, these two processes may exert control on each other. Wilcox (1962b) noted a stimulation of lateral root initiation following the cessation of root elongation in incense-cedar (Libocedrus decurrens (Torr.) Florin).

Lateral roots are usually initiated in the pericycle at the edge of the stele between the phloem and endodermis (Esau 1977, Kozlowski 1971, Bogar and Smith 1965, Wilcox 1968a; 1962a; 1954). They are often initiated at variable distances from the apical meristem. Wilcox (1968a; 1954) noted the faster the growth rate of the root the greater the distance between the apex and nearest lateral root. A lateral root is initiated by the formation of a root primordium from periclinal divisions, followed by periclinal and anticlinal divisions of several adjacent pericycle cells. The position of the primordium varies in relation to the vascular pattern of the parent root (Esau 1977, Kozlowski 1971, Bogar and Smith 1965, Wilcox 1955).

Once a primordium has formed, its continued growth is dependent on the dormancy status of the plant. Wilcox (1968a; 1954) reported latent root primordia frequently become quiescent before they emerge from mother roots that were entering a state of rest. However, if conditions are conducive for growth, the primordia will grow through the

tissues of the endodermis, cortex, and epidermis. Both digestion of the surrounding tissue and mechanical pressure have been implicated by McCully (1975) and Kozlowski (1971) as processes involved in the outgrowth of the lateral root. Esau (1977) noted delignification and removal of secondary walls preceded lateral root initiation if the primordia was formed under lignified tissue. Prior to emergence from the main root, a lateral root has developed a well-defined apical meristem, root cap, and vascular cylinder (Fahn 1982, Esau 1977, Kozlowski 1971). Bogar and Smith (1965) describe lateral root differentiation as being similar to that in the primary root.

Conifer seedling root systems have a long and short root branching pattern, termed heterorhizic (Sutton 1980b, Wilcox 1954). The long roots generally develop from larger primordia and emerge earlier than the smaller, slower-growing short root primordia (Wilcox 1968a). Wilcox (1962a and b) noted a correlation between the rate of extension and the diameter of a lateral root; large diameter new roots tended to be the long roots which grew more rapidly and for longer periods than the smaller diameter, short roots. The length of a lateral root also tends to be related to the diameter of the mother root. In his morphological studies of red pine (Pinus resinosa Ait.) seedling root systems

Wilcox (1968a and b) reported only lateral roots with diameters greater than 50 percent of the diameter of the mother root became long roots, and only 10 to 21 percent of emerging laterals attained this initial size. Additionally, Sutton (1967) reported the longer roots of Picea spp. commonly arose from the root collar region.

Despite the predominance of long roots, short roots (which are often mycorrhizal) are an important characteristic of heterorhizic root systems and can constitute a major percentage of the root branches (Wilcox 1968a and b). Wilcox (1962b) observed the presence of short roots in most of the Pinaceae but none in the Cupressaceae. He characterized short roots as originating from small primordia and having a slow rate of cell division. Short roots may live only a few days or several months (Bogar and Smith 1965, Wilcox 1962b).

Patterns of Lateral Root Growth

The growth of lateral roots shows both diurnal and seasonal variation (Hermann 1977) with root maturation often accompanied by a period of dormancy or quiescence. Roots in a state of rest are characterized by deposits of suberin in their cortex and root cap, and their cells become lignified giving the mature or resting root a brown appearance (Esau 1977, Kozlowski 1971, Wilcox 1954).

Suberized layers on outer root surfaces were generally assumed to make mature roots impermeable to water and salts. Kramer and Bullock (1966) reported permeability generally decreased with increases in root diameter or with increases in amounts of suberization. However, Kramer and Bullock (1966) and Chung and Kramer (1975) concluded significant amounts of water and salts can be absorbed through suberized roots of loblolly pine seedlings either through discontinuous periderm platelets, or through permeable lenticels and sites where dead lateral roots have left gaps. The ion barrier in suberized roots is presumed to be the vascular cambium, with the cork cambium functioning as an additional partial barrier (Chung and Kramer 1975).

There is considerable and yet unresolved debate on whether roots undergo a period of true dormancy, but there is consensus of inherent growth periodicity (Kozlowski 1971). Results of Wilcox (1968a) suggest growth cycles of individual roots of red pine seedlings vary in duration, intensity, and periodicity. Less than half of the lateral roots on Douglas-fir seedlings were found to be active during peak periods of root growth (Krueger and Trappe 1967). Nambiar (1980) reported at any given point in time, only 20 to 45 percent of the primary lateral roots of Monterey pine (Pinus radiata D. Don) seedlings grew new roots even in good environments.

Hermann (1977) suggested most tree species have more than one cycle of root activity/root rest during the growing season. Wilcox (1968b; 1962b; 1954) reported cyclic root growth of various conifer species occurred under uniform environmental conditions. He interpreted this cyclic root growth as reflecting quiescent or resting periods alternating with active root growth (similar to that of recurrent shoot growth patterns) rather than being the result of adverse environmental conditions. Merritt (1968) found similar periodicity in red pine root growth. He concluded environmental changes could modify the endogenously controlled patterns of root growth.

In contrast to species with cycles of no root growth, Krueger and Trappe (1967) reported Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) root growth occurred all year long. They suggested, however, that in natural situations growth is generally suppressed by unfavorable conditions, particularly cold soil temperatures. This apparent lack of an overall quiescent or dormant period in Douglas-fir root growth has also been noted in other studies (Bhella and Roberts 1975, Worrall 1971).

Cyclic variability depends on the stage of root development, branching, branch order, and the immediate environment. Therefore, even though the overall root system

is quiescent, there may be a few roots which show some new growth and make the root system appear to grow all year long (Wilcox 1968a). Additionally, Wilcox (1968a) reported finding occasional white tips throughout the winter in red pine seedlings, but noted these roots had well developed dormancy layers in outer layers of the root cap and were actually dormant.

Despite the variability in the periodicity of individual roots, root systems as a whole in most species tend to have an overall pattern in their root growth cycle which is generally different from the periodicity of any single root (Wilcox 1954). The most frequent pattern according to Hermann (1977) involves a high rate of growth in the early spring, a decrease in growth rate in the midsummer, followed by an increase in the fall.

Seedling Root Regeneration

Root growth of nondisturbed tree seedlings is influenced by many above-ground factors including air temperature, light, and daylength (Nambiar 1980), as well as soil factors such as temperature (Heninger and White 1974, Bowen 1970), bulk density, and water content (Nambiar 1980). Most of these factors also have an important impact on seedling root regeneration after transplanting (Ritchie and Dunlap 1980,

Stupendick and Shepherd 1980, Abod et al. 1979, Nambiar et al. 1979, Stone and Jenkinson 1970, Stone and Schubert 1959a).

When seedlings are lifted and transplanted many of their roots are broken off, with the apices of secondary and higher order laterals being particularly susceptible (Nambiar 1980, Stone and Schubert 1959a). The probability of survival is low unless these transplanted seedlings can rapidly elongate new roots (Ritchie and Dunlap 1980, Ritchie and Stevens 1979, Day and MacGillivray 1975, Stone and Jenkinson 1970, Stone and Benseler 1962, Stone and Schubert 1959a).

Stone and Schubert (1959a) defined a recently transplanted seedling's ability to rapidly elongate existing roots and initiate new roots as its root growth capacity. Root growth capacity has been useful in predicting performance and thus planting stock quality (Feret et al. 1985a and b; 1984, Sutton 1980a, Burdett 1979, Stone and Norberg 1979, Jenkinson 1978, Jenkinson and Nelson 1978, Rhea 1977, Krugman and Stone 1966, Stone et al. 1962, Stone 1955). The ability to grow new roots has been called a seedling's "root growth capacity" (Sutton 1980a, Burdett 1979, Stone and Norberg 1979, Jenkinson 1980; 1978; 1975), "root regeneration" (Nambiar et al. 1979, Day and

MacGillivray 1975, Dykstra 1974, Stone and Schubert 1959a; 1959b), "root growth potential" (Ferret et al. 1985a and b; 1984, Ritchie and Dunlap 1980), and "root regenerating potential" (Abod et al. 1979, Ritchie and Stevens 1979, Krugman and Stone 1966, Stone et al. 1963, Stone et al. 1962). These terms are used interchangeably in the literature. Since the new root system of transplanted seedlings is primarily due to elongation of existing roots (root growth) rather than root initiation (root regeneration) (Stone et al. 1962), the term root growth potential (RGP) will be used hereafter in reference to the ability of a seedling to regenerate its root system.

In their review of seedling RGP Ritchie and Dunlap (1980) formulated a model integrating internal and external factors affecting development and expression of RGP. Internal factors which sequentially influence RGP included stock characteristics, physiological condition at lifting (dormancy and carbohydrate status), physiological changes during storage (dormancy release, respiration), and physiological condition at the time of planting (dormancy, carbohydrate, and photosynthetic status). These factors interact with external factors such as the nursery environment, cultural practices (root pruning and wrenching, lifting date), storage conditions (temperature, moisture,

relative humidity, duration), handling procedures during outplanting operations, and site factors (soil temperature and moisture), to determine the final ability of a seedling to regenerate new roots following outplanting.

Anatomy of Root Regeneration

After root injury, regeneration of seedling root systems involves both elongation of old roots and the initiation and elongation of new lateral roots (Abod et al. 1979). The initiation of new laterals may be due to normal development, or it may be injury induced. If the latter case is true, the regenerated laterals are generally considered to be adventitious roots. These adventitious roots originate from preformed primordia or from induced primordia in tissue that would not have differentiated root primordia during normal development (Sutton 1980b, Haissig 1974a; b; c, Girouard 1967, Wilcox 1955).

Healing processes occur on wounded surfaces of injured roots resulting in the formation of five zones of cells. Wilcox (1955) described the outer zones of these five regions in noble fir (Abies procera Rehd.) as consisting of dried-up cells, followed by a region of disorganized and necrotic cells impregnated with wound substances. Beyond these zones is a region of wound cork, followed by a region

of callus, and finally, a region of transition to normal tissue. Adventitious roots develop either in undisturbed tissue or from derivatives of the callus approximately 1 mm beyond the wound cork layer in the callus zone. Davis (1984) reported the belief that root regeneration can occur anywhere on the root system is not supported by research, and states callus at severed ends of roots is the only significant site of root regeneration.

Normal and regenerated lateral roots differ in their early vascularization and in their method of vascular attachment to the mother root. Wilcox (1955) reported the primordium of a lateral root produced by regeneration shows earlier vascularization than normal lateral roots, and vascular elements of regenerated lateral roots attach only to secondary xylem while those of normal laterals (formed before secondary growth begins) attach to protoxylem strands. Additionally, the morphology of normal and regenerated laterals often differs. Horsley (1971) noted injury-induced lateral roots of paper birch (Betula papyrifera Marsh.) seedlings were larger and thicker than normal lateral roots. The diameter of regenerated lateral (long) roots was usually greater than 60 percent of the parent root tip diameter while this relationship for normal lateral (long) roots was only 25 to 59 percent.

The method of root regeneration varies among species. Stone et al. (1962) observed that after 30 days the regenerated root system of Douglas-fir seedlings was due to lateral root elongation rather than root initiation followed by elongation. In contrast, Nambiar et al. (1979) reported that the regenerated root systems of Monterey pine seedlings were primarily the result of initiation and elongation of secondary lateral roots. In their study, regenerated primary and secondary lateral roots accounted for 63 to 100 percent of the new apices and 85 to 100 percent of the new root length, depending on environmental conditions.

The method of root regeneration also varies with the age of the roots at the level of pruning (Bogar and Smith 1965). Stone et al. (1963) reported that the ratio of numbers of existing lateral roots which elongated to the number of newly initiated roots depended on the age of roots in ponderosa pine (Pinus ponderosa Laws.) seedlings. Generally, older roots tended to regenerate new roots primarily through the elongation of existing lateral roots while a seedling with younger, smaller roots regenerated roots by both elongation of old roots as well as by the initiation of new roots. Similar results have been reported for other coniferous species (Bogar and Smith 1965, Wilcox 1955), as well as for hardwoods (Horsley 1971, Wilson 1970).

The age of the root at the level of pruning influences the origin of regeneration because different tissues form callus at different stages of maturation in the root. Wilcox (1955) noted if a noble fir root was pruned at a stage prior to the formation of the entire circumference of vascular cambium, callus formation was primarily from the pericycle. New roots subsequently originate in the pericycle and develop as normal lateral roots (Esau 1977, Bogar and Smith 1965, Wilcox 1955). Once the circumference of the vascular cambium is complete, it plays a principal role in callus formation and wound healing. At this stage regenerated cambium cells and adjacent parenchyma cells in the transitional zone below the callus region initiate the new roots (Wilcox 1955).

Patterns of Root Regeneration

A seedling's inherent ability to grow new roots depends largely on its physiological status (Ritchie 1984a). This status changes with the seasons, each change increasing plant adaptivity to ambient conditions. Perry (1971) defined this cycling of physiological status as the dormancy cycle. Loblolly pine ceases shoot growth in the autumn (Saranthus 1968, Perry et al. 1966) but this quiescence is not necessarily true dormancy. In this case the quiescent

state is regulated by unfavorable growing conditions, primarily temperature and moisture, and resumption of shoot growth in the spring is not dependent on the satisfaction of a chilling requirement (Romberger 1963). Loblolly pine, for example, will grow all winter if kept under a 14.5-hour photoperiod (Kramer 1936).

While a seedling is passing through the stages of its shoot growth cycle, its RGP varies in a consistent manner. Stone et al. (1962) described ponderosa pine seedling RGP as being low in the late-summer, increasing after shoots have become dormant in the late-autumn, peaking in mid- to late-winter, and then a sharp drop occurs coinciding with budburst and renewed shoot growth. Similar seasonal patterns have been reported for Douglas-fir (Jenkinson 1984, Jenkinson and Nelson 1978), Jeffrey pine (Pinus jeffreyi Grev. and Balf.) (Jenkinson 1980), and Taxus spp. (Lathrop and Mecklenburg 1971).

Environmental conditions present during shoot dormancy or quiescence can modify RGP patterns. Stone and Norberg (1979) showed when environmental conditions caused budset in early September, RGP peaked twice prior to the resumption of top growth in ponderosa pine, white fir (Abies concolor Lindl. and Gord.), and red fir (Abies magnifica A. Murr.) seedlings. However, when shoot elongation continued into

late October only one peak occurred. Stone and Jenkinson (1971) reported similar results for ponderosa pine and concluded the exposure of seedlings to cold temperatures early in the autumn accelerated shoot dormancy and RGP development. Variability in seasonal RGP patterns have also been reported for Douglas-fir, Jeffrey pine, Monterey pine, red pine, loblolly pine, western hemlock (Tsuga heterophylla Sarg.), noble fir, white fir, Norway spruce (Picea abies (L.) Karst.), white spruce (Picea glauca (Moench) Voss), black spruce (Picea mariana Mill.), and Taxus spp. (Ritchie and Dunlap 1980). Despite variability in the specific seasonal patterns of RGP the tendency for a spring and autumn low, and late-winter peak is highly consistent.

Species which undergo shoot dormancy have autumn and winter RGP increases coinciding with accumulation of chilling hours, the RGP peak culminating with the fulfillment of the chilling requirement (Ritchie and Dunlap 1980). Stone and Schubert (1959a) found RGP changes directly correlated with the fulfillment of ponderosa pine's cold requirement. These results were supported by Stone et al. (1963). Krugman and Stone (1966) examined this relationship in more detail and found ponderosa pine seedlings had low RGP (less than 10 cm of new root growth per seedling) until the seedlings had received 90 cold

nights. After this time, RGP increased to approximately 100 cm of new root growth per seedling with continued cold exposure until 150 cold nights. Cold exposure beyond 150 cold nights did not increase new root growth any further. Similar cold requirement-RGP relationships have been reported for white fir, western hemlock, and Douglas-fir (Ritchie and Dunlap 1980).

Once the stage is reached where root growth can be initiated, and the environment is also favorable for new root growth, the rate of elongation of these new roots has been reported to be regulated by an internal carbohydrate source-sink regime (Ritchie and Dunlap 1980). It appears root regeneration periodicity is regulated by shoot growth cycles while the strength of the response reflects the internal carbohydrate status of the seedlings. Ritchie and Dunlap (1980) describe new root growth as an energy consuming process occurring at the expense of available metabolites, particularly the carbohydrates. Seasonal patterns of carbohydrate synthesis, storage, conversion, and metabolism are all related to a seedling's shoot growth cycle and have been suspected as modifying RGP responses. This relationship has been observed for Douglas-fir (Krueger and Trappe 1967, Winjum 1963), loblolly pine (Gilmore 1962), and white pine (*Pinus strobus* L.) (Shiroya et al. 1966).

In their review of RGP research, Ritchie and Dunlap (1980) summarized the carbohydrate-new root growth relationship. In early autumn seedlings are entering a dormant or quiescent state and their RGP is low; they are physiologically preparing to cease shoot growth and carbohydrate storage is the predominate metabolism. Prior to budburst seedlings are preparing to reinitiate growth and roots are the major metabolic sink, actively drawing upon currently assimilated carbohydrates. After budburst there is competition for currently photoassimilated carbohydrates between the shoots and roots. The sink strength of the roots is less than that of the shoots and, consequently, RGP is low. Despite all of the studies that lend support to Ritchie and Dunlap's (1980) hypothesis, no clear relation between carbohydrate concentration in the roots and root activity has been established (Ritchie 1984a; 1982).

Changes in Root Growth Potential Over Time and in Cold Storage

Changes in Root Growth Potential Over Time.

The periodicity of RGP has been related to the shoot growth cycle and there are theories relating it to carbohydrate availability. Therefore, nursery operations which affect these factors will undoubtedly influence RGP

development. Feret et al. (1984) found a significant amount of loblolly pine seedling RGP related to nursery and seedling management practices. They suggested although inherent seedling RGP for any planting year may vary depending on climatic and edaphic conditions, the degree to which this potential is expressed depends primarily on two factors; handling procedures and outplanting site conditions. Two cultural practices which appear to have a great impact on RGP are time of lifting and cold storage (Ritchie and Dunlap 1980).

Hermann (1967; 1964; 1962) observed the ability of Douglas-fir seedlings to withstand environmental stresses varied as they passed through their shoot growth cycle. Seedlings lifted before or after true dormancy were more likely to suffer extensive damage from handling and cold storage, and consequently, RGP was low (Ritchie 1984a and b). Stress due to handling during periods when seedling root systems are sensitive to disturbance may completely override RGP (Ritchie and Dunlap 1980, Lavender and Wareing 1972). However, lifting when seedlings are in the best physiological condition to endure stress not only increases outplanting success but Dierauf and Marler (1969) found the subsequent height growth of loblolly pine seedlings to also be improved.

Lavender and Wareing (1972) reported shoot cold hardiness and drought resistance varied seasonally in a similar manner to RGP, being low in the fall, high in the winter and low in the spring. Winter-lifted seedlings are, therefore, apparently in the best physiological condition to maintain RGP during handling. Similar conclusions have been arrived at by others (Ritchie 1982, Garber and Mexal 1980, Ritchie and Stevens 1979, Stone and Schubert 1959b).

The climatic conditions a seedling is exposed to will regulate its shoot growth cycle, therefore, determining the most appropriate time for lifting. In his root regeneration studies of western yellow pines, Jenkinson (1980) concluded one of the keys to successful plantation establishment is knowing when to lift seedlings from the nursery. He reported although climatic conditions are important for determining the stage of dormancy and thus when to lift, different seed sources will respond differently to the environmental stimuli controlling dormancy. Similarly, root regeneration responses to the environment also vary with the genetic origin of a seedling (Jenkinson 1980, Stone and Norberg 1979, Stone and Schubert 1959b).

