GREENHOUSE GROWTH OF *PINUS X RIGITAEDA* SEEDLINGS IN RESPONSE TO WATER STRESS AND CORRELATIONS WITH 7 YEAR PLANTATION PERFORMANCE

by

Gary R. Hodge

Thesis submitted to the Graduate Faculty of the

Virginia Polytechnic Institute and State University

in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

in

FORESTRY

APPROVED:

P.P. Feret, Chairman

Jon D. Johnson

Thomas E. Burk

February 1983

Blacksburg, Virginia

ACKNOWLEDGEMENTS

I would like to thank Dr. Peter Feret, Dr. Jon Johnson, and Dr. Tom Burk for their invaluable aid and advice on this project. I must also thank Linda Joyner for her cheerful help with the time-consuming data collection.

Special thanks to my wife Terry for her support and love.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

A major factor responsible for slowing the progress of forest tree breeding is the long period of time involved in determining the relative genetic value of individual trees and selecting those to be included in a tree breeding program. An early genetic screening technique could shorten the time required to identify genetically superior trees and, consequently, increase the rate at which genetic gains can be made. Another potential benefit of early genetic screening would be a decrease in field testing costs through the early elimination of a large number of genetic candidates. Therefore, the primary objective of this study was to correlate seedling greenhouse growth characteristics and plantation performance of *Pinus* x *rigitaeda* to examine the possibility of developing an early genetic screening technique.

Water stress may be the single most important environmental factor limiting tree growth (Kramer and Kozlowski, 1960). In view of this, an additional objective of this study was to examine seedling growth characteristics and water stress response in *P*. *rigida* Mill., *P*. *taeda* L., and *P*. x *rigitaeda*. Growth analysis, allometric growth functions, and stem unit information were utilized in identifying genetic variation in response to water stress.

LITERATURE REVIEW

Pinus taeda L. (loblolly pine) is the most important softwood species in the southern pine region (Dorman, 1976). Its natural range extends north into Maryland and central Delaware. *Pinus rigida* Mill. (pitch pine) ranges from central Maine to northern Georgia, through the Appalachian Mountains, and extends west to eastern Tennessee and Kentucky, and southeastern Ohio (Little, 1965). Generally, pitch pine is not a commercially important species (Dorman, 1976) because it exhibits both slow growth and poor form (Little and Trew, 1979).

The Pitch x Loblolly Pine Hybrid

In an attempt to combine the rapid growth of loblolly pine with the cold hardiness of pitch pine, tree breeders began developing hybrids between the two species as early as 1933. Despite the disappointing results of that early research (Little and Somes, 1951), interest in the potential of the pitch x loblolly hybrid remained strong. A great deal of improvement of the hybrid was done in Korea, and the result was a pitch x loblolly hybrid (*Pinus* x *rigitaeda*) that had better form than pitch pine, and exhibited a growth rate twice that of pitch. The hybrid also retained the cold hardiness of pitch pine, and could survive the frigid winters in Korea, while loblolly pine could not (Dorman, 1976).

In 1963, the Westvaco Corporation and personnel of the Northeast Forest Experiment Station (USDA-USFS) began a program to develop high quality, winter-hardy yellow pine, adapted to land in western Virginia, West Virginia, southern Ohio, and western Maryland (Little and Trew, 1979). The main objective of the program was to examine the feasibility of using *P. x rigitaeda* as a commercial species in those areas where loblolly pine was poorly adapted. A thorough discussion of the program is given by Little and Trew (1976, 1977). The pitch x loblolly hybrids grew well in areas outside the natural range of loblolly. The hybrids may even be more suitable than loblolly in certain areas within the natural range of loblolly because the hybrid exhibits a growth rate equivalent to loblolly pine and greater resistance to winter injury. Overall, the initial results were very promising, and the coordinators of the program began receiving requests for seed for mass planting.

Potential for Early Selection

The dual task of mass producing *P. x rigitaeda* for planting and improving the genetic superiority of the hybrid will require a great deal of genetic selection (Hyun, 1976). Selection for inclusion in a tree improvement program is usually accomplished through the use of extensive progeny tests, involving test periods of from 8 to 30 years. Juvenile-mature correlations could provide an alternative to time-consuming field tests by reducing the time span required to make reliable genetic evaluations of candidate material. This would increase genetic gain per unit time.

Juvenile growth traits in seedlings or saplings have been correlated with adult characteristics in various species, and have yielded mixed results. Mean family seedling or sapling heights have been shown to be poorly correlated with mature tree height in Douglas-fir (Pseudotsuga menziesii (Mirb) Franco)(Anon., 1964), slash pine (P. elliottii Engelm.), loblolly pine (LaFarge, 1975), and ponderosa pine (P. ponderosa Laws.) (Namkoong and Conkle, 1976). Other researchers have found significant correlations between juvenile characteristics and adult traits. Nanson (1976) found that nursery height could be used as a predictor for height at ages 25 to 60 in Pinus sylvestria L., Picea abies (L.) Karsten, and Pseudotsuga menziesii. Yeatman and Holst (1967) showed good correlations between four month seedling height and four year height in the nursery in Pinus banksiana Lamb. (jack pine). In work with loblolly pine, Robinson and van Buijtenen (1979) showed the selection of families on the basis of nurserybed traits would yield an 8% gain in volume at 15 years. Cannell et al. (1978) reported significant correlations between first year seedling growth traits and 8 year tree volume growth in families of loblolly pine. They suggested that if their findings are substantiated, seedling growth characteristics may provide a simple, inexpensive method of screening loblolly pine for volume growth. Waxler and van Buijtenen (1981) reported significant correlations between shoot weight and average family volume superiority in loblolly pine (volume superiority = (average volume of family/average of plantation) x 100). Feret (1981) showed comparable correlations in P. ponderosa.[1]

[1] Feret, P. 1981. Research completed at The Institute of Forest Genetics, Placerville, California. Manuscript in preparation.

Water Stress Relationships

The ability to avoid or tolerate water stress may contribute greatly to the potential of a tree to grow on a particular site. Zimmermann and Brown (1971) state that water stress is the single most important environmental factor limiting tree growth. Kramer and Kozlowski (1960) suggest that any decrease in soil water potential below -1 bar (1 bar = 0.1 MPa) will inhibit plant growth. In 66 out of 80 studies examined by Stanhill (1957), plant growth was limited by soil water potentials of less than -15 bars. Sands and Rutter (1959) found significant reductions in growth in first year seedlings of *P. sylvestris* due to the slight difference in soil water potential from -0.1 bars to -0.3 bars. In loblolly and shortleaf pine (*P. echinata* Mill.) seedlings, height growth was inhibited at a soil water potential of -2.5 bars, and growth stopped completely at -3.5 bars (Stransky and Wilson, 1964). Waxler and van Buijtenen (1981) showed that a decrease in soil water potential from -2.3 bars to -3.1 bars drastically impaired seedling growth of loblolly pine. Cannell *et al*. (1978) judged water stress to be the most critical factor limiting height and volume growth of loblolly pine in the south, even on the wettest sites. They hypothesized that small differences in the ability to tolerate water stress could result in large differences in height and diameter growth.

Shoot-Root Relationships

Differences in the partitioning of biomass to shoot and roots can play a major role in differences in plant growth. Plant physiologists have long supposed that there exists some optimum balance in the allocation of dry matter to the shoots and roots. Simple shoot-root ratios have often been used in an attempt to quantify the shoot-root relationship. Shoot-root ratios, however, are cumbersome to use because they change with plant age due to the differing rates of growth of the shoot and root (Ledig and Perry, 1965). Allometric growth equations can provide an effective method of describing the balance between shoot and root growth. The allometric equation:

$$\log_e \text{(shoot dry wt.)} = a + k \log_e \text{(root dry wt.)}$$

was used by Ledig et al. (1970) to characterize pine seedling growth. If tree growth is limited primarily by the ability to avoid water stress, plants allocating proportionally more dry matter to their roots would be expected to grow faster than those apportioning less assimilate to their roots. A relatively low k value would reflect a large investment of dry matter into the roots. Genotypes with low k values could be expected to perform better under moisture stress.

Growth Analysis

Growth analysis utilizes measurements from periodic harvests to partition growth among component characteristics. It is a relatively simple technique for elucidating genetic differences in and environmental effects on growth (Ledig, 1974).

This study utilized three classical formulas of growth analysis. Relative growth rate (RGR) is an overall growth index which can be used to compare growth rates of genetically different populations or of plants in different environments. Growth rate is expressed relative to the amount of starting material; thus, the effects of initial differences in size can be disregarded. Net assimilation rate (NAR) is the rate of dry weight increase per unit area of leaf, and is a measure of photosynthetic efficiency. Leaf area ratio (LAR) is the ratio of leaf area to dry weight and expresses the proportion of phytosynthetic surface to repiratory mass (Ledig, 1974).

Van den Driessche (1968) found RGR to be a good indicator of productivity in seedlings of four confier species, as it quickly reduced the effects of differences in original seedling size. He also found that NAR differences had a greater effect on RGR than did differences in LAR. His findings paralleled, to some degree, those of Sands and Rutter (1959) in a study on the effects of differences in soil water stress on seedlings of Pinus sylvestris (Scots pine). They found that the effects of water stress on RGR were due mainly to variations in NAR. Sands and Rutter used a formula expressing NAR as the rate of dry weight increase to leaf weight; however, this is still a measure of photosynthetic efficiency.

Shoot Growth Components

The length of leader produced each year by conifers will obviously have a great effect on total height growth variability. Shoot growth analysis, as presented by Cannell (1978), begins with the identification of fixed and free growth. The analysis then proceeds to the division of both major growth components into stem units.

Fixed and Free Growth: Fixed growth is defined as the elongation of stem units and leaf primordia which have overwintered in a bud. Free growth (Jablanczy, 1971) is defined as the elongation of stem units and leaf primordia in the same season as they were initiated, or without any dormancy period. Most conifers exhibit both types of shoot growth. Tepper (1963) examined the relative contributions of fixed and free growth in *Pinus echinata* and *P. rigida*. He found that pitch pine exhibits essentially only fixed growth, while shortleaf utilizes both modes of growth. Griffing and Elam (1971) found that *P. taeda* exhibits both fixed and free growth, and that although fixed growth contributed the largest proportion to shoot growth, those trees with the most free growth flushes were also those with the longest total leader length. In a study on a six year old *Pinus* x *rigitaeda* plantation, Bailey (1981) found that loblolly exhibited both fixed and free growth, pitch only fixed growth, and ten families of *P.* x *rigitaeda* exhibited proportions of free growth intermediate to the two parent species. Additionally, she found that the fixed growth increment of the hybrids was essentially equal, and differences in total shoot length were due to differences in the amount of free growth.

Germinants (first year seedlings) exhibit only free growth (Jablanczy, 1971). First year seedling growth characteristics, then, may be of use in predicting the performance of pitch x loblolly hybrid families.

Free growth, however, may not be of as much importance to older trees as to seedlings and saplings. In four year old *Picea mariana* (Mill.) B.S.P. (black spruce), differences in free growth accounted for difference in stem increment (Pollard and Logan, 1974). In 12 year old black spruce, Logan and Pollard (1975) found free growth in only 5 of 60 trees. Jablanczy (1971) suggested that free growth is absent in older spruce and begins to play a decreasing role at 5 to 10 years after germination. This pattern of diminishing free growth activity may also apply to *Pinus* species (Lanner, 1976).

Stem Units: A stem unit is the small section of stem associated with each needle, needle fascicle, or sterile scale (a node plus its internode; Doak, 1935). The number of stem units reveals the number of primordia produced in the apical meristem, while the length of the stem unit is attributable to sub-apical elongation. Cannell (1978) indicated that stem unit numbers and lengths could vary independently. Stem units have a demonstrated value in analyzing shoot growth in many species. Cannell *et al*. (1976) found in northern conifers that the length of a leader is often highly correlated with numbers of stem units. As mentioned above, Bailey (1981) found that differences in shoot growth increment in families of pitch x loblolly hybrids were due to differences in free growth. She also found that, in general, families with greater than average number of stem units in the free growth component had the longest free growth shoots (and, thus, the largest total shoot length). In examining the relationship of seedling growth characteristics to older growth in pitch x loblolly hybrids, it may be of use to identify growth components, i.e., stem unit numbers and lengths.

OBJECTIVES

The objectives of this study were:

1) To determine if greenhouse growth of *P. x rigitaeda* seedlings is correlated with one, two, three, four, five and seven year heights, and volume in seven year old trees.

2) To examine seedling growth characteristics, and genetic variation among families of *Pinus rigida*, *P. taeda*, and *P. x rigitaeda* in response to water stress.

MATERIALS AND METHODS

Two studies, similar in design, and under essentially identical experimental conditions, were performed in order to achieve the stated objectives. The first study involved only P. x rigitaeda seedlings. Seed parents were selected from a seven year test plantation at the Reynolds Homestead Research Center in Critz, Virginia. The plantation is one of 29 similar test plantations sponsored by Westvaco and the U.S.F.S. N.E. Forest Experiment Station to test hybrid performance. Criteria concerning the selection of the P. rigida and P. taeda parent material is given by Little (1965). Six hybrid crosses were selected for study, with two full-sib individuals per cross providing seed material. The crosses were selected mainly on the basis of the number of collectable good seed and, as a result, there was some degree of relatedness between the crosses (Table 1). The seed (F_2) was the result of wind pollination of the F_1 hybrids, and was collected in October, 1980, and placed in storage.

The second study involved two P. rigida families and four P. taeda families. Seed parents for the two P. rigida families were two check trees from the Reynolds test plantation. The P. taeda families were clones selected from a Westvaco seed orchard in Georgetown County, South Carolina. All seed was the result of open pollination. The pitch pine seed was collected in October, 1980, and placed in storage. The loblolly pine seed was collected in September, 1978, and placed in storage.

