Short Note: Shoot Elongation in Pinus rigida X taeda Hybrids

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Summary

Height growth components of ten F_1 families of the *Pinus rigida* × *taeda* hybrid and both parental species were examined. Hybrid families exhibited varying amounts of free and fixed growth and were intermediate between the parental species. Fixed growth shoot lengths were similar among the hybrid families while loblolly and pitch pine both had shorter fixed growth shoot lengths. Free growth shoot lengths were very different among all families and the parental species. Differences in height growth among the families and parental species could be explained by varying numbers and lengths of stem units in fixed and free growth shoot components.

Key words: Fixed Growth, Free Growth, Stem Units.

Zusammenfassung

Es wurden an Hand von 10 F_1-Familien von *Pinus rigida* × *P. taeda* Hybriden Komponenten des Höhenwachstums geschätzt und beide Elternarten untersucht. Die Hybrid-Familien zeigten in unterschiedlichem Ausmaß freies und fixiertes Wachstum und waren in Bezug auf die Elternarten intermediär. Das fixierte Wachstum der Trieblängen war zwischen den Hybrid-Familien gleich, während *Pinus taeda* und *Pinus rigida* beide ein kürzeres fixiertes Triebwachstum aufwiesen. Das freie Wachstum der Triebe war zwischen allen Familien und den Elternarten sehr unterschiedlich. Unterschiede im Höhenwachstum zwischen den Familien und den Elternarten können durch die unterschiedliche Anzahl und die variierenden Längen der Stammeinheiten in Bezug auf freie und fixierte Wachstumskomponenten erklärt werden.

Introduction

A knowledge of pine shoot growth components is essential to an understanding of height growth variability which in turn is necessary for maximizing genetic gain. Shoot growth studies have assessed the relative contributions of fixed and free growth (Pollard and Logan 1974, Cannell and Johnstone 1978, and Bongarten 1978) and in recent years have examined the shoot as a composite of stem units. The division of a pine shoot into stem units has been advocated by several authors (Lanner 1968, Clements 1970, Cannell *et al.* 1976, Cannell 1978, and Bollman and Sweet 1979) and provides a method for assessing genetic variation in shoot length. The genetic variability thus defined can subsequently be used in selecting trees for shoot component characteristics rather than conventional shoot length characteristics (Cannell 1974). Such information can be used to attenuate selection techniques.

A study involving several full-sib *Pinus rigida* × *P. taeda* hybrid families (Bailey 1981) found significant differences among families in height growth. The main objective of this work was to investigate genetic variation among hybrid families associated with a) fixed versus free growth and b) numbers and lengths of stem units formed.

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Materials and Methods

Full-sib families of pitch (female parent) and loblolly (male parent) pine planted in 1975 as part of a larger pitch × loblolly pine hybrid study sponsored by Westvaco Corporation and the Northeastern Forest Experiment Station (U.S.F.S., Durham, NH), were used in this study. The hybrid plantation is located at the Reynold's Homestead Research Center, Critz, Virginia. The hybrid families and commercial seedlings of pitch and loblolly were selected from the plantation for shoot growth analysis. All families were represented by one to five individuals in each of three blocks; a total of ten to fifteen individuals per family.

The distinction between fixed and free growth for the 1980 growing season was based on a preliminary investigation made in the spring of 1980. Growth cycles were counted in excised dormant terminal buds taken from a sample of lateral branches in early March. By late April it was possible to count growth cycles *in situ* in the elongating buds and this was done on the remaining laterals and the leaders. A significant positive correlation ($R = .75$, $p = .01$) was found between cycle numbers in dormant buds and cycle numbers in elongating buds for the lateral branches. Based on this relationship the growth cyles counted in the leader buds in late April were designated as fixed growth and additional cycles elongating during the growing season were designated as free growth.

