INHERITANCE OF STROBILI PRODUCTION AND GENETIC CORRELATION WITH GROWTH IN LODGEPOLE PINE

Mats Hannerz [1*], Sally N. Aitken [2], Tore Ericsson [3], Cheng C. Ying [4]

[1)] SkogForsk (The Forestry Research Institute of Sweden), Uppsala Science Park, SE-751 83 Uppsala, Sweden, Tel: +46-18-188500, Fax: +46-18-188600, E-mail: mats.hannerz@skogforsk.se
[2)] Department of Forest Sciences, University of British Columbia, 3041-2424 Main Mall, Vancouver, BC V6T 1Z4, Canada
[3)] SkogForsk (The Forestry Research Institute of Sweden), P.O. Box 3, SE-918 21 Sävar, Sweden
[4)] British Columbia Ministry of Forests, Research Branch, 712 Yates Street, Victoria, BC V8W 9C2, Canada
* Corresponding author

Received July 29, 2001; accepted January 3, 2002

ABSTRACT

Variation in flowering was analysed in a combined provenance-progeny trial with lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) in central British Columbia (BC). The study included 14 provenances from BC, western Alberta, and the Yukon, with 15 families per provenance and 12 trees per family. Female strobili production was assessed at 10, 11 and 29 years age, male strobili production at 11 and 29 years and height at 24 years age. Strobili production varied significantly among provenances. Provenances from the Yukon, northern BC and high elevation in southern BC had the slowest height growth and also the lowest production of male and female flowering at 29 years. Genetic correlations between height and flowering were generally weak. Narrow-sense heritabilities for strobili production varied from 0.13 to 0.64. Genetic correlations for strobili production in different years were positive both for female (0.53–0.78) and male flowering (0.32). Genetic correlations between male and female flowering were mostly negative but weak. The results demonstrate that selection of families for height in lodgepole pine should not notably affect the reproductive capacity. The results also suggest that male and female flowering capacity are two moderately to highly heritable but genetically rather independent characters.

Key words: *Pinus contorta*, flowering, growth, genetic correlation, heritability

INTRODUCTION

Selection of provenances or parent trees for primary traits such as growth might unintentionally affect other traits, and such responses are necessary to consider in tree breeding programmes and seed transfer guidelines. The genetic impact on the reproductive capacity is of great importance both from an ecological aspect, e.g. ability of the trees to self-regenerate and to provide a food-source for animals in a changing climate or with seed transfer, and from a practical perspective, e.g. quantity and quality of crops that may be obtained from seed orchards.

Seed and pollen production capacity among pines is inherited and show clonal variation (e.g. JONSSON *et al.* 1976), and this variation determines the quantity and genetic quality of seed orchard crops (YAZDANI & FRIES 1993; KANG & LINDGREN 1998). Considerable variation in seed and pollen production, as well as in reproductive phenology, has been shown both within and among provenances of lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) (NILSSON *et al.* 1980; YING *et al.* 1985; YING & ILLINGWORTH 1986; O'REILLY 1986). However, studies quantifying the degree of genetic control of reproductive output and the causal relationships between reproductive capacity and growth are scarce in pines. Such studies are needed in order to predict responses of reproductive traits to tree improvement, provenance transfer, and fecundity in a changing climate.

In this article, we analyse how female and male flowering abundance varies within and among provenances of lodgepole pine and over time, in terms of heritability and correlation estimates for strobili production and growth in a 29-year-old provenance-progeny trial of lodgepole pine.

MATERIAL AND METHODS

The field experiment

The combined provenance-progeny trial of lodgepole pine is located on a well-drained flat river bench at the BC Ministry of Forests' Red Rock Tree Improvement Station, near Prince George in central BC, (53°46' N, 122°43' W, 620 m a.s.l.) (Fig. 1). The test site was planted with 4-year-old stock in 1973 at 3.7 m square spacing. The total test includes 53 provenances from the Yukon, BC, and western Alberta. Each provenance is represented by 15 open-pollinated families. The experiment has a split-plot design with provenances as main plots and families within provenances represented by six-tree subplots in three completely randomised blocks. A more detailed description of the test, including a map with the origin of all provenances, is found in WU *et al.* (1996).