Germination and Pre-Treatment Procedures

Seed from the hybrid crosses was stratified for 42 days at 7°C. A total of ten seed from each individual tree were individually weighed

Table 1. *P.* x *rigitaeda* crosses, *P. taeda*, and *P. rigida* families examined in the study.

Hybrid Cross[1]	Pitch Parent Location	Loblolly Parent Location
22 x 64	Barnstable Co., MA	Worcester Co., MD
51 x 23	Amherst Co., VA	Worcester Co., MD
71 x 22	Plymouth Co., MA	Worcester Co., MD
71 x 23	Plymouth Co., MA	Worcester Co., MD
78 x 22	Oxford Co., ME	Worcester Co., MD
78 x 26	Oxford Co., ME	Somerset Co., MD

Loblolly Family	Location
7-56	Georgetown Co., SC
11-09	Georgetown Co., SC
11-10	Georgetown Co., SC
11-20	Georgetown Co., SC

VDF Pitch Family[2]	Location
15	unknown
33	unknown

[1] Pitch parent x Loblolly parent

[2] Va. Div. of Forestry pitch family ID numbers based on replication and tree numbers at the Reynolds Homestead Research Center, Critz, VA.

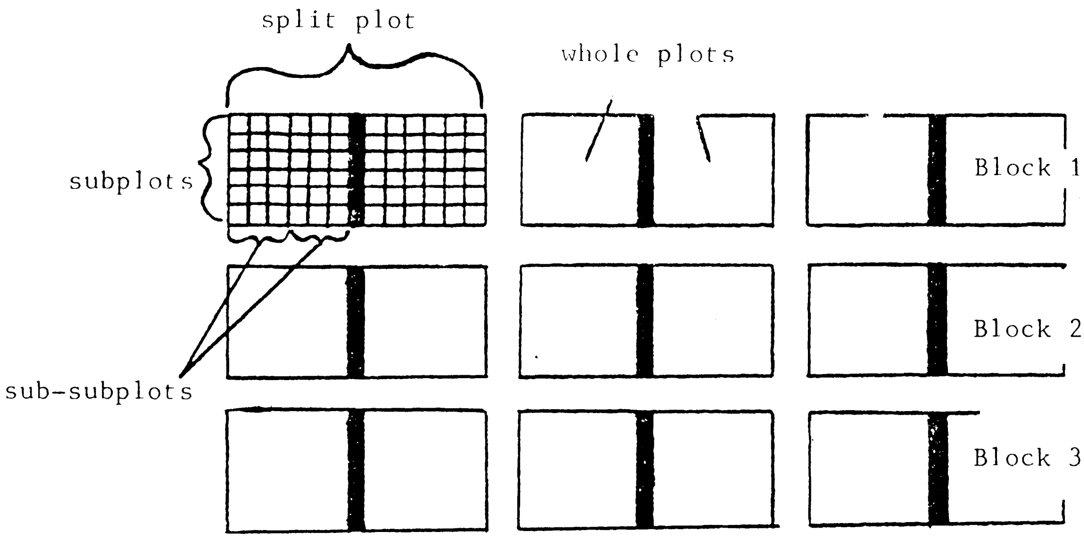
after stratification in order to obtain an estimate of seed weight. The seeds were then germinated in Petri dishes. When the radicle had grown to a length equal to that of the seed, the seed was placed in storage at 7°C until all seeds germinated. This was done to eliminate effects due to differences in time of germination. Germinated seeds were planted on August 9, 1981, into plastic tubes one inch in diameter and approximately eight inches deep. Each tube contained approximately 160 cm^3 of PROMIX BX, an artificial planting medium. The seedlings were kept in a greenhouse in Blacksburg, Virginia, and watered as needed until September 7, 1981, when moisture treatments began.

Seed from the *P. rigida* and *P. taeda* families were given a 24 hour cold water soak, ten seeds from each individual were weighed, and all seeds were germinated and planted as above. The germinated seeds were planted on August 27, 1981, and watered as needed until September 29, 1981, when moisture treatments began.

On September 14, 1981, both studies were moved from the original greenhouse where they were kept under ambient light and temperature conditions, to another greenhouse where they received a supplemental 16 hour photoperiod supplied by a bank of four General Electric Warm White flourescent tube lights.

Statistical Design

The germinated seeds were planted in a split plot design (Figure 1). Nine trays, holding the plastic planting tubes, were separated into three blocks. Each tray, or split plot, was then randomly partitioned into two whole plots, to be placed under one of two moisture regimes.



1) Control and water stress treatments were randomly assigned to each pair of whole plots.

2) Crosses were randomly assigned to subplots within each whole plot.

3) In the P. x rigitaeda study, families nested within crosses were randomly assigned to sub-subplots within each subplot.

4) One whole plot per block, selected at random, was harvested at each of three harvest dates.

Figure 1. The planting design.

The whole plots were further partitioned into subplots, in which seedlings of a single family were planted. In the hybrid planting scheme, where there were two trees representing each family, the subplots are broken into sub-subplots to accommodate seedlings from each tree.

Periodic harvests were made for growth analysis. One tray, or whole plot, from each of the three blocks was randomly selected for one of three harvests, made at approximately one month intervals.

The studies were treated in as similar a manner as possible throughout the experiment. The periodic fertilization of both studies took place at the same time from date of planting. Furthermore, the six blocks (three in each study) were shifted intact to random positions on benches in the greenhouse each two weeks. This was done to minimize bench effects, and to allow for a more meaningful comparison of growth parameters between the hybrid study and the pitch/loblolly study. In each study, 54 seedlings per tree were planted, yielding a total of 648 seedlings in the hybrid study, and 324 in the pitch/loblolly study.

Water Stress Treatments

Water stress treatments were randomly assigned to whole plots in the nine split plots in both studies. The control treatment consisted of a watering to field capacity every four days. The stress treatment consisted of a watering to field capacity every six days. Field capacity was determined to be reached when water drained from the bottom of the planting tubes. At the beginning of the treatments, all seedlings were fertilized with 7.5 ml of a 10% solution of Miricaid 30-10-10 liquid fertilizer. Seedlings were then fertilized every 12 to 24 days, when watering schedules coincided.

Plant Water Stress

To provide data on the effects of the watering regime on plant water stress, additional trays of seedlings, not included among those to be harvested and analyzed, were planted according to the experimental design and underwent both moisture treatments. Samples of the additional seedlings were measured in a pressure chamber (Scholander *et al*., 1965) to determine predawn water stress at the end of the drying cycles.

Harvest Procedures

Harvests of the hybrid seedlings were made on October 27, 1981, December 4, 1981, and January 20, 1982. Harvests of the *P. rigida* and *P. taeda* seedlings were made on November 17, 1981, December 23, 1981, and February 10, 1982. Length of time from planting to the 1st, 2nd, and 3rd harvest, respectively, were approximately 11, 17, and 23 weeks. At each harvest, the following measurements were made on each seedling: The height of the seedling to the tip of the tallest needle and to the apical meristem was measured. Additionally, 75% of the stem from the cotyledons to the apical meristem was excised, and stem units in this region were counted. This was done to insure that measurements of mean stem unit length were not biased by stem units which had not elongated. Leaf area was measured to provide estimates of net assimilation rate. It was suspected that new needles would be net sinks of photosynthate, while older needles would be more likely to be producing carbohydrate. Therefore, needles from the 75% region of the stem were stripped from the plant and projected leaf area measured with a LI-COR LI-3000 Portable Leaf Area Meter. The needles and excised stem, the remainder of the shoot, and the root were then dried at 65°C for 48 hours, and weighed.

In summary, these procedures measured shoot dry weight, root dry weight, total dry weight, total shoot height, apical meristem height, number of stem units, mean stem unit length and leaf area for each seedling. For convenience, these eight variables will be referred to as "raw variables."

Shoot-Root Relationships

Analysis of shoot-root relationships were made using the allometric equation (Drew and Ledig, 1980):

$$\log_e \text{(shoot d.wt.)} = a + k \log_e \text{(root d.wt.)}$$

F-tests for differences in k values among crosses, families, species and treatments were made according to Steele and Torrie (1960) using the SAS package (Helwig and Council, 1979).

Growth Analysis

Relative and absolute growth rates were calculated for each harvest interval using total plant dry weight, shoot dry weight, and root dry weight. Absolute growth rates were calculated using the formula:

$$AGR = (\text{d.wt.}_a - \text{d.wt.}_{a-1})\ (1/t)$$

where: a = harvest number

t = number of days between (a) and (a-1).

Relative growth rates were calculated using the formula (Radford, 1967):

$$RGR = (\log_e d.wt._a - \log_e d.wt._{a-1})(1/t)$$

where: a = harvest number

t = number of days between (a) and (a-1).

Net assimilation rates and leaf area ratios were calculated for each harvest interval using total dry weight and leaf area. Net assimilation rates were calculated using the formula (Radford, 1967):

$$NAR = \frac{(d.wt._a - d.wt._{a-1})(\log_e A_a - \log_e A_{a-1})}{t(A_a - A_{a-1})}$$

where: A = leaf area

a = harvest number

t = number of days between (a) and (a-1).

Leaf area ratios were calculated using the formula (Radford, 1967):

$$LAR = \frac{(A_a - A_{a-1})(\log_e d.wt. - \log_e d.wt._{a-1})}{(\log_e A_a - \log_e A_{a-1})(d.wt._a - d.wt._{a-1})}$$

where: A = leaf area

a = harvest number.

Average values of AGR, RGR, NAR, and LAR were also calculated by averaging values for separate harvest intervals.

Analysis of Variance

The data from the two experiments were analyzed separately. Analysis of the hybrid data with a full model was not possible because the combination of fixed and random factors in the model yielded no term with the proper expected mean square to test for cross differences or treatment differences. Therefore, initial analysis was made by treatment in order to test for differences among crosses, and by cross to test for differences between treatments. The models were, respectively:

$$Y_{ijkl} = mu + B_i + H_j + C_k + F(C)_{kl} + H \times F(C)_{jkl} + e_{ijkl}$$

where: mu = overall mean

	B = blocks	(fixed)
	H = harvest	(fixed)
	C = cross	(random)
	F(C) = family (cross)	(random)
	H x F(C) = pooled error term[1]	(random)
	e = random error	

and,

$$Y_{ijkl} = mu + B_i + H_j + T_k + F_l + HT_{jk} + HF_{jl} + HTF_{jkl} + e_{ijkl}$$

where: mu = overall mean

	B = blocks	(fixed)
	H = harvest	(fixed)

[1] Analysis was first performed including the harvest x cross interaction term and harvest x family (cross) term. All harvest x cross interaction were insignificant. The above model was then used to allow testing of the cross.

T = treatment (fixed)

F = family (random)

HT = harvest x treatment interaction (fixed)

HF = harvest x family interaction (random)

HTF = harvest x treatment x family interaction (fixed)

e = random error

Analysis of the pitch pine - loblolly pine study was initially performed using the following model:

$$Y_{ijklm} = mu + B_i + H_j + T_k + S_l + F(S)_{lm} + TS_{kl} + TF(S)_{klm} + HS_{jl} + HT_{jk} + HTS_{jkl} + HTF(S)_{jklm} + e_{ijklm}$$

where: mu = overall mean

B = blocks (fixed)

H = harvest (fixed)

T = treatment (fixed)

S = species (fixed)

F(S) = family (species) (random)

HS = harvest x species (fixed)

HT = harvest x treatment (random)

HTS = harvest x treatment x species (random)

HTF(S) = harvest x treatment x family (species) (fixed)

e = random error

As there was some seedling mortality, neither experiment was completely balanced. Therefore, all analyses were made using SAS package Type IV sums of squares as suggested by Helwig and Council (1979).

Growth analysis variables were calculated using mean values for each harvest-block-treatment-cross-family combination for the hybrid data, and using mean values for each harvest-block-treatment-species-family combination for the pitch pine and loblolly pine data. Each combination had a maximum of three observations. Assuming equal variances at time 1 and 2, the following would then be true:

at time 1, $\sigma^2_{\bar{x}_1} = \sigma^2/n_1$

at time 2, $\sigma^2_{\bar{x}_2} = \sigma^2/n_2$

where: n = number of live seedlings at time i.

Then:

$$VAR(\bar{x}_2 - \bar{x}_1) = \frac{1}{n_1}\sigma^2 + \frac{1}{n_2}\sigma^2 = \frac{(n_1 + n_2)}{n_1 n_2}\sigma^2$$

Therefore, analysis of variance on growth analysis variables was performed using a weight factor W according to the formula:

$$W = \frac{n_1 n_2}{n_1 + n_2}$$

Correlation Analysis

Pearson product moment and Spearman rank correlation coefficients were used to examine the relationship between greenhouse growth variables and mean field performance variables of the six *P.* x *rigitaeda* crosses.

Data for mean cross field performance were obtained from the Reynolds Homestead Research Center for the following variables: one, two, three, four, five and seven year heights, and a seven year volume index using the formula $V = D^2H$. Correlation matrices were generated between the above variables and mean cross values of the growth analysis variables for each interval-treatment combination. Additional matrices between field variables and overall means of greenhouse growth variables averaged over harvest or interval were generated. Correlations with k-value and seed weight were also examined.

RESULTS

Seed Weight

Analysis of variance revealed significant ($\alpha = 0.05$) cross and family within cross differences in seed weight for the hybrids. Mean cross seed weight ranged from 10.2 to 17.2 mg (Table 2). Analysis of the parent species data showed that loblolly had significantly ($\alpha = 0.001$) larger seed than pitch pine. Pitch seed averaged 7.9 mg while loblolly seed weighed an average of 30.0 mg, nearly a fourfold difference. Family within species differences were also highly significant ($\alpha = 0.001$).

