ROOT GROWTH POTENTIAL AND OUTPLANTING PERFORMANCE OF LOBLOLLY PINE SEEDLINGS RAISED AT TWO NURSERIES

by

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Thesis submitted to the Faculty of the
Virginia Polytechnic Institute and State University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

in

Forestry

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January, 1987
Blacksburg, Virginia

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(ABSTRACT)

Root growth potential (RGP) is the measure of seedling ability to grow new roots. Loblolly pine (Pinus taeda L.) seedlings from 5 seedlots were raised at two widely separated nurseries (Summerville, SC and New Kent, VA). In Experiment I, RGP was determined during the fall and winter of 1984-85 and 1985-86, and several morphological traits were measured. In Experiment II seedlings from the same seedlots were lifted during February 1985 and 1986 at both nurseries, and cold stored until subsequent outplanting; subsamples of outplanted seedlings were used for RGP determinations.

Root growth potential varied significantly by family, nursery, and lift date, and first order interactions were significant. Generally, the RGP of Summerville raised seedlings was higher than that of New Kent raised seedlings. RGP was not strongly correlated with common measures of shoot morphology, but RGP was consistently well correlated with lateral root dry weight.

In Experiment II, RGP varied significantly by family, nursery, and storage duration. The family x nursery effect was the only significant interaction. Summerville raised seedlings had higher RGP on each planting date. During each year RGP declined rapidly in storage. First year survival was significantly correlated with RGP ($r = .52$, $p < .001$). Height increment and RGP were also strongly correlated ($r = .80$, $p < .001$). These relationships and their implications for nursery management were discussed.

ACKNOWLEDGEMENTS

I acknowledge the valuable guidance of my advisor, Dr. Peter P. Feret, in completing this endeavor. My committee members also provided valuable assistance: Dr's John R. Seiler and David W. Smith, and Mr. Richard E. Kreh. I thank the Westvaco Corporation for providing the seedlings and for financial assistance. Mr. I. Fred Trew of Westvaco coordinated logistical support during lifting and outplanting operations. I appreciated the assistance of Mr. Jack Bird who helped in RGP data collection, and the assistance of Mr. Richard Haught and Mr. John McKinley who helped measure outplanting performance.

Thank you to my parents for their moral support while I continued my studies. The largest share of my gratitude goes to my wife, Dianne, who has tolerated my time away from home, and who worked by my side many days in the lab counting roots and weighing seedlings, and in the field recording data.

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INTRODUCTION AND OBJECTIVES

The decreasing survival rate of planted loblolly pine (*Pinus taeda* L.) seedlings is a major concern in the South. In a survey conducted from 1960 to 1978, Weaver et al. (1980) reported that pine plantation survival had decreased, while the acreage planted had nearly doubled. It has been estimated that approximately 30% of planted seedlings die, and that much of this mortality is due to poor planting stock quality and improper handling procedures (Venator 1981). Since over 1 billion bareroot seedlings are planted yearly in the South (Boyer and South 1984, Johnson et al. 1982), high mortality represents a substantial economic loss.

During routine lifting operations, a seedling typically loses 75% of its root mass (Nambiar 1980). During operational root pruning to a 14 cm (5 1/2") taproot, the seedling's absorptive surface is further reduced. The size of a seedling's root system may not be critical for growth in the nursery environment, due to it being well supplied with water and nutrients (Nambiar 1980). However, after being lifted and losing most of its roots, a seedling is planted in the field and subjected to moisture stress and low levels of available nutrients. As a result, initial survival of outplanted seedlings depends to a large extent on the ability of the injured root system to rapidly grow and re-establish intimate contact with the soil (Kozlowski and Scholtes 1948).

Root growth potential (RGP) is defined as the ability of a seedling to regenerate its root system after planting in a controlled environment. RGP has been demonstrated to be positively correlated with survival and/or field performance in *Pinus* spp. (Feret et al. 1985a; b, Feret and Kreh 1985, Sutton 1980, Burdett 1979, Stone and Norberg 1979, Jenkinson 1978, Rhea 1977, Stone 1955), *Abies* spp. (Stone 1955), and *Picea* spp. (Sutton 1980). Burdett (1979) concluded that differences in RGP may account for the wide variations in survival among different sources of stock. In his work with lodgepole pine (*Pinus contorta* Dougl.), first year mortality increased exponentially with decreasing RGP values (Burdett 1979). Sutton (1980) found similar results with jack pine (*Pinus banksiana* Lamb), black spruce (*Picea mariana* Mill.), and white spruce (*Picea glauca* Moench.). In loblolly pine, as RGP levels increase, survival and first year height also increase (DeWald et al. 1985b, Feret and Kreh 1985, Feret et al. 1985a; b; 1984).

RGP has been used in assessing the onset of seedling dormancy, and its relationship to lifting dates, storage effects, and field performance (DeWald et al. 1985a, Jenkinson 1980, Stone 1971). The expression of RGP also has a strong genetic component. DeWald et al.(1985b) and Carlson (1985) both showed significant differences in RGP between half-sib loblolly pine families. RGP has also been found useful in evaluating seedling degradation during handling or storage (Feret et al. 1985b).

Kramer and Rose (1985) have noted a thorough evaluation of seasonal and genetic variation of southern pine RGP was needed, and concluded that progress towards improving and standardizing seedling quality would be accomplished through a better understanding of how RGP variation is related to shoot dormancy. DeWald's (1986) recent work has provided much needed information in this area. Further work on the RGP of loblolly pine seedlings will result in a more efficient manipulation of seedling physiology, resulting in seedlings with greater survival and growth potential.

With the above considerations in mind, two experiments were conducted. The objectives of experiment I were to:

1. Quantify root growth potential changes during the lifting season over 2 nurseries and 5 seedlots;
2. Relate seedling morphology to RGP;
3. Relate shoot dormancy and chilling hours to RGP.

The objectives of experiment II were to:

1. Quantify root growth potential changes during cold storage over 2 nurseries and 5 seedlots;

2. Determine the relationship between RGP and subsequent outplanting performance.

LITERATURE REVIEW

Seedling quality concerns

Recurring instances of poor survival of planted loblolly pines (*Pinus taeda* L.) have caused serious concerns in the South (Weaver et al. 1981, Xydias 1980). It has been estimated that 30% of planted seedlings die (Venator 1981). Causes of low survival are generally thought to include poor quality planting stock and improper handling during lifting, grading, storage, transportation, and planting. Also, adverse soil and weather conditions after planting can increase mortality.

Common recommendations to improve seedling quality are to decrease seed bed density, undercut beds before lifting, and more intensive culling at the nursery (Venator 1981). All of these practices substantially increase the cost of seedlings. Considering that 1.3 billion southern pine seedlings are raised annually in the South (Boyer and South 1984, Johnson et al. 1982), the economic impact of poor seedling survival can be very large.

Indicators of seedling quality

Usual indicators of seedling quality involve morphological attributes (root/shoot ratio, stem caliper, foliage color, and height), which are mostly fixed at the time of lifting from the nursery. South and Mexal (1984) state that the ideal seedling has a large caliper (>4mm) and a heavy root system (dry weight >0.8g). Other desirable morphological characteristics were shoot height less than 30 cm, a prominent terminal bud, mature secondary needles, and numerous lateral roots. Correlations between seedling size and survival have been mixed, due to strong interactions between size and site characteristics. On droughty sites smaller seedlings may outperform larger seedlings (Baker et al. 1979). Morphological measures may be useful for separating seedlings with a low capacity for growth and survival from those with a high capacity, but they do not reflect physiological changes that occur after lifting (Duryea and McClain 1984, Venator 1981, Weaver et al. 1981, Xydias 1980, Williston 1974). In an early review, Wakely (1948) concluded that morphological grades are inadequate indicators of seedling quality. However, regeneration foresters and nurserymen still commonly judge seedlings by look and feel.

A long term study by South et al. (1985) has shown significant effects due to size of loblolly pine seedlings for survival, height, and volume at age 3 and 13 years after outplanting. Seedling grades were delineated based on root collar diameter. Grade 1 seedlings (>4.7 mm) were superior to grade 2 seedlings (3.2-4.7 mm) which also surpassed grade 3 seedlings (<3.2 mm). The differences in survival between the 3 groups actually increased from 3 to 13 years after planting. Clearly seedling size is sometimes an indicator of subsequent performance; however, it cannot be relied upon for consistent information. In the study by South et al. (1985) the history of the small seedlings could provide reasons why they performed poorly. Possibly the smaller seedlings were suppressed in the nursery bed by their more vigorous associates. As a result, the smaller seedlings were less physiologically fit. The outplanting was done on an unusually excellent site (loblolly pine site index 28.7 m (94 ft), base age 25). This may have resulted in intense vegetative competition which subsequently suppressed the smaller seedlings, while the larger seedlings could more quickly dominate surrounding vegetation.

The search for physiological indicators of seedling quality is marked by abundant literature (Duryea and McClaine 1984, Ritchie and Dunlap 1980). Among the techniques available for physiological testing, root growth potential (RGP) has emerged as a promising method. Stone (1955) developed the procedure which has become the standard method for determining RGP. The method involves obtaining a sample of seedlings, removing any new white root tips, root pruning to a specified length, and placing the seedlings in a controlled environment for a set period of days. At the conclusion of this period, the seedlings are excavated, and their new root growth quantified. RGP is thus a measure of a seedling's capacity to rapidly re-grow roots lost in lifting.

This measure of seedling ability to re-grow new roots has been termed its "root regeneration potential" (Abod et al. 1979, Ritchie and Stevens 1979, Day and MacGillivray 1975, Krugman and Stone 1966, Stone et al. 1963), "root growth capacity" (Johnson-Flanagan and Owens 1985, Jenkinson 1980, Sutton 1980, Burdett 1979, Stone and Norberg 1979), and "root growth potential" (DeWald 1986, Feret et al. 1985a, 1985b, 1984, Ritchie and Dunlap 1980). These terms are used interchangeably in the literature. Actually the new root production of a transplanted seedling is due primarily to elongation of existing roots (root growth), rather than root initiation (root regeneration), (DeWald 1986, Stone et al. 1962). Hence, the term root growth potential (RGP) will be used subsequently in reference to the ability of a seedling to rapidly expand its root system.

The new roots generated during RGP analysis are an indication of how quickly a seedling would produce roots in the field. These new roots establish soil contact beyond the planting hole, and are more efficient than suberized roots at water and nutrient uptake (Kozlowski and Scholtes 1948). Thus a seedling with high RGP is better at extracting the soil solution during the critical post-planting period, and has an increased probability of survival compared to the seedling with low RGP.

Previous RGP work

Stone (1955) was the first to report that tree seedlings varied greatly in their ability to regenerate roots. It is generally recognized that RGP depends primarily on the physiological status of the seedling, which is controlled in part by nursery cultural practices, and subsequent lifting and handling procedures (Smith 1986). RGP of many species has been studied using Stone's (1955) system. Extensive studies have been undertaken to measure the effects of soil temperature, soil moisture, cold storage temperature, and the impact of such nursery practices as lift date, root pruning, top pruning, and fertilization (Duryea 1984, Ritchie 1984a).

RGP has been demonstrated to be strongly related to field survival and growth in many species in the Coniferae genera, including Abies, Picea, Pinus, and Psuedotsuga (Feret and Kreh 1985, Feret et al. 1985a and b; Feret et al. 1984, Ritchie 1984a and b, Sutton 1980a, Burdett 1979, Stone and Norberg 1979, Jenkinson 1978, Jenkinson and Nelson 1978, Rhea 1977, Stone 1955). The widespread, positive correlation with field performance is a great improvement over the poor relationship of traditional morphological measures used in grading seedlings (Feret and Kreh 1985, Feret et al. 1985a; 1984, Lavender and Waring 1972, Wakeley 1954).

Patterns of Root Growth

A seedling's innate ability to grow new roots depends primarily on its physiological state (Ritchie 1984). In many species RGP appears to increase and decline in direct opposition to shoot growth (Drew and Ledig 1981). Variability in seasonal RGP patterns has been reported for many species, including Douglas-fir (Pseudotsuga menziesii Mirb.), Monterey pine (Pinus radiata D.Don.), red pine (Pinus resinosa Ait.), white fir (Abies concolor Gord.), Norway spruce Picea abies L.), white spruce)Picea glauca Moensch.), black spruce (Picea mariana Mill.), loblolly pine, jack pine, (Pinus banksiana Lamb.), and Taxus species (Ritchie and Dunlap 1980).

Much of the RGP work has involved the western conifers. Douglas-fir and ponderosa pine RGP cycles appear to be related to shoot dormancy status (Ritchie and Dunlap 1980). Autumn and winter increases in RGP coincide with accumulation of chilling hours, and the RGP peak indicates the fulfillment of this requirement (Ritchie and Dunlap 1980, van den Driessche 1977, Krugman and Stone 1966).

Krugman and Stone (1966) found that ponderosa pine seedlings averaged less than 10 cm of new root growth until the seedlings had been exposed to 90 cold nights. After this period RGP quickly increased to 100 cm of new roots , as cold exposure continued up to 150 cold nights. After 150 cold nights further chilling was not accompanied by RGP changes (Krugman and Stone 1966). Similar chilling sum-RGP relationships have been reported for other cool temperate region species, such as white fir, western hemlock (Tsuga heterophylla Raf.), and Douglas-fir (Jenkinson 1984, Ritchie and Dunlap 1980, Jenkinson and Nelson 1978).

When the seedling reaches its peak RGP level, and the environment is favorable for root growth, the elongation rate of new roots has been reported to be regulated by an internal carbohydrate source-sink regime (Ritchie and Dunlap 1980). It appears that RGP trends are regulated by shoot growth cycles (Drew and Ledig 1981), while the magnitude of the root growth response may reflect the level of internal carbohydrate reserves (Ritchie and Dunlap 1980). New root growth is an energy demanding process, occuring at the expense of available metabolites. Carbohydrate metabolism follows seasonal patterns related to the seedling's shoot growth cycle, and is thought to affect RGP responses (Rose and Whiles 1984), although results supporting this relationship have not been reported in the literature.

In autumn, seedlings enter 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. It is this stored energy which is thought to regulate the magnitude of RGP response. In early spring, prior to bud burst, seedlings are preparing to resume shoot growth and roots are the primary metabolic sink, actively drawing upon converted carbohydrate reserves. As shoot growth resumes there is competition between the shoot and the roots for current photosynthate. The shoot is a stronger metabolic sink than the roots, and consequently RGP decreases sharply as top growth commences (Drew and Ledig 1980, Ritchie and Dunlap 1980). Despite all of the studies which lend support to the above hypothesis, no clear relationship between carbohydrate concentration in the roots and root growth has been established (Rose and Whiles 1984, Ritchie 1982).

Loblolly pine ceases shoot growth in autumn, but this quiescence is not necessarily true dormancy (Perry et al. 1966). A dormant seedling will not resume normal shoot growth until a chilling requirement has been met, even under growth promoting conditions. A quiescent seedling does not have this specific requirement of a particular cold sum accumulation before shoot growth resumes. DeWald (1986) found significant negative correlations (r^2= -.45 to -.65) between average minimum soil and air temperatures and loblolly pine RGP. The quiescent state in loblolly pine is induced by unfavorable growing conditions, primarily low temperature and moisture levels. Actually, loblolly pine will grow all winter if kept under greenhouse conditions, with at least a 14.5 hour photoperiod (Kramer 1936,1957).

A study by Garber (1983) reported that a brief cold period resulted in much faster resumption of shoot growth under favorable conditions, but that a photoperiod of more than 14 hours could partially substitute for the cold requirement. Differences among loblolly pine seed sources have also been noted, with sources originating north of 34^{o} N. latitude apparently having some chilling requirement (Carlson 1985). Despite the apparent lack of true dormancy, loblolly pine RGP has a seasonal pattern of low values in the spring and autumn, and a consistent late winter peak (DeWald 1986, Feret et al. 1985a).

Genotypic effects on RGP

Root growth has a strong genetic component (Carlson 1985, DeWald 1985, Jenkinson 1980). Ponderosa pine provenances were shown to have RGP peaks at different dates, after being exposed to identical chilling hours at the same nursery (Jenkinson 1980). DeWald et al. (1985b) also found significant differences in timing of RGP peaks and their magnitude among half-sib loblolly pine families. The moderately strong heritability values of RGP on November to March lifted seedlings (h=.30-.50) indicate selection would probably be successful for improving this trait (DeWald et al. 1985b). It has been suggested that RGP tests be used to screen potential breeding tree selections, as an early indication of transplantibility (Johnson 1982).

Cold storage effects on RGP

Presently, regeneration practices in the South require periods of cold storage for most seedlings between lifting and field planting (Garber and Mexal 1980). It has been recognized that this storage period be as brief as possible to retain seedling vigor (Menzies et al. 1985, Dierauf 1974, Dierauf and Marler 1969). Storage is necessary to arrest the natural progression of shoot activity in the spring. Successful plantings are often made up to late May in Virginia, but seedlings must be lifted by mid-March to prevent shoot growth from resuming. Also, clearing the nursery beds early in spring allows seed bed preparation to begin for the following crop (Garber and Mexal 1980).

Cold storage has been shown to effect RGP in many studies (Barden and Feret 1986, DeWald 1986, Feret et al. 1985a; 1984, McCraken 1979, Jenkinson and Nelson 1978, Rhea 1977, Stone and Benseler 1962), but the effect is not consistent. Various studies have shown RGP increasing, decreasing, or remaining stable during periods of storage.

