

ON THE GENOTYPE-BY-TIME INTERACTION: GROWTH INCREMENTS AND THEIR EFFECT ON GENETIC GAIN

F. Zamudio

Abstract.- A method useful to quantify the effect of genotype-by-time interaction (GxTime) for the genetic gain of cumulative traits is presented. Results indicate that the response to selection for cumulative traits can be partitioned into two components which reflect the contribution from the additive effect of growth increments and the contribution from the interfamily stability over time. A selection index which combines information for the intra- and interfamily variation over time is also developed. Data from four progeny tests of *Pinus tecunumanii* established in South America, as part of the international program conducted by the CAMCORE cooperative, were used to assess the method. The estimation of selection efficiency can be used to diagnose the effect of time in response to selection in a breeding program, to compare the chances for early selection in different locations, and to select individual trees for greater and more steady growth over time. As expected, the predicted response from the index selection exceeded the predicted response to individual selection for cumulative height at every test site.

Keywords: Early selection, *Pinus tecunumanii*, provenance/progeny tests, selection index.

INTRODUCTION

As more information from genetic tests become available, tree breeders increasingly turn their attention to developing optimum procedures for selection within these tests. One of these procedures encompass the use of correlated trait selection. Its most important application in forestry is to estimate mature tree performance by assessing progenies when they are young. The economic advantages of being able to observe traits in young seedlings and possibly shorten the generation interval are often great enough that juvenile selection becomes highly desirable. The success of early selection relies on the assumption that the genes and growth processes involved in early and late stages of ontogeny are the same and hence juvenile expression is correlated with mature tree performance. However, this is rarely the case because both the physiological system and gene expressions can change with the accumulation of size and through ontogeny (Namkoong et al., 1988).

Even though juvenile growth processes might not exactly be the same as those in adult trees, some growth processes may be identical, and some traits may foretell what later behavior will be even if it is not identical (Namkoong and Kong, 1989). The search for these traits motivated Nanson (1970) to develop a theory for selection at young ages in forest trees. Baradat (1975) later proposed and provided computational procedures for including juvenile-mature

Research Assistant. CAMCORE cooperative. College of Forest Resources. North Carolina State University. Box 7626. Raleigh, NC 27695-7626.

genetic covariances in combined and multi-trait indexes. Nevertheless, it has been recognized that estimates of breeding values from young sibs may be unstable and subject to rank changes over time. Maternal effects, unique characteristics of juvenile physiology, or genotype by year interaction have been mentioned as some of the possible causes for such instability (Stonecypher and Arbez, 1976).

The main objectives of the paper is to present a method useful to quantify the effect of GxTime interaction on the genetic gain of cumulative traits. The method partitions the genetic gain for cumulative traits into different components which reflect the effect of growth increments, and develops a selection index which combines information from the intra- and interfamily variation over time. Data from four progeny tests of *Pinus tecunumanii* established in South America (Dvorak and Donahue, 1992) were used to assess consequences of GxTime interaction in genetic gain and index selection.

METHOD

Rationale.- Zamudio (1995) showed that the heritability estimate for a cumulative trait measured at age C can be expressed as a function of the genetic control at different growth periods adjusted by the phenotypic variance for the cumulative growth at age C, plus a function of the genetic association among growth increments:

$$h^2(\mathbf{C}) = E_{t'} h_{t'}^2 g_{t'}^2 \mathbf{NP}(\mathbf{C}) + (1/\mathbf{0}, \mathbf{y}) E_{t'} c_{t'} E_{t' < t} a_{t' t'} \mathbf{NP}(\mathbf{C}) \quad (1)$$

where 0_{xy} is the coefficient of coancestry; h^2 , a^2_{ft} , and $(3^{-2})_{pt}$ are the heritability, family variance component, and phenotypic variance for the growth increment at period t-th, respectively; and $a_{ftt'}$ is the family covariance components between growth periods t- and t'-th. The first element in expression (1) can be considered as a "relative cumulative genetic control" (RCGC) and the second element can be defined as a "time stability factor" (TSF). Its value is unique to a set of families established at a particular site and summarizes the effect of the interfamily stability component of the GxTime interaction (Zamudio, 1995). A high positive value for $a_{ftt'}$ means that family growth reflects a positive pattern during intervals t and t'; a value of $a_{ftt'}$ close to zero suggests that families did not show any relation in their growth increment between periods t and t'; and a negative value of $a_{ftt'}$ implies that families had a negative growth pattern from periods t to t'. As trees age, the inclusion of new family covariances as part of TSF can have a positive, neutral, or negative effect in the expression of genetic control at successive ages. Thus, it could be hypothesized that the higher the value of TSF for a particular site the better the chance for early selection to succeed. Zamudio (1995) also developed this idea by partitioning the genetic gain due to direct individual selection into two components:

$$\blacklozenge G(\mathbf{C}) = E_{t'} \mathbf{G}, \mathbf{A} \mathbf{G}, (\mathbf{a}, \mathbf{Y}'\mathbf{VP}(\mathbf{C})) + 2 E_{t'} c_{t'} E_{t' < t} \mathbf{A} \mathbf{G} (\mathbf{A}_{t'}, \mathbf{P}_{t'}) (\mathbf{op}_{t'} / \mathbf{i} / \mathbf{VP}(\mathbf{C})) \quad (2)$$

The first component of (2) is the contribution to the total genetic gain from the additive effect of growth increments, and it encompasses the sum of genetic responses for each increment (\bullet GO adjusted by the ratio of their phenotypic variance with respect to the phenotypic variance for the cumulative trait at age C. The second component is the contribution to the total genetic

gain due to the interfamily stability over time or TSF for a particular site. It corresponds to the sum of correlated responses due to selection at earlier growth periods [$\bullet \mathbf{G}(\mathbf{A}, \mathbf{P})$], and it is also adjusted by the ratio of phenotypic variance at earlier growth increments with respect to the phenotypic variance at age \mathbf{C} . It is clear that the higher the family contribution to the interfamily stability, the higher the TSF for a test will be, and the better the chance to increase the genetic gain for cumulative growth.

Numerical Example.- The data used in this example are from four provenance/progeny tests comprising open pollinated half-sibs families of *Pinus tecunumanii*, collected from mother trees in the Mountain Pine Ridge, Belize, and established during 1982 in four different locations in South America as part of the international program conducted by the CAMCORE cooperative and its members (Dvorak and Donahue, 1992). The tests included in this paper are recognized as ARACRUZ 1 and 2 (established by Aracruz Florestal in Brazil), PROFORCA (established by Productos Forestales del Oriente C. A. in Venezuela), and JARI (established on lands of JARI Florestal also in Brazil). Trials were planted following a randomized complete block design, where each family was planted at 3x3 m (10x 10 feet) spacing in six-tree row plots. More details about the trial establishment can be found in Jurado-Blanco (1989).

Measurements for total height (m) were obtained at three, five, and eight years of age after planting. Growth increments for individual trees were obtained by subtracting the cumulative growth at a particular age from the cumulative growth at the age immediately following. Considering H_t as the height increment at the t-th growth period after planting, there were three growth increments: H_1 = growth during ages 0 to 3; H_2 = growth during ages 3 to 5; and H_3 = growth during ages 5 to 8.

PROC MIXED (SAS Institute, Inc. 1992) was used to obtain restricted maximum likelihood (REML) estimators for the different variance components for each growth period and covariance components between different growth periods. The value of 24 (twice the coefficient of coancestry among individuals from the same family) was assumed to be 0.33, and used to estimate the additive genetic variances and heritability for each growth increment and additive genetic covariances between paired growth increments. Progenies established in the field tests originated from mother-trees occurring in natural stands, where there was a good chance for self-pollination and mating among related neighboring trees, which implied that families may present some degree of inbreeding (Squillace, 1974).

The genetic response to direct individual selection was calculated using expression (2) and the methodology presented by Zamudio (1995). The proportion selected (10%) was maintained constant through the comparison of responses (selection intensity = 1.76). Comparisons of the response to selection due to additive effects of increments and interfamily stability over time were made within each test and between tests to determine the effect of stability in the genetic response for cumulative growth. A selection index which maximizes the selection response for cumulative height at age 8 was developed. The index included the information about inter- and intrafamily variation for the three growth increments and was expressed as

$$\mathbf{I} = (\mathbf{b}_1 \mathbf{f}_1 \quad \mathbf{w}, \mathbf{e}_1) + (\mathbf{b}_2 \mathbf{f}_2 + \mathbf{w}_2 \mathbf{e}_2) + (\mathbf{b}_3 \mathbf{f}_3 + \mathbf{w}_3 \mathbf{e}_3),$$

where f_i respectively; b_i and e_t respectively. The genetic response in the index was compared to the response to direct selection for cumulative height at age 8.

