VARIATION IN BALSAM FIR SHOOT APEX CHARACTERISTICS AND SHOOT GROWTH[1/]

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Abstract.--Dormant terminal buds and subsequently developed shoots were removed from several whorls of 17-year old trees representing four balsam fir (Abies balsamea (L.) Mill) provenances and examined for variation in primordia and needle production, apical dome diameter and the relative contributions of stem unit number and length to shoot growth. Shoot apex primordia number and apical dome diameter were strongly correlated and generally paralleled provenance and interwhorl variation in shoot growth. Despite correlations between primorida and needle number, there were significantly more primordia initiated than needles subsequently produced on shoots from the same, trees. Apparently, the last formed primordia in the winter into bud scales rather than needles. Provenance variation in shoot length was due primarily to provenance differences in number rather than length of stem units. In contrast, shoot growth variation among individual trees within provenances resulted primarily from variation in stem unit length. Whorl to whorl variation in shoot growth was substantial and due to differences in both number of stem units and stem unit length.

Additional keywords: Abies balsamea, stem unit, primordia, apical dome.

INTRODUCTION

Variation in growth rate among provenances of several coniferous species has been partially attributed to general physiological events responsible for development of the shoot apex. In several spruce (Picea) and pine (Pinus) species and Douglas-fir (Pseudotsuga menziesii Mirb. Franco), genetic variation in embryonic shoot development has been documented and shown to be largely a function of the rate and/or duration of needle or axillary bud primordia initiation during summer and fall (Burley 1966; Pollard et al. 1975; Cannell and Willett 1975; Cannell et al. 1976; Bongarten 1978). Furthermore, variation in shoot growth has frequently been associated with variation in total primordia complement produced the previous growing season. Therefore, information concerning the extent and nature of genetic and developmental variation in bud morphogenesis may provide a foundation for interpreting and understanding growth rate variation within tree species.

Balsam fir (Abies balsamea (L.) Mill.) is an economically important species which exhibits considerable provenance variation in growth rate

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(Lester et al. 1976; Lowe et al. 1977). Although the physiology of shoot development in balsam fir has been described by Jablanczy (1971), the extent of genetic variation in shoot development and its relationship to growth has not previously been reported. At The University of Vermont, we have begun an investigation of genetic and developmental variation in bud morphogenesis and subsequent shoot development in balsam fir. This paper reports findings of preliminary studies designed to provide an estimate of variation within and among balsam fir trees and provenances in number of primorida and needles produced during a given growing season, diameter of the apical dome and relative contributions of stem unit number and length to total shoot growth.

MATERIAL AND METHODS

Plant material was obtained from trees representing four balsam fir provenances growing in a border row around the southern edge of a 17-year old provenance test plantation in Wolcott, VT. The four provenances, one each from eastern and western Ontario and the Upper and Lower Peninsulas of Michigan, were chosen because of their representation in border rows and not because of extreme performance in any characteristic. Border row trees were chosen because it was necessary to remove leaders and first-order terminals from several whorls and we did not wish to alter the growth or form of trees in the provenance test.

To determine the magnitude and distribution of variation in number of primordia and apical dome diameter, terminal buds were collected in February 1983 from leaders and two branches from each of whorls two through six from five randomly chosen trees per provenance. Terminal buds from the first whorl, which were fused to the terminal buds of the leader, were discarded. In the laboratory, the bud scale complex was removed to expose the apical dome and primordia arranged in spiral parastichies (fig. 1A and 1B). After confirming phyllotaxy (generally 8:13 for apices of whorls two through six and 13:21 for leader apices), the number of primordia per embryonic shoot was estimated by determining the average number of primordia in three parastichies and multiplying by the number of parastichies indicated by the phyllotaxy. Apical dome diameter was assumed equal to the diameter of a circular plane defined by the three most recently initiated primordia (fig. 1B).

To determine the relationship between number of primordia and subsequent needle production and to characterize variation (among and within trees and provenances) in shoot length, two shoots were collected following 1983 shoot elongation from the same whorls, trees and provenances that were previously sampled for primordia number determinations. Because leader and first whorl buds had been removed from these trees during the previous sampling, leaders and two shoots from the first whorl were collected from an additional five trees per provenance. The length of each shoot was measured and the number of needles per shoot were counted with an electronic seed counter. The number of needles per shoot were considered an estimate of the number of stem units per shoot, and the average interneedle distance was used as an estimate of stem unit length. The number and length of stem units were considered collectively as components of shoot length.