The time of lifting, relative to the seedling's shoot dormancy cycle, can have an influence on the RGP of cold stored seedlings. Cold storage of Douglas-fir has resulted in the improvement, decline, or maintanence of RGP levels depending on when a seedling was lifted (Ritchie 1984b). These results can be explained by the fact that cold storage can satisfy a seedling's chilling requirement and thus improve its RGP. This has been shown for Douglas-fir (Ritchie 1982, Ritchie and Stevens 1979, Lavender and Wareing 1972), western hemlock (Nelson and Lavender 1979), and ponderosa pine (Jenkinson 1980, Krugman and Stone 1966).

The shoot of a seedling must be fully dormant or quiescent to tolerate storage well. Thus, some chilling must be received before storage is successful. The chilling sum needed by Douglas-fir to maintain vigor in storage has been calculated as between 500 and 1,600 hours (Ritchie and Dunlap 1980, Ritchie and Stevens 1979). Ponderosa pine (<u>Pinus contorta</u> Dougl.) seedling RGP was reduced if lifted and stored prior to 300 hours or after 1,200 hours of natural chilling (Stone and Jenkinson 1971). Stone (1959) concluded the detrimental effects of cold storage were due to the failure of seedlings to achieve physiological hardening or readiness before lifting.

For species which undergo a true dormancy, the variable effects of cold storage can be explained by the following hypothesis (Ritchie and Dunlap 1980): A seedling's shoot must be completely dormant prior to lifting and cold storage, this is usually quantified using a minimum number of chilling hours. Subsequent cold storage then often results in RGP increases. If a seedling is lifted at its dormancy peak, RGP is usually maintained in storage. However, if seedlings are lifted before dormancy has been achieved, or after the shoot is resuming activity, then RGP decreases in cold storage (Ritchie and Dunlap 1980).

The effect of cold storage is less predictable for species or seed sources with little or no chilling requirement, like loblolly pine (Perry et al. 1966). Generally loblolly pine seedlings do not store well until they are fully quiescent. In the Virginia Coastal Plain, this does not occur until late November (Dierauf 1982). Garber and Mexal (1980) reported loblolly pine seedlings increased their tolerance of storage until mid-December. Seedlings lifted and stored before this time had low survival rates upon outplanting. However, lifting and storage after mid-December resulted in peak survival levels even after 9 weeks in storage (Garber and Mexal 1980). Another study by

Dierauf and Marler (1969), though, showed survival and 3 year height growth decreasing for stored seedlings lifted after late December. Rhea (1977) also reported similar results.

These apparent contradictions in loblolly pine seedling storage success may be due to differences in the physiological status of the seedlings used in the different studies. The Arkansas-raised seedlings in Garber and Mexal's (1980) study may have not been in a quiescent state until mid December. In Dierauf and Marler's (1969) study the environmental conditions may have induced earlier tolerance to cold storage in the Virginia-raised stock. The varying provenances used may also have contributed to the differential storage success of late winter lifts. Garber and Mexal (1980) suggested that a seed source x storage interaction may be a contributing factor in the variable results obtained from these studies.

The duration and temperature of cold storage, in addition to lift date, can also have an impact on storage success. Prolonged storage at temperatures below $-2^{\circ}C$ results in freeze damage due to tissue dessication and cell rupture, while prolonged exposure to temperatures above $+5^{\circ}C$ results in rapid respiratory depletion of carbohydrates, and increasing fungi growth on the seedlings (Ritchie and Dunlap 1980). Within this $-2^{\circ}C$ to $+5^{\circ}C$ range, temperatures just above freezing +1°C to +3°C are generally considered optimum. RGP has been reported to decline, even at these ideal temperatures, under extended storage for loblolly pine (Barden and Feret 1986, DeWald 1986, Garber and Mexal 1980), ponderosa pine (Stone and Norberg 1979, Stone and Schubert 1959b), and other species (Ritchie et al. 1985). Stone and Norberg (1979) suggested these decreases are not detrimental as long as RGP remains above a threshold level needed for survival in a specific environment. The length of time a seedling can maintain vigor in cold storage depends primarily on its current dormancy or quiescent status, and the environmental conditions in the storage unit.

Ritchie and Dunlap (1980) attributed the effects of cold storage duration on RGP to a shoot physiological status x carbohydrate reserve interaction. Root growth is an energy-expensive process. Significant weight losses following relatively brief periods of cold storage have been reported for a variety of conifer species by Garber and Mexal (1980). They suggested these weight losses are metabolic reductions of available food reserves needed for rapid root growth.

McCraken (1979) followed carbohydrate changes in Monterey pine and mugo pine (<u>Pinus mugo</u> Torr.) after 6, 12, and 18 weeks in storage. He found significant losses in total carbohydrate content of the roots after only 6 weeks.

Most of this decrease was due to respiratory consumption of starch which occurred immediately after lifting. Longer periods of storage resulted in further depletion of carbohydrates, but at much slower rates than the initial losses. A significant difference among species was also seen, as mugo pine retained much higher carbohydrate reserve levels than Monterey pine, particularly in the root system (McCraken 1979). Other studies have also noted species variability (Winjum 1963, Hellmers 1962).

Most reports have been in agreement with McCraken's (1979) data which show decreases in carbohydrate levels occurring in both the shoot and the roots of cold, dark stored seedlings. However, one study has shown unusual weight gains in seedlings cold-stored under an 8 or 16 hour photoperiod (Johnson 1983). Despite the circumstantial evidence indicating carbohydrate depletion in extended storage causes low RGP values, this has not been well supported in the literature. Root and shoot starch levels have shown poor correlations with RGP in several studies (Rose and Whiles 1984, Ritchie 1982).

The moisture status of seedlings can also affect subsequent RGP measures after storage. Menzies et al. (1985) recommend not lifting Monterey pine when needle water potential is lower than -.5 MPa. Free water or moisture holding materials are commonly added to seedlings before packaging for transport or storage (Burdett and Simpson 1984). Recently, however, excessive moisture has been shown to significantly reduce the RGP of loblolly pine seedlings stored in kraft-polyethylene bags (Barden and Feret 1986).

Applications of RGP

Morphological attributes generally have not been correlated well with RGP in loblolly pine (DeWald 1986, Feret 1985a). These studies have shown little relationship between RGP and various measures of seedling size, such as caliper, height, volume, or root-shoot ratio. However, Brissette and Roberts (1984) have shown lift date and seedling size effects on RGP for loblolly pine. In their study of 2 nurseries, large seedlings (grade 1) had higher RGP than medium seedlings (grade 2), which also surpassed small seedlings (grade 3) in 2 out of 3 lift dates. Most of the large seedlings originated from one nursery, and the small seedlings from another, so this bias in the data may result in erroneous conclusions (Brissette and Roberts 1984).

RGP has been positively correlated with early field performance in loblolly pine. Using linear regression analysis relating the number of new roots to first and second year height increment, r-squared values of .59 and

.28 were obtained, respectively (DeWald et al. 1985b). Due to the threshold effect of RGP (increases above a certain level having little influence on growth) non-linear analysis yields much stronger relationships. Feret et al. (1985a) reported r-squared values of .97 relating percent survival to number of new roots. This study used stock from 7 different nurseries and many different sources. With this variability, RGP patterns and levels varied considerably.

The ability of RGP to indicate stock degradation after root exposure to warm, drying conditions has also been shown by Feret et al. (1985b). In this experiment, entire seedlings were exposed to ambient day conditions for varying lengths of time. After exposure, samples were immediately outplanted, and a subsample used for RGP analysis. Following exposure over varying lengths of time RGP decreased sharply. Correlations between height, survival, and RGP were highly significant. The relationship, as measured by r-squared, between first year height, second year height, and the log (base 10) of new root length were both .85. The correlation between first year survival and $\log_{10}$ of new root length was .70 (Feret et al. 1985b).

Since peak RGP values are associated with deep shoot dormancy levels, a seedling's ability to handle environmental stresses during lifting, handling, and storage is also at a high level during this period (Ritchie and Dunlap

1980, Lavender and Waring 1972). Burdett (1979) concluded that differences in RGP may account for the wide variations in survival between various batches of stock, differing in lift date, cold storage duration, and nursery location. In his work with lodgepole pine, first year mortality increased exponentially with decreasing RGP (Burdett 1979).

Jenkinson (1980) reported that although climatic conditions are important for determining dormancy status and thus the ideal time to lift, different seed sources of ponderosa pine will respond differently to the environmental conditions controlling dormancy. Hence, the seed source is a major factor influencing the rate of increase and timing of the RGP peak in ponderosa pine (Jenkinson 1980).

In the western United States all of the above factors have been integrated when determining lifting schedules. Climatic data have been combined with genetic information to establish "lifting windows" for seedling lots. These lifting windows are scheduled on the basis of anticipated timing of the RGP peak for a particular area (based on chilling hour accumulation), modified by the species and seed source being grown (Ritchie and Dunlap 1980, Jenkinson and Nelson 1978). One of the keys to successful plantation establishment is the correct scheduling of lifting windows (Jenkinson 1980). The normally droughty summer conditions experienced in much of the ponderosa pine's range has placed a premium on seedlings with high RGP values, to ensure early root establishment and survival after outplanting.

Lifting schedules are not as thoroughly planned at most southern pine nurseries, with less consideration paid to the seed source and chilling hours received. At most nurseries, lifting begins when the equipment and labor is available, and proceeds as fast as weather conditions will allow, to ensure all seedlings are lifted before shoot growth resumes. Presently, no studies have been reported where the same genetic stock of loblolly pine was grown at different nurseries, and comparisons made between the seasonal RGP pattern, cold storage success, and outplanting performance.

METHODS AND MATERIALS

Experiment I

Hypotheses

Experiment I was performed to examine differences in 1-0 loblolly pine RGP over time, among 5 seedlots, and between 2 nurseries. The following null hypotheses were tested:

1. Ho: Root growth potential of the seedlings does not vary significantly over the lifting season;
2. Ho: The RGP of seedlings from the 2 nurseries does not vary significantly;
3. Ho: The RGP of seedlings from the 5 seedlots does not vary significantly;
4. Ho: RGP trends are not correlated with any morphological attributes measured.

Seedling Culture

Seed sources for the study included 4 half-sib families (designated as 6-8, 6-9, 6-20, and 11-137), and a seed orchard mix (designated as 42-M). All seed lots originated from the Westvaco Virginia Piedmont seed orchard in Summerville, South Carolina. The orchard mix seed (42-M) was sorted by size, hence in year 1 all seed was medium sized, (30,580/kg, 13,900/lb) and in year 2 all seed was large sized (28,160/kg, 12,800/lb).

Seed was hand sown in April 1984 and April 1985 at the Virginia Department of Forestry (VDF) nursery located at the New Kent Forestry Center (Providence Forge, Virginia) and the Westvaco nursery (Summerville, South Carolina). Each family was sown in 3 replicate locations within the nursery bed. Both nurseries are located on the Coastal Plain (Figure 1), on sand to loamy-sand soils of the Chipley series at Summerville, and the Statesville series at New Kent. Seedling density at the end of the 1984 and 1985 growing season was approximately 312 trees/m^2 (29 trees/ft^2) and 279 trees/m^2 (26 trees/ft^2) at the New Kent and Summerville nurseries, respectively.

Cultural practices normal to each nursery were followed. The New Kent nursery was under a continuous cropping system which did not allow fallow time for a cover crop to be grown and incorporated. However, sawdust was applied yearly at the rate of 1.3 cm and incorporated into the soil before seeding. Irrigation and rainfall resulted in at least 2.5 cm of water being applied weekly during the growing season. In both years the seedlings were mowed to a height of 21 cm twice in August and once in September, to prevent the seedlings from becoming too large, and to increase the root/shoot ratio. No root pruning was

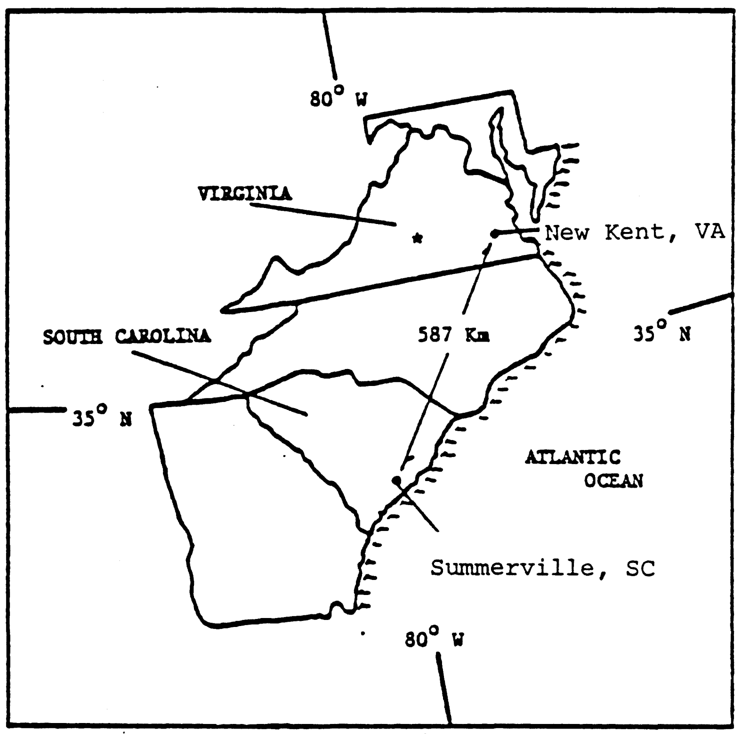

Figure 1. Locations of the VDF nursery, New Kent VA, and the Westvaco nursery, Summerville SC. The planting site (*) is located at Sprouses Corner, VA.

performed.

The rotational cropping of the Summerville nursery allowed sorgum and corn to be grown and incorporated during fallow years to maintain soil organic matter level. Also winter rye was grown as a cover crop during the cool season. Irrigation and rainfall resulted in at least 4.2 cm of water being applied to the seedbeds weekly during the growing season. The seedlings were mowed twice in 1984, on August 14 at 20 cm, and again on August 21 at 15 cm. In 1985 the seedlings were mowed in late September, to a height of 20 cm. In 1984 seedlings were root pruned by undercutting in late September. In 1984 and 1985 the beds were undercut and the lateral roots pruned in mid-October. At both nurseries routine applications of fertilizer and pesticides were made throughout the season.

Chilling hours were recorded during both years. Chilling hours were defined as the number of hours the temperature was between 0^{o} and 8^{o} C, at each nursery (Garber 1983; 1978).

Seedling sampling procedures

Seedlings were sampled 8 times from all 5 seedlots approximately every 2 weeks from early November until mid-February, at both nurseries and during both years. Occasionally lifting was postponed due to frozen ground in

January and February (Table 1). On each lift date 10 seedlings were hand dug from each nursery plot, for every treatment combination. The roots were dipped in water, then the seedlings were immediately placed in plastic bags, and laid in a cooler with ice. The coolers were shipped to the Reynolds Homestead Agricultural Experimental Station, in Critz, Virginia, to undergo RGP analysis. The seedlings were in transit for 2-3 days.

The root growth potential system

Seedling RGP was determined using a system similar to Stone (1955). New white root tips on seedlings were removed, and the root systems pruned to a length of 14 cm below the root collar. The 10 seedlings from each of the 3 nursery bed locations were mixed, then 2 samples of 15 seedlings each were placed in 2 replicate trays. The seedlings were planted in plexiglass trays 46cm x 10cm x 41cm (L x W x H), filled with 0.013 m^3 of Promix^R BX[1]. The trays were watered and allowed to drain. The drainage holes were plugged, and the trays immersed in a water bath held at

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[1] Promix^R BX, A. H. Hummert Seed Co., St Louis, Missouri, is a plant growth medium consisting of shredded peat moss, horticultural vermiculite, and perlite with the following nutrient amendments; dolomitic limestone, calcium nitrate, super phosphate, potash, and fritted trace elements.

Table 1. Calendar dates for each of the 8 loblolly pine seedling lifts conducted at the New Kent VA (NK) and Summerville SC (S) nurseries during the 1984-85 and 1985-86 lifting seasons.

	year			
	1984-86		1985-86	
	nursery			
lift	NK	S	NK	S
1	Oct. 30	Oct. 29	Nov. 4	Nov. 4
2	Nov. 13	Nov. 13	Nov. 18	Nov. 18
3	Nov. 27	Nov. 27	Dec. 2	Dec. 2
4	Dec. 11	Dec. 11	Dec. 16	Dec. 16
5	Dec. 26	Dec. 26	Dec. 30	Dec. 30
6	Jan. 8	Jan. 8	Jan. 13	Jan. 13
7	Jan. 29	Jan. 22	Jan. 27	Jan. 27
8	Feb. 13	Feb. 11	Feb. 10	Feb. 3

a constant 20° C, which has been found to be near optimum for root growth (Nambiar et al. 1979, Stupendick and Shepherd 1979). The trays were rewatered after 12 days.

A 16 hour photoperiod was maintained by supplementing natural light with Grolux flourescent lamps suspended 0.5 m above the seedlings. The greenhouse temperature was maintained above 15°C at night, and below 30°C during the day. After 24 days the seedlings were washed out of the trays, and measurements taken.

At the end of the RGP testing period new root growth was measured, along with several morphological attributes of each seedling. The total length and total number of new long roots (>1.5 cm) and the total number of new short roots (>0.5 cm and <=1.5 cm) were determined for each seedling. RGP was thus expressed as the total length or total number of roots produced. The following morphological attributes were also recorded at the time of RGP measurements:

1. root collar diameter (nearest 0.1 mm)
2. shoot length (nearest cm)
3. number of terminal buds present
4. number of terminal buds alive
5. top code (status of the terminal).

The following scale was adapted from Johnson (1983), to visually evaluate the status of the terminal.