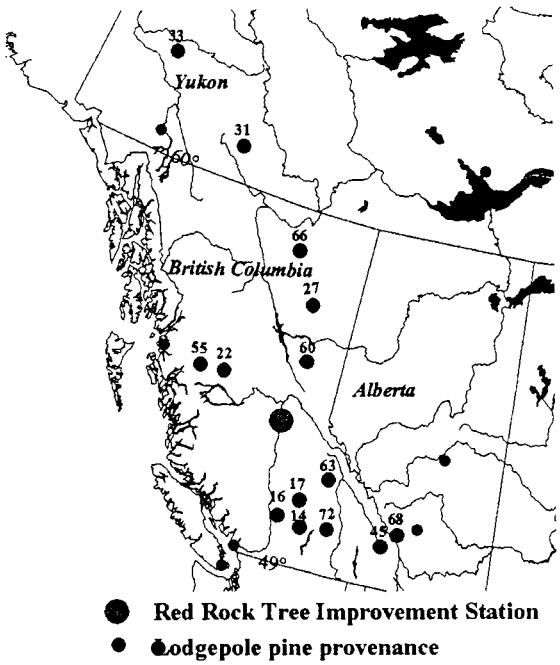

Figure 1. Location of the 14 provenances in the study and the test site at Red Rock.

Data collection

Both previously collected and new data were utilized in the present study (Table 1), since the field experiment has been subject to extensive earlier investigations. XIE & YING (1995; 1996) reported growth until 24 years from seed, and attacks of various pests at the same age were described in WU *et al.* (1996). YING & ILLINGWORTH (1986) and O'REILLY (1986) both investigated variation in production of strobili on 10–12-year-old trees on a restricted samples of provenances.

This study was restricted to 14 provenances extending from 50° to 63° N of latitude and from 115° to 136° W of longitude (Fig. 1). Seed source elevation varied from 500 to 1800 m (Table 2). In the last assessment, for the purposes of this study, all 15 families per provenance were evaluated. The number of trees was restricted to four per family in each of the three blocks, for a maximum of 180 trees per provenance. Due to mortality, the actual number of trees in the study varied from 70 to 180 (mean 150) per provenance, and in two provenances only 14 families were represented. Individual tree data from earlier measurements were matched with the new data set.

Assessment of strobili abundance was conducted on June 4–7 1998, when the trees were 29 years old from seed. The trees were generally between 8 and 12 meters tall, and the observations were carried out from about one tree-length distance. The timing of the inventory was judged as optimal, since all female and male strobili were well developed, and vegetative elongation had not yet advanced to the point of concealing the strobili. The weather conditions were favourable for observation during the four days of inventory. Abundance of female flowering was measured as the number of female strobili observed on one side of the previous year's leader and top lateral shoots. The inventory was made visually with binoculars with 9 times magnification by two persons from, on average, a southern aspect. The mean of the two scorer's estimates was recorded. Abundance of male flowering was recorded using five classes reflecting the number of potential pollen cone positions (shoots) that had pollen clusters. The classes were

0: without pollen clusters;
10: 1 to 20 %,
30: 21 to 40 %,
50: 41 to 60 %,
70: 61 to 80 % with pollen clusters;
90: more than 80 % with pollen clusters.

Data analysis

Apart from the initial descriptive analysis, estimation of genetic parameters was based on a reduced sample of provenances. Provenances 31, 33, and 66, from northern BC and the Yukon, and the high-elevation provenance 16 with extremely poor flowering, were removed in order to avoid overestimation of variance components. Data from earlier as well as current measurements were analysed as continuous variables in spite of the fact that most records were counts and even in one case class values (male flowering at age 29). During the analyses, no substantial deviations from normality were

Table 1. Tree variables used in the present study of the Red Rock trial. With reference to the studies where the data collection is described.

