

# Developmental Instability in Leaves of *Tectona grandis*

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## Summary

*Tectona grandis* clones were investigated for developmental instability of leaves at the top, middle and lower crown strata. Developmental instability was measured by asymmetry and two kinds of intraleaf variability of vein distribution. The instabilities varied among clones, trees and zones, suggesting that they are governed by genetic factors. Instabilities of leaf parts were positively and highly correlated with each other. Magnitudes of different instability indices of various clones vary, indicating that each of them are also governed by some common genetic mechanism. Directionality was found to be random, and developmental instability varies according to the stages of tree growth. Leaves developing from the middle portion of the crown possessed less instability in comparison to either end. Clones showing generally higher instability, are comparatively stable at the same stage which suggests that genes responsible for developmental error may become more active in certain growth stages than in others

**Key words:** *Tectona grandis* leaf, Intra-genotypic variability, Developmental instability, Genetic control, Correlation with bole length.

## Zusammenfassung

Klone von *Tectona grandis* wurden auf ihre entwicklungsmäßige Instabilität bezüglich der Blätter in hohen, mittleren und unteren Kronenregionen untersucht. Die Instabilität wurde durch Asymmetrie und zwei verschiedene Arten der Aderverteilung innerhalb eines Blattes festgestellt. Die Instabilität variierte zwischen Klonen, Bäumen und Zonen, was anzeigt, daß sie durch genetische Faktoren bestimmt wird. Die Instabilitäten der Blatt-Teile waren eng und positiv miteinander korreliert. Die Ausmaße der unterschiedlichen Instabilitätsindizes verschiedener Klone variierten, was anzeigt, daß sie ebenfalls von einigen gemeinsamen genetischen Mechanismen reguliert werden. Die Richtung war zufallsmäßig, die entwicklungsmäßige Instabilität variierte im Verlauf der Stadien der Baumentwicklung. Blätter, die sich in der Kronenmitte entwickelten, besaßen weniger Instabilität als die beiden Enden. Klone, die generell eine höhere Instabilität zeigten, waren im selben Stadium vergleichsweise stabil, was anzeigt, daß Gene, die für entwicklungsmäßige Fehler verantwortlich sind, in manchen Entwicklungsstadien aktiver sind, als in anderen.

## Introduction

Intragenotypic variability can be measured in two ways; by measuring different individuals of the same genotypes and by measuring the repetitive organs of a single individual. This intragenotypic variation is known as developmental instability and is thought to be the result of environmental fluctuation inside and outside of the plant and of lack of homeostatic buffering during the course of development of organs. PAXMAN (1956) showed that the developmental instability of various characters in *Nicotiana rustica* differed due to different genotypes and that such differences were specific for the genotype and individual characters. ROY (1963) reporting on instability in leaves and

flowers of *Jasminum multiflorum*, var. *rubescens*, var. *alba* and on *Nyctanthis arbor-tristis*, found significant differences among trees within and among seasons. LEVIN (1970a) evaluated developmental instability in *Liatris aspera*, *L. spicata*, *L. cylindraceae* and in their hybrids by analysis of intragenotypic variance, and by Kurtosis. The two methods gave different results, as a result of buffering and canalisation which are two functionally related but genetically different components. SAKAI and SHIMAMOTO (1965a, b) have shown in *Oryza sativa* that if two characters controlling pleiotropism by the same set of genes, take their own developmental pathway from a very early stage, a slight correlation exists between their developmental instabilities. If they take the same developmental path and the differentiation sets in late, the correlation coefficient will be high. In *Nicotiana tabacum* they showed that the developmental instabilities varied among varieties, that the instability is controlled by genetic factors and, that the high yielding varieties contains less instability than the lower yielding variety. BAGCHI and IYAMA (1984) showed that the developmental instability in *Arabidopsis thaliana* can be induced by irradiation, proving genetical control. They also showed that the developmental instability is susceptible to selection pressure by selecting lines with higher and lower instabilities, that these are heritable and that the magnitude of instability changes with changes in temperature.