Water Stress

Pre-dawn plant water potential readings for the well watered treatment had a sample mean of -1.3 bars and a standard deviation of -0.6 bars. The stress treatment mean was -4.2 bars with a standard deviation of -1.3 bars. These sample means were significantly different at $\alpha = 0.001$ using an approximate t-test suggested by Li (1964) for populations with different variances. There were significant treatment effects on many growth variables in both the hybrid and the pitch pine - loblolly pine study, as discussed below.

Hybrid Seedlings - Raw Variables

Examination of raw variable means by treatment suggested that the stress treatment decreased plant growth. Values for the stress treatment are lower than the well-watered control for every variable

Table 2. Seed weights and standard deviations for *P.* x *rigitaeda* crosses and families, and for *P. rigida* and *P. taeda* families.

P. x *rigitaeda* cross	Seed wt. (mg)	St.Dev.	Cross	Family	Seed wt. (mg)	St.Dev.
22 x 64	10.8	1.76	22 x 64	1	10.6	2.34
				2	11.0	1.01
51 x 23	10.3	3.94	51 x 23	1	8.1	4.27
				2	12.4	2.15
71 x 22	13.3	4.00	71 x 22	1	13.8	5.46
				2	12.7	1.97
71 x 23	14.3	3.76	71 x 23	1	12.7	2.22
				2	15.9	1.88
78 x 22	13.1	2.38	78 x 22	1	12.9	2.88
				2	13.2	1.89
78 x 26	17.2	4.29	78 x 26	1	16.9	6.04
				2	17.5	1.51

Parent Species	Seed wt. (mg)	St.Dev.	Species	Family	Seed wt. (mg)	St.Dev.
P. rigida	7.9	5.03	*P. rigida*	15	9.6	6.92
				33	6.3	0.40
P. taeda	30.3	7.90	*P. taeda*	7-56	24.6	9.81
				11-09	37.1	6.09
				11-10	29.6	3.88
				11-20	29.7	5.89

at each harvest (Table 3). The seedlings seemed to be increasing mass in a linear growth pattern, although height growth seemed to slow at the end of the study (Figure 2).

Analysis of variance by hybrid cross on the raw variables showed harvest effects to be significant in almost every case (Appendix A). Treatment effects were also significant for most variables in five of the six crosses. Cross 22 x 64 was unique in that almost no effects were significant in any variable. Seedlings from this cross grew very little; it ranked last for all variables under both treatments. Family differences were not often apparent, showing consistently only in two crosses.

In analyses of variance by treatment, harvest terms were again significant for all variables for both treatments (Appendix B). The analysis of the well watered treatment revealed significant cross differences in five of the eight variables: shoot weight, shoot length, apical meristem height, mean stem unit length, and leaf area. There were no family within cross differences. The stress treatment, however, elicited very different results. Cross effects were not significant for any variable, while there were significant family within cross effects in all variables except mean stem unit length.

The effect of the treatment on the variance components σ^2_C (variation due to cross) and $\sigma^2_{F(C)}$ (variation due to family within cross) reflects the different results obtained by ANOVA (Table 4). Treatment had little effect on the percent of total variation explained by the sum of the cross variance component and family within cross variance component. This ratio was approximately 0.21 for both treatments. Treatment did

Table 3. Means ± standard error for eight variables measured on *P. x rigitaeda* seedlings grown under two watering regimes.

	Well Watered	Stressed
Total dry weight (mg)		
11 weeks harvest 1	221 ± 11.5	167 ± 9.0
17 weeks harvest 2	489 ± 23.1	368 ± 16.0
26 weeks harvest 3	780 ± 34.7	578 ± 23.1
Shoot dry weight (mg)		
1	152 ± 7.5	115 ± 5.9
2	355 ± 16.2	258 ± 11.1
3	553 ± 25.0	410 ± 16.7
Root dry weight (mg)		
1	69 ± 4.1	51 ± 3.3
2	134 ± 7.3	110 ± 5.2
3	227 ± 10.7	167 ± 7.2
Shoot weight (mm)		
1	82 ± 1.9	70 ± 1.3
2	116 ± 3.1	91 ± 3.2
3	130 ± 4.2	98 ± 2.4
Apical meristem height (mm)		
1	43 ± 1.3	36 ±0.94
2	91 ± 3.0	63 ±2.11
3	103 ± 3.9	73 ±2.06
Number of stem units		
1	44 ± 1.4	37 ± 1.2
2	73 ± 1.7	64 ± 1.5
3	88 ± 2.2	79 ± 2.1
Mean stem unit length (mm)		
1	0.42 ± 0.02	0.37 ± 0.01
2	0.74 ± 0.03	0.53 ± 0.02
3	0.69 ± 0.03	0.49 ± 0.01
Leaf area (mm^2)		
1	718 ± 37	532 ± 28
2	1488 ± 75	954 ± 49
3	2384 ± 123	1924 ± 89

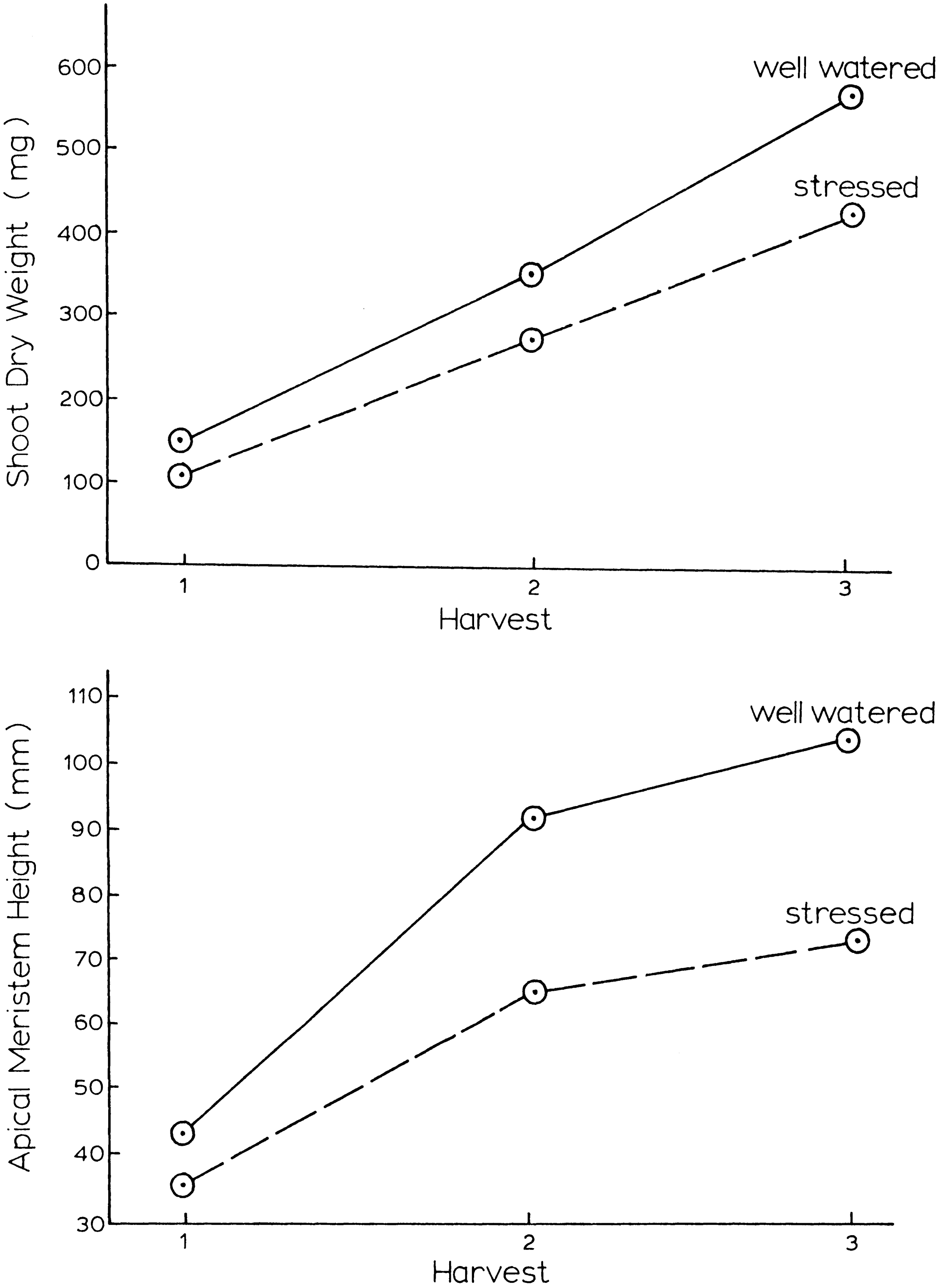


Fig. 2. Shoot Dry Weight and Apical Meristem Height of *P.* x *rigitaeda* seedlings grown under two watering regimes.

Table 4. Relative importance of variance components for *P.* x *rigitaeda* seedlings grown under two watering regimes.

Treatment	Var.Comp. ratio[1]	shoot weight	root weight	total weight	shoot length	meristem height	stem units	stem unit length	leaf area
well watered	$\frac{C}{C + F}$	0.774	0.702	0.747	1.000	1.000	0.699	0.881	0.780
	$\frac{F}{C + F}$	0.226	0.298	0.253	0	0	0.301	0.119	0.220
	$\frac{C + F}{T}$	0.218	0.247	0.238	0.170	0.159	0.196	0.093	0.211
stressed	$\frac{C}{C + F}$	0.553	0.618	0.570	0.328	0.067	0.047	0.344	0.604
	$\frac{F}{C + F}$	0.447	0.382	0.430	0.672	0.933	0.953	0.656	0.396
	$\frac{C + F}{T}$	0.249	0.263	0.295	0.157	0.106	0.163	0.123	0.241

[1] C = variance due to cross effects
F = variance due to family within cross effects
T = total variance

however, have an effect on variance distribution between σ^2_C and $\sigma^2_{F(C)}$. In every case, $\sigma^2_{F(C)}$ accounted for a greater percent of the variation under the stress treatment. This suggests that σ^2_C and $\sigma^2_{F(C)}$ represent different types of genetic variation and that the genetic components of $\sigma^2_{F(C)}$ are more important in eliciting differences under water stress than those of σ^2_C.

Pitch and Loblolly Pine Seedlings - Raw Variables

Examination of the means by treatment shows that water stress treatments did in fact reduce seedling growth (Table 5). Growth patterns presented in Figures 3 and 4 are less clear cut than was seen in the hybrids. It does seem clear, however, that height growth had reached a plateau under the stress treatment by third harvest, as was seen in the hybrids. These results paralleled those of Waxler and van Buijtenen (1981) who found that loblolly seedlings grown at a plant water stress of -4.0 bars ceased height growth after 18 weeks. In this study, loblolly grew very little from 17 to 23 weeks at a plant water stress of -4.2 bars.

Analysis of variance showed harvest effects to be significant for most of the variables (Appendix C). Treatment effects were highly significant (α = 0.01) for all variables. Species effects were also significant for all variables, with loblolly being larger than pitch in every case (Table 5). This seems to be primarily an effect of the relatively large seed of loblolly, since seed weight was significantly correlated with most variables. Family within species differences were apparent only in shoot length, stem units, and leaf area. Species and

Table 5. Means ± standard error for eight variables measured on *P. rigida* and *P. taeda* seedlings grown under two watering regimes.

	P. rigida		*P. taeda*	
	watered	stressed	watered	stressed
Total dry weight (mg)				
11 weeks harvest 1	195±19.5	126±10.1	236±13.0	157± 9.8
17 weeks harvest 2	277±35.4	213±31.9	301±25.1	313±14.5
26 weeks harvest 3	353±62.4	272±31.0	635±45.2	442±25.9
Shoot dry weight (mg)				
1	144±14.0	92± 7.4	176± 9.9	118± 7.7
2	196±24.4	151±21.7	219±17.4	225±10.8
3	223±68.4	186±21.3	438±30.3	316±18.8
Root dry weight (mg)				
1	51± 5.8	34± 3.4	60± 3.4	38±2.3
2	80±11.6	61±10.4	82± 8.1	87±4.4
3	129±26.4	85±10.7	196±15.6	126±7.5
Shoot height (mm)				
1	94±5.8	72±5.5	117±3.5	97±4.0
2	105±8.0	90±7.5	135±5.7	137±3.4
3	95±7.8	88±4.4	159±4.9	136±4.3
Apical meristem height (mm)				
1	52±4.3	37±4.6	86±2.8	69±3.5
2	70±7.8	57±6.2	108±5.1	107±3.5
3	65±7.6	60±4.0	135±4.5	111±4.1
Number of stem units				
1	41±3.0	32±2.3	57±2.0	45±2.1
2	56±4.8	48±3.0	86±2.7	78±2.0
3	51±4.8	52±3.0	101±3.5	91±2.1
Mean stem unit length (mm)				
1	0.56±0.04	0.38±0.04	0.65±0.04	0.55±0.03
2	0.61±0.04	0.53±0.06	0.70±0.04	0.67±0.04
3	0.61±0.07	0.50±0.03	0.74±0.02	0.60±0.02
Leaf area (mm)				
1	739± 73	487± 46	810± 97	511± 34
2	895±131	727±105	814± 77	824± 56
3	770±134	698± 98	1721±155	1255±104