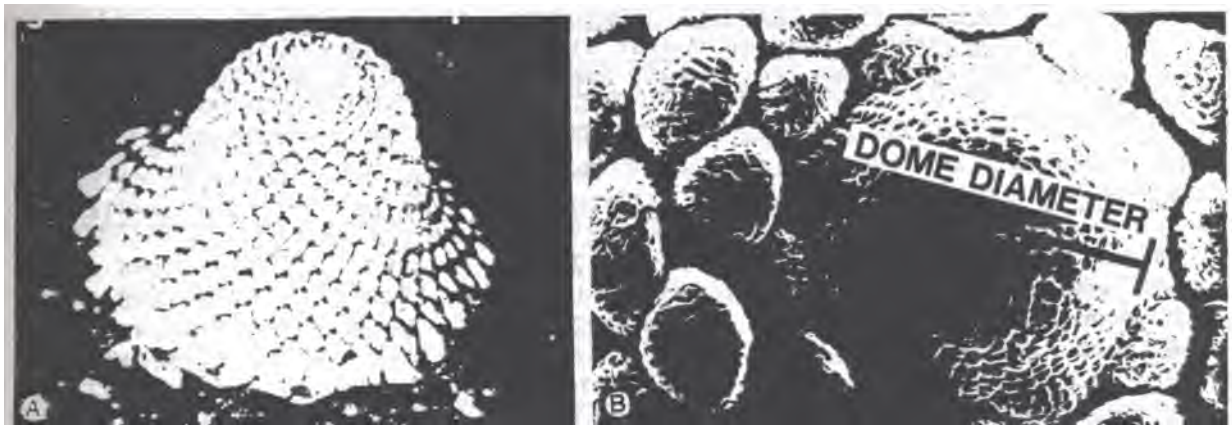

Figure 1A and 1B -- Fig. 1A, Photomicrograph of a typical balsam fir shoot with primordia arranged in spiral rows or parastichies. Fig. 1B, Scanning electron micrograph of an apical dome and surrounding primordia.

RESULTS AND DISCUSSION

Variation in Primordia Number and Apical Dome Diameter

Most of the variation in number of primordia (70%) and apical dome diameter (80%) was attributed to differences among provenances and whorls within trees, whereas tree-within-provenance and bud-within-whorl accounted for a relatively small portion of the total variation. On a mean basis, extreme provenances differed by 44% and 24% in number of primordia and apical dome diameter, respectively (table 1). In general, provenance mean primordia number paralleled provenance mean height whether considered separately by whorl or as an average over all whorls. For example, trees grown from seed collected in Floodwood, MI were tallest and had the most primordia on the embryonic shoots of each whorl, while those from Red Lake, ONT were shortest and had the fewest primordia in each whorl. Pollard and Logan (1976), working with black spruce (Picea mariana (Mill.) B.S.P.), also reported a significant positive correlation between provenance mean primorida number and height.

Variation in number of primordia among whorls averaged over all trees and provenances was greater than that attributed to provenance differences. In fact, embryonic shoots of leaders averaged more than twice the number of primordia than embryonic shoots in the sixth whorl (table 2). Although the number of primordia decreased with increasing whorl number (table 2), the degree of reduction was not consistent from whorl to whorl. The largest reduction (half of the total difference) in number of primordia among whorls occurred between buds of the leader and second whorl. Despite this difference, the number of primordia in embryonic shoots of leaders was strongly and positively correlated with the number in embryonic shoots of whorls two through six (range in $r=0.44$, $P<0.05$, to 0.79, $P<0.01$, 18 d.f.). As with provenance differences in number of primordia, differences among whorls also paralleled shoot elongation differences.

Table 1 -- Apical dome diameter, number of primorida, needle number and the difference between number of primordia and needles of four balsam fir provenances averaged over leaders and whorls two through six.

Source	Apical dome diameter (mu)	No. of Primordia	No. of Needles	Difference between number of primordia and needles
Balsam Creek, ONT	291	210	188	+22**
Red Lake, ONT	251	181	177	+ 4NS
Floodwood, MI	310	260	229	+31**
Roscommon, MI	272	214	200	+14**

** P≤.01, 18 d.f.
NS Non-significant

Table 2 -- Apical dome diameter, number of primordia, needle number and the difference between average number of primordia and needles of balsam fir leaders and whorls two through six averaged over all provenances.

