GENETIC VARIATION IN STEM GROWTH COMPONENTS IN WHITE SPRUCE SEEDLINGS AND ITS IMPLICATIONS TO RETROSPECTIVE EARLY SELECTION[1]

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ABSTRACT

We performed statistical and genetic analysis on stem growth components of white spruce greenhouse-grown seedlings to determine: (1) heritability of the second season branch increment (*BI*), the number of stem units (*NSU*) and mean stem unit length (*MSUL*), (2) the relative degree of determination of *BI* by *NSU* and *MSUL*, (3), the potential of *BI*, *NSU* and *MSUL* as early selection indicators for 11-year height. For data in original units, individual-tree heritability (h_i^2) for *NSU* and *MSUL* was 0.232 ± 0.097 and 0.264 ± 0.101, respectively. The Corresponding values for heritability of family means (h_f^2) were 0.457 ± 0.101 and 0.492 ± 0.106. Similar estimates were found with transformed data. Path coefficient analysis showed that *BI* was 58.29 % determined by *NSU* and 41.71 % by *MSUL*. We found that selection for *MSUL* in the greenhouse would yield 47.4 % and 85.1 % of genetic gain expected from direct selection for 11-year height at site A and B, respectively. The corresponding values due to selection for *NSU* were 19.1 % and -29.0 %. From this work, the following conclusions can be made: (1) variations in *NSU* and *MSUL* are equally but independently inherited, (2) although *NSU* contributed more to *BI* than *MSUL* did, both stem components are important if annual height growth is to be maximised, (3) for prediction of advanced-age field height, *MSUL* is a better indicator than *NSU*.

Keywords: genetic variance, genetic correlation, heritability, stem units, stem unit length, early selection, white spruce, *Picea glauca*

INTRODUCTION

Stem height growth is an important component of volume production and is often used in evaluation of yield potential of genotypes in forest trees (ZOBEL & TALBERT 1984; KREMER, 1992; DANJON 1994; KREMER & LASCOUX 1988). Height, however, is a composite trait composed of different growth components whose variation may be under different degrees of inheritance. Dissecting and studying the genetics of height growth components should lead to a better understanding of the genetics of height growth and simplify selection in tree breeding. Conifers play a dominant role in industrial forestry both in temperate and tropical areas. Therefore, understanding the *BI*ology and efficient selection techniques for conifers would aid success of industrial forestry.

The pattern of shoot development in the genus *Pinus* that may also be related to shoot development in other conifers was described in detail by LANNER (1976). Irrespective of the model of shoot growth (free or fixed), height growth in conifers takes place as annual increments that accrue in spring and summer. These annual height increments result from extension of stem units (needle primordia) that were deposited in the previous growing season (DOAK 1935; CANNELL 1974; CANNELL & WILLETT 1975). The number of stem units (*NSU*) correspond to the number of needles on a given stem segment normally representing an annual growth increment. Since the length between needles cannot be easily measured, the stem unit length (SUL) is normally expressed as the mean stem unit length (*MSUL*), which is the ratio of the annual increment and the number of needles (*NSU*) on it (BONGARTEN 1986).

Studies have shown that populations and families-within-populations vary considerably with respect to

NSU and *MSUL* (KREMER & LARSON 1983; BONGARTEN 1986; BRIDGWATER 1990; LI *et al.* 1991, 1992; JONSSON *et al.* 2000). The relative importance of *NSU* and *MSUL* in determining the annual height growth increment has been a subject of investigation and the results vary with species, genetic grouping (provenance or family) and test conditions. For example, in jack pine (*Pinus banksiana* Lamb.), KREMER & LARSON (1983) found that the annual height increment was more correlated to *NSU* than *MSUL* at the population level and *MSUL* than *NSU* at the family-within-population level. In Douglas-fir (*Pseudotsuga menziesii* var *glauca* (Beissn.) Franco.) populations, *NSU* and *MSUL* were approximately equally correlated with shoot growth increment, though the results differed when northern and southern populations were considered separately (BONGARTEN 1986). In blue spruce (*Picea pungens* Englm.), BONGARTEN (1986) found that, shoot growth increment was more correlated with *NSU* than *MSUL* at the population level and *MSUL* than *NSU* at the family-within-population level.

Stem growth component (*NSU* and *MSUL*) analysis is well documented in *Pinus* species from which the concept was introduced by DOAK (1935). However, the same concept applies to other conifers such as spruces and Douglas-fir (BONGARTEN 1986; CANNELL & WILLETT 1975). Genetic analysis of stem growth components and their relationship to height growth would facilitate the understanding of how superior height growth is achieved and thus aid early selection for height in slow growing species such as white spruce (STIELL 1976; SCOGGAN 1978).

