GENETIC EFFECT ON BIOMASS PARTITION AND TREE ARCHITECTURE IN SEEDLINGS OF *PINUS CONTORTA* SSP. *LATIFOLIA*, IN ALBERTA, CANADA

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ABSTRACT

Genetic variation in biomass partitioning (stem, branch, needle and root biomass) and in architecture traits (harvest index, shoot to root ratio and sturdiness quotient) was studied in a *Pinus contorta* spp. *latifolia* population of 116 open-pollinated families. Families were collected from 33 natural stands in Alberta, Canada and were grown for two seasons in the greenhouse. Family effect was significant ($P \leq 0.01$) for all traits, accounting for 4% to 9% of total variance. Stand effect accounted for 0% to 4% of the total variance and was only significant for needle, above-ground biomass and shoot-root ratio. The narrow-sense heritabilities ranged between 0.183 ± 0.064 for shoot-root ratio and 0.433 ± 0.092 for above-ground biomass. The corresponding family heritabilities were ranged from 0.396 ± 0.053 to 0.667 ± 0.052. The genetic correlations among stem, needle, root, above-ground and total biomass were larger than 0.8 while correlations between branch biomass and other biomass traits were less than 0.8, but above 0.5. Harvest index showed moderate correlation with stem ($r = 0.453\pm0.122$) and root biomass ($r = 0.370\pm0.143$). Shoot-root ratio significantly correlated with root ($r = -0.233\pm0.181$), needle ($r = 0.329\pm0.155$) and above-ground biomass (0.297 ± 0.152). Sturdiness quotient only correlated with stem biomass (0.293 ± 0.105). Among three architecture traits, harvest index showed correlation with shoot-root ratio (-0.344 ± 0.162) and sturdiness quotient (0.389 ± 0.141). Levels of heritability and genetic correlation in this study suggest that selection would be effective for biomass and tree architecture traits in lodgepole pine.

Key words: harvest index, shoot-root ratio, sturdiness quotient, heritability, genetic correlation.

INTRODUCTION

More effective partitioning of total biomass into harvestable parts has been a major cause of yield increase in agricultural and horticultural plants (EVANS 1975, GIFFORD & EVANS 1981, GIFFORD *et al.* 1984, RASMUSSON 1987). In forest trees, selective breeding has emphasized mainly on the superiority in growth and quality traits such as volume, stem straightness, fine branching, and narrow crown. Whether yield improvement from tree breeding is entirely due to increase of total biomass production or more effective partitioning of biomass into stem is relatively unknown since there are few reports about genetic variation of biomass partitioning and tree architecture traits. It is believed that narrow crown, harvest index, biomass partition were under genetic control in a Norway spruce mutant (*Picea abies* f. *pendula* (Lawson) Sylven) (PULKKINEN & PÖYKKÖ 1990, PULKKINEN 1991), Scots pine (*Pinus sylvestris* L.) (VELLING & TIGERSTEDT 1984, PÖYKKÖ & VELLING 1993), Virginia pine (*Pinus virginiana* Mill) (MATTHEWS *et al.* 1975), loblolly pine (*Pinus*

taeda L.) (LEDIG *et al.* 1970), slash pine (*Pinus elliottii* Engelm. var. *elliottii*) (VAN BUIJTENEN 1978). In sitka spruce (*Picea sitchensis* Carr.) and lodgepole pine (*Pinus contorta* Dougl.), sparsely branched clones were believed the most efficient stemwood producer and large genetic gains could be achieved from simultaneous selection for rapid growth and high harvest index (CANNELL *et al.* 1983).

The study of tree biomass partitioning and architecture has important implications to the breeding of ideotypes. Tree architecture refers to the number, size, shape, structure, arrangement, and display of tree parts (ADAMS 1982). An ideotype is a model tree with a balanced combination of improved characters that maximizes productivity. Tree productivity is closely related with tree architecture since it affects the effectiveness of biomass production and allocation. One strategy to increase tree productivity is breeding for ideotype combination (DICKMANN 1985). The proposed ideotype combination for trees includes tallness, compactness, narrow crown, fibrous root systems with strongly developed taproot, a phenology that allows for

full utilization of the growing season and greater harvest index (CANNELL 1978, DICKMANN 1985, KÄRKI & TIGERSTEDT 1985).

