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Genetic Variation, Heritability and Genotype × Environment Interactions of Resin Yield, Growth Traits and Morphologic Traits for *Pinus elliottii* at Three Progeny Trials

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Abstract: To better understand the genetic control of resin yield, growth traits and morphologic traits for *Pinus elliottii* families, genetic relationships among these traits were examined in three 27-year-old progeny trials located in Jingdezhen, Jian and Ganzhou, Jiangxi Province, China. In total, 3695 trees from 112 families were assessed at the three sites. Significant site, family and family × site effects were found for resin yield, growth traits and morphologic traits. Resin yield and growth traits were found to be under moderate genetic control for the three sites combined, with family heritability and individual narrow-sense heritability ranging from 0.41 to 0.55 and 0.11 to 0.27, respectively. The coefficient of genotypic variation (CV_G) of stem volume (SV) and crown surface area (CSA) were higher than those of other traits at each site. Genetic correlation estimates indicated that selection for growth traits might lead to a large increment in resin yield (RY), and most morphologic traits had moderate to strong correlations with growth traits at each individual site. One possible strategy in tree breeding would be to maximize resin production through selection for growth traits.

Keywords: families; *Pinus elliottii*; resin yield; growth traits; morphologic traits; heritability; genotypic correlation

1. Introduction

Pine resin is an important non-timber secondary forest product. It produces turpentine (monoterpenes and sesquiterpenes) and rosin (diterpenes). These compounds are widely used in pharmaceutical, cosmetics, food, chemical and other such industries [1–3]. China is the leading producer of resin in the world. During the 1990s, China annually exported a total of 200,000 tons of resin to more than 40 countries, accounting for about 50% of the resin traded in the world [4]. Of the pine resin resources, *Pinus elliottii* is one of the main resin tree species in China.

P. elliottii (slash pine), which originated from the Southeastern United States, is one of the most important coniferous timber species in the *Pinus* genus. Slash pine was introduced to China in the late 1940s and began to be planted in Southern China on a large scale in the late 1970s [5]. In addition to its wide use for the wood, pulp and paper industry, this species has also long been employed as a main source of resin. In recent years, the resin price has risen annually. For example, the resin purchased from forest farmers has an average price of 10 yuan (about 1.5 dollars) per kilogram in 2016. Nowadays, it is more profitable for farmers than harvesting trees for timber. However, due to its high commercial value, slash pine has been subjected to overexploitation during past decades.

The quantity of constitutive resin produced by pine species is influenced by genetic and environmental factors [6]. Much of the attention devoted for identifying the variables that have a bearing on resin production has concentrated on environmental attributes and cultural practices aimed to stimulate tree growth. A prominent focus of this research includes potential determinants that might alter resin production over the course of a growing season, including those that can cause carbon resources to be shifted to secondary metabolic processes involved in resin synthesis away from the dominant primary processes that contribute to tree growth. Allocation of photosynthates to primary and secondary metabolic processes is believed to result in a trade-off between growth and resin formation following plant growth differentiation principles formulated first by Loomis [7] and later modified to explain the relationship between growth and resin flow in pines by Lorio [8]. Previous studies have suggested that growth traits and morphologic traits can influence resin yield, with trees with a larger diameter and crown size yielding more resin than their smaller pine species counterparts [9,10]. Thus, accurately exploring the genetic correlation among resin yield, growth traits and morphologic traits is needed, as they have major implications for the development of selection and breeding strategies.

Similarly, a large effort has also been committed to determine how strongly genetic effects influence variation of resin yield in pine trees. Researches have demonstrated that resin yield is a highly heritable trait, and important genetic gains can be obtained from the selection of high resin yielders. For example, Roberds and Strom [11] estimated that the repeatabilities of gum yield in loblolly pine (*Pinus teada* L) (0.64–0.67), longleaf pine (*Pinus palustris*) (0.46–0.77) and slash pine (0.55) are quite high. Squillace and Bengston [12] found that narrow-sense heritability for gum resin yield in slash pine is around 0.55, indicating that this trait is under fairly strong genetic control. Experimental observations in maritime pine (*Pinus pinaster* Ait.) and masson pine (*Pinus massoniana*) likewise indicate that resin-yielding capability is under substantial genetic regulation in these species [13,14]. General methods for increasing resin yield including genetically improve associated trees and develop resin pine plantations. In China, the genetic improvement to increase resin yield was initiated in the mid-to-late 1980s, and these programs primarily focus on the selection of trees that yield high amounts of resin based on the phenotypic performance of unimproved plantations [14]. Research has demonstrated that large differences occur among half-sib families in resin yield, and some superior families and clones for further studies on genetic improvement have been selected [15,16]. However, the majority of seedlings used for afforestation have not been subject to genetic improvement, and pine plantations have made limited contributions to the increment of resin yields. Slash pine improvement programs to promote resin yield are still nascent, and more breeding practices needed to be made for this species.

In China, tree breeding programs for slash pine have mainly emphasized improvements in tree growth and wood properties [2,17]. Several studies have focused on the resin-yielding capacity. However, most of these studies on resin yield and growth traits have either been performed at a single site or are based on a small number of samples or families. Consequently, limited information is available on the ecological variation, reaction norms and phenotypic plasticity of the resin yield, growth traits and morphologic traits of *P. elliottii* families. Moreover, the sample size in these previous studies was insufficient. For tree improvement, quantitative parameter estimates require an examination of more genotypes at different locations than those used in previous studies.

To understand the quantitative genetics for resin yield, growth traits and morphologic traits of *P. elliottii* in China, we conducted a large study using 3695 trees from 112 open-pollinated families established at three sites in Jiangxi Province with the following study aims: (1) to describe the resin yield, growth traits and morphologic traits in the studied area; (2) to quantify genetic variation and inheritance for resin yield, growth traits and wood traits; (3) to explore the genotype × environment interactions for these traits; (4) to examine the genetic relationship among resin yield, growth traits and wood traits. These findings will be helpful to decide the appropriate breeding strategies for improvement programs of slash pine in China.