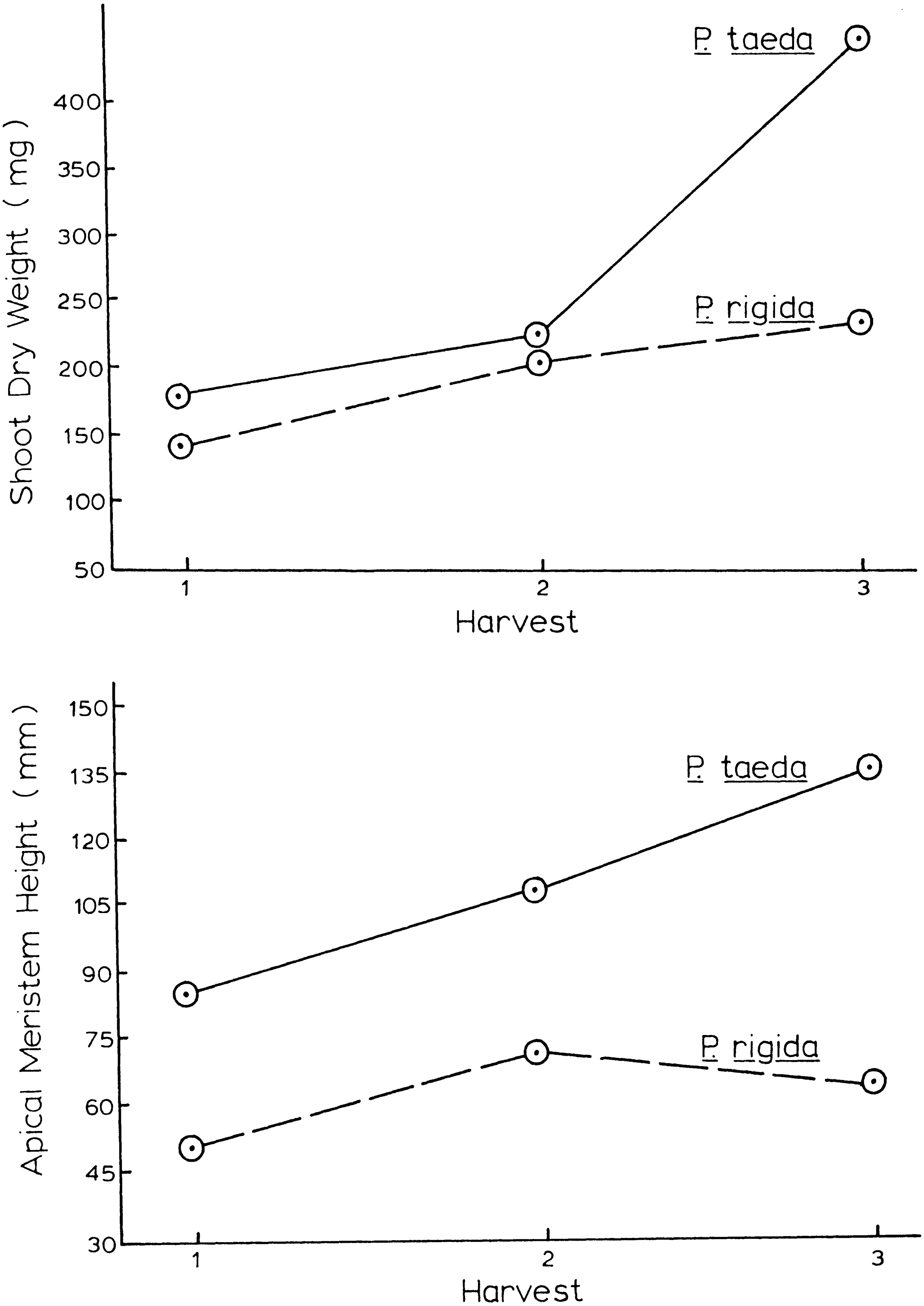


Fig. 3. Shoot Dry Weight and Apical Meristem Height of P. rigida and P. taeda grown under the well watered moisture regime.

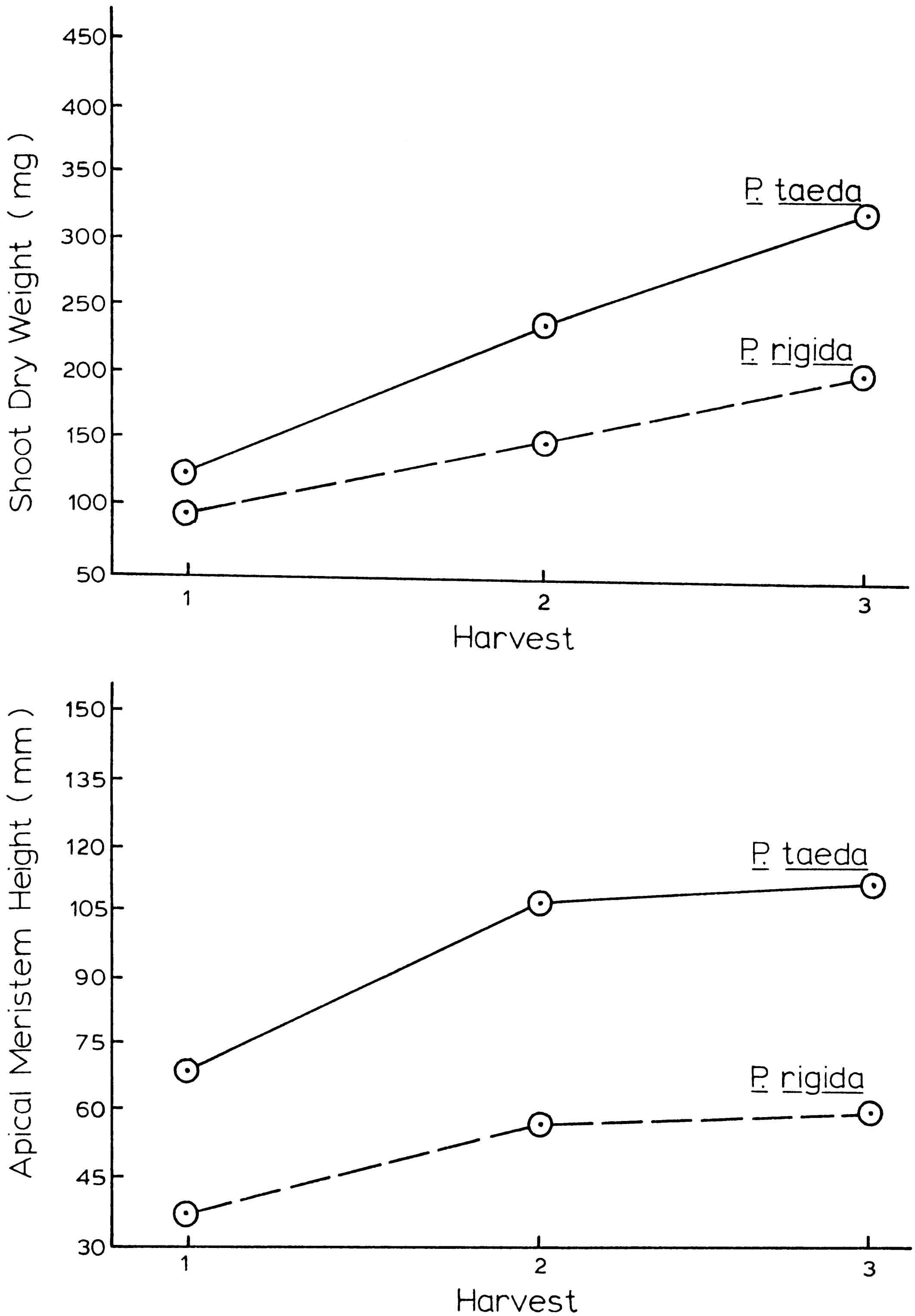


Fig. 4. Shoot Dry Weight and Apical Meristem Height of *P. rigida* and *P. taeda* grown under the stressed regime.

family interactions with treatment were not significant, suggesting that water stress does not lead to changes in family rank for the growth variables. There was, however, a significant harvest x species interaction for seven of the eight variables. This interaction was significant due to the fact that loblolly continued to grow well throughout the experiment (except in height under the stress treatment), while pitch grew very little between harvests 2 and 3. This may reflect the greater growth capacity of loblolly pine.

Analysis of variance was also done separately by treatment. The major difference between the two treatments was that the stress treatment elicited famiy within species differences that were not apparent under the well watered conditions (Appendix D). The harvest x species interaction discussed above was significant under both treatments.

Hybrid Seedling - Analysis Variables

In general, results of analysis of variance by cross on growth analysis variables showed no consistent pattern (Appendix E). Treatment effects were insignificant for most variables in all crosses except cross 78 x 26. Family differences were not apparent, and few interaction terms were significant. Harvest interval was the only term which was consistently significant. Separate analyses by treatment (Appendix F) showed no cross differences, but interval effects were again highly significant. The effect of interval seems to be due to a decrease in rate of growth; relative growth rates and net assimilation rate decreased significantly in each harvest interval (Table 6). The relatively high

Table 6. Mean values of growth variables for *P. x rigitaeda* seedlings grown under two watering regimes.

Interval	Treatment	Absolute Growth Rate mg/day			Relative Growth Rate percent/day			NAR $mg/mm^2/day$	LAR mm^2/mg
		total	shoot	root	total	shoot	root		
01	well watered	2.5	–[1]	–	3.2	–	–	0.0225	1.41
	stressed	1.8	–	–	2.9	–	–	0.0213	1.33
12	well watered	7.2	5.4	1.7	2.2	2.3	1.8	0.0071	3.08
	stressed	3.9	2.8	1.1	0.8	09.8	0.8	0.0027	2.86
23	well watered	5.1	3.5	1.6	0.7	0.7	0.9	0.0024	3.02
	stressed	3.9	2.8	1.1	0.8	0.8	0.8	0.0027	2.86

[1]No value since seed weight was used for calculations.

value for NAR seen in interval 0-1 (seed to harvest 1) for the hybrids, and for pitch and loblolly pine, is probably an inflated estimate. A relatively small percentage of the total needles were measured at the first harvest, as stems had not elongated a great deal at that time. It seems likely that many of the needles in the top portion of the shoot, which were not sampled to prevent measuring non-productive leaf area, were in fact producing photosynthate. Thus, the production of those needles were accounted to the measured leaf area, increasing the estimates of NAR. The effect of this bias was probably reduced by the second and third harvests as percentage of total needles measured increased. In fact, NAR's appear more reasonable in comparison with RGR's by the second harvest.

A final analysis of variance by interval (Appendix G) indicated the effects of the decrease in growth. Treatment and cross effects were both apparent in interval 0-1, less so in interval 1-2, and disappear by interval 2-3, when presumably seedlings in all crosses and both treatments had slowed growth markedly.

Multiple regression analyses of the relationship of relative growth rate to net assimilation rate and leaf area ratio showed that NAR accounted for more variation in RGR than did LAR. This is in agreement with the findings of Sands and Rutter (1959) with _Pinus sylvestris_ L. and van Den Driessche (1968) with _Pseudotsuga menziessi_ (Mirb.) Franco., _Picea sitchensis_ (Bongard) Carriere., _Picea glauca_ (Monench) Voss, and _Tsuga heterophylla_ (Raf.) Sarg.

Pitch and Loblolly Pine Growth Analysis Variables

Analysis of variance with the full model showed no treatment effects and almost no interval effects (Appendix H). Species differences are apparent in absolute growth rates of shoot, root, and total plant, but not in relative growth rates or NAR. The larger absolute growth rates of loblolly (Table 7) probably reflect the differences in seed size between the species, as seed weight was correlated significantly with AGR's. The absence of significant differences in relative growth rates suggests that at this seedling growth stage there is no tendency for loblolly to exhibit more efficient growth than pitch pine.

There was a significant interval x treatment effect in seven of the eight variables. This effect can be seen in Table 8 and Figure 5. The changes in AGR are reflected by changes in NAR and may be the results of asynchronous cycles of growth under the two treatments.

Analyses by treatment (Appendix I) showed that the stress treatment elicited species differences while the well watered treatment did not. Interval differences also seem more readily apparent under the stressed condition.

The final analysis by interval (Appendix J) showed a pattern similar to that obtained from the hybrid data. Treatment and species differences are most apparent in interval 0-1, and become progressively more obscure in intervals 1-2 and 2-3. The species difference in total RGR in interval 0-1 reflects the larger RGR for pitch pine, 0.038 versus 0.023 for loblolly (Table 7).

Table 7. Mean values of growth analysis variables for *P. rigida* and *P. taeda*.

Interval	Species	Absolute Growth Rate mg/day			Relative Growth Rate percent/day			NAR $mg/mm^2/day$	LAR mm^2/mg
		total	shoot	root	total	shoot	root		
01	pitch	2.0	-[1]	-	3.8	-	-	0.0213	1.92
	loblolly	2.4	-	-	2.3	-	-	0.0259	1.14
12	pitch	2.3	1.5	0.8	1.1	1.0	1.3	0.0036	3.52
	loblolly	3.1	2.1	1.0	1.3	1.2	1.5	0.0048	2.88
23	pitch	1.2	0.5	0.7	0.4	0.3	0.7	0.0016	2.80
	loblolly	4.8	3.2	1.6	1.1	1.0	1.3	0.0043	2.64

[1]No value since seed weight was used for calculations.

Table 8. Mean values of growth analysis variables for *P. rigida* and *P. taeda* seedlings grown under two watering regimes.