Jenkinson (1980) noted the seed source of ponderosa pine seedlings was a major factor controlling the timing of the RGP peak, both in the time of onset and rate of RGP

increase. Therefore, when evaluating a lifting schedule, seed source must also be considered. In nurseries in the Western United States, climatic data has been combined with information on the genetic background of the seedlings resulting in the establishment of lifting "windows". These lifting windows are based on the anticipated time of the RGP peak for the area, seed source, and species being grown (Ritchie and Dunlap 1980, Jenkinson and Nelson 1978).

Changes in Root Growth Potential in Cold Storage.

Current regeneration practices in the South often require periods of cold storage for a large proportion of nursery seedlings during the time between lifting and outplanting (Garber and Mexal 1980). Cold storage has been shown to affect RGP in many studies (McCracken 1979, Jenkinson and Nelson 1978, Rhea 1977, Stone and Jenkinson 1971, Winjum 1963, Hellmers 1962, Stone and Benseler 1962, Stone and Schubert 1959b). Normally, dormant hardwood stock can withstand prolonged cold storage without appreciable damage. Conifers, however, suffer damage after shorter periods of time (Hermann 1967).

Effects of cold storage on RGP depend on the time of lifting relative to the physiological status of the shoot, as well as the duration of storage. Ritchie (1984b) found cold storage to increase, decrease or maintain Douglas-fir

RGP depending on when a seedling was lifted. Generally, loblolly pine seedlings do not store well until they are fully quiescent. In Virginia, this does not usually occur until the last two weeks of November (Dierauf 1982).

Garber and Mexal (1980) reported the storage potential of loblolly pine seedlings increased until mid-December. Seedlings lifted and stored prior to this time had lower survival rates when outplanted. Lifting and storage after mid-December no longer resulted in decreased survival, even after nine weeks of cold storage. In contrast, Dierauf and Marler (1969) showed the storage potential and subsequent survival of loblolly pine decreased as the lifting season progressed into late December. These results were supported by Rhea (1977).

These anomalies in loblolly pine seedling cold storage success may be due to differences in the physiological status of the shoots of the seedlings in the different studies. The seedlings in Garber and Mexal's study may not have been in a state of quiescence appropriate for cold storage until mid-December. In the other two studies, however, environmental conditions may have triggered quiescence at a different time and the particular seed sources used were no longer physiologically tolerant to cold storage in late winter. Garber and Mexal (1980) also

suggested that a seed source X storage interaction may be a contributing factor in the disparity among results.

Other studies have linked the sensitivity of seedlings in cold storage to the stage of their shoot growth cycle. Hermann (1967) reported the sensitivity of Douglas-fir seedlings to root exposure decreased from November to January, and this change was associated with physiological changes in the dormancy cycle. Similar results were reported by Ritchie and Stevens (1979). Stone and Schubert (1959b) noted delays in lifting in the autumn improved survival rates of cold-stored ponderosa pine. In their study, no seedlings survived cold storage if lifted prior to mid-September, but survival increased to 82 percent if lifting was delayed until mid-October. Cold-stored seedlings lifted after November 1 had survival rates of 95 percent. There was some variation among seed sources in survival but the overall trend was consistent. Stone and Schubert (1959b) concluded the deleterious effect of cold storage was due to the failure of seedlings to achieve physiological hardening or readiness before being placed in storage.

The cold storage potential of a seedling has been related to the dormancy cycle through the number of chilling hours received. Stone and Jenkinson (1971) observed before 300

hours or after 1200 hours of chilling the buds of ponderosa pine seedlings were not tolerant to chilling and RGP was severely reduced in cold storage. The chilling sum needed for successful cold storage of Douglas-fir seedlings has been calculated in several studies and appears to be between 500 to 1600 hours (Ritchie and Dunlap 1980, Ritchie and Stevens 1979).

Cold storage can satisfy a species' chilling requirements if seedlings are lifted at the appropriate time. In these cases RGP tends to increase with storage until the cold requirement has been fulfilled. After this time prolonged cold storage may decrease or maintain RGP depending on the species and seed source (Ritchie and Dunlap 1980, Garber 1978). The satisfaction of chilling requirements through cold storage has been reported for Douglas-fir (Ritchie 1982, Ritchie and Stevens 1979, Lavender and Hermann 1970), spruce species (Nienstaedt 1967), western hemlock (Nelson and Lavender 1979), ponderosa pine (Jenkinson 1980, Krugman and Stone 1966), other western yellow pines, and true firs (Jenkinson 1980). Species or seed sources with either a short or no chilling requirement such as loblolly pine do not always follow this pattern and their response to cold storage is not fully understood.

In addition to time of lifting, the duration and temperature of cold storage can have a significant impact on storage success. Prolonged exposure to temperatures below -2°C results in tissue desiccation and cell damage while temperatures warmer than $+5^{\circ}\text{C}$ result in respiratory depletion of carbohydrates and fungi buildup (Ritchie and Dunlap 1980). Within the -2 to $+5^{\circ}\text{C}$ temperature range RGP has been observed to decrease as storage length increased for ponderosa pine (Stone and Norberg 1979, Stone and Schubert 1959b), loblolly pine (Garber and Mexal 1980, Dierauf and Marler 1969), jack pine (*Pinus banksiana* Lamb.), white and black spruce (Sutton 1980a), and white and noble fir (Stone and Norberg 1979). Stone and Norberg (1979) suggested these decreases are generally not harmful as long as RGP remains above a minimum necessary for survival at a particular site.

The length of time a seedling can be satisfactorily stored may depend on its state of dormancy or quiescence (Ritchie and Stevens 1979, Garber 1978, Dierauf 1974). Ritchie and Stevens (1979) reported the effects of storage duration interacted strongly with lifting date regardless of storage temperature in Douglas-fir seedlings. Ritchie and Dunlap (1980) attributed the effects of cold storage duration on RGP to a shoot status-carbohydrate reserve

interaction. In support of this hypothesis, Garber and Mexal (1980) reported significant weight losses in a variety of dormant and quiescent conifer species following relatively short periods of cold storage. They concluded these weight changes represented respirational depletions of available food reserves needed for renewed root growth.

In a study examining carbohydrate changes in Monterey and Mugho pine (Pinus mugo Turra) after 6, 12, and 18 weeks of cold storage, McCracken (1979) found decreases in total carbohydrates in the roots after only 6 weeks. Further examination revealed most of the decrease was due to respiratory consumption of starch which occurred immediately following lifting. Depletion of total carbohydrates continued with longer periods of storage but at a slower rate. There were also differences among the species examined. Mugho pine maintained a greater carbohydrate reserve than Monterey pine throughout cold storage, particularly in the root system. Similar species variability has been noted in other studies (Winjum 1963, Hellmers 1962). Most of the literature is in agreement with McCracken's (1979) study which showed decreases in carbohydrates occurring in both the shoots and the roots of cold-stored seedlings. However, one study reported an unusual weight gain among cold-stored seedlings where the

seedlings were subjected to an 8- or 16-hour photoperiod (Johnson 1983).

MATERIALS AND METHODS

Seedling Propagation

Three separate studies were conducted to examine changes in 1-0 loblolly pine seedling RGP over time, in cold storage, and among half-sib families. All of the seed used in these studies was donated by the Virginia Division of Forestry (VDF) and obtained from their seed orchard at the New Kent Forestry Center nursery, Providence Forge, Virginia. The studies involving genetic aspects used randomly selected half-sib families, while the studies examining the effects of time of lifting and cold storage utilized a bulked seed mix used operationally by the VDF which contains an unknown number of half-sib families. All of the seed had been moistened and then stratified by VDF personnel in polyethylene bags at 1.7°C for 60 days.

Seeds from 14 half-sib families and one bulked VDF seedlot were hand-planted for the genetics studies on April 26, 1983 and on May 4, 1984 in seedbeds at the New Kent nursery. The seeds were planted in a randomized complete block design in two adjacent seedbeds in 1983 and in one contiguous seedbed in 1984. Each half-sib family in every

block was represented by one row of 40 seeds, planted at an approximate 2 cm spacing. A border edge of 10 bulked VDF seeds was planted at both edges of every row, and a buffer of 10 rows of bulked VDF seed was planted between each block. The surrounding seedbeds were operationally planted (direct seeding) with bulked VDF seed on the same day. Seedlings from these seedbeds were used for the time of lifting and cold storage studies. Oxyfluorfen (Goal 2EC) preemergent herbicide was applied by the VDF at a rate of 0.19 kg ai. per hectare at the time of planting.

All of the seedlings were grown operationally at the nursery throughout the growing season. While in the nursery the seedlings were watered (approximately 2.5 cm of water per week is maintained in the soil by precipitation or irrigation until late-September) and top-pruned to a height of 21 cm by VDF personnel. The 1983 seedlings were top-pruned on August 10, 31, and September 20, and the 1984 seedlings were top-pruned on August 1, 20 and September 19.

On May 26, 1983 there were heavy rain storms accompanied by hail which caused flooding and considerable damage to the seedlings. Poor germination in some of the half-sib families in conjunction with the weather damage necessitated combining the 8 field blocks into 4 blocks in order to have an adequate number of seedlings for the 1983-84 genetics

study. High survival in 1984-85 enabled the use of all 8 nursery blocks.

On each lift-date, seedlings were excavated by hand with a shovel and immediately placed in double-layered polyethylene bags. The bulked VDF seedlings for the cold storage and time of lifting studies were removed from three randomly selected spots within a nursery bed adjacent to the half-sib families. When the half-sib families were lifted, two randomly selected blocks in 1983-84 were removed and the same half-sib families combined. In 1984-85 one nursery block was randomly removed for each lift-date. An estimate of block location variation was made in 1984-85 by handlifting bulked VDF seedlings from the centers of the border rows for each nursery block containing half-sib families, and then these blocks were statistically compared following the same root regeneration tests that the half-sib families had undergone.

Environmental Data Collection

Throughout the study the nursery environment was monitored to relate environmental changes over time to changes in loblolly pine seedling phenology and RGP. Beginning in late August and ending in early April, soil temperature, air temperature, and precipitation data were

recorded. Air temperature was continuously recorded by a hygrothermograph in a weather station positioned 46 m from the end of the nursery beds containing the half-sib families. Chilling hours were calculated from these data as the number of hours between 0 and 8°C (Garber 1983; 1978). Precipitation was collected in a rain gauge positioned adjacent to the weather station. Maximum and minimum soil temperatures were recorded every three days at a depth of 12 cm using a remote reading maximum-minimum probe thermometer located adjacent to the weather station. The soil temperature probe was positioned in an area subject to irrigation so that any temperature changes due to irrigation experienced by the seedlings would be recorded.

Root Growth Potential Testing Systems

Following lifting, seedlings were transported in a styrofoam cooler to either the Reynold's Research Center in Critz, Virginia, or to the Virginia Tech campus, Blacksburg, Virginia. The roots of the seedlings were pruned to 12 cm below the root collar and any new white roots removed. The root collar was defined as the groundline level on the main axis; the approximate area along the main stem-root axis where the primary vascular system changes from that of a stem to a root (Sutton and Tinus 1983). Root growth

potential of all seedlings was then measured utilizing two different testing systems. A 15-day hydroponic RGP testing system was established in a greenhouse on the Virginia Tech campus. The other RGP testing system, set up at the Reynold's Research Center, was a more traditional 24-day system similar to that described by Stone (1955). Greenhouse temperatures were monitored with hygrothermographs throughout all RGP tests. This data was used as a covariate in the analyses of RGP variation to remove greenhouse temperature variation from RGP variation over time.

15-Day Testing System

Root-pruned seedlings were grown hydroponically in 37.8 liter aquariums in a greenhouse for 15 days. The seedlings were floated on tap-water by inserting them at their root collars into slots cut in styrofoam rectangles, and air was bubbled into the water through two permeable stones in each aquarium using diaphragm pumps (Whisper 300 from Willinger Bros., Inc.). The water temperature was maintained at ambient air temperature (16 to 27°C) and 0.5 g of 20-20-20 (nitrogen-phosphorus-potassium) was added to the water to a final concentration of 13 ppm. The aquariums were covered with aluminum foil to prevent sunlight from reaching the

roots, to reduce algae growth, and to help maintain a relatively constant water temperature. The seedlings were grown under a 16-hour photoperiod, and the system was set up beneath shade cloth to create more constant air and light regimes.

24-Day Testing System

Root-pruned seedlings were hand-planted into 46 X 10 X 41 cm (length X width X height) plexiglass watertight trays (equipped with a drainage hole) containing Pro-Mix¹ growth medium. The seedlings were well watered and excess water was allowed to drain from a hole at the bottom of each tray. The trays were then stoppered and emersed in waterbaths held at a constant 20°C. The waterbath temperature was maintained with heaters or cooling units and the bath water was circulated around the trays with a water pump. The seedlings were grown for 24 days in a greenhouse under ambient air temperatures (16 to 27°C) and a 16-hour photoperiod. After 24 days of growth the seedlings were carefully excavated and their root systems washed, exposing the new white roots.

¹ Pro-Mix BX Premier[®] (A.H. Hummert Seed Co., St. Louis, Missouri) is a horticultural growth medium containing shredded sphagnum peat moss, horticultural vermiculite, and perlite with the following nutrient additives: dolomitic limestone, calcium nitrate, super phosphorus, potash, phosphate, and fritted trace elements.

Seedling Shoot and Root Measurements

Following the 15- and 24-day RGP tests, several root and shoot variables were measured on every seedling:

1. height from the root collar to the severed tip of the stem (nearest cm)
2. amount of new shoot elongation (nearest cm)
3. root collar diameter (nearest 0.1 mm)
4. shoot activity was a rated on a scale similar to that described by Johnson (1983) according to the criteria:
 - a) dead seedling
 - b) no apparent shoot activity
 - c) swollen or elongated buds (terminal bud if present or bud within top needle fascicle)
 - d) stem elongation just beginning
 - e) measurable stem elongation
 - f) elongating needles
5. seedling dry weights (measured only in 1984-85)
 - a) total shoot dry weight (nearest 0.01 g)
 - b) needle dry weight (nearest 0.01 g)
 - c) stem dry weight (nearest 0.01 g)
 - d) total root dry weight (nearest mg)
 - e) lateral root dry weight (nearest mg)
 - f) taproot dry weight (nearest mg)
6. total number and length (nearest cm) of lateral roots
 - a) elongated primary lateral roots
 - b) non-elongated primary lateral roots

c) elongated secondary lateral roots

d) non-elongated secondary lateral roots.

Primary lateral roots were defined as roots attached directly to the taproot. Secondary roots were lateral roots attached to primary lateral roots.

The RGP data collected included total number and length (nearest cm) of new short roots (those 0.5-1.5 cm in length) and new long roots (those >1.5 cm long) of seven different types of new roots. New root type was based on site of attachment to the old root and included:

1. new root arising directly from the end of a primary lateral root
2. new root arising from a primary lateral root at a site other than directly from the end
3. new root arising directly from the end of a secondary lateral root
4. new root arising from a secondary root at a site other than directly from the end
5. new root arising directly from the taproot
6. new root arising from a new root of type 1 or 2
7. new root arising from a new root of type 3 or 4.

Hypotheses for the Three Experiments

Experiment I: Changes in Loblolly Pine Root Growth Potential from September to April

The time of lifting experiment involved periodically lifting loblolly pine seedlings from the nursery from September to April in 1983-84 and in 1984-85. This study tested the following null hypotheses:

1. Ho: Changes in loblolly pine seedling RGP from September to April are not related to concurrent environmental changes.
2. Ho: Changes in loblolly pine seedling RGP are not related to their shoot growth cycle from September to April.
3. Ho: The origin(s) of regenerated roots in loblolly pine seedlings does not change over time.

Specific procedures for this experiment are described on pages 49 through 54.

Experiment II: Changes in Loblolly Pine Seedlings During Cold Storage

The cold storage experiment subjected loblolly pine seedlings to different lift-date X cold-storage combinations and compared them to seedlings fresh-lifted from the nursery. The cold storage experiment tested the following null hypotheses:

1. Ho: There are no effects of time of lifting on cold storage success as reflected in loblolly pine seedling RGP.
2. Ho: There are no RGP differences between loblolly pine seedlings held in cold storage for different durations.

3. Ho: There are no RGP differences between fresh-lifted and cold-stored loblolly pine seedlings.

Specific procedures for this experiment are described on pages 78 through 83.

Experiment III: Root Growth Potential Variation Among Half-sib Families of Loblolly Pine Seedlings

The genetics experiment compared relative and absolute RGP changes over time among half-sib families of loblolly pine seedlings. This experiment tested the following null hypotheses:

1. Ho: There are no RGP differences among half-sib families of loblolly pine seedlings.
2. Ho: There are no differences in RGP changes over time among half-sib families of loblolly pine seedlings.
3. Ho: There are no genetic differences in the origin(s) of regenerated roots among half-sib families of loblolly pine seedlings.

Specific procedures for this experiment are described on pages 102 through 108.

EXPERIMENT I

Changes in Loblolly Pine Root Growth Potential from September to April

Introduction

Characteristics of a high quality seedling include high survival and growth potential (Sutton 1979). Seedling quality can be described both morphologically and physiologically; however, morphology has been shown to be inadequate as a sole basis for evaluating seedling quality (Feret and Kreh 1985, Feret et al. 1985a and b, Nebgen and Meyer 1985, Feret et al. 1984, Sutton 1979, Blair and Cech 1974, Lavender and Wareing 1972, Wakeley 1954; 1948). There are growing concerns among foresters on how to evaluate seedling physiological quality (Brissette 1984, Johnson et al. 1982).

Among recent reviews on seedling quality evaluation (Ritchie 1985, Duryea and McClain 1984, Ritchie 1984a, Jaramillo 1980, Ritchie and Dunlap 1980, Sutton 1979) root growth potential (RGP), the readiness to initiate and elongate new roots (Sutton 1980c), was one technique noted for estimating seedling physiological quality.

Seasonal RGP development and its relation to shoot growth cycles have been described for many western species (Faulconer and Thompson 1984, Jenkinson 1980, Ritchie and Dunlap 1980, Stone and Norberg 1979, Lathrop and Mecklenburg 1971, Stone and Jenkinson 1971, Krugman and Stone 1966, Stone et al. 1962; 1963, Stone and Schubert 1959a and b). Jenkinson (1980) noted one of the keys to successful plantation establishment of western yellow pines is knowing when to lift seedlings from the nursery. Lifting "windows", based on anticipated RGP peaks, have been developed as guides for appropriate times to lift different seed sources and species at different nurseries (Jenkinson and Nelson 1978).

Despite a strong positive relationship between loblolly pine RGP and field performance (DeWald et al. 1985b, Feret and Kreh 1985, Feret et al. 1985a and b; 1984), a systematic evaluation of seasonal variation in loblolly pine RGP has not been done, and the relationship between RGP and loblolly pine shoot quiescence has not been described (Kramer and Rose 1985). In addition, although it has been noted that new root growth consists of both elongation of existing roots as well as initiation of new roots (Furuta 1982, Nambiar et al. 1979, Stone and Schubert 1959a) the relative importance of elongation versus initiation to new root systems has never been intensively examined.

The objectives of this study were to describe seasonal variation in loblolly pine seedling RGP from the end to the start of the shoot growing season, and to relate this variation to the shoot growth cycle and environmental variation over the same period. In addition, an attempt was made to describe the morphology of the regenerated root system.