Harvest index, shoot-root ratio and sturdiness quotient are three characteristics of tree architecture important to the breeding for ideotype combination. Harvest index is commonly referred to as the ratio of stem dry weight to the total dry weight at harvest (VELLING & TIGERSTEDT 1984). For practical reasons, most studies in trees have calculated ratio of stem dry weight to the above-ground dry weight as the harvest index (CANNELL 1985, PULKKINEN et al. 1989). A higher proportion of dry matter allocation into the stem increases the product recovery and the yield per unit area of land.

Shoot-root ratio refers to the proportion of above-ground biomass to the root biomass. Thus, it is a measure of balance between the transpirational area and the water absorbing area of plants. It was reported that seedlings with lower shoot-root ratios within same class of height exhibited better survival when water was a limit factor (HERMANN 1964, LOPUSHINSKY & BEEBE 1976). Shoot-root ratio has also been shown to influence the stability of trees to withstand wind (CANNELL & WILLETT 1976).

Sturdiness quotient is the ratio of tree height to basal diameter. It reflects the stocky or spindly nature of seedlings and influences the ability of seedlings to withstand wind, drought and frost damages (THOMPSON 1985). In mature trees, this ratio is an indicator of tree taper.

The present study provides knowledge on stand and family-within-stand differentiation, heritabilities and genetic correlations among components of total biomass (stem, branch, needle and root) and architecture traits (harvest index, shoot-root ratio and sturdiness quotient) in lodgepole pine. Data for analyses were based on 116 open-pollinated families from 33 stands studied for two growth periods in the greenhouse. Whether pattern of population differentiation and estimates of genetic parameters at young age would be maintained as seedlings mature must remain to be seen.

MATERIALS AND METHODS

Thirty-three stands of lodgepole pine of average and good quality were sampled in one of four lodgepole pine breeding regions in Alberta, Canada. The sampling breeding region covers the Swan Hills plateau area and some of the surrounding benchlands of central Alberta and is a lodgepole pine dominated extension of the Canadian Rocky Mountains foothills forest. The geographic area of the breeding region ranges from latitude 53°58' to 55°12', longitude 115°11' to 116°50'

and elevation 885 m to 1,160 m. Effort was made to sample stands evenly across the breeding region. Within each stand, four or less trees at a minimum of 300 m apart to decrease the risk of relatedness were selected as parents for collection of open-pollinated seeds. Criteria for selection were: (1) superior stem form (straight stem); (2) low taper (close to cylinder) and superior natural pruning characteristics; (3) crown and branching excellence (narrow and cylindric crown and short branches with relative large angle to stem; (4) height superior to dominant trees within a 300 m radius; and (5) freedom from disease, defect, or spiral grain.

Seeds were spot sown without stratification in plastic tube-containers filled with peat moss in the University of Alberta greenhouse and germination completed after 46 days with an average rate of 59.6% across families. Seedlings were transplanted into 5.6 litre plastic pots containing a mixture of peat, sand and sterilized soil using a completely randomized block design with single-tree plots in each of 20 replications. In order to accelerate seedling growth and to have two growing seasons within a year, daylight-length manipulation (shortening daylight-length) was used to induce seedling dormancy between two growth periods.

Temperatures were set at 25/20 °C for day / night and light regimes in the first and second growth period were set for 16/8 hours, supplemented by high pressure sodium vapour light (PPFD intensity of 300–340 $\mu mol \cdot m^{-2} \cdot s^{-1}$) if natural daylight was shorter than 16 hours. Fertilizing (1:1 of N–P–K 28–14–14 and 20–0–15 plus iron chelate) and watering took place once and twice weekly, respectively. Day/night shifted to 12/12 h for three weeks to induce dormancy at the end of the first growth period, and to 8/12 h for eight weeks of dormancy period. During dormancy period, fertilizer (1:1 of N–P–K 10–52–10 and 0–0–62 plus iron chelate) and water were applied weekly. The greenhouse study extended 36 weeks from transplanting to the end of second growth period.

Genetic variation and trend of genetic parameters on height, diameter, bud and branch characteristics in two growing seasons have been reported (WU et al. 1995). In this study, height and basal diameter were measured at the end of the second growth period for calculation of sturdiness quotient (HD). The average of seedling height was 15.9 cm with a maximum family mean of 22.3 cm and a minimum of 9.8 cm. The average of seedling basal diameter was 7.7 mm with a maximum family mean of 9.4 mm and a minimum of 5.4 mm. Seedlings were then harvested, separated into parts (stem, branch, needle, root) and oven dried at 80°C for 48 hours for biomass partitioning and computing harvest index (HI) and shoot-root ratio (SR).