Numbers of stem units were counted in each growth cycle for both fixed and free growth. Each cycle was divided into its constituent sterile and fertile stem unit zones (scale and short shoot components respectively). The length of each zone was measured to the nearest 0.5 cm and all stem units counted. Fertile stem units were enumerated while clipping off the top of each fascicile and sterile units by marking each with a felt tip marker. Mean stem unit length (MSUL) was calculated as zone length divided by the total number of stem units.

Results

An overall summary of shoot growth characteristics is presented in *Table 1*. An analysis of variance incorporating initial height as a covariable indicated significant differences in shoot length among families. A Fisher's protected least significant differences test was used to identify families with significantly longer or shorter shoots. These differences and the differences in numbers of fixed and free growth cycles prompted further analysis. The first stage of this analysis was to partition shoot length into fixed and free growth.

Fixed growth shoot lengths, mean stem unit numbers and short shoot MSUL's are presented in *Table 2*. Both pitch and loblolly families had significantly shorter shoots than any of the hybrid families. Despite differences in both stem unit numbers and lengths, however, there were essentially no differences in fixed growth shoot length among the hybrid families. Correlations suggest a strong

Table 1. — Mean values for shoot length, stem unit number and number of growth cycles for selected families.

FAMILY	NO. OF TREES	SHOOT LENGTH (cm)	FIXED CYCLES	FREE CYCLES	AVERAGE STEM UNIT NUMBERS
77X7-56	15	104.5a[1]	2	2	558
77X11-10	15	100.9ab	2	1	584
78X11-10	12	90.0 bc	2	1	557
Loblolly	12	89.7 bc	1	2	524
59X11-10	13	89.6 bc	1	2	578
59X7-56	15	89.1 c	2	2	528
71X15A	15	88.6 c	2	1	564
71X22	15	87.4 c	2	1	577
78X7-56	10	86.4 c	2	1	523
71X10	15	86.2 c	2	1	635
78X22	15	85.6 c	3	1	563
Pitch	12	43.7 d	4	0	336

[1] values connected by the same letter are not significantly different ($p < .05$).

Table 2. — Details of fixed growth by family (MSL = Mean length of fixed growth, MSUN = mean stem unit number, MSUL = mean stem unit length, R = correlation between MSUL and MSUN).

FAMILY	MSL	MSUN	MSUL	R
Loblolly	39.9a[1]	233*[2]	.19	-.46
Pitch	45.1a	336	.13*[3]	.03
59X7-56	59.1 b	319*	.20	-.47
59X11-10	60.7 bc	341*	.19	-.75*[4]
78X7-56	62.7 bc	376*	.18	-.47
78X22	64.1 bc	432*	.15	-.61*
71X15A	64.1 bc	389*	.18	-.71*
71X10	65.2 bc	465	.14	-.66*
77X11-10	65.5 bc	352*	.20	-.70*
77X7-56	65.9 bc	316*	.23	-.77*
71X22	66.3 bc	428*	.16	-.07
78X11-10	67.2 c	391	.18	-.75*
OVERALL	60.9	367*	.18*	-.57*

[1] values connected by the same letter are not significantly different ($p < .05$).
[2] indicates significant positive correlation of MSUL with shoot length.
[3] indicates significant positive correlation of MSUL with shoot length ($p < .05$).
[4] indicates significance at ($p < .05$).

positive relationship between shoot length and stem unit numbers and a strong inverse relationship between stem unit length and stem unit numbers for most of the families studied. These relationships may be useful in explaining the uniformity of fixed growth shoot length.

Differences among families in total 1980 shoot length were not explicable in terms of fixed growth which was essentially uniform among families. Free growth components were thus examined and the results summarized in *Table 3*. More significant differences in shoot length were apparent for the free growth with loblolly having significantly longer free growth shoots than any of the hybrids. Again stem unit numbers had a strong positive correlation with shoot lengths although in several families there was also a positive relationship between free growth shoot length and MSUL. No trend of decreasing MSUL with increasing stem unit number is apparent in the free growth. Although stem unit numbers and lengths are inversely related in the fixed growth, they are independent in the free growth.