1. dead, all foliage brown

2. no apparent activity
3. terminal buds swollen
4. terminal starting to flush
5. terminal flushing with measurable elongation
6. terminal flushing with measurable elongation and needles flushing
7. already growing, often with no buds reset.

For state 5 and 6 the length of the current growth flush was also recorded (nearest cm).

For year 1 the following dry weights were obtained on a per seedling basis:

1. total shoot dry weight (nearest 0.01 g)
2. foliage dry weight (nearest 0.01 g)
3. stem dry weight (nearest 0.01 g)
4. terminal buds dry weight (nearest mg)
5. total root dry weight (nearest mg)
6. lateral root dry weight (nearest mg)
7. tap root dry weight (nearest mg).

For year 2, dry weights were determined for the following variables on a per sample basis of 30 seedlings:

1. total shoot dry weight (nearest 0.01 g)
2. total root dry weight (nearest 0.01 g)
3. lateral root dry weight (nearest 0.01 g)
4. tap root dry weight (nearest 0.01 g).

Experimental Design and Analysis

The experiment consisted of a factorial combination of the 3 treatments (5 seedlots, 2 nurseries, and 8 lifts). Analysis of all data was performed using the SAS statistical package (SAS Institute, Cary, NC). Using the measures of total length and total number of new roots, Analysis of Variance (ANOVA) procedures were performed on the results to determine which effects and interactions were a significant component of seedling RGP variability. An alpha level of 0.01 was used for tests of significance.

The following general model was used:

$$RGP = N_i + F_j + L_k + N_iF_j + N_iL_k + L_kF_j + N_iF_j{+}L_k + error;$$

Where N = nursery effects (i = 1, 2)

F = family effects (j = 1, 2, 3, 4, 5)

L = lift date effects (k = 1, 2, 3,....8).

Correlation coefficients were determined between RGP and the morphological attributes on a per seedling basis during the 1984-85 lifting season, and on a 30 seedling sample basis during the 1985-86 lifting season. Correlation coefficients for chilling hour sum and RGP were calculated for each nursery and lift date combination. All data were also submitted to Duncan's New Multiple Range Test to determine where significant ($p < 0.05$) differences occurred.

Experiment II

Hypotheses

Experiment II was conducted to examine differences in 1-0 loblolly pine RGP and field performance over 5 storage durations (planting dates), among 5 seedlots, and between 2 nurseries. The following hypotheses were tested:

1. Ho: RGP does not vary significantly for seedlings stored for varying lengths of time;
2. Ho: RGP of stored seedlings from the 2 nurseries does not vary significantly;
3. Ho: RGP of stored seedlings from the 5 seedlots does not vary significantly;
4. Ho: RGP is not correlated with field performance.

Seedling sampling procedures

Seedling culture was identical to that in Experiment I. In February of both years an additional 6,600 seedlings were lifted. Seedlings were sorted and packaged at each nursery into bundles of 33 seedlings for every treatment combination. The seedlings were placed in kraft-polyethylene bags and transported to the VDF Charlottesville facility to undergo cold storage at $2^{o}C$.

The five outplanting dates were chosen as every 3 weeks from early March until late May, in both years. On each planting date the seedlings were transported to the site, seedling bundles were removed from the bags and 8 of the 33 seedlings randomly selected to undergo RGP analysis; the remaining 25 seedlings were outplanted. The total elapsed time between removal from cold storage until the last seedling was planted was usually less than 7 hours.

Seedlings for RGP tests were transported to the Reynolds Homestead Agricultural Experiment Station immediately after planting was completed. Upon arriving they were refrigerated at 4° C until placement in the trays the next day. RGP determinations were made as described in Experiment I.

The outplanting sites were on different tracts located in Buckingham county on the Virginia Piedmont (Figure 1). The stands were composed of mixed hardwoods (primarily Quercus spp., Carya spp., and Acer rubrum L.) and Virginia pine (Pinus virginiana Mill.). The sites were operationally harvested, then prepared with a drum-chopper and burned. Each field block contained fifty 6.1 m x 6.1 m plots, and was surrounded by operational hand plantings. In each plot 25 trees were hand planted on a 1.22 m x 1.22 m spacing.

The actual planting was done on a per block basis. The 8 seedlings for RGP determinations were held in a bucket of water until planting in that block was completed. They were then placed in plastic bags in a cooler with ice. The remaining 25 trees were also held in pails of water during planting in the designated plot. In this way all of the seedlings for a particular block were exposed to similar durations of ambient temperatures after leaving storage.

From each plot 16 seedlings were measured within 2 weeks after planting to determine initial heights. In October 1985 (for the year 1 planting), percent survival was determined for each plot, and the same 16 trees were remeasured to determine final height, to allow calculation of the height increment.

Experimental Design and Analysis

Experiment II consisted of a factorial combination of the 3 treatments (seedlot, nursery, and planting date) in a randomized complete block design. Analysis of all data was performed using the SAS statistical package (SAS Institute, Cary, NC). RGP analysis used the mean of the 8 seedlings sampled from each plot. Analysis of Variance (ANOVA) procedures were performed on the results to determine which effects and interactions were a significant component of seedling RGP variability.

The following general model was used:

$$RGP = N_i + F_j + P_k + N_iF_j + N_iP_k + P_kF_j + N_iF_j+P_k + error;$$

Where N = nursery effects (i = 1, 2)

F = family effects (j = 1, 2, 3, 4, 5)

P = planting date effects (k = 1, 2, 3,....8).

The angular transformation (arcsin (square root X)) on percent survival of the outplanted stock was analyzed with the ANOVA procedure to determine whether planting date, nursery, or family had a significant effect. Also first and second order interactions were examined. Outplanting results used the plot means from the 16 measured trees.

Correlations were calculated to determine the relationship between RGP values at the time of planting, and subsequent survival and height growth in the field. When comparing different planting dates the relationship is confounded due to different soil and weather conditions following each outplanting. Thus, correlations were also determined by planting date. Regression models were determined for various transformations of survival (logit = $\log_{10}$ (X/1-X)), height, and new root number ($\log_{10}$, square root), over all plantings, and by planting date. All data were submitted to Duncan's New Multiple Range Test to determine where significant differences occurred.

EXPERIMENT I RESULTS

Root growth potential was measured as the mean total length and mean total number of new roots produced. Due to the very strong correlation ($r=.929$, $p<.001$) between number and length, only number of roots is discussed here. All main effects and first order interactions were highly significant during both years of the study (Tables 2 and 3). The second order interaction was significant in year 2. Data is presented by family, nursery, lift date and year in Tables 4 and 5. The calendar dates of each lift at both nurseries for both years are in Table 1.

Trends during year 1

Summerville seedlings during year 1 had higher RGP on every sample date throughout the lifting season (Figure 2). However, the patterns of RGP exhibited at both nurseries were virtually identical during year 1. RGP increased from low levels in late October to a peak in late December, followed by a decrease through January, and a second slightly lower peak in mid-February. There was less difference between nurseries when RGP was high (Figure 2), resulting in a significant nursery x lift date interaction.

All families exhibited higher RGP overall when raised at Summerville as compared to New Kent (Table 6). However,

Table 2. ANOVA table for number of new roots (> 0.5 cm) for loblolly pine seedlings during the 1984-85 lifting season.

Source	df	SS	F	p
lift date	7	164092.5	112.84	.0001
nursery	1	88822.7	427.57	.0001
family	4	17977.5	21.64	.0001
nursery*family	4	13552.6	16.31	.0001
nursery*lift date	7	16673.4	11.47	.0001
family*lift date	28	15134.1	2.60	.0001
nursery*family *lift date	28	9359.6	1.61	.02
error	2302	478209.4		

Table 3. ANOVA table for number of new roots (> 0.5 cm) for loblolly pine seedlings during the 1985-86 lifting season.

Source	df	SS	F	p
lift date	7	159656.0	178.17	.0001
nursery	1	20215.8	157.92	.0001
family	4	10186.8	19.89	.0001
nursery*family	4	1850.6	3.61	.006
nursery*lift date	7	81142.8	90.55	.0001
family*lift date	28	15519.0	4.33	.0001
nursery*lift date *family	28	13084.1	3.65	.0001
error	2317	296598.0		

Table 4. Mean total number of new roots (> 0.5 cm) for loblolly pine seedlings from 5 families from the New Kent VA (NK) and Summerville SC (S) nurseries, for the 8 lifts of the 1984-85 season.

	lift							
	1		2		3		4	
family	NK	S	NK	S	NK	S	NK	S
11-137	0.87 b[1]	8.53 b	5.23 a	8.87 c	3.33 b	9.00 b	4.80 a	15.20 b
42-M	4.73 a	15.00 ab	8.47 a	20.37 ab	8.67 a	20.00 a	8.00 a	24.92 a
6-20	3.80 ab	16.33 a	10.27 a	18.87 ab	7.43 ab	16.17 ab	9.30 a	27.07 a
6-8	0.37 b	15.00 ab	9.33 a	24.63 a	4.70 ab	23.17 a	5.90 a	23.77 a
6-9	0.90 b	17.63 a	8.77 a	16.37 b	5.97 ab	20.97 a	3.87 a	26.00 a
mean	2.13 b	14.50 a	8.41 b	17.82 a	6.02 b	17.86 a	6.37 b	23.18 a

[1] Means within a column followed by the same letter are not significantly different using Duncan's New Multiple Range Test at the p < .05 level. Column means are compared within a lift.

Table 4. continued.

	lift							
	5		6		7		8	
	NK	S	NK	S	NK	S	NK	S
11-137	28.07 b	23.00 c	4.93 b	30.87 a	11.57 ab	9.70 b	23.07 a	16.80 b
42-M	41.80 a	46.9 ab	12.23 a	36.37 a	8.33 bc	10.90 b	27.67 a	28.03 a
6-20	27.70 b	35.20 bc	11.10 a	28.13 a	14.97 a	21.97 a	26.77 a	36.53 a
6-8	26.97 b	52.47 a	7.37 ab	36.70 a	10.33 abc	23.17 a	24.37 a	30.47 a
6-9	26.17 b	42.90 ab	9.33 ab	32.23 a	5.07 c	21.33 a	11.13 b	30.17 a
mean	30.14 b	40.29 a	8.99 b	32.86 a	10.05 b	17.41 a	22.60 b	28.40 a

[1] Means within a column followed by the same letter are not significantly different using Duncan's New Multiple Range Test at the p < .05 level. Column means are compared within a lift.

Table 5. Mean total number of new roots (> 0.5 cm) for loblolly pine seedlings from 5 families from the New Kent VA (NK) and Summerville SC (S) nurseries for the 1985-86 lifting season.

	lift							
	1		2		3		4	
family	NK	S	NK	S	NK	S	NK	S
11-137	5.17 b[1]	0.00 b	0.63 b	2.07 b	11.23 a	0.38 c	13.10 ab	3.23 b
42-M	11.9 a	0.47 a	3.37 a	2.83 a	10.17 a	3.33 b	21.33 a	7.63 ab
6-20	4.17 b	0.07 b	1.40 ab	2.97 b	11.67 a	7.80 a	18.73 ab	5.80 ab
6-8	2.23 b	0.10 b	0.90 b	1.07 b	2.33 b	0.47 c	11.27 b	5.33 ab
6-9	1.17 b	0.10 b	2.00 ab	6.67 b	8.03 ab	2.13 bc	19.27 ab	9.03 a
mean	4.93 a	0.15 b	1.66 a	3.12 a	8.69 a	2.84 b	16.74 a	6.21 b

[1] Means within a column followed by the same letter are not significantly different using Duncan's New Multiple Range Test at the p < .05 level. Column means are compared within a lift.

Table 5. continued.

	lift							
	5		6		7		8	
	NK	S	NK	S	NK	S	NK	S
11-137	0.33 b	18.37 b	3.97 b	17.17 bc	1.53 b	12.50 c	13.80 b	44.83 ab
42-M	7.20 a	26.67 a	9.87 a	13.03 c	7.77 a	19.23 bc	18.50 ab	49.20 a
6-20	7.33 a	23.17 ab	9.70 a	28.17 a	7.70 a	25.03 ab	18.67 ab	23.77 c
6-8	2.13 b	18.07 b	8.97 ab	12.23 c	1.87 b	13.97 c	18.27 ab	37.67 b
6-9	1.67 b	24.13 ab	13.47 a	23.17 ab	4.13 ab	29.50 a	22.00 a	49.37 a
mean	3.73 b	22.07 a	9.19 b	18.75 a	4.60 b	20.05 a	18.25 b	40.97 a

[1] Means within a column followed by the same letter are not significantly different using Duncan's New Multiple Range Test at the $p < .05$ level. Column means are compared within a lift.

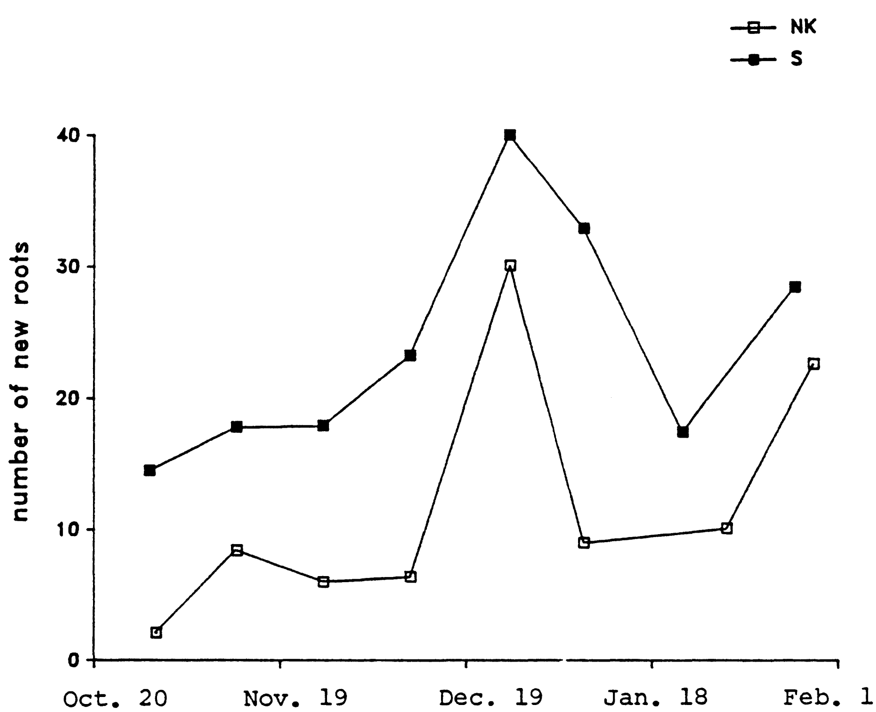

Figure 2. Mean number of new roots (> 0.5 cm) of loblolly pine seedlings plotted by lift date for the New Kent VA (NK) and Summerville SC (S) nurseries for the 1984-85 lifting season.

Table 6. Mean number of new roots (> 0.5 cm) for loblolly pine seedlings from 5 families at the New Kent VA and Summerville SC nurseries during the 1984-85 and 1985-86 lifting seasons.

	---- 1984-85 ----		---- 1985-86 ----	
family	New Kent	Summerville	New Kent	Summerville
11-137	10.23 b[1]	15.25 b	6.22 b	12.37 bc
42-M	14.99 a	25.34 a	11.26 a	15.35 ab
6-20	13.92 a	25.03 a	9.92 a	14.56 bc
6-8	11.17 b	28.67 a	6.00 b	11.11 c
6-9	8.90 b	26.07 a	8.97 a	18.01 a
mean	9.60 b	24.07 a	8.47 b	14.28 a

[1] Means within a column followed by the same letter do not differ significantly using Duncan's New Multiple Range Test at the $p < .05$ level. Overall nursery means are compared within a year.

the relative family rankings changed substantially over the lifting season from nursery to nursery (Table 4). A family x nursery interaction is evident as family 6-9 had the lowest RGP overall when grown at New Kent, but it was ranked second when raised at Summerville (Table 6). RGP values for all families except 6-20 peaked on the fifth lift date (Dec. 26). Family 6-20 had slightly higher RGP on the last lift (Feb. 11 and 13).

Trends during year 2

During year 2, Summerville seedling RGP was higher than New Kent seedling RGP for 5 of the 8 lifts (Figure 3). On the final 4 lifts (late December to mid-February), Summerville seedlings had higher RGP than New Kent seedlings. The RGP pattern at both nurseries was different, with the only similarities being low early values, and the highest values occurring on the final lift. The second highest RGP for Summerville seedlings was observed on the fifth lift (Dec. 30), while New Kent seedlings expressed their second highest RGP on December 16.

As in year 1, all families exhibited overall higher RGP when raised at Summerville (Table 6). Again, family 6-9 performed relatively better at Summerville than at New Kent. RGP peaked for all families on the last lift (Feb. 3 at Summerville, and Feb. 10 at New Kent).