Analyses of variance and covariance for all traits were conducted with the following model:

$$Y_{ijk} = \mu + S_i + F_{j(i)} + R_k + SR_{ik} + E_{ijk} \quad [1]$$

where μ is the grand mean, S_i is the ith stand effect (I = 1 to 33), $F_{j(i)}$ is the jth family effect within i^{th} stand (j = 1 to 4), R_k is the kth replication effect (k = 1 to 20), SR_{ik} is interaction between k^{th} replication and i^{th} stand, and E_{ijk} is the residual error. All effects in the model were assumed random and calculations of expected mean squares and mean cross-products followed the Hartley synthesis method (MILLIKEN & JOHNSON 1984). The effects of family-within-stand and replication-by-stand interaction could be examined directly by F-tests, but SATTERTHWAITE's (1946) approximate test procedure was required to synthesize mean squares and mean cross-products for other effects in the model.

The mating system is predominantly outcrossing in lodgepole pine (EPPERSON & ALLARD 1987). Thus, assuming no inbreeding, linkage, and epistasis, the component of variance and covariance among open-pollinated families estimates one-quarter of the additive genetic variance and covariance, respectively (NAMKOONG 1979). Heritabilities on the individual and family basis were computed as:

$$\text{Narrow-sense heritability, } h_i^2 = \frac{4\sigma_{f(s)}^2}{\sigma_e^2 + \sigma_{f(s)}^2} \quad [2]$$

$$\text{Family heritability, } h_f^2 = \frac{\sigma_{f(s)}^2}{0.06\sigma_e^2 + \sigma_{f(s)}^2} \quad [3]$$

where $\sigma_{f(s)}^2$ is family-within-stand variance, and σ_e^2 is residual variance.

The exact confidence interval could not be estimated for narrow-sense and family heritabilities due to imbalance in the data, caused by slow germination and mortality in six families. Therefore, standard errors of heritabilities were estimated through Taylor's expansion (KENDALL et al. 1987). Genetic correlations (r_g) among traits were estimated as cov(fx fy) $/\surd(\sigma_{fx}^2 \sigma_{fy}^2)$, where cov(fx fy), σ_{fx}^2 and σ_{fy}^2 were family covariance and variances of traits x and y, respectively. Standard errors of genetic correlations were approximated as TALLIS (1959).

RESULTS

Genetic variation in seedling biomass and architecture traits

Survival following two growth periods averaged 96 percent. Mortality was related mainly to the slow germination and subsequent poor seedling quality in six families. It is observed that the most of seedling biomass in lodgepole pine was allocated into needles after two growing periods, and it accounted for 61% of the total biomass. The second largest sink of photosyn-

Table 1. Results of the analysis of variance presented as percentage of total variance and overall means, percentage and coefficients of variation (C.V.) for stem, branch, needle, root, above-ground, total biomass and three seedling architecture traits[a]

Sources of variation	Trait								
	SB	BB	NB	RB	GB	TB	HI	SR	HD
Replication (R)	14**	6**	15**	9**	15**	14**	1**	3**	19**
Stand (S)	3	4	4*	2	4*	4*	1	2*	0
Family (stand)	8**	7**	9**	7**	9**	8**	9**	4**	6**
R x S	2	0	1	2	1	2	0	2	0
Residual	73	83	72	80	71	71	89	89	75
Mean [b]	277	91	1626	673	1995	2668	0.138	3.10	21.3
Percentage [c]	10.4	3.4	60.9	25.2	74.8				
C.V. [d]	26.3	36.2	21.5	21.6	22.0	21.3	10.0	12.6	8.6

[a] SB: stem biomass, BB: branch biomass, NB: needle biomass, RB: root biomass, GB: above-ground biomass (SB+BB+NB), TB: total biomass (GB+RB), HI: harvest index (SB/GB), SR: shoot-root ratio (GB/RB), HD: sturdiness quotient (height/diameter).

[b] unit = cg.

[c] percentage of total biomass.

[d] C.V.: coefficient of variation based on family means.

* P≤0.05; ** P≤0.01.

Table 2. Estimates of individual (h_i^2) and family (h_f^2) heritabilities and their standard errors (s.e.) for stem, branch, needle, root, above-ground, total biomass and seedling architecture traits [a].

