staining part of the chromosome (nucleolar organizer) could be seen to traverse the nucleolus (*Fig.* 16).

Discussion

The techniques described above were well suited for study of the early stages of microsporogenesis in *Pinus*. For the later stages of meiosis, these methods were less effective because the cytoplasm generally remained intact, thus preventing spreading of the chromosomes. The various chemical treatments designed to dissolve the callose walls of the meiocytes did not improve removal of the cytoplasm. It is not known if these treatments failed to remove the callose walls, thus inhibiting contact between the hot stain solvents and the cytoplasm, or if the cytoplasm in the later meiotic stages was less sensitive to the solvents than the cytoplasm in earlier stages. This failure to disintegrate the cytoplasm resulted in clumping of the chromosomes.

The most effective treatment to disintegrate the cytoplasm, and separate the chromosomes in the later stages of meiosis was prolonged boiling in EGW; the main drawback of this method being swelling of the chromosomes. However, the results were sufficiently promising to start a series of experiments to determine if this boiling technique could be modified to one that would cause less chromosome swelling. These experiments will be discussed in the next paper.

Literaturne Cited

Ballou, B., Sundharadas, G., and Bach, M. L.: Chloral hydrate: a solvent for biological membranes. Science 185: 531—533 (1974). — Beçak, M. L., Fukuda, K., and Carneiro, S. M.: Chromatin ultrastructure of lower vertebrates. Experientia 33: 1314—1316 (1977). — Boke, N. W.: Clearing and staining plant materials with lactic acid and pararosaniline hydrochloride. Oklahoma Acad. Sci. Proc. 49: 1—2 (1970). — Bonga, J. M.: A glycerine — water — DMSO — carmine stain used to determine the effect of IPC, EDTA, and aeration on the accumulation of metaphase figures in root tips of Pinus resinosa. Can. J. Bot. 55: 1696—1699 (1977). — Bonga, J. M., and Venketeswaran, S.: Fixing and staining of conifer tissues with lacto-propiono-dimethylsulfoxide-carmine. Stain Technol. 51: 197—199 (1976). — Borstel, R. C., von, and Lindsley, D. L.: Insect embryo chromosome techniques. Stain Technol. 34: 23—26 (1959). — Currier, H. B.: Callose substance in plant cells. Amer. J. Bot. 44: 478—488 (1957). — Gerlach, D.: Botanische Mikrotechnik. George Thieme, Stuttgart (1969). — Grimstone, A. V., and Skaer, R. J.: A guidebook to microscopical methods. Cambridge University Press, London (1972). — Heslop-Harrison, J.: Cytoplasmic continuities during spore formation in flowering plants. Endeavour 25: 65—72 (1966). — Lin, C. H., Falk, R. H., and Stocking, C. R.: Rapid chemical dehydration of plant material for light and electron microscopy with 2,2-dimethoxypropane and 2,2-diethoxypropane. Amer. J. Bot. 64: 602—605 (1977). — Sharma, A. K., and Sharma, A.: Chromosome techniques. Theory and practice. Buttenvorths, London (1972). — Shahma, C. B. S. R., Panda, B. P., and Sahu, R. K.: A macerating ammonium oxalate fixative and schedule for some root meristems. Biol. Plant. 19: 150—152 (1977). — Rupert, E. A., and Webster, G. L.: A procedure for staining pollen nuclei when obscured by cytoplasmic inclusions. Stain Technol. 47: 185—187 (1972).

Seedling Growth Rates, Water Stress Responses and Root-Shoot Relationships Related to Eight-year Volumes among Families of Pinus taeda L.

By M. G. R. Cannell[1]), F. E. Bridgwater[2]) and M. S. Greenwood[3])

(Received July / December 1978)

Summary

First-year seedling growth characteristics were correlated with mean individual-tree 8-year volumes of 16 North Carolina families of *Pinus taeda* L., with a view to developing seedling screening methods for early volume growth.

Rates of seedling height growth (mmlweek) were influenced by family differences in seed size until the seedlings were about 140 mm tall. Thereafter, until bud-set, the growth rates of well-watered seedlings became positively correlated with 8-year volumes, on a mean family basis, especially for families field tested on a poorly drained site. For families tested on a better-drained site, the correlations with seedling height growth rates were significant only when the seedlings were subjected to mild water stress: families which produced the greatest 8-year volumes grew fastest under mild water stress as seedlings. These families also tended to have high root to shoot relative growth rates, as revealed by regressions of shoot on root dry weights of seedlings grown in two contrasting media. This suggested that superior volume-producers on the better-drained site avoided water stress by producing extensive root systems.

There was little evidence that superior volume-producing families had prolonged seasonal periods of growth as seedlings.

It seems promising to further examine seedling height growth rates as a measure of future family field performance, taking measurements after seed size effects have disappeared and under environmental stresses that mimic those which influence growth in the field.

Key words: bud-set, early genetic evaluation, juvenile-mature correlations, progeny-test, root-shoot relationships, water stress responses.

Zusammenfassung

Einjährige Sämlinge von *Pinus taeda L.* aus *16* Familien in North Carolina wurden im Wachstum mit 8 Jahre alten Kiefern aus dein gleichen Familien verglichen. Hierbei wurde gefunden, daß bis zu einer Sämlingsgröße von etwa 14 cm eine Abhängigkeit zur mittleren Samengröße der jeweiligen Familie gegeben ist, während danach Standorteinflüsse, wie z. B. die Wasserführung des Bodens für den Holzzuwachs bestimmend sind. So waren später Beziehungen im Gesamtwachstum (Volumen) der Sämlinge zum mittleren

---

[1]) Tree Physiologist, Institute of Terrestrial Ecology, Bush Estate, Penicuik, Midlothian, Scotland. This work was done while on sabbatical leave with the Weyerhaeuser Company, Southern Forestry Research Center, Hot Springs, Arkansas, U.S.A.

[2]) and [3]) Geneticist and Tree Physiologist, respectively, Weyerhaeuser Company, Southern Forestry Research Center, Hot Springs, Arkansas, U.S.A.

Gesamtwachstum der betreffenden Familien nur bei ausreichender Wasserzufuhr zu erkennen.

Introduction and Literature Review

This paper reports significant and repeatable correlations between some first-year seedling growth traits and 8-year individual-tree volumes among families of loblolly pine (*Pinus taeda* L.). If further work substantiates these findings, we may have revealed some simple, cheap methods of screening loblolly pine families at the seedlings stage for early volume growth.

Mean family seedling or sapling heights are poorly correlated with mature-tree heights in many species (Nanson 1968, Namkoong *et al.* 1972, Lafarge 1975, Steinhoff 1974, Giertych 1974, Namkoong and Conkle 1976) and single morphological or physiological traits are rarely good predictors of future performance (e.g. photosynthetic rates, Zelawski 1976). The predictive value of multivariate or computer models of many morpho-physiological seedling attributes is promising, but these approaches are expensive (Ledig 1976, Gordon and Promnitz 1976).

The approach taken in these studies was to measure four aspects of the growth of open-pollinated orchard seedlings, namely (a) dates of bud-set, (b) height and diameter growth rates, recognizing that these are influenced by maternal factors as well as by differences inherent in the embryos, (c) growth responses to water stress, and (d) the distribution of dry matter between shoots and roots. These seedling studies were done in Arkansas. Eight-year-old control-pollinated families with the same female parents, and five of the same male parents, were growing in field tests in North Carolina. These families were measured in height and diameter to provide 8-year volume estimates which were correlated with the four aspects of seedling growth.

Our choice of four seedling traits was based on the following analyses of published literature.

(a) *Dates of bud-set.*

The best-growing loblolly pine provenances in many regions of the southern U.S.A. are those from coastal or southerly regions with frost-free seasons at least 20—30 days longer than the ones at the planting sites (climatic data: Thornthwaite 1941, Hocker 1955, provenance trial data: Thor and Brown 1962, Collins 1964, Barber 1966, Wells and Wakeley 1966, Kraus 1967, Thor 1967, Wells 1969, Grigsby 1973, 1977, Lafarge 1974). These provenances may be able to utilize summer rainfall better than the local provenances (Wells 1969), or they may respond more favourably to cooler night temperatures (Kramer 1957, Hellmers and Rook 1973), but a more obvious explanation, supported by studies of Perry *et al.* (1966), Krall (1969) and Woessner (1972) is that they have longer seasonal periods of growth.

Variation *within* provenances of loblolly pine has also been reported in (a) time of height growth cessation among 10 half-sib east Texas families (Bilan 1965), (b) seasonal duration of rapid net assimilation rates among 26 full-sib North Carolina families (Ledig and Perry 1969) and (c) apparent low temperature threshold for growth, among 10 individuals in Alabama (Boyer 1976).