Abbr.	Description	Age	Reference
HT24	Total height (m)	24	XIE & YING (1996)
FEM10	Total number of female strobili [a)]	10	YING & YLLINGWORTH (1986)
FEM11	Total number of female strobili [a)]	11	YING & YLLINGWORTH (1986)
FEM29	Number of female strobili on the leader and in the top whorl	29	This study
MAL11	Total number of pollen clusters[a)]	11	YING & YLLINGWORTH (1986)
MAL29	Abundance of pollen clusters in classes 0–10–30–50–70–90, where e.g. 50 corresponds to between 40 and 50 % of the shoot positions having male flowers	29	This study

[a)] Recorded in two of three blocks only.

detected.

In biological terms, the phenotypic trait value (P) of an individual tree was assumed to consist of $P = A + E$, where A is the additive genetic effect (breeding value), and E is the independent environment effect, which also includes a genetic residual. The phenotypic variance was thus assumed to be partitioned into $\sigma_P^2 = \sigma_A^2 + \sigma_E^2$. Non-additive genetic variance, thus included in the environmental variance σ_E^2, was subsequently overlooked. Similarly, the phenotypic covariance between two traits is subdivided into additive genetic and environmental covariance: $\sigma_{P_1P_2} = \sigma_{A_1A_2} + \sigma_{E_1E_2}$.

The statistical analyses were carried out using both single-trait (univariate) and two-trait (bivariate) linear modelling, including all combinations of assessed traits. The assumed base mixed model was $\mathbf{y} = \mathbf{X_b b} + \mathbf{X_p p} + \mathbf{Zu} + \mathbf{e}$, which in the two-trait case becomes

$$\mathbf{y}' = [\mathbf{y}_1', \mathbf{y}_2'],\ \mathbf{X_b} = \mathbf{X}_{b_1} \oplus \mathbf{X}_{b_2},\ \mathbf{X_p} = \mathbf{X}_{p_1} \oplus \mathbf{X}_{p_2},$$

$$\mathbf{Z} = \mathbf{Z}_1 \oplus \mathbf{Z}_2,\ \mathbf{u}' = [\mathbf{u}_1', \mathbf{u}_2'] \text{ and } \mathbf{e}' = [\mathbf{e}_1', \mathbf{e}_2']$$

An observation vector $\mathbf{y}_i$ (i = 1 or 2) had a maximum of 12 tree values per half-sib family, fewer when data was missing due to mortality, or when only two of three blocks were assessed. The design matrices, $\mathbf{X_b}$ for the fixed-effects of three blocks (**b**), and $\mathbf{X_p}$ for 10 provenances (**p**), reflected each observation's association as regards block and provenance. The incidence matrix **Z** indicated random family (parent, mother tree) effects (**u**) within provenances, over blocks.

The random family effects of $\mathbf{u}_i$ (with element u_{ip} for trait i, parent p) and the random residual effects of $\mathbf{e}_i$ were assumed to have independent multivariate normal distributions with zero means and common variances/covariances according to $Var\begin{bmatrix}\mathbf{u}\\ \mathbf{e}\end{bmatrix} = \begin{bmatrix}\mathbf{G}\otimes\mathbf{I} & \mathbf{0}\\ \mathbf{0} & \mathbf{R}\otimes\mathbf{I}\end{bmatrix}$,

where $\mathbf{G} = \{\sigma_{u_iu_j}\}$ is the variance/covariance matrix of family effects and $\mathbf{R} = \{\sigma_{e_ie_j}\}$ the residual variance/covariance matrix (i, j = 1 or 2, denoting variance when $i = j$, e.g. $=\sigma_{u_2u_2} = \sigma_{u_2}^2$). Estimates of $\sigma_{u_iu_j}$ and $\sigma_{e_ie_j}$ (in single-trait analysis, only σ_{ii}^2 and σ_e^2, respectively) were computed using the restricted maximum likelihood (REML) technique (e.g. SEARLE *et al.* 1992) with the computer program ASREML (GILMOUR *et al.* 1999) based on an average information (AI) algorithm.