Table 4 presents the results from a variable selection procedure used to summarize the variables important in determining total shoot length for each family. Initially, six variables were used in the model; free growth stem unit numbers and lengths, fixed growth stem unit numbers

Table 3. — Details of free growth by family (MSL = Mean shoot length, MSUN = Mean stem unit number, MSUL = Mean stem unit length, R = correlation between MSUL and MSUN).

FAMILY	Shoot Length (cm)	MSUN	MSUL	R
71X10	21.0a[1]	170*[2]	.13	-.28
71X22	21.0a	148*	.16*[3]	.24
78X22	21.5a	130	.18*	.31
78X11-10	22.7ab	165*	.15	.09
78X7-56	23.7ab	147	.18*	-.31
71X15A	24.2ab	175*	.14*	.21
59X11-10	29.0abc	238*	.12	-.55*[4]
59X7-56	30.0 bc	209*	.16	.02
77X11-10	35.5 cd	232*	.15	.09
77X7-56	38.6 d	241	.16*	.22
Loblolly	49.7 e	290*	.18	.28
OVERALL	28.7	194*	.15*	-.02

[1] values connected by the same letter are not significantly different ($p < .05$).
[2] indicates significant positive correlation of MSUL with shoot length.
[3] indicates significant positive correlation of MSUL with shoot length ($p < .05$).
[4] indicates significance at ($p < .05$).

Table 4. — Results of a variable selection procedure with shoot length as the dependent variable.

FAMILY	BEST MODELS 1 VAR.	2 VAR.	3 VAR.	4 VAR.
Loblolly	RN[1] (.81)[2]	RN RL (.91)	RN RL XN (.96)	RN RL XN XL (.99)
Pitch	XL (.69)	XL XN (.96)		
59X11-10	RN (.76)	RN XN (.88)	RN XN RL (.98)	RN XN RL XL (.99)
59X7-56	XL (.33)	XL XN (.73)	XL XN RN (.82)	XL XN RN RL (.99)
71X10	RN (.36)	XN XL (.68)	XN XL RN (.88)	XN XL RN RL (.97)
71X15A	RN (.46)	RL XN (.62)	XN XL RN (.93)	XN XL RN RL (.96)
71X22	XN (.51)	XN RN (.84)	XN RN XL (.93)	XN RN XL RL (.96)
77X11-10	RN (.51)	RN RL (.88)	RN RL XN (.94)	RN RL XN XL (.99)
77X7-56	RN (.64)	RN RL (.84)	RN RL XN (.94)	RN RL XN XL (.96)
78X11-10	XL (.33)	XL XN (.67)	XL XN RN (.84)	XL XN RN RL (.89)
78X22	XN (.50)	XN XL (.85)	XN XL RL (.90)	XN XL RN RL (.96)
78X7-56	RN (.70)	XN XL (.95)	XN XL RL (.98)	XN XL RN RL (.98)

[1] RN = free numbers RL = free MSUL XN = fixed numbers XL = fixed MSUL.
[2] R^2 value for model.

and lengths and sterile stem unit numbers and lengths. The sterile stem unit variables added only .02 to the R^2 value in an overall model and were left out of the final analysis. The results indicate the best 1, 2, 3, and 4 variable models for each family.

Discussion

Differences in shoot components were most obvious between the pitch and the loblolly pine controls. Pitch pine produced an average of four fixed and no free growth cycles while loblolly produced an average of one fixed and two free growth cycles. The interspecific hybrids were intermediate, all produced some fixed and some free growth. Differences in total shoot length were also apparent with three hybrid families ranking higher than loblolly and all ranking higher than pitch. These differences in shoot lengths and components suggest that different growth patterns were being followed by the pitch, the loblolly and the hybrids.

Trees producing a large percentage of free growth have growth patterns enabling them to initiate and elongate stem units in response to current environmental conditions. Such a pattern was exemplified by loblolly which produced over 50% of its 1980 shoot length as free growth. At the opposite extreme, trees producing mainly fixed growth are able to respond to current environmental conditions only by initiating stem units for the following year. This type of growth pattern was illustrated by pitch pine which depended entirely on the elongation of stem units formed in 1979 for its 1980 growth. The growth patterns of the hybrids in terms of fixed and free growth percentages were intermediate with some favoring the pitch and others the loblolly pattern. Since loblolly did not have the longest shoots it was not possible to explain shoot length in terms of capacity for free growth.