Our hypothesis was that some of the variation in 8-year volumes among half-sib North Carolina families might be due to differences in seasonal growth duration, detectable at the seedling stage as differences in time of bud-set in response to seedling size, temperature and/or photoperiod.

(b) *Seedling growth rates in relation to seed weights*

Seedling growth, in size, weight or numbers of needles, is the integrated expression of interacting component physiological processes, no one of which is likely to account for variation in the performance of a wide range of genotypes (Wallace *et al.* 1976). The success of early genetic evaluation may depend on measuring appropriate *integrated* aspects of seedling growth, over suitable time periods, and in environments that simulate those in the forest. We began by measuring height increments, during most of the first year, on outdoor grown seedlings without nutrient or water stress.

But the early growth rates of seedlings are influenced by endosperm and embryo weights (as well as by other maternal factors). In classical growth analysis it is assumed that seedlings increase in weight exponentially, so that their

Table 1. — Mean individual-tree stem volumes of *Pinus taeda* L. half-sib families at age 8 estimated from full-sib fertilized progeny tests, and mean weights of open-pollinated seeds collected from orchard clones of the same genotypes. The plus trees and progeny tests were either in north or south coastal regions of North Carolina, U.S.A.

Location of plus trees and progeny tests	Family	Mean stem volume*	Difference from** commercial check	Weight per seed***
		dm^3 ± S.E. (d.f.)	dm^3 ± S.E.	mg ± S.E.
North of Pamlico River N. Carolina (north coastal)	A	17.5 ± 3.26 (247)	3.18 ± 0.609	31.9 ± 3.17
	B	16.6 ± 3.74 (378)	2.24 ± 0.527	34.4 ± 4.31
	C	16.5 ± 2.07 (139)	2.22 ± 0.647	27.7 ± 4.26
	D	16.1 ± 3.84 (250)	1.78 ± 0.654	29.7 ± 2.71
	E	16.0 ± 2.51 (923)	1.69 ± 0.277	39.2 ± 4.35
	F	15.2 ± 2.73 (675)	0.88 ± 0.337	47.9 ± 5.18
	G	15.0 ± 2.86 (874)	0.67 ± 0.304	40.2 ± 3.32
	H	15.0 ± 2.96 (384)	0.65 ± 0.466	28.6 ± 2.52
	I	14.9 ± 3.24 (198)	0.55 ± 0.678	33.1 ± 3.65
	Commercial check	14.3 ± 2.43 (102)	0.00 ± 0.816	25.0 ± 5.82
South of Pamlico River N. Carolina (south coastal)	J	12.9 ± 1.45 (238)	1.67 ± 0.414	38.1 ± 4.34
	K	12.6 ± 1.16 (817)	1.34 ± 0.201	34.8 ± 4.34
	L	12.5 ± 1.40 (284)	1.31 ± 0.372	37.8 ± 4.67
	M	10.9 ± 1.13 (337)	—0.26 ± 0.308	39.0 ± 4.64
	N	10.7 ± 0.71 (311)	—0.52 ± 0.255	39.2 ± 4.18
	O	10.7 ± 0.77 (175)	—0.56 ± 0.354	42.8 ± 4.94
	P	10.6 ± 0.94 (376)	—0.66 ± 0.265	39.0 ± 5.09
	Commercial check	11.2 ± 1.91 (100)	0.00 ± 0.729	25.0 ± 5.82

* Regression means, and S.E.'s about those means, see text; divide by 1000 to give m^3.

** Realized genetic gain.

*** Means of 100 air-dried seeds before stratification.

Table 2. — Details of experiments to evaluate family differences in seedling growth traits of *Pinus taeda* L.

	I	II	III	IV	V
Purpose of experiments was to measure:	Growth rates in relation to seed weights and bud set	Water stress responses and bud-set	Repeat expt II in a glasshouse	Root-shoot relationships	Repeat expt IV in a different medium
Medium	Peaty	Peaty	Peaty	Peaty	Sandy
Date of sowing	29 June	29 June	25 August	29 June	25 August
Environment	Outside after 1 Aug.	Outside 1 Aug.—5 Sept. in open shelter in 14 h photoperiods from 5 Sept.—7 Oct.	Glasshouse	Glasshouse	Glasshouse
Treatments	Well-watered, soil-fungicide for first two weeks only	Same as I, with 2 levels of water stress begun 14 Sept., (see Fig. 5)	One level of water stress, begun 9 Dec., no control, soil fungicide applied throughout the experiment	Well-watered, soil fungicide applied throughout the experiment	Same as IV
Measurements, and dates when taken. (see Fig. 1)	Heights on 17, 24, 31 August, 7, 14, 20, 28 Sept., 5, 12, 26 Oct. Basal diameters on 28 Sept., 5, 12, 26 Oct., 9, 22 Nov. Percentage bud-set on 26 Oct.	Heights on 15, 17, 19, 21, 23, 25, 29 Sept. and 1, 3, 5, 7 Oct. Percentage bud-set on 7 Oct.	Heights on 10, 12, 14, 16, 18, 20, 22 Dec.	Shoot dry weights, root dry weights and total length of roots from 22—29 July	Same as Expt IV, from 28 Sept. to 3 Oct.
Experimental design	4 Seedlings of each of 19 families in 5 randomized blocks, analysis done on means of 4 seedlings	Split plot (see Table 4), analysis done on means of 4 seedlings in each sub-plot	Same as Expt I	4 seedlings of each of 15 families in 5 randomized blocks	Same as Expt IV

* 0.5 g Benlate + 0.5 g Dexon/litre, applied to control damping off

weight **W** at time **t** is equal to $W_0 x^t$, where W_0 was their initial weight and **x** their relative growth rate (Sweet and Wareing 1966, Perry 1976). But in practice, family variation in W_0 due to seed size becomes less important with time as W becomes increasingly closely correlated with x (Righter 1965). Our approach, then, was to measure each weekly height increment of outdoor-grown seedlings (**x**) and see how quickly family differences in **x** became poorly correlated with initial seed weights (W_0) and more closely correlated with seedling heights and 8-year volumes (W).

(c) *Water stress responses*

Internal water stress was judged to be the most critical factor limiting height and volume growth of loblolly pine during the growing season, even on wet sites, in the southern U.S.A. Consider the following observations. Yearly differences in basal area increment can be closely correlated with numbers of days when sufficient water is available to permit radial growth (Bassett 1964). Water stress commonly limits the number of shoot flushes (Wenger 1952, Zahner 1962), the distance between needle fascicles (Allen and Scarbrough 1970, working with *Pinus palustris* Mill.) and bud development (Zahner 1962). Seedlings close their stomata and stop growing in height at mild levels of water stress and are slow to begin growing again (e.g. Brix 1962, Stransky and Wilson 1964, Kaufman 1968). Diurnal changes in water potential may account for the fact that most radial and extension growth occurs at night (Reed 1939, Barney 1951, Zahner 1968). Provenances from areas with frequent summer rainfall perform well at a range of sites (Wells 1969, Grigsby 1973) possibly because they lack growth-restricting water-stress avoidance mechanisms to some small degree.

In view of these facts, we hypothesized that even small differences in water stress tolerance, avoidance or recovery might give rise to substantial differences in volume growth. We were not interested in drought survival, but rather in small differences in response to mild levels of water-stress that can check height and diameter growth.

(d) *Root-shoot relationships*

Small differences in dry matter partitioning between shoots and roots can have a major effect on total plant growth (e.g. Ledig 1969). The ratio of the relative growth rates of shoots and roots in young plants with exponential growth in given approximately by the allometric coefficient **k** in the equation: $\log_e$ shoot dry weight = a + **k** $\log_e$ root dry weight, which is more meaningful than the root : shoot ratio (see Ledig and Perry 1965). It is often argued that genotypes with high **k** values grow rapidly because they reinvest a high proportion of their assimilates in photosynthetic capital (Ledig 1975). On the other hand, if growth is limited by water and nutrient supply, genotypes with low **k** values may grow fastest because they may develop the largest root systems and make the greatest claims on soil water and nutrient resources. Rapid root development after transplanting is important for early growth in southern pines (Snyder 1961, Bieneke and Perry 1965, Kaufman 1968, van Buijtenen *et al.* 1976). There are known family differences in **k** (Ledig *et al.* 1970) and root morphology (Stonecypher *et al.* 1965) measured on seedlings of loblolly pine, and we hypothesized that such differences might be correlated with the rate of 'site-capture' and hence individual-tree growth in the field. We therefore measured **k** on young seedlings and looked for negative relationships with 8-year volumes.