Materials and Methods

Loblolly pine 1-0 seedlings were periodically lifted from September through mid-April in 1983-84 and 1984-85. Their RGP and several shoot and root characteristics were measured on each lift-date. In addition, the nursery environment was continuously monitored to relate it to changes in seedling shoot activity and RGP.

The seedlings used in this study were operationally grown by the Virginia Division of Forestry (VDF) at their New Kent Nursery, located in the Virginia Coastal Plain, near Providence Forge, Virginia. The seedlings were planted in April 1983 and 1984, regularly irrigated throughout the growing season, and were top-pruned on August 10, 31, September 20, 1983, and on August 1, 20, September 19, in 1984.

Air temperature was continuously monitored by a hygrothermograph in a weather station adjacent to the nursery beds being sampled. Precipitation was collected in a rain gauge adjacent to the weather station. Maximum and minimum soil temperatures were measured at a depth of 12 cm every three days.

In 1983-84 60 seedlings were hand-lifted at intervals approximately 17 days apart (September 1, 19, October 6, 25, November 10, 22, December 13, January 19, February 2, March 1, 13, and April 2). In 1984-1985 a more intensive sample was desired and 60 seedlings were hand-lifted each week from September 1 until April 8 with the exception of the week of January 23 when the ground was frozen. The seedling root systems were pruned to 12 cm below the root collar (ground line level on the main axis [Sutton and Tinus 1983]) and any new white root tips were removed. Seedling RGP was then measured using two different testing systems.

The RGP of 30 seedlings was measured by growing them in an aerated hydroponic system, which consisted of two replicate 37.8 liter aquariums. The seedlings were grown for 15 days in a greenhouse under a 16-h photoperiod. Water temperature was maintained at ambient air temperature (16-27°C) and 0.5 g of 20-20-20 (nitrogen-phosphorus-potassium) was added to each aquarium. The remaining 30

seedlings from each lift-date were measured in a more traditional testing system (Stone 1955) by planting them into two replicate 46 X 10 X 41 cm (length X width X height) trays containing Pro-Mix growth medium. The seedlings were grown for 24 days in a different greenhouse under ambient air temperatures (16-27°C) and a constant root temperature of 20°C. Daylength was set at 16 hours. Temperatures of both greenhouses were monitored with hygrothermographs throughout the study.

After each 15- and 24-day RGP test the seedlings were carefully removed and the following shoot and root variables were measured on each seedling:

1. height from the root collar to the severed tip of the stem (nearest cm)
2. amount of new shoot elongation (nearest cm)
3. root collar diameter (nearest 0.1 mm)
4. shoot activity was assigned a rating based on the level of visually detectable activity:
 - a) none apparent
 - b) swollen or elongated buds (terminal bud if present or bud within top needle fascicle)
 - c) stem elongation just beginning
 - d) measurable stem elongation
 - e) elongating needles
5. seedling dry weights (measured only in 1984-85)
 - a) total shoot dry weight (nearest 0.01 g)

- b) needle dry weight (nearest 0.01 g)
 - c) stem dry weight (nearest 0.01 g)
 - d) total root dry weight (nearest mg)
 - e) lateral root dry weight (nearest mg)
 - f) taproot dry weight (nearest mg)
6. total number and length (nearest cm) of lateral roots
- a) elongated primary lateral roots
 - b) non-elongated primary lateral roots
 - c) elongated secondary lateral roots
 - d) non-elongated secondary lateral roots.

Primary lateral roots were defined as roots attached directly to the taproot. Secondary roots were lateral roots attached to primary lateral roots.

Dry weights were not measured in 1983-84 because following each RGP test the seedlings were used to estimate dormancy status. Random samples of six seedlings from the 15-day testing system were planted into 1 liter (11 cm diameter) plastic pots containing Pro-Mix growth medium and grown in a greenhouse under the same conditions as the 15-day RGP tests. Shoot activity was recorded once per week using the scale previously described. The number of days required for the resumption of active shoot growth following lifting from the nursery was used to estimate the dormancy intensity parameter described by Ritchie (1984a). Chilling

hours were based on the loblolly pine results of Garber (1983; 1978) and calculated from the nursery hygrothermograph data as the number of hours in the nursery between 0 and 8°C.

The RGP data collected included total number and length (nearest cm) of new short roots (those 0.5-1.5 cm in length) and new long roots (those >1.5 cm long) of seven different types of new roots. New root type was based on site of attachment to the old root and included those originating directly from the end or from a site other than directly from the end of either a primary or secondary lateral root, new roots arising from the sides of other new roots, and new roots arising directly from the taproot.

The study was designed as a randomized complete block design with two blocks (two aquariums or trays), each containing 15 seedlings, nested in the lift-date X RGP testing system combinations. The data were analyzed utilizing analyses of variance, correlation analyses, and regression analyses (SAS Institute, Inc. 1985). The significance level used for all of the tests was $\alpha=0.05$. Air temperature variation of both greenhouses was monitored with hygrothermographs. Correlations of greenhouse temperature changes with RGP over time were very low and not significant. Therefore, it is assumed the effect of slight

changes in greenhouse temperatures over time on RGP was minimal.

The block effect was nonsignificant and subsequently included in the error term. All subsequent analyses were based on 2 replicates of plot means of $n=15$. Only lift-dates in common weeks between the two years were used in statistical comparisons among years. Most interactions among years and testing systems were significant, therefore, subsequent analyses were used to test these effects separately. Despite significant absolute RGP differences, relative differences from lift-date to lift-date did not vary significantly between the two RGP testing systems (DeWald et al. 1985a). Therefore, RGP results of the two systems will not be presented or discussed separately.

Results

Environmental Variation.

Environmental variation for both years is illustrated in Figure 1. Weekly total precipitation ranged from 0.0 to 1.7 cm in 1983-84 and 0.0 to 1.0 cm in 1984-85. The major difference between the two years was greater precipitation in 1983-84, particularly in the spring. Soil and air temperature ranges and means are listed in Table 1. Temperature variation was relatively consistent between

years (Table 1), although 1983-84 soil temperatures were slightly cooler in October and December, and warmer in January and mid-February than 1984-85 soil temperatures. Air temperatures warmed faster in the late-winter in 1984 (Figure 1). Simple linear correlations between air and soil temperatures, and among years were all significant (Table 1). The difference between air and soil temperatures averaged only 5°C.

Seedling Morphology.

Means and ranges of seedling morphological traits are summarized in Table 2. All morphological variables varied significantly among lift-dates and years. In general, seedlings grown in 1983 were smaller than those grown in 1984 (Table 2). All root and shoot size variables increased until early December, remained relatively constant through the winter, then increased again in early March when measurable shoot elongation in the RGP tests occurred. Exceptions to this pattern of variation were needle dry weights which decreased in the spring, and height variation which randomly increased and decreased among lift-dates.

Shoot Activity.

Seedling shoots remained active in the nursery until late-October and in the greenhouse until mid-November

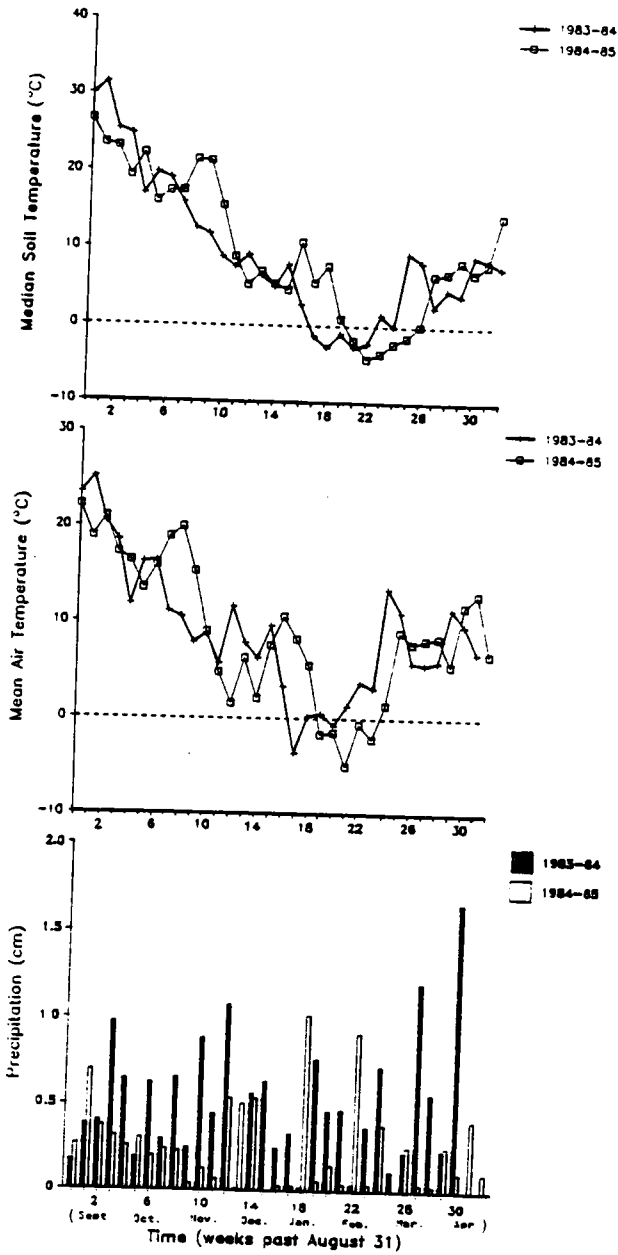


Figure 1. Precipitation, and air and soil temperature variation at the New Kent nursery, Providence Forge, Virginia.

Table 1. Air and soil temperature variation at the New Kent nursery, Providence Forge, Virginia in 1983-84 and 1984-85.

Temperature Parameter	Average Weekly Temperature Range (°C)		Correlation Between Years ¹ (r)
	1983-84	1984-85	
Soil Maximum	-2.2 to 33.3	-2.2 to 33.3	0.82
Soil Minimum	-4.4 to 30.4	-6.3 to 20.4	0.79
Soil Median	-2.8 to 31.5	-4.3 to 26.7	0.82
Air Maximum	0.5 to 32.1	1.9 to 29.8	0.70
Air Minimum	-8.2 to 20.0	-11.7 to 17.1	0.69
Air Mean	-3.6 to 25.2	-5.0 to 22.2	0.70

Correlation (r) Between Air and Soil ² :		
Maximum Temperature	0.95	0.89
Minimum Temperature	0.94	0.94
Median Temperature	0.96	0.93

¹All correlation coefficients significant at $\alpha=0.05$.

²All correlation coefficients significant at $\alpha=0.05$.

Table 2. Shoot and root characteristics of loblolly pine seedlings tested for root growth potential in 1983-84 and 1984-85.

Morphological Trait	1983-84		1984-85	
	Range	Mean	Range	Mean
Height (cm)	15.4-18.8	17.6a ¹	18.3-23.9	21.3b
Shoot Dry Weight (g)				
Stem	---	---	0.37-1.03	0.72
Needles	---	---	0.58-1.28	0.90
Total Shoot	---	---	1.13-2.16	1.63
Root Collar Diameter (mm)	2.3-4.0	3.6a	2.2-4.6	3.8b
Primary Lateral Roots				
Number	11.7-19.9	16.2a	13.4-29.4	22.9b
Length (cm)	40.4-116.1	76.9a	55.2-141.5	104.9b
Secondary Lateral Roots				
Number	3.0-17.8	9.5a	4.8-33.2	15.7b
Length (cm)	4.2-21.6	12.4a	5.6-43.7	20.7b
Root Dry Weight (g)				
Lateral Roots	---	---	0.04-0.30	0.19
Taproot	---	---	0.05-0.39	0.25
Total Root	---	---	0.14-0.67	0.44
Root/Shoot Ratio	---	---	0.12-0.39	0.27

¹Means followed by the same letter do not differ significantly between years ($\alpha=0.05$).

²Data not collected in 1983-84.

despite being in a environment which should have sustained growth (Kramer 1957, Barney 1951). The number of days until resumption of shoot activity decreased with each lift-date until late-March when seedlings in the nursery had swollen buds. By April, many seedlings in the nursery had measurable shoot elongation (Table 3).

Variation in shoot activity over time was highly consistent between years ($r=0.93$), however, resumption of shoot activity occurred earlier in 1983-84 than in 1984-85. Bud activity occurred during the 24-day RGP test on 1983-84 seedlings lifted in late-November. Seedlings had been exposed to nearly 500 chilling hours in the nursery by this time in 1983 but to less than 400 chilling hours in 1984. Shoot activity was not detected in the 1984-85 RGP tests until early January, after seedlings had been exposed to over 900 chilling hours (Table 3). After mid-January, shoot activity was similar between years.

Seedling Root Activity.

Percentage of primary lateral roots producing new roots ranged up to 30 and 55 percent in 1983-84 and 1984-85, respectively. In general, the proportion of primary lateral roots elongating on 1983-84 seedlings was 10 percent greater than on 1984-85 seedlings at any given point in time. Percentage of elongating secondary lateral roots ranged up

Table 3. Chilling hours at the New Kent nursery, Providence Forge, Virginia, and loblolly pine shoot activity following lifting.

Date Lifted	Accumulated Weekly Chilling Hours ¹		Number of Days Until Shoot Activity Ceased		Number of Days Until Renewed Shoot Activity ²	
	1983-84	1984-85	1983-84	1984-85	1983-84	1984-85
August						
30	0	0	-- ³	--	--	--
September						
1	0	0	47	--	128	--
6	0	0	--	--	--	--
13	0	0	--	--	--	--
19	14	--	51	--	111	--
21	--	6	--	--	--	--
27	64	6	--	--	--	--
October						
2	--	27	--	--	--	--
6	71	--	36	--	88	--
10	82	27	--	--	--	--
17	120	27	--	--	--	--
25	165	--	0	--	63	--
26	--	27	--	--	--	--
30	254	52	--	--	--	--
November						
5	--	114	--	0	--	--
10	333	--	0	--	42	--
14	445	217	--	0	--	--
19	--	365	--	0	--	--
22	498	--	0	--	22	--
29	565	465	--	0	--	>24
December						
5	667	602	--	0	--	--
13	718	681	0	0	22	>24
19	849	736	--	0	--	>24
28	1014	810	--	0	--	>24
January						
3	1165	934	--	0	--	22
8	1324	1089	--	0	--	22
16	--	1239	--	0	--	20
19	1471	--	0	--	11	--
31	--	1401	--	0	--	11
February						
2	1711	--	0	--	11	--
7	1829	1559	--	0	--	11
14	1832	1722	--	0	--	11
21	1885	1869	--	0	--	11
28	--	1947	--	0	--	6
March						
1	1986	--	0	--	6	--
7	2091	2045	--	0	--	6
13	--	2128	-- ⁴	--	0	--
15	2210	--	--	*	--	0
20	2254	2191	--	*	--	0
27	2314	2316	--	*	--	0
April						
2	--	2388	*	*	0	0
8	--	2423	--	*	--	0

¹Number of hours between 0 and 8 °C.

²After cessation of shoot activity.

³Data not collected.

⁴Seedling shoots were active prior to lifting from the nursery.

to 40 and 67 percent, respectively, in 1983-84 and 1984-85. Patterns of lateral root elongation were similar to RGP variation, the percentage elongating the greatest when RGP was high.

Root Growth Potential.

Mean total numbers and lengths of new roots varied significantly over time and among years (Table 4). Despite the fact that the overall percentage of lateral roots producing new roots was similar in both years, 1984-85 seedlings produced greater numbers and lengths of new roots, particularly at the late-winter peak (Figures 2 and 3, Table 4).

Seedling RGP varied with lift-date, but an overall trend of relatively low RGP in the autumn, increasing RGP through the winter to mid-March peak, followed by a spring RGP decrease, was consistent for both testing systems and years (Figures 2 and 3). A clear relationship between specific RGP changes and environmental variation over time was not apparent. Linear regressions of RGP on various environmental variable combinations explained 79 percent (R^2) of the monthly variation measured in 1983-84 but only 43 percent (R^2) of the 1984-85 weekly variation. Other regressions using many different algorithms and forms of the environmental data were even less successful than

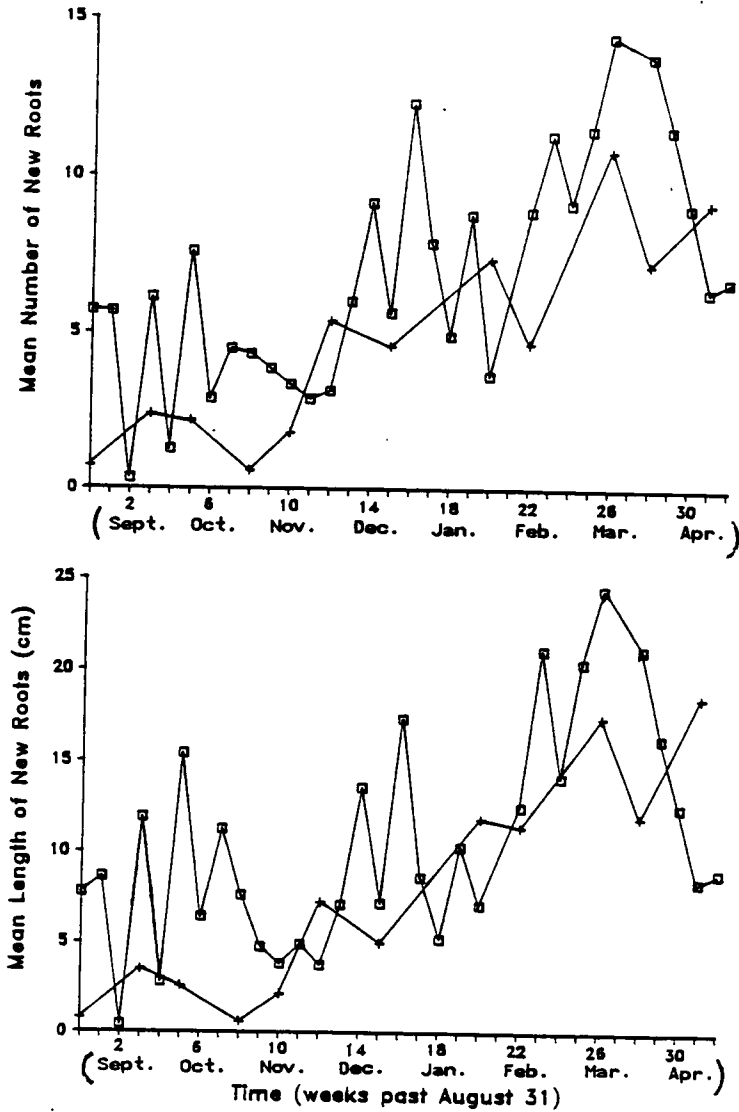


Figure 2. Root growth potential from September to April in 1983-84 (—+) and 1984-85 (—□) of loblolly pine seedlings from the 15-day test.