Although the fixed growth for both loblolly and pitch resulted in shoots of approximately the same length their strategies for attaining this length were different. Loblolly produced few long stem units while pitch produced many short stem units. This inverse relationship between numbers and lengths was also exhibited in the hybrids. All of the hybrids, however, produced more stem units than loblolly and/or longer stem units than pitch resulting in their having longer fixed growth shoots than either parent species. Despite differences among families in numbers and lengths of stem units their fixed growth shoots were of strikingly similar lengths.

The uniformity in fixed growth shoot length found among the hybrids is consistent with the findings of POLLARD and LOGAN (1974). In their work with black spruce they found that fixed growth formed the bulk of shoot production but was similar among provenances. Differences in shoot elongation among provenances apparently resulted from variation in the amount of free growth produced. Since no differences in fixed growth shoot length among families were found in this study, the differences found in total shoot length must also be due to free growth.

Correlations between fixed growth shoot length and stem unit numbers indicated a strong positive relationship for all families except pitch, 71 × 10 and 78 × 11-10. Correlations between shoot length and fixed MSUL were significant for pitch but not for any of the hybrid families. These results support the finding by many authors that numbers of stem units account for most of the variation in shoot length. Free growth shoot lengths were more variable and in several families MSUL was correlated with shoot length. Stem unit numbers were also important in free growth shoot length but were not the dominating factor as in the fixed growth.

Analysis of the free growth component indicated significant differences among families not only in stem unit numbers and lengths but also in shoot lengths. No trend of decreasing MSUL with increasing stem unit number was detected in the free growth; correlations indicated that these variables were independent in all families except 59 × 7-56. The lack of correlation between free growth stem unit numbers and lengths was in contrast to the inverse relationship found in the fixed growth. This may in some way be related to the fact that fixed growth stem units are initiated and elongated during different seasons while free growth stem units are initiated and elongated in the same season.

Results from the variable selection procedure indicate the relative importance of fixed and free growth stem unit numbers and lengths for each family. There are differences among families in the importance of these variables. For loblolly and the hybrid families 77 × 7-56 and 77 × 11-10 the free growth variables were most important. For pitch pine the two fixed growth variables, accounted for 96% of the variation in total shoot length. Although some hybrid families had over half of the variability accounted for by the fixed growth variables none had an R^2 value for these two variables as high as that for pitch, suggesting that height growth variation in these families is a function of free as well as fixed growth.

These results imply different patterns of maximizing shoot elongation among hybrids families. For some families free growth components accounted for the most variability in shoot length; for others, fixed growth components were most important. In loblolly pine free growth components accounted for 91% of the variability. For most of the hybrids, however, more than two variables were necessary to account for over 90% of the variability in shoot length.

Conclusions

In all of the hybrid families fixed growth constituted the bulk of the 1980 shoot growth but was consistent among families. Differences in total shoot length were due to the varying amounts of free growth produced. In loblolly fixed growth constituted less than half of the 1980 shoot length; free growth was significantly greater than in any of the hybrids, but not sufficient to compensate for the small amount of fixed growth.

The optimum growth pattern of trees on the Reynolds site seems to be the production of a certain minimum amount of fixed growth followed by as much free growth as site conditions allow. Loblolly pine did not produce this minimum amount of fixed growth and this could account for its poor relative performance compared with the hybrids. It would be of interest to relate these growth patterns to environmental variables, particularly moisture, over a more extended period. It may be that in a favorable growing season loblolly could surpass the hybrids in shoot length growth due to its capacity for large amounts of free growth.

In the future it may be possible to genetically select hybrid families with growth strategies highly adapted to site conditions. When this is done, height growth potential will be effectively utilized.

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