RESULTS AND DISCUSSION

Phenotypic correlations among growth increments and cumulative growth are given in table 1. The largest positive phenotypic correlations between H_1 and H_2 were almost zero but the largest negative value was -0.477 at PROFORCA. The largest positive correlation between H_1 and H_3 was 0.185 at ARACRUZ 1, and three out of four correlations between H_1 and H_3 were also negative. Results from this study clearly show that GxTime interaction is present in the four CAMCORE tests sites analyzed, as reflected by the low and/or negative phenotypic correlations among increments.

TABLE 1.- Phenotypic correlations between growth increments and between cumulative growth for height

TESTS	PHENOTYPIC CORRELATIONS				TESTS	CUMULATIVE GROWTH	
	GROWTH INCREMENTS					H5	H8
	H2	H3					
H_1	ARACRUZ 1	0.008 ns	0.185 ns	H3	ARACRUZ 1	0.781 **	0.669 **
	ARACRUZ 2	-0.191 ns	0.129 ns		ARACRUZ 2	0.724 **	0.685 **
	PROFORCA	-0.477 *	0.017 ns		PROFORCA	0.186 ns	0.220 ns
	JARI	0.068 ns	-0.089 ns		JARI	0.679 **	0.606 **
H_2	ARACRUZ 1		0.012 ns	H5	ARACRUZ 1		0.800 **
	ARACRUZ 2		-0.157 ns		ARACRUZ 2		0.840 **
	PROFORCA		-0.259 ns		PROFORCA		0.716 **
	JARI		-0.342 *		JARI		0.775 **

Not surprisingly, the estimators of correlations for cumulative growth were all positive. ARACRUZ 1 showed the largest correlation between H3 and H5, and PROFORCA the lowest value (despite having the largest phenotypic variance for H3, 1.2499). With the exception of PROFORCA, correlations between H3 and H8 decreased and the largest correlations were recorded between H5 and H8. These values ranged from 0.716 at PROFORCA to 0.84 at ARACRUZ 2.

Estimates of different genetic parameters are presented in table 2. Heritabilities for increments showed a tendency to diminish over the time. The PROFORCA and JARI test sites showed negative additive genetic covariances for height growth among periods 1 vs 2 and 2 vs 3. As a result, TSF was negative at PROFORCA and also low at JARI. The reasons for these negative covariances could be the results of adverse environmental conditions that predominate at both sites (Zamudio, 1992).

Predicted responses due to the effect of each increment and correlated responses due to interfamily stability among growth periods (TSF) are given in table 3. The largest contribution from the additive effect of increments to the total genetic response was recorded at PROFORCA (0.793/0.598=133 %). However, the correlated response due to interfamily stability was negative at this test site, which had the effect of subtracting gain from the response due to

the additive effects and reducing the total genetic response predicted at age 8. Nevertheless, the largest contribution of the correlated response due to stability to the total gain was recorded at ARACRUZ 1 (0.309/0.779=40 %), followed by ARACRUZ 2 (0.38/0.971=39 %), which implies that these sites present the best chances for early selection on height.

TABLE 2.- Genetic parameters for height. Subscript numbers represent the different growth periods. VP(8) and $h^2(8)$ are the phenotypic variance and heritability at age 8 respectively; w_t is the heritability for t-th growth period; $C(A_t, A_{t'})$ is the additive genetic covariance between growth increments t- and t'-th; RCGC is the relative cumulative genetic control; and TSF is the time stability factor.

TEST SITE	GENETIC PARAMETERS FOR HEIGHT INCREMENTS									
	VVP(8)	h^2_1	h^2_2	$w_{1/2}$	COVARIANCES			RCGC	TSF	$h^2(8)$
					$C(A_1, A_2)$	$C(A_1, A_3)$	$C(A_2, A_3)$			
ARACRUZ 1	1.855	0.322	0.149	0.071	0.048	0.075	0.040	0.144	0.095	0.239
ARACRUZ 2	1.317	0.337	0.109	0.143	0.032	0.028	0.082	0.255	0.163	0.418
PROFORCA	1.693	0.068	0.195	0.059	0.223	0.087	-0.230	0.266	-0.065	0.201
JARI	1.348	0.293	0.120	0.049	0.106	-0.052	-0.040	0.195	0.016	0.211

TABLE 3.- Genetic response to direct selection in cumulative height at age 8. Subscript numbers represent the different growth periods. AG_t is the genetic response for the t-th growth increment; AG(A_t, P_t) is the correlated response for growth increment t'-th after applying indirect selection at growth period t-th; and AG(8) is the total genetic response at age 8 and is the sum of responses due to additive affects for increments and the correlated response due to stability over time.