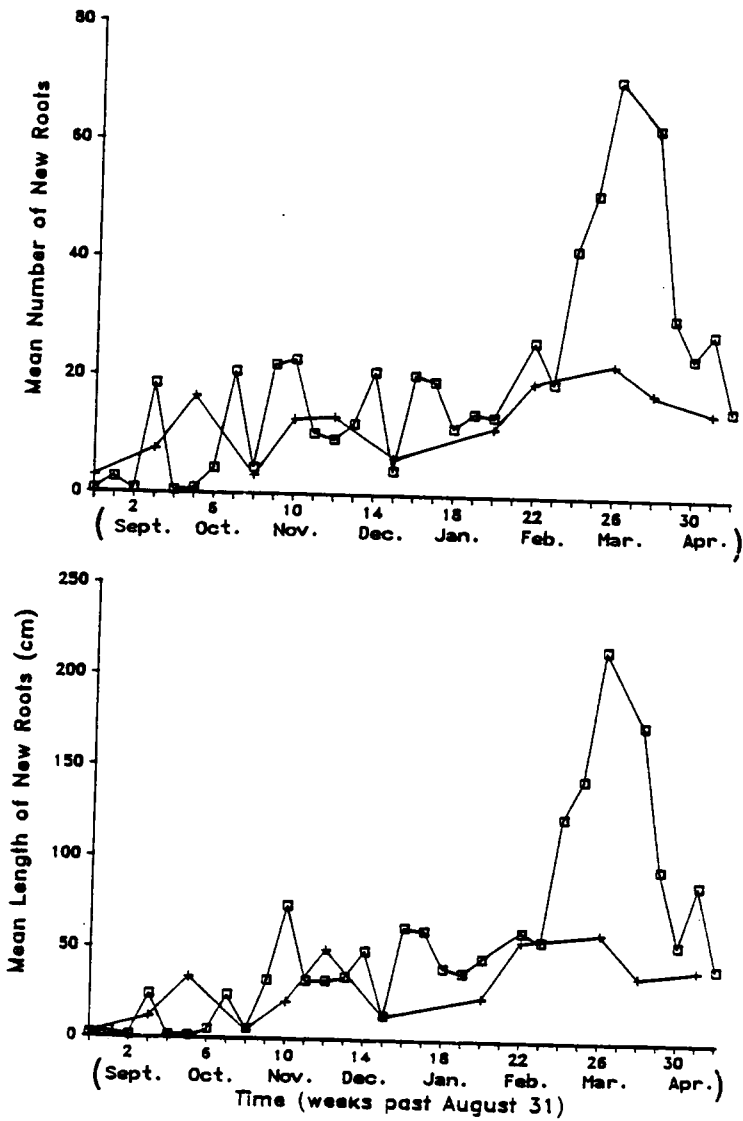


Figure 3. Root growth potential from September to April in 1983-84 (—+) and 1984-85 (—□) of loblolly pine seedlings from the 24-day test.

Table 4. Mean total number and length, and numbers and lengths of root types comprising loblolly pine seedling new root systems.

Type of New Root ¹	15-Day Testing System			24-Day Testing System		
	1983-84	1984-85	1984-85	1983-84	1984-85	1984-85
	Range	Mean	Range	Mean	Range	Mean
A	0.20-6.10	2.32	0.10-6.00	2.43	1.43-5.80	3.40
B	0.00-2.14	0.42	0.00-2.47	0.41	0.03-8.13	3.67
C	0.03-4.13	1.84	0.23-8.93	4.05	1.03-7.27	3.70
D	0.00-0.70	0.12	0.00-0.80	0.14	0.00-1.84	0.43
E	0.00-0.04	0.01	0.00-0.00	0.00	0.00-0.30	0.11
F	0.00-0.50	0.06	0.00-0.27	0.02	0.00-5.20	0.97
G	0.00-0.10	0.01	0.00-0.03	0.01	0.00-0.61	0.12
Short Roots ²	0.60-7.03	3.17	0.27-9.03	4.82	2.33-13.37	7.12
Total Number	0.60-10.83	4.76	0.33-14.47	7.03	2.93-22.63	12.40
						0.60-71.07
						19.97
						0.00-5.50
						0.07-15.17
						5.15
						0.00-12.4
						0.00-20.47
						3.50
						0.00-1.00
						0.00-15.97
						2.39
						0.00-6.50
						0.88
						0.10-35.53
						10.87
						0.60-71.07
						19.97
						0.00-45.53
						15.70
						0.07-40.90
						9.18
						0.00-67.17
						19.22
						0.03-33.07
						5.21
						0.00-2.97
						0.26
						0.00-6.30
						1.19
						0.00-26.63
						3.36
						0.00-8.40
						1.06
						0.10-35.53
						10.87
						1.03-215.70
						53.99

¹New root type was based on site of origin: new root attached to a primary or secondary lateral root directly from the end (A and C, respectively) or at a site other than directly from the end (B and D, respectively), new root attached directly to the taproot (E), new root attached to a new root on a primary (F) or secondary (G) lateral root.

²Short roots—summation of short roots (new root 0.5-1.5 cm in length) of all root types.

regressions with untransformed data. Only average weekly minimum soil and air temperatures were significantly correlated with RGP, coefficients ranged from -0.60 to -0.70 in 1983-84, and from -0.33 to -0.56 in 1984-85.

New Root System Morphology.

Seedling new root systems were primarily composed of short roots. The percentage of total new roots that were short roots averaged 60 to 70 percent (although it ranged 17 to 100 percent) (Table 4). This percentage tended to decline as RGP increased over time; seedlings lifted in the autumn averaged 10 to 15 percent more new short roots than long roots compared to seedlings lifted in the spring. Seedlings grown hydroponically had the highest percentage of short roots in the mid-winter (greater than 70 percent), which accounted for 90 percent of the total new root length. Seedlings from the 24-day system had the lowest percentage at mid-winter (less than 50 percent).

Of the seven types of roots comprising the new root system, those growing directly from the ends of lateral roots were the most common (types A and C in Table 4), accounting for greater than 60 percent of the new root systems. Of these two types of new roots, those with origins on primary lateral roots comprised a higher percentage of the new root system in 1983-84, but the

reverse was true the following year. In addition to these two types, seedlings tested in the 24-day system had a relatively high proportion of new roots originating on lateral roots at sites other than directly from the end (types B and D in Table 4), the percentage ranging 25 to 60, being particularly high in the autumn. Very few seedlings had new roots originating directly from the taproot, and the proportion of new roots originating on new roots attached to secondary lateral roots was also low (types E, F, and G in Table 4). These three types generally accounted for less than 20 percent of total new root numbers and lengths.

The proportion of the most common new root types remained relatively constant over time despite changes in RGP. Specific RGP increases and decreases were not associated with any consistent change in rank among the new root types; although, when RGP was low, there tended to be a lower proportion of the less common types. There was a greater diversity of new root types produced in the early autumn and after mid-February, particularly in the 24-day system. The early-autumn diversity was due to increased amounts of new roots originating on the sides of lateral roots. However, most of these new roots were short roots and did not contribute much to total root length. After mid-February, the relative proportion of the most common new root types

decreased slightly concomitant with increases in amounts of all other root types. Figure 4 illustrates this trend for percentage of total number in the 1984-85 24-day system at biweekly intervals.

Discussion

The overall RGP pattern observed for both years is consistent with other loblolly pine studies (Ferret et al. 1985a, Brissette and Roberts 1984, Rhea 1977), as well as with other species such as Douglas-fir (Ritchie and Stevens 1979, Jenkinson and Nelson 1978, Krugman et al. 1965, Winjum 1963, Stone et al. 1962) and ponderosa pine (Stone and Norberg 1979, Jenkinson 1977; 1975, Krugman and Stone 1966, Krugman et al. 1965, Stone and Schubert 1959a; b; c). The overall RGP variation pattern was similar for the 12 lift-dates in common between the two years (Figures 2 and 3) contrary to Brissette and Roberts' (1984) speculation that loblolly pine RGP on either side of the peak would vary considerably from year to year. Jenkinson (1984) reported RGP patterns were stable across years for western yellow pines.

There may be less difference in absolute RGP peak values between the two years than the data indicate. The late-winter temperatures in 1983-84 were at levels favorable for

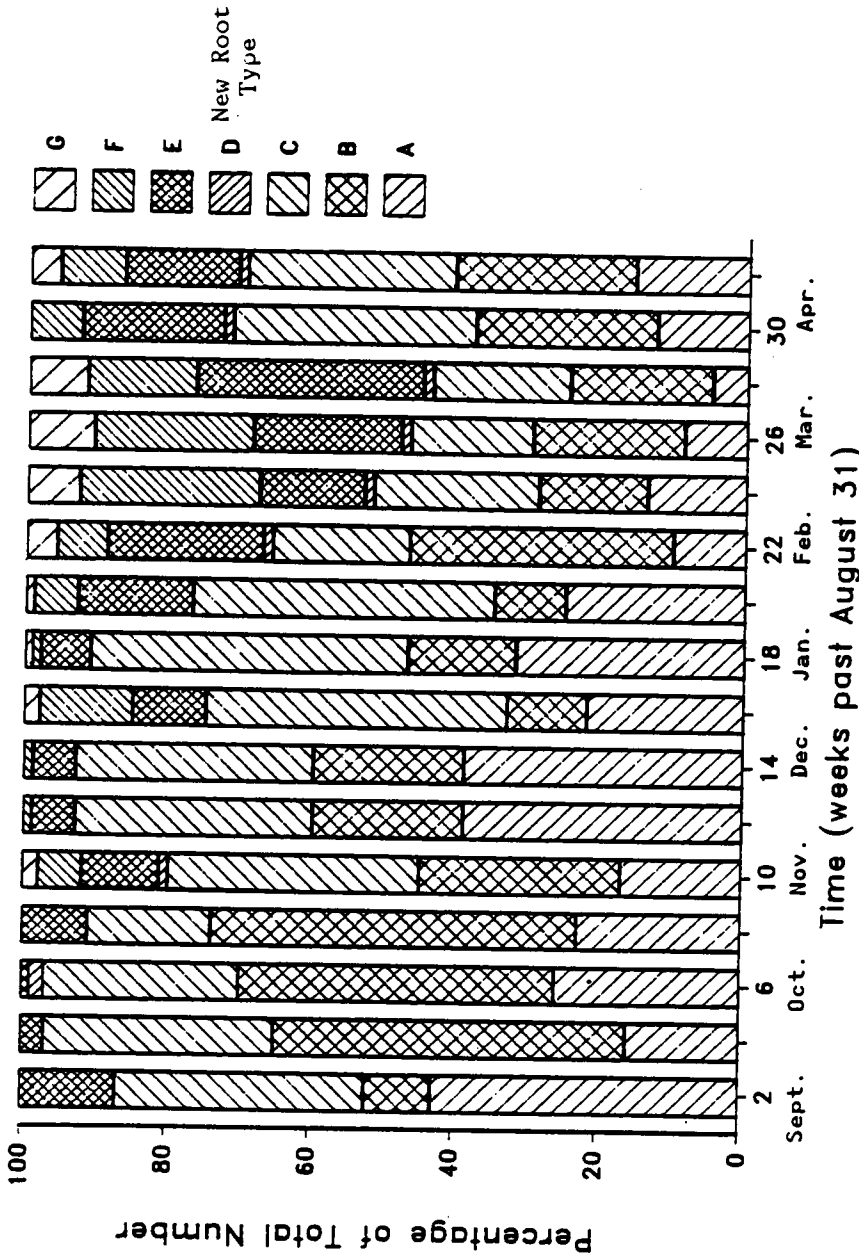


Figure 4. Biweekly proportion of new root types in the new root systems of loblolly pine seedlings tested in the 1984-85 24-day system. Root type is based on site of origin: new root attached to a primary or secondary lateral root directly from the end (A and C, respectively) or at a site other than directly from the end (B and D, respectively), new root attached directly to the taproot (E), new root origin on a new root attached to a primary (F) or secondary (G) root.

increased metabolic activity in loblolly pine (Drew and Ledig 1981, Barney 1951) and could have accelerated RGP development (Johnson-Flanagan and Owens 1985, Stone and Jenkinson 1971). However, since there is a one month gap in the 1983-84 data at this time it is possible the actual RGP peak was missed and a higher RGP peak than that recorded in week 26 occurred.

An alternative explanation for the differences in absolute RGP values between years may be the size difference of the seedlings. Root processes are mediated by the shoot (Ritchie and Dunlap 1980, Hay and Woods 1975, Gilmore 1962), therefore, more growth substances may have been available in 1984-85 to stimulate and support root initiation and elongation. In addition, both Rhea (1977) and Carlson (1985) reported relationships between lateral root size (numbers and lengths) and RGP. Therefore, the greater numbers and lengths in the lateral root systems in 1984-85 may have contributed to the greater overall RGP and the higher peak that year.

Root growth potential variation was more closely related to shoot phenology than to environmental variation. Seedling RGP was low during the cessation of shoot activity, increased when budburst occurred at the end of RGP tests, and declined as active shoot elongation began in the

nursery. The apparent relationship between RGP and shoot phenology, and the relative constancy of loblolly pine RGP variation over time suggests RGP is strongly internally regulated. Since the stimulus for root initiation and elongation is believed to originate in the shoot (Ritchie and Dunlap 1980, Hay and Woods 1975, Gilmore 1962) the environment may have an impact on loblolly pine RGP indirectly through its effect on shoot phenology.

Douglas-fir and ponderosa pine RGP variation appears to be related to their shoot dormancy cycle; mid-winter increases coinciding with the accumulation of chilling hours, the RGP peak representing the fulfillment of this requirement (Ritchie and Dunlap 1980, van den Driessche 1977, Krugman and Stone 1966). It is generally agreed that although southern seed sources of loblolly pine do not go fully dormant in the winter (Saranthus 1968, Perry et al. 1966), cessation of shoot activity in the winter of sources north of approximately 34°N latitude, is related partially to a chilling requirement of the buds (Boyer and South 1985, Cannell 1985, Lantz 1985, Garber and Mexal 1980, Garber 1978).

The increased rates of budburst with increasing chilling in loblolly pine seedlings from the New Kent nursery (located at 37.5°N latitude) is consistent with other

loblolly studies (Carlson 1985, Garber and Mexal 1980, Garber 1978, Kramer 1957) and suggests they require some form of chilling before normal shoot activity will resume. Although a specific chilling requirement for loblolly pine seedlings could not be determined from the present study, the development of rest for loblolly pine has been reported to occur from September through November (Cannell 1985), and the chilling requirement fulfillment in November through December (Garber 1978).

The low RGP in late-autumn and early-winter is likely the result of changes in seedling metabolism related to phenological events. Stone et al. (1962) reported lifting Douglas-fir in the autumn disrupted normal physiological sequences associated with seedling dormancy and caused poor RGP. Cannell (1985) reported the inability of loblolly pine roots to grow while buds are in a state of rest. Roots of lodgepole pine and spruce have been found to be mitotically inactive in the late-autumn when RGP was low (Johnson-Flanagan and Owens 1985). The fewer types of new roots produced by the seedlings in the autumn, even when RGP was occasionally high, suggests this may also be true in loblolly pine.

The dry weight increases in the autumn, which have also been reported in other studies (Munson and Stone 1984, Drew

and Ledig 1981, Garner and Dierauf 1976), may indicate shifts in photosynthate allocation between the root and shoot. Kramer and Kozlowski (1979) indicated southern pines accumulate most of their reserve carbohydrates during the autumn and winter after shoot growth ceased. Energy is directed to increasing seedling biomass rather than new root initiation until the late-winter when root elongation and initiation become the primary metabolism (Venator 1984, Chung and Barnes 1980, Ritchie and Dunlap 1980). Consequently, RGP is low in the autumn and increases in the winter.

In addition, since root growth tends to be cyclic (Hermann 1977, Merritt 1968, Wilcox 1968a and b; 1962b; 1954), low autumn RGP values may be partially due to injury caused by lifting seedlings with actively growing, unsuberized roots. Incompletely suberized roots are readily damaged and root suberization is more complete when root growth is minimal (Carlson 1985). Other reports have linked low RGP to the resistance of the root system to handling (Ritchie 1985, Ritchie and Stevens 1979, Hermann 1967).

After fulfillment of the chilling requirement, shoots send stimuli to the roots for elongation and initiation of new roots (Cannell 1985). Increased photosynthetic rates in late-February support increased root metabolic activity

(Ledig and Perry 1969, Davis et al. 1963), and RGP rises. The increased root metabolic activity is also reflected in the production of new roots from all types of sites on the old root system. Despite the large RGP decrease in the spring, the majority of the root system remained active; all types of new roots were produced, but in lesser amounts.

Decreases in RGP coinciding with renewed shoot growth in the spring is not unexpected for a species such as loblolly pine which typically shows an alternation of root and shoot growth. Just prior to the large spring RGP decrease, the sink strength of the root system is high, allowing a high rate of root metabolic activity (Drew and Ledig 1981, Chung and Barnes 1980, Ritchie and Dunlap 1980, Shiroya et al. 1966). However, once budburst begins the shoots are more effective competitors for translocatable reserves and current photosynthate (Cannell and Willett 1976, Eliasson 1971, Lathrop and Mecklenburg 1971, Zeimer 1971, Gordon and Larson 1968, Shiroya et al. 1966) and RGP decreases. The sink strength of loblolly pine's shoot is particularly great during renewed growth in the spring since approximately 26 percent of the season's growth occurs during this time (Boyer 1970, Saranthus 1968).

Despite the high level of root activity in the late-winter and early-spring, a maximum of only two-thirds of the

old lateral roots produced new roots. During the winter, less than half the lateral roots were active, and root growth consisted primarily of elongation of existing lateral roots (new roots growing directly from the ends of lateral roots) rather than initiation of new lateral roots (new roots originating at sites other than directly from lateral root ends). The late-winter RGP increase was accompanied by a large increase in root initiation. These results are consistent with limited observations made on other species (Johnson-Flanagan and Owens 1985, Krueger and Trappe 1967, Stone et al. 1962, Stone and Schubert 1959a). In the early-autumn there was also a relatively high proportion of root regeneration on primary lateral roots which reflects seedling biomass increases. Therefore, apparently only when seedling metabolism is relatively high will a significant amount of root regeneration occur.

It is interesting to note that although the 1984-85 seedling root systems were larger, the proportion of roots which elongated or initiated new roots was generally higher for primary lateral roots in 1983-84 but higher for secondary lateral roots in 1984-85 (e.g. compare types A and C in Table 4 between the two years for a given testing system). The 1984-85 seedling root systems could be considered more mature since they reached a given size

earlier than the 1983-84 root systems. Stone et al. (1963) noted the older the root, the more likely it was to regenerate roots through the elongation of younger lateral roots on it.

Similar to other species (Winjum 1963), the majority of loblolly pine new roots regardless of lift-date were short roots. This indicates a higher relative importance of new root number compared to new root length. Root number, as in other studies (Ferret et al. 1985a, Rhea 1977), explained nearly all new root length variation. Therefore, new root numbers may be a more relevant measure of RGP.

EXPERIMENT II

Changes in Loblolly Pine Seedlings During Cold Storage

Introduction

The ideal procedure in artificial regeneration systems would be to transplant seedlings immediately after they were lifted from the nursery. This is often not possible due to factors such as soil conditions, weather, and logistics (Kramer and Rose 1985). The loblolly pine seedling planting season in the Southeastern United States exceeds the lifting season by as much as three months. To avoid seedling quality decreases caused by lifting flushing seedlings in the spring, seedlings are lifted early and cold-stored until they can be planted.

Cold storage has been reported to improve, decrease, or have no effect on the subsequent survival of loblolly pine seedlings, depending on the date of lifting from the nursery and duration of storage (Venator 1984, Dierauf 1982, Garber and Mexal 1980, Rhea 1977, Dierauf 1974, Williston 1974, Dierauf and Marler 1969, Ursic et al. 1966, Kahler and Gilmore 1961). Similar variable effects have been reported when root growth potential (RGP), the readiness to initiate

and elongate new roots (Sutton 1980c), was used to evaluate seedling physiological quality following cold storage of various conifer species (Carlson 1985, Ritchie 1984a and b, McCracken 1979, Rhea 1977, Jenkinson and Nelson 1978, Stone and Jenkinson 1971, Winjum 1963, Hellmers 1962, Stone and Benseler 1962, Stone and Schubert 1959b).

