breeding program, a single breeding population may be established, tested and selected at sites similar to A. This strategy will not significantly affect selections for straightness, since selections made at site A predicted fairly well performance of straightness at site C. Since results of a single test are likely to overestimate gain across a region, as it ignores possible GXE, tests established should be replicated within the region represented by site A. Nursery period in *P. taeda* varies with altitude, being shorter at low altitudes, and therefore locating the nursery and genetic tests at site A, which is the lowest in elevation, should result in savings both in nursery and transport costs.

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Analyzing Parameters of Growth and Yield Models for Chinese Fir Provenances with a Linear Mixed Model Approach

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Abstract

Chinese fir is the preferred species for tree farm plantations in south Asia. Height growth and basal-area growth models were used to test the growth performance of Chinese fir originating from 26 provenances grown on two separate plantations in southern China. Parameters of the height growth and the basal-area growth models were statistically tested by way of a linear mixed-effects model approach in order to identify the growth parameters that are influenced by site and provenance. For the stand height growth model, it was found trees originating from the 26 provenances have different site indices when planted at similar sites. However, the slope coefficient was similar across provenances. Similarly for the basal-area growth model, the model intercept and the density-age related parameter showed no significant differences among provenances. No conclusive inference could be drawn concerning the site index-related parameter in the basal-area growth model.

Key words: basal area, Chinese fir provenances, growth and yield models, height, mixed-model approach, plantation, statistics.

Introduction

Chinese fir (*Cunninghamia lanceolata*) is a fast growing species that produces high quality lumber and attractive revenues up to 30 years. First commercial thinning can be done at about 8 years to 10 years following planting. As a result, Chinese fir constitutes one of the main commercial tree species in south Asia. As part of tree improvement research, many experimental plantations have been established in the past 20 years, with seed originating from many different geographic regions (BUFORD, 1986; MONTENEGRO *et al.*, 1997; YING, 1997). Growth and yield models are commonly used to evaluate growth performance. Parameters used in such models are normally site specific in nature. As a rule, these growth models need re-calibration (model parameter re-estimation) every time they are applied to new provenances or sites.

In theory, it is possible to design a growth and yield model to estimate stand growth for a single-species plantation. In designing such a model, efforts are required to determine which parameters in the growth and yield models are sensitive to provenance and site conditions, and which are not so sensitive.

Adequate testing of growth and yield models requires that repeated measurements be taken over many years. For data-

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sets that contain large amounts of repeated measurements, appropriate specification of the covariance structure of the data is crucially important to the model inference reliability (GREGOIRE *et al.,* 1995). Various approaches have been employed to deal with such datasets that contains repeated measurement. For example, BIGING (1985) uses a varying parameter approach to estimate the parameters of site index curves. He explicitly considers the differences between individual trees and the effect that these differences have on model parameters. The varying parameter approach can be considered as a type of linear mixed effect model. Linear mixed effects models have been used in the past to account for covariances among repeated measurements (BIGING, 1985; BUFORD and BURKHART, 1987; GREGOIRE *et al.,* 1995; LAPPI, 1997; TASISSA and BURKHART, 1998).

The data structure of seed-source and provenance experiments is more complex compare to conventional growth and yield experiments. The amount of data generated is often high as seeds from many seed sources are often planted at the same sites. However, the number of trees per provenance is often low. Currently, there are no scientific papers that discuss the use of linear mixed models for making statistical inference on parameters of growth and yield models based on data from provenance experiments.

The objective of this paper is to use linear mixed effect models to estimate and test the parameters of growth and yield models of Chinese fir provenances. The reported research also establishes a general procedure for using this approach to estimate and test growth and yield model parameters based on provenance experiments data.

Study Area and the Data

Chinese fir trees from each of 26 provenances were planted in 1980 in two separate experimental plantations in southern China. The Hongya forest farm (F1) is located in Sichuan province (29° 14' N, 103° 15' E) at an elevation of 900 m to 1000 m above mean sea level. Annual average temperature is 12 °C and precipitation is 2646 mm. Jigongshan forest farm (F2) is located in Henan province (31° 50' N, 114° 05' E) at an elevation of 340 m to 385 m. Annual temperature is 12.5 °C and annual precipitation is 1355 mm. Soils at both locations are characterized as yellow brunisols. Granite is the main parent material in both locations.

