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Genetic analysis of growth curves for a woody perennial species, *Pinus taeda* L.

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Abstract Inheritance of growth curves is critical for understanding evolutionary change and formulating efficient breeding plans, yet has received limited attention. Growth curves, like other characters that change in concert with development, often have higher heritability than age-specific traits. This study compared genetic parameters of height-growth curves with those of age-specific heights for a conifer, *Pinus taeda* L. Growth curves were fitted with: (1) a linear regression model, and (2) a non-linear model based on Richards' function using two sources of height data: two six-parent diallel tests assessed at age 2 to 10 years and two tests from a nested mating design with 222 parents assessed at 1 to 25 years. Additive genetic control of growth-curve parameters was moderate ($h^2 = 0.06$ to 0.26) and slightly lower than that for age-specific heights. Additive variance exceeded dominance variance for rate and shape parameters, but not for the asymptote. Genetic correlations among growth-curve parameters were high. Early selection on height was as efficient as selection on growth-curve parameters.

Keywords Richards' function · Heritability · Age–age correlations · Height · Conifers

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Introduction

Genetic analysis of growth curves has received limited attention. Growth curves are considered infinite-dimensional traits (Kirkpatrick and Heckman 1989) or function-valued traits (Pletcher and Geyer 1999) because the trait can be described by an infinite set of measurements. Growth curves are important in ecology because evolutionary changes in morphology shift during ontogeny (Alberch et al. 1979). They are important to breeding plans because growth curves shift in response to selection (Barbato 1991; Rekaya et al. 2000).

A response to selection altering the shape of the growth curve is feasible. Genetic analysis of growth curves has been applied to lactation curves of dairy cows (Shanks et al. 1981; Rekaya et al. 2000), body weight-age curves in beef cattle (DeNise and Brinks 1985), body weight-age curves in poultry (Barbato 1991), body weight-age curves in mice (McCarthy and Bakker 1979) and body length-age curves in fish (Rocchetta et al. 2000). Half-sib families vary in the asymptote but not in the shape parameter of growth curves in *Pinus taeda* (Nance and Wells 1981; Buford and Burkhart 1987). No genetic parameter estimates have been reported for these studies. Heritability for growth curves is moderate (individual $h^2 = 0.09$ to 0.14) and lower than that for age-specific heights in *Pinus pinaster* (Maugnussen and Kremer 1993). Estimates for growth curves in livestock (Shanks et al. 1981; DeNise and Brinks 1985; Rekaya et al. 2000) tend to be higher than those for plants, but genetic analysis of growth curves has received less attention in plants (Maugnussen and Kremer 1993).

Determining the genetic control of growth curves is important because they correct for irregularities in the data caused by human error or random environmental effects and allow for prediction of growth at ages where measurements are missing. Our first hypothesis is that heritability estimates of growth curves will be higher than those for age-specific heights because growth curves reduce environmental and measurement errors. Our second hypothesis is that early selection on the growth curves will result in higher gain at maturity compared to early selection on age-specific heights. This is based on the fact that genetic correlations between early height and height at harvest tend to be low. Growth-curve parameters may be better indicators of growth patterns and thus likely to be related to mature growth.

The study objectives were as follows: (1) to estimate the genetic parameters of growth-curve parameters for *P. taeda* and to compare these estimates to those of age-specific heights, and (2) to determine the efficiency of early selection.

Materials and methods

Source of genetic test data

The WEY dataset was from two six-parent diallels planted at six locations; four in North Carolina and two in Oklahoma. A total of 30 full-sib families from the U.S. Atlantic Coastal Plain were planted in single-tree plots in 36 replicates in each test. The WEY tests were assessed for height at ages 2 to 7 and 10 years.

The genetic test data were from the International Paper Company (IP) and the Weyerhaeuser Company (WEY). The IP tests are described in detail by Balocchi et al. (1993). The dataset is from 222 families mated in a nested mating design and planted in two first-generation genetic tests in Georgia. Seedlings were planted in 12-tree row plots with three replications. Systematic thinning was carried out in the tests at age 10 years. The tests were assessed at 1–10, 13–17 and 25 years of age. Statistical analyses were carried out only on trees that had measurements at 25 years and for height at ages greater than 3 years.