In their review of RGP, Ritchie and Dunlap (1980) conclude the effect of cold storage on RGP of seedlings with chilling requirements is through interactions with bud dormancy and carbohydrate reserves. In general, dormancy is released in western conifer species in cold storage as it is in the field, with concurrent increases in RGP until the fulfillment of the chilling requirement. Seedlings put in cold storage before they are dormant, or kept in storage after the fulfillment of the chilling requirement often show decreases in RGP (Jenkinson 1984, Ritchie et al. 1985, Ritchie 1984b, Jenkinson 1980, Nelson and Lavender 1979, van den Driessche 1977, Ritchie and Stevens 1979, Stone and Jenkinson 1971). The effect of cold storage on RGP of species adapted to warmer climates such as loblolly pine is less well understood (Ritchie and Dunlap 1980). Few studies have extensively examined the effects of cold storage on loblolly pine RGP, and a direct comparison of cold-stored with freshly lifted seedlings has not been made. The

objectives of this study were to describe changes in loblolly pine seedlings following different lift-date X storage duration combinations, and to relate these results to the RGP, shoot activity, and new root system morphology of fresh-lifted seedlings.

Materials and Methods

The 1-0 seedlings used in this study were operationally grown by the Virginia Division of Forestry (VDF) at their New Kent Forestry Center nursery located in the Virginia Coastal Plain, near Providence Forge. The seeds were planted in April 1983 and 1984, regularly irrigated throughout the growing season, and were top-pruned on August 10, 31, September 20, 1983, and on August 1, 20, September 19, in 1984. Air temperature was continuously monitored by a hygrothermograph in a weather station adjacent to the nursery beds being sampled. Chilling hours were based on the loblolly pine results of Garber (1983; 1978) and calculated from the hygrothermograph data as the number of hours in the nursery between 0 and 8°C.

Several lift-date X storage duration treatment combinations were compared to fresh-lifted seedlings. Seedlings were lifted on October 25 and 30, November 22 and 29, December 13 and 19, January 8 (1985 only), February 2

and 1 in 1983-84 and 1984-85, respectively. The January 8 lift-date treatment was not possible in 1984 due to frozen soil in the nursery.

On each lift-date 300 seedlings were hand-lifted and the RGP of 60 seedlings was immediately measured. The remaining seedlings were randomly divided into two approximately equal groups, placed into two double-layered polyethylene bags, and stored for durations of 3, 6, 9, and 12 weeks in a coldroom held at a constant 2°C and 50 percent relative humidity. Following the cold storage treatments 30 seedlings were removed from each of the two polyethylene bags, 60 seedlings were fresh-lifted from three random spots in the same nursery seedbed, and the RGP of all the seedlings was measured. Prior to the initiation of the RGP tests, the seedling root systems were pruned to 12 cm below the root collar (ground line level on the main axis [Sutton and Tinus 1983]) and any new white tips were removed.

The RGP of 30 seedlings removed from cold storage for each lift-date X storage duration treatment, and 30 fresh-lifted seedlings were tested by growing them in an aerated hydroponic system consisting of two replicate 37.8 liter aquariums in a greenhouse. Water temperature was maintained at ambient air temperature (16-27°C) and 0.5 g of 20-20-20 (nitrogen-phosphorus-potassium) was added to each aquarium.

The seedlings were grown under a 16-h photoperiod for 15 days. The remaining 30 cold-stored and 30 fresh-lifted seedlings from each treatment combination were measured in a more traditional testing system (Stone 1955) by planting them into two replicate 46 X 10 X 41 cm (length X width X height) trays containing Pro-Mix growth medium. The seedlings were grown for 24 days in a different greenhouse under ambient air temperatures (16-27°C) and a constant root temperature of 20°C. Daylength was set for 16 hours. Temperatures of both greenhouses were monitored throughout the study with hygrothermographs.

After each 15- or 24-day RGP test the seedlings were carefully removed and the following shoot and root variables were measured on each seedling:

1. height from the root collar to the severed tip of the stem (nearest cm)
2. amount of new shoot elongation (nearest cm)
3. root collar diameter (nearest 0.1 mm)
4. shoot activity (used to estimate the dormancy intensity parameter described by Ritchie [1984]) was assigned a rating based on the level of visually detectable activity:
 - a) none apparent
 - b) swollen or elongated buds (terminal bud if present or bud within top needle fascicle)
 - c) stem elongation just beginning
 - d) measurable stem elongation

- e) elongating needles
- 5. seedling dry weights (measured only in 1984-85)
 - a) total shoot dry weight (nearest 0.01 g)
 - b) needle dry weight (nearest 0.01 g)
 - c) stem dry weight (nearest 0.01 g)
 - d) total root dry weight (nearest mg)
 - e) lateral root dry weight (nearest mg)
 - f) taproot dry weight (nearest mg)
- 6. total number and length (nearest cm) of lateral roots
 - a) elongated primary lateral roots
 - b) non-elongated primary lateral roots
 - c) elongated secondary lateral roots
 - d) non-elongated secondary lateral roots.

Primary lateral roots were defined as roots attached directly to the taproot. Secondary roots were lateral roots attached to primary lateral roots.

The RGP data collected included total number and length (nearest cm) of new short roots (those 0.5-1.5 cm in length) and new long roots (those >1.5 cm long) of seven different types of new roots. New root type was based on site of attachment to the old root and included those originating directly from the end or from a site other than directly from the end of either a primary or secondary lateral root, new roots arising from the sides of other new roots, and new roots arising directly from the taproot.

The study was designed as a factorial experiment with 2 completely randomized blocks (two aquariums or two trays) nested in each lift-date (4 in 1983-84, 5 in 1984-85) X storage treatment (5 durations) X testing system (15-day or 24-day) interaction, each block containing 15 seedlings. The January 8 lift-date treatment was not used in the comparison between years.

The data were analyzed utilizing analyses of variance, correlation analyses, and regression analyses (SAS Institute Inc. 1985). Differences between fresh-lifted and cold-stored seedlings were also analyzed using multivariate profile analysis (Harris 1975) which multivariately compares overall slopes between two regression lines, and also compares data-point to data-point changes among the two regression lines. The significance level used for all of the above tests was $\alpha=0.05$. The nested block effect was not significant and was included in the error term. All subsequent analyses were based on two replicates of plot means of $n=15$. Most interactions among years and testing systems were significant, therefore, subsequent analyses were used to test these effects separately. Despite significant absolute RGP differences, relative differences from lift-date to lift-date did not vary significantly between the two RGP testing systems (DeWald et al. 1985a).

Therefore, RGP results of the two systems will not be presented or discussed separately. Correlations between greenhouse temperatures and RGP were very low and not significant. Therefore, it is assumed any temperature changes in the greenhouse environments over time had a minimal effect on seedling RGP.

Results

Seedling Morphology.

Cold-stored and fresh-lifted seedling shoot and root size variables did not vary significantly among lift-dates or among storage durations. However, some traits varied significantly between cold-stored and fresh-lifted seedlings, particularly in the autumn. October-lifted stored seedlings averaged 31.5 lateral roots compared to 36.0 for seedlings fresh-lifted from the nursery during these cold-storage treatments. In 1984 November-lifted stored seedlings averaged 39.1 lateral roots compared to 44.9 for fresh-lifted seedlings. In addition, dry weights of cold-stored seedlings were significantly less than fresh-lifted seedlings. Dry weights were variable, or showed either slight decreasing trends (cold-stored seedlings) or slight increasing trends (fresh-lifted seedlings) (Table 5).

Table 5. Dry weight changes over time in cold-stored and fresh-lifted loblolly pine seedlings in 1984-85.

Lift-Date	Time After Lift-Date (weeks)	0-Week Dry Weight		Percentage of Seedling 0-Week Dry Weight ¹ (by lift-date)			
		Shoot (gm)	Root (gm)	Shoot %	Root %	Stored Fresh %	Rt/Sht %
October 30	0	1.78	0.42	0.24			
	3				99	67	95
	6				101	81	100
November 29	9				89	77	98
	12				116	82	112
	0	1.46	0.43	0.29			
December 19	3				102	108	93
	6				105	103	100
	9				112	135	98
January 8	12				114	121	100
	0	1.68	0.45	0.27			
	3				95	95	107
February 2	6				104	125	118
	9				91	112	100
	12				105	133	109
January 8	0	1.67	0.54	0.33			
	3				98	132	100
	6				91	118	93
February 2	9				85	140	83
	12				92	111	87
	0	2.51	0.62	0.26			
February 2	3				75	90	81
	6				74	106	77
	9				62	83	79
February 2	12				62	-	81
	12						

¹Stored=seedlings lifted at each 0-week lift-date and stored at 2°C for 3, 6, 9, or 12 weeks.
 Fresh=seedlings fresh-lifted from the New Kent nursery each time seedlings were removed from cold storage.
 †Data not collected.

Shoot Activity.

Bud activity and subsequent spring shoot elongation of seedlings in the RGP tests varied significantly over time, increasing with later time of lifting and with cold storage duration (Table 6). In addition, differences between stored and fresh-lifted seedlings were also significant. Seedlings lifted in the autumn and early winter, and stored up to 9 weeks often had accelerated bud activity compared to seedlings fresh-lifted during this time. In contrast, bud activity of fresh-lifted seedlings was accelerated compared to seedlings lifted in January and February and cold-stored at least 6 and 3 weeks, respectively (Table 6). Fresh-lifted seedlings at these times had needle elongation and two to three times greater stem elongation than cold-stored seedlings, which had little or no needle elongation.

Seedling Root Activity.

The RGP and percentage of elongating lateral roots generally increased with time of lifting and storage duration (Figures 5, 6, 7, and 8). The RGP of seedlings from different lift-date and storage duration treatments removed from cold storage on the same date did not differ significantly. Exceptions to these trends were cold-stored seedlings lifted in October and February. Seedlings lifted in October had low RGP going into cold storage and RGP

Table 6. Bud activity and shoot elongation of cold-stored loblolly pine seedlings tested for root growth potential.

Month Storage Lifted	Chilling Hours ¹ 1983 1984 -84 -85	15-Day Testing System						24-Day Testing System					
		1983-84			1984-85			1983-84			1984-85		
		Bud Status ²	Shoot Elongation	Bud Status	Shoot Elongation	Bud Status	Shoot Elongation	Bud Status	Shoot Elongation	Bud Status	Shoot Elongation	Bud Status	Shoot Elongation
	(weeks)	(%)	(cm)	(%)	(cm)	(%)	(cm)	(%)	(cm)	(%)	(cm)	(%)	(cm)
October	0	165	52										
	3	445	365	2.5 (109) ³	0.0 (100)	2.0 (99)	0.0 (100)	1.8 (77)	0.0 (100)	1.9 (95)	0.0 (100)		
	6 ^a	718	736	2.1 (91)	0.0 (100)	2.0 (99)	0.0 (100)	2.5 (86)	0.0 (100)	1.9 (95)	0.0 (100)		
	9 ^b	1165	1089	3.3 - ⁴	0.0 -	1.9 (94)	0.0 (100)	2.6 -	0.0 -	2.7 (127)	0.1 (110)		
	12 ^c	1587	1559	3.3 (85)	0.1 (100)	2.3 (108)	0.0 (100)	2.1 (86)	0.0 (100)	1.7 (77)	0.0 (100)		
November	0	498	365										
	3 ^a	718	736	2.9 (125)	0.0 (100)	2.0 (100)	0.0 (100)	3.0 (105)	0.0 (100)	2.0 (100)	0.0 (100)		
	6 ^b	1165	1089	3.2 -	0.0 -	2.0 (101)	0.0 (100)	4.1 -	0.4 -	2.3 (100)	0.0 (100)		
	9 ^c	1587	1559	4.1 (108)	0.5 (100)	2.6 (110)	0.0 (100)	4.2 (113)	0.7 (100)	2.5 (86)	0.0 (100)		
	12 ^d	1832	1947	4.2 (94)	0.8 (78)	2.7 (82)	0.0 (100)	4.4 (86)	1.1 (25)	4.7 (100)	2.1 (100)		
December	0	718	736										
	3 ^b	1165	1089	2.9 -	0.0 -	2.1 (103)	0.0 (100)	3.8 -	0.3 -	2.4 (114)	0.0 (100)		
	6 ^c	1587	1559	4.1 (106)	0.2 (100)	2.4 (103)	0.0 (100)	4.3 (114)	0.8 (100)	3.7 (126)	0.2 (100)		
	9 ^d	1832	1947	3.9 (89)	0.2 (19)	3.6 (108)	0.1 (76)	4.5 (86)	1.3 (30)	4.9 (103)	2.5 (163)		
	12 ^e	2091	2191	4.2 (91)	0.5 (31)	4.3 (82)	0.6 (20)	4.9 (84)	3.4 (84)	5.2 (89)	3.7 (84)		
January	0	-	1089										
	3 ^c	-	1589	-	-	2.2 (94)	0.0 (100)	-	-	3.4 (116)	0.1 (100)		
	6 ^d	-	1947	-	-	2.5 (90)	0.1 (81)	-	-	4.5 (94)	1.6 (105)		
	9 ^e	-	2191	-	-	3.8 (72)	0.1 (13)	-	-	5.3 (91)	4.6 (68)		
	12 ^f	-	2423	-	-	4.9 (88)	0.9 (32)	-	-	5.1 (86)	2.7 (57)		
February	0	1587	1559										
	3 ^d	1832	1947	3.7 (84)	0.0 (0)	3.4 (102)	0.0 (18)	4.6 (90)	2.5 (58)	4.8 (101)	2.8 (185)		
	6 ^e	2091	2191	3.9 (84)	0.3 (18)	3.9 (73)	0.2 (7)	4.7 (81)	2.6 (66)	4.9 (83)	3.1 (46)		
	9 ^f	-	2423	4.4 (82)	1.1 (35)	4.9 (89)	1.1 (40)	5.5 (102)	2.7 (90)	4.9 (84)	1.8 (38)		
	12	-	-	4.3 -	1.0 -	5.0 -	1.3 -	4.8 -	1.9 -	5.4 -	2.3 -		

¹Number of hours in the New Kent nursery, Providence Forge, Virginia between 0 and 8°C.
²Rated on a scale: 1=dead seedling, 2=no apparent bud activity, 3=swollen or elongated buds, 4=bud flushing, 5=measurable stem elongation, 6=elongating needles.
³Percentage of the value recorded for seedlings fresh-lifted on dates seedlings were removed from cold storage.
⁴Seedlings from month lifted X storage length combinations followed by the same letter were removed from cold storage on the same date.
⁵No data collected.

remained low. In addition, mold was found in the bags containing the seedlings after 12 weeks of cold storage. Cold-stored seedlings lifted in February generally showed no significant RGP changes with time in storage (Figures 5, 6, 7, and 8).

The multivariate profile analysis indicated overall differences between cold-stored and fresh-lifted seedlings were not significant. On a per lift-date basis, however, the RGP and percentage of elongating lateral roots of stored seedlings lifted in October both years and in November 1984 were significantly less than comparable fresh-lifted seedlings (Figures 5, 6, 7, and 8). These cold-stored seedlings had 14 and 10 percent fewer elongating primary and secondary lateral roots, respectively, than fresh-lifted seedlings. The reverse trend was true in November and December, 1983. Cold-stored seedlings lifted these months had up to two times greater RGP than seedlings fresh-lifted during these times (Figures 5, 6, 7, and 8). In addition, these 1983 cold-stored seedlings, as well as 1984 February-lifted cold-stored seedlings, had 25 percent more elongating lateral roots than comparable fresh-lifted seedlings.

New Root System Morphology.

In general, variation over time and among storage durations was significant for the numbers and lengths of all

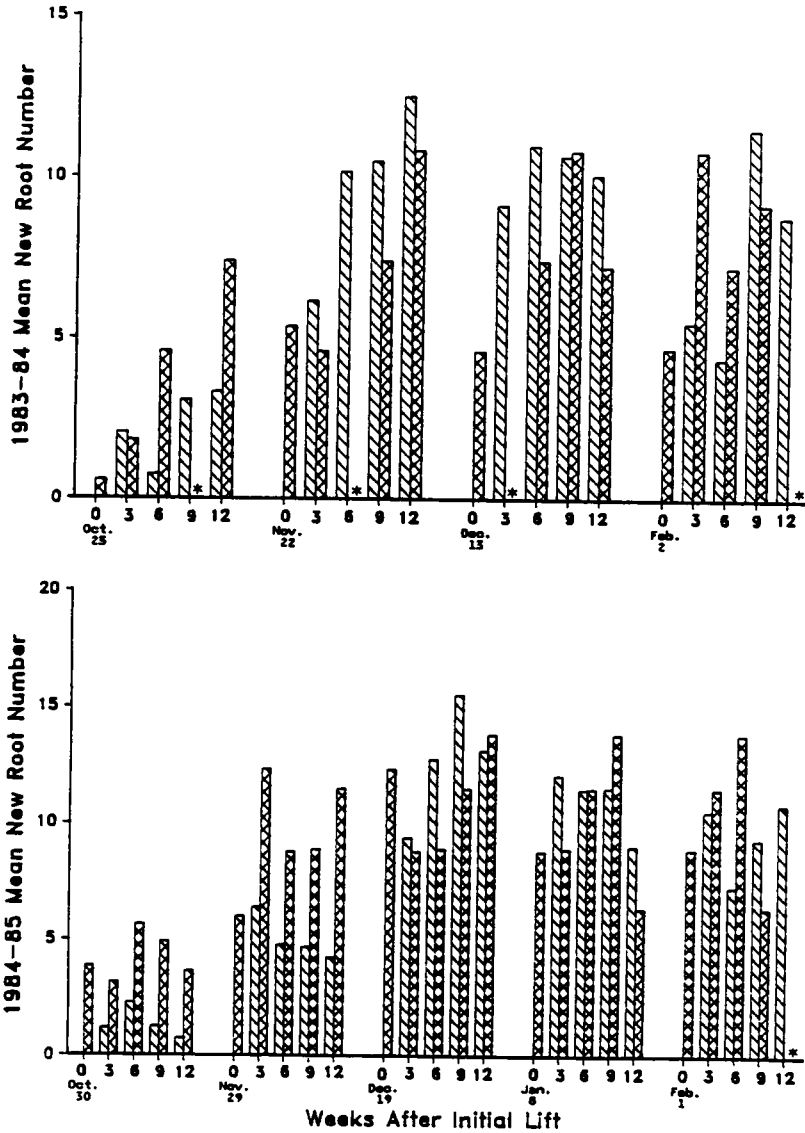


Figure 5. Changes in new root number over time of cold-stored (▨) and fresh-lifted (⊠) loblolly pine from the 15-day test. *= no fresh-lift data available.