Fourteen trees from each provenance were planted at Jigonshan farm, and 30 trees from each provenance were planted at Hongya farm. The initial density was 2 by 2 meters for all plantations, resulting in 2500 stems per hectare. All sites within the same farm area were assumed to have similar site quality. Only dominant trees were used in our model analysis. Measurements were taken every two years from stands of 6 years to 17 years old. During each measurement period, height of dominant trees and the diameter at breast height (DBH, 1.3 m above ground level) of all living trees were recorded. However, only 56 dominant trees from Hongya and 40 dominant trees from Jigongshan were used in testing model parameters.

The Linear Mixed Effects Model

The linear mixed effects model of this paper is of the general form

$$y = Xb + Zn + e \qquad [1]$$

where

$E(e) = 0$, $Cov(e) = R$,

$E(n) = 0$, $Cov(n) = G$, and

y = a vector of n observations,

X = a known 'n x p' design matrix of fixed effects,

b = an unknown p-vector representing fixed effects,

n = unknown random vector representing random effects with model matrix Z.

e = n-vector representing random errors.

We can set $x = Zb + e$, then $E(x) = 0$, and let $V = Cov(x) = Cov(y) = ZGZ' + R$.

Usually, we do not know the elements of the covariance matrix V. Unlike the elements of V, there are at least three methods to estimate the elements of matrices G and R. These methods are the maximum likelihood (ML), restricted-residual maximum likelihood (REML), and minimum norm quadratic unbiased estimate (MINQUE) methods (CHRISTENSEN, 1996). However, SWALLOW and MONAHAN (1984) present simulation evidence favoring REML and ML over MINQUE. In this paper, we chose the REML method to estimate the elements of matrices G and R.

To obtain estimates of b and n, the standard method is to solve the mixed model equations (HENDERSON, 1984), i.e.,

$$\begin{bmatrix} X'\hat{R}^{-1}X & X'\hat{R}^{-1}Z \\ Z'\hat{R}^{-1}X & Z'\hat{R}^{-1}Z + \hat{G}^{-1} \end{bmatrix} \begin{bmatrix} \hat{\beta} \\ \hat{\nu} \end{bmatrix} = \begin{bmatrix} X'\hat{R}^{-1}y \\ Z'\hat{R}^{-1}y \end{bmatrix}, \qquad [2]$$

where $\hat{G}$ and $\hat{R}$ are estimates of G and R.

Statistical inferences concerning the fixed- and random-effects of parameters in the mixed model can be obtained by testing the following null hypothesis:

$$L\begin{bmatrix} \beta \\ \nu \end{bmatrix} = [M \ K]\begin{bmatrix} \beta \\ \nu \end{bmatrix} = M\beta + K\nu = 0, \qquad [3]$$

in which L=[M K] is a block matrix. Matrix M is the contrast of fixed effects and matrix K is the contrast of random effects. For example, suppose that $n' = [n_1, n_2, n_3]$ and we test null hypothesis n_1, n_2, n_3, then

$$K = \begin{bmatrix} 1,0,-1 \\ 0,1,-1 \end{bmatrix}. \qquad [4]$$

Under the assumption of normality for b and *n*, then statistic

$$F = \frac{\begin{bmatrix} \hat{\beta} \\ \hat{\nu} \end{bmatrix}' L'(L'\hat{C}L)^- L \begin{bmatrix} \hat{\beta} \\ \hat{\nu} \end{bmatrix}}{rank(L)}, \qquad [5]$$

where "H" is a generalized inverse of "H", and $\hat{C}$ is a generalized inverse of the coefficient matrix C, *i.e.,*

$$\hat{C} = \begin{bmatrix} X \hat{R}^{-1}X & X \hat{R}^{-1}Z \\ Z \hat{R}^{-1}X & Z \hat{R}^{-1}Z + \hat{G}^{-1} \end{bmatrix}^-. \qquad [6]$$

Equation [5] can be compared against an approximate F-distribution with degrees of freedom rank(L) in the numerator and n-rank (X Z) in the denominator (SAS, 1992). Statistical inference about b and *n* can be made with Equation [5].

The restricted-residual maximum likelihood (REML, SWALLOW and MONAHAN, 1984) can be used to estimate the covariance matrix of the vector of the error term of the regression [R= cov(e) is n x n matrix and e = n-vector representing random error] and covariance matrix of the vector random

effect [G= cov(n) is q x q matrix and n = p-vector representing an unknown random effect]. Based on our experience, matrix R is a block diagonal matrix, because trees of the same age have the same residual variance and trees of different ages have different residual variance (*Table 1*). The covariance matrix G uses a simple diagonal matrix $G = g^2 I$, because different plantations or seeds are independent from one another.