TEST SITE	RESPONSE TO INDIVIDUAL SELECTION FOR CUMULATIVE HEIGHT AT AGE 8								
	AG _t (m)	$\bullet G_2$ (m)	$\bullet G_3$ (m)	DUE TO ADDITIVE EFFECTS	AG(A ₂ , P ₁) (m)	$\bullet G(A_3, P_1)$ (m)	AG(A ₃ , P ₂) (m)	DUE TO INTERFAMILY STABILITY	TOTAL RESPONSE $\bullet G(8)$ (m)
ARACRUZ 1	0.550	0.217	0.141	0.470	0.087	0.136	0.085	0.309	0.779
ARACRUZ 2	0.563	0.149	0.179	0.591	0.059	0.052	0.186	0.380	0.971
PROFORCA	0.134	0.596	0.128	0.793	0.351	-0.137	-0.233	-0.195	0.598
JARI	0.428	0.205	0.077	0.462	0.225	-0.110	-0.072	0.038	0.500

A better way to compare results is by dividing the total genetic response by the test means at age 8. The largest predicted response was at ARACRUZ 2 (0.971/12.5=7.8 %), followed by ARACRUZ 1 (0.779/11.6=6.7%), PROFORCA (0.598/14.4=4.2%), and JARI (0.5/14.4=3.5%). These results demonstrate the effect of interfamily instability. ARACRUZ 2 presented a low relative contribution of response due to additive effects of increments (0.591/0.971=61 %) than PROFORCA (0.793/0.598=133 %), but families established at PROFORCA were more unstable over the time than families at ARACRUZ 2. This triggered a lower total response to selection in PROFORCA than in ARACRUZ 2. This type of analysis warns breeders to be cautious when comparing genetic response at different sites. A negative contribution from the interfamily stability implies that the progeny of some trees with unstable growth could produce progenies that may perform well during the first five years but may change enough to decrease their growth in the next period(s). This would result in losing potential gain over time in the next breeding generation.

Values for the regression coefficients and response to selection in the index are given in table 4. The percentage of genetic response with respect to the test mean for cumulative growth at age 8 is also given for each test site. The ARACRUZ 1 test site ranked first for the predicted response. Conversely, JARI had the lowest predicted response.

TABLE 4.- Regression coefficients and response to selection in the index for height. The percentage of genetic response with respect to the test mean for cumulative height at age 8 is also given for each test. The efficiency was calculated as the ratio between the genetic response in the index and the genetic response due to direct individual selection for the cumulative growth at age 8.

TEST SITE	REGRESSION PARAMETERS FOR TOTAL HEIGHT AT AGE 8						GENETIC RESPONSE IN THE AG(AI)	TEST MEAN AGE (m)	PERCENTAGE OF GAIN (RANKING)	EFFICIENCY OF RESPONSE IN THE INDEX OVER SELECTION
	b ₁	b ₂	w ₂	b ₃	w ₃	INDEX (m) EIGHT (%) THE INDIVIDUAL				
ARACRUZ 1	1.050	0.729	1.044	0.376	1.054	0.124	1.60	11.6	13.8 (1st)	205
ARACRUZ 2	1.053	0.806	1.054	0.707	1.036	0.577	1.71	12.5	13.7 (2nd)	176
PROFORCA	-7.865	0.875	0.417	0.571	-9.323	-0.044	1.67	14.4	11.6 (3rd)	276
JARI	1.058	0.584	1.008	0.180	1.030	0.018	1.10	14.4	7.4 (4th)	129

Implications to Breeding. Results in this study indicate that the simple observation of age-age phenotypic correlations for cumulative growth can be misleading. Because GxTime interaction is mainly the effect of two components, namely interfamily and intrafamily stability (Zamudio, 1995), and the cumulative growth is a function of successive increments, the gain from early selection should be tested by analyzing how the performance of different families can affect the covariances among family and residual effects over time for the different growth increments. There will be families whose contribution to the covariance among family effects over time will be positive, but their covariance for residual effects over time can be positive or negative which affects the estimation of genetic gain at cumulative ages. This happened at the PROFORCA test site. Thus, families should not only be classified by their cumulative growth but also by their contribution to the two GxTime interaction components. The next logical step is a further comparison with their growth rate to fully detect which individuals and/or families are good candidates for early positive response to selection.