Materials and Methods

Seedling studies were done in Arkansas using open-pollinated seed of 16 families of *Pinus taeda* L., taken from two first-generation seed orchards, both located near Washington on the Pamlico River estuary, North Carolina (77° 15' W, 35° 35' N, *ca* 5 m altitude). Nine families (A—I, *Table 1)* were from a 'north coastal' orchard, consisting of clones (grafts) from candidate plus trees selected on the coastal plain north of the estuary, and 7 families (J—P) were from a 'south coastal' orchard consisting of clones selected on the coastal plain south of the estuary. These families had been included in full-sib genetic tests in North Carolina as part of the North Carolina State University — Industry Cooperative Tree Improvement Program as described below (*Evaluation of 8-year volumes).* Three additional seed lots were included for comparison in our seedling experiments, namely (a) a North Carolina 'commercial check' seed lot collected from native forests in the south coastal region, (b) a mixture of 5 select-tree half-sib families from southern Louisiana, and (c) a mixture of 5 select-tree half-sib families from Arkansas and Oklahoma.

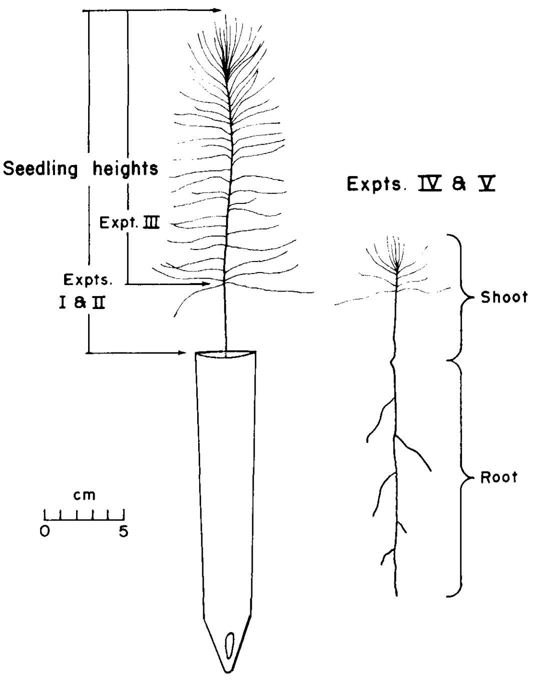

Figure 1. — Appearance of *Pinus taeda* seedlings and their containers when evaluations were made of height growth rates (experiments I—III) and shoot and root dry weights (experiments IV and V).

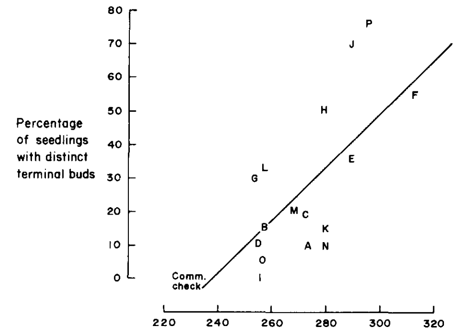

Figure 2. — Relationship between (a) the percentage of seedlings of 16 *Pinus taeda* families (A—P, Table 1) and a commercial check population having terminal winter buds on 26 October, and (b) the mean heights of the seedlings (experiment I). Seedlings were growing outside at Hot Springs, Arkansas. Correlation coefficient r = 0.71, significant P = 0.01.

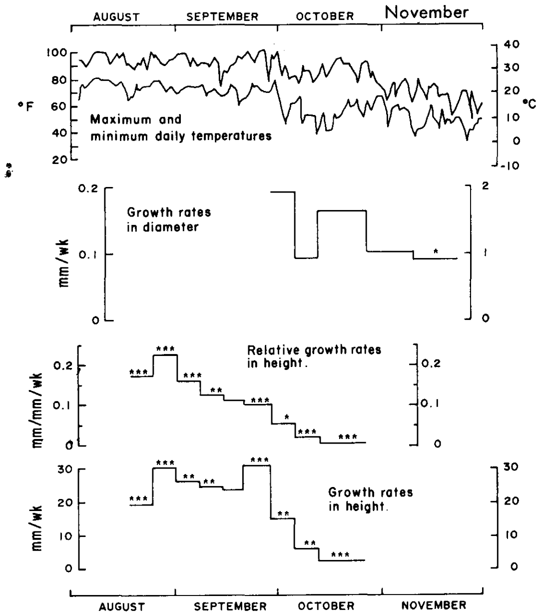

Figure 3. — Mean height and diameter growth rates of *Pinus taeda* seedlings growing outside at Hot Springs, Arkansas, shown in relation to ambient screen temperatures. Asterisks indicate the presence of significant differences among 16 families (A—P, Table 1) and 3 check populations- at *P = 0.05, **P = 0.01 and ***P = 0.001.

Evaluation of first-year seedling traits

Five experiments (I—V) were done at Hot Springs, Arkansas (95° 5' W, 34° 30' N, 210 m altitude) as detailed in *Table 2.*

Stratified seeds were sown in 164 cm^3 well-drained tube-shaped plastic containers *(Fig. 1)* in a glasshouse in either peat : vermiculite : perlite (5 : 5 : 1 by volume) or sandy loam (from Magnolia, Arkansas) in both cases with added slow-release fertilizer containing about 80 mg N, 30 mg P_2O_5 and 60 mg K_2O per seedling (11.3 g 'Osmocote' in 4.5 l of medium). Additionally, experiments I—III received complete Hoagland's solution weekly. The peaty and sandy media contained about 45% and 1% organic matter, with bulk densities of 0.13 g cm^{-3} and 1.33 cm^{-3}, respectively. While in the glasshouse *(Table 2)* the seedlings were in 14 h photoperiods under incandescent lights, at temperatures which fluctuated between 16° C and 32° C. While outside the seedlings experienced ambient temperatures (e.g. *Fig. 5)* and natural photoperiods of 14.4 h in mid-June, decreasing to 11.4 h by mid-October. Competition was minimized by spacing the seedlings 8 cm apart.

Treatments. Experiment I recorded the height and diameter growth of well-watered seedlings growing outside, up to and after winter bud-set.

Experiment II recorded the height growth of seedlings outside in open shelter in 14 h photoperiods, given three water stress treatments beginning 14 September, 77 days after sowing: (1) well-watered control, (2) mildly stressed seedlings, not watered for 5 days on two occasions (14—19

Sept. and 24—29 Sept., see *Fig. 5*), producing pre-dawn shoot water potentials of —3.8 atm. compared with —2.9 atm. on the controls and (3) moderately stressed seedlings which were not watered for 6 days in the first stress cycle (14—20 Sept.) which caused daytime wilting following pre-dawn shoot water potentials of only —5.6 atm. Care was taken to ensure that the medium was rewetted on rewatering. Bud-set began on 1 October.

Experiment III was a repeat, from seed, of experiment II, but with the seedlings growing in a glasshouse, with no control, and only one mild water stress treatment. Two water stress cycles were given (10—12 and 16—18 Dec.) beginning 106 days after sowing. Bud-set began on 20 December.

Experiments IV and V recorded the root-shoot relationships of glasshouse-grown seedlings harvested 23—30 days and 34—39 days after sowing, respectively, before their root morphologies became modified by the containers.

Measurements. Heights and basal stem diameters were measured in experiments I—III (*Table 2*) using an electronic device described by Ingram (1978). The base reference for height measurements was changed from the rims of the containers in experiments I and II to the cotyledons in experiment III (*Fig. 1*) to avoid error resulting from movement of the seedlings within the tubes during water stress cycles. The upper reference points were always the tips of newly-emerging needles, and to ensure that they were rigid and erect it was important not to extend the photoperiod beyond 14 h, and also to take measurements at the end of each water stress cycle 2 h after rewatering at dawn.

In experiments IV and V the roots were washed out, floated on paper, and every root was measured in length. Roots and shoots were separated (*Fig. 1*) and dried at 95° C for 24 h. All root weighings were done twice.

Statistical analyses. A few abnormal seedlings (never exceeding 5% in any experiment) were omitted from the analyses. Analyses of variance in experiments I—III were done

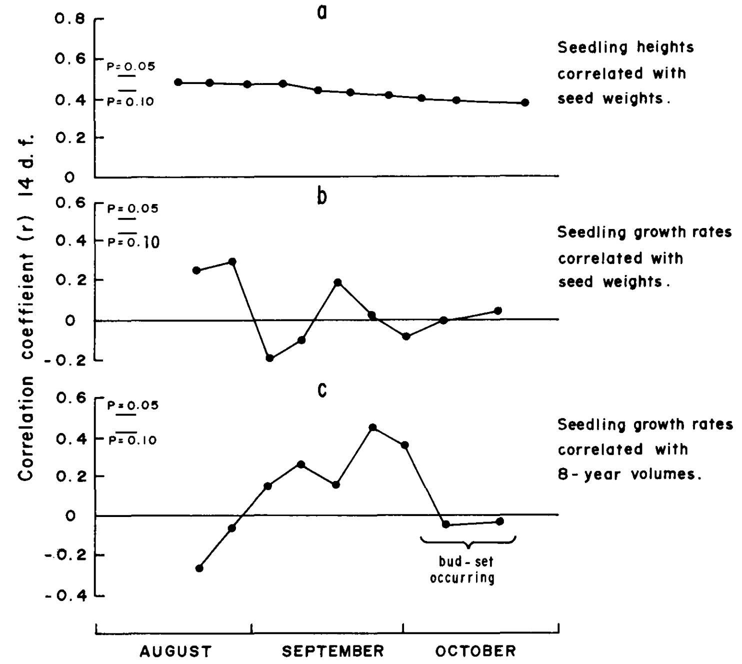

Figure 4. — Correlation coefficients for 16 *Pinus taeda* families (A—P, *Table 1*) between family mean seedling heights or height growth rates during August—October outside at Hot Springs, Arkansas, and family mean seed weights or 8-year volumes (from *Table 1*). Bars indicate r values significantly different from zero at P = 0.05 and 0.01.