Growth and Yield Models

It is generally accepted that a growth and yield model can be defined by a system of equations including a height growth model and a basal area growth model (TANG *et al.,* 1994). In this study, a height growth model is used to estimate site indices and slope parameters using data from dominant trees of several provenance plots. The estimated site indices are used as fixed parameters in basal area growth model.

Height Growth Model: Parameter Testing

A simple log-transformed exponential function was used to model dominant height growth in Chinese fir, i.e.,

$$\ln H = \ln S + b(1/t - 1/t_o) \qquad [7]$$

where: t = stand age (year)

$\quad$ t_o = index age (year = 15)

$\quad$ S = site index (m)

$\quad$ b = slope coefficient.

A test was applied in order to determine whether the Chinese fir trees originating from the different provenances with the same site index S and the same slope b.

BIGING (1985) used the generalized least square (GLS) method to estimate parameters of site index curves. His method explicitly considered the differences between individual trees and the impact of tree-specific differences on parameters. BUFORD and BURKHART (1987) addressed similar questions, with mixed-effects to account for correlation among within tree observation in their statistical treatment. Such methods have a common basis to the linear mixed-effects model approach considered in this paper.

Similar with BIGING (1985), we assume that $Y_{ijk} = \ln(H_{ijk})$ for the ith provenance and j^{th} tree at age k. For the ith provenance, we define the site index related parameter a_i and slope factor b_i as following:

$$a_i = \ln S_i = a + a_i \qquad [8]$$

and

$$b_i = b + b_i \qquad [9]$$

where: a = lnS

$\quad$ b = average slope

$\quad$ S = average site index

$\quad$ S_i = site index of the ith provenance

a_i and b_i represent the parameter differences for provenance i. Then the statistical model has the following form:

$$Y_{ijk} = [a + b \, X_{ijk}] + [a_i + b_i \, X_{ijk} + r_{ij} \, X_{ijk}] + e_{ijk}, \qquad [10]$$

where: r_{ij} = random effect of the jth tree from the ith provenance

$\quad$ X_{ijk} = $1/t_{ij} - 1/t_o$

$\quad$ t_{ij} = tree age of the jth tree from the ith provenance

$\quad$ r_{ij} = random effect of the jth tree from the ith provenance

$\quad$ e_{ijk} = random error with N(0, R) distribution.

If we assume that the trees from the different provenances have the same site index, *i.e.,* $a_i = 0$ and $b_i = 0$, then Equation [10] would be equivalent to the mixed model implementation of the varying parameter model used by BIGING (1985), and which can be used to estimate the fixed effects of parameters a and b.

In this model, we can test whether the site index and slope for different provenances are different from the average value with null hypothesis Ho: $a_i = 0$, i = 1, ..., m; and Ho: $b_i = 0$, i = 1, ..., m.

Following BIGING *et al.* (1985), tree-age related variability and impacts of tree-to-tree variability is considered as a random effect.

Considering that the seeds from one provenance used in a plantation represent a random sample for that particular provenance, a_i and b_i should be considered as random effects when the intention is to test the differences in a_i and b_i among provenances.

The proposed testing procedure can be used to test whether all provenances share the same site index and slope. The procedure also considers the impacts of tree-to-tree variabilities. Using the SAS procedure PROC GLM (LITTELL *et al.,* 1996), the testing procedure proceeds as follow:

1. Two null hypotheses can be stated according to the linear mixed model [10]:

$$H_{o1} : a_i = 0, i = 1, ..., m$$

$$H_{o2} : b_i = 0, i = 1, ..., m$$

2. The F-value is calculated with equation [5] and is used to carry out statistical inference. The results are provided in *table 2*. Results from both plantations suggest that hypothesis $H_{o1}:a_i = 0$ is rejected, and hypothesis $H_{o2}: b_i = 0$ is not rejected. This means that trees from the different provenances grown in the same region generally possess different site indices, but similar slopes. According to these results, the differences exhibited in $a_i = a + a_i$ can not be attributed to simple random error, and thus a_i can be considered as a fixed effect. Parameter b_i should be considered as the sum of the fixed-effect component b and the random-effect components b_i and be retested in step 4 based on the assumption that a_i are fixed effects.

