

insects in the greenhouse that could have influenced the induction of PI, at least for some clones where the s. d. were high (Tab. 2). However, for most of the clones we think that these data are representative. For wound induced PI it has previously been shown that ethylene induced the expression of PI genes (KERNAN and THORNBURG, 1989). Furthermore, systemic expression of *win2* in *Solanum tuberosum* required both a putative wound signal and ethylene (WEISS and BEVAN, 1991). In this study the poor correlation between ethylene accumulation and PI production indicates that ethylene alone is not an inducer of PI (Fig. 3A).

No significant correlations between ethylene production and resistance to gall midge and rust were observed (Figs. 3B and C). Both resistance to gall midge and rust varied considerably in the clones studied, so the lack of correlation indicates that we do not have a clear relationship between ethylene production and these traits. The resistance to leaf beetle was less variable among the genetic units observed which makes it impossible to exclude a relationship between ethylene production and leaf beetle resistance ($r^2=0.2$) (Fig. 3D). The lack of correlation between the wound-induced metabolic changes studied and resistance could perhaps be explained by insufficient ethylene and PI being formed. However, that is not very probable since the amount of ethylene produced exceeds the levels of exogenously applied ethylene that in fact have been shown to increase other defence enzymes such as for example chitinase 40 to 50 times (BROGLIE et al., 1989). Obviously more detailed studies are required for evaluating induced defence reactions in *Salix*.

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Quantitative Genetic Parameters for Seven Characters in a Clonal Test of *Salix eriocephala*

II. Genetic and Environmental Correlations and Efficiency of Indirect Selection

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Summary

The relationship between seven characters that are important in biomass production was examined using 20

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clones of *Salix eriocephala*. Biomass was positively correlated with number of stems, number of branches and wood moisture content, with significant genetic correlation coefficients of 0.794, 0.740 and 0.521, respectively. Wood specific gravity was negatively correlated with stem height, stem basal diameter and wood moisture content, with significant genetic correlation coefficients of -0.872, -0.750 and -0.868, respectively.

The efficiency of indirect selection via correlated responses were assessed for number of stems, wood moisture content, wood specific gravity, and biomass. Number of stems, number of branches, and wood moisture content were identified as the potential secondary characters to which selection can be applied for more rapid improvement in biomass. No indirect selection, however, was found to be more efficient than direct selection for number of stems, wood moisture content, and wood specific gravity.

Key words: *Salix eriocephala*, quantitative genetic parameters, genetic correlation, environmental correlation, indirect selection, selection efficiency, correlated response.

Introduction

The characters to be improved in a willow breeding program vary with the purposes of the operational programs in which the material will be used. In a program for biomass production, the greatest need is to increase the growth rate (i.e., dry matter per unit of time; STOTT, 1984). Growth rate may depend on morphological characters such as tree height, diameter, and number of coppices per stool. Also, wood moisture content and specific gravity are considered to be important physical characters related to biomass growth (SENNERBY-FORSSE, 1985; KENNEY, 1990). However, the relationship between the physical and morphological characters important to willow biomass production are not known. Furthermore, examination of heritabilities and genetic gains (LIN and ZSUFFA, 1993) indicates that only limited improvement is possible in biomass. It is therefore necessary to identify secondary character(s) to which selection can be applied for more rapid improvement in biomass production.

In this paper, we discuss results of a correlation analysis for 7 characters in *Salix eriocephala* M. and their implications in actual selection for biomass production.

Materials and Methods

The plant materials and experimental designs on which this paper is based are described in a companion paper (LIN and ZSUFFA, 1993). The analysis of covariance between characters was conducted using the General Linear Model (GLM) procedure on SAS (SAS Institute Inc., 1988). The cross product matrices were computed for clone and site \times clone components. The genetic covariances between characters were obtained according to their expected mean cross products (Table 1).

The product-moment (PEARSON) correlation coefficient, or phenotypic correlation coefficient (r_p), was computed as:—(1)

$$r_p = \frac{\text{cov}(x,y)}{\text{Std}(x) \cdot \text{Std}(y)} \quad (1)$$

where $\text{cov}(x,y)$ is the phenotypic covariance between characters x and y ; $\text{Std}(x)$ and $\text{Std}(y)$ are the phenotypic standard deviations of characters x and y , respectively.

