VARIATION IN SPECIFIC GRAVITY AND TRACHEID LENGTH AMONG BALSAM FIR PROVENANCES[1]

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ABSTRACT.--In a northern Vermont test plantation balsam fir provenances varied considerably in growth rate, specific gravity and tracheid length. In general, trees grown from seed collected in the eastern and central portions of the balsam fir range were faster growing, had lower specific gravities and longer tracheids than those grown from seed collected in the western portion of the range. Mean provenance specific gravity and tracheid length were strongly correlated with growth rate, however, significant provenance differences in specific gravity and tracheid length existed after adjusting for growth rate.

INTRODUCTION

Balsam fir (*Abies balsamea* (L.) Mill.) is a common component of North America's boreal forest regions and is an important Christmas tree and pulpwood species. During recent years, considerable research in balsam fir has focused on its taxonomic affiliation with related species and the nature and extent of intraspecific variation. Balsam fir provenance tests in the Lake States and New England have revealed considerable genetic variation in growth rate, leafing out phenology (Lester et al. 1976; Lowe et al. 1977), foliar moisture and drying rate (DeHayes et al. 1978), and the concentration of foliar monoterpenes (Lester 1974). Phenotypic variation studies have shown population differences in cone bract to scale ratios and the concentration of cortical monoterpenes (Myers and Bormann 1963; Zavarin and Snajberk 1972). For most traits, an east-west pattern of variation has been evident.

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Specific gravity and tracheid length of the wood are important properties that influence the commercial value and utility of species. Specific gravity determines the yield per unit volume of dry wood produced, while tracheid length influences the strength and quality of wood products. Balsam fir compares poorly with other conifers for timber production because of its relatively low density. However, due to its abundance and satisfactory tracheid length and quality, it is an important source of pulp throughout much of its range (Bakuzis and Hansen 1965). Although considerable information has been gathered on provenance variation in balsam fir in recent years, little is known about the extent and pattern of variation of its wood properties.

Provenance and phenotypic variation in wood properties has been demonstrated for many coniferous species (Echols 1958; Posey et al. 1970; Ledig et al. 1975; Zobel et al. 1960), and improvement in wood quality has been a primary objective of several tree improvement programs. For instance, Zobel (1971) has shown that specific gravity and tracheid length are strongly and independently inherited in southern pines and that considerable gain in wood quality can be achieved through selection. There has been little investigation of intraspecific variation in wood properties of any fir species, except for a phenotypic variation study to determine the taxonomic status of southern Appalachian *Abies*. In that study, Thor and Barnett (1972) found differences in specific gravity and tracheid length among stands within three purported varieties of balsam fir. However, environmental and genetic differences among stands were confounded so that the nature of the variation could not be determined. Our objective was to determine the extent and nature of genetic variation in specific gravity and tracheid length among balsam fir provenances in a northern Vermont provenance test.

MATERIALS AND METHODS

In spring 1971, 3-2 seedlings representing 21 provenances from throughout most of the balsam fir range (Fig. 1) were planted at the Wolcott Research Forest in northern Vermont. The plantation was laid out in a randomized complete block design with two 7-tree row plots of each provenance within each of four blocks. The seedlings were planted at a 1.5 x 1.5 meter spacing. Three rows of border trees surround the plantation to minimize edge effects. Weed competition was controlled by herbicides and mowing for the first few years after planting. Details on plantation establishment and early measurements are described by Lowe et al. (1977).

By fall 1978 (age 13 from seed), the crowns of most adjacent trees had begun to overlap and the plantation was in need