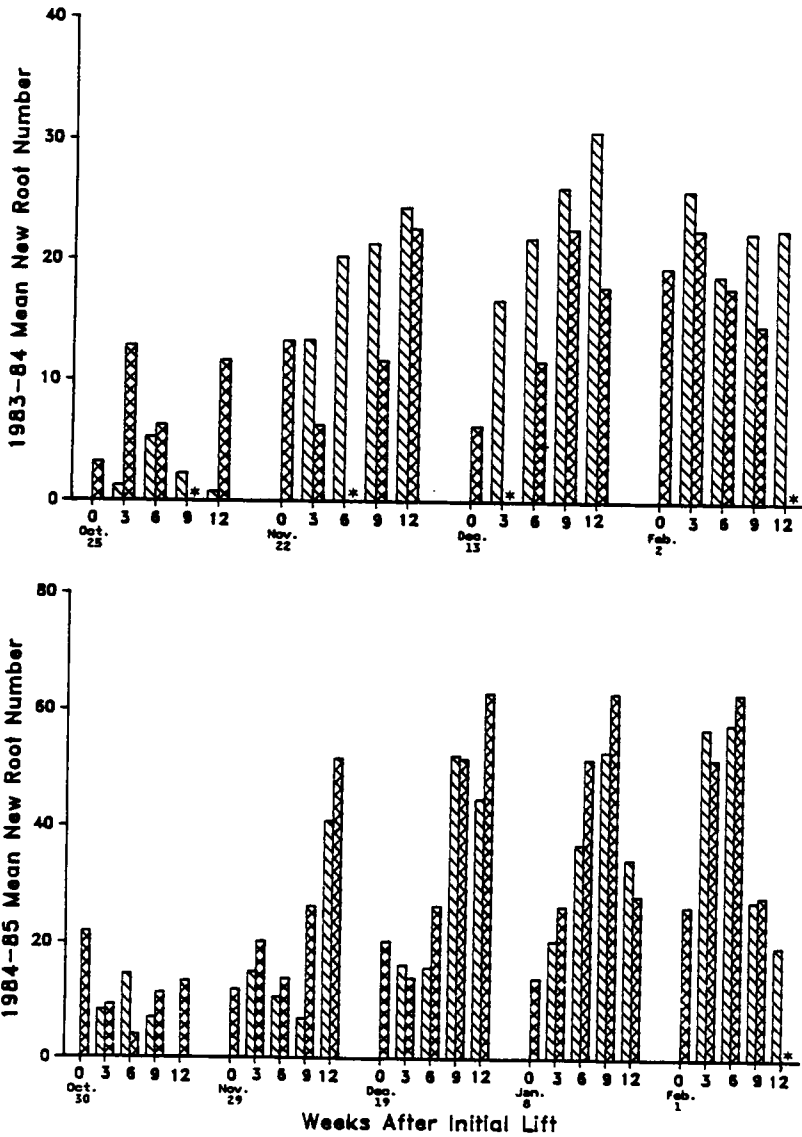


Figure 6. Changes in new root number over time of cold-stored (▨) and fresh-lifted (⊠) loblolly pine from the 24-day test. * = no fresh-lift data available.

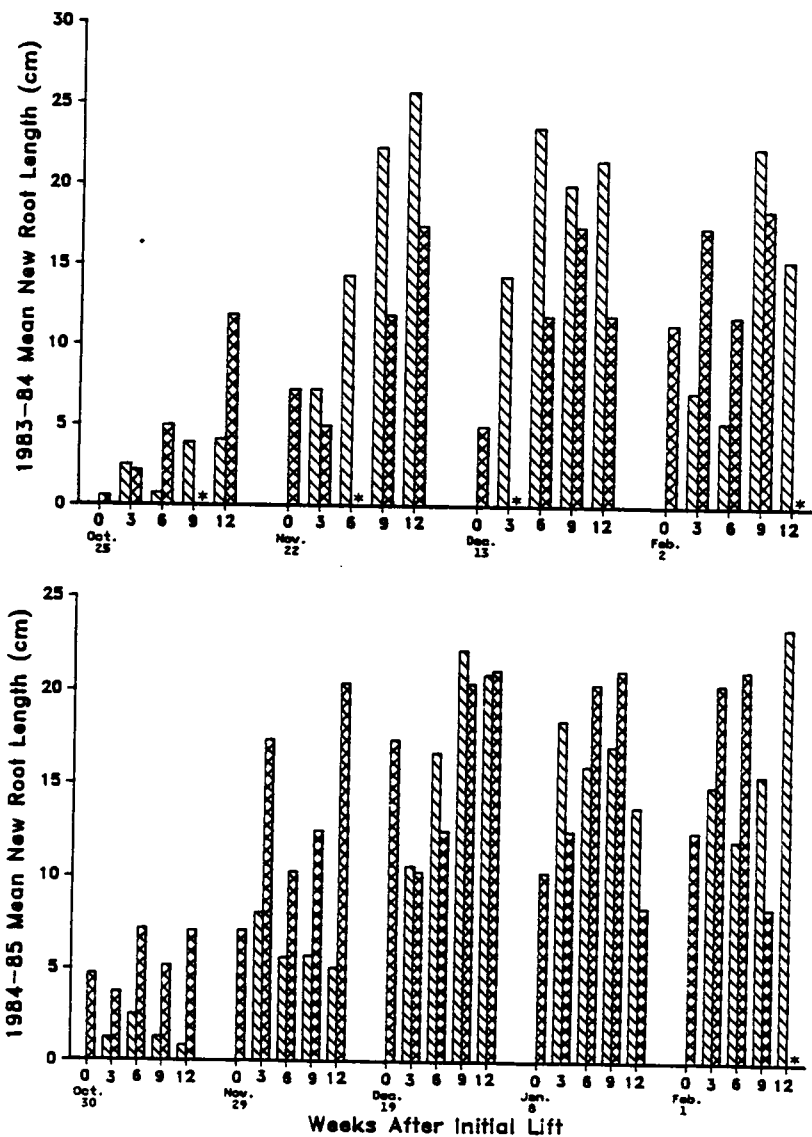


Figure 7. Changes in new root length over time of cold-stored (▨) and fresh-lifted (⊠) loblolly pine from the 15-day test. *= no fresh-lift data available.

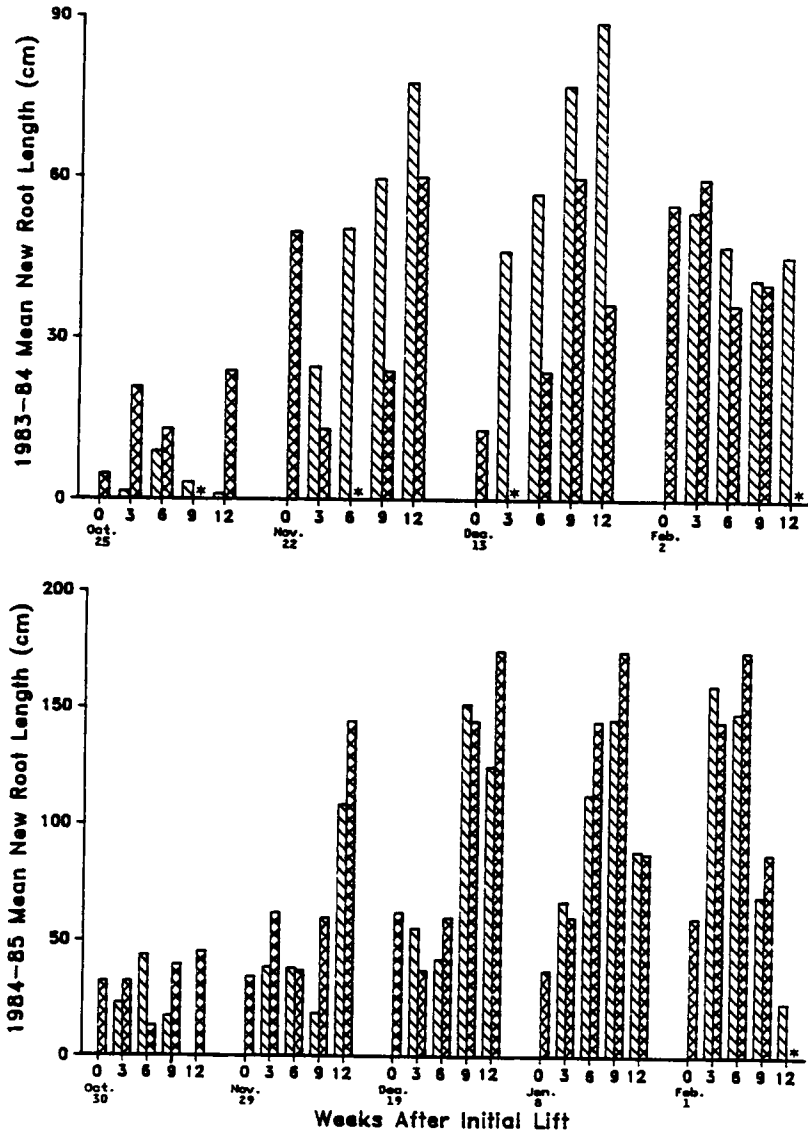


Figure 8. Changes in new root length over time of cold-stored (▨) and fresh-lifted (⊠) loblolly pine from the 24-day test. * = no fresh-lift data available.

major types of new roots comprising the new root systems of fresh-lifted or cold-stored seedlings. This variation was similar to that described for total number and total length of new roots. In addition, percentages of new root types generally did not differ significantly among seedlings of different lift-date X storage duration combinations removed from cold storage at the same time. Occasional significant differences were due to new root systems of stored seedlings lifted in October which had less diverse types of new roots. Significant differences between cold-stored and fresh-lifted seedlings occurred most commonly for new roots originating at sites other than directly from the ends of lateral roots. However, the differences appeared to be random and were not associated with any particular lift-date X storage duration treatment.

The diversity of new root types comprising the new root systems was lowest in the autumn when RGP was low and greatest when RGP was high. However, greater than 50 percent of the new roots originated directly from the ends of lateral roots regardless of lift-date. The remainder of the new root systems included (in order of decreasing abundance): new roots originating from primary and secondary lateral roots at sites other than directly from the ends, new roots originating on new roots attached to

primary and secondary lateral roots, and new roots attached directly to the taproot.

In addition, greater than 50 percent of the numbers of new roots were short roots, the percentage decreasing significantly with lift-date and storage duration until February. Stored seedlings lifted in February, and fresh-lifted seedlings after the third week in February had significant increases in the percentage of short roots in their new root systems.

Discussion

The similarity of bud activity between fresh-lifted seedlings and seedlings removed from cold storage prior to the late-winter supports the results of Carlson (1985) and Garber (1978) who reported loblolly pine bud dormancy was reduced as rapidly in cold storage as in nature. Cold storage has also been reported to fulfill the chilling requirements of other species, including Douglas-fir (Jenkinson 1984, van den Driessche 1977) and ponderosa pine (Jenkinson 1980, Krugman and Stone 1966).

The cold-stored loblolly pine seedlings may have had their chilling requirement fulfilled faster than seedlings growing in the nursery in the early-winter. Although the effect was not significant, the slightly accelerated bud

activity of November- and December-lifted seedlings once they were removed from cold storage (Table 6) may be due to lack of exposure to occasional warm temperatures experienced by seedlings growing in the nursery. Ritchie (1984b) reported warm temperatures negated cold temperature contributions to the satisfaction of chilling requirements in Douglas-fir.

The lag in late-winter bud activity and shoot elongation in the RGP tests of cold-stored seedlings relative to fresh-lifted seedlings is not surprising since cold-stored seedlings were not exposed to the warming nursery environment which undoubtedly had previously accelerated shoot metabolism of fresh-lifted seedlings. Similar results have also been reported for Douglas-fir (Ritchie 1984b, Ritchie and Stevens 1979, Hermann 1967), and Ritchie (1984b) attributed this delay in stored Douglas-fir seedlings to lack of exposure to photoperiod and warming temperatures.

After the chilling requirements have been met, RGP has been reported to decrease or remain unchanged in cold storage depending on the species and seed source (Ritchie et al. 1985, Ritchie 1982, Jenkinson 1980, Ritchie and Stevens 1979, Stone and Norberg 1979, Garber 1978, van den Driessche 1977, Krugman and Stone 1966). In the current study, RGP of seedlings removed from cold-storage in the spring was

variable. It is uncertain if this represents a decrease in storability. Other studies reported successful (Dierauf 1984; 1974) and unsuccessful (Venator 1984) cold-storage of loblolly pine seedlings lifted in the late-winter and early-spring.

Ritchie et al. (1985) concluded RGP decreases of cold-stored western conifer species in the spring were due to increased metabolism in the buds. Shoot metabolic activity of stored loblolly pine seedlings in the spring had increased (Table 6) despite the lack of a photoperiod and warming temperatures, and although shoot activity lagged behind that of fresh-lifted seedlings, the level of activity of stored seedlings was at a point where RGP of fresh-lifted seedlings was declining.

The results of this study indicated seedling size and new root characteristics generally do not differ among stored and fresh-lifted seedlings. The relatively smaller size of stored seedlings lifted in October and November is probably the result of the steady increase in size until December of seedlings growing in the nursery. The decreasing dry weight trends of stored seedlings lifted in December, January, and February when compared to the increasing dry weight trends of fresh-lifted seedlings during these times likely caused the significant difference between stored and fresh-lifted seedlings.

The lack of significant dry weight changes during cold storage is in contrast to Garber and Mexal's (1980) report of significant weight losses in loblolly pine. They attributed these decreases to respirational depletion of food reserves with increased time in cold storage. Similar weight losses have been reported for Mugho and Monterey pine (McCracken 1979), Sitka spruce (Picea sitchensis (Bong.) Carr.) (Buckley and Lovell 1974) and Douglas-fir (Hermann 1967).

The increase, decrease, or lack of change in loblolly pine seedling RGP following different lift-date X storage duration treatment combinations is consistent with other loblolly pine studies (Carlson 1985, Garber and Mexal 1980, Rhea 1977) as well as with results of other studies (Ritchie et al. 1985, Jenkinson 1984, Ritchie and Stevens 1979, Stone and Norberg 1979, Krugman and Stone 1966, Stone and Schubert 1959b). All of these previous studies attributed RGP changes to effects of cold storage, and Ritchie and Dunlap (1980) hypothesized RGP decreases in cold storage are due to the depletion of food reserves needed for regrowth.

Whether cold storage caused RGP changes in the previous studies is uncertain since cold-stored seedlings were not compared to fresh-lifted seedlings. In the only other study directly comparing cold-stored to fresh-lifted seedlings,

Winjum (1963) reported no differences between cold-stored and fresh-lifted seedlings of noble fir and Douglas-fir. This is consistent with the results of the current study where root activity of cold-stored loblolly pine lifted after November was generally not different than fresh-lifted seedlings for any of the variables examined.

The only major differences between cold-stored and fresh-lifted seedlings occurred when cold-stored seedlings had been lifted in October and (in 1984) November. The relatively poor performance of early-lifted cold-stored loblolly pine seedlings has been noted in other loblolly pine studies (Carlson 1985, Dierauf 1982, Garber and Mexal 1980), as well as with ponderosa pine (Stone and Schubert 1959b) and Douglas-fir (Jenkinson 1984, Ritchie and Stevens 1979). Seedling quality changes in cold storage of early-lifted stock has been related to chilling requirements; quality decreasing if seedlings are stored prior to bud dormancy.

The inconsistent results between the two years of cold-stored seedlings lifted in November has been noted in other studies (Kahler and Gilmore 1961) and may relate to variable levels of dormancy due to differences in chilling hour accumulation. Only 165 and 52 chilling hours had accumulated at the New Kent nursery in 1983 and 1984,

respectively, prior to the cold storage of seedlings lifted in October. Almost 500 chilling hours had accumulated prior to the November lift-date in 1983 but less than 400 hours had accumulated in 1984 (Table 6).

It is not certain the number of chilling hours required by loblolly pine at the New Kent nursery (34°N latitude) to attain dormancy, but apparently between 400 and 500 hours are needed for subsequent satisfactory cold storage. Nurseries located further south may have to delay cold storage until mid-winter before enough chilling hours have accumulated. Ursic et al. (1966) and Ursic (1963) reported poor results if loblolly pine seedlings were stored prior to January in a southern Mississippi nursery.

The detrimental effect of cold storage on early-lifted stock has been attributed to a lack of physiological readiness for chilling in nondormant stock (Kramer and Rose 1985, Ritchie and Dunlap 1980, Stone and Schubert 1959b), the greater susceptibility to damage of incompletely suberized autumn roots, and higher root metabolism in the autumn (Carlson 1985, Kramer and Rose 1985). Kramer and Rose (1985) hypothesize seedlings need enough time in the autumn to accumulate sufficient food reserves to maintain physiological processes in order to tolerate cold storage.

Fully dormant seedlings can be successfully stored for many weeks. In the current study, loblolly pine seedlings lifted after November consistently retained their physiological quality even after 12 weeks of cold storage. The successful long term cold storage of dormant loblolly pine seedlings has been reported in other studies (Boyer and South 1985, Carlson 1984, Dierauf 1984; 1982; 1974, Williston 1974; 1965, Kahler and Gilmore 1961). Similar results have also been noted for Douglas-fir (Jenkinson and Nelson 1984, Ritchie and Stevens 1979, Hermann 1967) and other western conifers (McDonald et al. 1983).

EXPERIMENT III

Root Growth Potential Variation Among Half-Sib Families of Loblolly Pine Seedlings

Introduction

Over a billion bareroot pine seedlings are annually produced in southern United States nurseries (Boyer and South 1984). Subsequent plantation establishment with these seedlings is variable; and according to Weaver et al. (1981) and Venator (1981), survival rates have been decreasing since 1960. Jenkinson (1980) determined one of the keys to successful plantation establishment of western yellow pines is knowing when to lift seedlings from the nursery and when to plant them in the field. Different seed sources differ in their optimal lifting periods and "lifting windows" have been developed as a guide for lifting western yellow pines (Jenkinson 1980) and Douglas-fir (Jenkinson 1984, Jenkinson and Nelson 1978).

The lifting windows have been related to seasonal patterns of root growth potential (RGP) of different seed sources (Jenkinson 1980). Four typical RGP (the readiness to initiate and elongate new roots [Sutton 1980c]) patterns

described by Jenkinson (1975; 1980) include: a) an autumn RGP peak, b) mid-winter peak, c) RGP plateau from late-autumn through the winter, and d) a bimodal pattern with autumn and mid-winter RGP peaks.

Early reports by Beineke (1966) and Beineke and Perry (1965) showed a clear genetic relationship among loblolly pine progenies in their ability to be successfully transplanted as bare-root seedlings. They noted a strong positive relationship between transplantability and the ability of the progenies to regenerate new roots. However, this aspect of loblolly pine seedling regeneration was largely ignored until the recent research efforts of Carlson (1985) and DeWald et al. (1985b). Results of these studies support the earlier research of Beineke (1966) and Beineke and Perry (1965). In their discussion on southern pine regeneration research needs, Kramer and Rose (1985) stress a need for more work in seedling RGP. It was the objective of the research reported here to describe genetic variation in RGP among 14 half-sib families of 1-0 loblolly pine seedlings.

Materials and Methods

Seeds for the 1-0 loblolly pine seedlings used for the study were donated by the Virginia Division of Forestry (VDF) and were obtained from the seed orchard at their New Kent Forestry Center nursery, located in the Virginia Coastal Plain, near Providence Forge. Fourteen randomly selected half-sib families were used along with the bulked seed mix (containing an unknown number of half-sib families) used operationally by the VDF. All of the seed had been moistened and then stratified by VDF personnel in polyethylene bags at 1.7°C for 60 days.

The seeds were hand-planted on April 26, 1983 and on May 4, 1984 in a randomized complete block design in two adjacent seedbeds in 1983 and in one contiguous seedbed in 1984 at the New Kent nursery. Each seedlot (half-sib family) in every block was represented by one row of 40 seeds, planted at an approximate 2 cm spacing. A border edge of 10 bulked VDF seeds was planted at both edges of every row, and a buffer of 10 rows of bulked VDF seed was planted between each block.