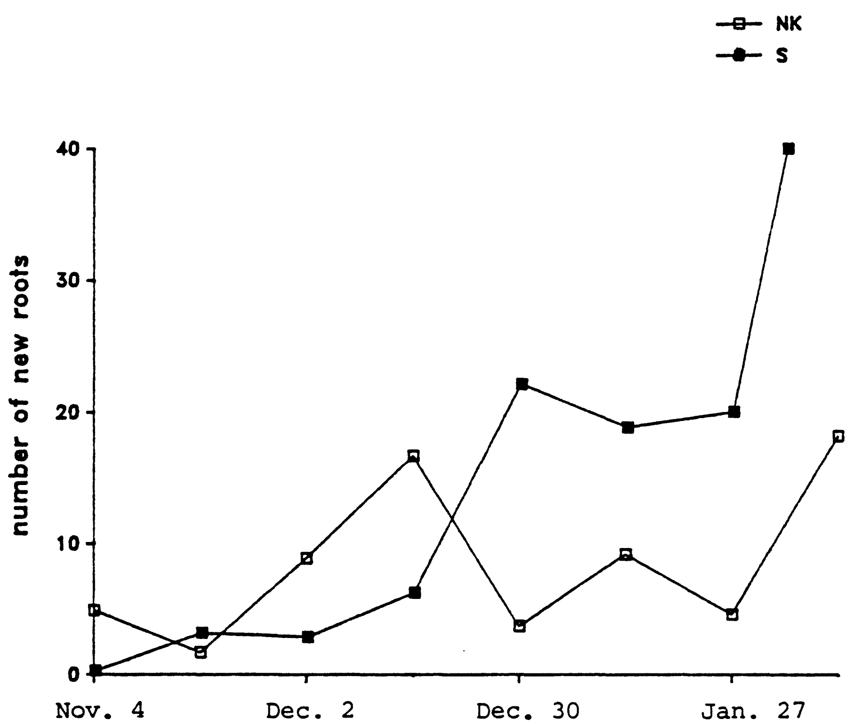

Figure 3. Mean number of new roots (> 0.5 cm) of loblolly pine seedlings plotted by lift date for the New Kent VA (NK) and Summerville SC (S) nurseries for the 1985-86 lifting season.

Comparisons between years

Comparing RGP from year to year was difficult, as the lift dates did not correspond exactly (Table 1); however overall mean RGP values were higher during the 1984-85 lifting season (Table 6). This was due primarily to the high RGP peak on December 26 (Figure 2), and to the much higher values exhibited during the early lifts by Summerville seedlings during the 1984-1985 season (Figure 4).

On the last lift Summerville seedlings had higher RGP in year 2 than in year 1, while for New Kent the opposite was true (Figures 4 and 5). Family 6-20 and 42-M were the top-ranked seedlots during both years at both nurseries (Table 6). Family 6-8 was equivalent to these families in year 1, but was ranked last in year 2. For family 6-9 the reverse was true; it performed much better in year 2 than in year 1. Family 11-137 had low RGP during both years (Table 6).

Results by family, nursery, lift date, and year

The data are presented by lift date, family, and nursery, for each year in Tables 4 and 5. Family rank appeared to fluctuate randomly over the lift dates. In year 1 when Summerville outperformed New Kent on every lift date,

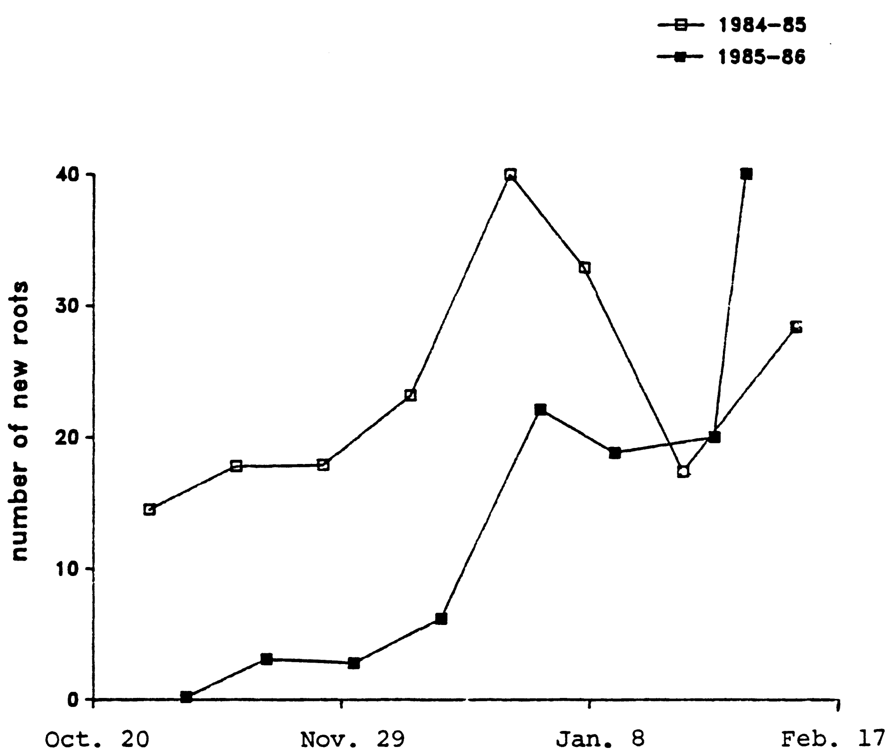

Figure 4. Mean number of new roots (> 0.5 cm) of loblolly pine seedlings plotted by lift date for the Summerville SC nursery during the 1984-85 and 1985-86 lifting seasons.

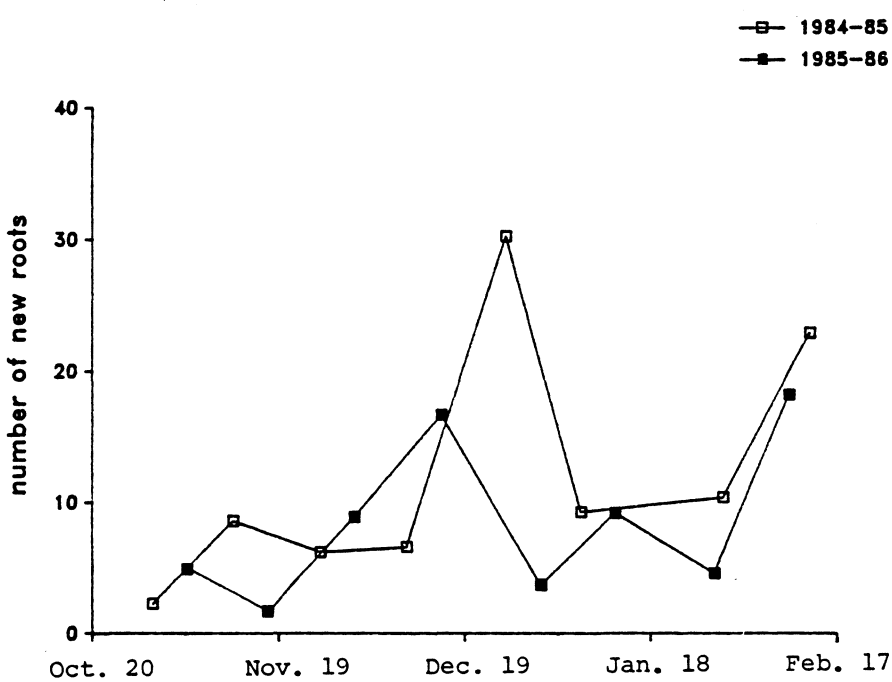

Figure 5. Mean number of new roots (> 0.5 cm) of loblolly pine seedlings plotted by lift date for the New Kent VA nursery during the 1984-85 and 1985-86 lifting seasons.

only one family (11-137) ever had higher values when raised at New Kent. This only occurred on the peak lifts 5 and 8 (Table 4). In year 2 nursery rankings were much more variable, with New Kent seedling RGP generally higher than Summerville RGP during the first 4 lifts, and much lower during the last 4 lifts (Figure 3, Table 5).

Shoot and Root Morphology

The means and ranges of the various seedling morphological variables for each nursery and both years are in Tables 7 and 8. New Kent seedlings had significantly larger shoots during both years, whether measured by root collar diameter, shoot height or shoot weight. Summerville seedlings had heavier root systems in 1984-85. In 1985-86 only the lateral root weight of Summerville seedlings exceeded that of New Kent seedlings.

In year 1 other morphological parameters measured were terminal bud weights and foliage weights. Summerville had heavier buds than New Kent raised seedlings, but foliage weights were identical between the 2 nurseries. During both years Summerville seedlings had a significantly higher root shoot ratio, and a more fibrous root system, as evidenced by a higher lateral root/tap root ratio (Tables 7 and 8).

Table 7. Means and ranges of loblolly pine seedling morphological traits by nursery for the 1984-85 lifting season, n = 2382.

seedling character	New Kent, VA mean	New Kent, VA range	Summerville, SC mean	Summerville, SC range
root collar diameter (mm)	4.51 a[1]	3.0-7.9	4.25 b	2.3-7.6
shoot height (cm)	23.1 a	17.0-32.0	18.9 b	9.0-31.5
shoot weight (g)	2.50 a	0.94-6.39	2.08 b	0.47-7.80
foliage weight (g)	1.31 a	0.30-4.69	1.31 a	0.28-3.89
bud weight (g)	0.008 b	0.0-0.066	0.027 a	0.0-0.27
root weight (g)	0.49 b	0.13-4.05	0.67 a	0.19-2.40
tap root weight (g)	0.33 b	0.090-3.71	0.37 a	0.08-1.33
lateral root weight (g)	0.30 a	0.15-0.71	0.30 a	0.03-1.15
lateral:tap root ratio	0.50 b	0.06-2.09	0.87 a	0.14-4.81
root:shoot ratio	0.20 b	0.07-1.22	0.35 a	0.07-4.25

[1] Means within a row followed by the same letter do not differ significantly using Duncan's New Multiple Range Test at the $p < 0.05$ level.

Table 8. Means and ranges of loblolly pine seedling morpological traits by nursery for the 1985-86 lifting season. n = 2397 for root collar diameter and height. n = 80 for dry weight data.

	nursery			
	New Kent, VA		Summerville, SC	
seedling character	mean	range	mean	range
root collar diameter (mm)	4.3 a[1]	2.6-6.5	3.9 b	1.9-5.8
shoot height (cm)	24.8 a	17.0-30.0	22.0 b	12.0-30.0
shoot weight (g)	2.70 a	2.44-3.31	1.93 b	1.24-2.32
root weight (g)	0.50 a	0.32-0.76	0.50 a	0.22-0.83
tap root weight (g)	0.33 a	0.22-0.45	0.28 b	0.13-0.42
lateral root (g) weight	0.18 b	0.09-0.33	0.22 a	0.09-0.43
lateral:tap root ratio	0.53 b	0.36-0.78	0.77 a	0.53-1.57
root:shoot ratio	0.18 b	0.12-0.28	0.26 a	0.14-0.36

[1] Means within a row followed by the same letter do not differ significantly using Duncan's New Multiple Range Test at the $p < 0.05$ level.

Year 1 correlations of morphological measures with RGP

The correlation coefficients for the various morphological measures and RGP are in Table 9. Shoot variables had weak but significant correlations with number of new roots (Table 9). Shoot height was the only variable negatively correlated with RGP, and this is likely an artifact due to the nursery top-pruning to different heights. The significance of the very low r-values are due in part to the very large sample sizes ($n > 2,000$). The various measures of root dry weight resulted in stronger, highly significant correlations with RGP ($p < .001$; Table 9). The strongest relationship was found with lateral root weight ($r = .54$).

When the data was analyzed by nursery, height was then very weakly, positively correlated with RGP (New Kent, $r = .078$; Summerville, $r = .073$). The number of terminal buds and the top code rating were correlated with the RGP of New Kent seedlings, but not with Summerville seedlings. Other correlations did not vary markedly by nursery (Table 9). Analysis of the correlation coefficients for each nursery-lift date combination did not consistently improve the correlations, nor was a trend evident.

Year 2 correlations of morphological measures with RGP

Correlations between morphological variables and RGP

Table 9. Correlation coefficients (r) relating morphological traits and number of new roots grown by loblolly pine seedlings during the 1984-85 and 1985-86 lifting seasons for the New Kent (NK) and Summerville (S) nurseries.

	------ 1984-85[1] ------			------ 1985-86[2] ------		
	combined	NK	S	combined	NK	S
root collar	.118 ***[3]	.156 ***	.219 ***	.220 ***	.155 ***	.399 ***
height	-.126 ***	.078 **	.073 *	ns	.067 *	.142 ***
top code	ns	.063 *	ns	.391 ***	.346 ***	.474 ***
number of buds	.294 ***	.309 ***	ns	.204 ***	.146 ***	.198 ***
shoot weight	.052 *	.074 *	.169 ***	ns	ns	.680 ***
tap root weight	.226 ***	.154 ***	.231 ***	.468 ***	.349 ***	.721 ***
lateral root weight	.538 ***	.533 ***	.459 ***	.853 ***	.544 ***	.923 ***
total root weight	.428 ***	.356 ***	.378 ***	.752 ***	.495 ***	.874 ***
root/shoot ratio	.236 ***	.370 ***	.119 ***	.753 ***	.517 ***	.836 ***

1 Morphological data in year 1 was obtained on a per seedling basis, n = 2382.

2 Dry weight data in year 2 was obtained as a 30 seedling mean for every treatment combination, n = 80. Other morphological data was obtained on a per seedling basis, n = 2397.

3 *** denotes significance at the $p < 0.001$ level.
** denotes significance at the $p < 0.01$ level.
* denotes significance at the $p < 0.05$ level.
ns denotes no significant correlation.

were inconsistent from year to year (Table 9). The results that differed the greatest in year 2 were: height was not significantly correlated with RGP, and top code was the strongest correlated shoot variable (Table 9). After analyzing the data by nursery, some relationships changed. Height was again weakly, positively correlated with RGP (New Kent, r = .067; Summerville, r = .142).

In year 2 dry weight correlations with RGP were determined on a 30 seedling sample basis for each treatment combination, so specific comparisons among years can not be made. As in year 1, root variables were more highly correlated with RGP than were shoot variables (Table 9). Again in year 2, lateral root dry weight was the measure most highly correlated with RGP (r = .85).

After analyzing the data by nursery, correlation coefficients for all morphological measures were higher for Summerville seedlings than for New Kent seedlings (Table 9). The correlation coefficients for lateral root weight was particularly high for Summerville seedlings (r = .92). Shoot weight also was well correlated with RGP for Summerville seedlings (r = .68), but was not significant overall, nor for the New Kent nursery. When the data was analyzed by lift date, the correlations did not consistently improve nor was there a trend evident.

Status of the terminal

Rating the activity of the shoot on a scale from 1 to 7 (top code) essentially resulted in a 24 day dormancy release test. A plot of top code over chilling hour sum revealed an inconsistent relationship from year to year (Figures 6 and 7). In year 1, seedling shoots appeared most dormant after approximately 350 chilling hours had been accumulated. In year 2, top code generally increased over the lifting season as the chilling sum increased. Similarly, top code was not correlated with RGP in year 1, but was significantly correlated in year 2 ($r = .39$; Table 9). There also was no trend of stronger correlations as the lifting season progressed, in either year.

Chilling hour correlations with RGP

The New Kent nursery, located at a more northerly latitude in a colder hardiness zone, received chilling hours earlier in the season, and they accumulated faster. Summerville recorded no chilling hours until after the first lift (early November) in year 1, and after the third lift (early December) in year 2. During both years New Kent received chilling hours more than a month before the first lift.

Linear correlations between chilling hour sum and RGP over both nurseries were very inconsistent among years

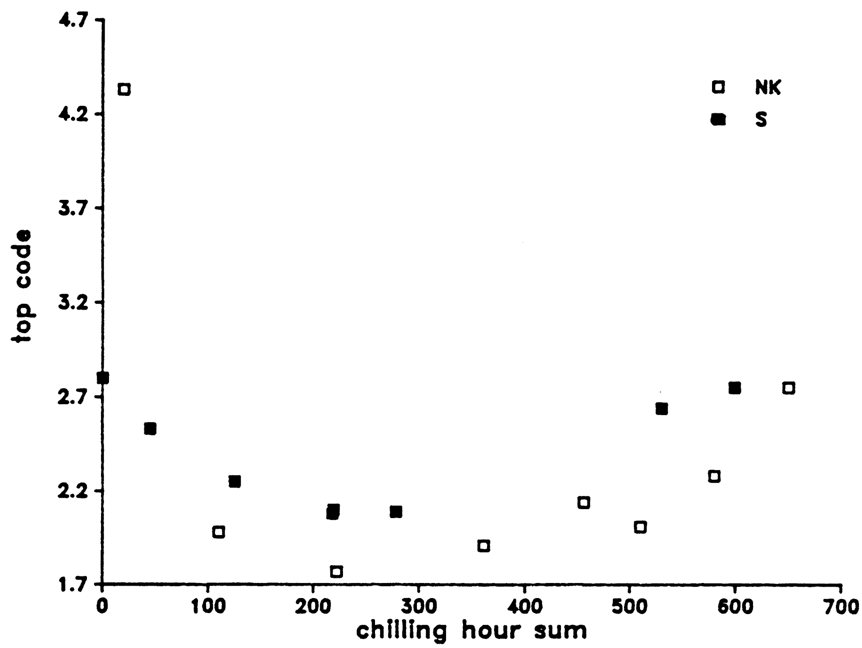

Figure 6. Loblolly pine seedling top code (status of the terminal) plotted over chilling hour sum for the New Kent VA (NK) and Summerville SC (S) nurseries during the 1984-85 lifting season.