Interval	Treatment	Absolute Growth Rate mg/day			Relative Growth Rate percent/day			NAR $mg/mm^2/day$	LAR mm^2/mg
		total	shoot	root	total	shoot	root		
01	well watered	2.7	-[1]	-	2.9	-	-	0.0258	1.36
	stressed	1.8	-	-	2.4	-	-	0.0230	1.22
12	well watered	1.1	1.2	0.7	0.8	0.7	1.0	0.0027	3.10
	stressed	3.6	2.5	1.1	1.7	1.6	1.9	0.0062	3.08
23	well watered	5.1	3.2	1.9	1.1	0.9	1.5	0.0045	2.75
	stressed	2.1	1.4	0.7	0.6	0.6	0.7	0.0023	2.64

[1]No value since seed weight was used for calculations.

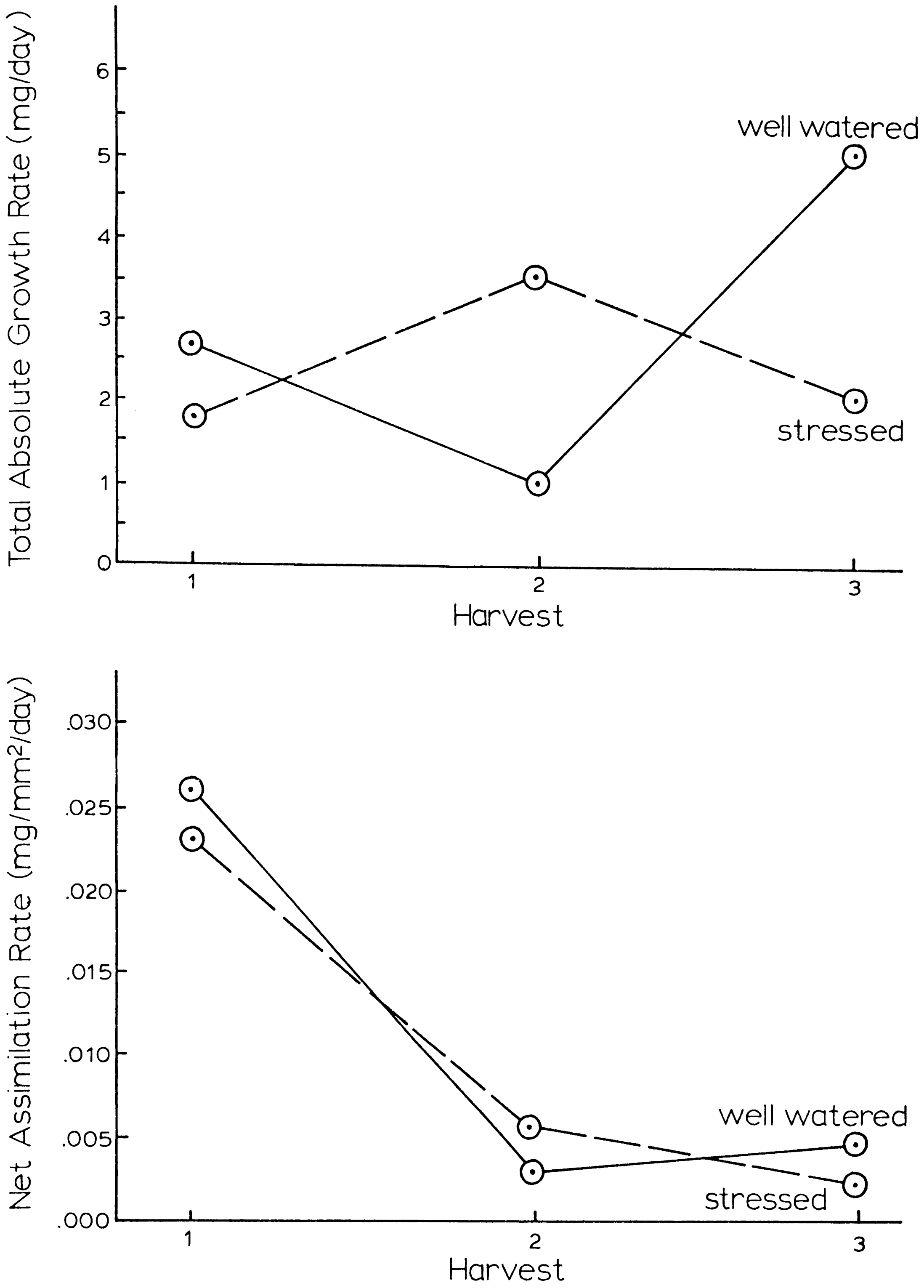


Fig. 5. Total Absolute Growth Rate and Net Assimilation Rate by Harvest Interval from Combined Data for 2 P. *rigida* and 4 P. *taeda* families grown under two watering regimes.

Allometric Growth

Analysis of shoot-root relationships of P. rigida and P. taeda revealed no significant k-value differences between treatments, species, or among families. K-values for the six pitch and loblolly pine families ranged from 0.757 to 0.844 (Table 9). Similarly, analysis of shoot-root relationships in the hybrid study revealed no significant differences in k-values between treatments or between families nested within crosses. There were, however, significant differences ($\alpha = 0.001$) in k-value among crosses. Values ranged from 0.736 to 0.890. The differences were apparent under both water treatments.

Correlations between k-values for each treatment, and a k-value obtained from the combined data, with means for all raw variables and growth analysis variables for each treatment were calculated for the hybrid crosses and the pitch and loblolly families. This was done to examine the relationship between k-value and growth under the two watering regimes. No significant correlation with k-value was found.

Correlation Analysis

There were no significant correlations found with height at age 1, 2, 3, 4, or 5. There were, however, many significant correlations with 7 year height and 7 year volume. Tables 10-17 present the results of Pearson product moment and Spearman rank correlations. Examination of matrices produced by the different methods on the same data suggests that the Pearson method is more likely to yield significant correlations with height than Spearman's technique, while the reverse is true of of correlations with volume.

Table 9. Summary of allometric coefficients for *P. x rigitaeda* crosses, and *P. rigida* and *P. taeda* families.

Hybrid Cross		k	st. error
22 x 64		0.890	0.026
51 x 23		0.749	0.027
71 x 22		0.849	0.027
71 x 23		0.892	0.031
78 x 22		0.736	0.029
78 x 26		0.863	0.030
Species	**family**	**k**	**st. error**
pitch	15	0.783	0.038
	33	0.757	0.048
loblolly	7-56	0.844	0.039
	11-09	0.762	0.029
	11-10	0.786	0.029
	11-20	0.843	0.035

It is possible to make some generalizations about the correlation results. Seed weight did not correlate with growth analysis variables with the exception of AGR's in the 0-1 interval. Seed weight did correlate with raw variable values from the well-watered control treatment, but not with values from the stress treatment, nor with overall experimental means from either treatment. The significant correlations coefficients with both techniques were quite high, $R > 0.80$ in every case. Significant correlations were found with raw variables as often, and perhaps more often, than were found with growth analysis variables. Total, shoot, and root dry weight seemed most valuable, correlating more often than did seedling heights, number of stem units, mean stem unit length, or leaf area.

Table 10. Pearson product moment correlation coefficients between growth variables at harvest 1 or interval 0-1 and plantation traits for 6 P. x rigitaeda crosses.[1]

Variable	Treatment					
	Well watered			Stressed		
	7 year height	7 year volume	Seed weight	7 year height	7 year volume	Seed weight
total weight	NS	0.864	0.888	0.899	0.908	NS
shoot weight	NS	0.899	0.874	0.904	0.904	NS
root weight	NS	NS	0.897	0.880	0.908	NS
shoot height	0.968	NS	NS	0.915	NS	NS
apical meristem height	0.947	0.891	NS	NS	NS	NS
stem units	NS	NS	0.877	NS	NS	NS
mean stem unit length	0.850	NS	NS	NS	NS	NS
leaf area	NS	NS	NS	0.921	0.903	NS
AGR total	NS	0.862	0.888	0.908	0.897	NS
AGR shoot	-[2]	-	-	-	-	-
AGR root	-	-	-	-	-	-
RGR total	0.955	NS	NS	0.835	NS	NS
RGR shoot	-	-	-	-	-	-
RGR root	-	-	-	-	-	-
NAR	NS	NS	NS	NS	NS	NS
LAR	NS	NS	NS	NS	NS	NS

[1]Values presented are significant R.
NS - not significant at $\alpha = 0.05$.

[2]No value since seed weight was used for calculation.

Table 11. Spearman rank correlation coefficients between growth variables at harvest 1 or interval 0-1 and plantation traits for 6 *P. x rigitaeda* crosses.[1]

Variable	Treatment					
	Well watered			Stressed		
	7 year height	7 year volume	Seed weight	7 year height	7 year volume	Seed weight
total weight	NS	NS	0.886	0.829	1.000	NS
shoot weight	NS	NS	NS	0.829	1.000	NS
root weight	NS	NS	NS	0.943	0.943	NS
shoot height	0.943	0.943	NS	0.943	0.943	NS
apical meristem height	0.943	0.943	NS	NS	NS	NS
stem units	NS	NS	0.886	NS	NS	NS
mean stem unit length	0.886	0.886	NS	NS	NS	NS
leaf area	0.829	NS	NS	0.829	1.000	NS
AGR total	NS	NS	NS	0.829	1.000	NS
AGR shoot	-[2]	-	-	-	-	-
AGR root	-	-	-	-	-	-
RGR total	NS	NS	NS	NS	0.943	NS
RGR shoot	-	-	-	-	-	-
RGR root	-	-	-	-	-	-
NAR	NS	NS	NS	NS	0.943	NS
LAR	NS	NS	NS	NS	NS	NS

[1] Values presented are significant R.
NS - not significant at $\alpha = 0.05$.

[2] No value since seed weight was used for calculation.

Table 12. Pearson product moment correlation coefficients between growth variables at harvest 2 or interval 1-2 and plantation traits for 6 P. x rigitaeda crosses.[1]

Variable	Well watered			Stressed		
	7 year height	7 year volume	Seed weight	7 year height	7 year volume	Seed weight
total weight	0.824	0.963	0.823	NS	0.841	NS
shoot weight	NS	0.968	0.822	NS	0.817	NS
root weight	0.848	0.936	0.815	NS	0.869	NS
shoot height	NS	NS	NS	NS	NS	NS
apical meristem height	NS	NS	NS	NS	NS	0.813
stem units	NS	NS	NS	NS	NS	NS
mean stem unit length	NS	NS	NS	NS	NS	NS
leaf area	NS	0.915	0.844	NS	NS	NS
AGR total	NS	NS	NS	NS	NS	NS
AGR shoot	NS	0.955	NS	NS	NS	NS
AGR root	NS	NS	NS	NS	NS	NS
RGR total	NS	NS	NS	NS	NS	NS
RGR shoot	NS	NS	NS	NS	NS	NS
RGR root	NS	NS	NS	NS	NS	NS
NAR	NS	NS	NS	NS	NS	NS
LAR	NS	NS	NS	NS	NS	NS

[1]Values presented are significant R.
NS - not significant at $\alpha = 0.05$.

Table 13. Spearman rank correlation coefficients between growth variables at harvest 2 or interval 1-2 and plantation traits for *P.* x *rigitaeda* crosses.[1]

Variable	Treatment					
	Well watered			Stressed		
	7 year height	7 year volume	Seed weight	7 year height	7 year volume	Seed weight
total weight	0.943	0.943	NS	NS	NS	NS
shoot weight	0.829	1.000	NS	NS	NS	NS
root weight	0.886	0.829	NS	NS	NS	NS
shoot height	NS	NS	NS	NS	NS	NS
apical meristem height	NS	NS	NS	NS	NS	0.829
stem units	NS	NS	NS	NS	0.812	NS
mean stem unit length	NS	NS	NS	NS	NS	NS
leaf area	NS	NS	NS	NS	NS	NS
AGR total	NS	0.829	NS	NS	NS	NS
AGR shoot	NS	0.829	NS	NS	NS	NS
AGR root	NS	NS	NS	NS	NS	NS
RGR total	NS	NS	NS	NS	NS	NS
RGR shoot	NS	NS	NS	NS	NS	NS
RGR root	NS	NS	NS	NS	NS	NS
NAR	NS	NS	NS	NS	NS	NS
LAR	NS	NS	NS	NS	NS	NS

[1]Values presented are significant R.
NS - not significant at $\alpha = 0.05$.

Table 14. Pearson product moment correlation coefficients between growth variables at harvest 3 or interval 2-3 and plantation traits for 6 P. x rigitaeda crosses.[1]

Variable	Well watered			Stressed		
	7 year height	7 year volume	Seed weight	7 year height	7 year volume	Seed weight
total weight	NS	NS	0.869	0.938	NS	NS
shoot weight	0.924	NS	NS	0.926	NS	NS
root weight	NS	NS	NS	0.975	NS	NS
shoot height	NS	NS	NS	NS	NS	NS
apical meristem height	NS	NS	NS	NS	NS	NS
stem units	NS	NS	NS	NS	NS	NS
mean stem unit length	NS	NS	NS	NS	NS	NS
leaf area	0.889	NS	NS	0.854	NS	NS
AGR total	NS	NS	NS	0.812	NS	NS
AGR shoot	NS	NS	NS	0.836	NS	NS
AGR root	NS	NS	NS	NS	NS	NS
RGR total	NS	NS	NS	NS	NS	NS
RGR shoot	NS	NS	NS	NS	NS	NS
RGR root	NS	NS	NS	NS	NS	NS
NAR	NS	NS	NS	NS	NS	NS
LAR	NS	NS	NS	NS	NS	NS

[1]Values presented are significant R.
NS - not significant at $\alpha = 0.05$.