Growth-curve parameters

Most of the trees in the WEY dataset were still actively growing and thus had no apparent asymptote. In these young tests a simple linear model was fitted for estimating the rate parameter. The linear model for the WEY dataset was:

$$H = \beta_0 + \beta_1 * \mathrm{age} + \varepsilon, \qquad (1)$$

where H is the height at a given age, β_0 is the intercept, β_1 is the rate parameter and ε represents the random error.

The IP tests were older and most of the trees were approaching, or had reached, their asymptotes. A non-linear model based on the Richards' function (Richards 1959) was fitted to the IP dataset. Parameters of the growth curves from the Richards' function have meaningful interpretation in forestry (Fekedulegn et al. 1999). The Richards' function has been used for smoothing growth curves (Balocchi et al. 1993) in *P. taeda*. The Richards' function is a flexible model that fits a unique growth function to each tree:

$$H = A(1 - \exp(-b * \mathrm{age}))^c + \varepsilon, \qquad (2)$$

where H is the height at a given age, A is the asymptotic or maximum height, b is the rate parameter, c is the shape parameter and ε represents the random error. The asymptote represents the maximum height of trees and the rate parameter is the rate at which height approaches the asymptote. The shape parameter is the rate at which height approaches the asymptote at inflection point (Fitzhugh 1976). A linear model, similar to the one used for the WEY dataset, was fitted to 4 to 10 year data from the IP dataset and the estimated rate parameter compared with that estimated from the WEY dataset.

The parameters for the growth functions and predicted values for height were estimated using PROC NLIN and PROC REG functions in SAS (SAS Institute Inc 1985). The parameters of each curve were estimated using the least squares method. For non-linear models, the asymptote was constrained on the biological assumption that the asymptote is reached by age 50 years. A growth model developed by Amateis et al. (1984) for *P. taeda* from the Coastal Plain region was used to estimate the maximum height or asymptote. The model is as follows:

$$\mathrm{Ln}(H_{50}) = \mathrm{Ln}(H_{25})(25/50)^{b_1 exp(b_2(1/50-1/25))}, \qquad (3)$$

where H_{50} = maximum height at age 50 (asymptote), H_{25} = maximum height at age 25 (33 m from the IP dataset), $b_1 = -0.11092$, $b_2 = -1.9036$.

Using this model, the maximum height at 50 years was estimated to be 44 meters. For calculations of growth curve parameters, the asymptotes for the trees were constrained to be equal or less than 44 meters. A sensitivity analysis using three asymptotes (40, 44 and 47 m) tested whether the site index values changed the genetic parameter estimates. Three different values of A, b and c were obtained from the non-linear model.

Genetic parameter estimates

Genetic parameters for height, predicted height and growth curves were estimated using the individual tree model ASREML (Gilmour 1996). Individual-tree heritabilities and their standard errors were estimated using the following univariate model:

$$Y_{ijkl} = \mu + S_i + R_j + F_k + A_l + \varepsilon_{ijkl}, \qquad (4)$$

where Y_{ijkl} is the observation on the k^th^ tree in the i^th^ replication and in the j^th^ family, μ is the overall mean, S_i is random effect of the i^th^ location, R_j is random effect of the j^th^ block, F_k is random effect of the k^th^ family (male × female interaction), A_l is additive effect of the l^th^ tree and ε_{ijkl} the within-plot error. The individual tree model fits a random effect for the additive genetic merit or breeding value of each tree, both for trees with records and those that are represented as parents, and incorporates all relationship information in the analysis. Since the additive variance was estimated by A_l in the model, the full-sib family variance component (σ^2_F) was interpreted as $1/4\sigma^2_D$ where σ^2_D is the dominance genetic variance. Epistatic variance was assumed to be zero.

The relative importance of the dominance variance (D) was determined as a proportion of the additive variance ($D_A = \sigma^2_D/\sigma^2_A$) and as a proportion of the phenotypic variance ($D_P = \sigma^2_D/\sigma^2_P$). Genetic and phenotypic correlations were estimated using a bivariate individual tree model.