Position within tree	Apical dome diameter (mu)	No. of Primordia	No. of Needles	Difference between number of primordia and needles
Leader	431	358	389	-31NS
Whorl 2	329	266	242	+24**
Whorl 3	300	231	217	+14*
Whorl 4	275	210	199	+11NS
Whorl 5	254	197	183	+14NS
Whorl 6	243	174	156	+18*

* P≤.05, 18 d.f.
** P≤.01, 18 d.f.
NS Non-significant

Apical dome diameters were strongly and positively correlated with number of primorida (r=0.89, P<0.01, 94 d.f.) and the pattern of variation among provenances and whorls closely paralleled that for number of primordia. In general, whorls, trees and provenances with many primordia had proportionately larger apical domes (tables 1 and 2). For instance, trees from Floodwood, MI and Red Lake, ONT provenances represented extremes in apical dome diameter as well as number of primordia (table 1) and the average apical dome diameter in embryonic shoots of leaders was nearly twice that of whorl six (table 2). Although significant at all whorls, the relationships between dome diameter and number of primordia was stronger in the lower whorls (r=0.86, P<.01, 18 d.f. in whorl 6) than in leaders (r=0.50, P<0.05, 18 d.f.) and upper whorls. The relationship between apical dome diameter and number of primordia is consistent with findings from developmental studies of spruce (Picea) and pine (Pinus) seedlings (Gregory and Romberger 1972; Cannell et al. 1976).

Relationship Between Primordia and Needle Number

When compared over all trees and whorls, the number of primordia initiated on the shoot apex was strongly correlated ($r=0.78$, $P<0.01$, 98 d.f.) with the number of needles subsequently born on extended shoots. This relationship was strongest for buds and shoots in the uppermost whorl sampled ($r=0.86$, for whorl 2, $P<0.01$, 18 d.f.) and tended to diminish somewhat basipetally ($r=0.55$, for whorl 5, $P<0.05$, 18 d.f.).

Despite a strong correlation between number of primordia and needle number, there were generally more primordia initiated in buds than needles subsequently produced on comparable shoots of the same trees. In fact, paired t-tests revealed that differences between number of primorida initiated and subsequent needle production were significant for three of the four provenances (table 1) and three of the five whorls studied (table 2). Apparently, the last-formed 15 to 30 primordia initiated in the winter bud differentiate into bud scales rather than needles the following spring. However, provenances and whorls seem to vary somewhat in the number of primordia which differentiate into bud scales. These data indicate that free growth (needle production and internote elongation during growing season of elongation) is unimportant in shoot development on these 17-year old balsam fir and that variation in needle complement must therefore be a function of variation in the development of winter bud and, to a lesser extent, the proportion of primordia which differentiate into bud scales rather than needles. A generally greater number of primordia than needles and provenance variation in that difference has also been reported for 7-year old blue spruce (Picea pungens Engelm.) (Bongarten 1978) and 11-year old white spruce (Picea glauca (Moench) Voss) (Pollard 1973). In contrast, a greater number of needles than primordia, and therefore evidence for free growth, has been reported in a few 12-year old black spruce provenance (Pollard and Logan 1976) and most provenances of 15-year old Douglas-fir (Bongarten 1978).

The reverse relationship between number of primordia and needles that were observed on leaders (table 2) must be interpreted with considerable caution. Unlike in whorls two through six, leader buds and shoots were necessarily from different trees and only one bud or shoot could be sampled per tree to represent the leader (two buds or shoots were sampled and averaged per whorl). As a result, sampling error was high in leaders and chance alone may have been responsible for a greater needle than primordia count.

Variation in Shoot Length as a Function of Stem Unit Number and Length

Shoot length varied significantly among provenances in whorls one through six (table 3) and among trees within each provenance. Variation in shoot length among whorls within trees accounted for 70% of the variation in shoot length. When considered collectively over all whorls, trees and provenances, shoot length was positively correlated with both number of stem units ($r=0.91$, $P<0.01$, 138 d.f.) and stem unit length ($r=0.84$, $P<0.01$, 138 d.f.). That is, relative to short shoots, long shoots generally had a greater number of stem units (estimated by number of needles) and longer stem units (estimated by average interneedle distance). To further characterize variation in shoot growth, we examined the contributions of stem unit number and length to variation in shoot length among provenances, individual trees within provenances and whorls within trees.

Variation among provenances. There were too few provenances to assess the relationship between shoot length and stem unit characteristics by correlation analyses. Therefore, we performed a separate analysis of variance for each sampling position to determine the significance of provenance differences in stem unit number and length. In the uppermost whorls, where provenance differences in shoot length were greatest, stem unit number but not length varied significantly among provenances (table 3). In other words, provenance variation in shoot growth in the uppermost whorls is primarily a function of the number of stem units. The reverse pattern was evident in whorls five and six. Bongarten (1978) also found that geographic variation in shoot growth among blue spruce provenances was due to number of stem units, but both stem unit number and length contributed to provenance variation in shoot growth of Douglas-fir. In addition, shoot length variation among pitch (Pinus rigida Mill.), loblolly (P. taeda L.), and several hybrid (pitch x loblolly) pine families was also associated with variation in stem unit number (Bailey and Feret 1982).