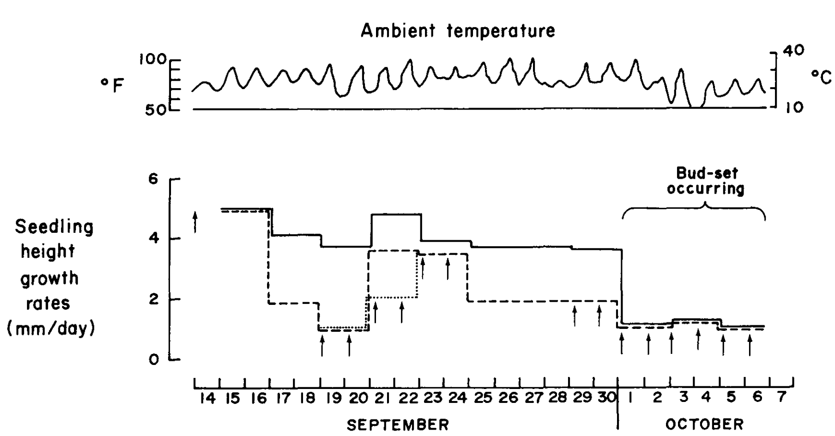

Figure 5. — Height growth rates of seedlings of *Pinus taeda* subjected to varying watering regimes growing in an open shelter outside at Hot Springs, Arkansas, shown in relation to ambient screen temperatures. These are the overall means of 16 families and 3 check populations. ——— control, watered daily; — — — watered as indicated by ↑, ... not watered on 19 September.

on the means of each row of seedlings (4 before elimination) per family per block per treatment, for the variates: heights, diameters, height and diameter increments in each measurement period, relative increment in each period (increments per mean heights or diameters in the incremental periods). Family means were then correlated with mean family seed weights and 8-year volumes for each of the north and south coastal types *(Table 1)*.

In experiments II and III covariance analyses were done adjusting height increments on seedling heights, but in most instances adjustments were not significant, or family ranks changed very little (rank correlations before and after adjustment always exceeded $r = 0.8^{***}$). Consequently only unadjusted values are reported.

In experiments IV and V linear regressions of shoot dry weights on root dry weights and lengths were calculated for each family. Regressions were not significantly nonlinear. Tests were made for family differences in the overall regressions and regression coefficients following RAO (1965, p. 281—4). Regression coefficients were then correlated with 8-year volumes

Evaluation of 8-year volumes given in Table 1. Genetic material.

Five early pollen producers in each of the north and south coastal seed orchards had been used as male parents in two separate tester mating schemes. These testers included F and G within the north coastal orchard and K within the south coastal orchard. Within each scheme, each tester was to have been mated with every other individual within its seed orchard (north and south coastal) and each full-sib family was to have been included in three genetic tests planted in successive years within its coastal region (north and south). However, because some crosses could not be made, or failed, each test had a different genetic constitution. That is, each full-sib family was not planted in all three tests in its coastal region, but instead occurred in any one, two or three tests.

Even though the data were not balanced in a genetic or an experimental design context, estimates of 8-year volumes for half-sib families in this study were based on many trees *(Table 1)* growing in several tests. The relative performance of half-sib families is therefore though to be reliable.

Sites, layout and treatments. The five north coastal tests were planted at a site north of the Pamlico River estuary (76° 50' W, 36° 00' N) in 1964, '65, '66, and '67, and in 1968 at a nearby site (76° 40' W, 36° 10' N) chosen for its similar physical and soil water characteristics. These were moderately well-drained sites favouring rapid growth. The five south coastal tests were planted at one site south of the Pamlico River estuary (76° 55' W, 35° 15' W) which was poorly-drained, with a water table closer to the surface, and had less rapid growth. The water table at the south coastal site was approximately 0.0—0.3 m and 0.3—0.6 m below the surface during winters and growing seasons, respectively. Drawdown rates at the north coastal site were about twice those at the south coastal site (HUGHES, pers. comm.).

Each test (2 sites, 5 planting years) was a randomized complete block with six blocks each containing full-sib families arranged in 10-tree row plots. Three of six blocks in each test were randomly chosen to receive dolomitic lime at the beginning of the first field season and triple superphosphate and muriate of potash at the beginning of the first and third growing seasons. A complete fertilizer (N, P and K) was applied as crown closure occurred (during the 6th, 7th or 8th field season). Data from only these fertilized blocks were used to calculate volumes because growth can be enhanced on these sites by the addition of phosphate fertilizers (MATZIRIS and ZOBEL 1976) and it is an operational practice to do so on Weyerhaeuser Company lands in this region.

Statistical analyses. Individual-tree stem volumes *(Table 1)* were calculated after the eight growing season in the field using the equation of SCHMITT and BOWER (1970). Stem volumes were estimated for half-sib families only for clones which occurred as males or females in at least two full-sib crosses in each of three test years. If there had been no mortality, this gave 180 individual tree values (2 full-sib families, 3 out of 5 test years, 3 blocks, 10-tree rows).

As mentioned, the amount of information available for each test year varied among full-sib families, and hence among the half-sib means to which they contributed. Consequently, we took the volumes of all trees in each test as in a stability analysis (FINLAY and WILKINSON 1963). The mean volume of each half-sib family was then taken as the predicted volume of that family at the mean of all five tests *(Table 1*, column one). Standard errors were calculated for each regression mean *(Table 1)*. Statistical comparisons were not made among means because some full-sib values were used to estimate both their male and female parent half-sib means.

Results

Families are listed alphabetically in order of their mean 8-year volumes at the two test locations (A—I north coastal, J—P south coastal). Note that A, B and C were outstanding volume producers, whereas M, N, O and P were poorer than the commercial check *(Table 1)*.

Family mean values for the first-year seedling traits and their correlations with 8-year volumes *(Table 1)* are summarized in *Table 3*.

Percentage Bud-set (Expts I and II)

Using chi-square, large significant family differences were found in the percentage of outdoor-grown seedlings, sown 29 June, which had set buds in September—October *(Table 3)*. Some of this variation could be attributed to differences in mean seedling size because loblolly pine seedlings need to reach a critical size in order to set buds. Thus, mean family percentage bud-set values were positively correlated with mean seedling heights *(Fig. 2*, $r = 0.71^{***}$); the intercept in *Fig. 2* of about 220 mm height was the apparent mean critical height for bud-set. Assuming that the variation in percentage bud-set about the regression line in *Fig. 2* was genetic, families P, J, H, L and G seemed prone to early bud-set, whereas the outstanding volume producers at age eight, families A, B and C, all set buds relatively late as seedlings. However, the evidence that families prone to early bud-set in their first year were poor volume producers was rather weak *(Table 3)*.

Seedling growth rates in relation to seed weights (Expt. I)

Mean seedling heights in experiment I increased from 99 mm on 17 August to 270 mm on 26 October, and basal stem diameters increased from 3.2 mm on 28 September to 4.2 mm on 23 November. Height growth exceeded 30 mm wk^{-1} during the last weeks in August and September *(Fig. 3)*. Height growth decreased to zero in October, while diameter growth continued at about 0.1 mm wk^{-1} until frost in November. Relative height growth rates decreased from about 20% per week in August to zero in October *(Fig. 3)* while relative stem diameter growth continued to late November at about 3% per week.

Significant family differences in both absolute and relative height growth rates, in all but one measurement period *(Fig. 3)*, accounted for about 30% of the variance in height growth. Family differences in diameter growth were probably masked by large measurement errors.

Family mean seedling heights were positively correlated with mean seed weights, but the correlations decreased

Table 3. — Seedling traits of families of *Pinus taeda* and their correlations with 8-year volumes.