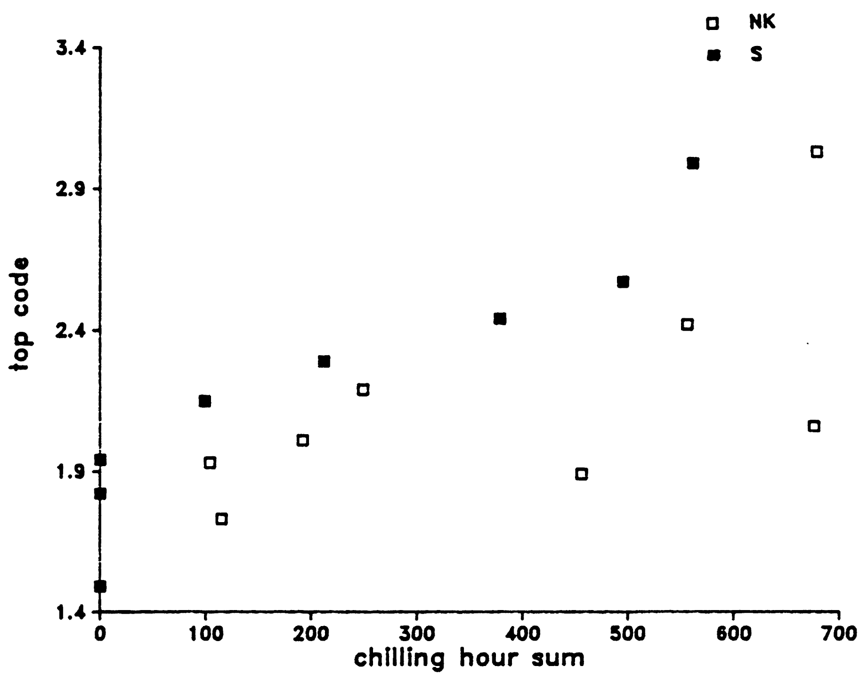

Figure 7. Loblolly pine seedling top code (status of the terminal) plotted over chilling hour sum for the New Kent VA (NK) and Summerville SC (S) nurseries during the 1985-86 lifting season.

(Table 10). Also a plot of RGP over chilling hour sum does not indicate a broad relationship with both nurseries (Figures 8 and 9). The correlation between chilling hours accumulated over both nurseries and RGP was not significant in year 1, but was highly significant in year 2 (r = .47, Table 10). During both years the correlation between Julian date (days after October 1) and RGP was much stronger than the chilling hour correlation, and was highly significant (Julian date 1984-85, r = .38; 1985-86, r = .62; Table 10).

After analyzing the data by nursery, the results changed greatly, as the New Kent seedlings were exposed to cooler temperatures, but overall had lower RGP values. In year 1 the RGP of New Kent seedlings was well correlated with chilling hours (r = .54; Figure 8) and with Julian date (r = .52; Table 10). However, the RGP of Summerville seedlings in year 1 was not significantly correlated with chilling hours, but was strongly correlated with Julian date (r = .41; Table 10).

During year 2, the relationship from nursery to nursery reversed completely. The RGP of New Kent seedlings was not significantly correlated with chilling hours, but was correlated with Julian date (r = .41; Table 10). In year 2 Summerville seedling RGP was very strongly correlated with chilling hour sum (r = .86; Figure 9) and Julian date (r = .83; Table 10).

Table 10. Correlation coefficients relating number of new roots (> 0.5 cm) for loblolly pine seedlings, chilling hour sum, and Julian date (days after October 1), for the New Kent and Summerville nurseries, and combined, during the 1984-85 and 1985-86 lifting seasons. n = 8.

	---------- 1984-85 ----------		
	combined	New Kent	Summerville
chilling hours	ns[1]	.54 *	ns
Julian date	.38 *	.52 *	.41 *
	--------- 1985-86 ---------		
chilling hours	.47 *	ns	.86 *
Julian date	.62 *	.41 *	.83 *

[1] ns indicates no significant correlation.
* denotes significance at the p < .001 level.

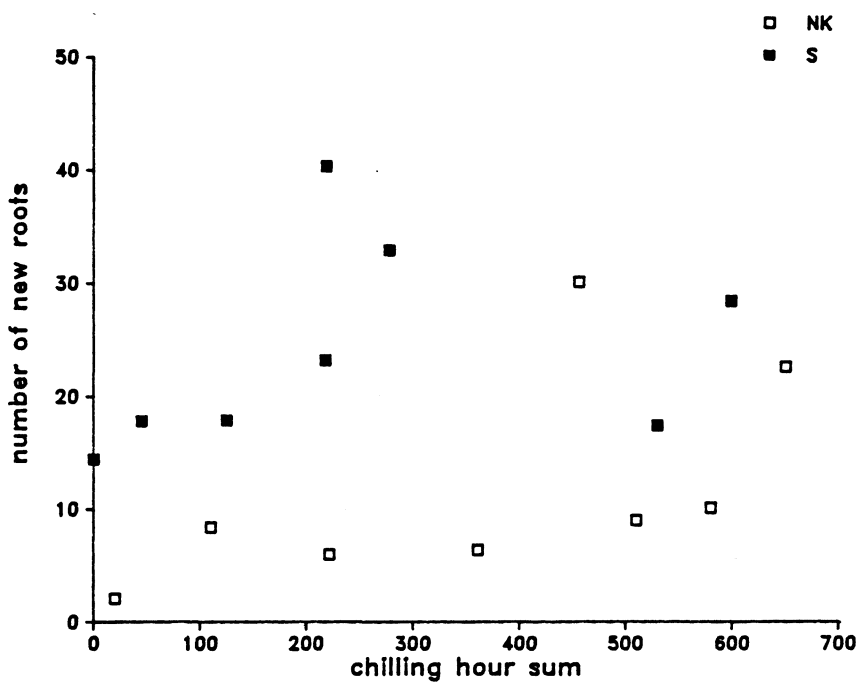

Figure 8. Mean number of new roots (> 0.5 cm) plotted over chilling hour sum for the New Kent VA (NK) and Summerville SC (S) nurseries for the 1984-85 lifting season.

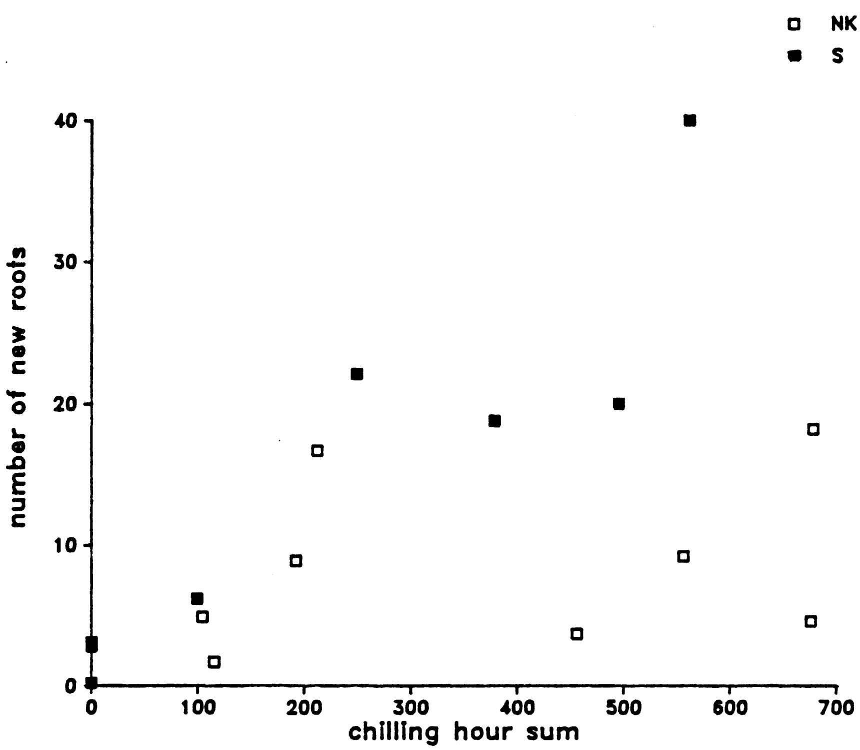

Figure 9. Mean number of new roots (> 0.5 cm) plotted over chilling hour sum for the New Kent VA (NK) and Summerville SC (S) nurseries for the 1985-86 lifting season.

EXPERIMENT I DISCUSSION

The overall RGP patterns were not similar from year to year, (Figures 4 and 5), except in the broadest sense. During both years RGP was low during the autumn, increased in December, then declined in January before another large increase in February. This pattern agrees with other loblolly pine studies, except for the December peak (Feret et al. 1985a, Brissette and Roberts 1984, Rhea 1977). Mean values were higher at both nurseries during the 1984-85 season (Table 6), primarily due to the very high peak on December 26.

No lifts were done after mid-February, thus the RGP decline often associated with the resumption of height growth in the spring was not observed in this study. The last 2 lifts in both years were between January 22 and February 13, and RGP values were very similar between years, for these lifts (Figures 4 and 5). The most notable difference from year to year was the very high peak in late December 1984, which resulted in the highest observed RGP for year 1, at each nursery. The second highest RGP levels in 1985-86 for each nursery occurred in December, although the lifts were 2 weeks apart (Figure 3). The possibility that mutual, higher peaks may not have been sampled between lifts has been hypothesized by DeWald (1986). If this was the case, the peak date could have corresponded identically with the peak in year 1.

RGP levels were much higher during year 1 at the Summerville nursery (Table 6), yet the RGP pattern was much more consistent than at the New Kent nursery (Figures 4 and 5). However, at New Kent the overall RGP levels were much more similar from year to year (Table 6), with the 1984-85 season having slightly higher RGP. DeWald's (1986) study compared loblolly pine seedlings from the New Kent nursery during the 1983-84 and 1984-85 seasons, and found RGP levels to be higher in the second year. She noted that the 1984-85 seedlings were larger, with heavier root systems, than the 1983-84 seedlings. Root growth is a shoot mediated process (Ritchie and Dunlap 1980), and presumably seedlings with larger shoots could provide more metabolites for the root system. No evidence of this relationship was found in the present study as there were only weak correlations between shoot size and RGP (Table 9).

Summerville seedlings were larger in year 1 than in year 2 by every measure except height (Tables 7 and 8). Root systems, especially lateral roots, were much heavier at Summerville in year 1. Others (DeWald 1986, Carlson 1985, Rhea 1977), have reported relationships between lateral root size and RGP. The strong relationship between lateral root dry weight and RGP is expected, as DeWald (1986) has shown that most of the new root growth during the RGP test originated on the lateral roots. New Kent seedling size was more consistent from year to year, and overall RGP levels were more consistent from year to year. However, measures of seedling size (shoot height and weight, caliper) were poorly correlated with RGP during both years, and at both nurseries (Table 9).

The large consistent differences between nurseries could be due to many factors. Summerville seedlings had heavier lateral root systems, and smaller shoots than New Kent seedlings (Tables 7 and 8), which resulted in a higher root/shoot ratio. The undercutting and lateral root pruning practiced at the Summerville nursery likely influenced both morphological attributes.

The relationship between RGP and shoot phenology (top code) was somewhat contradictory from year to year. RGP was well correlated with top code in year 2, but not in year 1 (Table 9). In the early lifts in year one, the shoots were still growing, and top code values were high (Figure 6) when RGP values were low. Later, the unusually high RGP peak on December 26 occurred when seedling shoots were very dormant (Figure 6). In year 2 seedling shoots and roots were dormant during the early lifts, as evidenced by low RGP and top code, and both shoots and roots became progressively more active later in the season (Figures 7 and 9). Hence, in year 2 top code was well correlated with RGP. A relationship between dormancy release in the late winter and RGP is believed to be present because the stimulus for root growth apparently comes from the shoot (Ritchie and Dunlap 1980). However, in this experiment top code and RGP were not consistently related from year to year.

In other species RGP is closely correlated with the number of chilling hours received, with peak RGP values occurring at the fulfillment of this requirement (Ritchie and Dunlap 1980, van den Driessche 1977). Although southern provenances of loblolly pine do not become fully dormant in the winter (Saranthus 1968, Perry et al. 1966), cessation and later commencement of shoot activity of sources north of approximately 34° N latitude may be related to a chilling requirement (Boyer and South 1985, Cannell 1985, Garber and Mexal 1980). The increasing activity of the terminal bud through the lifting season supports these findings, as the seed sources were from the Virginia Piedmont, well north of 34th parallel.

A strong relationship between chilling hours and RGP was not found (Figures 8 and 9, Table 10). Chilling sum and RGP were strongly correlated during year 1 for New Kent seedlings. However, Summerville seedling RGP in year 1 was not correlated with the number of chilling hours received, but was strongly correlated with Julian date (days after Oct. 30). In year 2 these findings were completely reversed by nursery. The milder climate at the Summerville nursery resulted in slower accumulation of chill hours, yet New Kent seedling RGP surpassed Summerville seedling RGP during the early lifts only in year 2.

The early advantage in RGP of New Kent over Summerville seedlings may have been caused by the Summerville location not receiving any chilling hours during the first 3 lifts in year 2. Possibly some chilling hours are needed for the seedling to enter the metabolic phase marked by increasing RGP, whereas shoot dormancy release requires a greater number of chilling hours. In year 1, Summerville RGP exceeded New Kent RGP on every lift date, and the first chilling hours at Summerville were recorded 6 weeks earlier than in year 2. Also in year 1, the first chilling hours were recorded only 1 lift later at Summerville than at New Kent.

The low RGP in the early lifts (before mid-December) may be related to changes in seedling metabolism. Southern pines were found to accumulate reserve carbohydrates after shoot growth had ceased in the autumn (Kramer and Kozlowski 1979). The seasonal carbohydrate cycle is thought to affect RGP responses (Rose and Whiles 1984). Cannell (1985) concluded, largely from the report by Carlson (1985), that loblolly pine roots do not grow when the buds are in a state of rest. Year 1 results of the present study disagrees with Cannell's (1985) conclusion because RGP peaked in year 1 when the shoots were most dormant (Dec. 26). However in year 2, RGP and shoot activity (top code) where significantly correlated.

RGP is usually low in the autumn and increases during the winter. It is often hypothesized that after fulfillment of the chilling requirement the shoot sends stimuli to the roots triggering rapid initiation and elongation of new roots, under favorable conditions (Cannell 1985). Commonly reported high RGP levels in early spring may also be linked to increased photosynthetic rates at this time (Ledig and Perry 1969, Davis et al. 1963). Possibly if lifting had continued through February and March, a much higher RGP peak would have been observed at both nurseries, before the RGP decline associated with the resumption of shoot growth occurred.

An alternative explanation for low RGP values are due to the breaking and damaging of unsuberized roots during lifting. New white root tips were observed at both nurseries during the earliest lifts (before late November). Root suberization is most complete when root growth is at a minimum, ie. mid to late winter (Carlson 1985). Possibly the active root systems were damaged during early lifts resulting in low RGP levels. Other studies have also indicated that the root system is most tolerant of handling during periods of high RGP (Ritchie et al. 1985, Ritchie and Stevens 1979).

RGP levels between families were markedly different overall, and the rank order changed a great deal by lift date (Tables 4 and 5) as was reported by DeWald (1986). However, the peak values occurred at both nurseries on the same dates, and all but one family (6-20), in one year (1984-85), exhibited peaks on the same date. DeWald (1986) reported that various families did peak on different dates, but she thought that a central, larger peak may not have been sampled.

The fact that peaks also were observed at both nurseries simultaneously, indicates that RGP patterns are under internal control (Drew and Ledig 1981), and the absolute levels are mediated by current seedling status (shoot dormancy, available carbohydrates, etc.) which is influenced by cultural practices and environmental conditions (Ritchie and Dunlap 1980). DeWald (unpublished) also examined the effect of greenhouse temperature fluctuations on RGP and found few correlations between RGP and the mean, maximum, or minimum daily temperatures experienced during the RGP test period.

Strong RGP patterns by seed source have been reported for Douglas-fir (Jenkinson 1984, Jenkinson and Nelson 1978), and ponderosa pine (Jenkinson 1980; 1975), but were not observed for loblolly pine by Dewald (1986) or in the current study. Only 4 half-sib families were used, and they were not typical, as the seed orchard mix of many families (42-M) usually outperformed the other seedlots. Also, all of the seedlots used originated from the same Virginia Piedmont provenance, hence markedly different RGP patterns were not expected.

No seedlot-specific windows of high RGP levels were found, as have been reported for other species (Jenkinson 1984, Ritchie et al. 1985). RGP tended to increase and decline sharply, with family rank changing markedly by lift date. These sharp fluctuations may have been due to sampling error. Freyman and Feret (1987), have applied sampling size equations to RGP analysis, and concluded that a sample of 45-60 seedlings is required to differentiate 80% of the time between means that differ by 30%, at a significance level of 0.05. They used a hydroponic growing system and the square root transformation of new root number. Using untransformed new root number would require a larger difference between means to be detectable. Hence, the 30 seedling samples used in this study may have been inadequate to detect actual differences between individual family, nursery, and lift date combinations. However, all other analyses of this study were done on combined samples. Hence for the nursery x lift date effect 300 seedlings were sampled on each lift date, and for the family x lift date effect 60 seedlings from each family were sampled on each lift date.

A minimum of 10 new roots may be considered a threshold value, to indicate that seedlings are in good physiological condition for lifting, storage, and planting (Barden et al. 1987). If a minimum of 10 new roots is used as a lifting criteria, all seedlots at Summerville except 11-137 were ready to be lifted after late October in year 1 (Table 4). However in year 2, Summerville seedlings did not average over 10 new roots until late December (Figure 4).

At the New Kent nursery, no 2 consecutive lifts averaged over 10 new roots, during either year (Figure 5). During the 1984-85 lifting season at New Kent, only family 6-20 sustained a high level of RGP for more than 2 consecutive lifts (Table 4). In year 2, no family exceeded 10 new roots for longer than 2 lifts (Table 5). Therefore, with these 5 seedlots, a broad lifting window appears to occur at Summerville, while at New Kent RGP rarely reached an acceptable level (defined as 10 new roots).

EXPERIMENT II RESULTS

All main effects (planting date, nursery, family and field block), were highly significant during both years of the study (Tables 11 and 12). The only significant interactions were nursery x planting date and nursery x family, which occurred during both years. Means separated by Duncan's New Multiple Range Test for all planting dates, family, nursery, and year combinations are in Tables 13 and 14.