The genetic correlation coefficient (r_G) between characters x and y was calculated as (BECKER, 1984; FALCONER, 1989):—(2)

$$r_G = \frac{\text{COV}_G}{\sigma_x \cdot \sigma_y} = \frac{\text{COV}_c}{\sigma_x \cdot \sigma_y} \quad (2)$$

where COV_G is the genetic covariance between characters x and y ; COV_c is the covariance between characters x and y due to clones; σ_x and σ_y are the genetic (clonal) standard deviations of characters x and y , respectively.

The standard deviations of the genetic correlation coefficients (r_G) were calculated as (ROBERTSON, 1959):—(3)

$$\sigma(r_G) = \sqrt{\frac{(1-r_G^2)^2}{2H_x^2 H_y^2} \sigma_{(H_x^2)} \sigma_{(H_y^2)}} \quad (3)$$

where σ 's are the standard deviations; H_x^2 and H_y^2 are the heritabilities of characters x and y , respectively.

The relationship of phenotypic, genetic and environmental correlations (r_E) can be expressed mathematically (FALCONER, 1989) as:—(4)

$$r_p = H_x H_y r_G + e_x e_y r_E \quad (4)$$

where H_x and H_y are the square roots of the broad sense heritability of either individual ramets or clonal means of characters x and y , respectively; e_x and e_y are the environmental standard deviations of characters x and y , respectively

$$(e_x = \sqrt{1-H_x^2} \text{ and } e_y = \sqrt{1-H_y^2}).$$

The environmental correlation between characters x and y can thus be derived from equation (3) as:—(5)

$$r_E = \frac{r_p - H_x H_y r_G}{\sqrt{(1-H_x^2)(1-H_y^2)}} \quad (5)$$

The correlated response (CR_y) of the desired character y brought about from the selection based on a secondary character x was calculated according to the following expression (FALCONER, 1989):—(6)

$$CR_y = i H_x H_y r_G \sigma_{py} \quad (6)$$

and the percentage of CR_y is:—(7)

$$CR_y \% = \frac{i H_x H_y r_G \sigma_{py}}{\bar{y}} \times 100 \quad (7)$$

where σ_{py} and \bar{y} are the phenotypic standard deviation and the mean of character y , respectively.

Results and Discussion

Phenotypic correlations

Table 2 summarizes the results of the analysis of the phenotypic correlations (above diagonal) between the pairs of characters. At the phenotypic level, stem height was positively correlated with stem basal diameter, number of branches, and wood moisture content with significant phenotypic correlation coefficients of 0.667, 0.219, and 0.132, respectively.

Stem basal diameter was negatively correlated with number of stems ($r_p = -0.274$) and positively with wood

Table 1. — Expected mean cross products for the analysis of covariance.

Source ^a	DF	Expected mean cross products ^b
S _i	1	COV _e + 2.1176 COV _{BxC} + 6.3529 COV _{SxC} + 42.3530 COV _B + 127.0588 COV _S
B _{j(i)}	4	COV _e + 2.2329 COV _{BxC} + 44.6576 COV _B
C _k	19	COV _e + 2.1630 COV _{BxC} + 6.4890 COV _{SxC} + 12.9779 COV _C
SC _{ik}	19	COV _e + 2.1630 COV _{BxC} + 6.4890 COV _{SxC}
BC _{j(i)k}	76	COV _e + 2.3554 COV _{BxC}
e _{(ijk)l}	170	COV _e
TOTAL	289	

^a) Source of variation: S_i, site; B_{j(i)}, block within site; C_k, clone; SC_{ik}, site x clone; BC_{j(i)k}, block x clone; e_{(ijk)l}, within plot error.

^b) COV, covariance.

specific gravity ($r_p = 0.134$). The phenotypic correlation between number of stems and number of branches was highly significant ($r_p = 0.794$). A significant positive correlation was found between number of stems and wood moisture content, while a negative correlation was apparent between number of stems and wood specific

gravity, and between wood moisture content and wood specific gravity.

Biomass was significantly correlated with stem height, stem basal diameter, number of stems, and number of branches, with positive correlation coefficients ranging from 0.520 to 0.702, while the correlations between biomass

Table 2. — Phenotypic (above diagonal, N = 290) and genetic (below diagonal, N = 20) correlation coefficients, with standard deviations^a for r_G in parentheses, between seven characters of *Salix eriocephala*.