In this article, we present results of stem growth component analysis from a retrospective greenhouse study involving 53 open-pollinated families of white spruce from Peace River, Alberta, Canada. Our objective was to establish the degree of genetic control of the variation in *NSU* and *MSUL* and their relationship with annual shoot growth on primary branches and the main stem. We also attempted to establish the relationship between growth components assessed on seedlings in the greenhouse environment with 11-year height on two field sites in Alberta. The potential of these growth components as early selection indicators is discussed in terms of selection efficiencies.

MATERIALS AND METHODS

Description of the Test Material

Seeds for 69 families were collected in the period between 1979 and 1983 by Alberta Lands and Forest Service and its co-operators. Collection was limited to

tall trees with straight bole, right-angled branches and free from disease or insect damages. The sampled region lies within the Peace River Basin, northwestern Alberta, Canada (54°31'–58°03' N, 117°35'–119°22' W, 365–945 metres above the sea level). All families originated from open-pollinated seeds collected without population structure.

Field and Greenhouse Tests

In 1988, Alberta Lands and Forest Service in co-operation with Weyerhaeuser Canada Ltd., established two field trials described as follows: (1) Chinchaga River Forest located at 57°50' N, 118°12' W and 470 metre above sea level. It was originally a dense aspen stand with 80 % well-drained soil and 20 % poorly drained pockets, with soil pH between 6.5 and 7.5. In this article, this site is designated site A. Saddle Hill Forest located at 55°31' N, 119°40' W and 914 metre above sea level. It was originally a mixture of spruce, pine and aspen stand, with a mixture of loam, silt and clay soil that is better drained than site A. In this article, this site is designated site B. The experimental design on both sites was a randomised complete block with 69 families, 6 replications and 6-tree row plots with 2.5 m × 2.5 m spacing. At the age of 11-years from seeds (8 years in the field), total height was assessed on both sites.

A retrospective greenhouse test was established at the University of Alberta in Edmonton in May 1996 using 58 of the 69 families from the original collection. The growth medium was a 2:1 peat to vermiculite mixture with 5.0 g·litre⁻¹ of lime added to bring the pH to about 5.0. Seed germination and seedling growth were conducted in 700 millimetre-cavity styroblocks. Prior to sowing, seeds were cold stratified at 2 °C for 21 days. The design of the experiment was a randomised complete block with single-tree plots, replicated 30 times. With this design, each seedling in the block represented a different family. Families were randomly assigned in each of the 30 blocks.

Seedlings were raised at an extended photoperiod of approximately 20 hours per day, from a combination of natural and artificial light. The temperature was set at 23 °C day and night, except during the hardening period when the temperature was reduced by 2 °C every week to bring about complete rest before the seedlings could be taken outside the greenhouse for over-wintering. These temperature reductions did not go below 14 °C. Temperature of 14 °C is not expected to hinder needle initiation, since needle initiation in white spruce has been found to continue into October when temperatures are much lower that 14 °C (POL-

LARD 1973). Seedlings were watered once every two days and fertilised once a week. Following budset at the end of the first growing season (August 1996), seedlings were take out of the greenhouse and kept in protected boxes for overwintering. Continuous snow cover was maintained on the seedlings to protect them from desiccation by wind. In the first week of May 1997, seedlings were returned to the greenhouse to start the second growing season that ended at the end of August of the same year.

Stem growth components covered in this article were assessed at the end of the second season (August 1997) as described below. The two longest branches were selected for all seedlings whose growth during the second season was considered adequate in that it reflected the general performance of the experiment. Only those seedlings with health branches that retained all needles in the second season segment were included in the study. Needles were plucked from the second season segment of the selected branches and counted to obtain the number of stem units (*NSU*). Then the length of the segment from which *NSU* was assessed was measured to obtain segment length, here called branch increment (*BI*). *BI* and *NSU* were then used to derive the mean stem unit length as *MSUL* = SL ÷ *NSU*.

Statistical and Genetic Analysis

A family was included in the analysis only if it was represented by at least five seedlings. Thus, only 53 of the 58 families that were planted in the progeny test were involved in the analysis of stem growth components. The data corrected from the greenhouse seedlings were used to perform two types of analysis as follows: (1) data were first analysed in original units to provide statistical tests and estimate heritability and correlation coefficients, and (2) data were then analysed in logarithmic standard units to provide statistical tests, estimate of heritability and correlation coefficients, and perform path coefficient analysis to determine the relative contribution of *NSU* and *MSUL* to *BI*.