Table 15. Spearman rank correlation coefficients between growth variables at harvest 3 or interval 2-3 and plantation traits for 6 *P.* x *rigitaeda* crosses.[1]

Variable	Treatment					
	Well watered			Stressed		
	7 year height	7 year volume	Seed weight	7 year height	7 year volume	Seed weight
total weight	NS	NS	0.943	0.886	0.829	NS
shoot weight	0.886	0.829	NS	NS	NS	NS
root weight	NS	NS	NS	0.943	0.943	NS
shoot height	NS	0.829	NS	NS	NS	NS
apical meristem height	NS	0.829	NS	NS	NS	NS
stem units	NS	NS	NS	NS	NS	NS
mean stem unit length	NS	NS	NS	NS	NS	NS
leaf area	0.886	0.829	NS	0.829	NS	NS
AGR total	NS	NS	NS	NS	NS	NS
AGR shoot	NS	NS	NS	NS	NS	NS
AGR root	NS	NS	NS	NS	NS	NS
RGR total	NS	NS	NS	NS	NS	NS
RGR shoot	NS	NS	NS	NS	NS	NS
RGR root	NS	NS	NS	NS	NS	NS
NAR	NS	NS	NS	0.838	NS	NS
LAR	NS	NS	NS	NS	NS	NS

---

[1]Values presented are significant R.
NS - not significant at $\alpha = 0.05$.

Table 16. Pearson product moment correlation coefficients between overall mean values of seedling growth variables and plantation traits for 6 *P.* x *rigitaeda* crosses.[1]

Variable	Treatment					
	Well watered			Stressed		
	7 year height	7 year volume	Seed weight	7 year height	7 year volume	Seed weight
total weight	0.876	0.881	NS	0.885	0.826	NS
shoot weight	0.889	0.881	NS	0.885	NS	NS
root weight	0.841	0.874	NS	0.873	0.865	NS
shoot height	NS	NS	NS	NS	NS	NS
apical meristem height	NS	NS	NS	NS	NS	NS
stem units	0.850	NS	NS	NS	NS	NS
mean stem unit length	NS	NS	NS	NS	NS	NS
leaf area	0.869	0.857	NS	0.899	NS	NS
AGR total	0.827	NS	NS	NS	NS	NS
AGR shoot	0.882	NS	NS	NS	NS	NS
AGR root	NS	NS	NS	NS	NS	NS
RGR total	0.816	NS	NS	NS	NS	NS
RGR shoot	NS	NS	NS	NS	NS	NS
RGR root	NS	NS	NS	NS	NS	NS
NAR	NS	NS	NS	0.838	NS	NS
LAR	NS	NS	NS	NS	NS	NS

[1]Values presented are significant R.
NS - not significant at $\alpha = 0.05$.

Table 17. Spearman rank correlation coefficients between overall mean values of seedling growth variables and plantation traits for 6 *P.* x *rigitaeda* crosses.[1]

Variable	Treatment					
	Well watered			Stressed		
	7 year height	7 year volume	Seed weight	7 year height	7 year volume	Seed weight
total weight	0.886	0.829	NS	0.886	0.829	NS
shoot weight	0.943	0.943	NS	0.886	0.829	NS
root weight	NS	NS	NS	0.943	0.943	NS
shoot height	NS	0.829	NS	NS	NS	NS
apical meristem height	NS	0.829	NS	NS	NS	NS
stem units	NS	0.943	NS	NS	0.829	NS
mean stem unit length	NS	0.829	NS	NS	NS	NS
leaf area	0.886	0.829	NS	0.886	0.829	NS
AGR total	0.886	NS	NS	NS	NS	NS
AGR shoot	0.943	0.943	NS	NS	NS	NS
AGR root	NS	NS	NS	NS	NS	NS
RGR total	NS	NS	NS	NS	NS	NS
RGR shoot	NS	NS	NS	NS	NS	NS
RGR root	NS	NS	NS	NS	NS	NS
NAR	NS	0.829	NS	NS	0.829	0.829
LAR	NS	NS	NS	NS	NS	NS

[1]Values presented are significant R.
NS - not significant at $\alpha = 0.05$.

DISCUSSION

Seed Weights

Differences in seed weights have been known to be correlated with differences in growth (Righter, 1965). This occurred in the hybrid seedlings grown under well watered conditions, but not in seedlings grown under the stress treatment. Apparently, under luxurious conditions, seedlings can rely heavily on stored nutritive tissue, but under stress conditions differences in metabolic efficiency become more important. This may not hold true for all ranges of seed weights. With three to fourfold differences in seed weight, the pitch pine and loblolly pine seedling growth characters remained correlated with seed weight even under the stress treatment. The large differences in seed size of loblolly and pitch pine are not peculiar to this study. Loblolly averages 18,200 seed per pound and pitch pine averages 61,700 seed per pound (U.S.D.A. Handbook 450, 1974). Simple computations yield a seed weight average of 24.9 mg and 7.4 mg, respectively. In comparison, the averages in this study were 30.3 mg and 7.9 mg. The slightly larger than average size of the loblolly seed may reflect their seed orchard origin.

Hybrid Raw Variables: Genetic Variance Components

A very interesting result of the analysis of variance of the hybrid raw variables was the change in size of the variance components σ^2_C and $\sigma^2_{F(C)}$ under the two moisture treatments. Normally, one interprets the genetic meaning of variance components such as these using quantitative genetics theory. In most quantitative genetics work with forest trees, it is common to collect open pollinated seed and to assume a half-sib relationship among seedlings from a single mother tree. Assuming this half-sib relationship, and no epistatic effects, the variance components σ^2_C and $\sigma^2_{F(C)}$ have the following genetic expectations (Falconer, 1960):

$$\sigma^2_C = \text{average covariance of cousins} = 1/8\ \sigma^2_A$$

$$\sigma^2_{F(C)} = \text{average covariance of half-sibs minus } \sigma^2_C = 1/4\ \sigma^2_A - 1/8\ \sigma^2_A = 1/8\ \sigma^2_A$$

where: σ^2_A = additive genetic variance.

With the above expectations, one would expect σ^2_C and $\sigma^2_{F(C)}$ to tend to be significant under the same conditions. This is not the case; therefore, the genetic expectations of σ^2_C and $\sigma^2_{F(C)}$ must be substantially different.

Libby et al. (1969) list four possible biases that may enter into quantitative genetics work with open pollinated seed:

a) not all trees produce abundant seed, thus biasing the study toward fruitful parents;

b) the parents may be related, producing inbred seedlings;

c) males related to each other but not to the females will produce seedlings which are more closely related than half-sibs; and

d) if males contribute more than one offspring per family, the average relationship will be greater than half-sibs.

This study was performed using open pollinated seed collected from a production progeny test, where full sibs were planted in ten tree row plots. There is, therefore, a strong possibility that all four biases are confounding the genetic expectations of σ^2_C and $\sigma^2_{F(C)}$. An additional source of confusion lies in the inter-relationship of the six hybrid crosses. This makes it extremely difficult even to speculate as to whether additive, dominance, or epistatic variance is most important under particular environmental conditions. The results obtained, however, do suggest that the importance of specific genetic variance components may vary with environmental conditions. These results parallel those of Waxler and van Buijtenen (1981) with loblolly pine in a similar experiment. They found changes in genetic variance between four different moisture regimes. A similar type phenomenon was observed by Feret *et al*. (1979) in *Pinus pungens* Lamb. They found no relationship between family dry weight accumulation rankings of seedlings grown on two different soils. From their results, they inferred that genes important to the species for growth on one soil were different than the genes required for growth on the other.

A study performed using *P*. x *rigitaeda* seed from controlled crosses could provide estimates of additive and dominance variance components under different moisture regimes.

Allometric Growth Equations

The results of this study do not support a hypothesis that differences in k-value reflect differences in abilities to grow under moisture stress. One should not necessarily conclude, however, that k-value differences are biologically insignificant in *P*. *taeda*, *P*. *rigida* or

P. x rigitaeda. The range of k-values reported here was substantially smaller than documented by other workers. Ledig and Perry (1965) reported a range of 0.42 to 0.92 in loblolly pine, in comparison to the range of 0.76 to 0.84 found in loblolly and pitch, and 0.74 to 0.89 found in P. x rigitaeda in this study. It may be that slight differences in k-values at the upper portion of the range are not meaningful.

Variations in light intensity, soil nutrition, atmospheric humidity and photoperiod do not alter the allometric coefficient k (Ledig and Perry, 1965; Wareing, 1960). It is not clear whether differences in soil moisture lead to differences in k-value. Ledig et al. (1970) found some evidence that k-value in loblolly pine differed between two moisture regimes, although the difference was significant only at the 0.10 level of probability. The results of this study suggest that k-value in loblolly, pitch, and pitch x loblolly pine do not change under different moisture regimes. This implies that a particular plant cannot adapt to environmental conditions by changes in relative allocation of dry matter to shoots and roots, rather that this particular aspect of its growth pattern is determined solely by its genotype.

Pitch and Loblolly Pine

The fast growth rate of loblolly pine relative to pitch pine, is apparent even at the very early seedling stage. At every harvest, loblolly had a larger dry weight, was taller, had more stem units, and more leaf area than pitch pine. The species showed few differences in relative growth rates and the only difference was in total RGR in interval 0-1, where pitch pine grew more efficiently than loblolly. The results imply that the faster growth of loblolly pine was not due to a greater growth efficiency. Two alternate explanations are suggested by an examination of the data. The first is the correlation of growth variables with seed weight, and the differences in relative seed size discussed above. The second is the tendency of loblolly to exhibit free growth as opposed to the essentially fixed-growth pattern exhibited by pitch pine. This was observed in this experiment when the pitch pines slowed and stopped growth earlier than did loblolly. Perhaps these two factors, loblolly pine's large seed and percentage of free growth, are the major contributors to the recognized superiority in growth of loblolly over pitch pine.

Correlation Analysis

The many significant correlations with 7 year height and volume presented in Tables 10-17 indicate the potential of juvenile-mature correlation analysis as a genetic screening technique for *P.* x *rigitaeda*. It seems particularly promising that many variables consistently have high correlations with field performance, regardless of harvest-treatment combination. For example, using the Pearson technique, shoot dry weight correlated significantly with either height or volume at each harvest-treatment level, and with mean values averaged over harvest. The presence of these consistently significant correlations suggests that there may be a biological relationship between greenhouse growth of seedlings and field performance. The fact that correlations were significant at each harvest indicates that this relationship is apparent over a relatively long period of time, and not only at a particular stage in seedling development. This suggests that a genetic screening technique based on greenhouse growth of seedlings would have the added convenience of flexible harvest scheduling.

The lack of relationship with height at ages one through five, and the "sudden" appearance of relationship in year seven, may be the result of changes in rank during this period. Bailey (1980) did a comprehensive study on changes in rank from 1975 to 1979 for the 53 hybrid crosses planted at Reynolds Homestead Research Center. The comparison-wise error rate was set at $\alpha = 0.001$ to insure that the experiment-wise rate was less than 0.05. One cross (22 x 64) examined in this study went from rank 43 in 1975 to rank 22 in 1979. Changes in rank of this nature from 1975 to 1981 could account for the non-significant correlations obtained with early height measurements.

The growth analysis variables did not correlate often with the field traits, nor were there consistent relationships as seen in the raw variables. This may be due in part to the relatively small size of the experiment. The data may not have given good estimates of the true growth analysis parameters, and consequently, possible relationships with field performance may not have been reflected in the correlations. However, the lack of relationship reported here concurs, in a general way, with the results of Campbell and Rediske (1965) in a study on photosynthetic efficiency and dry weight gain in Douglas-fir seedlings. They concluded that selection for photosynthetic efficiency in nearly mature trees would be less efficient than selection on the desired growth traits themselves. The usefulness of a general application of this idea to *P. x rigitaeda* is supported by the comparison of results obtained with simple plant dry weight measurements to those obtained with the more sophisticated growth analysis techniques.

One should be somewhat cautious in interpreting the predictive value of a variable that is correlated with height or volume if it also happens to be correlated with seed weight. This is particularly important in this study, where correlations were made between seedling growth characteristics and parental field performance. A variable correlated with volume and seed weight may simply reflect the fact that a large tree produces large seed and, therefore, large seedlings. One should probably place more faith in those variables which correlate with field performance and not with seed weight. In seedlings grown under water stress, the variables total weight and shoot weight satisfy these conditions.

The small size of this experiment leads to some problems in assuming the broad applicability of these results to *P. x rigitaeda*. Of the 53 crosses planted at Reynolds Homestead Research Center, the six examined in this study were ranked 21, 25, 28, 29, 40 and 46 for 5th year height growth. The crosses then represented a range from the 60th percentile to the 13th percentile, or approximately half the range for height growth.

Another potential problem is suggested by the work of Cannell *et al.* (1978) and Feret (1981)[1]. Feret found correlations between seedling

---

[1] Feret, P.P. 1981. Research completed at the Institute of Forest Genetics, Placerville, California. Manuscript in preparation.

growth and field performance in ponderosa pine to be plantation specific; i.e., variables of apparent potential in predicting growth in one plantation often had no value in another. Cannell *et al.* (1978) found in loblolly pine that the significance of correlations between juvenile growth and field performance depended on how closely greenhouse moisture conditions mimicked those found in a particular plantation. One should not be surprised to find some type of this plantation to plantation variation in *P.* x *rigitaeda*.

Further research would shed light on the situation. A suitable experiment would involve repeating particular pitch x loblolly crosses that are represented in a number of *P.* x *rigitaeda* plantations with varying degrees of water availability. One should insure that the crosses examined represent a large portion of height and volume ranges in all plantations to be studied.

SUMMARY AND CONCLUSION

Seedlings of two *P. rigida* and four *P. taeda* families and six *P. x rigitaeda* crosses were grown in a greenhouse under two moisture regimes. Water stress decreased growth in every case in every variable measured. Water stress also elicited some genetic differences in the pitch pine and loblolly pine that were not apparent under the control treatment. The major differences between pitch and loblolly seedlings seemed to be primarily a function of large differences in seed size. The continued growth of loblolly throughout the experiment indicated that free growth may also play a major role in differences between the two species.