	Traits								
	SB	BB	NB	RB	GB	TB	HI	SR	HD
h_f^2	0.401	0.308	0.424	0.317	0.433	0.422	0.369	0.183	0.315
s.e.	0.088	0.078	0.091	0.079	0.092	0.091	0.093	0.064	0.095
h_f^2	0.647	0.579	0.661	0.586	0.667	0.660	0.574	0.396	0.550
s.e.	0.056	0.067	0.054	0.066	0.052	0.054	0.085	0.053	0.071

[a] SB: stem biomass, BB: branch biomass, NB: needle biomass, RB: root biomass, GB: above-ground biomass (SB+BB+NB), TB: total biomass (GB+RB), HI: harvest index (SB/GB), SR: shoot-root ratio (GB/RB), HD: sturdiness quotient (height/diameter).

Table 3. Estimates of genetic correlations (above the diagonal) and their standard errors (below the diagonal) among stem, branch, needle, root, above-ground, total biomass and seedling architecture traits [a].

Trait	Traits								
	SB	BB	NB	RB	GB	TB	HI	SR	HD
SB		0.687	0.912	0.936	0.939	0.959	0.453	0.134	0.293
BB	0.088		0.711	0.576	0.749	0.722	−0.048	0.192	−0.173
NB	0.260	0.082		0.867	0.996	0.985	0.076	0.329	0.161
RB	0.021	0.119	0.041		0.885	0.934	0.370	−0.233	0.185
GB	0.018	0.072	0.001	0.035		0.993	0.133	0.297	0.165
TB	0.012	0.079	0.005	0.021	0.003		0.196	0.171	0.173
HI	0.122	0.161	0.169	0.143	0.156	0.159		−0.344	0.389
SR	0.140	0.182	0.155	0.181	0.152	0.167	0.162		−0.025
HD	0.151	0.162	0.159	0.153	0.165	0.162	0.141	0.105	

[a] SB: stem biomass, BB: branch biomass, NB: needle biomass, RB: root biomass, GB: above-ground biomass (SB+BB+NB), TB: total biomass (GB+RB), HI: harvest index (SB/GB), SR: shoot-root ratio (GB/RB), HD: sturdiness quotient (height/diameter).

thetic output was the root system and it accounted for 25.2% of total biomass. The branches had the least biomass, at 3.4% of total biomass. Large among-family variation was observed for all biomass traits (coefficient of variation based on family varied from 21.5 to 36.2). In contrast, the among-family variation was less in harvest index, shoot-root ratio and sturdiness quotient (coefficient of variation based on family varied from 8.6 to 12.6, Table 1).

Significant family differences at 1% probability level were observed among 116 lodgepole pine families for all biomass traits and three seedling architecture traits. Families accounted for 4–9% of total variance while stands only accounted for 0–4% of variance. Stand effects were only significant for needle and above-ground biomass and shoot-root ratio at 5% probability level. The effect owing to replications was significant at the 1% level of probability and explained

1–19% of the total variance. This indicates block of experiment in the greenhouse was effective to reduce environmental variation. The largest percentage of total variances in biomass and architecture traits, from 71% to 89%, was due to differences among seedlings within families (Table 1).

Narrow-sense heritabilities (h_i^2) were estimated from 0.183±0.064 for shoot-root ratio to 0.433±0.092 for total above-ground biomass (Table 2). The corresponding family heritabilities (h_f^2) were from 0.396 ±0.053 to 0.667±0.052.

Genetic correlations among seedling biomass and architecture traits

The seedling biomass components in lodgepole pine showed strong covariation. The estimated genetic correlations among stem, needle, root, above-ground

and total biomass were larger than or equal to 0.8 although genetic correlations between branch biomass and other biomass traits were less than 0.8. But genetic correlations between branch biomass and other biomass traits were still above 0.5 (Table 3). Harvest index showed a moderate correlation with stem biomass (r = 0.453±0.122) and root biomass (r = 0.370±0.143), but had weak relationship with above-ground biomass (r = 0.133±0.156) and total biomass (0.196±0.159). In addition, genetic correlations between harvest index and branch, needle biomass traits were weaker or near zero (Table 3). Shoot-root ratio was correlated negatively with root biomass (r = −0.233±0.181), but correlated positively with needle (r = 0.329±0.155) and above-ground biomass (0.297±0.152). Genetic correlations between shoot-root ratio and other biomass traits (stem, branch and total biomass) were low (all below 0.2) and shoot-root ratio was also negatively correlated with harvest index (−0.344±0.162). Seedling sturdiness quotient was observed positively correlated with stem biomass (0.293±0.105) and harvest index (0.389± 0.141). However, seedling sturdiness quotient was correlated weakly with other biomass traits and shoot-root ratio. Judging from the size of standard errors for estimated genetic correlations, it seems estimated genetic correlations were relatively precise since all genetic correlations above 0.2 had their standard errors less than the estimates.