It is understood that seedling size may influence the number of needle primordia formed in the winter bud, especially in the early weeks of seedling development (POLLARD 1974a). In other words, large seedlings may produce large number of stem units (*NSU*) just because they are large. The opposite may be the case for small seedlings. Thus, to control the effects of seedling size on the variation in *NSU*, the 18-week seedling height (H18), which is the total height of the seedling at the end of the first growing season was entered in the analysis as a covariate. The analysis of covariance used the general linear model procedure (PROC GLM) in the

SAS software (SAS INST. 1994) to fit the following statistical equation:

$$Y_{i,j} = \mu + R_i + F_j + E_{ij} + X_{ij} \qquad [1]$$

where, Y_{ij} = measurement of *BI*, *NSU* or *MSUL* for family *i* in replication *j*, μ = general mean; R_i, F_j and E_{ij} are respectively, effect due to replication *i*, family *j* and residual of family *i* in replication *j*. X_{ij} is a covariate, which is H18 for family *i* in replication *j*. All effects in the model were considered random, additive and independently normally distributed with zero expectations and respective variances.

The mean squares from equation 1 were equated to expected mean squares and used to estimate variance components that were then used to calculate individual-tree heritability (h_i^2) and heritability of family means (h_f^2) as follows:

$$h_i^2 = \frac{3 * \sigma_f^2}{\sigma_e^2 + \sigma_f^2} \quad \text{and} \quad h_f^2 = \frac{\sigma_f^2}{\frac{\sigma_e^2}{k} + \sigma_f^2} \qquad [2]$$

where σ_e^2 and σ_f^2 are residual and family variance components, respectively, and k is a coefficient representing the average number of seedlings per family. Although predominantly out-crossing, white spruce exhibits a considerable amount of inbreeding. Survival and growth vigour of seedlings from inbred seeds is the same as that of out-crossed ones until many weeks after germination when inbreeding depression takes effect (FOWLER & PARK 1983; PARK *et al*. 1984). As a result, seedlings from open-pollinated seed contain a mixture of half- and full-sib families. Thus, to prevent overestimation of heritability, the family variance was multiplied by 3 instead 4 to obtain the additive genetic variance needed to calculate heritability. The standard error of h_i^2 and h_f^2 was, respectively, calculated as described by BECKER (1975) and WRIGHT (1976).

The genetic, phenotypic and environmental correlation coefficients were calculated by substituting the appropriate covariance and variances into the following general formula:

$$r_{xy} = \frac{\sigma_{xy}}{\sigma_x * \sigma_y}$$

where r_{xy} = genetic, phenotypic or environmental correlation, σ_{xy} = genetic, phenotypic, or environmental covariance, σ_x and σ_y = genetic, phenotypic, or environmental standard deviations for the two traits. The standard error for the genetic correlation was calculated as described by ROBERTSON (1959).

In addition to the correlation coefficients between

stem growth components, we performed path coefficient analysis to estimate the relative degree of determination of *BI* by *NSU* and *MSUL*. To do this, we followed the method described in details by KREMER & LARSON (1983) and BONGARTEN (1986). A brief outline of this method is provided below:

The relationship between *BI*, *NSU* and *MSUL* is such that *BI* = *NSU* × *MSUL*. In logarithmic scale, this can be represented as log(*BI*) = log (*NSU*) + log (*MSUL*). If a correlation exist between *NSU* and *MSUL*, the following relationship applies:

$$Var(\log(BI)) = Var(\log(NSU)) + Var(\log(MSUL)) + 2*cov(\log(NSU),\log(MSUL))$$

If we replace *BI*, *NSU* and *MSUL* by x, y and z, respectively, and use Greek script for the variance, the above expression becomes:

$$\sigma_x^2 = \sigma_y^2 + \sigma_z^2 + 2*cov(y,z) \qquad [4]$$

Since $r_{yz} = \dfrac{cov(y,z)}{\sigma_y \sigma_z}$ then $Cov(y,z) = \sigma_y \sigma_z r_{yz}$

Therefore, equation [4] is equivalent to equation [5]:

$$\sigma_x^2 = \sigma_y^2 + \sigma_z^2 + 2*\sigma_x \sigma_z r_{yz} \qquad [5]$$

where r_{yz} is the correlation between *NSU* and *MSUL*. Dividing each component of equation 5 by the total variance (σ_x^2), i.e., the variance of *BI*, we obtain equation [6]:

$$p_x^2 = p_y^2 + p_z^2 + 2*p_x p_z r_{yz} \qquad [6]$$

where p_x, is the path coefficient for log (*BI*) to itself (thus $p_x = 1$), p_y and p_z are, respectively, path coefficients for log (*NSU*) and log (*MSUL*) to log (*BI*). When *BI*, *NSU* and *MSUL* are standardised, the relative contributions of *NSU* and *MSUL* to *BI* are, respectively, calculated as follows:

$$c_y = p_y r_{xy} \quad \text{and} \quad c_z = p_z r_{xz} \qquad [7]$$

where c_y and c_z are, respectively, the relative degree of determination of *BI* by *NSU* and *MSUL*, r_{xy} and r_{xz} are respectively, correlation between *BI* and *NSU*, and *BI* and *MSUL*, and $cy + cz = 1$.