3. According to the results obtained in step 3, equation [10] can be rewritten as:

$$Y_{ijk} = [a_i + b \, X_{ijk}] + [b_i \, X_{ijk} + r_{ij} \, X_{ijk}] + e_{ijk} \qquad [11]$$

where a_i and b are due to fixed effects. Equation [11] can be used to test hypothesis:

$$H_{o2} : b_i = 0, i = 1, ..., m$$

The F-values and test results are shown in *table 3*. Test results confirm that hypothesis $H_{o2}: b_i = 0$, i = 1,..., m is not

Table 1. – Estimates of residual variances of log-transformed dominant tree height at different ages [log(H)]

Location	Estimate variances					
	age=6	age=8	age=10	age=12	age=14	age=16/17
F1 (*Hongya*)	0.0236	0.0051	0.0018	0.0032	0.0017	0.0022
F2 (*Jigongshan*)	0.0125	0.0065	0.0088	0.0034	0.0016	0.0013

Table 2. – Testing results for random site index and random slope.

Location	Parameter	N.	Numerator df[a]	Denominator df[a]	F	Pr>F
F1 (*Hongya*)	Site index (α)	312	26	259	10.09	<0.0001
	slope (β)	312	26	259	0.26	0.9999
F2 (*Jigongshan*)	site index (α)	312	26	414	3.45	<0.0001
	slope (β)	312	26	414	1.36	0.1018

[a]) df denotes the degrees of freedom

Table 3. – Testing results for fixed site index and random slope.

Location	Parameter	N	Numerator df[a]	Denominator df[a]	F	Pr>F
F1 (*Hongya*)	slope (β)	312	26	259	0.52	0.9743
F2 (*Jigongshan*)	slope (β)	468	26	416	0.39	0.9975

[a]) df denotes the degrees of freedom

Table 4. – Site indices of plantations with various seed sources.

Seed source number	F1 (*Hongya*)		F2 (*Jigongshan*)	
	a_i	Site index	a_i	Site index
1	2.08384	16.50	2.78419	16.19
2	2.82065	16.79	2.73399	15.39
3	2.90365	18.24	2.77904	16.10
4	2.84898	17.27	2.74282	15.53
5	2.78446	16.19	2.73223	15.36
6	2.78961	16.27	2.81430	16.68
7	2.95525	19.21	2.73976	15.48
8	2.78239	16.15	2.71910	15.16
9	2.83110	16.96	2.78099	16.13
10	2.81880	16.75	2.75097	15.65
11	2.78323	16.17	2.73326	15.38
12	2.88710	17.94	2.73848	15.46
13	2.80619	16.55	2.74320	15.54
14	2.78937	16.27	2.74680	15.59
15	2.71259	15.07	2.76167	15.82
16	2.84734	17.24	2.73417	15.39
17	2.86899	17.62	2.70981	15.02
18	2.86423	17.53	2.72855	15.31
19	2.78546	16.21	2.79086	16.29
20	2.79497	16.36	2.74571	15.57
21	2.64009	14.01	2.71805	15.15
22	2.81631	16.71	2.71415	15.09
23	2.74709	15.60	2.74259	15.53
24	2.71594	15.11	2.70350	14.92
25	2.75375	15.70	2.68875	14.70
26	2.72353	15.23	2.76811	15.93

bote: site index = $\exp(a_i)$
intercept, a = 2.72353 for Fl, a = 2.76811 for F2.
slope, b = 10.7671 for Fl, b = 10.0321 for F2.

rejected, and that the trees from the different provenances have the same slope value. The observed differences are mainly due to random error.

According to this analysis, the site index curves can be written as:

$$H_i = S_i \exp [b(1/t - 1/20)], \qquad [12]$$

with b = –10.1671 for Hongya Forest Farm (F1) and b = –10.0321 for Jigongshan Forest Farm (F2). The values for site indices S_i and a_i are given in *table 4*.

Inter-model Comparisons

In order to compare the results of the linear mixed effects model and those of the traditional fixed effects model, we constructed the following tests:

$$H_{o3}: a_i - a_1 = 0, i = 1, ...,m$$
$$H_{o4}: b_i - b_1 = 0, i = 1, ...,m.$$

where ai and bi are treated as fixed effects. Test results using fixed-effects only are shown in *table 5*. Comparing results obtained with and without random effects (*Tables 3* and *5*, respectively), the fixed-effect only null hypothesis test found that the slope of trees from different provenances tended to be different (*Table 5*). This is expected because hypotheses H_{o3} and H_{o4} test the differences of a particular sample of seeds used. The test of fixed effects can be used to test the differences that are caused by the combined effects of the random observational error, random growth factor, provenance difference, and model error on parameters a_i and b_i. Thus, the test should have a greater tendency to cause the rejection of the null hypotheses, indicating that significant differences exist between trees from different provenances.