DISCUSSION

Similar to our previous study on seedling morphological traits (height, diameter, bud, branch characteristics) (WU et al. 1995), differentiation of seedling biomass and architectural traits was well expressed among families after two growing seasons of seedlings in lodgepole pine (Table 1). Our data agree with the view that seedlings in many conifers can rapidly express their inherent variation under optimal growth condi-

tions (HANOVER & REICOSKY 1972, BONGARTEN & HANOVER 1985, WILLIAMS 1988, CARTER et al. 1990, PHARIS et al. 1991). A question concerning effectiveness of estimating genetic parameters in early seedling growth is whether maternal effect contributed significantly to family differentiation. If maternal effect is significant, then genetic differentiation and parameters in the seedling stage would be overestimated. Effects of seed size and seedling emergency rate have been proposed as two major maternal or preconditioning factors to be related to seedling performance in some conifer species (BONNER 1988). To understand whether seed size and seedling emergency rate have contributed to the family differentiation and the estimates of heritabilities in biomass traits in this study, two analyses were further conducted. In the first analysis, Pearson's correlations between average seed weight per family and seedling biomass traits were computed (Table 4). This analysis indicated only marginal correlations between seed weight and above-ground biomass (r = 0.17) and total biomass (r = 0.18). In addition, family seed weight was not significantly correlated with needle and branch biomass. Although correlations with stem biomass, root biomass were significant (5% probability level), the relationships were weak (r_w less than 0.22). In the second analysis, parameter of seedling emergency rate was calculated from probit analysis described by CAMPBELL and SORENSON (1979), and correlations between seedling emergency rate and seedling biomass traits were computed (Table 4). In general, correlations between seedling emergency rate and seedling biomass traits were smaller than the correlations between seed weight and seedling biomass traits. Therefore, there is little or no evidence that seedling biomass is related to seed size and seedling emergency rate. We also observed there was little contribution of maternal effect to 16 seedling morphological traits (WU et al. 1995).

Stand effect was significant only for shoot-root

Table 4. Family-mean correlations between seed weight (r_w), seedling emergency rate (r_s) and seedling biomass traits [a].

	Traits					
	SB	BB	NB	RB	GB	TB
r_w	0.215	0.076	0.165	0.188	0.170	0.179
P	0.021*	0.254	0.078	0.043*	0.069	0.054
r_s	0.108	0.061	0.145	0.126	0.137	0.138
se.	0.250	0.421	0.121	0.179	0.135	0.141

[a] SB: stem biomass, BB: branch biomass, NB: needle biomass, RB: root biomass, GB: above-ground biomass (SB+BB+NB), TB: total biomass (GB+RB), HI: harvest index (SB/GB), SR: shoot-root ratio (GB/RB), HD: sturdiness quotient (height/diameter).
* $P \le 0.05$; ** $P \le 0.01$.

biomass ratio, needle and above-ground biomass (Table 1). Non-significant and very little stand effect on lodgepole pine seedlings also has been observed for seedling morphological traits. This is probably expected since the 33 stands were confined within a narrow range, from latitude 53°58' to 55°12' and longitude 115°11' to 116°50' and lodgepole pine distribution is mainly continuous in this region. The predominance of within-family variability (Table 1) is probably indicative of the large number of effective pollen parents (large effective population size) and the maintenance of considerable genetic variation in this conifer.

There is increasing emphasis to exploit the genetic relationships among traits for breeding trees with a balanced union of improved attributes (CANNELL 1978, KÄRKI & TIGERSTEDT 1985, DICKMANN 1991, PULK-KINEN 1991, PÖYKKÖ & VELLING 1993). Harvest index differed significantly among families (Table 1), varied from 0.107 to 0.179 and with an average of 0.138. Heritabilities appropriate for mass selection (0.369 ±0.093) and family selection (0.574±0.085) were relatively high. Hence, there is a genetic basis for improving harvest index in this sample of lodgepole pine. Since harvest index was correlated positively with stem and root biomass, selection for increased harvest index would simultaneously increase seedling stem and root biomass.