Prior to performing the analyses of covariance, the data for *BI*, *NSU* and *MSUL* were standardised by dividing each trait by its mean. This makes it possible for the variances to be compared when computing the path coefficients, since by this standardisation each trait has a mean of 1 (BONGARTEN 1986). It also facilitates

the estimation of the degree of determination of *BI* by *NSU* and *MSUL* (KREMER & LARSON 1983). To ensure that standardisation did not affect the amount of variation and as a result the values of the genetic parameters that existed for the data in the original units, the variance components, heritability and correlation coefficients were calculated for both data in original units and standardised data. Results from both analyses appear in this article for comparison.

The statistical and genetic analyses and results of 11-year height on two field trials that were used in this study for evaluating the genetic worthiness of *BI*, *NSU* and *MSUL* as early selection indicators were submitted for publication in a separate article by RWEYONGEZA *et al.* (in press). Thus, those results do not appear in this article; only the genetic correlation between *BI*, *NSU* and *MSUL* with 11-year height on field site A and B, and the resulting efficiencies of indirect selection are presented.

Prior to calculating the genetic correlation between greenhouse-assessed stem growth components and 11-year height in the field, data for all traits were converted to standard units as described by ROBERTSON (1959). The general linear model procedure (SAS Inst. 1994) was employed to fit the following statistical equation to the data and extract the mean squares:

$$Y_{ijn} = \mu + S_i + F_j + SF_{ij} + E_{ij(n)} \qquad [8]$$

where, Y_{ijn} = observation on tree n in j family on site i (site = field or greenhouse), μ = general mean, S_i = effect due to test site (field or greenhouse), F_j = effect due to family, SF_{ij} = site × family interaction, and $E_{ij(n)}$ = error. The genetic correlation (r_A) between greenhouse and field traits was estimated from the mean squares generated by equation 8 as described by ROBERTSON (1959) in the following expression:

$$r_A = \frac{ms_f - ms_{sf}}{ms_f + ms_{sf} - 2*ms_e} \qquad [9]$$

where, *ms* stands for mean squares and subscripts f, sf and e denote family, site × family interaction and error, respectively. The standard error for this correlation was calculated as described by ROBERTSON (1959).

Selection efficiency was a measure used to determine the percentage of the genetic gain in 11-year height that could be expected from selection on *BI*, *NSU* and *MSUL* in a greenhouse retrospective test. Selection efficiencies were computed as the ratio of gain from indirect selection (correlated gain) to gain from direct selection assuming that the same selection intensity would be applied for both greenhouse and field traits (FALCONER 1981; LAMBETH 1980) as

follows:

$$E(\%) = \frac{CG_f}{\Delta G_f} * 100 = \frac{h_g h_f \sigma_{pf} r_A}{h_f^2 \sigma_{pf}} * 100$$

where $E(\%)$ = selection efficiency in percentage, CG_f = correlated gain in field height, ΔG_f = gain from direct selection on field height, and h_g and h_f = square roots of the heritability for the greenhouse trait and field height, respectively, σ_{pf} = phenotypic standard deviation for field height, and r_A = genetic correlation between greenhouse trait and field height.

RESULTS

Descriptive statistics, percentages of variance components and heritability values for stem growth components estimated from data in original and logarithmic

standard units appears in Table 1. Statistically, there was highly significant variation among families for BI, NSU and $MSUL$. This variation among families was almost the same for BI, NSU and $MSUL$. Table 1 shows that irrespective of whether data were transformed or not, variation among families accounted for 7.18 - 8.89 % of the total variance. Individual-tree heritability (h_i^2) values were 0.222 ± 0.095 – 0.283 ± 0.097. Values of heritability for family means (h_f^2) were 0.445 ± 0.100 – 0.511 ± 0.109. Generally, Table 1 shows that heritabilities for $MSUL$ were slightly higher than those of NSU.