2. Materials and Methods

2.1. Materials

The present study comprised of 112 open-pollinated families of *P. elliottii* plus trees randomly selected from a seed orchard in Georgia (12 plus trees), Mississippi (60 plus trees) and Florida (50 plus trees) in United States. Plus trees were selected for high resin yield, high growth rate, and straight stem form. Open-pollinated families from these trees were included in three trials established in the spring of 1990 at three locations in Jiangxi Province, Jingdezhen, Jian and Ganzhou, and the characteristics of the three trials are presented in Figure 1 and Table 1. The annual temperature and rainfall data in Table 1 were collected from the local meteorological bureau. The trials used a randomized complete block design with plots containing four trees per row and five replications, with a total of 2240 trees per site. The seedlings were planted with 3.0 m × 4.0 m spacing. Specific silvicultural treatments were not performed prior to the experiments. In 2016, all trees were measured; the survival rate for Jindezhen, Jian and Ganzhou were 55.8%, 56.1% and 53.1%, respectively; the survival rate was not high for the three trials, which reflected the snow disaster in 2008. The total number of trees sampled for the three sites were 1249, 1257 and 1189, respectively.

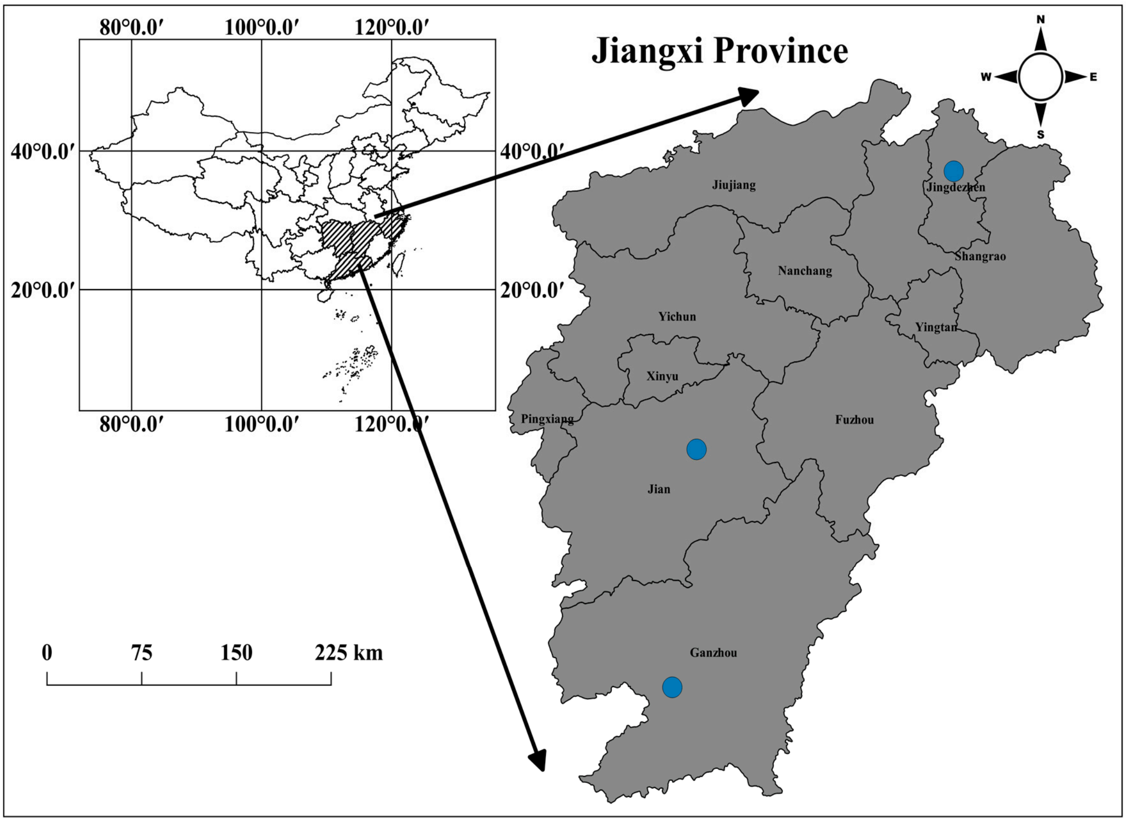

Figure 1. Location of the progeny trails (blue dots) in Jiangxi Province and main growing regions (shaded area) of *P. elliottii* in China.

Table 1. Location, climatic conditions and description of the three progeny trials.

Site	Latitude N (°)	Longitude W (°)	Mean Annual T (°C)	Rainfall mm/year	Survival (%)	Sample Trees
Jingdezhen	29.37	117.25	17.2	1805	55.8	1249
Jian	27.22	115.13	18.3	1487	56.1	1257
Ganzhou	25.38	114.93	20.2	1318	53.1	1189

2.2. Measurement of Resin Yield, Tree Growth and Evaluation of Morphologic Properties

Resin yield (RY) was measured using the bark streak wounding method for resin tapping [16]. After removing the outer bark at breast height using a sharp hatchet, a streak was incised in the bark-shaved face. The streak was 2 mm wide and 5 mm deep and had a side gutter angle of 45° and tapping load rate of less than 45% (Figure 2). Resin from each wound was funneled into open plastic bags attached to the base of the wounds. Rewounding was performed every 2 days throughout the experimental period in August, with 15 cuts performed on each tree. The sampled trees were measured for RY (in kilograms) at the end of August.

Figure 2. Bark streak wounding method for resin tapping.

Total height (HT) was measured in meters. Stem diameter at breast height (DBH) was measured in centimeter. The height (HGT) and DBH were used to calculate the stem volume (stem volume (SV), in m^3) of the outer bark of individual trees:

$$SV = \frac{0.527 \times \pi D^2 H}{4} \quad (1)$$

Morphologic traits including height under live crown (HLC), crown width (CW) and crown length (CL). The CW and CL were used to calculate the crown surface area (CSA) of an individual tree according to Chen et al. [18] and Huang et al. [19]:

$$\mathrm{CVA} = \frac{\pi \mathrm{CW}}{4}\sqrt{\mathrm{CL}^2 + \frac{\mathrm{CW}^2}{4}} \tag{2}$$

2.3. Statistical Models and Analysis

Univariate restricted maximum likelihood (REML) analyses were undertaken separately to obtain estimates of variance components for each trait using statistical software ASReml-R (v. 3.0, Queensland Department of Primary Industries and Fisheries, Brisbane, Australia) package in R [20,21]. The following linear mixed models (family models) were used for separate analyses (1) of individual site and for joint analyses (2) of the three sites together:

$$y = \mu + Xb + Z_1 f + Z_2 fb + e \tag{3}$$

$$y = \mu + X_1 s + X_2 b_{(s)} + Z_1 f + Z_2 fs + Z_3 fb_{(s)} + e \tag{4}$$

where y is the vector of observations, μ is the intercept, s, b, $b(s)$ are the fixed site, block and block within site effects, f, fb, fs, $fb(s)$, e refers to random family, family-site, family-block and family-block within site and residual effects, and X and Z are the known incidence matrices relating the observations in y to the fixed and random effects, respectively, assuming $f \sim N(0, \sigma_f^2 I)$, $fs \sim N(0, \sigma_{fs}^2 I)$, $fb_{(s)} \sim N(0, \sigma_{fb_{(s)}}^2 I)$, $e \sim N(0, \sigma_e^2 I)$, where σ_f^2, σ_{fs}^2, $\sigma_{fb_{(s)}}^2$, and σ_e^2 are family, family-site, family-block and family-block within site and residual error variances, respectively, I is an identity matrix.