The efficiency of early selection per generation was estimated assuming that the selection intensities at the young age and at mature ages are equal (Falconer 1989):

$$E = h_J \cdot r_A \cdot h_M^{-1}, \qquad (5)$$

where r_A is the additive genetic correlation between juvenile and the mature traits, and h_J and h_M are the square roots of the narrow-sense heritabilities of juvenile and mature traits, respectively.

Results

Trees in the WEY tests grew faster than those in the IP tests (height 10 was 11.14 m for WEY and 10.15 m for IP, Table 1). Height-age relationship in the younger WEY tests was essentially linear but the relationship of the older IP tests was non-linear (Fig. 1, 2). Phenotypic variation was moderate in all the three growth-curve parameters (coefficients of variation: 9 to 24%) and highest for the shape parameter. The regression sum of squares for the linear and non-linear models exceeded 98% of the total sum of squares. The analyses of variance showed that families differed significantly in all growth-curve parameters ($P<0.05$).

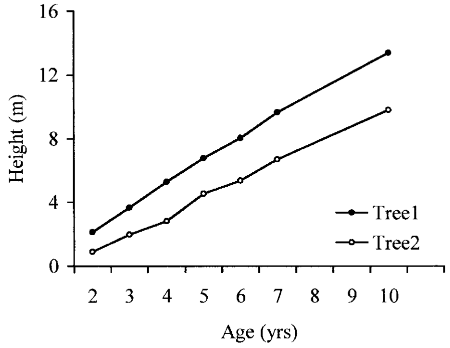

Fig. 1 Age-height relationships for two typical trees in the WEY tests

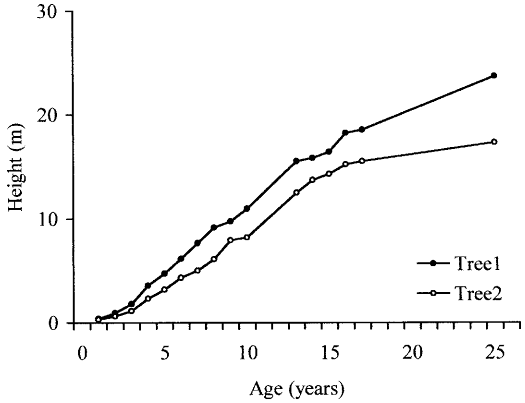

Fig. 2 Age-height relationship for two typical trees in the IP study

Table 1 Number of trees, means and standard deviations (SD) for height (m) for the WEY and IP tests

Trait	No. of trees		Mean ± SD	
	WEY	IP	WEY	IP
HT1[a]	–	4279	–	0.44 ± 0.16
HT2	5049	–	1.35 ± 0.52	1.06 ± 0.36
HT3	6063	–	2.47 ± 0.84	1.98 ± 0.62
HT4	6041	4279	3.88 ± 0.79	3.07 ± 0.80
HT5	5066	4279	5.47 ± 0.86	4.05 ± 0.94
HT6	4062	4279	6.82 ± 0.87	5.02 ± 1.02
HT7	2063	4279	8.21 ± 1.08	6.08 ± 1.11
HT8	–	4279	–	7.38 ± 1.11
HT9	–	4279	–	8.85 ± 1.14
HT10	6027	4279	11.14 ± 1.29	10.15 ± 1.21
HT11	–	–	–	–
HT12	–	–	–	–
HT13	–	–	–	13.64 ± 1.44
HT14	–	4279	–	14.66 ± 1.47
HT15	–	4279	–	15.68 ± 1.51
HT16	–	4279	–	16.63 ± 1.59
HT17	–	4279	–	17.58 ± 1.63
HT25	–	4279	–	23.54 ± 2.38
β_1	6065	–	1.24 ± 0.16	–
β_1	–	4279	–	1.19 ± 0.15
b	–	4279	–	0.09 ± 0.03
A	–	4279	–	30.75 ± 6.05
c	–	4279	–	1.98 ± 0.48

[a] HT = height; number is age

Heritability estimates

Heritability estimates for growth-curve parameters derived from non-linear models (h^2 = 0.06–0.18, see Table 3) were generally lower than those for age-specific heights. Heritability estimates derived from the linear models (h^2 = 0.15 and 0.26) were comparable to those of height at the oldest assessment age (10 years). The model used for predicting growth-curve parameters influenced the magnitude of heritability estimates. Rate-parameter estimates derived from the linear model were higher than those from the non-linear model. Using the non-linear model, the shape parameter had the highest heritability estimate (h^2 = 0.18) compared to the other two curve parameters (h^2 = 0.06 and 0.09, see Table 3).