Table 2 presents the correlation coefficients between pairs of stem growth components (BI, NSU and $MSUL$) and the correlations between stem growth components with the second season height growth increment on the main stem (HI). The genetic, phenotypic and environmental correlations between NSU and BI were higher than the corresponding values between $MSUL$ and BI. The general picture, one can see (Table

Table 1. Least square means, percentages of variance components and heritability of stem growth components computed from data in original units (above) and standard units (below).

Trait	Mean	Range of family means	σ_e^2	σ_r^2	σ_f^2	h_i^2	h_f^2
BI	75.2±1.3	48.3–96.0	90.04	2.78*	7.18***	0.222±0.095	0.445±0.100
NSU	234±3	194–279	90.69	1.72	7.59***	0.232±0.097	0.457±0.101
$MSUL$	0.32±0.0	0.26–0.36	86.00	5.70***	8.30***	0.264±0.101	0.492±0.106
BI			88.68	3.32*	8.00***	0.248±0.099	0.476±0.104
NSU			90.36	1.69	7.95***	0.243±0.098	0.469±0.103
$MSUL$			84.44	6.67***	8.89***	0.283±0.097	0.511±0.109

BI – branch increment (mm); NSU – number of stem units; $MSUL$ – mean stem unit length (mm); σ_e^2, σ_r^2 and σ_f^2 – error, replication and family variance component respectively; h_i^2 and h_f^2 – individual tree and family mean heritability, respectively. * – P < 0.05; *** – P < 0.001.

Table 2. Correlation coefficients for stem growth components measured on branches and second season height increment of the seedling main stem for data in original units (above) and data in logarithmic standard units (below).

Trait	Mean	Data in original units			Data in logarithmic standard unit		
		r_A	r_P	r_e	r_A	r_P	r_e
BI	NSU	0.745±0.133	0.796	0.800	0.762±0.119	0.805	0.809
BI	$MSUL$	0.693±0.149	0.632	0.628	0.683±0.144	0.638	0.632
NSU	$MSUL$	0.002±0.283	0.061	0.063	0.047±0.272	0.063	0.064
BI	HI	0.567±0.217	0.467	0.458			
NSU	HI	0.521±0.245	0.416	0.407			
$MSUL$	HI	0.274±0.251	0.261	0.260			

BI – branch increment; NSU – number of stem units; $MSUL$ – mean stem unit length; HI – main stem second season height increment; r_A, r_P and r_e – genetic, phenotypic, and environmental correlations, respectively.

Table 3. Degree of determination (%) of the annual growth increment (*BI*) by the number of stem units (*NSU*) and mean stem unit length (*MSUL*)

Trait	Genetic	Phenotypic	Environmental
NSU	58.29	63.51	63.99
MSUL	41.71	36.49	36.01

NSU - number of stem units; *MSUL* - mean stem unit length

2), however, is that both *NSU* and *MSUL* were comparatively highly correlated with *BI*. Irrespective of whether the data were transformed or not, *NSU* and *MSUL* were not correlated in any way. Table 2 also shows that the correlations for HI with *BI* and *NSU* were moderate, whereas the corresponding correlations between *MSUL* and HI were low.

Table 3 presents results from the path coefficient analysis showing the percentages with which *BI* was genetically, phenotypically and environmentally determined by *NSU* and *MSUL*. It shows that genetically, *BI* was 58.29 % determined by *NSU* and 41.71 % by *MSUL*. The corresponding phenotypic and environmental degrees of determination were much higher for *NSU* than *MSUL*.

The genetic correlation between greenhouse-assessed stem growth components and 11-year height on the two field test sites appear in Table 4. Genetic correlations and efficiencies of early selection were higher for *MSUL* than *BI*, and higher for *BI* than *NSU* for both site A and B. Selection for *MSUL* could yield 47.4 % and 85.1 % of the gain expected form direct selection for 11-year height on site A and B, respectively. A 29.0 % loss in the mean 11-year height at site B could be incurred if genotype with high *NSU* were selected.

DISCUSSION

Heritability of Stem Growth Components

The heritability estimates for *NSU* and *MSUL* generally shows that variation in these two components of stem growth were under equal genetic control. This, however, does not underrate the fact that heritabilities for *MSUL* were slightly higher than corresponding values for *NSU*. It simply means that the amount by which heritabilities for *MSUL* exceeded those of *NSU* was not high enough to conclude that variation in *MSUL* is more heritable than variation in *NSU*.

Studies with other conifers elsewhere had mixed results and heritabilities often depended on the test conditions. For example, during a fixed growth phase in *Pinus taeda* L. LI *et al.* (1992) found that *NSU* had higher heritability than *MSUL* for those seedlings receiving more water and more fertiliser as well as in those receiving less water and less fertiliser. For the summer growth phase, *NSU* and *MSUL* had equal heritability in seedlings receiving more water and more fertiliser, whereas in those receiving less water and less fertiliser *NSU* had slightly higher heritability than *MSUL*.