Table 3 -- Range and significance of provenance mean differences in shoot length, number of stem units and stem unit length at each of several crown positions in balsam fir.

Position within tree	Range and significance of provenance mean differences for		
	Shoot length (cm)	Number of stem units	Stem unit length (mm)
Leader	43.4-57.6NS	345-432NS	12.5-13.5NS
Whorl 1	22.9-31.6**	218-304**	10.2-10.9NS
Whorl 2	20.9-31.5**	206-292**	9.5-13.0NS
Whorl 3	14.4-20.6*	205-257*	7.0- 9.1NS
Whorl 4	12.2-16.0*	177-216NS	6.4- 7.8NS
Whorl 5	9.8-15.2*	153-210NS	5.9- 7.3**
Whorl 6	5.8-10.5*	130-174NS	4.8- 7.0**

* $P \leq .05$
** $P \leq .01$
NS Non-significant

Stem unit number, determined by activity of the apical meristem, is influenced largely by the rate and duration of primordia initiation and the degree of free growth. Like other phenological characteristics in woody plants, the duration of primordia initiation during summer and fall has been shown to be a genetically variable characteristic, especially among geograpically separated provenances (Bongarten 1978; Pollard 1973; Cannell and Willett 1975; Burley 1966). Since free growth was unimportant in these balsam fir trees, it is possible that provenance variation in stem unit number and shoot length result, at least in part, from provenance variation in the phonology of shoot apex development. Developmental studies are currently underway to test this hypothesis.

Variation among trees within provenances. To characterizie variation in shoot length among trees within provenances, average shoot length, number

of stem units and stem unit length per tree and whorl were expressed as a percentage of the provenance mean for that whorl and correlations were calculated between the adjusted values. The resulting R values indicate the proportion of variation in shoot length among individual trees, independant of provenance, explained by stem unit number and length. In contrast to provenance differences in shoot length, most of the variation in shoot length among individual trees was attributed to stem unit length, especially in the leaders and upper whorls (table 4). Number of stem units became increasingly more important in the lower whorls and explained most of the variation in shoot length among trees in whorls five and six.

Table 4 -- Proportion of variation (R^2) in shoot growth among individual balsam fir trees, adjusted for provenances, explained by number of stem units and stem unit length.

Position within tree	Proportion of variation in shoot length due to number stem units	stem unit length
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Leader	14NS	44**
Whorl 1	19NS	52**
Whorl 2	13NS	14NS
Whorl 3	44**	62**
Whorl 4	42**	58**
Whorl 5	79**	52**
Whorl 6	81**	16NS

** $P \leq .01$, 18 d.f.
NS Non-significant

Stem unit length, determined by the activity of the subapical or rib meristem, is influenced largely by growing season conditions during the relatively brief period during which elongation occurs. As such, one might expect stem unit length to be under relatively weak genetic control and for variation in stem unit length among individual trees to be largely a function of internal physiological and localized external conditions. In support of this suggestion, Bongarten (1978) found longer stem units on Douglas-fir trees which suffered frost damage the spring prior to sampling than on undamaged trees. Presumably, frost-damaged trees were able to funnel photosynthetic reserves into surviving shoots, thereby stimulating greater elongation than normal.

Variation among whorls within trees. To examine variation in shoot

stem unit length were expressed as a percentage of individual tree means to remove individual tree and provenance influences. These adjusted values for stem unit number and stem unit length were then independently correlated with adjusted shoot length values. Stem unit length explained 72% (R^2) of

length among whorls within trees, average shoot length, stem unit number and

the variation in shoot length among whorls. Differences in number of stem units among whorls exlained 61% of whorl to whorl variation in shoot

length. In contrast to the relatively long shoots found on leaders and in upper whorls, shoots characteristic of lower whorls in balsam fir are short because they are composed of both relatively few stem units and short stem units.

Variation in number of stem units and stem unit length unquestionably contribute to shoot growth differences among and within balsam fir trees and provenances. Because there was no evidence of free growth or spring primordia initiation in these 17-year old balsam fir trees, the number of stem units are determined solely by number of primordia initiated during the previous growing season. Clearly, the physiology of shoot apex development and the degree of genetic influence on that development are significant contributing factors to shoot growth variation among balsam fir provenances.

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