The significance of the variance components for each trait was tested using the likelihood ratio test (LRT, [22]). Approximate standard errors for estimated variances were estimated using the Taylor series expansion method [23].

Open pollinated mating was assumed to have created true half-sibs and among which the genetic variation accounts for one quarter of the total additive genetic variance, thus additive genetic variance

$$\hat{\sigma}_a^2 = 4\hat{\sigma}_f^2 \tag{5}$$

phenotypic variance

$$\hat{\sigma}_p^2 = \hat{\sigma}_f^2 + \hat{\sigma}_{fb}^2 + \hat{\sigma}_e^2 \tag{6}$$

and

$$\hat{\sigma}_p^2 = \hat{\sigma}_f^2 + \hat{\sigma}_{fs}^2 + \hat{\sigma}_{fb_{(s)}}^2 + \hat{\sigma}_e^2 \tag{7}$$

for individual site and joint analyses, respectively. Variation at genetic, phenotypic and residual level (CV_G, CV_P and CV_E), individual narrow-sense heritability ($\hat{h}_i^2$), and family mean heritability ($\hat{h}_f^2$) were calculated, respectively, as follows [14]:

$$CV_G = \hat{\sigma}_f / \overline{\mathrm{X}} \times 100\% \tag{8}$$

$$CV_P = \hat{\sigma}_p / \overline{\mathrm{X}} \times 100\% \tag{9}$$

$$CV_E = \hat{\sigma}_e / \overline{\mathrm{X}} \times 100\% \tag{10}$$

$$\hat{h}_i^2 = \frac{\hat{\sigma}_a^2}{\hat{\sigma}_p^2} \tag{11}$$

$$\hat{h}_f^2 = \frac{\hat{\sigma}_f^2}{\hat{\sigma}_f^2 + \hat{\sigma}_{fb}^2 / n_b + \hat{\sigma}_e^2 / (n_b \times n_k)} \tag{12}$$

$$\hat{h}_f^2 = \frac{\hat{\sigma}_f^2}{\hat{\sigma}_f^2 + \hat{\sigma}_{fs}^2/n_s + \hat{\sigma}_{fb_{(s)}}^2/(n_s \times n_b) + \hat{\sigma}_e^2/(n_s \times n_b \times n_k)} \quad (13)$$

Formula (10) and (11) were used in individual site and joint analyses, respectively. Terms n_s, n_b and n_k are the number of sites, blocks within sites and the harmonic mean of the number of trees per family, respectively.

Genetic correlations (r_g) were estimated using bivariate analyses for all possible combinations of traits and calculated as [14]:

$$r_g = \frac{\hat{\sigma}_{g(xy)}}{\sqrt{\hat{\sigma}_{g(x)}^2 \times \hat{\sigma}_{g(y)}^2}} \quad (14)$$

where the $\hat{\sigma}_{g(xy)}$ refers to the genotypic covariance between traits x and y, $\hat{\sigma}_{g(x)}^2$ denotes the genotypic variance component for trait x and $\hat{\sigma}_{g(y)}^2$ is the genotypic variance component for trait y.

To evaluate the extent of genotype × environment interaction (G × E) for each trait, between-site type-B genetic correlations obtained from bivariate models were used [24], and their approximate standard errors were estimated using the Taylor series expansion method [23]. The type-B genetic correlation was calculated as:

$$r_B = \frac{\hat{\sigma}_{g(a1a2)}}{\sqrt{\hat{\sigma}_{g(a1)}^2 \times \hat{\sigma}_{g(a2)}^2}} \quad (15)$$

where $\hat{\sigma}_{g(a1a2)}$ is the covariance between genotypic effects from bivariate models of the same traits in different sites and $\hat{\sigma}_{g(a1)}^2$ and $\hat{\sigma}_{g(a2)}^2$ are estimated genotypic variances for the same traits in trial 1 and trial 2, respectively.

To evaluate the expected response in resin yield at each site by using different selection criteria, and developed implications for tree improvement. The expected gain in trait y was predicted from the correlated response to individual selection in trait x using the following formula [25]:

$$\Delta \mathrm{G} = \mathrm{i}\ \hat{\mathrm{h}}_{\mathrm{x}}\ \hat{\mathrm{h}}_{\mathrm{y}}\ \mathrm{r}_{\mathrm{g}}\ \hat{\sigma}_{\mathrm{py}} \quad (16)$$

where i is the selection intensity (according to the sample size in this study, the selection intensity is assumed to equal 1.76, which corresponds to the selection of ten parental trees out of 100); $\hat{\mathrm{h}}_{\mathrm{x}}$ and $\hat{\mathrm{h}}_{\mathrm{y}}$ are the square roots of individual tree heritability for direct-selection x trait and correlated y trait; r_{g} is the estimated genetic correlation between traits x and y; and $\hat{\sigma}_{\mathrm{py}}$ is the phenotypic standard deviation for trait y.

3. Results

3.1. Mean Values and Site Effects

The mean values, range of variation and standard error of the mean for all traits in each of the three progeny trials are presented in Table 2. The trees at the Jian site had the lowest RY. The highest RY was observed at the Ganzhou site, with a 6.9 difference was observed between the lowest and highest average RY (Table 2). At the Jingdezhen site, the HGT of *P. elliottii* was the highest but the DBH was the lowest; thus, the SV of *P. elliottii* was not high at this site. Nevertheless, at the Jingdezhen site, the CSA was the highest, which was supported by the highest CW and moderate CL at this site, whereas at the Jian site, the CSA was the lowest. The HLC of trees at the Jingdezhen site was 33.66% higher than that of the tress at the Ganzhou site. An analysis that combined all three trials showed significant site effects ($p < 0.01$) for RY, growth traits and morphologic traits (Table 3).