In another study with *Pinus taeda*, LI *et al.* (1991) found that *NSU* had higher heritability a lower level of nitrogen than at a higher level. To the contrary, *MSUL* was not genetically variable irrespective of the level of nitrogen. For *Pinus elliottii* Engelm. *NSU* had higher heritability than *MSUL* at both low and high nitrogen treatments during the free growth phase. During the fixed growth phase, *NSU* had higher heritability than *MSUL* only at high nitrogen treatment (SMITH *et al.* 1993). While studying stem growth components in *Pinus sylvestris* L. JONSSON *et al.* (2000) observed higher heritability for *NSU* than *MSUL* at both wide and low spacing. Stem growth component analysis in *Pinus banksiana* Lamb. showed that *MSUL* had higher heritability than *NSU* at low and high temperature during a free growth phase, and only at high tempera-

Table 4. Genetic correlation between seedling stem growth components measured in the greenhouse and 11-year height from the field trials and efficiencies of indirect retrospective early selection.

Field Test side	*BI*		*NSU*		*MSUL*	
	r_A	E (%)	r_A	E (%)	r_A	E (%)
Chinchaga River (A)	0.524±0.155	40.2	0.243±0.193	19.1	0.566±0.142	47.4
Saddle Hill (B)	0.236±0.243	33.4	- 0.200±0.241	-29.0	0.551±0.178	85.1

BI - branch increment; *NSU* - number of stem units; *MSUL* - mean stem unit length; r_A - genetic correlation; *E* - selection efficiency.

ture during a fixed growth phase. At low temperature *NSU* and *MSUL* had equal heritability during fixed growth (KREMER & LARSON 1983). In *Picea pungens* Englm., BONGARTEN (1986) reported heritability of 0.28 for *NSU* and 1.01 for *MSUL*.

These cited examples generally indicate a tendency for heritability of *NSU* and *MSUL* to vary with species, test environment (temperature, nutrient levels, spacing) and whether analysis is made on stems from fixed or free growth. Growth components for the present study of white spruce were assessed on branches and only for one growing season of fixed growth. The results support a general tendency towards equal heritability for *MSUL* than *NSU*. Since studies in other species have indicated that comparative genetic control for the variation in *NSU* and *MSUL* may change with time, test conditions, and the nature of growth (free or fixed), we cannot speculate on whether or not the results would have been the same if we had extended this study to more than one period of fixed growth, or even assessed growth components during the first growing season, which is a free growth phase. However, our study shed more light on the extent of genetic control of the variation in stem growth components. Also, our spruce study provides additional information to a body of literature on the stem growth component subject that is overwhelmingly dominated by studies in the genus *Pinus* compared to other conifers with similar modes of growth.

Determination of Annual Growth Increment

Our study showed that *NSU* not *MSUL* was a greater determinant of annual growth increment for the first order branches. Approximately, *NSU* and *MSUL* determined 58 % and 42 % of *BI*, respectively. However, these percentages are not overwhelmingly different to suggest that one can achieve superior growth by selecting for *NSU* in the exclusion of *MSUL*. Instead, our results suggest that, though to different extents both *NSU* and *MSUL* are important for ensuring adequate annual growth. A tree breeder intending to improve traits such as height growth that is often correlated with branch length would need to select for both high *NSU* and high *MSUL*.

Results from studies in other species are mixed in support of *NSU* and *MSUL* as main determinant of *BI*. In *Pinus banksiana* for example, KREMER & LARSON (1983) found that *MSUL* was a greater determinant of *BI* at both low and high temperature during a free growth phase. During a fixed growth phase, *NSU* was an overwhelming determinant of *BI* (93.6 %) compared to *MSUL* (6.4 %) at low temperature. At high tempera-

ture, however, the relative contributions to *BI* were 45.9 % for *NSU* and 54.1 % for *MSUL*. The latter case is consistent with our finding and conclusion that both *NSU* and *MSUL* are important in determining *BI*. While studying stem growth components in *Pinus elliottii* SMITH *et al.* (1993) found that in both low and high nitrogen treatments, free and fixed height growth increments were more correlated with *NSU* (r_A = 0.93 –0.94) than *MSUL* (r_A = 0.62–0.78). This is also consistent with our findings of greater correlation between *NSU* and *BI* than *MSUL* and *BI*. In *Picea pungens* the correlation between *MSUL* and *BI* was greater than that of *NSU* and *BI* (BONGARTEN 1986).