In terms of the biological model, the additive genetic variance was estimated using $\hat{\sigma}_{A_i}^2 = 4\hat{\sigma}_{u_i}^2$, where $A_{i_p} = \mu + 2u_{i_p}$ is the additive breeding value of parent tree p. The phenotypic variance was estimated with

$\hat{\sigma}_{P_i}^2 = \hat{\sigma}_{u_i}^2 + \hat{\sigma}_{e_i}^2$, and the environmental variance with

$\hat{\sigma}_{E_i}^2 = \hat{\sigma}_{P_i}^2 - \hat{\sigma}_{A_i}^2 = \sigma_{e_i}^2 - 3\sigma_{u_i}^2$. The corresponding equations for covariances are

$\hat{\sigma}_{A_iA_j} = 4\hat{\sigma}_{u_iu_j}$, $\hat{\sigma}_{P_iP_j} = \hat{\sigma}_{u_iu_j} + \hat{\sigma}_{e_ie_j}$, and

$\hat{\sigma}_{E_iE_j} = \hat{\sigma}_{e_ie_j} - 3\hat{\sigma}_{u_iu_j}$, respectively. Correlations were

estimated using $\hat{r}_{E_{ij}} = \frac{\hat{\sigma}_{E_i E_j}}{\sqrt{\hat{\sigma}^2_{E_i}\,\hat{\sigma}^2_{E_j}}}$ for environmental, and $\hat{r}_{A_{ij}} = \frac{\hat{\sigma}_{A_i A_j}}{\sqrt{\hat{\sigma}^2_{A_i}\,\hat{\sigma}^2_{A_j}}}$ for additive genetic. The covariance and correlation estimates were computed for each pair of traits using a post-processing module of ASREML, which also provided estimates of heritabilities and parameter standard errors. Narrow-sense heritability estimates, that is $\hat{h}^2 = \hat{\sigma}^2_A / \hat{\sigma}^2_P$, were calculated both from single-trait analyses and as means of estimates obtained from two-trait analyses. Estimates of heritability will be biased upwards somewhat by the use of a single test site as genotype-by-environment interaction variance could not be estimated. Correlation matrices were assembled for all traits from the two-trait runs. They were positive definite and thus without incongruous estimates. Standard errors of the parameters were moderate to high due to the character of the data in combination with relatively small sample sizes.

RESULTS

Variation among provenances

At the age of 29, female strobili and pollen clusters were recorded on 75 and 60 % of the trees, respectively. The mean number of female strobili observed on the leader and in the top whorl was 2.4, from an individual range between 0 and 14 (Table 2). For height and all the flowering variables, the fixed effect of provenance was always highly significant ($p < 0.0001$). With the exception of female flowering at 10 and 11 years, provenances from southern and central BC had more abundant flowering than those from the Yukon (31, 33) and northern BC (66). The most high-elevation provenance (16) from southern BC was an exception, since it produced the fewest strobili of all sources in all years. At 10 years, there was an opposite tendency with the lowest amount of flowers on southern provenances. Outstanding provenances, for both prolific female and male flowering in all years, were Settler's Road (45) and Albreda (63). Telkwa Low and High (22, 55) were from the introgression zone with shore pine (*P. contorta* var. *contorta*) and prolifically produced female strobili in all years, although had poor male production (particularly obvious for provenance 55).

Genetic parameters

The heritability estimates for strobili production ranged from 0.13–0.64 with the lowest value for female strobili at age 29. The single-trait estimates (Table 3) were

Table 2. Number, names, and geographical origins of the 14 provenances in the Red Rock trial, ordered from north to south, with mean heights at 24 years of age and numbers of pollen clusters and seed cones at ages 10, 11, and 29.