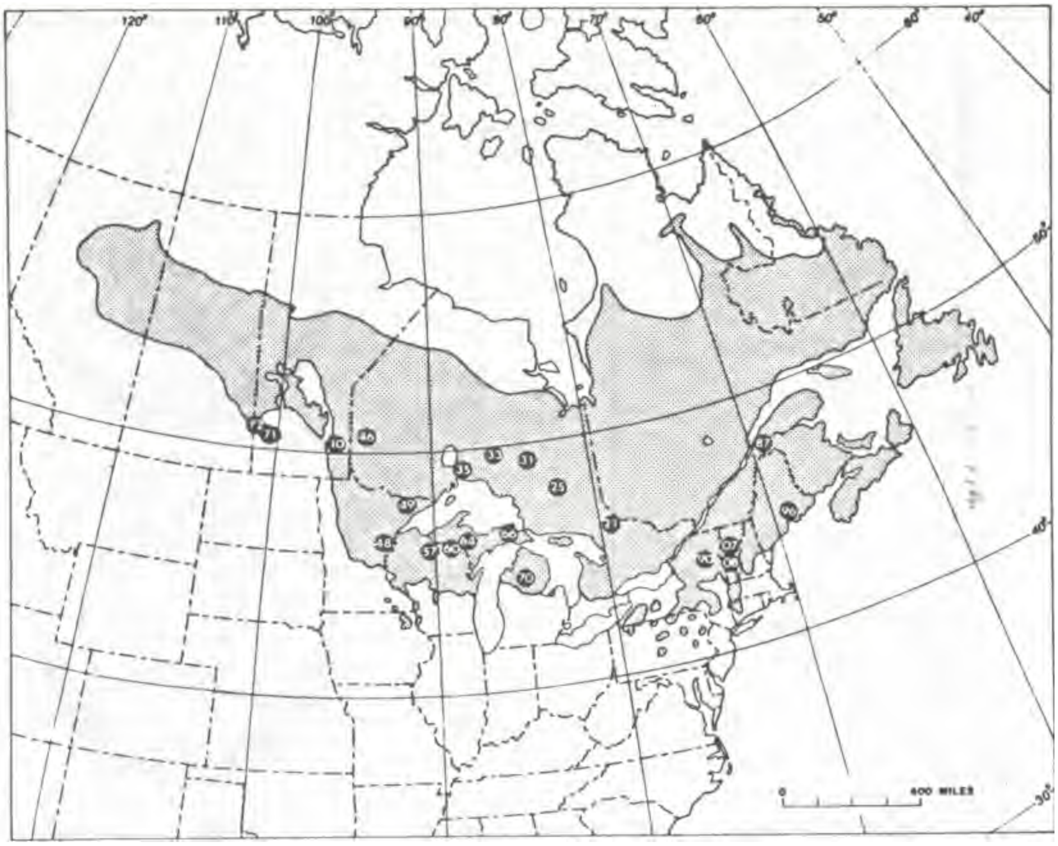

Figure 1. The natural range of balsam fir and location of 21 provenances represented at the Wolcott, Vermont plantation.

of thinning. At that time, height and diameter (15 cm above the ground) measurements were made and the plantation was thinned to remove two trees from each 7-tree plot. The smallest tree and an average size tree in each plot were selected for thinning. The average size tree removed from the two plots per block of each provenance provided the material for wood property analyses. A total of eight trees from each of 19 of the 21 provenances were included in the study.

The internode containing six annual growth rings was selected from each stem for wood property analyses. Preliminary analyses showed this internode to be most representative of each tree because its wood characteristics were approximately equal to the average of those from the remainder of the tree. Two adjacent cross-sectional disks, 2 cm in thickness, were cut from the center of the selected internode from each tree (Fig. 2). Care was taken to avoid compression wood, nodal swelling or any other stem deformities at the point of disk removal. A 2 cm