Improvement of tree stem form in lodgepole pine is also possible since sturdiness quotient differed among families, varying from 0.168 to 0.256 with an average of 0.213 (Table 1), and heritabilities appropriate for mass and families selection were 0.315±0.095 and 0.550±0.071, respectively (Table 2). Genetic difference in sturdiness quotient has been reported in other conifers. Sturdiness quotient in Scots pine at age 16 differed among families, was correlated negatively with diameter and stem weight, but had no correlation with harvest index (VELLING & TIGERSTEDT 1984).

Comparing with genetic parameters for 16 seedling morphological traits (height, diameter, bud and branch characteristics), heritabilities for biomass traits, harvest index and sturdiness quotient were lower than the estimates for height measurements, but higher than estimates for bud and branch characteristics traits. However, heritabilities of biomass traits were similar to estimates for diameter measurements (WU *et al.* 1995). Estimated genetic correlation between sturdiness quotient and total height was 0.598 (±0.090), and between sturdiness and diameter was near zero (r = –0.022±0.221). This suggests that selection for sturdiness quotient would have an increase in stem volume with a more uniform lower and upper logs. Selection to increase sturdiness quotient would also increase harvest

index due to their positive correlation (r = 0.389± 0.141) (Table 3). Thus, breeders can improve lodgepole pine by directing more biomass into the stem and simultaneously reducing tree taper.

Significant genetic differences in shoot-root ratio have been widely reported in many conifers (LEDIG & PERRY 1965, CANNELL & WILLETT 1976, CANNELL ET AL. 1978, JIANG 1988). The expression of large genetic variation and effective individual and family heritabilities (0.183±0.064 and 0.396±0.053, respectively) for shoot-root ratio suggest there is potential for improvement of shoot-root ratio in this sample of lodgepole pine. Due to negative genetic correlation between harvest index and shoot-root ratio, selection for increasing the shoot-root ratio would have a negative effect on harvest index in the lodgepole pine seedlings. However, selection for increasing shoot-root ratio would not have much impact on height and diameter since their genetic correlations were low, at 0.032±0.208 and 0.113±0.181, respectively.

Study of lodgepole pine seedling architecture here may serve as a model for further study in older trees. Caution should be exercised, however, in extrapolating results from seedling studies to those of older stands. Following two factors are believed to contribute to the possible poor extrapolation of results from seedling study to mature trees. First, the environment in which seedlings are grown may be sufficiently different from the environment in which improved trees are grown that interaction between genotypes and environments becomes important. Spacing, water, nutrition and light competition effects on biomass allocation and seedling sturdiness quotient have been reported (KEYES & GRIER 1981, LEDIG 1983, JIANG 1988). Thus, one should simulate field environmental condition in early seedling growth to maximize early-mature genetic correlation. Second, inference of seedling studies to older materials may be affected if different genes are involved in the expression of traits at different ages. For example, partitioning to various plant parts may involve expression of different sets of genes after the onset of flowering or competition. The very small portion of biomass allocated into branches (3.4%) in the seedlings may well reflected the different developmental stages between seedlings and older trees. Therefore, a period of two-growth periods in the greenhouse can hardly be considered sufficient for a serious evaluation of pattern of biomass partition and architecture traits since these traits are expected to be subject to progressive change over the life of a tree. Nevertheless, seedling studies may serve as a model for the physiological processes in older trees and is a first approximation to what can be expected in applied tree breeding programs. The destructive nature on estimat-

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ing harvest index and biomass partition have prohibited the genetic study of tree architecture in the mature trees since large sample size is necessary for quantitative genetics study. This is why only a few studies of harvest index in conifer species have been conducted, and all are based on very small data sets (PULKKINEN et al. 1989). The small trees at early ages can provide the opportunity to study genetic variation on harvest index and biomass partition based on a large population such as this lodgepole pine study and it can rapidly provide at low cost estimates of additive genetic variance and covariance in the breeding population. Levels of heritability and genetic correlation, and the small standard errors of these estimates, suggest that selection procedures that exploit additive genetic variance and covariance in architectural traits would be promising for this sample of lodgepole pine.

REFERENCES

ADAMS, M. W. 1982: Plant architecture and yield breeding. *Iowa State J. Res.* **56**:225–254.