Provenance		Lat. (° ' N)	Long. (° ' W)	Elev. (m)	Height at age 24 (m)	Seed cones at age			Pollen clusters at age	
No.	Name					10[a]	11[a]	29[b]	11[a]	29[c]
33	Ethel L., Yukon	63 18	136 28	876	4.8	12.0	23.4	0.7	9.7	12.4
31	Frances L; Yukon	61 10	129 20	884	5.8	17.0	23.4	0.9	2.6	8.9
66	Stone Mt; BC	58 39	124 46	1173	6.7	17.2	26.8	1.2	7.0	14.9
27	Pink Mt; BC	57 00	122 24	1113	8.0	18.6	24.7	2.3	14.8	23.1
60	Mt. Lemoray, BC	55 33	122 33	732	9.2	12.6	25.5	2.9	20.1	27.3
22	Telkwa Low, BC	54 39	127 03	518	9.4	17.2	33.8	3.9	45.2	28.7
55	Telkwa High, BC	54 38	127 26	1005	8.5	17.8	32.2	3.3	13.6	15.0
63	Albreda, BC	52 35	119 10	975	9.3	15.9	46.4	3.5	105.5	38.4
17	Oie L; BC	52 00	121 12	991	10.0	8.5	21.3	2.2	31.6	27.7
16	Lime L/O, BC	51 06	121 40	1814	5.8	9.0	13.9	0.6	1.9	3.4
68	Kananaskis, AB	51 01	115 02	1501	8.4	15.2	28.2	2.6	61.1	23.4
14	Wentworth Cr; BC	50 58	120 20	1059	9.7	9.2	26.2	2.4	23.0	31.3
72	Larch Hills, BC	50 42	119 11	777	10.6	7.0	30.3	2.1	81.6	47.0
45	Settler's Road, BC	50 31	115 44	1036	10.1	22.1	67.8	2.8	172.6	45.6
Mean					8.6	14.4	31.4	2.4	45.8	26.7
Abbreviation					HT24	FEM10	FEM11	FEM29	MAL11	MAL29

[a] Mean total number of pollen clusters or seed cones per tree
[b] Mena number of seed cones on the leader and on shoots in the top whorl
[c] Mean percent of potential positions in the crown having male flowers

Table 3. Estimated means $\bar{x}$, phenotypic variances σ_P^2, additive genetic variances σ_A^2, and heritabilities (h^2), ±standard errors, and genetic coefficients of variation $\sigma_A/\bar{x}$ for height and fecundity traits from 7 univariate analyses of 148 half-sib families from 10 provenances in the Red Rock trial. Provenances 16, 31, 33, and 66 were excluded from the analyses.

Trait	$\bar{x}$	σ_P^2	σ_A^2	h^2	$\sigma_A/\bar{x}$
HT 24	9.31±0.3	0.872±0.027	0.358±0.067	0.410±0.071	0.06
FEM 10	14.4±0.5	183±8	67.9±19.5	0.371±0.101	0.57
FEM 11	33.6±1.1	764±34	319±85	0.418±0.104	0.53
FEM 29	2.80±0.06	5.17±0.18	0.664±0.296	0.128±0.057	0.29
MAL 11	56.7±3.6	7816±314	5001±901	0.640±0.101	1.25
MAL 29	30.7±0.8	545±20	213±47	0.391±0.080	0.48

Table 4. Estimated environmental correlations (r_E, above the diagonal), heritabilities (h^2, mean values from bivariate runs, in the bold typeface diagonal), and additive genetic correlations (r_A, below the diagonal) ± standard errors for height and fecundity traits from 15 bivariate analyses of 148 half-sib families in the Red Rock trial. Underline correlations exceed twice the standard error.

Trait	HT 24	FEM 10	FEM 11	FEM 29	MAL 11	MAL 29
HT 24	**0.410 ±0.071**	0.173±0.099	0.053±0.102	0.219±0.061	0.142±0.127	0.095±0.084
FEM 10	−0.222±0.162	**0.369±0.101**	0.507±0.087	0.102±0.076	0.148±0.140	0.158±0.109
FEM 11	−0.074±0.158	0.532±0.140	**0.416±0.104**	0.001±0.085	0.421±0.139	0.085±0.110
FEM 29	0.038±0.202	0.720±0.234	0.784±0.222	**0.124±0.056**	0.055±0.097	0.124±0.066
MAL 11	−0.145±0.128	0.089±0.160	0.156±0.150	−0.081±0.199	**0.640±0.101**	0.182±0.126
MAL 29	0.056±0.143	−0.287±0.174	−0.030±0.171	−0.203±0.224	0.319±0.129	**0.390±0.080**

nearly identical with the means of estimates from two-trait analyses (Table 4), for all traits.

