INFLUENCE OF SPECIFIC GRAVITY AND GROWTH RATE ON DRY WOOD PRODUCTION IN PLANTATION-GROWN WHITE SPRUCE

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ABSTRACT

Two hundred and thirty-two white spruce trees were sampled from 29 plots in 6 localities in southern Ontario. Specific gravities of discs cut at four-foot intervals were determined for each tree. The amount of dry wood substance contained in each tree was obtained by multiplying weighted, whole tree specific gravity by tree volume. Although specific gravity was negatively correlated with growth rate, this reduction in dry weight per unit volume was minor in relation to the increased volumes associated with rapid growth rates.

The equation using the regression of the logarithm of dry wood production on tree age was determined. Trees having dry wood production of more than 1.5 times the standard error of estimate indicated by the regression lines were selected as superior trees. The characteristics of these superior trees together with the environments in which they grew were examined. The absence of any relationship with environmental factors suggested a genetic cause of above-average wood production. Superiority of a tree was mainly due to fast radial growth rate. The prospect of designing a tree breeding program to improve rate of dry wood production is discussed.

INTRODUCTION

Specific gravity variation of wood has been studied extensively in the past hundred years. Although no universally accepted conclusion has been reached on the question of what factors may influence wood specific gravity and to what extent each factor may affect it, investigators generally agree that for spruces, growth rate is important in controlling wood density. Fast growth rate is usually associated with low wood specific gravity in spruce (Hale and Fensom, 1931; Hale and Prince, 1940; Aldridge and Hudson, 1958; Hall, 1961; Keith, 1961; Hale, 1962; Bernhart, 1964).

This fact is somewhat discouraging because the beneficial effect of fast growth rate on the volumetric growth of trees may be offset by a reduction in density of wood. Therefore, the overall effect of growth rate on the rate of wood substance production becomes uncertain. Since increasing the rate of wood production should be one of the main goals of tree breeding programs, it becomes important to investigate how rate of wood substance production varies from tree to tree and how it is related to growth rate. The present study is an effort to clarify the above questions.

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MATERIALS AND METHODS

Field Procedures

Samples for his study were supplied in 1964 by Professor D. V. Love of the Faculty of Forestry, University of Toronto. White spruce (*Picea glauca* (Moench.) Voss) trees were sampled from 29 plots in 6 localities throughout plantations in southern Ontario. A total of 232 trees ranging in age from 17 to 41 years was thereby obtained.

Diameter at breast height of every tree within a plot had previously been measured and arranged in a frequency distribution table with a class interval of two inches. One white spruce tree was then selected randomly from each class. For the class of highest frequency, one additional tree was taken. These trees were subsequently felled to a stump height of approximately six inches, and total tree heights were recorded. Sample discs one to two inches thick were removed from the base upwards at four-foot intervals. A total of 1758 discs were thus made available for laboratory study.

Office and Laboratory Procedure

The growth rate for each disc was calculated in terms of number of rings per inch from data for age and average radius supplied by Prof. Love.

Information concerning two environmental factors, stand density and soil moisture regime (Hills, 1952), was obtained for each sample plot. Stand density was expressed as total basal area per acre. Soil moisture regime of the sampling plots was determined by Mr. J. R. M. Williams.¹ Moisture regime varied from grade 0 to 6 with grade 2 equivalent to "fresh" grade² in the universal scale.

From each sample disc, a defect-free sector with an included angle of 45° from the average growth zone was selected. The water immersion method described by Brown *et al.* was used for green-volume determination. Specimens were then oven dried at 103° ± 2° C. until continued loss of weight was negligible as indicated by repeated weighings. Specific gravities of specimens were then calculated.

Because of the commonly occurring character of great taper in white spruce and also because of the wide variation in growth rate and tree height in the sample trees, a simple average of the sample specific gravities at different height in the tree could not give an accurate estimation of the whole tree specific gravity. Therefore, a weighted-average method (Pronin, 1966) was used to estimate whole-tree specific gravity of the entire tree. A Fortran IV computer program was written to calculate the estimated tree volume without bark as well as the weighted-average, whole tree specific gravity. The program then proceeded to calculate the oven-dry weight of wood for each tree by multiplying its specific gravity by its tree volume.