BONGARTEN, B.C. & HANOVER, J. W. 1985: Accelerating seedling growth through photoperiod extension for genetic testing: a case study with blue spruce (*Picea pungens*). *Forest Science* **31**:631–643.

BONNER, F. T. 1988: Importance of seed size in germination and seedling growth. *In* Karmra, S.K. & Ayling, R.D. (Eds). Proc. of Intern. Symp. on For. Seed Prob. in African, Harare, Zimbabwe, pp.53–61.

CAMPBELL, R. K. & SORENSEN, F. C. 1979: A new basis for characterizing germination. *J. Seed Tech.* **4**:324–340.

CANNELL, M.G.R. & WILLETT, S. C. 1976: Shoot growth phenology, dry matter distribution and root:shoot ratios of provenances of *Populus trichocarpa, Picea sitchensis* and *Pinus contorta* growing in Scotland. *Silvae Genet.* **25**:49–59.

CANNELL, M. G. R. 1978: Improving per hectare forest productivity. p. 120–148 *In:* Proc. 5th North Amer. For. Biol. Workshop, Gainesville, FL.

CANNELL, M. G. R.,. BRIDGWATER, F. E. & GREENWOOD, M. S. 1978: Seedling growth rates, water stress responses and root-shoot relationships related to eight-year volumes among families of *Pinus taeda* L. *Silvae Genet.* **27**:237 –247.

CANNELL, M. G. R., SHEPPARD, L. J., FORD, E. D. & WILSON, R. H. F. 1983: Clonal differences in dry matter distribu tion, wood specific gravity, and foliage "efficiency" in *Picea sitchensis* and *Pinus contorta*. *Silvae Genet.* **32**:195–202.

CANNELL, M. G. R. 1985: Dry matter partitioning in tree crops. p. 160–193 *In:* Attributes of trees as crop plants. M.G.R. Cannell and J.E. Jackson (eds.). Institute of Terrestrial Ecology, Penicuik, Scotland.

CARTER, K. K., ADAMS, G. W. GREENWOOD, M. S. & NITSCH- KE, P. 1990: Early family selection in jack pine. *Can. J. For. Res.* **20**: 285–291.

DICKMANN, D. I. 1985: The ideotype concept applied to forest

trees. p. 89–101 *In:* Attributes of trees as crop plants. M.G.R. Cannell and J.E. Jackson (eds.). Institute of Terrestrial Ecology, Penicuik, Scotland.

DICKMANN, D. I. 1991: Role of physiology in forest tree improvement. *Silva Fennica* **25**:248–256.

EPPERSON, B. K. & ALLARD, R. W. 1987: Linkage disequilib- rium between allozymes in natural populations of lodge- pole pine. *Genetics* **115**:341–352.

EVANS, L. T. 1975: The physiological basis of crop yield. *In:* Crop physiology, some case histories. L.T. Evans (ed.). Cambridge Univ. Press. Cambridge. pp. 327–355.

GIFFORD, R.M. & L.T. EVANS, L. T. 1981: Photosynthesis, carbon partitioning, and yield. *Ann. Rev. Plant. Physiol.* **32**:485–509.

GIFFORD, R. M., THORNE, J. H., HITZ, H. D. & GIAQUINTA., R. T. 1984: Crop productivity and photoassimilate partition- ing. *Science* **225**:801–808.

HANOVER, J. W. & REICOSKY, D. A. 1972: Accelerated growth for early testing of spruce seedlings. *Forest Science* **18**: 92–94.

HERMANN, R. K. 1964: Importance of top-root ratios for survival of Douglas-fir seedlings. *Tree Planters' Notes* **64**:7–11.

JIANG, I. B. J. 1988: Analysis of multidata sets with example from genetic tests of provenances of *Pinus contorta* (Lodgepole pine) and full-sib progenies of *Pinus sylves- tris* (Scots pine). Ph.D. Dissertation, Swedish University of Agriculture Sciences, Uppsala.

KÄRKI, L. & TIGERSTEDT, P. M. A. 1985: Definition and exploitation of forest tree ideotypes in Finland. p. 102–109 *In:* Attributes of trees as crop plants. M.G.R. Cannell and J.E. Jackson (eds.). Institute of Terrestrial Ecology, Penicuik, Scotland.

KENDALL, S.M., STUART, A. & ORD, J. K. 1987: Kendall's advanced theory of statistics. 5th edition, Volume 1, Distribution theory. Charles Griffin and Company, London.