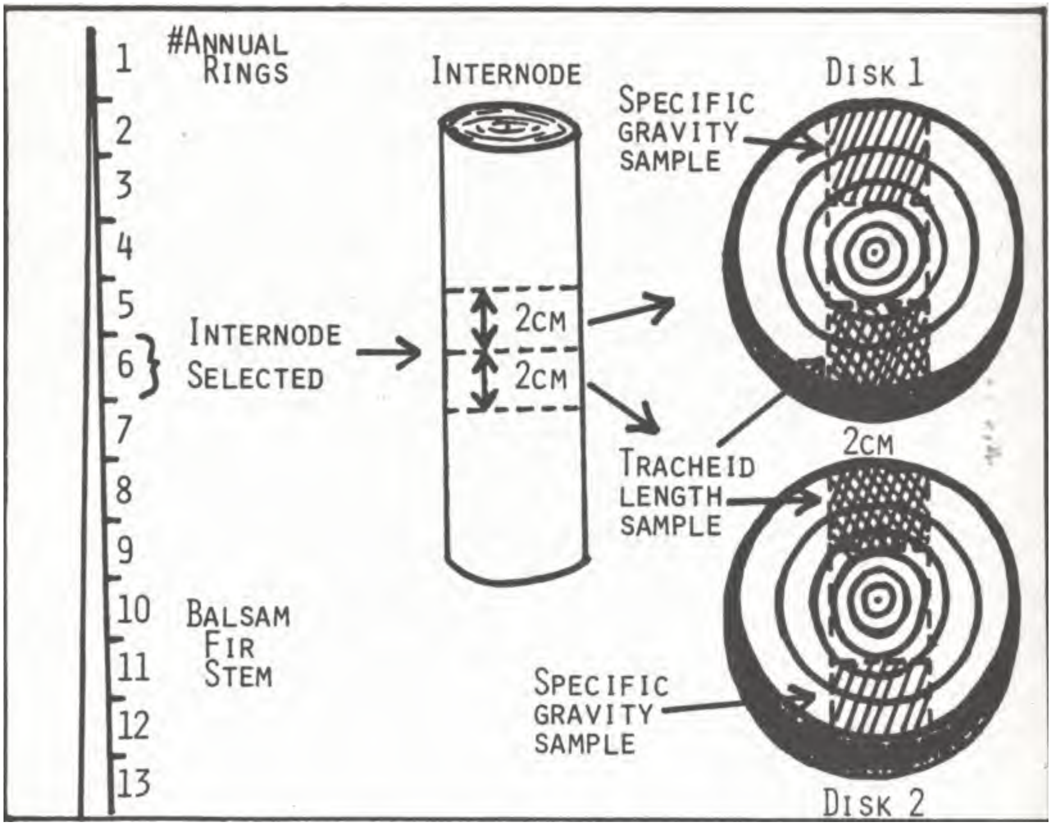

Figure 2. Balsam fir internode and cross-sectional samples from each of two disks used for specific gravity and tracheid length measurements.

wide cross section was then cut through the center of each disk. Portions of the cross-sectional samples containing the last three years' growth from both sides of each disk were used for wood property analyses. Two samples each, one from opposite sides of each disk, were used for specific gravity and tracheid length measurements.

Samples used for specific gravity determination were oven-dried, weighed and immersed in molten paraffin to prevent water absorption. Unextracted specific gravity was determined for each sample by the oven-dry weight, oven-dry volume method (Brown et al. 1952). Since there is evidence of a high correlation between unextracted and extracted specific gravity in the juvenile wood of conifers (Meier and Goggans 1977; Ledig et al. 1975), extractives were not removed.

Wood slivers, including both earlywood and latewood, were removed from the remaining two samples per tree and prepared for tracheid length measurements. Since provenances did not differ in the proportion of latewood to earlywood (Dery 1980), no bias was introduced by including both types of wood. The wood slivers from each of the two trees per provenance per block were bulked and macerated in Jeffreys' fluid. The tracheids were rinsed in distilled water and stained with basic fuchsin. Tracheids were mounted on slides by the liquid dispersion method described by Echols (1961). The mounted tracheids were projected with a bioscope and measured with Vernier calipers to the nearest .01 mm. The mean length of 50 tracheids per block for each provenance was used in data analysis. A total of 3,800 tracheids were measured.

Analysis of variance was used to assess the significance of provenance differences in each measured trait. Growth characteristics were analyzed using plot means as observations, whereas wood properties were analyzed using the mean of two trees per block from each of the 19 provenances as observations. Analyses of covariance were used to evaluate provenance differences in specific gravity and tracheid length after adjusting for height. Simple correlations, using provenance means as observations, were computed to assess relationships among traits and between traits and seed origin variables.

RESULTS AND DISCUSSION

Balsam Fir Wood Properties

The unextracted specific gravity of balsam fir wood from the 19 provenances averaged .428 on an oven-dry volume basis (Table 1). This figure is comparable to the value of .41 reported previously for balsam fir (U.S. Forest Products Laboratory, 1955). When converted to a green volume basis, the average unextracted specific gravity of balsam fir in our study was .38, which is somewhat higher than the values of .34 to .36 reported by others (Bendtsen 1974; Thor and Barnett 1972).

The average tracheid length of 13-year-old balsam fir from the 19 provenances was 1.92 (Table 1) which is considerably shorter than the 3.5 mm reported for mature balsam fir (U.S. Forest Products Laboratory 1953). The discrepancy can be attributed to the juvenile nature of the wood which consisted of an extremely high proportion of earlywood. The trees analyzed in our study had live crowns extending to the ground, which for balsam fir results in a high production of juvenile wood that is characterized by almost a complete absence of relatively long latewood tracheids (Heger 1974).

Table 1. Relative unextracted specific gravity, tracheid length, height and diameter of 13-year-old balsam fir representing 19 provenances growing in Vermont.

UVM No.	Origin	Relative: Specific gravity	Tracheid length	Height	Diameter
		- - - - - - - % of Plantation Mean - - - - - - -			
East & Central					
07	VT	95	110	119	130
87	QUE	96	109	105	112
66	MI	96	107	104	112
31	ONT	96	98	104	101
90	NY	97	107	107	114
60	WI	97	100	101	98
21	ONT	98	102	112	113
70	MI	98	95	106	104
25	ONT	99	104	109	109
64	MI	99	100	111	110
57	WI	100	102	104	105
Mean		97	103	107	110
West					
72	MAN	99	98	88	90
10	MAN	101	100	100	94
33	ONT	101	93	91	91
46	ONT	102	94	93	88
48	MN	102	96	86	79
49	MN	103	97	89	84
71	MAN	105	93	86	86
35	ONT	116	91	74	79
Mean		104	95	88	86
Actual mean		.428[a]	1.92 mm	283 cm	6.59 cm
Range in provenance means		.405[a] to .497	1.75 mm to 2.12 mm	210 cm to 338 cm	5.19 cm to 8.57 cm

[a] Ovendry Weight/Ovendry Volume method of determination.