Table 5. – Testing results for site index and slope as fixed effects.

Location	Parameter	N.	Numerator df[a]	Denominator df[a]	F	Pr>F
F1 (*Hongya*)	Site index (α)	312	25	259	6.80	<0.0001
	slope (β)	312	25	259	1.73	0.0189
F2 (*Jigongshan*)	site index (α)	468	25	414	2.33	0.0004
	slope (β)	468	25	414	2.69	<0.0001

[a]) df denotes the degrees of freedom

Differences Between Plantations

Differences between plantations should be treated as a fixed effect. A model of between-plantation effects is constructed as follows:

$$Yf_{ijk} = [a_f + b_f X_{fijk}] + [b_{fi} X_{fijk} + r_{fij} X_{fijk}] + e_{fijk} \quad [13]$$

where $f = 1, 2$ represent the two plantations. Test of the null hypothesis

$$H_{o5} : b_1 - b_2 = 0,$$

suggests that the null hypothesis cannot be rejected on the basis of the generated F-values provided in *table 6*. This implies that the slope coefficients b of trees from the different plantations are not significantly different from one another.

Table 6. – Testing results for slope (slope) of height growth model for trees from the two plantations (i.e., F1 and F2).

Parameter	N	Numerator df[a]	Denominator df[a]	F	Pr>f
b (*location*)	780	1	3	0.01	0.9107

[a]) df denotes the degrees of freedom

Basal-area Growth Model: Parameter Testing

The same procedure can be used to test parameters for basal area growth (Li *et al.,* 1988; Tang *et al.,* 1994); namely, parameters of the model equation

$$Ln\ G = b_1 + b_2 \ln S + b_3 \ln(1 - \exp[-c_4(t - t_b)(DI/1000)^{c_5}], \quad [14]$$

Where: G is the basal area of the stand ($m^2\ ha^{-1}$)

S = site index (m)

t = stand age (year)

DI = site density index (stem/ha)

t_b = breast height age (=3 years for Chinese fir)

b_1, b_2, b_3, c_4 and c_5 are model parameters.

Parameters c_4 (=0.003213229) and c_5 (= 4.89714) are set according to values published in Li *et al.* (1988). We want to test whether parameters b_1, b_2 and b_3 are different for trees from different provenances. A statistical model is constructed as follows:

$$Y_{ik} = (b_1 + b_{1i}) + (b_2 + b_{2i})X^1_{ik} + (b_3 + b_{3i}) X^2_{ik}] + e_{ik} \quad [15]$$

where $X^1 = \ln S$

$X^2 = \ln\{1 - \exp[-c_4(t - t_b)(DI/1000)^{c_5}]\}$

Associated null hypotheses are:

$H_{o6}: b_{1i} = 0, i = 1, ..., m$

$H_{o7}: b_{2i} = 0, i = 1, ..., m$

$H_{o8}: b_{3i} = 0, i = 1, ..., m$

The contrast matrices of random effects are 'm x m' unit matrices. The F-values are calculated as before and the results are provided in *table 7*. For plantation F2, null hypotheses are accepted. This implies that the basal area growth model [14] is applicable across provenances considered in this study. For the other plantation F1, null hypothesis [6] is not rejected and the other two hypotheses are rejected. From this, parameter b_1 can be considered as a fixed parameter applicable to all provenances. Further studies are needed to substantiate the roles of parameters b_2 and b_3 in the basal area growth model. Assuming b_1 is constant, model equations [14] to [15] can be used to construct a statistical model to test the random effects of parameters b_2 and b_3 with hypotheses H_{o7} and H_{o8}. The statistical model to be used in these tests is as follows,

$$Y_{ik} = b_1 + (b_2 + b_{2i})X^1_{ik} + (b_3 + b_{3i}) X^2_{ik} + e_{ik} \quad [16]$$

Table 8. – Testing results for b_2 and b_3 in basal area growth model for plantation F1 (Hongya).