KEYES, M. R. & GRIER, C. C. 1981: Above- and below- ground net production in 40-year-old Douglas-fir stands on low and high productivity sites. *Can. J. For. Res.* **11**:599–605.

LEDIG, F. T. & PERRY, T. O. 1965: Physiological genetics of the shoot-root ratio. p. 39–43. *In:* Proc. Soc. Amer. Foresters 1960, Detroit, Mich.

LEDIG, F. T., BORMANN, F. H. & WENGER, K. F. 1970: The distribution of dry matter growth between shoots and roots in loblolly pine. *Bot. Gaz.* **131**:349–359.

LEDIG, F. T. 1983: The influence of genotype and environ- ment on dry matter distribution in plants. p. 427–454 *In:* Plant Research and Agroforestry. P.A. Huxley (ed.). International Council for Research in Agroforestry, Nairobi. Kenya.

LOPUSHINSKY, W. & BEEBE, T. 1976. Relationship of shoot- root ratio to survival and growth of outplanted Douglas- fir and ponderosa pine seedlings. USDA. For. Serv. Pacific Northwest and Range experiment Station. Re- search Notes PNW–274 7p.

MATTHEWS, J. A., FERET, P. P., MADGEWICK, H. A. I. & BRAMLETT, D. L. 1975. Genetic control of dry matter distribution in twenty half-sib families of virginia pine. p. 234–241 *In:* Proc. 13th South. For. Tree Improv. Conf.,

Raleigh, NC.

MILLIKEN, G. A. & JOHNSON, D. E. 1984: Analysis of messy data. Volume I, Designed experiments. Van Nostrand Reinhold Company, New York.

NAMKOONG, G. 1979. Introduction to quantitative genetics in Forestry. Technical bulletin no. 1588. USDA. For. Serv.

PHARIS, R. P., YEH, F. C. & DANCIK, B. P. 1990: Superior growth potential in trees: what is its basis, and can it be tested for at an early ages? *Can. J. For. Res.* **21**:368–374.

PÖYKKÖ, T. & VELLING, P. 1993: Inheritance of the narrow-crowned Scots pine E 1101, "Kanerva pine". *Silva Fennica* **27**:219–226.

PULKKINEN, P., PÖYKKÖ, T., TIGERSTEDT, P. M. A. & VELLING, P. 1989: Harvest index in northern temperate cultivated conifers. *Tree Physiol.* **5**:83–98.

PULKKINEN, P. & PÖYKKÖ, T. 1990: Inherited narrow crown form, harvest index and stem biomass production in Norway spruce (*Picea abies*). *Tree Physiol.* **6**:381–391.

PULKKINEN, P. 1991: Crown form and harvest increment in pendulous Norway spruce. *Silva Fennica* **25**:207–214.

RASMUSSON, D. C. 1987: An evaluation of ideotype breeding. *Crop Sci.* **27**:1140–1146.

SATTERTHWAITE, F. E. 1946: An approximate distribution of estimates of variance components. *Biom. Bull.* **2**:110

–114.

TALLIS, G. M. 1959: Sampling errors of genetic correlation coefficients calculated from the analysis of variance and covariance. *Aust. Jour. of Stat.* **1**:35–43.

THOMPSON, B.E. 1985: Seedling morphological evaluation--What you can tell by looking. p. 59–71 *In*: Proceedings of evaluating seedling quality: principles, procedures, and predictive abilities of major tests. M.L. Duryea (ed.) Forest Research Laboratory, Oregon State University, Corvallis.

VAN BUIJTENEN, J. P. 1978: Genetic differences in dry matter distribution between stems, branches and foliage in loblolly and slash pine. p. 235–241 *In*: Proc. 5th North Amer. For. Biol. Workshop, Gainesville, FL.

VELLING, P. & TIGERSTEDT, P. M. A. 1984: Harvest index in a progeny test of Scots pine with reference to the model of selection. *Silva Fennica* **18**:21–32.

WILLIAMS, C. G. 1988: Accelerated short-term genetic testing for loblolly pine families. *Can. J. For. Res* **18**:1085–1089.

WU, H. X., YEH, F. C., PHARIS, R. P., DANCIK, B. P., JIANG, I. B., DYMOCK, I. &. DHIR, N. K. 1995: Genetic parameters of greenhouse growth and performance of 2-year *Pinus contorta* subsp. *latifolia*. *Scand. J. For. Res.* **10**:12–21.