Character ^b	HT ^c	BD	NS	NB	MC	SG	WT
HT		0.667**	0.079	0.219**	0.132*	-0.075	0.702**
BD	1.319** (0.709)		-0.274**	0.081	-0.099	0.134*	0.555**
NS	-0.979** (0.036)	-0.483* (0.318)		0.794**	0.151**	-0.204**	0.520**
NB	-1.376** (0.669)	-0.406 (0.297)	0.985** (0.010)		-0.012	-0.085	0.694**
MC	1.050** (0.066)	0.923** (0.045)	-0.210 (0.266)	-0.054 (0.238)		-0.623**	0.014
SG	-0.872** (0.150)	-0.750** (0.130)	0.176 (0.263)	0.038 (0.232)	-0.868** (0.049)		0.007
WT	-0.217 (0.887)	0.254 (0.413)	0.794** (0.149)	0.740** (0.156)	0.521* (0.216)	-0.281 (0.266)	

^a) Standard deviations of r_G were calculated using heritabilities of clonal means.

^b) Characters: HT, stem height; BD, stem basal diameter; NS, number of stems/stool; NB, number of branches/stool; MC, wood moisture content; SG, wood specific gravity; WT, oven-dry biomass/stool.

^c) * significant at 0.05 level; ** significant at 0.01 level.

and wood moisture content or specific gravity were not significant statistically.

Genetic and environmental correlations

The genetic correlation coefficients and their standard deviations are also presented in table 2. At the genotypic level, stem height was negatively correlated with number of stems and wood specific gravity, with highly significant correlation coefficients of -0.979 and -0.872 , respectively, indicating that selection for higher stem height growth will be accompanied by a reduction in number of stems and wood specific gravity.

A significant negative genetic correlation was obvious between stem basal diameter and number of stems ($r_G = -0.483$), and between stem basal diameter and wood specific gravity ($r_G = -0.750$), while a significant positive correlation was evident between stem basal diameter and wood moisture content ($r_G = 0.923$), and between number of stems and number of branches ($r_G = 0.985$). Wood specific gravity was negatively related to wood moisture content, and the correlation between them was highly significant statistically ($r_G = -0.868$).

Biomass was highly correlated with number of stems ($r_G = 0.794$) and number of branches ($r_G = 0.740$). A plant with more stems and branches may occupy a larger area of growing space and have a larger leaf area. SENNERBY-FORSSE²⁾ (Personal communication), working with three *Salix* species, found that at the early growing stage, total leaf area is negatively correlated with the stem biomass. When the trees become older, however, the correlation becomes positive and stronger. This is because at the early stage, leaf growth takes away part of the total resource from stem biomass growth, thus there is a negative correlation between leaf area and stem biomass. Once development reached a certain point, the leaves produce more photosynthates than they consume, which contributes to stem biomass growth. If this is the case, a plant with more stems and branches will eventually exhibit a higher biomass yield.

A significant, positive correlation ($r_G = 0.521$) exists between wood moisture content and biomass. However, biomass was not significantly related to stem height, stem basal diameter and wood specific gravity at the genetic

²⁾ Swedish University of Agricultural Sciences, Uppsala, Sweden.

level, although the phenotypic correlations were significant. This indicates that the significant phenotypic correlations between biomass and the latter characters were mainly under environmental influence, and can only be important in a selection index to correct for environmental influences (FALCONER, 1989).

The genetic correlation coefficients between stem height and stem basal diameter, number of branches and wood moisture content exceeded the theoretical limits of 1 or -1 . Genetic correlation coefficients exceeding unity are not uncommon in forest genetics literature. For example, in another willow clonal test, KENNEY (1990) found that 3 of the genetic correlation coefficients between the chemical characters exceeded theoretical limits. Other examples were found in Caribbean pine (LEDIG and WHITMORE, 1981); in Norway spruce (BENTZER *et al.*, 1989); in black locust (MEBRAHTU and HANOVER, 1989); and in *Pinus caribaea* var. *hondurensis* (HARDING *et al.*, 1991).