	Experiment	Bud-set (%) Seedlings sown 29 June evaluated		Mean height growth rates of regularly watered seedlings 31 Aug — 5 Oct		Mean height growth rates of water-stressed seedlings mm/day		Shoot-root regression coefficients			
		26 Oct (n = 20	7 Oct (n = 60)	Absolute growth rates mm/day	Relative growth rates	Mildly water-stressed 17—19 and 25—29 Sept	Mildly water-stressed 10—12 and 16—18 Dec	$\log_e$ shoot d.wt / $\log_e$ root d.wt (mg) Peat	$\log_e$ shoot d.wt / $\log_e$ root d.wt (mg) Sand	Shoot d.wt (mg) / Total root length (mm) Peat	Shoot d.wt (mg) / Total root length (mm) Sand
		I	II	I	I	II	III	IV	V	IV	V
Families tested north of the Pamlico River, N. Carolina	A	10	3	3.36	0.117	2.65	2.95	—	—	—	—
	B	15	8	3.13	0.117	2.47	2.81	0.38***	0.09	3.69***	0.60*
	C	20	12	3.43	0.121	2.58	2.54	—	—	—	—
	D	10	0	3.20	0.121	2.07	2.49	0.32***	0.19	4.84***	0.71***
	E	35	23	3.19	0.101	1.75	2.05	0.52***	0.21*	5.15***	0.82***
	F	55	23	3.45	0.103	1.34	1.99	0.39***	0.37***	6.92***	0.88***
	G	30	8	2.69	0.097	1.71	1.93	0.50***	0.51***	7.62***	0.95***
	H	50	22	3.13	0.106	1.15	1.74	0.48***	0.22**	5.04***	1.18***
	I	0	0	3.10	0.115	1.57	2.13	0.55***	0.24***	6.68***	0.55***
Correlations with 8-year volumes (r)		—0.43	—0.29	0.47	0.59	0.90***	0.91***	—0.58	—0.67*	—0.80**	—0.46
Families tested south of the Pamlico River, N. Carolina	J	70	25	3.33	0.110	1.00	1.66	0.60***	0.34***	5.95***	0.71***
	K	15	3	3.33	0.114	1.58	2.54	0.56***	0.26**	5.35***	0.69**
	L	30	12	3.27	0.125	1.72	2.01	0.41***	0.22***	3.96***	1.17***
	M	20	8	3.22	0.112	1.71	2.33	0.59***	0.18**	6.11***	0.23
	N	10	8	3.07	0.100	1.01	1.61	0.34**	0.38**	3.55*	1.10***
	O	5	0	3.16	0.118	2.41	1.90	0.75***	0.34***	6.27***	0.98***
	P	75	67	3.15	0.101	1.53	1.97	0.65***	0.37***	7.80***	1.06***
Correlations with 8-year volumes (r)		0.22	—0.19	0.90**	0.50	—0.30	0.16	— 0.20	—0.32	—0.30	—0.10
Control populations	Commercial check	0	3	2.93	0.109	2.62	2.72	0.61***	0.34***	7.26***	1.08***
	Arkansas/ Oklahoma	25	9	2.63	0.114	1.90	1.52	—	—	—	—
	South Louisiana	0	2	3.49	0.128	2.36	2.07	—	—	—	—
Test statistics applied to all families plus the three controls		275***	315***	0.262	0.0103	0.694	0.847	(a)6.3*** (b)2.8***	8.1*** 1.6	12.2*** 2.1**	13.9*** 3.0***
		Chi-squares testing signif. from mean % bud-set		Least significant differences, P = 0.05				F-ratios testing hypotheses of equal (a) regressions and (b) slopes			

* ** *** significant at P = 0.05, 0.01 and 0.001, respectively.

during the course of the experiment *(Fig. 4 a)*, indicating that height growth during September—October was less influenced by seed weights than growth earlier on. This was confirmed by correlations between seed weights and seedling growth rates *(Fig. 4 b)*, which were positive in mid-August but fluctuated around zero during September—October. Although most individual correlation coefficients in *Fig. 4* are not significantly different from zero, the time trends are thought to be real. Similar trends were found in two additional studies, one on 15 loblolly pine families

Table 4. — Statistics from analyses of variance of height growth rates (mm/day) of 16 families, plus 3 check populations, of *Pinus taeda* seedlings subjected to three watering regimes. (Experiment II, see also *Figures 5* and *6*).

		SEPTEMBER																	OCTOBER						
		14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	1	2	3	4	5	6	7
Dates of watering (w)	Control	w	w	w	w	w	w	w	w	w	w	w	w	w	w	w	w	w	w	w	w	w	w	w	w
	Mildly stressed	w					w	w	w	w	w	w					w	w	w	w	w	w	w	w	w
	Moderately stressed	w						w	w	w	w	w					w	w	w	w	w	w	w	w	w
F-ratios	Blocks (4 d.f.)		5.1*		1.2		3.1		2.6		5.8*			2.0			2.7		3.5		2.2		7.6**		
	Treatments (2 d.f.)		1		99***		299***		169***		11**			219***			129***		5*		16**		1		
	Error mean square (a)		1.58		1.99		0.78		1.06		1.05			0.47			0.71		0.31		0.23		0.14		
F-ratios	Families[1]) (18 d.f.)		6.3***		4.2***		5.1***		2.8***		7.4***			5.2***			2.6***		2.3***		2.8***		3.4***		
	Families × treatments (36 d.f.)		1.0		2.6***		1.8***		1.3		1.2			2.0***			2.3***		0.8		1.7*		1.2		
	Error mean square (b)		0.72		0.61		0.37		0.44		0.55			0.30			0.45		0.25		0.21		0.20		

* ** *** Significant at P = 0.05, 0.01 and 0.001, respectively.

[1]) Including controls.

from west of the Mississippi River (Cannell 1978 a)[4]) and another on a separate set of 12 coastal North Carolina families. In all studies, seed weights were no longer correlated with seedling height growth rates once the seedings exceeded about 140 mm in height, about 2 months after sowing.

Seedling height growth rates became positively correlated with 8-year volumes by the end of August, and remained so until early October when many seedlings had set buds *(Fig. 4 c)*. That is, once the effects of seed weights on seedling growth rates disappeared (at the end of August when the seedlings were about 140 mm tall) seedling growth rates appeared to reflect the inherent growth potential of the families in field tests. This was true for both the north and south coastal families, for both absolute and relative seedling height growth rates (see correlations with 8-year volumes, *Table 3*). Again, we base this conclusion on the existence of meaningful time trends in *Fig. 4 c* and fully appreciate that, when many correlation coefficients are calculated, a few can be significant by chance.

Seedling heights, as opposed to their growth rates, were negatively and very poorly correlated with 8-year volumes (r = —0.25 in August, r = —0.10 in October) because seedling heights always showed the early effects of seed weights; and seed weights happened to be non-significantly negatively correlated with 8-year volumes for this set of families (r = —0.34 and —0.65, for north and south coastal families, respectively). In other progeny tests seed weights have sometimes been positively correlated with inherent field performance (Righter 1965, and unpublished Weyerhaeuser data).

Seedling water stress responses (Expts II and III)

Experiments II and III were carried out on seedlings over 150 mm tall, when seedling height growth rates were no longer positively correlated with seed weights, but at the ends of both experiments treatment effects were masked by bud-set, and growth rates throughout the experiments were influenced by fluctuating ambient temperatures (e.g. *Fig. 5*).

In experiment II the water stress treatments severely and significantly depressed growth from 17—20 September *(Fig. 5, Tab. 4)*. Rewatering from 19 or 20 September to 24 September brought about little recovery for 2 days, and did not restore growth to those of the controls even by 23—25 September *(Fig. 5)*. The moderately stressed seedlings (rewatered on 20 September instead of 19 September) grew significantly less than the mildly stressed ones from 21—23 September. The second stress cycle, beginning 24 September, significantly depressed growth again *(Table 4)* and rewatering from 29 September to 6 October brought about little recovery because the seedlings in all treatments began setting buds.

In experiment III similar water-stress treatments depressed height growth rates of glasshouse-grown seedlings from 10—12 and 16—18 December.

Significant family differences occurred in the height growth rates of both well-watered control seedlings (as in experiment I) and seedlings subjected to water stress, accounting for about 30% of the total variance in both experiments II and III. But families which grew fastest when regularly watered were not necessarily those that grew fastest when water stressed. That is, during the periods of water stress in experiment II there were significant family × water stress treatment interactions *(Table 4)*. Family rank correlations between control and water stressed seedlings were less than r = 0.2.

Family rankings in height growth rates, produced by subjecting the seedlings to water stress, were similar for

---

[4]) Cannell, M. G. R., 1978 a. Seedling growth rates and seed weights of *Pinus taeda* L. families related to 4- or 8-year field performance. Unpublished Weyerhaeuser Company Technical Report, 042-3206/78/16.

both experiments II and III (*Table 3*), especially for the north coastal families (rank correlations between expts II and III, r = 0.94***). Neither covariance adjustment on seedling heights, nor calculating relative growth rates substantially changed family ranks.