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² Condition where sufficient moisture is available for optimum growth of mesophytic vegetation without surplus.

RESULTS

Table 1 summarizes the characteristics of the trees sampled. They had an average age of 30 years, and were fairly fast grown (9 rings per inch). The average whole-tree specific gravity was 5 per cent lower than the published figure for Canadian white spruce (Kennedy, 1965) and 6 per cent lower than the average whole-tree specific gravity of white spruce obtained by Wahlgren *et al.* (1966) in Maine.

The coefficient of variation for both diameter and growth rate at breast height was more than 30 per cent and for tree height more than 25 per cent. This large variation reflects the fact that sample trees were selected from the complete range of diameter classes available in each sampling plot.

TABLE 1
CHARACTERISTICS OF SAMPLE TREES

	Age at stump	D.B.H.	Growth rate (breast height)	Tree height	Sp. gr. (vol. green)
Mean	29.8 yrs.	7.05 in.	9.01 rings/in.	34.9 ft.	0.335
Maximum	41	11.10	3.90	57.5	0.422
Minimum	17	1.70	23.30	18.5	0.270
Standard Deviation	4.70	2.40	3.34	9.03	0.027
Coefficient of Variation (%)	15.8	33.8	35.9	25.9	8.0

Growth Rate - Specific Gravity Relationship

The following linear regression equation between specific gravity (Y) and growth rate in rings per inch (X) was calculated for 1758 discs:

$$Y = 0.29050 + 0.00532 X$$

$$S_{y.x} = 0.0225$$

$$r = 0.5766 **$$

From the highly significant correlation coefficient obtained, it is apparent that specific gravity of these discs decreased as ring width increased. Inclusion of height above ground (as a proportion of total tree height) in a two-factor regression with growth rate resulted in a correlation coefficient of 0.6278. This expression of proportional height was more effective than either height above ground or distance from apex in increasing the degree of correlation with specific gravity (Chang, 1966).

Age - Dry Wood Production Relationship

According to Snedecor (1956), the regression equation associated with growth phenomena is mostly of the form

$$W = A B^x$$

where W is the weight of the subject and x its age. Since logarithm of weight is linearly related with age of the growing subject, data of the oven-dry weight of sample trees were transformed into logarithmic values (base 10). The regression equation of logarithm of wood production on tree age was then calculated.

In elucidating the relationship between wood production and tree age, suppressed trees were not considered. This is because they neither represent the typical wood production for trees of a given age nor should they be selected for the purpose of tree breeding. In this study, trees with either heights or diameters at breast height less than two standard deviations from the average of sample trees were excluded arbitrarily as suppressed.

From visual observation of the scatter diagram of log. dry weights vs. age class (Fig. 1), a trend of linear relationship could be seen from trees 20 to 39 years old. The six trees younger than 20 years or older than 39 years were not in the range of the linear relationship, and were thus deleted from consideration.

FIGURE 1. Regression of log. oven-dry wood production on tree age.

Analysis of variance showed significant differences in log. dry wood production between different ages classes, and a test of linearity showed that the log. function was linearly related with tree age, while deviation from linearity was not significant (Table 2). The regression line

$$\text{Log. } Y = 0.93809 + 0.02910 X$$

represents the best fit for the data. This calculated regression line and the lines of 1.5 standard errors of estimate above and below it are included in Fig 1.