Parameter	N	Numerator df[a]	Denominator df[a]	F	Pr>F
b_2 (*site index*)	156	26	103	11.38	0.0001
b_3 (*density-age*)	156	26	103	1.38	0.1279

[a]) df denotes the degrees of freedom

The results indicate that null hypothesis H_{o8} cannot be rejected. Hence, parameters b_1 and b_3 should be the same for different provenances, and the variation exhibited is caused by random error. Parameter b_2, however, could be different for trees grown from different provenances.

Conclusion

1. Trees from different provenances of Chinese fir should have different site indices and the same slope parameters. The slope parameters for trees grown in different geographic locations did not show significant differences.

2. For the basal area growth model, data from both plantations confirmed that the model intercept and density-age related parameter remain the same for different provenances. For other site index-related parameters, no conclusive inference can be made because results from the two plantations considered are significantly different.

3. Using traditional general linear models for statistical inference, the model tests the differences caused by the combined effects of the random observational error, random growth factor, provenance differences, and model error on the parameters, and thus there is greater likelihood of rejecting proposed null hypotheses. It is suggested that a linear mixed model of the type described should be used to discriminate between the random and fixed effects on model parameters.

Table 7. – Testing results for parameter intercept b1, site index-related parameter b_2, and density age-related parameter b3 of basal growth model

Location	Parameter	N	Numerator df[a]	Denominator df[a]	F	Pr>F
F1 (*Hongya*)	b_1	156	26	78	0.21	1.0000
	b_2	156	26	78	5.36	0.0001
	b_3	156	26	78	2.11	0.0062
F2 (*Jigongshan*)	b_1	156	26	78	0.02	1.0000
	b_2	156	26	78	0.20	1.0000
	b_3	156	26	78	0.35	0.9980

[a]) df denotes the degrees of freedom

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Genetic Variation of Subalpine fir (Abies lasiocarpa (Hook.) Nutt.) in the Olympic Mountains, WA, USA

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Summary

This study examines the genetic structure of subalpine fir along an elevation gradient in the Olympic Mountains, Washington. Starch gel electrophoresis was used to resolve 15 isozyme loci from 9 populations on 3 mountains. First, we describe the genetic variation of these 9 populations in the Olympic Mountains, and compare these results to those of other tree species. Then we compare genetic differentiation (G_{ST}) among populations to test if selective pressures alter genotypic frequencies in response to steep environmental gradients over the elevation range of this species. Genetic variation is relatively uniform throughout most of the sites sampled (H_o range = 0.103-0.139 in the eastern Olympic Mountains), with notably lower diversity observed at the western extent of subalpine fir's range (H_o=0.70 in the central Olympic Mountains). Lower diversity in the western Olympics may result from either founder effects as the species expanded its range from a glacial refugium, or from selection pressures on the loci considered. Genetic differentiation is greater among high elevation sites on different mountains, than among different elevation sites on the same mountain, or lower elevation sites on different mountains. Estimates of gene flow (N_m=7.8) are high among all sites.

Key words: Abies lasiocarpa, genetic diversity, gene flow, isozyme, Olympic Mountains.

Introduction

Genetic variation is high in most conifer species (HAMRICK et al., 1979; HAMRICK and GODT, 1990). While most of this variation occurs within populations, resulting in relatively uniform genetic structure among populations (TIGERSTEDT, 1973; GURIES and LEDIG, 1982), variation does occur among populations in response to environmental gradients (reviewed by LINHART and GRANT, 1996). Genetic variation in conifers has been found among stands on sites with varying water availability (STUTZ and MITTON, 1988; SHEA, 1990), elevation (GRANT and MITTON, 1977; MITTON et al., 1980; HIEBERT and HAMRICK, 1983), and slope aspect (MITTON et al., 1977), and in some cases natural selection for specific genotypes has been suggested in response to site differences (e.g., FRYER and LEDIG, 1972; MITTON et al., 1977; GRANT and MITTON, 1977; LINHART and GRANT, 1996). Differentiation of genetic structure in species occurs even when migration rates are high, suggesting that selection forces where environmental gradients are steep may be sufficient to cause genetic differentiation in spite of adequate gene flow (JAIN and BRADSHAW, 1966; GRANT and MITTON, 1977; MITTON et al., 1977, 1980; LINHART et al., 1981; WOLF and SOLTIS, 1992). In a review of the evolutionary significance of genetic differentiation in plants, LINHART and GRANT (1996) conclude that environmental heterogeneity generates genetic heterogeneity by causing differing selection pressures and creating significant barriers to gene flow through differences in phenology.

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