The North Carolina commercial check seedlings were small, and grew slower than most families when well-watered. But curiously, they were among the fastest growing populations during the periods of water stress, in both experiments II and III (*Table 3*). The Arkansas/Oklahoma seedlings, which were smaller than the commercial check, did not respond so favourably to water stress. The southern Louisiana seedlings were relatively stress-tolerant in experiment II, but were not above average in experiment III.

As in experiment I, correlations between the growth rates of *regularly watered* seedlings (in experiment II), and 8-year volumes were positive, and much greater for the south coastal families than the north coastal ones (*Fig. 6*, compare *Table 3* expt I). Taking relative rather than absolute seedling height growth rates made little difference to the correlations with 8-year volumes for the south coastal families, and only slightly increased those for the north coastal families.

Correlations between the growth rates of *water stressed* seedlings and 8-year volumes were not significant for the south coastal families, but exceeded r = 0.8*** for the north coastal families in both water stress cycles in both experiments II and III (i.e. during the periods 17—19 and 25—29 September in expt II, and 10—14 and 16—18 December in expt III). These high correlations were peculiar to the periods when the seedlings were under water stress (*Fig. 6*). Adding the growth increments of the seedlings during the 2 water stress cycles in each experiment (e.g. 17—19 plus 25—29 September in expt. II) produced correlations of r = 0.9*** with 8-year volumes for the north coastal families (*Table 3*), but did not improve the poor correlations with 8-year volumes for the south coastal families.

In summary, 8-year volumes of the *south* coastal North Carolina families could be most accurately predicted from the height growth rates of *well-watered* seedlings, whereas 8-year volumes of the *north* coastal families could be most accurately predicted from the height growth rates of seedlings when subjected to *water stress*.

Seedling root-shoot relationships (Expts IV and V)

The shoots and roots in the peaty medium were, on average 35 and 7 mg in dry weight, respectively, whereas in the sandy medium they were 32 and 10 mg. Regression coefficients between $\log_e$ shoot and $\log_e$ root dry weights were significantly different among families growing in both media (*Table 3*). That is, the allometric coefficents **k** reflecting the functional relationships between shoots and roots differed among families (*Fig. 7*). Significant differences also occurred when shoot dry weights were regressed on total root lengths (tap plus lateral roots) (*Table 3, Fig. 7*).

The values of the regression coefficients were negatively correlated with 8-year volumes especially among the north coastal families (r values ranging from —0.46 to —0.80**, *Table 3*). That is, superior volume producers tended to have higher ratios of root to shoot relative growth rates, producing proportionately greater root weights and lengths with increase in shoot weights (*Fig. 7*). Commercial check seedlings behaved like inferior families.

Discussion

These studies suggested that genetic differences in 8-year volumes among loblolly pines families, may be foreseen, to some extent, by measuring the growth rates of first-year seedlings at the right time in appropriate environmental or stress conditions. If these findings can be repeated it may be possible to reject families with poor

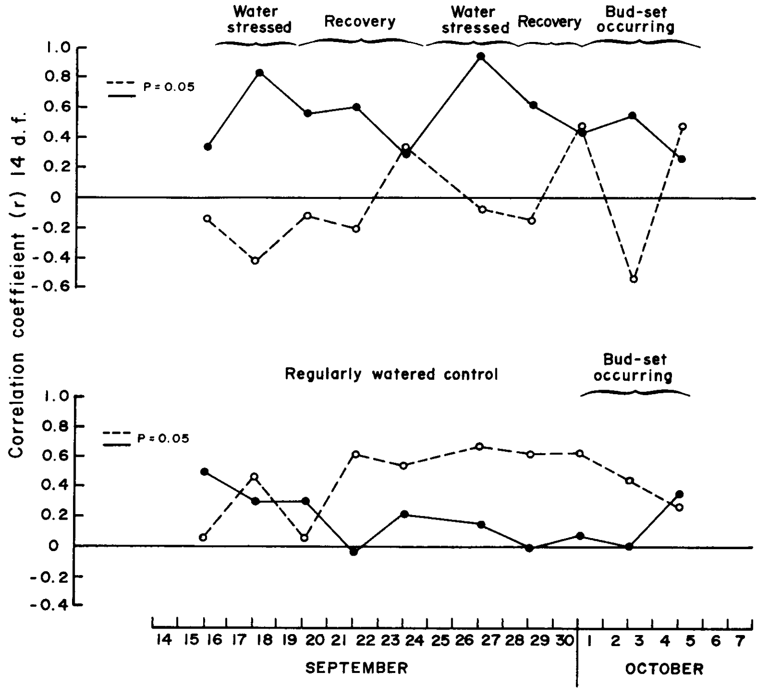

Figure 6. — Correlation coefficients for 9 north coastal North Carolina families of *Pinus taeda* (●———●) and 7 south coastal North Carolina families (O— — —O) between family mean seedling height growth rates during varying watering regimes (see *Fig. 5*), and their 8-year volumes (*Table 1*). Data for the two water stress regimes shown with dots and broken lines in *Fig. 5* have been pooled.

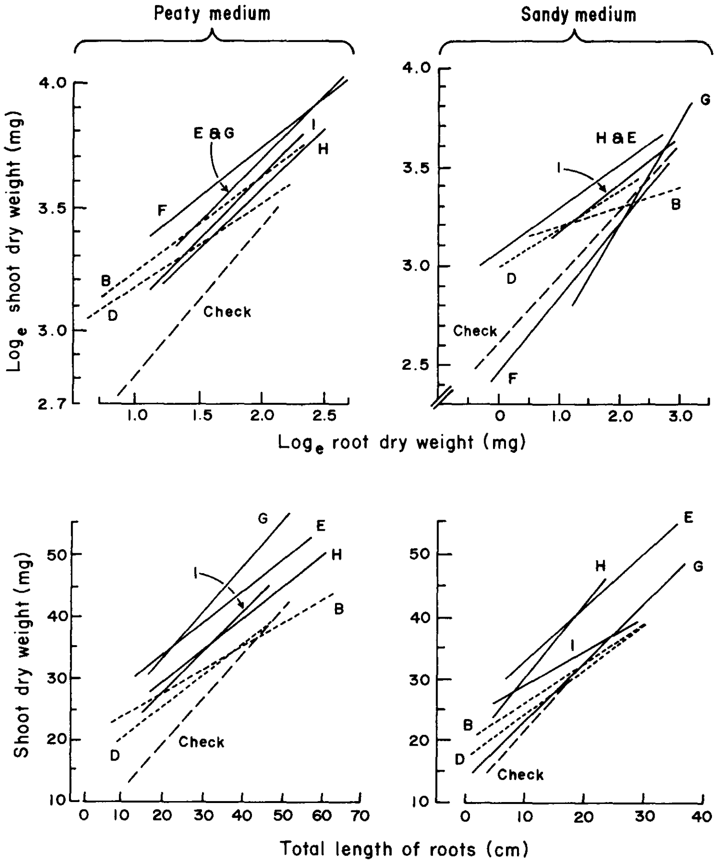

Figure 7. — Relationships between shoot and root parameters for seedlings of 7 north coastal North Carolina families of *Pinus taeda* and a commercial check population (— — — —) growing in a peaty and a sandy medium. The regression lines span the range of individual seedling values for each family. Regression coefficients given in *Table 3*. Families B and D (- - - - -) were superior in volume at age 8 in progeny tests (*Table 1*).

early field performance at the seedling stage. There were two important findings.

First, rankings in 8-year volumes could be crudely predicted (phenotypic juvenile-mature correlations $r \simeq 0.4$) from the height growth rates of first-year seedlings without water or nutrient stress. The condition for this prediction was that the seedlings were measured at least 7 weeks after germination when their growth rates were no longer positively correlated with seed weights, but before the seedlings began to set buds. In both experiments I and II, and in two other studies with different sets of 12—15 loblolly pine families (Cannell 1978 a[1])) family differences in rates at which the seedlings grew from about 120 to 200 mm in height (measured from the cotyledons to the tips of the uppermost needles) accounted for at least 20% of the known family variation in mean individual-tree volumes or heights 4 or 8 years after planting on various fertilized sites in North Carolina and Arkansas.

Secondly, the above seedling growth/eight-year volume correlations could be markedly improved by measuring seedling growth rates under environmental stresses chosen to mimic conditions believed to have influenced family differences in eight-year volume in the field. Thus, high correlations were obtained for the north coastal North Carolina families by measuring seedling growth rates during periods of mild water stress (experiments II and III). The north coastal families had been progeny-tested on well-drained sites where family differences in water stress avoidance and tolerance were probably important. By contrast, the south coastal progeny-test site was virtually waterlogged each winter, and had a water table nearer the surface during each growing season. At that site, family differences in water stress responses may have had relatively less effect on 8-year volumes. Accordingly, 8-year volumes of the south coastal families were poorly correlated with the growth rates of seedlings under water stress but were highly correlated with the growth rates of well-watered seedlings (*Table 3*). These results were repeatable, and suggested that there were genotype-site interactions between well and poorly-drained sites in coastal North Carolina. Such interactions have been found using unpublished Weyerhaeuser Company data for other loblolly pine families.