3.2. Genetic Variation and Heritability

Significant differences among families in the RY, growth traits and morphologic traits were observed when analyzing the three sites together (Table 3). Growth traits showed higher estimated family heritability ($h^2{}_f$ = 0.42–0.55) and estimated individual tree heritability ($h^2{}_i$ = 0.14–0.27) than resin yield and most morphologic traits (Table 3).

The estimates of variances, heritability, coefficients of genotypic, residual, and phenotypic variations at each individual site are presented in Table 4. Significant differences were observed among the families for most of the traits examined at the three sites except for the DBH, HLC and CW at Jian and the RY at Ganzhou. In general, the coefficient of genetic variation (CV_G) values for the SV and CSA were higher than those for other traits at each site (Table 4). The family and individual tree heritabilities for all traits at the Jindezhen site ranged from 0.46 to 0.65 and 0.41 to 0.73, respectively, which were high compared with those estimated at the other two sites.

Table 2. Mean values, standard error of the mean (SE) and range of variation based on individual values of the resin yield, growth traits and morphologic traits of *P. elliottii* for the three progeny trials.

Trait (Site)	Jingdezhen			Jian			Ganzhou		
	Mean	**SE**	**Range (Min–Max)**	**Mean**	**SE**	**Range (Min–Max)**	**Mean**	**SE**	**Range (Min–Max)**
RY (kg)	1.17	0.006	0.3–2.2	1.16	0.011	0.3–2.8	1.24	0.009	0.3–3.25
HGT (m)	14.68	0.083	6.4–23.0	13.02	0.072	5.4–18.6	12.15	0.061	5.8–16.7
DBH (cm)	25.26	0.114	13.7–39.5	27.82	0.132	16.2–43.9	28.05	0.120	17.5–41.8
SV (m^3)	0.418	0.005	0.06–1.37	0.441	0.005	0.09–1.12	0.412	0.004	0.11–0.96
HLC (m)	9.69	0.059	3.1–16.8	7.51	0.055	1.8–13.1	7.25	0.054	1.9–12.7
CW (m)	5.37	0.029	2.1–8.9	4.71	0.028	2.1–8.4	5.36	0.030	2.4–9.9
CL (m)	4.98	0.045	1.0–15.0	5.50	0.043	0.7–10.6	4.89	0.040	0.8–9.5
CSA (m^2)	24.9	0.316	4.7–106.0	22.9	0.258	3.2–61.4	24.2	0.254	6.0–65.7

Resin yield (RY), diameter at breast height (DBH), height (HGT), stem volume (SV), height under live crown (HLC), crown width (CW), crown length (CL) and crown surface area (CSA).

Table 3. Estimates of variances ($\hat{\sigma}^2_f$, $\hat{\sigma}^2_{fs}$, $\hat{\sigma}^2_{fb_{(s)}}$, $\hat{\sigma}^2_e$) for family, family-site, family-block within site interactions and residual variances, respectively, family mean and individual narrow sense heritability ($\hat{h}^2_f$, $\hat{h}^2_i$) (with standard error in parenthesis), and coefficient of variation at genetic, phenotypic and residual level (CV_G, CV_P and CV_E) for various traits from site combined analysis.

Trait	*p* Value of Site Effect	$\hat{\sigma}^2_f$ (SE)	$\hat{\sigma}^2_{fs}$ (SE)	$\hat{\sigma}^2_{fb_{(s)}}$ (SE)	$\hat{\sigma}^2_e$ (SE)	$h^2{}_f$ (SE)	$h^2{}_i$ (SE)	CV_G (%)	CV_E (%)	CV_P (%)
RY	<0.01 **	0.003 (0.001)	0.003 (0.001)	0.006 (0.002)	0.1 (0.003)	0.41 (0.09)	0.11 (0.04)	4.58	26.45	28.00
HGT	<0.001 ***	0.45 (0.12)	0.33 (0.11)	2.07 (0.16)	3.86 (0.12)	0.55 (0.07)	0.27 (0.06)	5.06	14.77	19.46
DBH	<0.001 ***	0.65 (0.21)	0.56 (0.23)	1.06 (0.37)	16.3 (0.49)	0.45 (0.09)	0.14 (0.04)	2.99	14.94	15.94
SV	<0.001 ***	0.001 (0.001)	0.002 (0.001)	0.005 (0.001)	0.03 (0.001)	0.42 (0.09)	0.16 (0.05)	7.45	39.43	44.71
HLC	<0.001 ***	0.26 (0.06)	0.04 (0.06)	1.34 (0.1)	2.31 (0.07)	0.59 (0.06)	0.26 (0.06)	6.23	18.62	24.35
CW	<0.001 ***	0.03 (0.01)	0.04 (0.01)	0.09 (0.02)	0.88 (0.03)	0.41 (0.09)	0.13 (0.04)	3.53	18.20	19.83
CL	<0.001 ***	0.05 (0.03)	0.04 (0.17)	0.34 (0.05)	1.73 (0.05)	0.26 (0.12)	0.08 (0.04)	4.31	25.63	29.45
CSA	<0.001 ***	2.91 (1.24)	6.26 (1.59)	13.5 (2.08)	73.07 (2.22)	0.35 (0.10)	0.12 (0.05)	7.10	35.60	40.75

Degrees of freedom are 2 for site, 12 for block. Resin yield (RY), diameter at breast height (DBH), height (HGT), stem volume (SV), height under live crown (HLC), crown width (CW), crown length (CL) and crown surface area (CSA). *** $p < 0.001$; ** $0.001 < p < 0.01$, level of significance of effects.

Table 4. Estimates of variances ($\hat{\sigma}_f^2$, $\hat{\sigma}_{fb}^2$, $\hat{\sigma}_e^2$) for family, family-block and residual variances, respectively, family mean and individual narrow sense heritability ($\hat{h}_f^2$, $\hat{h}_i^2$) (with standard error in parenthesis), and coefficient of variation at genetic, phenotypic and residual level (CV_G, CV_P and CV_E) for various traits at each site.