Environmental correlations (Table 4) were positive but rather weak with the exception of female flowering at age 10 and male flowering at age 11, which both correlated substantially with female flowering at age 11. Tree height was more weakly but nonetheless positively correlated with female flowering at 29 years.

The additive genetic correlations (Table 4) displayed another pattern since the estimates of correlations between male and female flowering, respectively, were generally low and were not much greater in magnitude than their standard errors. However, flowering for a given gender between years, was consistently positively correlated with estimated r_A of 0.53–0.78 for female and 0.32 for male flowering. Genetic correlations between tree height and flowering were, on the contrary, very indistinct and seemingly negligible (although, with negative estimates in two cases where their magnitude slightly exceeded the standard errors).

DISCUSSION

Provenance variation

The geographical variation for flowering at 29 years followed the same pattern as for height growth, with southern and low-elevation provenances flowering more prolifically than more northern and higher elevation ones. The trend was not continuous, since there was an abrupt transition from the provenances in southern and central BC to the ones in northern BC and the Yukon. This pattern was weaker for flowering in the early years, and even reverse for female flowering at 10 years. Based on a subsample from the same experiment, YING & ILLINGWORTH (1986) concluded that northern provenances were more precocious but less prolific than the southern latitude provenances. YING *et al.* (1985) and O'REILLY (1986) also found a higher seed and pollen cone production in central and southern BC provenances than in more northern provenances.

The results are somewhat in conflict with those from a Swedish provenance test reported by NILSSON *et al.* (1980), who found that northern-latitude and high-altitude provenances flowered more abundantly than southern ones. Their test was located at 62° 30' N, and the best flowering provenances were still transferred northwards, compared to their origin in Canada. One explanation provided by NILSSON *et al.* (1980) was that southern provenances may need higher temperatures to initiate flowers than do northern provenances, and the test site was located in a rather cool area of Sweden. This demonstrates the importance of considering

conditions at the test site when comparing different experiments.

Genetic parameters

The most important finding of this study was the low, or absent, genetic correlation between height and flowering, which indicates that selecting genotypes for growth will have no or small effects on flowering. An absent or low correlation between height growth and flowering was found also in *Picea glauca* (Moench) Voss. (NIENSTAEDT 1985), in *Picea abies* (L.) Karst. (HANNERZ *et al.* 1999; ALMQVIST *et al.* 2001), and in *Pinus taeda* L. (BYRAM *et al.* 1986). In contrast, SCHMIDTLING (1981) found a negative genetic correlation between early flowering (precocity) and height growth in a *Pinus taeda* study based on 10 parents.

The positive environmental correlation between flowering and height implies that the number of strobili is dependent on the size of the tree, when the genetic effect is excluded. Tree size seems to be especially important for the first flowering of a tree (BOLSTAD *et al.* 1992; CHAŁUPKA & CECICH 1997). A larger crown has the potential for more flowers, and many reports have found a positive phenotypical relationship between tree size and flowering abundance (ERIKSSON *et al.* 1973; SCHMIDTLING 1981; CHAŁUPKA & CECICH 1997). This relationship is probably also important for explaining differences among provenances in the study. On the other hand, reproductive organs compete for nutrient resources within a plant (LINDER & TROENG 1981), and abundant flowering may therefore lead to reduced vegetative growth the same or subsequent years. Consequently, negative phenotypic correlations between growth and cone production have occasionally been reported (CHAŁUPKA *et al.* 1975; TEICH 1975).