The estimation of the effect of instability on response to individual selection at cumulative ages is function of the heritability for each growth increment and genetic covariances between increments at different periods. It assumes that the same individuals selected at age 8 are also selected for each period but, given the effect of instability over time (reflected as imperfect phenotypic correlations between paired growth increments), probably some individuals would have to be replaced by others at different periods. Thus the first component in expression (2) may be underestimating the potential response to direct selection. Nevertheless, the usefulness of partitioning the estimated genetic response into cumulative effects and instability contributions has to be regarded as a diagnostic tool for breeders interested in knowing how much gain is lost due to the effect of GxTime interaction.

Genetic covariances or correlations among age-specific trait values quantitatively describe the genetic link between expressions of the same trait at different points in ontogeny. These genetic links between age-specific trait values have been mentioned to be the result of pleiotropy and linkage disequilibrium (Cherevud et al, 1983). In this case, the effects of one gene on the

phenotype is expressed at more than one age. But the differences in results indicate that there is also a strong influence of non-genetic factors on the expression of the trait through ontogeny. The fact that the interfamily stability component of GxTime interaction changed in different environments reflect the presence of genotype-by-time-by-environment interaction. This higher order interaction should suggest that breeders carefully assess selection strategies by measuring the impact of genotype-by-environment interaction as a main criteria, and also by considering how progenies evolve through ontogeny within each population test.

Though the response in the index looks promising at PROFORCA, results should be critically reviewed. A careful observation of the regression parameters for the index at this test site show that the b_1 and b_3 coefficients were the largest negative value among the total number of parameters estimated for the trait. This implies that if a candidate family had a highly positive family effect (family mean deviation from the total test mean) for the first or third growth period, or both, its index value can be very low. Because of the negative genetic correlations among periods 1 vs 3 and 2 vs 3, the interfamily instability component of GxTime in PROFORCA had a negative impact on the genetic response to selection for cumulative height at age 8. The high efficiency in response from using the index (table 4) and the negative regression coefficients imply that the index can successfully increase the genetic response to selection in height, but it will tend to favor families which on the average will grow less during periods 1 and 3 (negative family effects). Negative parameters have also been reported elsewhere. For example, Namkoong and Matzinger (1975) also estimated a mixture of positive and negative regression parameters to various growth points when selecting *Nicotiana tabacum* based on eight periodic heights. They hypothesized that some physiological constraints prevented the simultaneous seasonal increase in height growth causing a midseasonal drop in the index coefficients. Magnussen and Kremer (1993) also recorded negative index regression coefficients derived for selection of height in maritime pine (*Pinus pinaster* Ait.). They indicated that phenotypic height between ages 5 and 15 were inefficient as indicators of overall potential good height growth.

CONCLUSIONS

A comparison of the efficiency of response to selection in the index v/s individual selection for the cumulative height can be used to diagnose the effect of time in a breeding program. to compare the chances for early selection in different tests, and to select individual trees for higher and steady growth over time. As expected from theory, the predicted response in the index always exceeded the predicted response to individual selection for cumulative height at every test site.

A selection strategy based on the index suggests that ARACRUZ 1 had trees with the largest and most stable growth. The presence of a strong GxTime interaction for cumulative height in PROFORCA indicates that early selection will be less successful there than at other locations.

The results indicate the presence of a genotype-by-time-by-environment interaction that should be further investigated. Changes in the response to individual selection for cumulative height from one test to another suggests that progenies from *P. tecunumanii* can strongly and simultaneously interact over the time and planting location.

It was shown that the genetic response to individual selection depends on covariances between increments. Consequently, an early selection procedure can be optimized by selecting families and/or individuals which maximize the response function due to interfamily stability over time and thus choosing the moment when the response function due to stability over time show a maxima. This hypothesis needs to be further supported by the assessment of data collected at later ages.

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