Genetic correlation coefficients exceeding the theoretical limits are a consequence of particularly low estimates of heritabilities for the character(s) concerned (LEAMY, 1977), as seen in LEDIG and WHITMORE (1981) and KENNEY (1990). In the current study, the coefficients over the limits were all associated with stem height which has very low heritability ($H^2_i = 0.01$, $H^2_c = 0.05$) (LIN and ZSUFFA, 1993).

Correlations over the theoretical limits should not be interpreted as highly (strongly) positive or negative. In the current study, the genetic correlation coefficients exceeding unity generally have very large standard deviations, and also have significant or highly significant environmental correlation coefficients (Table 3). These indicate that the significant phenotypic correlations between these pairs of characters were determined not only by genetic correlations but also by environmental correlations.

Correlated responses and efficiency of indirect selection

Table 4 shows the correlated responses, expressed as a percentage of the means, for the characters on the vertical axis (i. e., number of stems, wood moisture content, wood specific gravity, and biomass) when selection is applied to the characters on the horizontal axis. The direct selection responses (expected gains) were presented for comparison. A negative value suggests that the 2 characters respond to selection in opposite directions due to their negative genetic correlation.

Table 3. — Environmental correlation coefficients (r_E) between 7 characters of *Salix eriocephala*. Above diagonal: r_E calculated using heritabilities of individual ramets. Below diagonal: r_E calculated using heritabilities of clonal means.

Character	HT ^a	BD	NS	NB	MC	SG	WT
HT		0.665**	0.118	0.288	0.022	0.0002	0.732**
BD	0.615**		-0.249	0.145	-0.293	0.385	0.580**
NS	0.280	-0.171		0.760**	0.236	-0.345	0.496*
NB	0.650**	0.405	0.639**		-0.001	-0.134	0.698**
MC	-0.549*	-0.958**	0.517*	0.045		-0.512*	-0.062
SG	0.300	0.936**	-0.622**	-0.258	-0.193		0.071
WT	0.904**	0.687**	0.378	0.687**	-0.424	0.274	

**) significant at 0.05 level; **) significant at 0.01 level.

Table 4. — Genetic gains (bold) and correlated responses of the characters on vertical axis (% of mean) when clonal selection is applied to the characters on horizontal axis: ($i = 1.372$).

	HT	BD	NS	NB	MC	SG	WT
Selection based on clonal means:							
NS	-5.9	-6.9	16.2	19.0	-4.4	3.8	11.7
MC	2.0	1.7	-0.4	-0.1	2.7	-2.4	1.0
SG	-1.8	-2.4	0.6	0.2	-4.0	4.7	-0.9
WT	-0.7	1.8	6.4	6.9	5.4	-3.0	7.4
Selection based on individual ramets:							
NS	-2.3	-3.8	9.6	10.3	-2.8	3.0	5.2
MC	0.8	0.9	-0.3	-0.1	1.8	-1.9	0.4
SG	-0.7	-1.3	0.4	0.1	-2.6	3.8	-0.4
WT	-0.2	1.0	3.8	3.8	3.5	-2.4	3.3

FALCONER (1989) pointed out that indirect selection is practically preferable to direct selection when: 1) the desired character is difficult to measure with precision such that the errors of measurement reduce heritability; 2) the desired character is measurable in one sex only, but the secondary character is measurable in both; and 3) the desired character may be costly to measure and it may be economically preferable to select for an easily measured correlated character (see also SEARLE, 1965; WEISSENBERG, 1976). However, indirect selection can only be more efficient than direct selection when the secondary character has a substantially higher heritability, and the genetic correlation between the 2 characters is high.

Number of Stems

Number of stems was examined as a desired character since it represents the coppicing ability of a willow stool after harvesting. The correlated responses identified in selection based on clonal means indicate that a large genetic gain (16.2%) was possible through direct selection for number of stems. The only correlated response that surpassed this gain was from the indirect selection for number of branches (19.0%), because number of branches had a higher heritability, and was highly correlated with number of stems (Table 2).

Selection for stem height or diameter growth, or wood moisture content may hinder the progress in number of stems by 4.4% to 6.9% because of the negative genetic correlations between them, while selection for higher biomass growth would bring about 11.7% improvement in number of stems.