Site	$\hat{\sigma}_f^2$ **(SE)**	$\hat{\sigma}_{fb}^2$ **(SE)**	$\hat{\sigma}_e^2$ **(SE)**	$h^2{}_f$ **(SE)**	$h^2{}_i$ **(SE)**	CV_G **(%)**	CV_E **(%)**	CV_P **(%)**
Jian								
RY	0.009 (0.003)	0.003 (0.006)	0.157 (0.008)	0.35 (0.09)	0.21 (0.08)	8.16	34.16	35.37
HGT	0.38 (0.20)	3.17 (0.34)	3.25 (0.17)	0.28 (0.11)	0.22 (0.11)	4.71	13.84	20.01
DBH	0.49 (0.35) ^{ns}	0.05 (0.72)	21.54 (1.08)	0.20 (0.11)	0.10 (0.06)	2.51	16.68	16.89
SV	0.001 (0.001)	0.002 (0.001)	0.035 (0.002)	0.27 (0.10)	0.15 (0.07)	7.17	42.52	44.17
HLC	0.000 (0.000) ^{ns}	2.59 (0.21)	1.49 (0.08)	0.00 (0.00)	0.00 (0.00)	0.00	16.23	26.67
CW	0.014 (0.016) ^{ns}	0.06 (0.03)	0.86 (0.04)	0.13 (0.12)	0.06 (0.05)	2.52	19.65	20.52
CL	0.09 (0.05)	0.21 (0.09)	2.03 (0.11)	0.27 (0.10)	0.16 (0.08)	5.48	25.88	27.74
CSA	2.22 (1.46)	4.57 (2.93)	75.21 (3.84)	0.21 (0.11)	0.11 (0.07)	6.51	37.87	39.54
Ganzhou								
RY	0.003 (0.002) ^{ns}	0.001 (0.004)	0.110 (0.006)	0.20 (0.11)	0.10 (0.06)	4.38	26.53	27.02
HGT	0.28 (0.12)	1.19 (0.20)	3.01 (0.16)	0.34 (0.10)	0.25 (0.10)	4.30	14.27	17.41
DBH	0.64 (0.30)	0.000 (0.000)	16.67 (0.72)	0.28 (0.09)	0.15 (0.06)	2.85	14.55	14.83
SV	0.001 (0.001)	0.001 (0.001)	0.023 (0.001)	0.33 (0.10)	0.20 (0.08)	7.67	36.99	38.34
HLC	0.28 (0.10)	0.84 (0.15)	2.39 (0.13)	0.41 (0.09)	0.32 (0.11)	7.35	21.30	25.83
CW	0.03 (0.02)	0.000 (0.000)	1.03 (0.04)	0.24 (0.11)	0.12 (0.06)	3.28	18.91	19.19
CL	0.06 (0.04)	0.30 (0.08)	1.59 (0.08)	0.22 (0.12)	0.13 (0.08)	5.04	25.71	28.45
CSA	4.11 (1.701)	4.16 ((2.70)	68.92 (3.56)	0.35 (0.10)	0.22 (0.08)	8.36	34.25	36.25
Jingdezhen								
RY	0.005 (0.002)	0.016 (0.002)	0.031 (0.002)	0.46 (0.08)	0.41 (0.11)	6.31	14.92	19.37
HGT	1.59 (0.34)	1.85 (0.31)	5.30 (0.28)	0.64 (0.05)	0.72 (0.13)	8.60	15.69	20.14
DBH	2.41 (0.57)	3.98 (0.63)	9.88 (0.53)	0.57 (0.06)	0.59 (0.12)	6.14	12.44	15.96
SV	0.008 (0.002)	0.01 (0.002)	0.03 (0.001)	0.61 (0.05)	0.68 (0.13)	21.36	37.65	50.10
HLC	0.63 (0.14)	0.64 (0.15)	3.09 (0.16)	0.59 (0.06)	0.57 (0.12)	8.16	18.12	21.52
CW	0.16 (0.04)	0.25 (0.04)	0.72 (0.04)	0.56 (0.06)	0.55 (0.12)	7.38	15.77	19.77
CL	0.47 (0.10)	0.50 (0.09)	1.58 (0.08)	0.65 (0.05)	0.73 (0.13)	13.75	25.16	32.03
CSA	20.32 (4.65)	31.88 (4.86)	74.39 (3.96)	0.60 (0.06)	0.64 (0.13)	18.10	34.62	45.17

Degrees of freedom are 4 for block. Resin yield (RY), diameter at breast height (DBH), height (HGT), stem volume (SV), height under live crown (HLC), crown width (CW), crown length (CL) and crown surface area (CSA); ^{ns} no significance of effects.

3.3. Genotype × Environment Interaction

In the present study, the family × site interaction was significant for RY, growth traits and morphologic traits (Table 3). Inter-site genotypic correlations between HLC with pairs of Jindezhen-Jian and Ganzhou-Jian sites were not estimated because significant differences in HLC were not observed among the families at Jian (Table 5). Most of inter-site genotypic correlations between the same traits at Jingdezhen-Jian and Jingdezhen-Ganzhou sites were moderate or weak (Table 5). However, the type B genotypic correlations between Ganzhou and Jian for all traits were higher, indicating that these traits were stable across Ganzhou and Jian. Compared with the resin yield and morphologic properties, the growth traits generally showed higher inter-site genotypic correlations (0.18–0.68).

Table 5. Type B genetic correlations (with standard error in parenthesis) between sites for the resin yield, growth traits and morphologic traits of *P. elliottii*.

Traits Correlations	RY	HGT	DBH	SV	HLC	CW	CL	CSA
JDZ-JA	0.34 (0.14)	0.53 (0.18) **	0.18 (0.22)	0.30 (0.18)	0.00 (0.00)	0.17 (0.21)	0.19 (0.18)	0.22 (0.19)
JDZ-GZ	0.29 (0.20)	0.48 (0.16) *	0.29 (0.19)	0.35 (0.19) *	0.43 (0.17) *	0.16 (0.20)	0.13 (0.18)	0.15 (0.18)
GZ-JA	0.55 (0.18) **	0.68 (0.12) **	0.54 (0.15) **	0.40 (0.12) *	0.00 (0.00)	0.37 (0.15) *	0.22 (0.13)	0.23 (0.13)

Type B genetic correlations were used to measure the importance of G × E interactions for RY and measure the growth traits and morphologic traits of *P. elliottii* from the combined sites analysis. Resin yield (RY), diameter at breast height (DBH), height (HGT), stem volume (SV), height under live crown (HLC), crown width (CW), crown length (CL) and crown surface area (CSA). JDZ (Jingdezhen), GZ (Ganzhou) and JA (Jian). ** $0.001 < p < 0.01$; * $0.01 < p < 0.05$, level of significance of effects.