All of the seedlings were grown operationally at the nursery, being regularly irrigated throughout the growing season, and top-pruned by VDF personnel on August 10, 31, and September 20, 1983, and on August 1, 20 and September 19

in 1984. Air temperature was continuously monitored by a hygrothermograph in a weather station positioned 46 m from the end of the nursery beds containing the seedlots. Chilling hours were based on the loblolly pine results of Garber (1983; 1978) and were calculated from the hygrothermograph data as the number of hours in the nursery between 0 and 8°C.

On May 26, 1983 there were heavy rain storms accompanied by hail which caused flooding and considerable damage to the seedlings. Poor germination in some of the seedlots in conjunction with the weather damage necessitated combining the 8 field blocks into 4 blocks in order to have an adequate number of seedlings for the 1983-84 study. High survival in 1984-85 enabled the use of all 8 nursery blocks.

On each lift-date seedlings were excavated by hand with a shovel and immediately placed in double-layered polyethylene bags. In 1983-84 two randomly selected blocks were lifted and the same seedlots combined on October 25, November 22, February 2, and March 13. In 1984-85 one nursery block was randomly chosen to be lifted on each of the following dates: October 30, November 29, December 19, January 8, January 31, February 21, March 15, and April 8.

Following lifting, seedlings were transported in a styrofoam cooler to the Virginia Tech campus, Blacksburg

Virginia, where the root systems were pruned to 12 cm below the root collar and any new white roots removed. Four seedlings per family were then randomly assigned to each of seven 37.8 liter aquariums and grown hydroponically in a greenhouse for 15 days, under a 16-hour photoperiod, and temperature regime ranging from 16 to 27°C. In addition, 0.5 g of 20-20-20 (nitrogen-phosphorus-potassium) was added to each aquarium. Greenhouse temperatures were monitored throughout the study with a hygrothermograph.

After 15 days of hydroponic growth the seedlings were carefully removed and the following shoot and root variables were measured on each seedling:

1. height from the root collar to the severed tip of the stem (nearest cm)
2. amount of new shoot elongation (nearest cm)
3. root collar diameter (nearest 0.1 mm)
4. shoot activity (used to estimate the dormancy intensity parameter described by Ritchie [1984]) was assigned a rating based on the level of visually detectable activity:
 - a) none apparent
 - b) swollen or elongated buds (terminal bud if present or bud within top needle fascicle)
 - c) stem elongation just beginning
 - d) measurable stem elongation
 - e) elongating needles
5. seedling dry weights (measured only in 1984-85)

- a) total shoot dry weight (nearest 0.01 g)
 - b) needle dry weight (nearest 0.01 g)
 - c) stem dry weight (nearest 0.01 g)
 - d) total root dry weight (nearest mg)
 - e) lateral root dry weight (nearest mg)
 - f) taproot dry weight (nearest mg)
6. total number and length (nearest cm) of lateral roots
- a) elongated primary lateral roots
 - b) non-elongated primary lateral roots
 - c) elongated secondary lateral roots
 - d) non-elongated secondary lateral roots.

Primary lateral roots were defined as roots attached directly to the taproot. Secondary roots were lateral roots attached to primary lateral roots. Seedlot size and bud activity variation were measured to quantify variation among the seedlots that might influence RGP variation.

The RGP data collected included total number and length (nearest cm) of new short roots (those 0.5-1.5 cm in length) and new long roots (those >1.5 cm long) of seven different types of new roots. New root type was based on site of attachment to the old root and included those originating directly from the end or from a site other than directly from the end of either a primary or secondary lateral root, new roots arising from the sides of other new roots, and new roots arising directly from the taproot.

The experiment was arranged as a randomized complete block design with blocks nested within lift-date. For each of the lift-dates there were 7 blocks (aquariums) each containing plots of 4 seedlings per half-sib family nested within lift-date. Differences in root regeneration due to lifting date and genetic origin were analyzed using analyses of variance, correlation analyses, and regression analyses (SAS Institute Inc. 1985). In addition, cluster analysis (SAS Institute Inc. 1985, Tryon and Bailey 1970) which multivariately places individuals which respond similarly into groups, was used to group seedlots which had similar RGP values for each lift-date and similar RGP changes among lift-dates. The significance level used for all of the above tests was $\alpha=0.05$.

The nested block effect in the analyses was nonsignificant and was included in the error term. All subsequent analyses were based on 7 replicates of plot means of $n=4$. Most interactions were significant, and subsequent analyses were used to test main effects separately. Seedlings lifted on January 31, 1985 were excavated from partially frozen soil at the nursery. Despite extreme care during lifting considerable injury occurred to the root systems and RGP results were subsequently very poor. Consequently, data from this lift-date were removed from all analyses.

An estimate of block location variation was made in April 1985 by hand-lifting bulked VDF seedlings from the centers of the border rows for each nursery block containing seedlots, and then these blocks were statistically compared following the same root regeneration tests the seedlots had undergone. Subsequent statistical comparisons of these nursery blocks revealed no significant differences among blocks for any of the variables measured. It was, therefore, assumed that any nursery block effect and the resulting confounding effects with lift-date were minimal. In addition, correlations between greenhouse temperatures and RGP were very low and nonsignificant. Therefore, it is assumed any temperature changes in the greenhouse environment over time had a minimal effect on seedling RGP.

Half-sib family heritabilities were determined for total number, total length, and number and length of the different types of new roots for data showing significant seedlot variation in the analyses of variance. Heritabilities were calculated as four times the intraclass correlations, which were based on the ratios of family variance to total variance (Falconer 1983) from the analyses of variance. Plot means were not used in these analyses of variance. Estimates were calculated separately for each lift-date due to significant seedlot X lift-date interactions. Standard

errors of the heritabilities were calculated using the formula of Falconer (1983) for the intraclass correlation variance:

$$\frac{2[1+(n-1)t]^2(1-t)^2}{n(n-1)(N-1)}$$

where: t = intraclass correlation
 N = number of half-sib families
 n = number of individuals per family

Results

Seedlot Size.

Seedling size varied among seedlots but all of them increased significantly in size in the autumn. The only size variable which showed a spring decrease was needle dry weight. Size variation among seedlots was random among years and lift-dates, and had no relation to seedlot differences in RGP.

Bud Activity.

Bud activity varied significantly among seedlots only in October and February; the differences were caused by delays in budset (October) and/or budburst (February). Bud activity among different seedlots was consistent among lift-dates and years, although all seedlots tended to set bud later and flush earlier in 1983-84. In 1983-84 all but approximately one-quarter of the seedlings per seedlot were

dormant by the October lift-date. In 1984-85 only half of the seedlings had ceased activity by the this time. The seedlings had been exposed to 165 chilling hours in the nursery by the end of October in 1983 but only 52 in 1984. In November, 500 and 465 chilling hours had been received by the seedlings in 1983 and 1984, respectively, (see Table 3 for chilling hour accumulation) and in both years all seedling bud activity had ceased by this time.

Budburst and shoot elongation during the RGP tests was observed in late-January and early February on all seedlings in 1983-84 but only on approximately half of the seedlings per seedlot in 1984-85. The seedlings had been exposed to over 1700 chilling hours by this time in 1983-84 and to over 1500 in 1984-85. Nearly all seedlings had measurable shoot elongation following their RGP tests in late-February and many had needle growth as well. Shoot elongation varied among seedlots in the spring; some seedlots had greater shoot elongation in March but less in April, while the reverse was true for other seedlots. These differences in bud activity and shoot elongation among seedlots were not related to changes in their RGP.

Lateral Root Elongation.

Variation in percentage of elongating lateral roots among lift-dates generally paralleled RGP variation. Variation

among seedlots ranged only 10 to 25 percent for elongating primary lateral roots in the winter (RGP was high), and 0 to 15 percent in the autumn and spring (RGP was low). Comparable figures for elongating secondary lateral roots are 15 to 40, and 10 to 30 percent, respectively. The lift-date X seedlot interaction was not significant for percentage of elongating primary or secondary lateral roots.

When the relative rankings of percentage elongating lateral roots on a seedlot are compared to seedlot RGP rankings, some seedlots with high RGP also had a relatively high percentage of elongating roots. However, approximately half the seedlots had RGP either greater or less than expected relative to their percentage of elongating roots. Rank correlations between the number of new roots and percentage elongating primary lateral roots generally decreased until the spring, while correlations with percentage elongating secondary roots increased (Table 7). In the spring, rank correlations for percentage elongating primary and secondary lateral roots increased and decreased, respectively. Rank correlations in March 1984 and February 1985 were not significant.

Root Growth Potential.

All new root variables varied significantly among years, seedlots, lift-dates, and seedlot X lift-date combinations.

Table 7. Loblolly pine seedlot rank correlations between percentage of lateral roots elongating and root growth potential.

Lift-Date	Root Growth Potential	Percentage of Roots that Elongated:	
		Primary Laterals	Secondary Laterals
New Root Number			
1983-84			
October		0.64	0.80
November		0.67	0.73
February		0.66	0.62
March		0.47 (ns) ¹	0.95
1984-85			
October		0.83	0.59
November		0.83	0.87
December		0.70	0.82
January		0.77	0.74
February		0.34 (ns)	0.93
March		0.76	0.65
April		0.72	0.87
New Root Length (cm)			
1983-84			
October		0.63	0.86
November		0.72	0.61
February		0.67	0.52
March		0.48 (ns)	0.84
1984-85			
October		0.84	0.57
November		0.79	0.86
December		0.72	0.81
January		0.81	0.72
February		0.35 (ns)	0.90
March		0.76	0.54
April		0.73	0.86

¹Correlation not significant ($\alpha=0.05$).

Seedlot means for total numbers and lengths of new roots for each lift-date are listed in Tables 8 and 9.

In 1983-84 most seedlots had their greatest RGP in early February, although March values were usually also high. In 1984-85 the greatest RGP values for all seedlots were recorded at the mid-February lift-date (Tables 8 and 9). In general, the RGP measured in February and March was significantly greater than RGP in the autumn and April. October RGP values were significantly lower than all other lift-dates both years.

Most seedlots had consistent relative RGP both years. However, in the spring seedlots K14-66 and F511 (length only) increased in rank while K531 and S526 (number only) decreased in rank in 1983-84 compared to 1984-85. These changes between the two years resulted in a significant seedlot X year interaction for the March lift-date.

Although in 1983-84 all seedlots produced relatively low lengths of new roots in November, the number of new roots produced by half of the seedlots (F511, G506, JJ4-17, K14-66, K531, S526, VDF) was as great or greater than in February and/or March. The other seedlots, which generally had lower RGP in November, had March and February RGP values approximately equal to each other (Tables 8 and 9).

Table 8. Seedlot mean number of new roots for each lift-date in 1983-84 and 1984-85.

Seedlot	Cluster Number ¹	Lift-Date										
		1983-84				1984-85						
		10/25	11/22	2/2	3/15	10/30	11/29	12/19	1/8	2/21	3/15	4/8
AA18-5	1	0.21	2.71	6.54	5.25	2.29	3.46	4.96	4.04	9.68	5.96	3.00
BB536	1	0.39	5.89	7.61	7.32	2.21	3.00	5.12	5.89	11.07	6.93	3.50
D14-15	2	--	--	--	--	--	--	--	--	--	--	--
E512	2	0.14	5.89	9.50	5.64	2.79	8.37	7.93	8.68	18.68	8.36	3.96
F511	1	0.35	4.89	6.96	4.39	2.75	4.21	4.59	5.92	11.83	7.29	4.25
G506	1	0.36	4.07	7.18	6.82	3.04	4.46	4.25	5.57	10.89	6.86	2.93
H508	1	0.36	4.07	7.18	6.82	3.36	3.50	7.79	5.71	12.96	8.25	2.89
H540	3	1.14	7.79	9.50	10.39	3.79	5.82	6.89	8.32	12.89	10.46	5.39
J2-8	3	--	--	--	--	3.93	5.79	5.29	7.57	14.00	9.46	5.46
JJ4-17	3	0.50	7.15	7.00	11.79	--	--	--	--	--	--	--
K531	3	0.68	6.64	7.14	11.11	1.96	4.75	5.29	6.43	14.75	8.11	4.50
K14-66	3	0.36	6.93	10.25	7.25	5.32	6.86	7.46	12.64	15.11	10.93	4.32
L517	2	0.64	4.74	9.43	7.71	--	--	--	--	--	--	--
P5-21	--	--	--	--	--	2.52	6.25	5.43	8.29	17.29	8.36	4.14
R523	3	0.36	6.00	9.93	9.68	3.68	5.36	6.33	7.89	18.14	9.07	6.21
S526	2	0.29	7.39	6.79	7.78	2.66	4.67	3.93	5.25	11.93	6.79	2.93
S529	4	0.68	9.25	18.36	13.42	7.29	7.36	12.07	13.71	26.07	12.29	9.75
U546	2	0.21	6.50	9.46	8.71	--	--	--	--	--	--	--
VDF	1	0.32	5.96	5.32	6.57	3.29	5.04	5.25	7.43	10.61	5.93	5.08
Lift-Date Mean		0.44	6.12	8.73	8.25	3.38	5.26	6.17	7.56	14.39	8.34	4.55
Standard Deviation ²		0.61	2.94	4.37	4.68	2.65	2.73	3.02	3.72	5.93	3.05	2.47

¹Cluster number refers to cluster group in Figure 9.

²Based on 7 plot means (n=6) per seedlot.

Table 9. Seedlot mean length of new roots for each lift-date in 1983-84 and 1984-85.

Seedlot	Cluster Number ¹	Lift-Date 1983-84				Lift-Date 1984-85						
		10/25	11/22	2/2	3/15	10/30	11/29	12/19	1/8	2/21	3/15	4/8
AA14-5	1	0.21	3.11	13.25	10.50	2.39	6.14	5.96	4.96	16.54	8.64	3.96
BB536	1	--	--	--	--	2.21	3.21	6.08	6.71	17.21	9.96	4.89
D14-15	1	0.39	7.54	13.39	15.39	--	--	--	--	--	--	--
E512	2	--	--	--	--	2.96	9.79	8.82	9.68	26.14	11.14	4.93
F511	2	0.14	7.15	21.95	9.61	2.93	5.07	5.19	7.00	18.17	10.00	7.07
G506	2	0.38	6.48	15.93	8.46	3.21	5.00	5.29	6.64	18.21	8.61	4.32
H508	1	0.36	4.67	15.21	13.36	3.68	3.68	9.11	6.50	22.07	11.46	3.18
H540	3	1.14	10.32	19.07	17.86	4.36	6.89	8.18	10.14	17.86	14.54	7.39
J2-8	3	--	--	--	--	4.04	6.61	6.29	8.96	23.18	15.21	7.64
JJ4-17	3	0.50	8.50	12.11	19.36	--	--	--	--	--	--	--
K531	3	0.68	7.61	13.86	19.54	2.14	5.32	6.21	7.86	23.00	11.04	6.18
K14-66	2	0.36	8.29	21.50	13.57	5.86	7.82	9.25	14.39	23.63	14.50	6.04
L517	2	0.68	5.21	17.04	13.11	--	--	--	--	--	--	--
P5-21	2	--	--	--	--	2.52	7.32	6.25	9.54	25.86	11.07	5.89
R523	3	0.36	7.41	20.79	18.18	3.79	6.07	7.30	9.04	31.18	12.71	8.61
S526	2	0.29	9.79	16.25	12.22	2.75	5.67	4.36	6.36	19.64	9.79	4.25
S529	4	0.71	12.07	33.82	22.25	8.32	8.21	14.86	15.21	39.50	17.39	11.89
U546	3	0.21	7.18	16.71	15.11	--	--	--	--	--	--	--
VDF	1	0.32	7.30	10.36	11.82	3.50	5.54	5.93	8.46	16.00	7.46	6.37
Lift-Date Mean		0.45	7.51	17.42	14.69	3.64	6.02	7.27	8.76	22.55	11.57	6.17
Standard Deviation ²		0.64	3.97	8.86	9.04	3.04	3.49	3.77	4.33	9.64	4.74	3.28

¹Cluster number refers to cluster group in Figure 10.
²Based on 7 plot means (n=4) per seedlot.

In 1984-85 relative RGP changes among seedlots over time were similar. However, while half of the seedlots had similar RGP in November, December, and January (H540, J2-8, K14-66, K531, P521, R523, VDF) other seedlots had relatively high RGP in mid-January compared to their RGP the previous two lift-dates. In addition, seedlots BB536, H508, and S529 had relatively poor RGP in November, 1984 compared to their maximum RGP. The rates of increase toward the maximum RGP value attained varied slightly among the seedlots. Most seedlots had reached only 50 percent of their maximum RGP by January but H540, K14-66, and VDF were within 30 percent of their maximum new root number and within 40 percent of their maximum new root lengths (Tables 8 and 9). In addition, these latter three seedlots had relatively broad RGP peaks, increasing toward their maximum sooner and decreasing less in March compared to other seedlots.

Other differences were noticeable in the magnitude of the spring RGP drop. The RGP of half of the seedlots in the spring (particularly for new root number) dropped below levels prior to their peak. Other seedlots also showed decreased RGP in March but only to levels as high or higher than in the autumn and winter. In addition, the RGP of seedlots AA14-5, BB536, F511, G506, H508, H540, J2-8, and K14-66 decreased only to levels approximately 30 to 40

percent of their maximum RGP values in the spring, while the RGP of the remaining seedlots decreased to values less than 40 percent of their maximum values.

Figures 9 and 10 illustrate results of the cluster analyses which multivariately placed seedlots into four groups based on their RGP relative to each lift-date mean. The R^2 values for these analyses were all greater than 0.80. The clusters formed for total number varied slightly from those formed for total length (Tables 8 and 9). Cluster Group 1 (Figures 9 and 10, Tables 8 and 9) contained seedlots whose RGP was generally at least 15 percent lower than each lift-date mean, while Group 4 contained only seedlot (S529) which had an RGP generally greater than 50 percent of each lift-date mean.

Cluster Groups 2 and 3 were similar but separated by seedlots in Group 2 which generally had means equal to or less than the overall mean for the October and March lift-dates, while RGP values of Group 3 seedlots were generally greater than the lift-date mean at these times. In the late-winter the reverse was true, with Group 3 seedlot RGP greater than the overall lift-date mean while Group 2 seedlot RGP was less than the lift-date mean.