Heritability estimates for the growth curves were robust to changes in the site index (Table 2). Heritability estimates for the asymptote varied from 0.05 to 0.08 and those for the rate and shape parameters were not affected by the site index.

Heritability estimates for age-specific heights in the IP tests were previously reported (Balocchi et al. 1993). Heritability for observed age-specific heights in WEY tests increased with age from 0.08 to 0.17 (Table 3). Heritability estimates from predicted values were slightly higher than those from observed values due to either less residual variance or higher additive variance in the former.

Variance components

Additive genetic variance exceeded dominance genetic variance ($D_A < 0.8$) for rate and shape parameters (Table 4). In contrast dominance was about twice the additive variance for the asymptote. Variance components for age-specific heights in the IP tests were reported previously (Balocchi et al. 1993). In the WEY tests, additive variance for age-specific heights increased with age (σ_A^2: 0.006 at age 2 to 0.199 at age 10) and the additive variances from predicted heights were slightly higher than those from observed heights (Table 2). Additive variance for age-specific height exceeded dominance variance at all ages ($D_A < 0.8$, Table 2).

Genetic correlations among traits

Genetic correlations among growth-curve parameters derived from a non-linear model were high. The asymptote was negatively correlated to the other two curve parameters (see Table 6). The genetic correlation between the rate and shape parameters was positive and high ($r_g = 0.90$). The rate and shape parameters derived from the non-linear model were poorly correlated with age-specific heights (see Table 6). The asymptote was well correlated with height at 25 years.

Genetic correlations between rate parameter and age-specific heights increased with age and were high-

Table 2 Sensitivity of estimates of variance components, ratio of dominance to additive variance (D_A), ratio of dominance to phenotypic variance (D_P) and heritability (standard error) for growth-curve parameters to different maximum heights in the IP tests

Parameter	Asymptote (m)	σ_A^2	σ_D^2	σ_E^2	D_A	D_P	h^2 (SE)
A	40	1.670	2.307	19.458	1.382	0.11	0.08 (0.04)
	44	1.533	3.447	23.831	2.249	0.13	0.06 (0.04)
	47	1.476	4.051	26.435	2.745	0.14	0.05 (0.03)
b	40	0.482	0.299	4.801	0.62	0.06	0.09 (0.04)
	44	0.484	0.370	5.051	0.77	0.07	0.09 (0.04)
	47	0.483	0.401	5.153	0.83	0.07	0.08 (0.04)
c	40	0.030	0	0.135	0	0	0.18 (0.06)
	44	0.030	0	0.139	0	0	0.18 (0.06)
	47	0.030	0	0.140	0	0	0.18 (0.06)

Table 3 Estimates of variance components (and their standard errors), ratio of dominance to additive variance (D_A), ratio of dominance to phenotypic variance (D_P), and heritability (and their standard errors) for height (H) and predicted height ($\hat{H}$) for pooled data across all WEY tests