Comparison of RGP among planting dates and between years

During both years RGP declined sharply during storage from fresh lift levels (Figures 10 and 11). During year 1, however, RGP increased greatly on the fourth planting date, after approximately 12 weeks in cold storage. This resulted in the highest RGP values for New Kent seedlings, and the second highest values for Summerville seedlings over the entire storage duration (Figure 10). In year 2 RGP declined greatly in storage. After only 3 weeks of storage RGP fell by more than 50% in seedlings from both nurseries (Figure 11). RGP continued to decline in year 2, but at a slower rate during the subsequent storage durations. No temperature or humidity problems were noted at the VDF Charlottesville storage facility.

Table 11. ANOVA table for number of new roots (> 0.5 cm) for loblolly pine seedlings sampled from the 1985 planting season.

Source	df	SS	F	p
planting date	4	5525.0	54.62	.0001
nursery	1	2783.3	110.16	.0001
family	4	752.8	7.44	.0001
block	3	316.4	4.17	.007
nursery*family	4	340.1	3.36	.01
nursery*planting date	4	1248.0	12.34	.0001
family*planting date	16	572.7	1.42	.1
nursery*family *planting date	16	354.9	0.88	.6
error	147	3717.5		

Table 12. ANOVA table for number of new roots (> 0.5 cm) for loblolly pine seedlings sampled from the 1986 planting season.

Source	df	SS	F	p
planting date	4	1554.5	16.19	.0001
nursery	1	5280.9	219.99	.0001
family	4	1578.8	16.44	.0001
block	3	317.6	4.41	.005
nursery*family	4	515.8	5.37	.0005
nursery*planting date	4	641.1	6.68	.0001
family*planting date	16	541.2	1.41	.1
nursery*family *planting date	16	331.0	0.86	.6
error	147	3528.7		

Table 13. Mean total number of new roots (> 0.5 cm) for loblolly pine seedlings from 5 families and the New Kent VA (NK) and Summerville SC (S) nurseries, over the 5 planting dates in 1985.

family	planting date: -- Mar. 4 -- NK	S	-- Mar. 26 -- NK	S	-- Apr. 17 -- NK	S	-- May 9 -- NK	S	-- May 30 -- NK	S
11-137	7.13 a[1]	17.91 b	4.38 b	8.81 b	1.84 b	6.09 bc	14.00 a	16.81 a	1.72 a	2.19 bc
42-M	9.34 a	25.03 ab	11.56 a	20.88 a	6.34 a	14.69 a	14.22 a	19.49 a	1.72 a	6.59 a
6-20	4.84 a	18.44 b	3.13 b	11.13 b	2.66 b	1.16 c	14.20 a	22.56 a	2.23 a	1.00 c
6-8	5.56 a	32.50 a	2.06 b	14.31 ab	2.16 b	14.13 a	12.59 a	23.22 a	2.91 a	1.31 c
6-9	6.66 a	18.91 b	4.81 b	12.97 ab	2.44 b	9.69 ab	14.50 a	20.56 a	3.00 a	4.66 ab
mean	6.71 b	22.56 a	5.20 b	13.62 a	3.09 b	9.15 a	13.90 b	20.53 a	2.84 a	3.15 a

[1] Means within a column followed by the same letter are not significantly different using Duncan's New Multiple Range Test at the p < .05 level. Column means are compared within a planting date.

Table 14. Mean total number of new roots (> 0.5 cm) for loblolly pine seedlings from 5 families and the New Kent VA (NK) and Summerville SC (S) nurseries, over the 5 planting dates in 1986.

	planting date									
	-- Mar. 3 --		-- Mar. 25 --		-- Apr. 16 --		-- May 8 --		-- May 29 --	
family	NK	S	NK	S	NK	S	NK	S	NK	S
11-137	4.16 ab[1]	12.44 b	0.94 ab	10.78 c	2.84 ab	4.23 c	1.19 a	4.29 a	0.41 a	3.41 b
42-M	10.97 a	18.57 ab	2.19 a	19.81 ab	6.09 ab	20.41 ab	3.41 a	9.22 a	2.53 a	5.69 b
6-20	2.60 b	14.87 ab	0.88 ab	16.88 ab	0.75 b	9.41 bc	0.82 a	7.54 a	0.44 a	8.60 ab
6-8	2.97 b	19.69 ab	0.44 b	12.72 b	2.66 ab	13.72 abc	1.10 a	6.59 a	0.84 a	10.37 ab
6-9	8.69 ab	24.69 a	0.63 b	24.59 a	10.72 a	24.20 a	2.29 a	8.54 a	1.91 a	18.13 a
mean	5.88 b	18.05 a	1.01 b	16.96 a	4.61 b	14.39 a	1.76 b	7.23 a	1.23 b	9.24 a

[1] Means within a column followed by the same letter are not significantly different using Duncan's New Multiple Range Test at the $p < .05$ level. Column means are compared within a planting date.

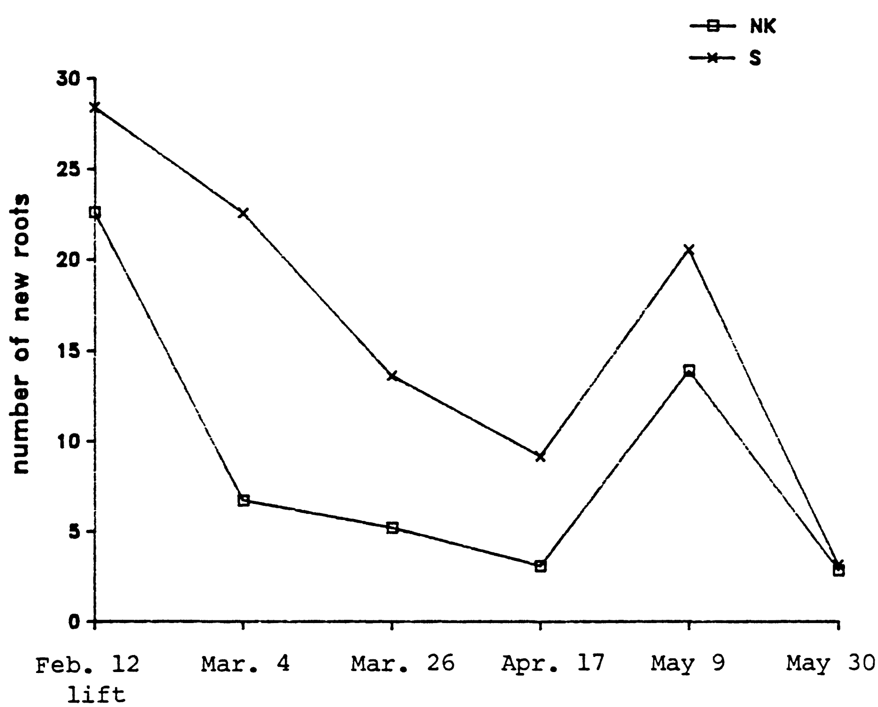

Figure 10. Mean number of new roots (> 0.5 cm) of loblolly pine seedlings plotted over planting date for the New Kent VA (NK) and Summerville SC (S) nurseries during the 1985 planting season.

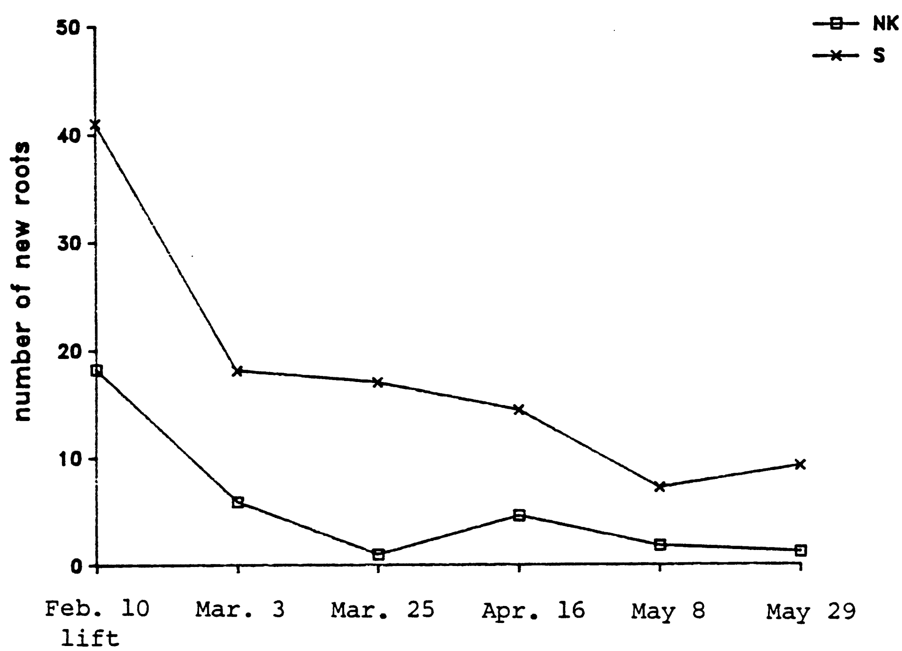

Figure 11. Mean number of new roots (> 0.5 cm) of loblolly pine seedlings plotted over planting date for the New Kent VA (NK) and Summerville SC (S) nurseries during the 1986 planting season.

Comparing RGP among families and between years

The rankings of the families by RGP after storage were similar from year to year, with the exception of the 6-8 and 6-9 families which were juxtaposed (Table 15), as they were over the 2 lifting seasons. The seed orchard mix (42-M) was the only seedlot ranked first or second during both years.

In both years the ranking of the families on lift 8 of Experiment I (which was the source for the outplanted seedlings), was very similar to the ranking over the planting season. In year 1 family 6-20 deviated from this pattern. 6-20 had the highest RGP on the last lift, but was ranked fourth over the planting season (Table 15). The variable family rankings by nursery resulted in the significant family x nursery interaction (Table 15).

Comparing RGP among nurseries and years

During both planting seasons Summerville seedlings had significantly higher RGP levels than New Kent seedlings (Figures 10 and 11), for every planting date, except the last planting in 1985. Summerville seedling mean RGP over all storage durations was virtually identical from year to year (Table 15). The mean RGP of New Kent seedlings was significantly lower during year 2 plantings (Table 15), due to the absence of the large increase after extended cold

Table 15. Mean number of new roots (> 0.5 cm) for loblolly pine seedlings of 5 families from the New Kent VA and Summerville SC nurseries during the 1985 and 1986 outplantings.

	---- 1985 ----		---- 1986 ----	
family	New Kent	Summerville	New Kent	Summerville
11-137	5.84 ab[1]	10.39 b	3.72 bc	7.30 d
42-M	9.19 a	17.35 a	6.02 ab	14.74 b
6-20	5.41 b	10.84 ab	1.82 c	11.46 c
6-8	5.07 b	17.11 a	3.01 c	12.70 bc
6-9	6.29 ab	13.39 ab	7.11 a	20.03 a
mean	6.36 b	13.82 a	4.34 b	13.25 a

[1] Means within a column followed by the same letter do not differ significantly using Duncan's New Multiple Range Test at the $p < .05$ level. Column means are compared within a year.

storage which occurred in 1985. Within each year, RGP of seedlings from both nurseries declined similarly in storage (Figures 10 and 11).

New Kent seedlings averaged less than 7 new roots on every planting date, except planting 4 in year 1, while Summerville seedlings averaged more than 7 new roots for each storage duration, except planting 5 in year 1 (Figures 10 and 11). The decreasing differences between seedlings from the 2 nurseries over the longer storage durations caused the strong nursery x planting date interactions.

1985 outplanting survival

The ANOVA results for the transformed survival data are in Table 16. Planting date, nursery, and family all had highly significant effects on survival. No interactions were significant.

There was no obvious trend in survival across the planting dates (Table 17), possibly due to the opposing influences of increasing rainfall (Table 17), and decreasing RGP (Figure 10) over the planting season. The seed orchard mix (42-M) had significantly higher survival than the 4 half-sib families (Table 18). For New Kent raised seedlings survival did not vary significantly among the half-sib families. For Summerville raised seedlings the only significant difference among seedlots was that 6-20 was

Table 16. ANOVA table for the angular transformation of first year survival (plot means) of loblolly pine seedlings planted during 1985.

Source	df	SS	F	p
planting date	4	0.707	5.34	.0006
nursery	1	2.365	69.28	.0001
family	4	0.526	3.86	.005
block	3	0.061	0.59	.6
nursery*family	4	0.174	1.27	.3
nursery*planting date	4	0.285	2.08	.2
family*planting date	16	0.662	1.21	.3
nursery*family planting date	16	0.374	0.69	.8
error	147	5.018		

Table 17. Mean first year survival and height increment (cm) of loblolly pine seedlings planted in 1985, by planting date, n = 40. Rainfall values are total rainfall (cm) received from 2 weeks before until 2 weeks after each planting date.

planting date	survival (%)	height (cm)	rainfall[2] (cm)
March 4	72.2 b[1]	14.5 a	1.30
March 26	80.2 a	14.7 a	2.56
April 17	70.2 b	11.8 b	0.94
May 9	82.0 a	12.4 b	6.07
May 30	72.2 b	9.5 c	11.76

[1] Survival and height means followed by the same letter do not differ significantly using Duncan's New Multiple Range at the $p < .05$ level.

[2] Rainfall data was obtained from the Buckingham VA Station of the State Climatology Office.

Table 18. Mean first year survival for loblolly pine seedlings from 5 families raised at the New Kent VA and Summerville SC nurseries, averaged over all 1985 outplantings.

family	New Kent	Summerville	mean
11-137	67.4 b[1]	82.2 ab	74.8 b
42-M	76.2 a	89.0 a	82.6 a
6-20	64.6 b	78.8 b	71.7 b
6-8	61.0 b	87.6 ab	74.3 b
6-9	65.6 b	80.8 ab	73.2 b
mean	67.0 b[2]	83.7 a	

[1] Means within a column followed by the same letter do not differ significantly using Duncan's New Multiple Range Test at the $p < .05$ level.

[2] Column means are compared between nurseries.

ranked last, and 42-M was ranked first. Summerville seedlings had significantly higher survival overall (Table 18).

Relating survival to RGP

Field survival was significantly correlated with RGP on all planting dates except the last one (Table 19, Figure 12). The overall correlation was strong and highly significant ($r = .52$). Simple linear regression was used to model survival over all planting dates as a function of new root number. New root number regressed on the logit ($\log_{10}$ $(X/1-X)$) of survival percentage provided the best fitting linear model ($r^2 = .31$; Figure 13). When the data was analyzed by family there were no significant correlations between survival and RGP.

Non-linear regression (Gauss-Newton method) was used to relate untransformed survival to the number of new roots. A satisfactory model could not be formed. Various transformations of new root number did not improve results. Using the logit of survival yielded only a fair model, with a pseudo r-square of .20. The residual plots were randomly distributed. After deleting values from the fifth planting date, the pseudo r-square increased to .28, which indicates the effect of the fifth (last) planting date anomaly.

After analyzing the data by planting date to

Table 19. Correlation coefficients between first year survival, height increment (cm), and number of new roots, for loblolly pine seedlings outplanted in 1985, by planting. n = 10.

	planting date					
	overall	Mar. 4	Mar. 26	Apr. 17	May 9	May 30
survival	.52 ***[1]	.84 **	.79 **	.73 **	.56 *	.27 ns
height increment	.80 ***	.91 ***	.85 **	.80 **	.81 **	.31 ns

1 *** indicates signifance at the p < .001 level.
** denotes significance at the p < .01 level.
* denotes significance at the p < .1 level.
ns denotes no significant correlation.