Relatively high heritabilities for female and male flowering in the early years imply that these traits should be considered in both operational breeding and mass propagation. The heritability for both female and male flowering was lower at 29 years than at 10–11 years. Contrary, NIENSTAEDT (1985) and SCHMIDTLING (1981) found higher heritabilities for mature flowering than for precocious flowering in *Picea glauca* and *Pinus taeda* respectively. The lower value for mature female flowering in this study may partly be a result of the observation method, where seed cones were counted only in the uppermost whorl, thereby not revealing the full flowering potential of each tree.

The positive year-to-year correlations in female and male flowering, respectively, means that the flowering ability of a tree is maintained over time. The same positive correlations have been reported in many other studies (SCHMIDTLING 1981; YING *et al.* 1985; NIENSTAEDT 1985; KJÆR 1996).

The correlations between male and female reproductive organs tended to be negative but were weak and variable. In other tree species, there are reports of both negative (SAVOLAINEN *et al.* 1993), positive (SCHMIDTLING 1983; KJAER 1996; BURCZYK & CHAŁUPKA 1997) and absent (KANG & LINDGREN 1998) correlations between male and female flowering.

CONCLUSIONS

Strobili production differs among provenances of lodgepole pine and the amount of flowering and height growth show a similar geographic pattern. Hence, selection of lodgepole pine provenances for good growth will usually not involve any risks of reduced flowering capacity.

There is a relatively strong genetic component for flowering capacity in lodgepole pine. The moderately high year-to-year correlation for female and male flowers, respectively, means that the flowering ability of a tree is maintained over time. The low correlation between height and flowering implies that selection for good growth will have small or negligible effects on flowering. Furthermore, profound and early flowering can be selected for without any negative influence on growth.

ACKNOWLEDGEMENTS

The NSERC Industry Research Chair in Genetics provided funding for the inventory in 1998 and the analysis. We are grateful to the staff at Red Rock Tree Improvement Station for maintaining the test, and especially to Carole Fleetham for providing all the information needed for the inventory. We also acknowledge Lesley McKnight at BC Ministry of Forests for providing the old data sets.

REFERENCES

ALMQVIST, C., JANSSON, G. & SONESSON, J. 2001: Genotypic correlations between early cone-set and height growth in *Picea abies* clonal trials. *Forest Genetics* **8**(3): 197–204.

BOLSTAD, S. B., KANG, H. & CECICH, R. A. 1992: Promoting and selecting for early flowering in jack pine in a controlled environment. *In*: Proceedings of the First Northern Forest Genetics Association Conference, July 23–25, 1991, Burlington, V. T. Edited by D. DeHayes and G. J. Hawley. Pp. 140–149.

BURCZYK, J. & CHAŁUPKA, W. 1997: Flowering and cone production variability and its effect on parental balance in a Scots pine clonal seed orchard. *Ann. Sci. For.* **54**: 129–144.

BYRAM, T., LOWE, W. J. & MCGRIFF, J. A. 1986: Clonal and annual variation in cone production in loblolly pine seed orchards. *Forest Sci.* **32**(4): 1068–1073.

CHAŁUPKA, W. & CECICH, R. A. 1997: Control of the first

flowering in forest trees. *Scand. J. For. Res.* **12**: 102-111.

CHAŁUPKA, W., GIERTYCH, M. & KROLIKOWSKI, Z. 1975: The effect of cone crops on growth in Norway spruce (*Picea abies* (L.) Karst.). *Arboretum Kronickie* **20**: 201-212.

ERIKSSON, G., JONSSON, A. & LINDGREN, D. 1973: Flowering in a clone trial of *Picea abies* Karst. *Studia Forest. Suec.* **110**: 1-45, Stockholm.

GILMOUR, A. R., CULLIS, B. R., WELHAM, S. J. & THOMPSON, R. 1999: ASREML Reference Manual, 210 pp. NSW Agriculture, Orange, Australia.

HANNERZ, M., ALMQVIST, C. & EKBERG, I. 1999: Rooting success of cuttings from young *Picea abies* (L.) Karst. in transition to flowering competent phase. *Scand. J. For. Res.* **14**: 498-504.

JONSSON, A., EKBERG, I. & ERIKSSON, G. 1976: Flowering in a seed orchard of *Pinus sylvestris* L. *Studia Forest. Suec.* **135**: 1-38.