The physiological basis for the family differences in seedling water stress responses were not investigated directly. But the studies on root-shoot relationships suggested that the superior north coastal families, which grew well when water was withheld, may have avoided stress by producing greater root masses and lengths in proportion to their shoot weights. Family differences in root resistances to water uptake could have been important in the peaty medium used in experiments II and III which contained 40—60% water by weight at —5 to —10 atmospheres. The variation among the north coastal families in seedling shoot-root regressions was negatively related to their 8-year volumes (Table 3, $r = -0.46$ to -0.80^{**}), and negatively related to their growth rates under water stress ($r = -0.5$). This was much less true for the south coastal families *(Table 3)*. It is claimed by some authors (Ledig *et al.*, 1970; Wareing and Patrick 1975) that inherent functional relationships described by root-shoot allometric coefficients can be stable with age over a wide range of environments in conifers. If so, it is possible that the high volume producing north coastal families owed their superiority on their well-drained site to their ability to produce extensive root systems rapidly after planting, capturing surrounding nutrient and water resources at the expense of competing vegetation. That is, they may have been good 'isolation' and 'competitive' genotypes (Cannell 1978). This is contrary to the expectations of Ledig *et al.* (1970) and Ledig (1975) who assumed that families with high shoot-root regression coefficients would grow fastest, because they would reinvest a larger proportion of their assimilates in shoots and photosynthetic capital. This did not seem to be true even on the very wet south coastal site.

Shoot-root dry weight regressions provided a useful second trait for early genetic evaluation. When combined in multiple correlations with seedling growth rates of either well-watered or water stressed seedlings, 89% and 92% of the variation in 8-year volumes was accounted for among the north and south coastal families, respectively.

There are a few points for concern. First, the commercial check seedlings often grew equally as much as the superior families, even under water stress *(Table 3)*. The commercial check seedlings were not unusually small, compared with the Arkansas/Oklahoma population for instance, and they did not germinate particularly poorly. Secondly, the rankings of families G and O were different under water stress in experiments II and III. Thirdly, the correlations between the growth rates of well-watered seedlings of north coastal families and 8-year volumes were poorer in experiment II *(Fig. 6)* than in experiment I *(Table 3)*. And fourthly, we have re-examined Stonecypher *et al.*'s (1965) data on loblolly pine and can find little relationsship between seedling shoot-root dry weight regressions and 8-year volumes of their full-sib families growing in Georgia. However, in our view, these inconsistencies do not invalidate the weight of evidence in support of our conclusions.

There is little evidence from our observations of bud-set that high volume producing families selected within coastal North Carolina had prolonged seasonal periods of growth. Loblolly pines can grow considerably during the winter (Barney 1951; Perry 1971; Strain *et al.* 1971) and rates and durations of winter bud development were not recorded. However, no significant family differences could be found in rates of height growth of small seedlings (sown 25 August) placed in progressively cooler, shorter-day, controlled environments, or placed outside in October-November (Cannell 1978 b)[5].

The influence of seed weights (and other maternal factors) on early seedling *growth* decreased as the seedlings aged. This was assumed to be the reason why, towards the end of the first year, family rankings in seedling height growth rates (with or without water stress) began to reflect inherent differences in future field performance. It is important to realize, however, that mean family seed weight/plant *size* correlations remained positive until the end of the first year, because inherent differences in seedling growth rates and water stress responses had not had time to override the early effects of seed weights. In many progeny tests these early effects may persist for 1—2 years after outplanting, and in some circumstances for much longer (e.g. Barber and Haverbeke 1961, Zarger 1965, Perry 1976).

---

[5] Cannell, M. G. R., 1978 b. Genetic variation in seasonal growth phenology within *Pinus taeda* L.: literature review and seedling studies on dates of bud-set. Unpublished Weyerhaeuser Company Technical Report, 042-3206/78/15.

References

Allen, R. M., and Scarbrough, N. M.: Morphology and length correlated in terminal flushes of longleaf pine saplings. U.S.D.A. Forest Service, Res. Paper SO-53. 15 p. (1970). — Barber, J. C.: Variation among half-sib families from three loblolly pine stands in Georgia. Georgia For. Res. Paper 37, 5 pp. (1966). — Barber, J. C., and van Haverbeke, D. F.: Growth of outstanding nursery seedlings of *Pinus elliottii* Englm. and *Pinus taeda* L. U.S. Forest Serv. Southeast Exp. Sta., Paper 126 (1961). — Barney, C. W.: Effect of soil temperature and light intensity on root growth of loblolly pine seedlings. Plant Physiol. 26: 146—163 (1951). — Bassett, J. R.: Tree growth as affected by soil moisture availability. Soil Sci. Soc. Amer. Proc. 28: 436—438 (1964). — Beineke, W. F., and Perry, T. O.: Genetic variation in ability to withstand transplanting shock. Eighth South. Forest Tree Improv. Conf. Proc. 106—109 (1965). — Bilan, M. V.: Some morphological variations among loblolly pine seedlings. Eight South. For. Tree Improv. Conf. Proc. 124—125 (1965). — Boyer, W. D.: Thermal efficiency: a possible determinant of height growth potential in young loblolly pines. For. Sci. 22: 279—282 (1976). — Brix, H.: The effect of water stress on the rates of photosynthesis and respiration in tomato plants and loblolly pine seedlings. Physiol. Plant 15: 10—20 (1962). — Buijtenen, J. P. van, Bilan, M. V., and Zimmermann, R. H.: Morpho-physiological characteristics related to drought resistance in *Pinus taeda*. *In:* Tree Physiology and Yield Improvement. Eds M. G. R. Cannell and F. T. Last. Academic Press, London and New York. p. 349—360 (1976). — Collins, A. B.: Tenth-year results of loblolly pine seed source planting in Georgia. U.S.D.A. For. Service Res. Note SE-20, 4 pp. (1964). — Finlay, K. W., and Wilkinson, G. N.: The analysis of adaptation in a plant-breeding programme. Aust. J. Agric. Res. 14: 742—754 (1963). — Giertych, M.: Inadequacy of early tests for growth characters as evidenced by a 59-year old experiment. Proc. Joint IUFRO Meeting S.02.041-3. Royal College of Forestry, Stockholm (1974). — Gordon, J. C., and Promnitz, L. C.: Photosynthetic and enzymatic criteria for the early selection of fast-growing *Populus* clones. *In:* Tree Physiology and Yield Improvement. Eds M. G. R. Cannell and F. T. Last. Academic Press, London and New York. p. 79—98 (1976). — Grigsby, H. C.: South Carolina best of 36 loblolly pine seed sources for southern Arkansas. U.S.D.A. For. Service Res. Paper SO-89. 10 pp (1973). — Grigsby, H. C.: A 16-year provenance test of loblolly pine in southern Arkansas. Fourteenth South. For. Tree Improv. Conf. Proc. p. 261—268 (1977). — Hellmers, H., and Rook, D. A.: Air temperature and growth of radiata pine seedlings. N.Z. Jl For. Sci. 3: 271—285 (1973). — Hocker, H. W.: Climatological summaries for selected stations in and near the southern pine region, 1921—1950. U.S.D.A. For. Service, Southeast For. Expt Stn. Paper 56. 12 pp (1955). — Ingram, M.: A device for measuring tree seedlings. For. Sci. (in preparation) (1978). — Kaufmann, C. M.: Growth of horizontal roots, height, and diameter of planted slash pine. For. Sci. 14: 265—276 (1968). — Kaufmann, M. R.: Water relations of pine seedlings in relation to root and shoot growth. Plant Physiol. 43: 281—288 (1968). — Krall, J.: Growth of loblolly pine in Uruguay. J. For. 67: 481 (1969). — Kramer, P. J.: Some effects of various combinations of day and night temperatures and photoperiod on the height growth of loblolly pine seedlings. For. Sci. 3: 45—55 (1957). — Kraus, J. F.: A study of racial variation in loblolly pine in Georgia — tenth years results. Ninth South. For. Tree Improv. Conf. Proc. pp. 78—85 (1967). — LaFarge, T.: Genetic variation among and within three loblolly pine stands in Georgia. For. Sci. 20: 272—275 (1974). — LaFarge, T.: Correlations between nursery and plantation growth in slash and loblolly pine. For. Sci. 21: 197—200. (1975). — Ledig, F. T.: A growth model for tree seedlings based on the rate of photosynthesis and the distribution of photosynthates. Photosynthetica 3: 263—275 (1969). — Ledig, F. T.: Increasing the productivity of forest trees. *In:* Forest tree improvement — the third decade. Ed. B. A. Thielges. Louisiana State Univ., Baton Rouge, La, U.S.A. p. 189—206 (1975). — Ledig, F. T.: Physiological genetics, photosynthesis and growth models. *In:* Tree Physiology and Yield Improvement. Eds M. G. R. Cannell and F. T. Last. Academic Press, London and New York. p. 21—54 (1976). — Ledig, F. T., and Perry, T. O.: Physiological genetics of the shoot : root ratio. Proc. Soc. Amer. Foresters, Detroit, Michigan. p. 39—43 (1965). — Ledig, F. T., and Perry, T. O.: Net assimilation rate and growth in loblolly pine seedlings. For. Sci. 15: 431—438 (1969). — Ledig, F. T., Bormann, F. H., and Wenger, K. F.: The distribution of dry matter growth between shoot and root in loblolly pine. Bot. Gaz.