LASCOUX *et al.* (1994) analysed the relative contribution of *NSU* and *MSUL* to *BI* in *Pinus sylvestris* at different nutrient levels. They found that at nutrient levels considered suboptimal, most of the variation in *BI* was due to variation in *MSUL*. At optimal nutrient conditions, however, *NSU* and *MSUL* had approximately equal role in determining *BI*. KREMER & LASCOUX (1988) studied stem growth in *Pinus pinaster* for six consecutive growing seasons and found that *NSU* not *MSUL* was the main contributor to *BI*. Similar results were found in a study with *Pinus banksiana* (MAGNUSSEN & YEATMAN 1989).

In this study, we also correlated stem growth components assessed on second season branch increment with the second season height increment assessed on the main stem of the seedling (*HI*). This would shed more light on the relative role of *NSU* and *MSUL* to annual growth. The genetic correlation between HI and *NSU* was much higher than that between *HI* and *MSUL* (Table 2). This is consistent with the higher correlation between *BI* and *NSU* than *BI* and *MSUL*, and thus, affirms the greater role of *NSU* than *MSUL* in the determination of annual growth increments.

NSU – MSUL Correlation

Stem growth component studies such as BONGARTEN (1986), KREMER & LARSON (1983), MAGNUSSEN & YEATMAN (1989), KREMER & LASCOUX (1988), have found negative genetic and phenotypic correlation between *NSU* and *MSUL*. Others, however, have found both negative and positive correlations for the same test materials measured in different growing seasons (LASCOUX *et al.* 1994; 1993). The reported negative correlation between *NSU* and *MSUL* has led some to conclude that *NSU* and *MSUL* may have less significance as selection criteria (MAGNUSSEN & YEATMAN 1989; BONGARTEN 1986). We did not find such a correlation between these two components. Table 2 shows that genetic, phenotypic and environmental

correlations between NSU and MSUL are positive and not far from zero. It should be noted that most of the reported negative correlations between NSU and MSUL are small negative values. Since most of the articles that report small negative correlations do not include standard errors of the correlation, those correlations may actually be close to zero. It may also be that the often-reported negative correlation between NSU and MSUL is just a manifestation of the way in which MSUL is computed. By expressing MSUL as a ratio of BI and NSU (MSUL = BI ÷ NSU), the negative correlation between NSU and MSUL is a more likely result.

Stem Growth Components and other Traits

In a white spruce study, POLLARD (1974b) found that some northern provenances ceased needle initiation earlier than southern ones. This suggests that NSU may be related to the latitude of seed origin or any other geographic factor related to seedling growth rhythm. In the present study of white spruce, we calculated correlations for latitude, longitude and elevation of seed origin with the family means. Both Pearson's and Spearman' rank order correlations were very low and only one was statistically significant (Table 5). We also calculated simple correlations for NSU and MSUL with the date of budburst. The date of budburst was recorded as the number of days from the date when seedlings were returned to the greenhouse to start the second growing season to the date when the scale on the terminal bud of the seedling ruptured to expose needles (RWEYONGEZA 2002). These correlations (Table 5) show that NSU was not related to the date of budburst, which in this case is a measure of growth rhythm. The

Table 5. Correlation coefficients for NSU and MSUL with latitude, longitude and elevation of seed origin, and date for budburst and seedling terminal bud size.

Variable pair		r_p	r_s
NSU	Latitude	−0.044	−0.041
NSU	Longitude	−0.149	−0.084
NSU	Elevation	0.062	−0.062
MSUL	Latitude	0.200	0.164
MSUL	Longitude	−0.039	0.000
MSUL	Elevation	−0.321*	−0.181
NSU	BB	0.021	−0.037
MSUL	BB	−0.290*	−0.231
NSU	BS	0.273*	0.176
MSUL	BS	0.194	0.161

SU - number of stem units, MSUL - mean stem unit length; BB - date for budburst; BS - bud size; r_p - Pearson's correlation; r_s - Spearman rank correlation; * - P < 0.05.

correlation between the date of budburst and MSUL was negative and statistically significant (r_A = −0.29, P = 0.035). In terms of strength, this significant negative correlation is too weak for us provide a reasonable generalisation about the relationship between stem growth components and seedling growth rhythms.