TABLE 2

TEST OF LINEARITY BETWEEN LOG. DRY WOOD PRODUCTION AND AGE CLASSES
Analysis of variance

	D.F.	SS	MS	F
Total	201	19.75392		
Age	19	5.45072	0.28689	43.65**
linearity	1	3.79183	3.79183	48.25**
Dev. from linearity	18	1.65889	0.09216	1.17 ^{n.s.}
Error	182	14.30320	0.07859	

Characteristics of Superior and Inferior Trees

Nine trees had a dry weight production more than 1.5 standard errors of estimate above the average and hence could be considered as superior trees. The characteristics of these trees and their environments are summarized in Table 3.

From Table 3 it is evident that the 9 superior trees were from 8 sample plots and 5 sampling areas. Sampling area 4 was the only area where no superior tree was found. The superior trees occurred in plots having soil moisture regime values 1, 2, 4, and 5. Stand density ranged from 172 to 238 square feet per acre, which can be considered as medium to dense.

It is evident that the superior trees were invariably taller than the average sample tree in the same plot. Growth rate at breast height was considerably faster than the average growth rate of 9 rings per inch, and specific gravities were lower than the average of 0.335 without exception (compare with Table 1).

For comparison and contrast, the environments and tree characteristics of the 15 trees which were further than 1.5 standard errors of estimate below the regression lines are summarized in Table 4. These inferior trees were found in all sampling areas except area 3, and were distributed among 13 different sampling plots. Stand densities of these plots ranged from 122 to 185 square feet per acre. All classes of soil moisture regime were found in these plots. Tree height, radial growth rate and specific gravity all tended to be opposite those of the superior trees.

DISCUSSION

Since phenotypic characters provide the basis for selection in tree breeding programs, the common features of superior trees are of interest. From Table 3, the most striking feature common to the superior trees was their extremely fast growth rate both in diameter and height. The average radial growth rate at breast height in the superior trees was 5.5 rings per inch, i.e., their ring widths were 64 per cent wider than the average trees. Because dry wood production is

TABLE 3
CHARACTERISTICS OF THE NINE SUPERIOR TREES AND THEIR ENVIRONMENTS

Sampling area	Plot No.	Soil moisture regime	Stand density (ft. ² /acre)	Average tree height in the plot (ft.)	Superior tree height (ft.)	Age at stump (yrs.)	Growth rate (rings/in.)	Sp. gr. (green vol.)
1	10	4	174.0	30.7	52.5	20	3.9	.292
2	14	2	177.8	39.5	53.5	34	5.4	.318
2	16	1 +	195.7	37.8	45.5	33	6.0	.320
2	17	1	206.1	40.1	48.6	33	5.3	.292
3	18	4	210.9	44.3	51.5	38	6.0	.325
3	19	2	238.3	50.7	57.5	37	6.2	.309
5	24	4	172.2	34.4	43.5	27	4.9	.333
6	29	5	173.3	45.4	53.5	32	6.0	.298
6	29	5	173.3	45.4	51.5	33	5.4	.301
Average			191.3	40.9	50.8	31.9	5.5	.310

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TABLE 4
CHARACTERISTICS OF THE FIFTEEN INFERIOR TREES AND THEIR ENVIRONMENTS

Sampling area	Plot No.	Soil moisture regime	Stand density (ft. ² /acre)	Average tree height in the plot (ft.)	Superior tree height (ft.)	Age at stump (yrs.)	Growth rate (rings/in.)	Sp. gr. (green vol.)
1	3	1+	176.5	42.3	32.5	32	14.8	.389
1	5	4	158.7	31.4	29.5	27	10.1	.329
1	5	4	158.7	31.4	26.5	25	9.7	.319
1	6	5	165.5	36.6	27.5	30	12.0	.373
1	10	4	174.0	30.7	24.5	21	7.7	.308
2	13	0	124.0	27.3	27.5	34	13.7	.377
2	14	2	177.8	39.5	32.5	36	13.2	.385
4	21	1	142.4	32.8	19.5	34	13.0	.337
4	22	3	165.7	31.6	24.5	29	11.5	.368
4	22	3	165.7	31.6	26.5	28	11.4	.386
5	23	4	185.0	26.6	21.5	29	12.0	.363
5	25	5	170.7	36.5	21.5	27	12.3	.370
5	26	6	121.6	29.8	22.5	31	11.6	.365
5	27	6	149.6	31.5	24.5	35	13.9	.368
6	30	2	185.4	42.9	39.5	36	11.2	.312
Average			161.4	33.5	26.7	30.3	11.9	.358