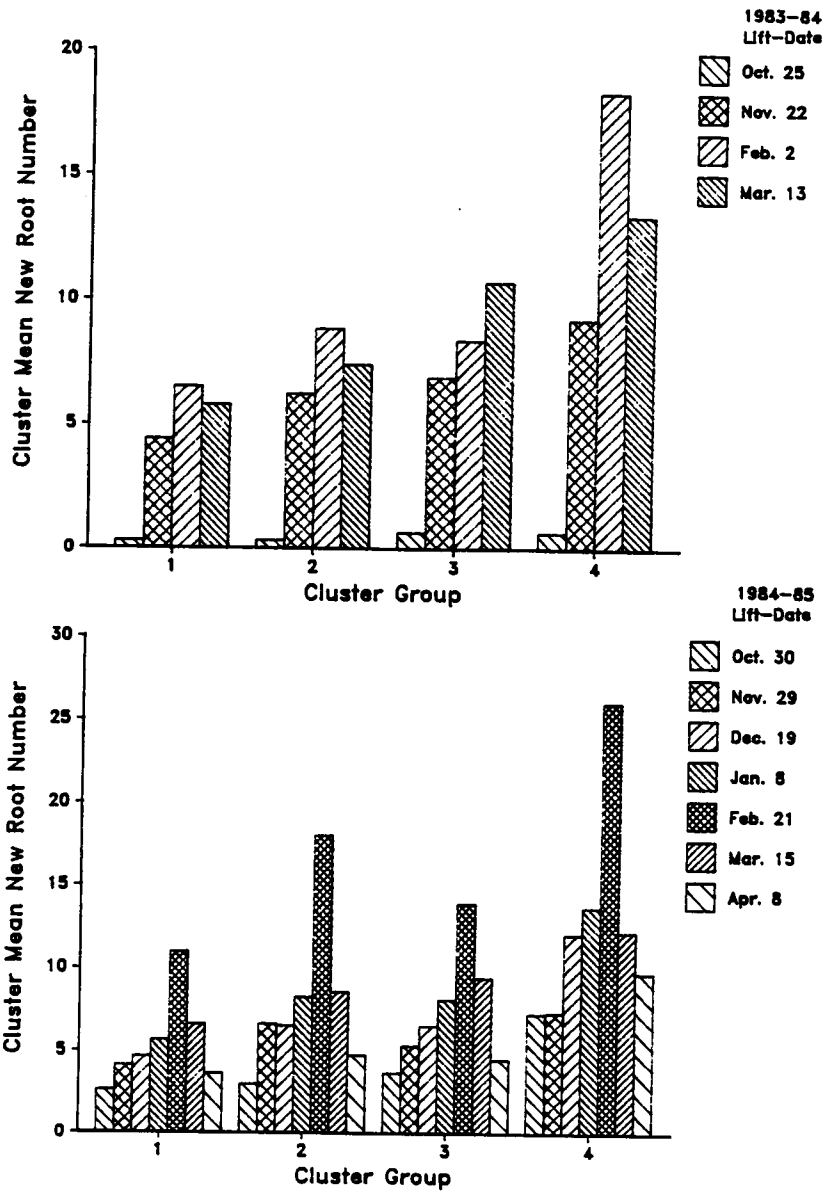


Figure 9. Mean new root number variation among lift-dates in 1983-84 and 1984-85. (Seedlots included in each cluster are listed in Table 8.)

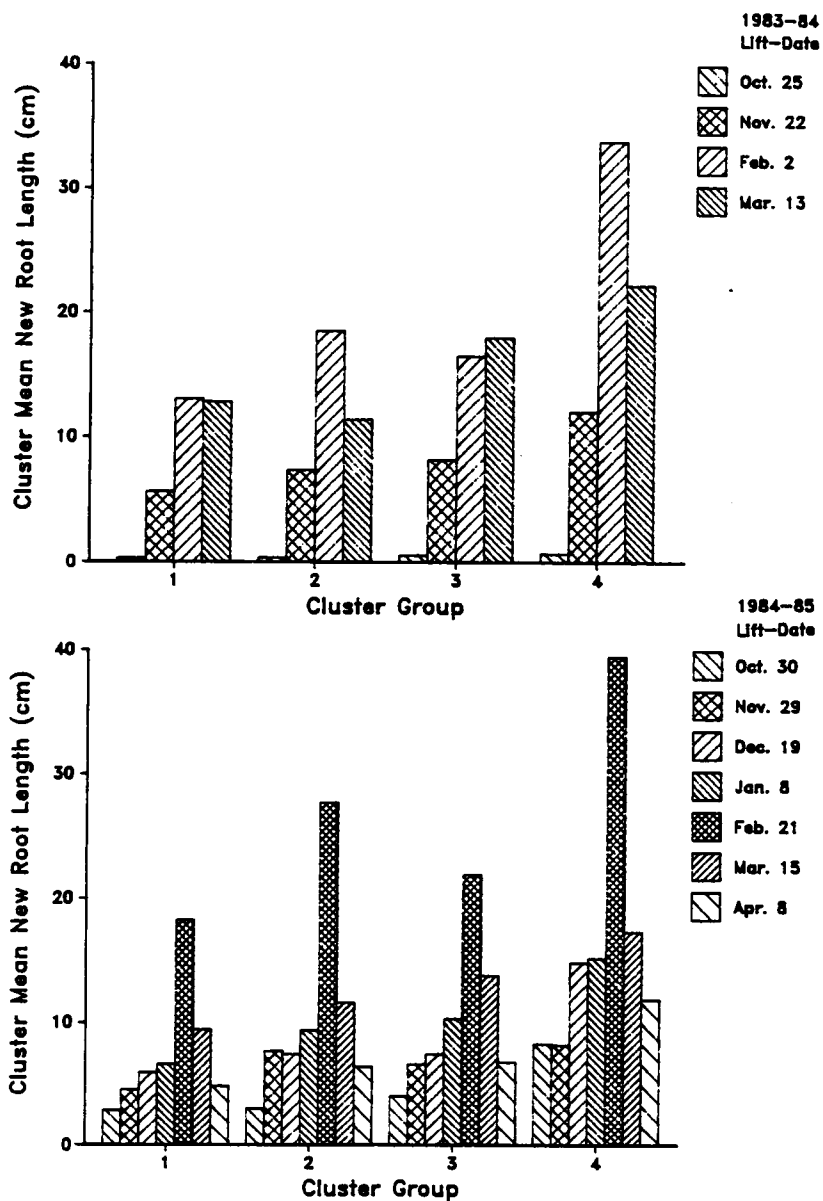


Figure 10. Mean new root length variation among lift-dates in 1983-84 and 1984-85. (Seedlots included in each cluster are listed in Table 9.)

New Root System Morphology.

The percentages of new root number and length comprised of short roots (those 0.5-1.5 cm) were consistent among seedlots, lift-dates, and years. On a per lift-date basis, and seedlots varied significantly from each other only in February, 1985 and the differences in percentage of new short roots averaged only 14 percent. The average 1984-85 values were 22 percent greater than 1983-84. Less than half the seedlots showed significant variation over time, generally the percentage of short roots was greatest in the late-autumn and early winter (>70 percent for number, >60 percent for length), and lowest (although still greater than 50 percent) in October and after January.

None of the seedlots produced new roots directly on the taproot; however, lift-date, seedlot, and year varied significantly for all other new root types. Years differed significantly due to greater RGP of most new root types in 1984-85 in October, but less in November compared to 1983-84. Greater than 90 percent of all new root numbers and lengths were comprised of roots originating directly from the ends of primary and secondary lateral roots. Changes in numbers and lengths of these two new root types followed patterns similar to total new root number and length.

New roots originating on lateral roots at sites other than directly from the ends were present in low amounts (less than 10 percent) for all lift-dates except October, where none of these types were produced. New roots originating on secondary lateral roots were present on all seedlots only in the spring. New roots originating from other new roots generally occurred only in the late-winter and early spring when RGP was relatively high, and they were present in amounts less than 5 percent. Seedlot variation was significant only in the late-winter for both of these types of new roots.

Most of the time seedlots had either a greater (>60 percent) or equal percentage of new roots originating from primary versus secondary lateral roots. However, in the late-winter, when RGP was high, this pattern was reversed for over half the seedlots. This shift caused a significant seedlot X lift-date interaction. In the spring the ratio of new roots elongating from primary versus secondary lateral roots returned to 60:40. In addition, new roots originating from new roots on primary lateral roots were more common than these root types on secondary lateral roots.

On a per lift-date basis, seedlots S529, K14-66, P5-21, R523, E512, and H540 had relatively higher amounts of new roots originating on the sides of primary lateral roots.

These seedlots also tended to have relatively higher amounts of new roots attached to these new root types. Seedlots H508, R523, S529, and K531 had relatively higher amounts of new roots originating from the sides of secondary roots than other seedlots.

Heritability values for RGP and the different types of roots are listed in Table 10. Values were highest in the late-winter and also were relatively high in the spring. Heritability values were lowest in the autumn. Values were consistent for total numbers and lengths of new roots, although values were generally greater for total number. Heritabilities for the different types of roots followed the same temporal pattern as total new root numbers and lengths. However, only new roots originating directly from the ends of lateral roots had heritability values greater than 0.10. Heritabilities of new roots originating directly from the ends of secondary lateral roots were particularly high, and occasionally greater than those for total new root number and length.

Discussion

The overall RGP seasonal pattern was consistent with previous reports for loblolly pine (Carlson 1985, Feret et al. 1985a, Rhea 1977, Brissette and Roberts 1984) as well as

Table 10. Half-sib family heritability values for loblolly pine seedling new root systems.¹

New Root Origin	Lift-Date 1983-84		Lift-Date 1984-85								
	10/25	11/22	2/2	3/15	10/30	11/29	12/19	1/8	2/21	3/15	4/8
----- Number of New Roots -----											
Directly from the end on a:											
Primary Lateral Root	ns ²	0.30	0.11	0.24	0.25	0.22	0.32	0.40	0.28	0.29	0.19
Secondary Lateral Root	ns	0.20	0.55	0.39	0.37	0.28	0.63	0.72	0.65	0.25	0.70
From other than the end on a:											
Primary Lateral Root	ns	ns	0.26	ns	ns	ns	0.12	ns	0.32	ns	ns
Secondary Lateral Root	-- ³	ns	ns	0.18	--	ns	ns	0.11	0.07	ns	0.10
From a New Root on a:											
Primary Lateral Root	--	ns	ns	ns	--	--	--	--	--	ns	ns
Secondary Lateral Root	--	--	ns	ns	--	--	--	--	--	0.24	--
Total New Root Number	ns	0.30	0.50	0.37	0.40	0.33	0.69	0.77	0.74	0.25	0.67
----- Length of New Roots -----											
Directly from the end on a:											
Primary Lateral Root	ns	0.36	0.16	ns	0.31	ns	0.39	0.29	0.22	0.32	0.19
Secondary Lateral Root	ns	0.20	0.44	0.36	0.38	0.30	0.58	0.66	0.50	0.27	0.59
From other than the end on a:											
Primary Lateral Root	ns	ns	ns	ns	ns	ns	0.09	ns	0.25	ns	ns
Secondary Lateral Root	--	ns	ns	0.18	--	ns	ns	0.11	ns	ns	0.10
From a New Root on a:											
Primary Lateral Root	--	ns	ns	ns	--	--	--	--	--	ns	ns
Secondary Lateral Root	--	--	ns	ns	--	--	--	--	--	0.24	--
Total New Root Length	ns	0.34	0.35	0.22	0.44	0.28	0.69	0.62	0.55	0.25	0.49

¹Standard errors ranged from ±0.03 to ±0.05.
²Seedlot variation was not significant (α=0.05).
³No new roots of this type were produced.

with other species such as Douglas-fir (Ritchie and Stevens 1979, Jenkinson and Nelson 1978, Krugman et al. 1965, Winjum 1963, Stone et al. 1962) and ponderosa pine (Stone and Norberg 1979, Jenkinson 1977, 1975, Krugman and Stone 1966, Krugman et al. 1965, Stone and Schubert 1959a; b; c). As in other studies (Cannell 1985, Ritchie and Dunlap 1980, van den Driessche 1977), the interaction of the seasonal loblolly pine RGP pattern with shoot phenology was evident; low autumnal RGP during the cessation of bud activity, RGP increased with accumulating chilling hours, and RGP decreased in the spring coinciding with renewed shoot activity. In addition, other types of root activity (percentage of roots elongating, percentage of new short roots and variety of types of new roots) were low in the autumn during the accumulation of shoot and root biomass, while root activity and diversity of new root types were high at the RGP peak and in the spring.

In contrast to the distinctive seed source dependent RGP patterns reported for ponderosa pine (Jenkinson 1980; 1975) and Douglas-fir (Jenkinson 1984, Jenkinson and Nelson 1978), there appeared to be only subtle differences among RGP patterns of the loblolly pine seedlots. The few differences in the date of the RGP peaks in 1983-84 (Figures 9 and 10) were likely due to the fact that the sampling dates missed

the actual peak. Data for bulked VDF 1983-84 seedlings indicated the peak occurred at the end of February, which was not sampled with 1983-84 seedlots. In 1984-85 the peak for bulked VDF seedlings occurred in late-February (Figures 2 and 3) which was when maximum RGP was recorded for all the 1984-85 seedlots.

Jenkinson (1975; 1980) reported the main differences among seed source RGP patterns were the onset and rate of RGP increase, duration of the peak, and time of spring RGP decrease. The loblolly pine results indicate some differences among the seedlots in these factors. The three seedlots with relatively less difference between their RGP peak and RGP values on either side of the peak may have broader RGP peaks, resulting from earlier increases toward the peak, and later (or slower) decreases from the peak than other seedlots. The difference in percentage drop from the RGP peak among the seedlots could also indicate differences in the time of RGP decrease.

Jenkinson (1984) also reported a three month difference in the opening and closing of lifting windows, although two-thirds of the 51 sources had open windows by December. Only three of the loblolly pine seedlots in the current study appeared not to be ready to be lifted in November. However, this should be interpreted with caution since the

storability of bulked VDF seedlings varied among years when lifted in November depending on the chilling hours received (Figures 5, 6, 7, and 8). All of the seedlots appeared suitable for lifting through mid-March, although depending on the amount of spring RGP decrease some seedlots are perhaps less suitable for spring lifting relative to others.

It is difficult to determine if the variability in RGP patterns is due to actual differences in responses to the environment, or to differences in absolute levels of RGP variability ranges among the seedlots unrelated to overall seasonal patterns. Jenkinson (1984) reported strong correlations between RGP and latitude and elevation combinations (and thus environmental and phenological differences) of the seedlot origins. In the current study, variability in bud activity and shoot elongation were unrelated to RGP variability among the seedlots. Carlson (1985) also reported no relation between loblolly pine dormancy release and RGP rank of half-sib families despite the fact that Coastal Plain seed sources required less chilling than those from the Piedmont Plateau.

Beineke (1966) found differences among seedlots in their time of budburst were unrelated to their transplantability, and Saranthus (1968) reported bud swell and elongation to occur within a 7 day period in his loblolly pine provenance

test in Louisiana. Therefore, the lack of variation in RGP patterns among loblolly pine seedlots compared to western species may be due to the relative uniformity in the environment of origin and uniformity of phenology. An alternative hypothesis is that there are larger differences in RGP seasonal variation among half-sib loblolly pine families but the sample of only 14 seedlots was too small to detect them.

Differences in the absolute levels of RGP illustrated by the cluster analyses are perhaps more important than the small seasonal pattern differences. There was a great deal of difference in absolute RGP levels among the seedlots, most of it associated with the level of the RGP peak. Total RGP and the major types of new roots produced were highly heritable. In addition, the relative constancy of the types and percentage of short new roots produced suggests the major difference between seedlots with poor versus seedlots with high RGP appeared to be the ability to produce more new roots at more sites on the old roots; seedlots which could produce new roots on the sides as well as directly on the ends of old roots generally had the greatest RGP values.

Campbell and Sorensen (1984) suggested if RGP varies genetically, then field mortality due to low RGP is likely to favor some genotypes over others. Beineke (1966) and

Beineke and Perry (1965) reported a relation between root regeneration to transplantability, and Beineke (1966) reported that most seedlots were consistently good or poor survivors on all lift-dates. In addition, more recent results with loblolly pine seedlots (DeWald et al. 1985b) showed 59 percent of the first-year height increment and 28 percent of second-year height increment variation among half-sib families of loblolly pine could be explained by their RGP differences. These early height differences are important to the ability of seedlings to dominate competing vegetation (Burdett et al. 1983).

If differences in absolute RGP levels result in preferential survival and height growth in the field, losses other than seedlings are likely occurring. Not only is the genetic variation in the plantation being decreased, but there is a potential loss of the best of other attributes. Beineke (1966) reported that the poorest progeny came from the seed of one of the best phenotypes. Seedlots with desirable traits but poor RGP should perhaps be used only in containerized seedling systems. In addition, selection for transplanting success should be considered (Kramer and Rose 1985, Beineke 1966) or at least screening for transplanting success should be incorporated into improvement programs.

SUMMARY AND CONCLUSIONS

Loblolly pine seedling RGP changed significantly in the nursery from September to April. The pattern of variation over time was typical of RGP variation for many other species; RGP was low in the autumn, increased in the early winter to a late-February peak, and then RGP decreased. This pattern was constant among years and among seedlots of loblolly pine. The only difference in this RGP pattern among seedlots appeared to be in the rate of increase to, and decrease from, the late-winter RGP peak. However, only a small number of seedlots were tested, and greater differences may in fact exist. If this is true, then the practice of bulking all seedlots in the nursery prevents the nursery manager from being able to use these differences. Seedlots with RGP patterns which increase faster toward the peak may be appropriate for earlier lifting in the autumn, and these seedlots may be more suitable for earlier cold storage. Conversely, it may be important to lift seedlots with rapid RGP decreases earlier than seedlots with less rapid RGP spring decreases.

The constancy of RGP patterns among years and seedlots is not surprising since RGP changes appear to be regulated by seedling metabolic events associated with shoot phenology rather than by environmental changes. All of the seedlots had similar phenology, and this may have contributed to the lack of difference among overall RGP patterns. In the early autumn overall seedling biomass is still increasing at a rapid rate, and shoot metabolism is high until the shoots become quiescent. Seedlings are sensitive to disturbance at this time and will generally have poor RGP. In addition, loblolly pine seedlings placed in cold storage at this time will not store well, even for short periods of time. As the autumn progresses chilling hours accumulate, seedling shoots become quiescent, energy is directed toward RGP, and RGP rises. If enough chilling hours have accumulated, seedlings can also be successfully cold-stored. The exact number of chilling hours needed at the New Kent nursery before seedlings can be satisfactorily cold-stored could not be determined from this study, but it appears to be between 400 and 500 hours of air temperatures between 0 and 8 °C.

Seedling RGP continues to rise from the late-autumn throughout the winter both in the nursery and in cold storage, until late-February when it peaks. The RGP peak coincided with the point where measurable shoot elongation

was beginning in the RGP tests, and then RGP subsequently decreased as metabolic energy was directed to renewed spring shoot growth. Seedlings removed from cold storage at this time had slightly delayed phenology compared to fresh-lifted seedlings, but RGP still tended to decrease. This may indicate cold storage might not be useful at extending the lifting season. However, spring cold storage results between years and RGP test systems were slightly variable, and more research is needed in this area before more definite conclusions and recommendations can be made.

The major RGP differences among half-sib families and among years were absolute levels of RGP. Seedling RGP in 1984-85 was much greater than in 1983-84, particularly at the peak. Similarly, some seedlots had much greater RGP regardless of the lift-date. Although specific statistical comparisons between size and RGP were not made, the differences in absolute RGP levels may be related to numbers and lengths of lateral roots. The 1984-85 root systems were larger than in 1983-84, and some seedlots also had large root systems. The data collected for all three experiments will subsequently be used to more thoroughly examine this possible root-size-RGP relationship on a per seedling basis. Not all of the differences in absolute RGP among seedlots was related to root size. Some seedlots with high numbers

and lengths of roots had relatively poor RGP and vice versa. Seedlots with higher RGP could produce more new roots on a given length of old root.

The new root systems were primarily composed of roots elongating directly from the ends of lateral roots. The winter RGP increase was accompanied by an increase in the types of new roots produced, primarily increases in new root initiation (new roots arising from the sides of lateral roots). This diversity was maintained in the spring, despite the RGP decrease. Therefore, it appears when seedling metabolism is high, both root elongation and initiation can occur, but when metabolism is low, root elongation primarily contributes to new root systems. In addition, half-sib families with low RGP had less new root initiation regardless of the lift-date. Cold-stored seedlings produced new root systems similar to fresh-lifted seedlings in terms of root initiation versus elongation. Therefore, cold storage does not appear to alter the manner in which new roots can be produced.

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