The above experiments show that the developmental instability and the within-genotype-variability are genetically controlled. Apart from the immense importance of developmental instability on adaptation, survival and fitness, the trait can be used as a marker for increased production. SAKAI and SHIMAMOTO (1965a) showed that high-yielding lines of *N. tabacum* contains lower instability. This may be a specific case where the correlation is accidental or specific for that species or it may be a general phenomena where developmental instability is inversely related to important vegetative characters. The high-yielding lines might have resulted from repeated selection, but it is obvious that commercial selections were made on productivity, not on lower-instability. This needs to be verified for forestry where orthodox selection of long duration crops through provenance or progeny tests may take years to complete at a massive investment and by the time results are available, the value might diminish considerably. In fact, TODA (1965) has negated the practical utility of progeny trials with reference to *Cryptomeria japonica*.

In the present investigation, assessment has been made of the teak clones for: 1) inter-clonal variability in developmental instability, 2) intra-clonal differences of the different indices of the same parameter, 3) differences among growth zones, and 4) relationship analysis between selected parameters and other vegetative characters.

## Materials and Methods

Twenty clones of teak were field grafted in 1966 onward in a latin square layout having twenty-ramets each in two blocks to form a seed orchard. The details of the clones used in this study are given in table 1.

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Table 1. — Clonal identification of the materials used.

Sl. No.	Clone	Accession No.	Places where collected
1.	K	-	Dhan Singh Tree, Dehra Dun, U.P. India.
2.	G	-	Dandeli, Karnataka, India.
3.	M	-	Kurseong, West Bengal, India.
4.	A	-	Nilambur, Kerala, India.
5.	N	-	Laos.

Five clones with three trees per clone were selected randomly. The crown lengths were visually divided into a top, middle and bottom zone. From each zone 5 mature leaves were taken, making a total of 15 leaves per tree and quantitative characters were measured from each leaf (Fig. 1).

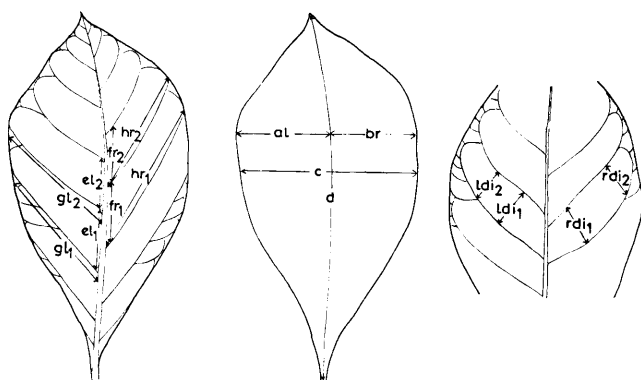


Fig. 1. — Schematic diagram on the method of leaf measurements.

From these measurements, developmental instability of leaves was measured in three ways: (1) Asymmetry (A), the absolute difference between the sides of a leaf divided by the maximum width of the leaf,

$$A = \frac{|al - br|}{c}$$

2) Vein-distance variability (D), Intra-leaf variation expressed in standard deviation of inter-vein distance on the mid-rib divided by average inter-vein distance,

$$D = \frac{\sigma d}{\bar{d}} = \frac{\sigma \text{ of } (el_1, el_2, fr_1, fr_2)}{\text{mean of } el_1, el_2, fr_1, fr_2}$$

3) Vein deviation index (I), Absolute difference between the largest and smallest distance of two adjoining veins divided by the average length of the two veins,

$$I = \frac{|di_1 - di_2|}{mi} = \text{where, } mi = \frac{\text{1st vein length} + \text{2nd vein length}}{2}$$

The vein-deviation index (I) was obtained both for the left half ( $I_L$ ) and right half ( $I_R$ ) of the lamina separately,

$$I_L = \frac{|Ldi_1 - Ldi_2|}{mi_L}$$

$$I_R = \frac{|rdi_1 - rdi_2|}{mi_R}$$

where  $mi_L$  and  $mi_R$  stands for the  $mi$  (already described) of the left half and right half of the lamina respectively.