The theory that allometric coefficients are a good indicator of performance under varying conditions of water stress was not substantiated by this experiment. In addition, k-values were found to remain relatively constant despite changes in water stres. For the range of stress examined in this study, it appears that water stress does not affect the relative allocation of dry matter to shoots and roots.

Genetic variance components in *P. x rigitaeda* may have importance under one set of environmental conditions and not under another. Interrelationship and confounding of genetic expectations, however, make it difficult to speculate which variance components are most important under moisture stress.

Numerous correlations between seedling growth characteristics and 7 year height and volume of *P. x rigitaeda* were significant, and they indicate that greenhouse experiments may be useful as a genetic screening technique for superior hybrid crosses, although a need for further research was identified.

LITERATURE CITED

Anonymous. 1964. The 1912 Douglas fir study, Annual Report. U.S.D.A. For. Serv., Pac. NW For. and Range Expt. Sta. p. 4-7.

Bailey, D. 1981. Height growth differences among P. rigida x P. taeda hybrids and an assessment of stem unit information in relation to shoot length in selected families. Virginia Polytechnic Institute and State University M.S. Thesis. 87 pp.

Campbell, R.K. and J.H. Rediske. 1966. Genetic variability of photosynthetic efficiency and dry matter accumulation in seedling Douglas-fir. Silvae Genetica 15: 65-72.

Cannell, M.G.R. 1978. Commponents of conifer shoot growth. Proceedings of the 5th North American Forest Biology Workshop. University of Florida, Gainesville, Florida. p. 313-318.

Cannell, M.G.R., F.E. Bridgewater and M.S. Greenwood. 1978. Seedling growth rates, water stress responses and root-shoot relationships related to eight year volumes among families of Pinus taeda L. Silvae Genetica 27:237-248.

Cannell, M.G.R., S. Thompson, and R. Lines. 1976. An analysis of inherent differences in shoot growth within some North Temperate conifers. In: Tree Physiology and Yield Improvement. Ed. M.G.R.Cannell and F.T. Last. p. 173-205.

Doak, C.C. 1935. Evolution of foliar types, dwarf shoots and cone scales of Pinus. Illinois Biological Monograph 13. 106 pp.

Dorman, K. 1976. The Genetics and Breeding of Southern Pines. U.S.D.A. Forest Service Agriculture Handbook No. 471.

Falconer, D.S. 1981. Intro. to Quant. Genetics. Longman Inc., New York. 340 pp.

Feret, P.P., D. Wm. Smith and H.M. Rauscher. 1979. Dry matter accumulation in twenty Wind Pollinated Pinus pungens families from southeast Virginia. Silvae Genetica 28: 194-196.

Grifing, C.G., and W.W. Elam. 1971. Height growth patterns of loblolly pine saplings. For. Sci. 17:52-54.

Helwig, J.T. and K.A. Council. 1979. SAS users Guide. SAS Institute. Cary, North Carolina. 494 pp.

Hyun, S.K. 1976. Interspecific hybridization in pines with the special reference to P. rigida x taeda. Silvae Genetica 25(6): 188-191.

Jablanczy, A. 1971. Changes due to age in apical development in spruce and fir. Can. Forest Service Bimonthly Research Notes 27, p. 10.

Kramer, P.J. and T.T. Kozlowski. 1960. Physiology of Trees. McGraw-Hill, New York. 642 pp.

Lafarge, T. 1975. Correlations between nursery and plantation height growth in slash and loblolly pine. Forest Science 21:197-200.

Lanner, R.M. 1976. Patterns of shoot development in Pinus and their relationship to growth potential. In: Tree Physiology and Yield Improvement. Ed. M.G.R. Cannell and F.T. Last. p. 224-243.

Ledig, F.T. 1974. Concepts of growth analysis. In: C.P.P. Reid and G.H. Fechner (eds.). Proceedings of the 3rd North American Forest Biology Workshop. Colorado State Univ. Ft. Collins. Colorado. p. 166-182.

Ledig, F.T., F.H. Bormann and K.F. Wenger. 1970. The distribution of dry matter growth between shoots and roots in loblolly pine. Bot. Gaz. 131:349-359.

Ledig, F.T. and T.O. Perry. 1965. Physiological genetics of the shoot-root ratio. Proc. Soc. American Foresters, Detroit, Michigan. p. 39-43.

Li, J.C.R. 1964. Statistical Inference I. Edward Brothers, Inc. Ann Arbor, Michigan. 658 pp.

Libby, W.J., R.F. Stettler, and F.W. Seitz. 1969. Forest Genetics and Tree Breeding. In: Annual Review of Genetics 3:469-493.

Little, E.L., Jr. 1965. In: Silvics of Forest Trees of the United States. U.S.D.A. Forest Service Agriculture Handbook No. 271.

Little, S. 1965. Loblolly-pitch pine breeding orchards. N.E. For. Tree Imp. Conf. Proc. 12:56-57.

Little, S. and H.A. Somes. 1951. No exceptional vigor found in hybrid pines tested. Northeast Forest Experiment Station Research Notes 10. 4 pp.

Little, S. and I.F. Trew. 1976. Breeding and testing pitch x loblolly pine hybrids for the Northeast. Northeast Forest Tree Improvement Conference Proceedings 23:71-85.

Little, S, and I.F. Trew. 1977. Progress reports on testing pitch x loblolly hybrids and on producing hybrid seed for mass planting. Northeast Forest Tree Improvement Conference Proceedings 24:14-28.

Little, S., and I.F. Trew. 1979. Pitch x loblolly hybrids; Loblollies for the North? J. For. 77(11):709-713.

Logan, K.T. and D.F. Pollard. 1975. Mode of shoot growth in 12 year old black spruce provenances. Canadian Journal of Forest Research 5:539-540.

Nanson, A. 1976. Juvenile-mature relationships, mainly in provenance and progeny tests. In: Proceedings of the I.U.F.R.O. joint meeting of the genetic workinng parties on advanced generation breeding. Bourdeaux. Fr. Publ. by I.N.R.A., 33610 Cestas, France. p. 99-119.

Namkoong, G., and M.T. Conkle. 1976. Time trends in genetic control of height growth in ponderosa pine. Forest Science. 2:2-12.

Pollard, D.F., and K.T. Logan. 1974. The role of free growth in differentiation of provenances of black spruce. Canadian Jour. of For. Research. 4:308-311.

Radford, P.J. 1967. Growth analysis formulae -- their use and abuse. Crop Science 7:171-175.

Righter, F.I. 1965. Pinus: The relationship of seed size and seedling size to inherent vigor. J. For. 43: 131-137.

Robinson, J.F., and J.P. van Buijtenen. 1979. Correlation of seed weight and nurserybed traits with 5-, 10-, and 15-year volumes in a loblolly pine progeny test. Forest Science 25:591-596.

Sands, K., and A.J. Rutter, 1959. Studies in the growth of young plants of Pinus sylvestris L. II, The relation of growth to soil moisture tension. Annals of Botany 23:269-284.

Scholander, P.F., H.T. Hammel, E.D. Bradstreet, and E.A. Hemmingsen. 1965. Sap pressure in vascular plants. Sci. 148:339-346.

Stanhill, G. 1957. The effect of differences in soil moisture status on plant growth: A review and analysis of soil moisture regime experiments. Soil Science 84:205-214.

Steele, R.G.D., and J.H. Torrie. 1960. Princ. and Proc. of Statistics. McGraw Hill, New York. 481 pp.

Stransky, J.J., and D.R. Wilson. 1964. Terminal elongation of loblolly and short-leaf pine seedlings under soil moisture stress. Soil Science Society Proceedings, p. 439-440.

Tepper, H.B. 1963. Leader growth of pitch and shortleaf pines. Forest Science 9(3):344-353.

U.S.D.A. For. Serv. 1974. Seeds of Woody Plants of the U.S. U.S.D.A. Ag. Handbook No. 450. 883 pp.

van den Driessche, R. 1968. Growth analysis of four nursery grown conifer species. Canadian Journal of Botany 46:1389-1395.

Waxler, M.S. and J.P. van Buijtenen. 1981. Early genetic evaluation of loblolly pine. Ca. J. For. Res. 11:351-355.

Yeatman, C.W. and M.J. Holst. 1967. Correlations between controlled environment and nursery grown seedlings of jack pine provenances. 14th NEFTIC Proceedings. Toronto, Canada. p. 24-29.

Zimmermann, M.H. and C.L. Brown. 1971. Trees: Structure and Function. Springer-Verlag, New York. 336 p.

Appendix A

Summary of ANOVA on eight variables measured on seedlings of *P. x rigitaeda*.[1]

Cross	Source	Dependent Variable							
		shoot weight	root weight	total weight	shoot length	apical meristem height	stem units	stem unit length	leaf area
22 x 64	harvest	NS	*	NS	NS	NS	NS	NS	NS
	block	NS	NS	NS	NS	NS	NS	NS	NS
	treatment	NS	NS	NS	NS	NS	NS	NS	NS
	family	NS	NS	NS	NS	NS	NS	NS	NS
	har x treat	NS	NS	NS	NS	NS	NS	NS	NS
	har x family	NS	NS	NS	NS	NS	NS	NS	NS
	har x trt x fam	NS	NS	NS	NS	NS	NS	NS	NS
51 x 23	harvest	*	NS	NS	***	***	**	*	*
	block	NS	NS	NS	NS	NS	NS	NS	NS
	treatment	*	NS	NS	**	**	*	**	NS
	family	NS	NS	NS	**	***	*	*	NS
	har x treat	NS	NS	NS	NS	NS	NS	NS	NS
	har x family	NS	NS	NS	NS	NS	NS	NS	NS
	har x trt x fam	NS	*	NS	NS	NS	NS	NS	NS
71 x 22	harvest	**	*	*	*	*	*	*	**
	block	NS	NS	NS	NS	NS	NS	NS	NS
	treatment	**	**	**	***	***	**	**	*
	family	NS	NS	NS	NS	NS	NS	NS	NS
	har x treat	NS	*	*	**	*	NS	NS	NS
	har x family	NS	*	*	*	NS	NS	NS	NS
	har x trt x fam	NS	NS	NS	NS	NS	NS	NS	NS

[1]NS – not significant
* – significant at $\alpha = 0.05$
** – significant at $\alpha = 0.01$
*** – significant at $\alpha = 0.001$

Appendix A (continued)

Cross	Source	Dependent Variable							
		shoot weight	root weight	total weight	shoot length	apical meristem height	stem units	stem unit length	leaf area
71 x 23	harvest	**	*	**	***	**	**	*	**
	block	*	**	NS	NS	NS	**	NS	NS
	treatment	*	**	*	**	**	NS	*	NS
	family	*	NS	NS	NS	NS	NS	NS	NS
	har x treat	NS	*	NS	*	*	NS	**	NS
	har x family	NS	NS	NS	NS	NS	NS	NS	NS
	har x trt x fam	NS	NS	NS	NS	NS	NS	NS	NS
78 x 22	harvest	*	*	*	**	**	**	*	*
	block	NS	NS	NS	NS	NS	NS	*	NS
	treatment	*	*	*	NS	NS	*	NS	**
	family	*	*	*	**	*	**	NS	*
	har x treat	NS	NS	NS	NS	NS	NS	NS	**
	har x family	NS	NS	NS	NS	NS	NS	NS	*
	har x trt x fam	NS	NS	NS	NS	*	NS	*	NS
78 x 26	harvest	**	*	**	NS	**	*	*	*
	block	NS	NS	NS	**	NS	**	NS	NS
	treatment	***	***	***	*	**	*	*	**
	family	NS	NS	NS	NS	NS	NS	NS	NS
	har x treat	**	**	***	NS	NS	NS	NS	NS
	har x family	NS	*	*	NS	NS	NS	NS	NS
	har x trt x fam	NS	NS	NS	NS	NS	NS	NS	NS

[1]NS - not significant
* - significant at $\alpha = 0.05$
** - significant at $\alpha = 0.01$
*** - significant at $\alpha = 0.001$

Appendix B

Summary of ANOVA on eight variables measured on seedlings of P. x rigitaeda crosses grown under well watered and stressed treatments.[1]

Treatment	Source	Dependent Variable: shoot weight	root weight	total weight	shoot length	apical meristem height	stem units	stem unit length	leaf area
well watered	harvest	***	***	***	***	***	***	***	***
	block	NS	NS	NS	NS	NS	***	NS	NS
	cross	*	NS	NS	**	***	NS	*	*
	fam(cross)	NS	NS	NS	NS	NS	NS	NS	NS
	harv x fam(cr)	*	**	**	*	*	*	NS	*
stressed	harvest	***	***	***	***	***	***	***	***
	block	NS	NS	NS	**	***	***	***	NS
	cross	NS	NS	NS	NS	NS	NS	NS	NS
	fam(cross)	*	*	*	*	*	***	NS	NS
	harv x fam(cr)	*	NS	*	NS	NS	NS	NS	**

[1]NS - not significant
* - significant at $\alpha = 0.05$
** - significant at $\alpha = 0.01$
*** - significant at $\alpha = 0.001$

Appendix C

Summary of ANOVA on eight variables measured on seedlings of two *P. rigida* and four *P. taeda* families.[1]

Source	shoot weight	root weight	total weight	shoot length	apical meristem height	stem units	stem unit length	leaf area
	Dependent Variable							
harvest	***	***	***	***	***	***	NS	***
block	***	***	***	**	**	NS	***	NS
treatment	**	**	**	**	**	**	**	**
species	*	*	*	**	**	**	*	NS
fam(species)	NS	NS	NS	*	NS	*	NS	*
treat x species	NS	NS	NS	NS	NS	NS	NS	NS
trt x fam(species)	NS	NS	NS	NS	NS	NS	NS	NS
harvest x species	**	*	**	*	*	**	NS	**
harvest x treatment	*	**	*	NS	NS	NS	NS	NS
har x trt x species	NS	NS	NS	NS	NS	NS	NS	NS
har x trt x fam(species)	NS	NS	NS	*	*	NS	**	NS

[1] NS – not significant
 * – significant at $\alpha = 0.05$
 ** – significant at $\alpha = 0.01$
 *** – significant at $\alpha = 0.001$

Appendix D

Summary of ANOVA on eight variables measured on seedlings of two *P. rigida* and four *P. taeda* families grown under well watered and stressed treatments.