Age (years)	Trait	σ_A^2	σ_D^2	σ_E^2	D_A	D_P	h^2 (SE)
2	H	0.006 (0.003)	0.005 (0.001)	0.075 (0.002)	0.75	0.06	0.08 (0.04)
2	$\hat{H}$	0.012 (0.007)	0.070 (0.013)	0.126 (0.004)	0.59	0.05	0.09 (0.04)
3	H	0.019 (0.009)	0.005 (0.001)	0.152 (0.005)	0.28	0.03	0.11 (0.05)
3	$\hat{H}$	0.021 (0.010)	0.006 (0.003)	0.154 (0.006)	0.25	0.03	0.12 (0.05)
4	H	0.046 (0.021)	0.006 (0.003)	0.250 (0.011)	0.12	0.02	0.15 (0.06)
4	$\hat{H}$	0.034 (0.016)	0.008 (0.004)	0.194 (0.009)	0.24	0.04	0.15 (0.06)
5	H	0.071 (0.034)	0.025 (0.011)	0.382 (0.019)	0.35	0.05	0.15 (0.07)
5	$\hat{H}$	0.059 (0.028)	0.017 (0.008)	0.284 (0.015)	0.28	0.05	0.17 (0.07)
6	H	0.092 (0.043)	0.022 (0.012)	0.490 (0.024)	0.24	0.04	0.16 (0.07)
6	$\hat{H}$	0.100 (0.046)	0.023 (0.012)	0.387 (0.025)	0.23	0.05	0.20 (0.08)
7	H	0.103 (0.051)	0.025 (0.023)	0.689 (0.035)	0.25	0.03	0.13 (0.06)
7	$\hat{H}$	0.104 (0.051)	0.027 (0.021)	0.584 (0.032)	0.26	0.04	0.15 (0.07)
10	H	0.199 (0.091)	0.049 (0.023)	0.986 (0.050)	0.25	0.04	0.17 (0.07)
10	$\hat{H}$	0.212 (0.097)	0.047 (0.023)	1.012 (0.052)	0.22	0.04	0.17 (0.07)

Table 4 Estimates of variance components (standard error), ratio of dominance to additive variance (D_A), ratio of dominance to phenotypic variance (D_P) and heritability (standard error) for the growth-curve parameters

Trait	Model	σ_A^2	σ_D^2	σ_E^2	D_A	D_P	h^2 (SE)
A	Non-linear	1.533 (0.960)	3.447 (1.748)	23.831 (0.725)	2.249	0.13	0.06 (0.04)
β_1 (WEY)	Linear	0.0025 (0.0011)	0.0005 (0.0003)	0.0137 (0.0006)	0.21	0.03	0.15 (0.06)
β_1 (IP)	Linear	0.0040 (0.0014)	0.0010 (0.0018)	0.0113 (0.0007)	0.24	0.06	0.26 (0.08)
b[a]	Non-linear	0.484 (0.225)	0.370 (0.358)	5.051 (0.162)	0.77	0.07	0.09 (0.04)
c	Non-linear	0.030 (0.011)	0 (0.014)	0.139 (0.006)	0	0	0.18 (0.06)

[a] Variance components multiplied by 10^4

est with 10 years height in the WEY tests (Table 5). Genetic correlations (r_g) varied from 0.44 with height at 2 years to 0.97 with height at 10 years. These correlations were slightly lower than those observed between height at 10 years and height at younger ages (r_g = 0.61 to 0.98). For the IP tests, height at 10 years and the rate parameter derived from 4–10 year data were well correlated (r_g = 0.92, Table 6). Both traits were well correlated with height at 25 years (r_g = 0.72 and 0.78, Table 6).

Table 5 Genetic correlations and their standard errors (below diagonal), and phenotypic correlations (above diagonal) of predicted heights and rate parameter for the WEY tests

Item	HT2	HT 3	HT 4	HT 5	HT 6	HT 7	HT 10	β_1
HT2		0.95	0.84	0.69	0.59	0.48	0.38	0.06
HT3	0.94 (0.04)		0.97	0.90	0.83	0.76	0.66	0.35
HT4	0.85 (0.09)	0.98 (0.01)		0.98	0.95	0.90	0.82	0.57
HT5	0.73 (0.15)	0.94 (0.04)	0.99 (0.01)		0.99	0.97	0.91	0.70
HT6	0.67 (0.17)	0.88 (0.07)	0.97 (0.02)	1		1	0.96	0.81
HT7	0.72 (0.16)	0.90 (0.07)	0.97 (0.02)	0.99 (0.01)	1		0.98	0.86
HT10	0.61 (0.20)	0.84 (0.09)	0.93 (0.04)	0.96 (0.02)	0.98 (0.01)	1		0.93
β_1	0.44 (0.25)	0.69 (0.17)	0.81 (0.11)	0.87 (0.08)	0.91 (0.05)	0.95 (0.03)	0.97 (0.02)	