The measurements of veins arising at both the extreme directions of upper and lower ends of lamina were excluded. The broad guidelines of the method is from SAKAI and SHIMAMOTO (1965a).

## Results

### A. Clonal differences in developmental instabilities of teak leaves

The teak leaves of various clones differed structurally in their size, shape and symmetry. The degree of inconsistency or accidents in development of a leaf was measured by analyses of variance of four indices of foliar instability (Table 2). Mean values for the five clones are shown in table 3. From table 2, it may be seen that asymmetry, vein-distance-variability and vein-deviation-index (R) are statistically highly significant among clones. The clone vs. tree interaction is highly statistically significant which means that the trees of a clone may influence developmental instability of leaves. The magnitude of the indices, in terms of mean values of asymmetry, vein-distances variability and vein deviation index are given in table 4.

Clone A from the southern part of India (Nilambur) possesses the highest mean instability, while Clone G from the local collection possesses the lowest (Table 4). The local clone with its lesser instability causes one to conclude that the differential adaptability is possibly due to latitudinal

Table 2. — Anova for four indices of developmental instability.

Sources of variation	df	Asymmetry	Vein-distance variability	Vein-deviation Index (L)	Vein-deviation Index (R)
Bn clone	4	0.0298***	0.0769***	0.0017	0.0045***
Bn tree	2	0.0025	0.0033	0.0016	0.0001
clone x tree	8	0.0021	0.0255***	0.0013	0.0013
Error	210	0.0013	0.0044	0.0009	0.0008

\*\*\* Significant at 0.1% level. R - right-side of the lamina, L - left of lamina.

Table 3. — Mean values of clones for different indices and bar diagrams.

Indices	Clones					Zones		
Asymmetry	M 0.0956	A 0.0447	G 0.0382	N 0.0361	K 0.0356			
vein-distance								
Variability	A 0.2107	N 0.1761	G 0.1451	K 0.1342	M 0.1024			
Vein deviation								
Index (Left)	A 0.0688	K 0.0637	M 0.061	N 0.0568	G 0.0533			
Vein deviation								
Index (Right)	A 0.0694	K 0.0604	M 0.0581	N 0.0567	G 0.0417	T 0.0656	L 0.0636	M 0.0522

T - Top; M - Middle; L - Lower zone.

Table 4. — Magnitudes of instability indices in different clones.

Clones	Asymmetry x 100	vein-distance variability x 100	vein-deviation Index (L) x 100	vein-deviation Index (R) x 100	Mean instability values
G	3.81	12.56	5.33	4.17	6.47
N	3.61	15.16	5.56	5.68	7.51
M	9.56	8.87	6.10	5.81	7.56
A	4.47	18.25	6.88	6.93	9.13
K	3.56	11.62	6.37	6.04	6.90

variability which might be related to the expression of developmental instability.

*B. Interrelationships among different parameters of instability indices*

Table 5, shows the correlation coefficients among different parameters of instability indices in leaves of teak. The positive coefficients are highly significant, which indicates that the factors or groups of factors responsible for developmental instability in leaves are similar.

*C. Directionality in teak leaves*

Asymmetry in teak leaves was concluded from absolute differences between the left-side and right-side of the lamina. The next step was to determine whether, i) the left-sidedness or right-sidedness, i.e. the directionality of asym-

metry is clone-specific or genotype specific, or ii) the asymmetry is not directional, and is fixed in a clone or genotype, with one plant being left-sided while another was right-sided and the sum total of this type of individual directionality may make a non-directional clone.