Provenance Variation

Significant differences were found among balsam fir provenances in unextracted specific gravity, tracheid length, height and diameter. Trees from provenances 07 (Granville, VT) and 35 (Beardmore, ONT) represented the extremes in all four traits (Table 1). Trees grown from seed collected in Granville, VT were largest (338 cm tall; 8.57 cm in diameter), had the longest tracheids (2.12 mm) and the lowest specific gravity (.405), while those grown from seed collected in Beardmore, ONT were smallest (283 cm tall; 5.19 cm in diameter), had the shortest tracheids (1.92 um0 and the highest specific gravity (.497) (Table 1). Growth traits exhibited the greatest amount of genetic variation with a difference between extreme provenances of 45-50% in height and diameter. The extreme provenances differed by about 20% in tracheid length and specific gravity.

Relationship Among Traits

Provenance mean specific gravity and tracheid length were strongly correlated with each other and with provenance mean height and diameter (Table 2). In general, trees from fast growing provenances had lower specific gravities and longer tracheids than trees from slow growing provenances. Selection for rapid growth could be expected, therefore, to be accompanied by a favorable increase in tracheid length but a sacrifice in wood density. However, the reduction in yield due to lowered specific gravity may be countered by increased volume associated with rapid growth.

A similar relationship between wood properties and growth rate was reported by Echols (1958) and Dorn (1968) for Scotch pine (*Pinus sylvestris* L.) in New Hampshire and New York provenance test plantations. Matziris (1979) also reported a weak but significant negative correlation between specific gravity and diameter in radiata pine (*Pinus radiata* D. Don) but no relationship between specific gravity and height. Dinwoodie and Richardson (1961) found a positive relationship between height growth and tracheid length in Sitka spruce (*Picea sitchensis* (Bong.) Carr.) seedlings. Despite such correlations, there does not appear to be a consistent relationship between specific gravity, tracheid length and growth rate over all species. For instance, Lee (1973) found a strong positive correlation between specific gravity and height among provenances of eastern white pine (*Pinus strobus* L.), but found no provenance variation in tracheid length. Sohn and Goddard (1974) found no relationship between specific gravity and height or diameter among open pollinated families of slash pine (*Pinus elliottii* Engelm.). In a study of phenotypic variation in wood properties of loblolly pine (*Pinus taeda* L.), Zobel et al. (1960) found that growth rate accounted for less than 2% of the variation in specific gravity, but tracheid length was significantly correlated with growth rate in a negative fashion. Apparently, the relationship between specific gravity, tracheid

Table 2. Correlation coefficients (r), both unadjusted and adjusted ( ) for height, among measured traits and between traits and seed origin variables for 13-year-old balsam fir from 19 provenances.

	Specific gravity	Tracheid length	Height	Diameter
	- - - - - - - - - - - - - - - r - - - - - - - - - - - - - - -			
Tracheid length	-.70** (-.45)	---	---	---
Height	-.82** (-.64**)	.78** (.52*)	---	---
Diameter	-.73** (-.55*)	.86** (.66**)	.94**	---
Latitude	.46* (.33)	-.58** (-.45)	-.62**	-.65**
Longitude	.45 (.31)	-.69** (-.58**)	-.66**	-.77**
Elevation	-.06 (-.11)	.05 (.10)	-.07	-.03
Average Jan. ppt.	-.49* (-.39)	.68** (.61**)	.58**	.69**
Average Jan. temp.	-.44 (-.29)	.67** (.55*)	.67**	.70**

* P ≤ .05, 17 d.f.
** P ≤ .01, 17 d.f.

length and growth rate varies by species with no one particular pattern predominating.

The magnitude and distribution of provenance variation in balsam fir wood properties closely paralleled the pattern of variation in growth rate and may largely be a function of provenance differences in height and diameter. To examine this relationship more thoroughly, analyses of covariance were used to determine the significance of provenance differences in specific gravity and tracheid length adjusted for height. Provenance differences in both wood properties remained highly significant after adjustment, but some rank changes were noted between adjusted and unadjusted provenance means. Trees from provenances 07 and 35 remained below average in specific gravity and tracheid length respectively, but no longer represented the extreme low for these traits. After adjusting for height, trees from provenance 70 (Roscommon, MI) had the shortest tracheids and trees from provenance 31 (Mattice, ONT) had the lowest specific gravity. Although growth rate influenced the expression of balsam fir wood properties, it was not solely responsible for provenance differences in tracheid length and specific gravity.