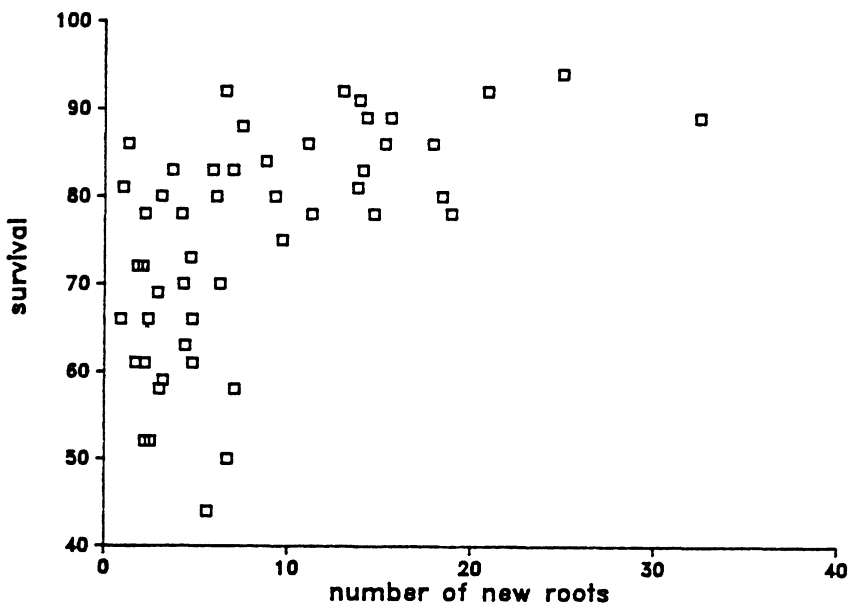

Figure 12. First year survival plotted over new root number for the 1985 planting season. Each point represents a mean across blocks of 64 seedlings for survival, and 32 seedlings for new root number.

logit of survival = .3206 + .0264 (nroots)

$r^2 = .31 \quad p < .001$

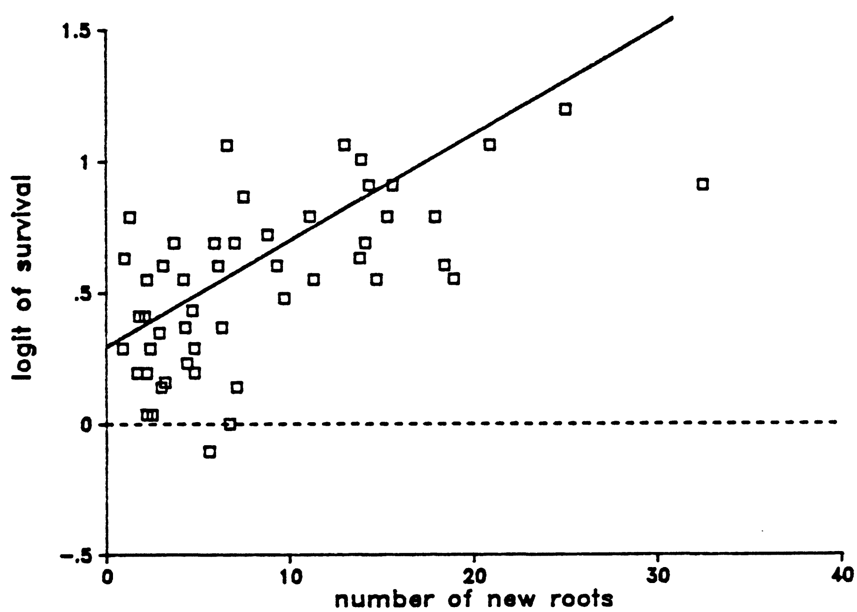

Figure 13. Relationship over all plantings of the logit of survival to new root number. Each point represents a mean across blocks of 64 seedlings for survival, and 32 seedlings for new root number. ——— indicates the regression line.

eliminate the confounding effects of different soil and weather conditions, the fit of the various models improved greatly. The $\log_{10}$ transformation of number of new roots resulted in a good fit. A small improvement in the r-square value could be obtained by relating the logit of survival to the square root of new root number. For simplicity the model using the $\log_{10}$ of new root number and untransformed survival was used (Figures 14 to 18). Only the final planting date failed to show a significant relationship between survival and RGP.

1985 height increment

The ANOVA results for height increment are in Table 20. All main effects were highly significant, including field block. Only the nursery x family interaction was significant.

There was a steady decline in height increment over the planting dates (Table 17). There were differences among families, and overall differences among nurseries were the most consistent effect (Table 21). New Kent seedlings averaged only 48% of the height increment that Summerville seedlings averaged. The 42-M seedlot had the largest height increment, when grown at either nursery. The nursery x family interaction is evident in Table 21, as 6-20 was ranked second in height increment when raised at New Kent,

Survival = .1597 + .5198 ($\log_{10}$ (nroots)

$r^2 = .76 \quad p < .001$

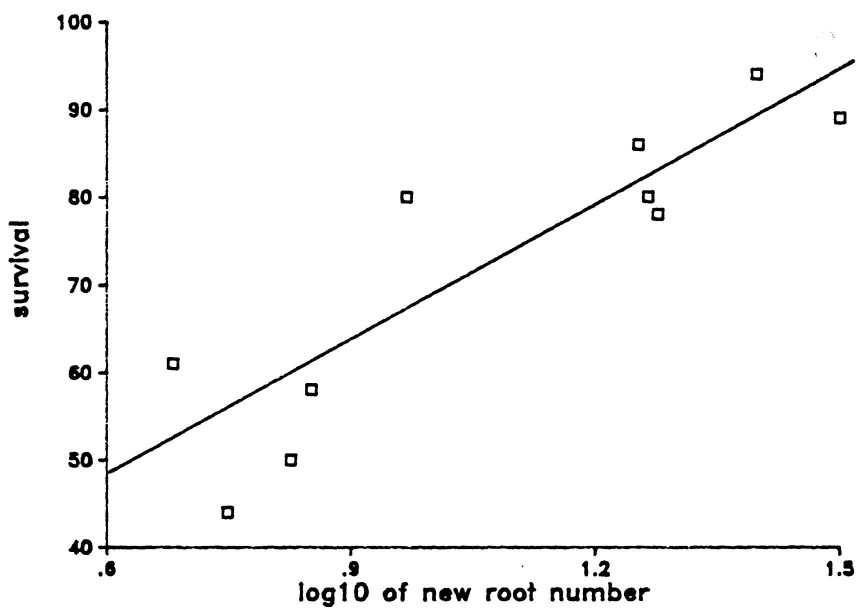

Figure 14. Relationship of survival to the $\log_{10}$ of new root number, for the March 4 planting. ——— indicates the regression line.

Survival = .5905 + .2411 ($\log_{10}$ (nroots)

$r^2 = .51$, $p < .01$

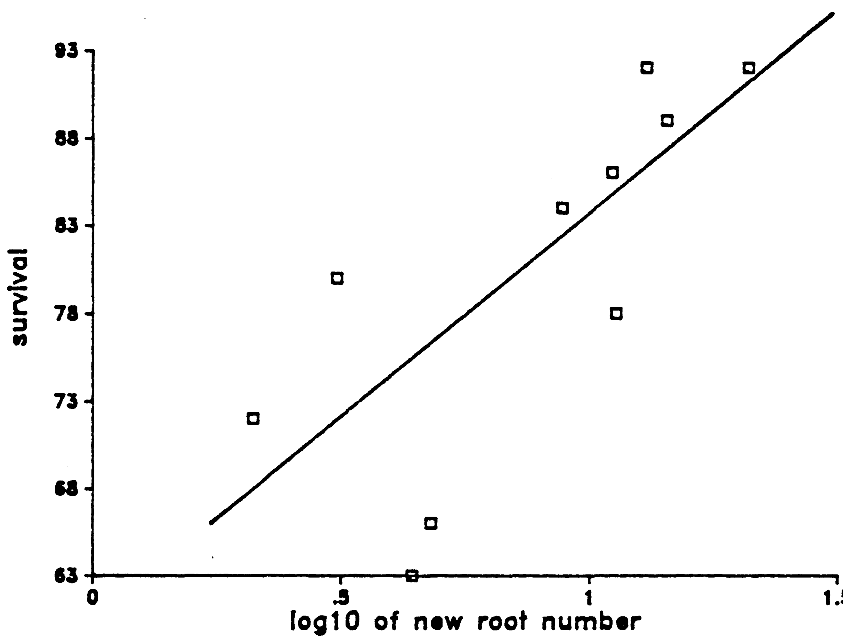

Figure 15. Relationship of survival to the $\log_{10}$ of new root number, for the March 26 planting. ——— indicates the regression line.

Survival = .6052 + .1573 ($\log_{10}$ (nroots)

$r^2 = .41 \quad p < .05$

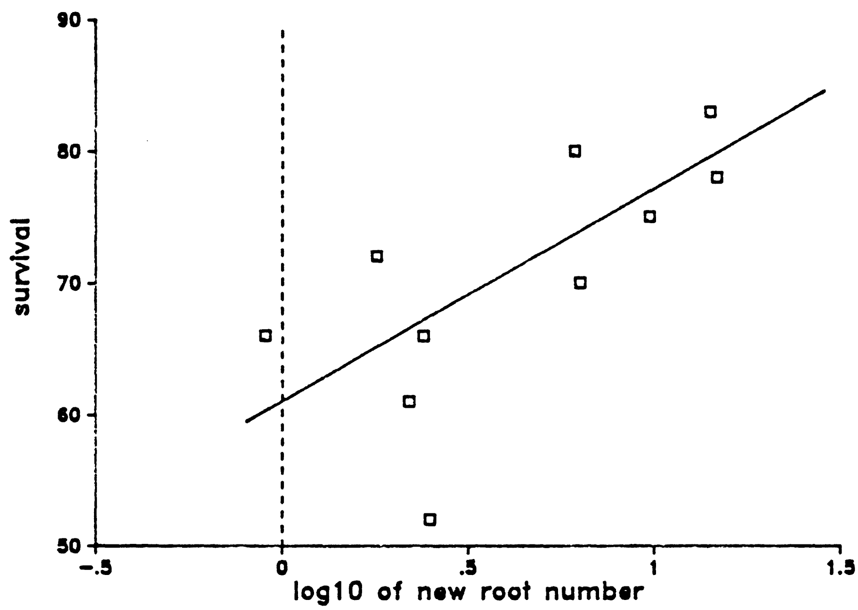

Figure 16. Relationship of survival to the $\log_{10}$ of new root number, for the April 17 planting. ——— indicates the regression line.

Survival = .7371 + .1446 ($\log_{10}$ (nroots)

$r^2 = .65$ $t < .005$

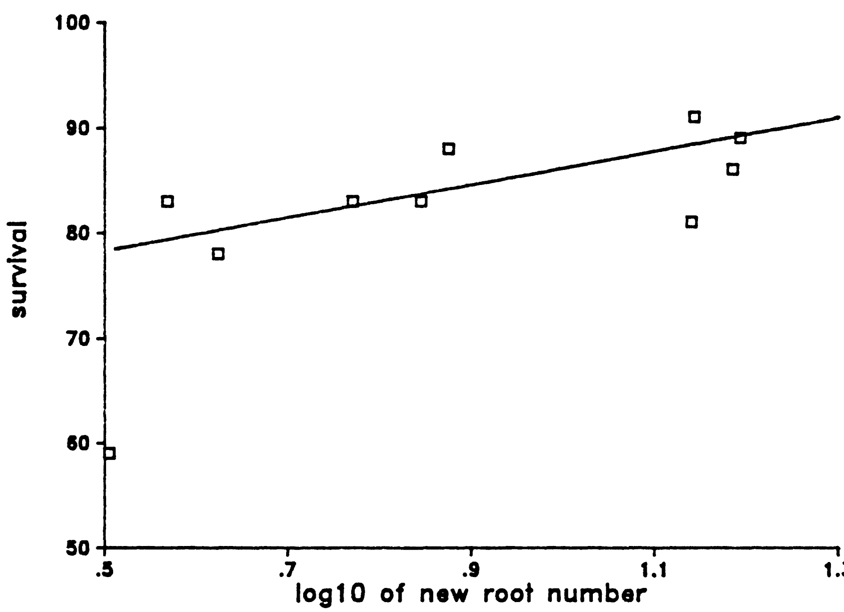

Figure 17. Relationship of survival to the $\log_{10}$ of new root number, for the May 9 planting. ——— indicates the regression line.

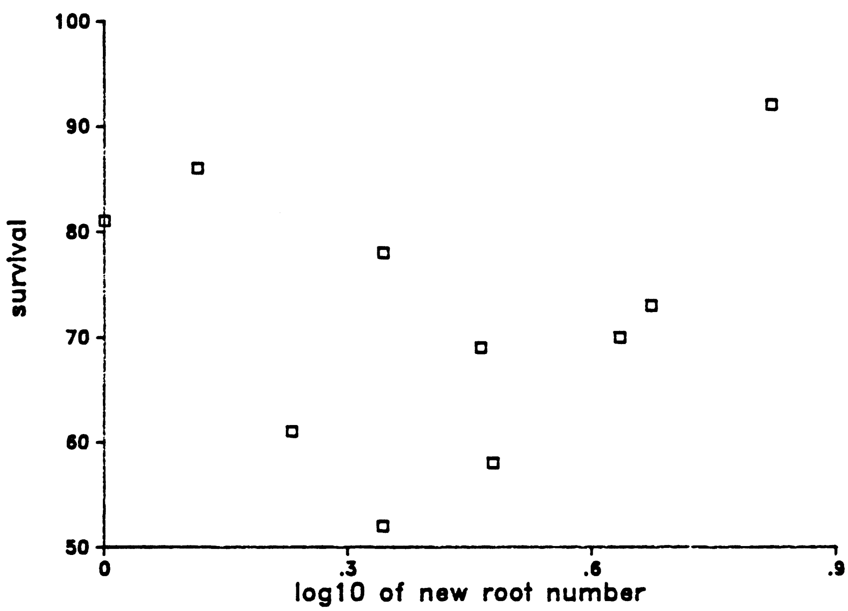

Figure 18. Relationship of survival to the $\log_{10}$ of new root number, for the May 30 planting. No significant regression was formed.

Table 20. ANOVA table for plot means of first year height increment (cm) of loblolly pine seedlings planted in 1985.

Source	df	SS	F	p
planting date	4	704.51	16.00	.0001
nursery	1	3800.18	345.28	.0001
family	4	337.54	7.67	.0001
block	3	221.70	6.71	.0003
nursery*family	4	130.45	2.96	.02
nursery*planting date	4	50.35	1.14	.3
family*planting date	16	70.72	0.41	.9
nursery*family planting date	16	105.40	0.60	.9
error	147	1617.87		

Table 21. Mean first year height increment (cm) of loblolly pine seedlings outplanted in 1985, by family and nursery.

	------ nursery ------		
family	New Kent	Summerville	mean
11-137	9.5 ab[1]	16.5 ab	13.2 bc
42-M	12.1 a	20.4 a	16.4 a
6-20	11.0 a	15.2 ab	13.2 c
6-8	9.0 b	17.9 ab	14.1 b
6-9	7.4 b	16.8 ab	12.6 c
mean	8.2 b	17.0 a	

[1] Means within a column followed by the same letter do not differ significantly using Duncan's New Multiple Range Test at the $p < .05$ level. Column means are compared by nursery.

but was ranked last when raised at Summerville. The height increment differences among blocks ranged from 11.7 cm to 14.3 cm.

Relating height increment to RGP

Height increment was significantly correlated with RGP over the first 4 planting dates. The overall correlation was very strong and highly significant (r = .80; Table 19). The trend of increasing height increment over increasing number of new roots was more nearly linear than the survival trend over RGP (Figure 19). Thus, various transformations only improved the model slightly. The final model used the square root of new root number (r = .65; Figure 20). Non linear regression was attempted, but no models were found superior to the simple linear regression, either in percent variation explained or the residual plots obtained. When the height increment data was analyzed by family, correlation coefficients between height and RGP were significant for every family.

After analyzing the data by planting date to eliminate the confounding effects of planting conditions, the fit of the models increased greatly (Figures 21 to 25). Untransformed new root number provided the best fit, but the last planting date resulted in no significant relationship between height increment and RGP for any transformation of

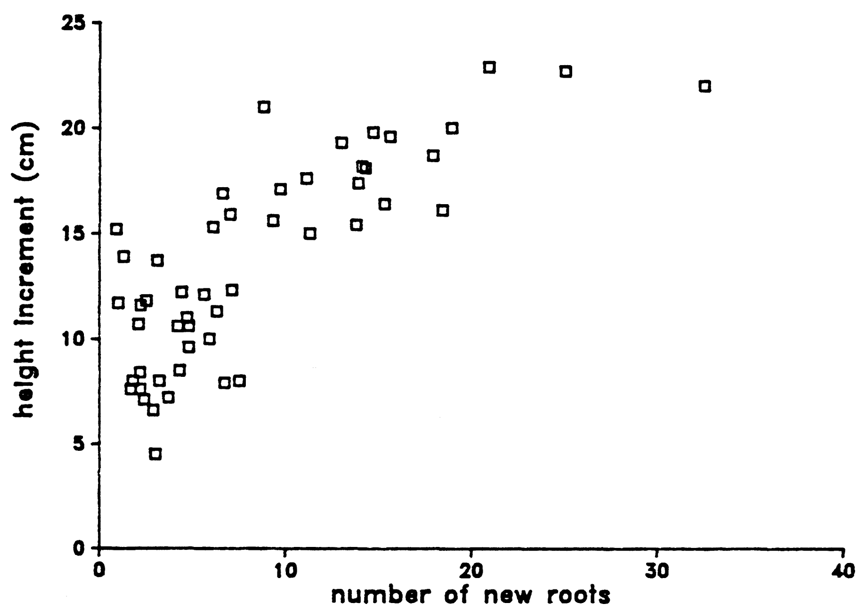

Figure 19. First year height increment (cm) plotted over new root number for the 1985 planting season. Each point represents a mean across blocks of surviving seedlings for height increment, and 32 seedlings for new root number.

height increment = 5.105 + 3.336 (square root (nroots)

$r^2 = .65 \quad t < .001$

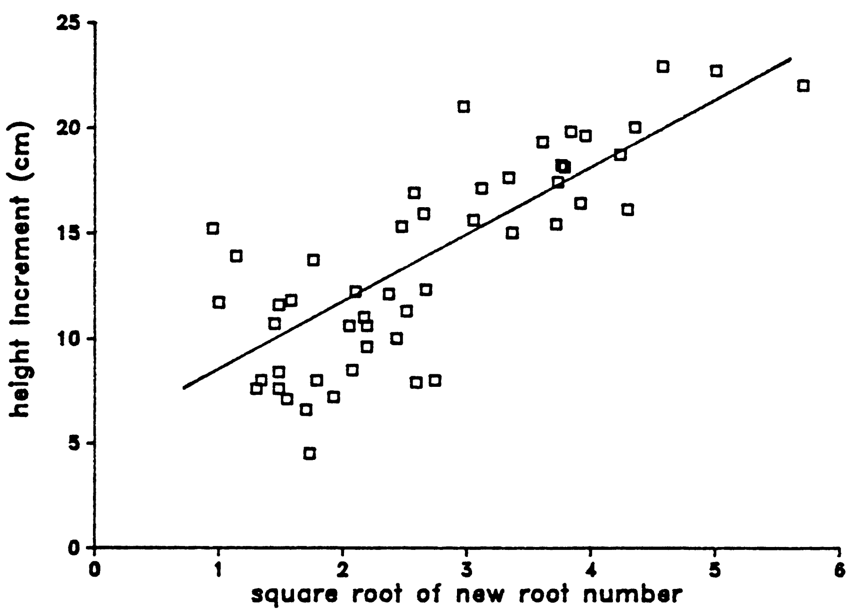

Figure 20. Relationship over all plantings of first year height increment (cm) to the square root of new root number. —— indicates the regression line.