POLLARD (1974a) reported a relationship between seedling size and NSU, in which large seedlings were more likely to produce more needle primordia than small seedlings. Previous analysis for the present study found a similar relationship for NSU and MSUL with 18-week seedling height (H18), though the correlation was greater for MSUL and H18 than NSU and H18. This was a reason for using H18 as a covariate for both statistical and genetic analysis of BI, NSU and MSUL. Prior to using H18 as a covariate, heritability values for NSU were much lower than those of MSUL and the correlations and degrees of determination were greater between BI and MSUL than BI and NSU. The use of H18 as a covariate increased considerably the heritabilities for NSU while reducing slightly the heritabilities for MSUL. This led to a conclusion that variations in NSU and MSUL were under almost equal genetic control, even though heritabilities for MSUL remained higher than those of NSU. Also, by using H18 as a covariate, the correlations and degrees of determination of BI by NSU exceeded that of MSUL. This shows that if the genetics of NSU and MSUL has to be well analysed, either seedlings of relatively uniform size should be used or adjustment be made to control the effect of seedling size on variation in NSU.

Some studies such as (HALLGREN & HELMS 1992) found a positive relationship between NSU and the size of the apical dome. This may be another way of relating NSU and subsequently MSUL to seedling size. At the beginning of the second growing season, we visually scored the size of the terminal bud of all seedlings as 1 (small), 2 (medium), and 3 (large). The simple correlations for NSU and MSUL with bud size appear in Table 5. The Pearson's correlation between NSU and MSUL was marginally significant (r = 0.27, P = 0.048). Again, in terms of strength this correlation is too weak for us to make a reasonable conclusion. However, the positive relationship between NSU and the size of the apical dome may be justified in so far as it relates NSU to seedling size.

Stem Growth Components and Early Selection

This study showed that selection for MSUL would capture a greater percentage of gain expected from direct selection for 11-year height at both site A and B than selection for NSU. Similarly, BI was a better

predictor of 11-year height than *NSU* but less than *MSUL*. This is similar to what was observed in *Pinus sylvestris* by JONSSON *et al*. (2000), in which selection for *MSUL* measured on a third season increment would capture 64.46 % (wide spacing) and 51.67 % (dense spacing) of gain expected from direct selection for 28-year height. The corresponding selection efficiencies for *NSU* were 18.97 % and −16.56 %, which relates well to our findings. The results of our study differ from those of LI *et al*. (1991) in *Pinus taeda* in which 12-year height was more genetically correlated with *NSU* at both low (r_A = 0.54) and high (r_A = 0.35) nitrogen treatments than *MSUL*. The corresponding correlations for *MSUL* were 0.02 and 0.18. This clearly shows that selection for *NSU* would be more efficient in improving 12-year height than selection for *MSUL*. In *Pinus elliottii*, 15-year height was weakly negatively correlated with both *NSU* and *MSUL* at low nitrogen content, and weekly positively correlated with *NSU* at high nitrogen treatment (SMITH *et al*. 1993). This case, though not strong, suggests that selection for *NSU* at high nitrogen content would be more efficient in improving 15-year height than selection for *MSUL*. Also, ZHANG and FINS (1993) reported that 9-year height of *Larix occidentalis* Nutt. correlated more with *NSU* than *MSUL*. Since there are only very few cases in which stem growth components have been assessed in spruce, more studies are needed to establish a clear trend for the usefulness of *NSU* and *MSUL* for early selection in white spruce.

A note of caution should be made for selection efficiencies involving field site B. Genetic variation and heritability values at this site were much lower than that of site A such that only low genetic gain in 11-year height could be expected from direct selection. In such a case, even a relatively small gain from indirect selection on traits such as *MSUL* (Table 4) would produce high selection efficiency. Thus, a better picture of what could be achieved by early selection in this study is given by site A.

CONCLUSIONS

The results from our present study of stem growth components in white spruce lead us to the following main conclusions:

Variation in the number of stem units (*NSU*) and mean stem unit length (*MSUL*) was under moderate genetic control, and variation in both growth components may be equally inherited.

Although *NSU* not *MSUL* was a greater determinant of the annual growth increment (*BI*), our results suggest that both *NSU* and *MSUL* are important if annual growth increment is to be maximised. Breeding to improve annual growth would require selection for higher values of both *NSU* and *MSUL*. This should be possible, since *NSU* and *MSUL* are not necessarily negatively correlated as it has been widely reported. Also, where negative correlations have been found, most of those correlations are small suggesting that with high selection intensity enough genotypes could be found that combine favourably high values of *NSU* and *MSUL*.

MSUL was a better early selection indicator than *NSU* for 11-year height, largely due to a high genetic correlation with 11-year height compared to that of *NSU* and a slightly better heritability compared to that of *NSU*.

In this study, there was no indication that *NSU* was related to growth rhythms, since no relationship was found for mean *NSU* with date of budburst, latitude, longitude and elevation or seed origin.

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