The covariance adjustment had a greater influence on the relationship between specific gravity and tracheid length than on the magnitude of provenance variation. Provenance mean specific gravity and tracheid length were negatively correlated prior to adjustment, but were not significantly correlated after adjusting for height (Table 2). The correlation between the two wood properties apparently resulted from an indirect relationship with height.

Geographic Variation Pattern

Provenance mean tracheid length, height and diameter were strongly correlated with latitude, longitude, average January precipitation and average January temperature at the seed origin, while specific gravity was only weakly correlated with these seed origin variables (Table 2). In general, trees grown from seed collected in the relatively warm and moist eastern portion of the range were faster growing and had longer tracheids than those grown from seed collected in the relatively cool and dry western portion of the range. After adjusting for height, tracheid length was still significantly correlated with all the aforementioned seed origin variables except latitude, thus confirming an east-west pattern of variation independent of growth rate. Despite weak correlations between provenance mean specific gravity (both unadjusted and adjusted for height) and seed origin variables, an east-west regional pattern of variation is still evident (Table 1). Trees from provenances north and west of Lake Superior were generally above average in specific gravity, while those from the central Lake States and further east had relatively low wood densities. East-west patterns of provenance and phenotypic variation have been reported for other traits in balsam fir, including growth rate (Lester et al. 1976; Lowe et al. 1977), monoterpene concentrations (Lester 1974; Zaverin and Snajberk 1972), cone scale-bract ratio (Myers and Bormann 1963) and susceptibility to insect injury (DeHayes 1980).

The longitudinal variation pattern in balsam fir tracheid length suggests a direct or indirect adaptive response to environmental conditions encountered throughout its natural range. In several species, phenotypic or genetic variation in tracheid length has been associated with seed source temperature conditions and a tendency for increased tracheid length from relatively cold to warm climates is evident (Echols 1958; Dinwoodie and Richardson 1961; Ledig et al. 1975). A similar pattern of variation is apparent in balsam fir, but a direct adaptive relationship between temperature and tracheid length is not clear. Tracheid length is determined largely by the size of originating fusiform cambial cells with post-divisional tracheid elongation contributing only slightly. As a result, any factor affecting the size of the fusiform initials will indirectly influence the length of derived vascular elements. Barman (1967) has shown that the frequency of anticlinal (multiplicative) cell divisions influ ences the length as well as number of fusiform initials. He has further demonstrated that intraspecific as well as within tree variation in the rate of anticlinal division of fusiform cambial cells is inversely related to tracheid length. That is, trees with a rapid rate of anticlinal divisions generally have shorter tracheids than trees with a slow rate of division. Thus, it is possible that trees from cold climates compensate for a relatively short growing season by an increased rate of anticlinal divisions which concommitantly results in the development of shorter tracheids. If this hypothesis is correct, then provenance variation in tracheid length of balsam fir is an indirect result of natural selection for a rapid multiplication of fusiform cambial cells and rate of circumferential growth in areas with a short growing season.

CONCLUSION

Balsam fir provenances varied considerably in specific gravity, tracheid length and growth rate. Trees grown from seed collected in the eastern portion of the range, particularly those from eastern Ontario, Quebec, New York and New England, were fastest growing, had the longest tracheids, and appear well suited for pulpwood production in Vermont. The relatively low specific gravity of trees from these provenances is offset by their rapid growth and associated increase in volume. Trees from western provenances, although of high specific gravity, can be expected to produce less biomass because of their relatively slow growth rate.

Based on our results, selection of fast-growing provenances of balsam fir will result in the production of wood with relatively long tracheids and low density. However, considerable provenance variation existed in both wood properties independent of growth rate. In addition, after adjusting for the influence of growth rate, provenance mean specific gravity and tracheid length were, at best, only weakly related, suggesting that the two wood properties may be selected for independently. Therefore, it should be possible to breed balsam fir for increased growth rate, longer tracheids, and higher density. Increased dry matter production and a better quality of wood fiber should result from a carefully designed breeding program.

The data in this study was obtained from relatively young trees at one provenance test site in Vermont, and the results must be interpreted accordingly. Despite limitations, these results may provide a starting point in balsam fir wood quality improvement by identifying superior provenances for future selection and breeding programs in Vermont.

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