KANG, K. S. & LINDGREN, D. 1998: Fertility variation and its effect on the relatedness of seeds in *Pinus densiflora*, *Pinus thunbergii* and *Pinus koraiensis* clonal seed orchards. *Silvae Genetica* **47**: 196-201.

KJÆR, E. D. 1996: Estimation of effective population number in a *Picea abies* (Karst.) seed orchard based on flower assessment. *Scand. J. For. Res.* **11**: 111-121.

LINDER, S. & TROENG, E. 1981: The seasonal cours of respiration and photosynthesis in strobili of Scots pine. *Forest Science* **2**: 267-276.

NIENSTAEDT, H. 1985: Inheritance and correlations of frost injury, growth, flowering, and cone characteristics in white spruce, *Picea glauca* (Moench) Voss. *Can. J. For. Res.* **15**: 498-504.

NILSSON, J.-E., ERIKSSON, G. & RUDIN, D. 1980: Studies on flowering biology in 14 provenances of *Pinus contorta* in a Swedish field trial. *In: Pinus contorta* as an exotic species. (ed. A. Persson). *Dept. of Forest Genetics, Swed. Univ. Agri. Sciences, Research Notes* **30**: 299-311.

O'REILLY, C. J. 1986: Phenology and development of vegetative and reproductive structures in provenances of lodgepole pine. PhD thesis, Dept of Biology, University of Victoria.

SAVOLAINEN, O., KÄRKKÄINEN, K., HARJU, A., NIKKANEN, T. & RUSANEN, M. 1993: Fertility variation in *Pinus sylvestris*: a test of sexual allocation theory. *Am. J. Bot.* **80**: 1016-1020.

SCHMIDTLING, R. C. 1981: The inheritance of precocity and its relationship with growth in loblolly pines. *Silvae Genetica* **30**: 188-192.

SCHMIDTLING, R. C. 1983: Genetic variation in fruitfulness in a loblolly pine (*Pinus taeda* L.) seed orchard. *Silvae Genetica* **32**: 76-80.

SEARLE, S. R., CASELLA, G. & MCCULLOCH, C. E. 1992: Variance Components, 501 pp. Wiley, New York, 501 pp.

TEICH, A. H. 1975: Growth reduction due to cone crops on precocious white spruce provenances. *Bi-monthly Research Notes* **31**(1): 6. Petawawa For. Exp. Sta, Canada.

WU, H. W., YING, C. C. & MUIR, J. A. 1996: Effect of geographic variation and jack pine introgression on disease and insect resistance in lodgepole pine. *Can. J. For. Res.* **26**: 711-726.

YAZDANI, R. & FRIES, A. 1993: Flower abundance, phenology and pollination pattern in a *Pinus contorta* seed orchard. *In:* Proceedings from IUFRO WP 2.02.06 and Frans Kempe Symposium, Umeå: *Pinus contorta* - from untamed forest to domesticated crop. (ed. D. Lindgren), *Dept of Forest Genetics and Plant Physiology, Swed. Univ. Agri. Sciences, Report* **11**: 375-387.

YING, C. C. & ILLINGWORTH, K. 1986: Variation in cone and seed production from natural stands, plantations, and clonal banks of lodgepole pine. USDA Forest Service, Inter-mountain research station Ogden, UT. General Technical Report INT-203. pp 191-199.

YING, C. C., MURPHY, J. C. & ANDERSEN, S. 1985: Cone production and seed yield of lodgepole pine grafts. *Forestry Chronicle* **61**: 223-228.

XIE, C.-Y. & YING, C. C. 1995: Genetic architecture and adaptive landscape of interior lodgepole pine (*Pinus contorta* ssp. *latifolia*) in Canada. *Can. J. For. Res.* **25**: 2010-2021.

XIE, C.- Y. & YING, C. C. 1996: Heritabilities, age-age correlations, and early selection in lodgepole pine (*Pinus contorta* ssp. *latifolia*). *Silvae Genetica* **45**: 101-107.