In case of directional asymmetry which may be clonally or genotypically fixed, the value of left-side width minus the right side width for every leaf will be invariably positive or invariably negative within a given clone or genotype. If the asymmetry is directional and individually fixed then the values of asymmetry obtained from leaves of a single plant would be either definitely positive or definitely negative. As a result, the sum of individual leaf values of asymmetry per plant would show a bimodal frequency distribution with a depression around the zeropoint. The following studies were conducted to answer these questions.

i) the width of the left half and right half of the blades were measured for all 5 leaves from each of 3 crown strata of 3 trees each from 5 clones. To see whether there is a clone-specific or tree-specific directional asymmetry the difference between the left-half and the right half width of the lamina of each clone (3 trees × 3 zones × five leaves) were subjected to paired t-test. The formula used is:

$$t_{n-1} = \frac{\bar{d}}{s/\sqrt{n}}, \text{ where } \bar{d} = \frac{1}{n} \sum_{i=1}^n d_i, s^2 = \frac{1}{n-1} \sum_{i=1}^n (d_i - \bar{d})^2$$

$d_i$ , being the differences between left side width and right side width of the  $i$ -th leaf. Only clone N showed some

Table 5. — Correlations among different indices of developmental instability.

Indices	D	I <sub>R</sub>	I <sub>L</sub>
A	0.4316**	0.2221**	0.8422**
D		0.2216**	0.1829**
I <sub>R</sub>			0.1739*

\*, \*\* - Significant at 5% and 1% respectively. (df = 74).

Table 6. — Distribution and significance of left — or right — sidedness.

Clone	G	N	M	A	K
<b>Trees</b>					
Tree 1	** (-)	*** (+)	*** (-)	* (+)	*** (-)
2	N.S.	*** (-)	* (+)	*** (+)	*** (+)
3	*** (+)	*** (-)	* (+)	* (-)	N.S.
<b>Overall</b>	<b>N.S.</b>	<b>*</b>	<b>N.S.</b>	<b>N.S.</b>	<b>N.S.</b>

\*, \*\*, \*\*\* - Significant at 5%, 1% and 0.1% levels respectively. (+) Left-sided, (-) right-sided, N.S. - Not significant.

Table 7. — Anova of four indices of foliar instability in three zones.

Sources of variation	df	Mean-Squares			
		Asymmetry	Vein-distance variability	Vein-deviation Index (L)	Vein-deviation Index (R)
Between clones	4	0.0298**	0.0769***	0.0017	0.0045***
Between Zones	2	0.0026	0.0191*	0.0039*	0.0008
Clones x Zones Interaction	8	0.0032**	0.0047	0.0005	0.0006
Error	210	0.0013	0.0051	0.0010	0.0008

\*, \*\*, \*\*\* - Significant at 5%, 1% and 0.1% levels respectively.

directionality (significant at 5% level), i.e. the left side was larger than the right side of the leaf.

To examine the directionality (significant at 5% level), i.e. the left side was larger than the right side of the leaf or not, the directionality within plants of the same clone and within zone of the same tree was assessed by the paired t-test for observations of each of the 15 trees and 45 zones. The results for within plants are given in Table 6.

Except for 2 trees (one in clone G and one in clone K) all trees had directionality of one or the other type. Each clone has at least one tree of positive directionality (left side larger than the right side) and at least one of negative directionality. The t-test for zones revealed non-significance in all cases. The conclusion is that positive directionality or negative directionality is neither clone specific nor zone specific, while tree specific directionality is either positive or negative, and the sum total of this type of individual directionality results in a non-directional clone.

#### D. Developmental instability and stages of plant growth

Examination of the data to study developmental instabilities in top, middle and lower portions of the crown revealed that the top and lower portions of the crown can be grouped together, whereas the middle portion is significantly different (lower) from the two others (Table 3). The computation of correlation coefficients for instability values among the three zones of top, middle and lower revealed that while top vs. lower ( $r = 0.3235^{**}$ ) and middle vs. lower ( $r = 0.6143^{**}$ ) are significantly correlated, there is no apparent correlation between top vs. middle ( $r = 0.0096$  N.S.)

#### E. Developmental order of leaves and instability

To study the developmental instability of leaves according to the stages of plant growth of all five clones were divided into three crown zones for determination of the instability indices of asymmetry, vein distance variability

and vein deviation index. From the analysis of variance (Table 7) the zonal effect was not found significant on asymmetry but significant on vein-deviation index and vein-distance variability. In the top and lower zones the vein-distance variabilities are high, in the middle zone it is significantly low. Figure 2 shows the interrelationship between zones and vein-distance variability for all five clones.