Table 6 Estimates of heritability and its standard error (on diagonal), genetic correlation and its standard error (below diagonal), and phenotypic correlation (above diagonal) of age-specific heights and growth-curve parameters for the IP tests

Item	HT10	HT25	β_1	A	b	c
HT10[a]	0.25 (0.08)	0.49	0.80	–0.06	0.15	–0.31
HT25	0.78 (0.05)	0.20 (0.07)	0.40	0.78	–0.60	–0.49
β_1	0.92 (0.02)	0.72 (0.06)	0.26 (0.08)	0	0.15	–0.02
A	–0.06 (0.13)	0.74 (0.06)	0.20 (0.12)	0.06 (0.04)	–0.86	–0.67
b	0.30 (0.11)	–0.37 (0.11)	0.11 (0.12)	–0.87 (0.04)	0.09 (0.04)	0.89
c	–0.33 (0.11)	–0.38 (0.10)	–0.10 (0.12)	–0.70 (0.07)	0.90 (0.03)	0.18 (0.06)

[a] HT10 = height at 10 years, HT25 = height at 25 years

Efficiency of selection

Selection efficiency was estimated for the IP dataset because data at maturity were available in this dataset. Early selection at height 10 years was compared with early selection on rate parameter as selection criteria to improve height at 25 years. Selection response was high and similar (efficiency values of 0.87 and 0.82, respectively). The high selection efficiencies were due to the high juvenile - mature correlations for height 10 and for the rate parameter (Table 6).

Discussion

Heritability estimates for growth curves tended to be lower than those for age-specific heights. This was also observed for *P. pinaster* (Maugnussen and Kremer 1993) and for mice (McCarthy and Bakker 1979). The heritability estimates tended to be particularly low for the nonlinear growth-curve parameters, particularly the asymptote and the rate parameter. The differences in heritability estimates in growth-curve parameters may be due to differential gene expression through ontogeny (Cheverud et al. 1983).

There are few estimates of heritability on growth curves, and are few in woody perennial species and none for *P. taeda*. The moderate heritability estimates for the growth curves reported here were similar to those of height-age curves of *P. pinaster* reported by Magnussen and Kremer (1993). In general, the heritability estimates for forest trees were lower than those of growth curves in beef cows ($h^2 = 0.21$ to 0.44) estimated using the Richards' function (DeNise and Brinks 1985) and those in mice ($h^2 = 0.46$ to 0.87) using the Gompertz function (McCarthy and Bakker 1979). The heritability difference between vertebrate animals and woody perennial plants shows divergence in the genetic control of ontogeny.

Heritability estimates for observed age-specific heights were consistent with those from earlier *P. taeda* studies (Balocchi et al. 1993; Gwaze et al. 1997, 2000) and slightly lower than those from predicted heights. The latter was expected since fitting growth curves reduces errors by smoothing irregularities of actual data. Higher heritability estimates from predicted than from observed values were also reported by Balocchi et al. (1993).

Growth-curve parameters were highly correlated. In *P. pinaster*, growth-curve parameters for height were reported to be moderately to highly correlated (Maugnussen and Kremer 1993). The high negative correlation between the asymptote and the rate parameter shows that trees with smaller asymptotes reach maximum height earlier. The negative correlation between the asymptote and the shape parameter shows that trees with smaller asymptotes reach maximum height at a younger age compared to trees with higher asymptotes.

Age-age genetic correlations between age-specific height and growth-curve parameters were moderate to high. Genetic correlations between age-specific heights and the rate parameter increased with age indicating that the rate parameter and the height at the oldest age were essentially the same trait.

The value of the asymptote and the shape parameter as selection criteria may be questionable because they are measured late in the life of the stand and early selection is a priority in tree-breeding programs. Efficiency of early selection based on the rate parameter was similar to that based on height at 10 years for predicting height at 25 years.

This study provided an insight into the genetic control of growth curves in *P. taeda*. Genetic control of growth-curve parameters in *P. taeda* is moderate and early selection on age-specific height is as efficient as selection on growth-curve parameters.

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