Moisture content

The gain in wood moisture content obtainable from direct selection was not large (2.7% and 1.8%, respectively, based on clonal means and individual ramets), but could be worthwhile, since wood moisture content may become one of the criteria in selection of superior clones, especially for drier sites. Selection for greater stem height, stem basal diameter or biomass growth will not affect the improvement in wood moisture content. However, the

correlated response of wood moisture content to selection for higher wood specific gravity should not be overlooked, since a 2.4% and 1.9% reduction in wood moisture content based on clonal means and individual ramets, respectively, could be expected from selection for higher wood specific gravity due to their negative genetic correlation.

Although the indirect selection for lower wood specific gravity can theoretically bring slightly greater improvement for wood moisture content than direct selection based on individual ramets (Table 4), wood specific gravity should not be used as a secondary character because wood specific gravity is more difficult to measure than moisture content, and low specific gravity is not desirable in biomass production.

Specific gravity

KENNEY (1990) pointed out that while moisture content has relatively little effect on the biochemical conversion process, specific gravity should be taken into consideration in energy conversion using willow feedstock. Specific gravity is also important to yield. SENNERBY-FORSSE (1985) found that an increase in specific gravity from 0.3 g/cm³ to 0.4 g/cm³ would raise dry matter production by 25% provided that volume growth remained the same.

Progress in improving wood specific gravity may be offset by selection for other characters with which it is negatively correlated. For example, the reduction in wood specific gravity resulting from selection for higher wood moisture content was large (4.0% and 2.6% based on clonal means and individual ramets, respectively).

Since wood specific gravity had the highest heritability among the characters examined, no indirect selection was identified to be more efficient than direct selection.

Biomass

A 7.4% genetic gain in biomass was achievable from direct clonal selection based on clonal means, while a 6.4%, 6.9% and 5.4% increase in biomass (correlated response) could be expected from indirect selection for number of stems, number of branches, or wood moisture content, respectively. A 3% and 2.4% reduction in biomass

could result from selection for higher wood specific gravity, based on clonal means and individual ramets, respectively.

If clonal selection is based on the performance of individual ramets, selection for more stems or branches, or higher moisture content is 8% to 16% more efficient than direct selection for biomass (Table 4), although the gain in biomass may still not be significant. Therefore, number of stems, number of branches and moisture content should be identified as potential secondary characters in indirect selection for willow biomass.

Indirect selection for biomass may be of practical advantage even though gains are not as large as those predicted for direct selection. In order to assess biomass, the trees must be harvested, and both green weight and moisture content measured to calculate oven-dry weight. It is therefore more difficult to measure biomass with precision than to count the number of stems or branches. Furthermore, harvesting the trials is not always an option since a genetic test usually serves multiple purposes. Selection for more stems or branches or higher wood moisture content based on clonal means will result in slightly less improvement in biomass than direct selection, but still be a potential alternative in a willow breeding program.

Conclusions

Many characters examined in this paper are correlated phenotypically, but are not necessarily correlated genetically. Only significant genetic correlations can readily be utilized in indirect selection for the characters important to willow biomass production. For number of stems, wood moisture content, and wood specific gravity, direct selection is better than indirect selection. For biomass, however, more rapid improvement can be achieved through indirect selection on individual ramets for more stems or branches, or higher wood moisture content.

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Temporal Variation in the Outcrossing Rate in a Natural Stand of Western White Pine

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Abstract

Population and individual-tree multilocus outcrossing rates were estimated for three successive pollination years (1983 to 1985) in a natural stand of white pine (*Pinus monticola*) using allozyme variation at 6 loci. Population outcrossing rate estimates were nearly static and did not differ significantly over the three years studied. Individ-

ual-tree outcrossing rate estimates were dynamic and varied within and among years. Some consistent "in-breeders" and "outcrossers" were identified, however, the outcrossing rate of most trees varied, indicating that these variations were caused by the pollination biology, phenology, or ecology. Our results parallel those reported in most conifer outcrossing-rate studies and support the hypothesis that outcrossing rate is under genetic control and that the among-tree temporal variation is mainly environmental. The observed fluctuation of individual-tree outcrossing-rate estimates indicates that parental ranking using wind-pollinated seeds requires statistical adjustment on the individual tree within a crop year.

Key words: *Pinus monticola*, mating system, temporal variation, outcrossing, selfing.

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