131: 349—359 (1970). — Matziris, D. I., and Zobel, B. J.: Effect of fertilization on growth and quality characteristics of loblolly pine. Forest Ecology and Management 1: 21—30 (1976). — Namkoong, G., and Conkle, M. T.: Time trends in genetic control of height growth in ponderosa pine. For. Sci. 22: 2—12 (1976). — Namkoong, G., Usanis, R. A., and Silen, R. R.: Age-related variation in genetic control of height growth in Douglas-fir. Theor. and Appl. Genet. 42: 151—159 (1972). — Nanson, A.: The value of early tests in forest tree selection especially for growth (in French). Dissert. Doct. Gembloux; Sta. Rech. Eaux et For., Groenendaal, H.S. No. 38, 242 pp (1968). — Perry, T. O.: Dormancy of trees in winter. Science 171: 29—36 (1971). — Perry, T. O.: Maternal effects on the early performance of tree progenies. *In:* Tree Physiology and Yield Improvement. Eds M. G. R. Cannell and F. T. Last. Academic Press, London and New York. p. 473—481 (1976). — Perry, T. O., Wang, C. W., and Schmitt, D.: Height growth of loblolly pine provenances in relation to photoperiod and growing season. Silvae Genetica 15: 61—64 (1966). — Ralston, C. W.: Some factors related to the growth of longleaf pine in the Atlantic coastal plain. J. For. 49: 408—412 (1951). — Rao, C. R.: Linear statistical inference and its implications. (2nd ed.) John Wiley and Son, New York, London, Sydney and Tokyo (1965). — Reed, J. F.: Root and shoot growth of shortleaf and loblolly pines in relation to certain environmental conditions. Duke Univ. N.C. School of For. Bull. 4, 52 pp. (1939). — Righter, F. I.: *Pinus:* the relationship of seed size and seedling size to inherent vigor. J. For. 43: 131—137 (1965). — Schmitt, D., and Bower, D.: Volume tables for young loblolly, slash and longleaf pines in plantations in South Mississippi. U.S.D.A. For. Ser. Res. Note SO-102 (1970). — Snyder, E. B.: Racial variation in root form of longleaf pine seedlings. Sixth South. Forest Tree Improv. Conf. Proc. p. 53—59 (1961). — Steinhoff, R. J.: Juvenile-mature correlations in ponderosa and western white pines. Proc. IUFRO meeting S.02.04.1-3. Royal College of Forestry, Stockholm (1974). — Stonecypher, R. W., Cech, F. C., and Zobel, B. J.: Estimates of components of variance and covariance in root and shoot characteristics of loblolly pine after one growing season. Eighth South. Forest Tree Improv. Conf. Proc. p. 86—94 (1965). — Strain, B. R., Higginbotham, K. O., and Mulroy, J. C.: Temperature preconditioning and photosynthetic capacity of *Pinus taeda* L., Photosynthetica 10: 47—53 (1976). — Stransky, J. J., and Wilson, D. R.: Terminal elongation of loblolly and shortleaf pine seedlings under soil moisture stress. Soil Sci. Soc. Amer. Proc. 28: 439—440 (1964). — Sweet, G. B., and Wareing, P. F.: The relative growth rates of large and small seedlings in forest tree species. Supplement to Forestry p. 110—117 (1966). — Thor, E.: A ten-year-old loblolly pine seed source test in Tennessee. J. For. 65: 168—176 (1967). — Thor, E., and Brown, S. J.: Variation among six loblolly pine provenances tested in Tennessee. J. For. 60: 476—480 (1962). — Thornthwaite, C. W.: Atlas of climatic types in the United States, 1900—1939. U.S.D.A. Misc. Publ. 421. 7 pp (1941). — Wallace, D. H., Peet, M. M., and Ozburn, J. L.: Studies of CO_2 metabolism in *Phaseolus vulgaris* L. and applications in breeding. In: CO_2 metabolism and plant productivity. Eds R. H. Burris and C. C. Black. Univ. Park Press, Baltimore, Md. (1976). — Wareing, P. F., and Patrick, J.: Source-sink relations in the partition of assimilates in the plant. In: Photosynthesis and productivity in different environmens. Ed. J. P. Cooper. Camb. Univ. Press, London (1975). — Wells, O. O.: Results of the southwide pine seed source study through 1968—9. Tenth South. For. Tree Improv. Conf. Proc. pp. 117—129 (1969). — Wells, O. O., and Wakeley, P. C.: Geographic variation in survival, growth and fusiform-rust infection of planted loblolly pine. For. Sci. Monogr. 11, 40 pp. (1966). — Wenger, K. F.: Effect of moisture supply and soil texture on the growth of sweetgum and pine seedlings. J. For. 50: 862 (1952). — Woessner, R. A.: Growth patterns of one-year-old loblolly pine seed sources and inter-provenance crosses under contrasting edaphic conditions. For. Sci. 18: 205—210 (1972). — Zahner, R.: Terminal growth and wood formation by juvenile loblolly pine under two soil moisture regimes. For. Sci. 8: 345—352 (1962). — Zahner, R.: Water deficits and growth of trees. In: Water deficits and plant growth II. Ed. T. T. Kozlowski. Academic Press, London and New York. p. 191—254 (1968). — Zelawski, W.: Variation in the photosynthetic capacity of *Pinus sylvestris.* In: Tree Physiology and Yield Improvement. Eds M. G. R. Cannell and F. T. Last. Academic Press, London and New York. p. 99—110 (1976).

Free or Lammas Growth and Progeny Performance in Picea sitchensis

By M. G. R. Cannell*) and R. C. B. Johnstone**)

Received August / December 1978)

Summary

Free growth is an efficient mode of leader growth expressed most by young trees of southerly provenances of *Picea sitchensis,* and to varying degrees by different open-pollinated progenies. With free growth, the stem units (needle internodes) are elongated sooner, become longer, and fewer are used to produce bud scales. Progenies which produced large amounts of free growth at a favourable site in Britain tended to improve their height rankings during the first six years after planting. These were progenies of plus trees selected within particular plantations in Britain, which were considered to be of southerly provenance. Some of these progenies performed outstandingly at the favourable site and selection for such 'responsive' progenies could be improved by selecting for an ability to produce free growth. At two less favourable sites, free growth production had little influence on progeny height rankings. However, progenies which were better-adapted to the poorest site were among those that were least able to produce free growth. These were progenies of plus trees in other particular plantations in Britain which were considered to be of more northerly provenance.

Thus, free growth was considered a useful criterion to select (or reject) progenies which contributed to genotype × site interactions. But it was not a reliable criterion to select for good general performance at a range of sites. Free growth was not necessarily associated with greater leader growth or stem unit production.

Key words: Free growth, genotype × environment interaction, physiological-genetics, progeny evaluation.

Zusammenfassung

Freies Wachstum oder Johannistriebbildung und die Wüchsigkeit von Nachkommenschaften von *Picea sitchensis.*

„Freies Wachstum" ist eine effiziente Weise des Haupttriebswachstums, welches überwiegend bei jungen Bäumen südlicher Herkünfte von *Picea sitchensis,* aber auch in unterschiedlichem Maße bei verschiedenen Nachkommenschaften, beobachtet wurde. Beim freien Wachstum strecken sich die Stammeinheiten (Nadel-Internodien) bereits eine Wachstumsperiode früher. Diese werden insgesamt länger und es werden weniger verbraucht, um Knospenschuppen zu bilden. Nachkommenschaften, die an einem günstigen Standort an der schottischen Westküste größere Anteile freien Wachstums produziert hatten, zeigten die Tendenz, ihren Rang hinsichtlich des Höhenwachstums im Laufe der

---

*) Institute of Terrestrial Ecology, Bush Estate, Penicuik, Midlothian, Scotland.

**) Forestry Commission, Northern Research Station, Roslin, Midlothian, Scotland.