3.4. Genotypic Correlations between Traits, Genetic Gain, and Correlated Genetic Response

The estimated genetic correlations among the RY, growth traits and morphologic traits are presented in Table 6. Strong and positive genotypic correlations between RY and HGT, DBH and SV were observed across the three sites. This finding suggests that selection for growth traits might lead to a large increment in RY. Moderate to strong and positive correlations were observed between RY and the morphologic traits at specific localities except between HLC and RY at Ganzhou, which was negatively correlated. Most morphologic traits showed moderate to strong correlations with growth traits at each individual site.

Predicted genetic gains, assuming observed individual tree heritability and genotypic correlations and correlated genetic response in resin yield, with different selection criteria used, are presented for individual sites in Table 7. The predicted gains in RY were comparable at Jian and Jindezhen (11.08% and 9.53%, respectively), whereas the Ganzhou site had a lower gain (4.18%). Selection for growth traits resulted in a higher gains in RY at Jindezhen (10.97–11.53%). Overall, predicted gains from growth traits selection in RY were higher than the selection for morphologic traits.

Table 6. Estimated intertrait genetic correlations (with standard error in parenthesis) among resin yield, growth traits and morphologic traits across the three study sites.

Trait	HGT	DBH	SV	HLC	CW	CL	CSA
Jian							
RY	0.68 (0.26) **	0.82 (0.18) ***	0.73 (0.17) ***	0.00 (0.00)	0.34 (0.4)	0.61 (0.22) **	0.56 (0.24) **
HGT		0.95 (0.14) ***	0.98 (0.11) ***	0.00 (0.00)	0.20 (0.61)	0.99 (0.17) ***	0.95 (0.33) ***
DBH			0.97 (0.07) ***	0.00 (0.00)	−0.11 (0.85)	0.97 (0.24) ***	0.60 (0.31) **
SV				0.00 (0.00)	−0.01 (0.60)	0.98 (0.15) ***	0.73 (0.23) ***
HLC					0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
CW						0.67 (0.46) *	0.98 (0.18) ***
CL							0.90 (0.09) ***
Ganzhou							
RY	0.58 (0.16) **	0.72 (0.17) ***	0.58 (0.20) **	−0.22 (0.27)	0.89 (0.20) ***	0.92 (0.19) ***	0.95 (0.13) ***
HGT		0.53 (0.19) **	0.85 (0.08) ***	0.88 (0.05) ***	−0.06 (0.27)	0.31 (0.18) *	0.12 (0.20)
DBH			0.89 (0.05) ***	0.10 (0.23)	0.66 (0.20) **	0.88 (0.16) ***	0.78 (0.12) ***
SV				0.52 (0.16) **	0.37 (0.25) *	0.72 (0.14) ***	0.54 (0.16) ***
HLC					−0.50 (0.25) *	−0.19 (0.19)	−0.36 (0.18) *
CW						0.91 (0.24) ***	0.98 (0.08) ***
CL							0.98 (0.05) ***

Table 6. *Cont.*

Trait	HGT	DBH	SV	HLC	CW	CL	CSA
Jindezhen							
RY	0.90 (0.04) ***	0.96 (0.02) ***	0.94 (0.03) ***	0.67 (0.09) ***	0.66 (0.08) ***	0.88 (0.04) ***	0.86 (0.04) ***
HGT		0.95 (0.02) ***	0.98 (0.01) ***	0.88 (0.03) ***	0.62 (0.08) ***	0.84 (0.04) ***	0.81 (0.05) ***
DBH			0.99 (0.01) ***	0.74 (0.07) ***	0.66 (0.08) ***	0.91 (0.03) ***	0.89 (0.03) ***
SV				0.79 (0.06) ***	0.63 (0.08) ***	0.91 (0.03) ***	0.87 (0.04) ***
HLC					0.45 (0.11) ***	0.48 (0.11) ***	0.49 (0.11) ***
CW						0.63 (0.08) ***	0.86 (0.04) ***
CL							0.94 (0.02) ***

Resin yield (RY), diameter at breast height (DBH), height (HGT), stem volume (SV), height under live crown (HLC), crown width (CW), crown length (CL) and crown surface area (CSA). *** $p < 0.001$; ** $0.001 < p < 0.01$; * $0.01 < p < 0.05$, level of significance of effects.

Table 7. Expected response ($\Delta G/\bar{x} \times 100$, ΔG is the genetic gains, and $\bar{x}$ is the mean values) in resin yield at each site when different selection criteria used.

Selection Criterion (Site)	Response (%)		
	Jian	Ganzhou	Jindezhen
RY	11.08	4.13	9.53
HGT	7.71	3.79	11.36
DBH	6.27	3.64	10.97
SV	6.83	3.39	11.53
HLC	0.00	−1.63	7.53
CW	2.01	4.03	7.28
CL	5.90	4.33	11.19
CSA	4.49	5.82	10.24

Resin yield (RY), diameter at breast height (DBH), height (HGT), stem volume (SV), height under live crown (HLC), crown width (CW), crown length (CL) and crown surface area (CSA).

4. Discussion

4.1. Mean Values and Site Effects

According to the three progeny trials in the present study, the mean RY values of *P. elliottii*, varied from 1.16 kg/tree to 1.24 kg/tree month (38.6–41.3 g/tree day) and were somewhat higher than some other pine species [14,16,26]. However, the present RY values for *P. elliottii* families were slightly lower than those reported for 15-year-old families of *P. massoniana* because these values were higher than 45 g/tree day [27]. These differences might reflect species variation within *Pinus*, differences in environment, the influence of climate variables, and differences in the sampling age. Moreover, the effects of tapping methods on RY should not be disregarded.

The mean annual growth rate for the HGT and DBH in the present study was slower than that of the 10-year-old and 13-year-old open-pollinated progeny tests for *P. elliottii* [28,29], and this finding might reflect the rapid growth of *P. elliottii* in the young stage (before age 12–13); however, after age 13, the growth was drastically reduced, which led to the slower mean annual growth rate for 27-year-old families of *P. elliottii* in the present study than that of the young plantation of *P. elliottii* [30]. Additionally, previous studies have suggested that *P. elliottii* exhibited different growth effects in different climatic provinces [31], and the slower annual growth rate for HGT and DBH in the present study might partially reflect the influence of climate variables on growth.