proportional to the radius squared, productivity would be increased by 2.7 times due to this increase in radial growth rate, if specific gravity and tree height were held constant and ring width increased at the same magnitude at all heights. The average tree height of superior trees was 23.6 per cent higher than the average tree of equivalent age classes. Since dry wood production is directly proportional to tree height, the improved productivity of these trees due to increase in height is also 23.6 per cent. Compared with the influence of radial growth rate, however, the effect of faster height growth is only minor.

The faster radial growth rate caused a decrease in density. However, the reduction in specific gravity in the superior trees was only 7.5 per cent compared with the average tree specific gravity. The adverse effect due to increased growth obviously is almost negligible compared with the beneficial effect of faster growth rate. It seems clear that the best management policy should be to increase the tree growth rate and disregard the minor reduction in density, if amount of dry wood production is chosen as the only criterion in considering the superiority of trees.

How much benefit could accrue from an intensified tree-breeding program if tree growth rate were used as a criterion for selection of seed orchard stock? This question cannot be answered with any certainty because the heritability of growth rate in white spruce is not known. However, based on a literature review of coniferous species, Campbell (1964) assigned a narrow-sense heritability of 20 per cent to breast-height diameter growth in order to estimate genetic gain to be obtained following one generation of selection in Douglas-fir. Campbell considered his heritability estimates to be conservative in comparison with reported values.

The following estimation of genetic gain based on reasonable assumptions might be a useful argument for future tree-breeding programs in white spruce. For this example, 33 year old trees were selected because this age class had more superior trees than any other. In this age class, the estimated total dry wood production for the average tree is 79 lb. (Fig. 1). Genetic gain through breeding of superior trees can be determined from the equation:

$$\text{Genetic gain} = \text{narrow sense heritability} \times (\text{mean of selection} - \text{mean of population})$$

Assuming a narrow-sense heritability for growth rate of 0.2, the genetic gain becomes

$$0.2 \times (237.11 - 79.14) = 31.59 \text{ lb.}$$

Compared with the estimated production in the average tree of 79 lb., the genetic gain value is strikingly high. An intensive tree-breeding program using fast radial growth rate as a criterion of selection might therefore be highly promising.

Finally, from Table 3, it is found that the superior tree on plot 24 had a growth rate at breast height of 4.9 rings per inch, which is 1.85 times faster than the average tree, yet its whole-tree specific gravity was 0.333. Although the specific gravity of this tree was still slightly lower than the average of 0.335, the superiority of this tree becomes outstanding when its extremely fast growth rate is considered. This tree not only produced a high volume of wood, but the quality of this wood did not suffer. Although only one such tree was found out of 232 examined, the fact that it is possible to find trees with both fast growth

rate and average density is still encouraging to those attempting to breed superior white spruce trees.

CONCLUSIONS

1. Number of rings per inch is positively correlated with specific gravity. However, dry wood substance production per unit of time increases with increasing growth rate, in spite of reduction in density.
2. No evidence could be found that any gross environmental factor was related to the occurrence of trees producing a superior amount of dry wood. It is therefore probable that inherent genetic factors are important.
3. Superior trees selected according to the linear regression line of log. dry wood production vs. tree age all had faster radial growth rate at breast height and higher tree height, but lower specific gravity when compared with the overall means of trees.
4. Radial growth rate is the most important factor affecting the amount of dry wood production per tree. Reduction in density due to increase in growth rate is negligible compared with the increase in tree volume.
5. It is possible to find trees with ring width 85 per cent wider than the average but still of average density. Extensive field surveys to locate such high-quality trees and breeding programs to propagate them would be of benefit in future forest management.

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