height increment = 8.711 + .4859 (nroots)

$r^2 = .80 \quad p < .001$

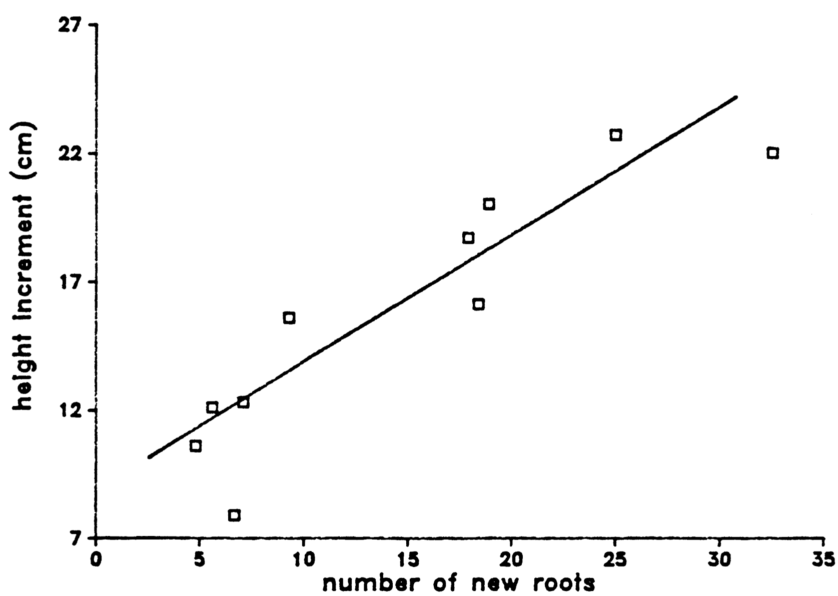

Figure 21. Relationship of first year height increment (cm) to new root number, for the March 4 planting. ——— indicates the regression line.

height increment = 10.023 + .6379 (nroots)

$r^2 = .68 \quad p < .005$

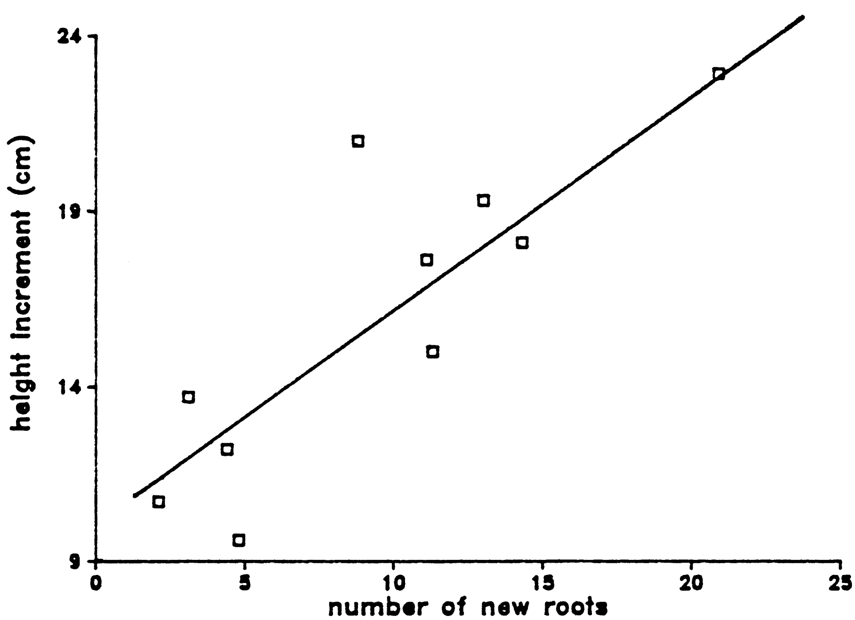

Figure 22. Relationship of first year height increment (cm) to new root number, for the March 26 planting. ——— indicates the regression line.

height increment = 8.795 + .7219 (nroots)

$r^2 = .60 \quad p < .005$

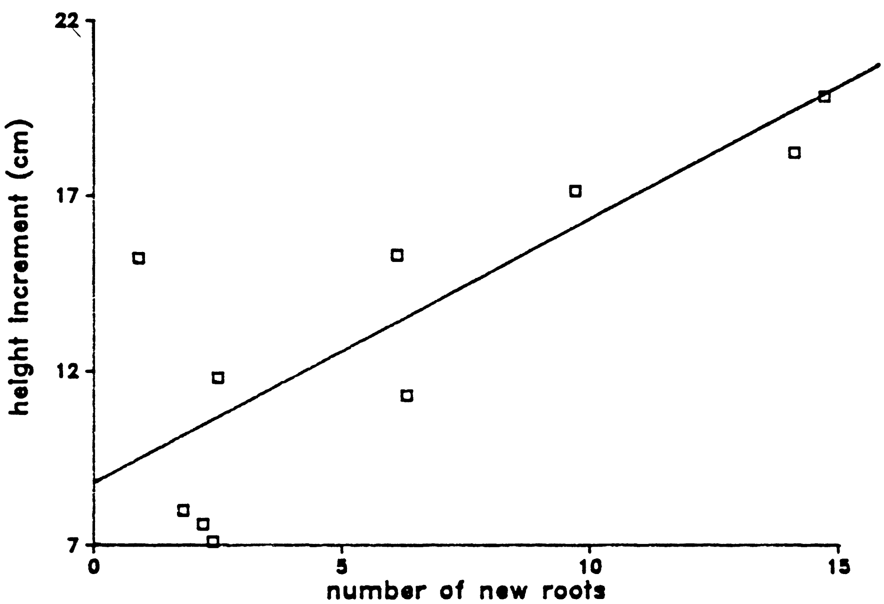

Figure 23. Relationship of first year height increment (cm) to new root number, for the April 17 planting. —— indicates the regression line.

height increment = 8.218 + .7677 (nroots)

$r^2 = .61 \quad p < .005$

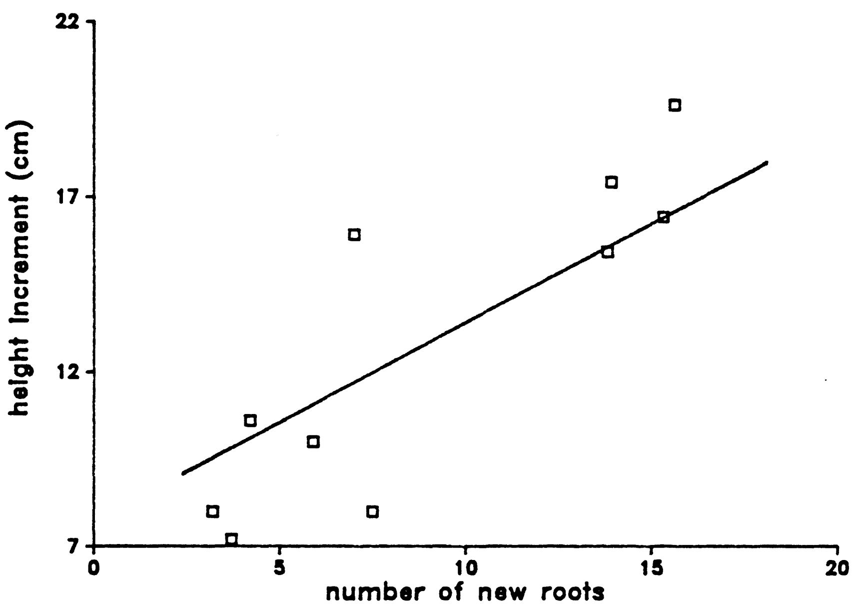

Figure 24. Relationship of first year height increment (cm) to new root number, for the May 9 planting. —— indicates the regression line.

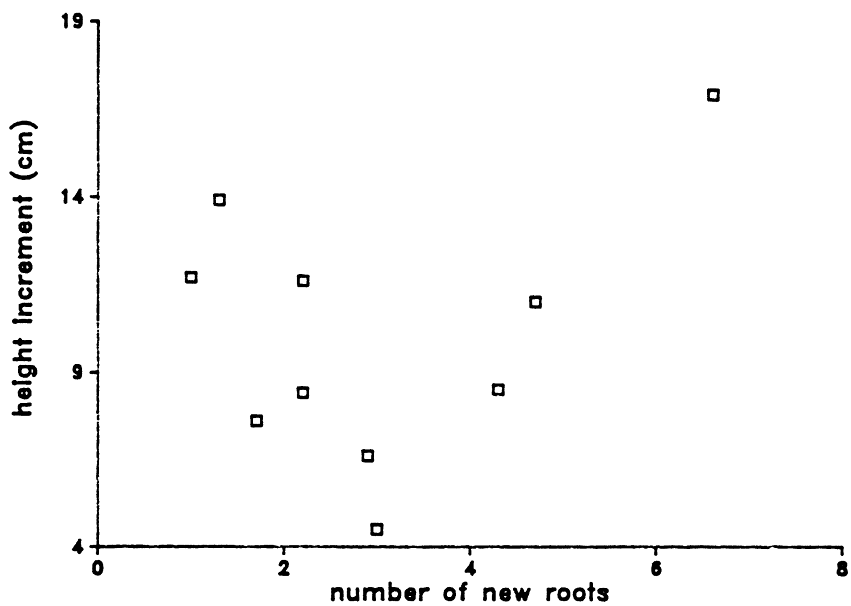

Figure 25. Relationship of first year height increment (cm) to new root number, for the May 30 planting. No significant model was formed.

RGP variables attempted.

EXPERIMENT II DISCUSSION

The rapid decline of RGP in storage during both years was unexpected and unusual. In year 2 RGP fell by more than 50% after only 3 weeks in storage. Other reports have shown loblolly pine can maintain high RGP for at least 12 weeks in cold storage (Barden and Feret 1986, Feret et al. 1985a). During both years the RGP of seedlings was high on the lift date which was stored for subsequent outplanting (Figures 10 and 11). The seedlings were hand lifted at both nurseries, roots were kept wet by dipping in water, and all sorting and packaging was done in an unheated shed, sheltered from the sun and wind.

Possible explanations for the decline in RGP are that the seedlings were stored too wet; this has recently been shown to reduce the RGP of seedlings cold stored in K-P bags (Barden and Feret 1986). No temperature or humidity problems were reported for the storage facilty. The sorting and packaging were done carefully to minimize seedling exposure, but they possibly were damaged at this time.

Many examples of poor storage success with early lifted seedlings have been reported (Ritchie 1984b, Ritchie and Dunlap 1980, Ritchie and Stevens 1979, Stone and Jenkinson 1971). However in this study, the seedlings from both nurseries had high RGP (> 18 new roots), on the lift that was stored both years. The most plausible explanation appears to be the possibility of excess moisture on the seedlings entering storage.

The 2 nurseries followed virtually identical trends in storage within each year. In year 1 early, rapid declines in RGP were followed by a sharp increase after 12 weeks in storage for seedlings from both nurseries (Figure 10). Large increases have been observed in other studies (Barden and Feret 1986, Feret et al. 1985c), just before and after rapid declines took place. An explanation for this "burst" of RGP may be that it is a response of the seedling to a stressful, anoxic environment. Evidence reported by Parrish and Davies (1977) for pea (Pisum sativum L.) seedlings indicates that auxins may be released from previously unavailable compartments following exposure to anoxic conditions. The apparent release of auxins caused pea stems to elongate 100% to 200% more than well oxygenated controls. Growth of pea seedlings is only an indirect indication of what may have occurred with the loblolly pine seedlings in storage, but auxins are known to stimulate root growth in many tree species (Kramer and Kozlowski 1979).

The high RGP levels of the fourth planting date coincided with the heaviest rainfall and the highest survival rates of the study (Table 17). During year 2 a rapid decline occurred in the first 3 weeks of storage, then

RGP levels fell slowly during subsequent storage durations. No "burst" of RGP was observed (Figure 11).

Summerville seedlings maintained higher RGP levels on all planting dates during both years, and the differences between nurseries were significant except for the fifth planting in year 1. The RGP rankings by family over the storage durations were very similar to the rankings at the time seedlings were lifted in February, with the exception of 6-20 in year 1. 6-20 had the highest RGP on the last lift but was ranked fourth over the storage durations. The seed orchard mix was ranked first or second each year (Table 15).

Summerville raised seedlings had significantly higher survival than New Kent seedlings for every family and planting date. Only 42-M had significantly higher survival among the seedlots over all plantings and both nurseries. No interactions were significant. The lack of a trend in survival over the planting season may have been due to the opposing influences of decreasing RGP and increasing rainfall.

RGP was shown to be a good predictor of survival. RGP and survival were significantly correlated overall (Table 19). Other studies have shown strong positive relationships between RGP and survival in loblolly pine (Feret et al. 1985a; b; c) and in other species (Burdett 1979, Jenkinson 1980, Ritchie and Dunlap 1980).

Upon analyzing the data by planting date, to remove confounding factors, the relationship between RGP and survival was strengthened, with the exception of the fifth planting date. The lack of correlation on the last planting date was probably due to the narrow range of RGP values, only 1-6 new roots, and the wet field conditions. Planting 4 had similar planting conditions and had the regression equation with the highest intercept and the shallowest slope of any of the models. RGP would logically be less critical for survival under well watered conditions, which would make the planted but suberized roots adequate for moisture and nutrient uptake.

An asymptotic trend in survival was evident. RGP in excess of 10-12 new roots yielded little improvements in survival (Figure 12). A value of 10 or more new roots seemed to be necessary to ensure survival of at least 80 %, although fewer roots occasionaly resulted in adequate survival. The family rankings by survival and RGP were similar, yet when correlation coefficients were calculated by family, no significant relationships were found. This may have been due to the strong confounding with planting date. Over the planting season there was not a consistent trend in survival and RGP declined erratically.

Height growth was more strongly correlated with RGP than survival. RGP has been positively correlated with growth increments in loblolly pine (DeWald 1985b, Feret et al. 1985a; b, and other species (Ritchie and Dunlap 1980, Sutton 1980). The linear trend persisted up to RGP levels of 18 new roots. An asymptotic trend was evident, with RGP increases over 18 new roots resulting in little further increase in height increment (Figure 15). Few seedling samples exhibited very high RGP levels (> 18 new roots), so height increment may continue to increase above these levels.

Seedlot 42-M exhibited the largest height increments and the highest RGP, and there were few significant differences in height increment among half-sib families. Overall the New Kent seedlings only averaged 48% of the height increment that Summerville seedlings averaged. The slight decreasing trend in height increments over the planting season may have been due to growth being less sensitive to early rainfall variability. The seedlings planted later also experienced a shorter growing season.

The rankings of the families by RGP and height increment were very similar. When correlation coefficents were calculated by family, all families had significant correlations between RGP and height increment. This indicates that RGP is a more robust predictor of first year height increment than of survival.

After analyzing the data by planting date to remove confounding factors, the relationship between height and RGP strengthened greatly, except for the last planting date. The fifth planting date anamoly my be due to the narrow range in RGP and the abundant rainfall late in the planting season. These early, large height increments may be important in the ability of a pine seedling to rapidly dominate its site, and compete successfully with other species.

SUMMARY AND CONCLUSIONS

This study has shown RGP to vary greatly by nursery, family, lift date, and storage duration. Number and length of new roots were very highly correlated. RGP was not strongly correlated with common shoot morphological measures of seedling "quality", but was consistently well correlated with lateral root weight. The Summerville nursery consistently produced seedlings with higher RGP, and lifts after mid-December had consistently higher RGP than earlier lifts, at both nurseries. The seed orchard mix seedlot that was used had excellent RGP, and overall had the highest outplanting survival rates and height growth increments. RGP was strongly correlated with survival and height increment. Ramifications of these results are several-fold:

1. Using family block plantings in the nursery would allow use of specific practices to improve the RGP of low RGP seedlots, i.e. additional undercutting or later lifting;

2. If feasible, some families should not be grown at the New Kent nursery, due to the strong nursery x family interaction;

3. The seed orchard mix must contain families with superior RGP, survival, and growth characteristics, as it usually outperformed the 4 half-sib families;

4. In manipulating seedlings for increased RGP, it

should be noted that managment should strive for good RGP (15-20 new roots), for all seedlings, rather than simply maximizing RGP; RGP increases above certain levels (10 to 12 new roots) resulted in little improvement in field survival. Growth was related to the square root of new root number and increases in height increment may still be gained at very high RGP levels.

In conclusion, RGP changes over time were found to follow similar patterns between nurseries but not between years, although the levels of RGP varied greatly between nurseries, and to a lesser extent between years. During both years RGP peaks occurred in December and February (Figures 2 and 3). Mean RGP values were much higher for Summerville raised seedlings, than for New Kent raised seedlings. Correlations between RGP and chilling hour sums were inconsistent, indicating that lobolly pine seedling RGP patterns are under primarily internal control, and the absolute levels are influenced by cultural and external factors, other than chilling hours. The heavy lateral root systems of Summerville seedlings correlated well with observed RGP values.

RGP was found to explain much of the observed variation in survival and height growth among outplanted seedlings from the 2 nurseries, 5 seedlots, and over the various planting dates. The relationship between field performance and RGP was strengthened when the data were separated by planting date, to remove the confounding effects of different weather conditions associated with each planting date.

Overall, the seed orchard mix outperformed the 4 half-sib families, and Summerville, SC raised seedlings outperformed the New Kent, VA raised seedlings in RGP and field performance.

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