Site effects reflect the reaction of trees to the combined effects of edaphic and as local and regional climatic conditions [32]. Moreover, the physiological age, genotype and culture method may also impact the trees. Significant site effects were observed for RY, growth traits and morphologic traits (Table 3). The results indicated that edaphic and regional climatic conditions have significant RY, growth traits and morphologic property effects. These significant site effects on RY, growth traits and morphologic traits have previously been described and reported [33–35]. Comparisons of the growth rates between sites showed that the SV at Jindezhen and Ganzhou was lower and presented 5–7.5% less growth than that at Jian. This tendency corresponds to expectations that site conditions are more favorable for *P. elliottii* in Jian than the two other sites. As in Jiangxi Province, the most suitable place for the growth of *P. elliottii* was in the Jitai Basin, which lies in central Jiangxi Province and presents a climate and growth environment similar to that of their original regions.

The highest resin yield was not observed for the most productive Jian site, as expected, but at the least productive Ganzhou site. This disparity could result from of a variety of causes, but differences in within-site environmental heterogeneity are a likely contributing factor. The ability of an individual to produce resin is modulated by the environmental conditions because the environmental conditions have various effects on the properties of the resin duct, where resin is synthesized and stored. Sites with high radiation (favoring photosynthesis processes), high summer temperatures (delaying radial resin canal sealing), and low rainfall (inducing resin canal formation) will be highly productive or determine high resin production [26]. During the tapping season, warm springs and summers with low humidity percentages could correspond to higher resin yield values. Follow this pattern, Jindezhen site should have the highest resin yield, as the highest annual temperature and the least rainfall were observed at this site.

4.2. Genetic Variation and Heritability

The family effects in the joint analysis for RY, growth traits and morphologic traits were significant (Table 3). Previous studies [27,36,37] have also reported a significant family/clonal effect on the RY and growth traits of *Pinus* tree species, as well as for morphologic properties [38]. The present study shows the important genetic variation in resin yield among *P. elliottii* families and the heritabilities for resin yield were moderately high. Resin flow is extremely variable, depending on genetics, climate and environmental factors such as soil fertility and disturbances [39,40]. Therefore, the ability of a tree to produce resin and resin ducts is likely related to the degree of constraints imposed by genetic and environmental factors.

Many studies have shown that growth traits are under substantial genetic control for coniferous species. The heritabilities for growth traits of the three sites combined were moderate to high (Table 3). In general, the estimates of heritability were higher for HGT ($h^2{}_f = 0.55$, $h^2{}_i = 0.27$) than for DBH ($h^2{}_f = 0.45$, $h^2{}_i = 0.27$), indicating that HGT has higher genetic control than DBH and more genetic gain in terms of tree volume can be expected from the selection for HGT than for DBH. The heritability estimates of *P. elliottii* for morphologic traits in the present study for the three sites combined were not high except for HLC. Similar studies on other trees have drawn the same conclusions and indicated that most variation in morphological traits is caused by environmental factors not genetic factors, thereby limiting the achievable gains from selection [36,41].

For most observed traits, family heritabilities were higher than individual heritabilities for the three sites combined or at each individual site. This result indicates that higher genetic gains can be achieved with family selection in *P. elliottii* populations. In fact, the results of previous studies on other pines also support this view [15,42]. The heritability values of the observed traits in the present study varied from site to site. Overall, the heritabilities at Jindezhen were higher than those at Jian and Ganzhou, and this finding may have been related to the experiment site topography at Jindezhen, which was flat ground and may have had a relatively low environmental influence on these traits.

The CV_G, that is, the genetic variance standardized to the trait mean, is considered the most suitable parameter for comparisons of genetic variation and the ability to respond to natural or artificial selection [43]. In the present study, both the CV_G and heritability exhibited the same pattern, with higher values at Jindezhen and relatively lower values at Jian or Ganzhou. The CV_G values of the growth traits, which ranged from 2.99% to 7.45% in the present study, were of the same magnitude as the CV_G values of the morphologic traits, which ranged from 3.53% to 7.10%. These results indicate an equivalent genetic potential for the improvement of growth traits as that for morphologic traits. In the present study, the CV_G of SV was higher than the CV_G of HGT or DBH. The finding may reflect the fact that volume is a function of both HGT and DBH. The CV_G of HGT (5.06%) was higher than the

CV_G of DBH (2.99%), indicating that the scope for selection of HGT among families is larger than that for DBH.

4.3. Genotype by Environment Interaction

Because *P. elliottii* breeding programs are focused on developing families suitable for different environments, G × E interactions may have a significant impact on the precision of breeding values estimates because they can reduce genetic gain. With incongruence between test locations and deployment zones, the G × E, if improperly accounted for, could result in bias estimates and decreased genetic gain [32]. The significant family × site interaction variation observed for the RY, growth traits and morphologic traits (Table 3) indicated that the families exhibited differences in ecological variation and reaction norms under different growth conditions. Significant G × E interactions have previously been reported for growth traits and resin yield [38]; however, few morphologic trait results have been reported for *Pinus* tree species.

The type B genetic correlation is a measure of the importance of environment interactions on genotype, and it provides a more precise estimate of G × E interactions [24]. Overall, the inter-site type B genetic correlations observed in the present study ranged from 0.13 to 0.68 (Table 5), suggesting a large amount of variation reflective of changes in rank among families across sites. The absence of significant positive type B genotypic correlations between genotypic values at the Jingdezhen-Jian and Jingdezhen-Ganzhou sites for most traits (Table 5) indicated a true G × E, and the differences between these sites might reflect the family × site interaction. However, the type B genotypic correlations between Ganzhou and Jian for all traits were higher than those at Jingdezhen-Jian and Jingdezhen-Ganzhou sites (Table 5), indicating that these traits were more stable across Ganzhou and Jian. The trails at Ganzhou and Jian are relatively close in distance so does the climatic condition, but no significant difference of mean annual temperature between these two trails and the one located at Jingdezhen was observed. However, the annual rainfall is around 1800 mm at Jingdezhen, which is higher than Ganzhou and Jian (~1400 mm) (Table 1). As far as we know, the optimum annual precipitation for slash pine is about 1400 mm at Jiangxi province. Therefore, we speculated that the rainfall was the most important factors driving G × E. But more environmental and climatic factors as soil type, soil fertility are required to investigate further to delimit the deployment regions.