Treatment	Source	Dependent Variable							
		shoot weight	root weight	total weight	shoot length	apical meristem height	stem units	stem unit length	leaf area
well watered	harvest	***	***	***	*	**	***	NS	**
	block	**	**	**	NS	NS	NS	*	NS
	species	**	*	**	**	***	**	NS	*
	fam(species)	NS	NS	NS	NS	NS	NS	NS	NS
	harvest x sp	*	NS	*	NS	NS	**	NS	**
	harv x fam(sp)	NS	NS	NS	*	*	NS	***	NS
stressed	harvest	***	***	***	***	***	***	**	**
	block	*	**	*	*	*	NS	***	NS
	species	*	NS	NS	**	**	**	**	NS
	family (sp)	*	*	*	**	*	**	NS	NS
	harv x sp	*	*	*	*	*	***	NS	NS
	harv x fam(sp)	NS	NS	NS	NS	NS	NS	NS	NS

[1]NS - not significant
* - significant at $\alpha = 0.05$
** - significant at $\alpha = 0.01$
*** - significant at $\alpha = 0.001$

Appendix E

Summary of ANOVA on growth analysis variables calculated for seedlings from *P.* x *rigitaeda* crosses.[1]

Cross	Source	Dependent Variable: shoot AGR	shoot RGR	root AGR	root RGR	total AGR	total RGR	NAR	LAR
22 x 64	interval	*	*	NS	*	*	*	**	**
	block	NS	NS	NS	NS	NS	NS	NS	NS
	treatment	NS	NS	NS	NS	NS	NS	NS	NS
	family	NS	NS	NS	NS	NS	NS	NS	NS
	int x tr	NS	NS	NS	NS	NS	NS	NS	NS
	int x fam	NS	NS	NS	NS	NS	NS	NS	NS
	int x trt x fam	NS	NS	NS	NS	NS	NS	NS	NS
51 x 23	interval	NS	NS	NS	NS	NS	**	***	***
	block	NS	NS	NS	NS	NS	NS	NS	*
	treatment	NS	NS	NS	NS	NS	NS	NS	NS
	family	NS	NS	NS	NS	NS	NS	NS	NS
	int x tr	NS	NS	NS	NS	NS	NS	NS	*
	int x fam	NS	NS	NS	NS	NS	NS	NS	NS
	int x trt x fam	NS	NS	NS	NS	NS	NS	NS	NS
71 x 22	interval	NS	*	NS	NS	***	*	**	***
	block	NS	NS	NS	NS	NS	NS	NS	NS
	treatment	NS	NS	NS	NS	*	NS	NS	NS
	family	NS	NS	NS	NS	NS	NS	NS	NS
	int x tr	NS	NS	NS	NS	NS	NS	NS	NS
	int x fam	NS	NS	NS	NS	**	NS	NS	NS
	int x trt x fam	NS	NS	NS	NS	NS	NS	NS	NS

[1]NS - not significant
 * - significant at $\alpha = 0.05$
 ** - significant at $\alpha = 0.01$
 *** - significant at $\alpha = 0.001$

Appendix E (continued)

Cross	Source	Dependent Variable							
		shoot AGR	shoot RGR	root AGR	root RGR	total AGR	total RGR	NAR	LAR
71 x 23	interval	NS	NS	NS	*	*	**	***	***
	block	NS	NS	NS	NS	NS	NS	NS	**
	treatment	NS	NS	*	NS	*	NS	NS	NS
	family	NS	NS	NS	NS	NS	NS	NS	NS
	int x tr	NS	NS	*	NS	NS	NS	NS	NS
	int x fam	NS	NS	NS	NS	NS	NS	NS	NS
	int x trt x fam	NS	NS	NS	NS	NS	NS	NS	NS
51 x 23	interval	NS	NS	NS	NS	NS	NS	**	***
	block	NS	NS	NS	NS	NS	NS	NS	*
	treatment	NS	NS	NS	NS	NS	NS	NS	*
	family	*	NS	NS	NS	NS	NS	NS	NS
	int x tr	NS	NS	NS	NS	NS	NS	NS	NS
	int x fam	NS	NS	NS	NS	NS	NS	NS	NS
	int x trt x fam	NS	NS	NS	NS	NS	NS	NS	NS
71 x 22	interval	**	**	NS	*	***	***	**	**
	block	NS	NS	NS	NS	NS	NS	NS	NS
	treatment	**	*	*	NS	***	*	NS	NS
	family	NS	NS	NS	NS	NS	NS	NS	NS
	int x tr	NS	*	*	NS	**	NS	NS	NS
	int x fam	*	*	NS	NS	***	*	NS	NS
	int x trt x fam	NS	NS	NS	NS	NS	NS	NS	NS

[1]NS - not significant
* - significant at $\alpha = 0.05$
** - significant at $\alpha = 0.01$
*** - significant at $\alpha = 0.001$

Appendix F

Summary of ANOVA on growth analysis variables calculated for _P._ x _rigitaeda_ seedlings grown under well watered and stressed treatments.[1]

Treatment	Source	Dependent Variable							
		shoot AGR	shoot RGR	root AGR	root RGR	total AGR	total RGR	NAR	LAR
well watered	interval	*	**	NS	**	***	***	***	***
	block	*	**	NS	NS	NS	NS	NS	NS
	cross	NS	NS	NS	NS	NS	NS	NS	**
	family(cross)	NS	NS	NS	NS	NS	NS	NS	NS
	int x fam(cross)	NS	NS	NS	NS	NS	NS	NS	NS
stressed	interval	NS	**	NS	**	***	***	***	***
	block	NS	NS	NS	NS	NS	NS	NS	NS
	cross	NS	NS	NS	NS	NS	NS	NS	NS
	family(cross)	NS	NS	NS	NS	NS	NS	NS	*
	int x fam(cross)	NS	*	*	NS	NS	**	**	NS

[1]NS - not significant
* - significant at $\alpha = 0.05$
** - significant at $\alpha = 0.01$
*** - significant at $\alpha = 0.001$

Appendix G

Summary of ANOVA on growth analysis variables calculated for P. x rigitaeda seedlings over three harvest intervals.[1]

Interval	Source	shoot AGR	shoot RGR	root AGR	root RGR	total AGR	total RGR	NAR	LAR
		Dependent Variable							
01	treatment	–	–	–	–	**	*	NS	*
	block	–	–	–	–	*	NS	NS	*
	cross	–	–	–	–	**	*	**	*
	trt x cross	–	–	–	–	NS	NS	NS	NS
	trt x fam(cross)	–	–	–	–	**	NS	NS	NS
12	treatment	*	NS	NS	NS	NS	*	NS	NS
	block	*	*	NS	NS	NS	NS	NS	*
	cross	NS	NS	NS	NS	NS	NS	*	NS
	trt x cross	NS	NS	NS	NS	NS	NS	NS	NS
	trt x fam(cross)	NS	NS	NS	NS	NS	NS	NS	NS
23	treatment	NS	NS	NS	NS	NS	NS	NS	NS
	block	*	NS	NS	NS	*	NS	NS	NS
	cross	*	NS	NS	NS	NS	NS	NS	NS
	trt x cross	NS	NS	NS	NS	NS	NS	NS	NS
	trt x fam(cross)	NS	NS	NS	NS	NS	NS	NS	NS

[1] NS – not significant
* – significant at $\alpha = 0.05$
** – significant at $\alpha = 0.01$
*** – significant at $\alpha = 0.001$

Appendix H

Summary of ANOVA on growth analysis variables calculated for seedlings from two *P. rigida* and four *P. taeda* families.[1]

Source	Dependent Variable							
	shoot AGR	shoot RGR	root AGR	root RGR	total AGR	total RGR	NAR	LAR
interval	NS	NS	*	NS	NS	NS	NS	**
block	**	*	***	**	**	*	**	***
treatment	NS	NS	NS	NS	NS	NS	NS	NS
species	**	NS	*	NS	*	NS	NS	*
fam(species)	NS	NS	NS	NS	NS	NS	NS	NS
treat x species	NS	NS	NS	NS	NS	NS	NS	NS
treat x fam(species)	NS	NS	NS	NS	NS	NS	NS	NS
interval x species	NS	NS	NS	NS	NS	NS	NS	NS
interval x treatment	*	*	***	**	**	**	**	NS
int x trt x species	NS	NS	*	*	NS	*	*	NS
int x trt x fam(species)	NS	NS	NS	NS	NS	NS	NS	NS

[1] NS - not significant
* - significant at $\alpha = 0.05$
** - significant at $\alpha = 0.01$
*** - significant at $\alpha = 0.001$

Appendix I

Summary of ANOVA on growth analysis variables calculated for seedlings of two *P. rigida* and four *P. taeda* families grown under well watered and stressed treatments.[1]

Treatment	Source	Dependent Variable							
		shoot AGR	shoot RGR	root AGR	root RGR	total AGR	total RGR	NAR	LAR
well watered	interval	NS	NS	*	NS	*	NS	NS	*
	block	**	*	**	*	**	**	**	*
	species	NS	NS	NS	NS	NS	NS	NS	NS
	family(sp)	NS	NS	NS	NS	NS	NS	NS	NS
	interval x sp	NS	NS	NS	NS	NS	NS	NS	NS
	int x fam(sp)	NS	NS	NS	NS	NS	NS	NS	NS
stressed	interval	NS	*	*	**	NS	*	*	*
	block	NS	NS	*	*	NS	NS	*	**
	species	*	NS	*	*	*	NS	*	*
	family(sp)	NS	NS	NS	NS	NS	NS	NS	NS
	interval x sp	NS	NS	NS	NS	NS	NS	NS	NS
	int x fam(sp)	NS	NS	NS	NS	NS	NS	NS	NS

[1] NS - not significant
* - significant at $\alpha = 0.05$
** - significant at $\alpha = 0.01$
*** - significant at $\alpha = 0.001$

Appendix J

Summary of ANOVA on growth analysis variables calculated for seedlings of two *P. rigida* and four *P. taeda* families over three harvest intervals.[1]

Interval	Source	Dependent Variable							
		shoot AGR	shoot RGR	root AGR	root RGR	total AGR	total RGR	NAR	LAR
01	treatment	–	–	–	–	**	**	NS	NS
	block	–	–	–	–	*	NS	NS	NS
	species	–	–	–	–	NS	*	*	*
	fam(species)	–	–	–	–	NS	*	NS	NS
	trt x species	–	–	–	–	NS	NS	NS	NS
	trt x fam(sp)	–	–	–	–	NS	NS	NS	NS
12	treatment	*	*	NS	NS	*	NS	*	NS
	block	NS	NS	*	*	NS	NS	*	**
	species	NS	NS	NS	NS	NS	NS	NS	*
	fam(species)	NS	NS	NS	NS	NS	NS	NS	NS
	trt x species	NS	NS	NS	NS	NS	NS	NS	NS
	trt x fam(sp)	NS	NS	NS	NS	NS	NS	NS	NS
23	treatment	NS	NS	*	*	*	NS	NS	NS
	block	**	**	**	*	***	**	**	NS
	species	*	NS	NS	NS	*	NS	NS	NS
	fam(species)	NS	NS	NS	NS	NS	NS	NS	NS
	trt x species	NS	NS	NS	NS	NS	NS	NS	NS
	trt x fam(sp)	NS	NS	NS	NS	NS	NS	NS	NS

[1] NS – not significant
* – significant at $\alpha = 0.05$
** – significant at $\alpha = 0.01$
*** – significant at $\alpha = 0.001$

The vita has been removed from the scanned document

GREENHOUSE GROWTH OF *PINUS* X *RIGITAEDA* SEEDLINGS

IN RESPONSE TO WATER STRESS

AND CORRELATIONS WITH 7 YEAR PLANTATION PERFORMANCE

by

Gary R. Hodge

(ABSTRACT)

Seedlings of two *P. rigida* and four *P. taeda* families and six *P.* x *rigitaeda* crosses were grown in a greenhouse under two moisture regimes. Water stress decreased growth in every case in every variable measured. Water stress also elicited some genetic differences in the pitch pine and loblolly pine that were not apparent under the non-stressed treatment. The major differences between pitch and loblolly seedlings seemed to be primarily a function of large differences in seed size. Free growth may also play a major role in differences between the two species.

The theory that allometric coefficients are a good indicator of growth under moisture stress was not substantiated by this experiment. In addition, k-values were found to remain relatively constant despite changes in moisture stress.

It appears that genetic variance components in *P.* x *rigitaeda* may have importance under one set of environmental conditions, and be unimportant in another. Inter-relationship of crosses and confounding of genetic expectations, however, make it difficult to speculate which variance components are most important under moisture stress. Correlations were made between seedling growth characteristics and 1, 2, 3, 4, 5 and 7 year height and a 7 year volume index. Many significant correlations were found with 7 year height and volume. These correlations indicate that greenhouse experiments may be useful as an early genetic screening technique in *P.* x *rigitaeda*.