The ranges of genetic type B correlation were low to moderate (0.29–0.55) for resin flow, indicating that the genetic performance measured in the present study was generally inconsistent across sites and the environmental conditions in the study locations were different. Similar results were observed among *P. sylvestris* and *P. elliottii* families planted at different sites [44,45]. Westbrook [46] performed an association analysis and observed that 81% of the SNPs (Single Nucleotide Polymorphism) significantly associated with resin flow in loblolly pine were specific to individual sites, implying that environmental context has a significant impact on the effects of the alleles underlying quantitative genetic variation in resin flow via complex molecular mechanisms. Generally, there are two approaches used to deal with G × E in tree improvement programs. The first one is to choose the best genotypes for each site-type based on well-characterized environments. As mentioned before, the lack of enough environmental information for the tested sites limited the utilize of independent selection. Alternatively, it was more suitable to identify and select those stable genotypes that perform well across all the environments. Tree HGT showed less G × E than resin flow and resin flow showed a strong positive correlation with tree HGT at Jingdezhen (Table 6), suggesting that selection based on tree HGT would increase the stability of the genetic entries around Jingdezhen without decreasing resin production.

4.4. Genotypic Correlations between Traits

Previous studies on *P. elliottii* have reported that RY and growth traits (DBH and HGT) present a strong positive correlation [15,28]. This finding indicates that genetic factors act concurrently to increase RY and growth. The explanations from previous studies on the relationship between RY and growth traits are often varied, and overall, the resource availability hypothesis (RAH) and growth-differentiation balance hypothesis (GDBH) are the main explanations for the relationship between RY and growth in pines. *Pinus* species have an extensive system of constitutive and induced defenses to resist attacks from bark beetles and associated fungi [47]. The primary defense is resin, which is synthesized and stored in an interconnected network of axial and radial resin ducts in the secondary phloem and xylem [48]. Both resin and resin ducts are costly to produce, and these costs could lead to trade-offs between growth and defense [49]. A tradeoff likely occurs between growth and defense based on the allocation of acquired resources because acquired resources are limiting; thus, the relationship between growth and defense is expected to be negative. In practice, however, studies on the relationship between growth and defense have reported mixed results, with certain studies finding a negative relationship [40,50] and other studies reporting a positive relationship [51,52]. These results highlight one of the difficulties of testing defense theories [53] because defenses could be either positively or negatively correlated with growth depending on the metric used. For example, Hood and Sala [54] reported that when only relative defense measures (i.e., duct density or relative duct area) were included, defense showed a negative correlation with growth, thus supporting the RAH. This finding predicts that constitutive defenses are favored in slower-growing species, which reflects the higher costs of replacing tissues. However, when absolute measures of defense (i.e., duct size, duct production and duct area) were included, defense showed a positive correlation with growth, which contradicts the RAH. Therefore, faster-growing trees have larger ducts and higher total duct areas, thereby leading to higher resin yield than slower-growing trees. Notably, slower-growing trees invest more in resin duct defenses per unit area of radial growth (i.e., duct density and relative duct area) and are likely to produce less resin than a larger tree with lower relative resin duct investment. The results of the present study support this pattern because the estimated genetic correlations between growth traits and resin yield were positive and strong.

In the present study, the estimated genetic correlations between most morphologic traits and RY were moderate to strong. Thus, a tree with a larger crown size typically produces more resin. This finding could be explained by the GDBH, which predicts that any resource limitation that reduces growth more than photosynthesis (e.g., water and nutrients) will increase the carbohydrates available for defense with little to no trade-off to growth. If the resource is limited, then the carbon demand for growth decreases but photosynthesis continues, presumably causing a shift of carbohydrate allocation from growth to defense (resin production and resin duct formation). Based on this logic, trees with larger crown sizes would produce more constitutive resin than slower-growing trees because trees with larger crown biomasses would have greater carbon surpluses later in the season to invest in resin and resin duct formation. Therefore, morphologic traits, particularly CW, CL and CSA, could be used as indirect assisted traits for selecting high-yielding trees.

4.5. Implications for Tree Improvement

The moderate heritability for resin yield and growth traits indicated that selective breeding according to the breeding merit ranks of parental trees (backward selection) would be effective. Forward selection was not recommended before the unknown paternal trees of the half-sibs were identified using pedigree reconstruction method. Unexpected G × E were observed for all the traits across the three trails suggesting determination of the environmental factors driving the important G × E was necessary to delimit deployment areas. The annual rainfall was probably the main factors but more climatic and soil factors should be investigated in future studies. Alternatively, the genotypes with stable performance over all the environments and higher breeding values were the proper candidates for further breeding and deployment programs.

On the whole, significant positive genetic correlations among resin yield, growth and morphologic traits indicate that selection for faster growth and larger crown size can increase resin yield. On the other hand, the inclusion of resin yield into tree breeding programs can lead to a partial enhancement of growth. Simultaneous improvement of resin yield, growth and morphologic traits of *P. elliottii* was concluded to be practical when strong positive correlations exist between these traits. Expected genetic gains and the correlated responses estimated in this study are based on genotypic correlations, genotypic variances, and individual tree heritability. The results obviously indicated that there would be important benefit in using the growth traits as selection traits together with resin yield if the objectives were to improve resin yield and growth increment.

5. Conclusions

We used 3695 samples from 112 families at three sites for a genetic study in resin yield, growth and morphologic properties of *P. elliottii* in Jiangxi Province, China to estimate the genetic parameters (heritability, type b genetic correlation, and among traits genetic correlation) and correlated response. These results are summarized as:

(1) Significant site, family and family × site effects were found for resin yield, growth and morphologic traits. The differences between the three sites might reflect the family × site interaction, and rainfall might be the main driver of the interaction.

(2) Heritabilities were moderate to high for resin yield and growth traits for the three sites combined, whereas with relatively lower heritabilities for morphologic traits.

(3) The genetic correlations of *P. elliottii* among resin yield, growth traits and morphologic traits were moderate to strong, these findings suggested that selection for growth and morphologic traits might lead to increment in resin yield, and genetic factors act concurrently to increase resin yield, growth and morphologic traits. Selection based on growth traits will have moderate to strong effects on resin yield.

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