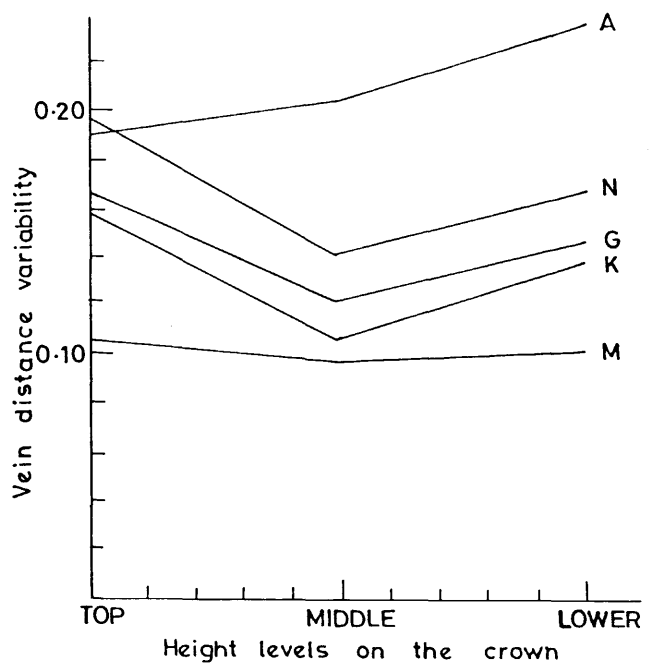


Fig. 2. — Relationship between vein distance variability and development order of leaves.

Table 8. — Relationship between instability indices and vegetative characters.

Characters	Indices		Vein- distance variability	Vein- deviation Index (R)	Vein deviation Index (L)
	Asymmetry				
Leaf length	0.0411		-0.6370**	0.1344	0.2060
Leaf breadth	0.2307		-0.8560**	-0.0650	0.0298
Bole-length	0.3026		-0.2070	-0.0284	-0.6164*

\*, \*\* - Significant at 5% and 1% levels respectively. (df = 14).

#### F. Developmental instability vs. vegetative characters

To observe the inter-relationships between indices of instabilities and vegetative characters, correlation coefficients were calculated (Table 8). Leaf length, leaf breadth and bole length are negatively correlated with instability. While the former two are related to the vein-distance variability, the later is related to vein-deviation Index, and all are inversely related. Dissimilar relationships among varying instability indices with those of different vegetative characters may also suggest that the factors or groups of factors which governs developmental instability in vegetative characters may be functionally similar but genetically dissimilar.

#### Discussion

The study of bilateral asymmetry, in the leaves and flowers of plants like *Nicotiana*, *Nictanthes*, *Jasminum*, *Arabidopsis*, etc., as shown by JINKS and MATHER (1955), PAXMAN (1956), ROY (1963), SAKAI and SHIMAMOTO (1965), and BAGCHI and IYAMA (1982) suggests that developmental instability is a genetically determined trait, but studies on broad-leaved forestry species are nil. Further, developmental instabilities of vegetative and reproductive parts are not correlated, but instabilities within vegetative and reproductive parts are correlated. This suggests that the foliar instabilities may also be correlated with other vegetative characters. The importance of this type of study in forest species is to determine whether foliar instability is correlated with other growth characters like leaf length, leaf breadth and bole-length, which might aid in indirect selection of higher bole-length. In fact, SAKAI and SHIMAMOTO (1965) has observed that highly productive lines are comparatively more stable developmentally.

The finding that the clones of teak differ in developmental instability in leaves suggests that the instability should also be genetic and the comparatively lesser asymmetry in local clones suggests a similar role of developmental instability towards adaptation as described for woody and non-woody plants. Further, the negative correlation between developmental instability and bole-length suggests a direct effect in production which is of potential importance. Future studies are, however, required to establish that higher production is related to lower instability within forest species.

PAXMAN (1956) showed that developmental instabilities in reproductive organs are correlated. BERG (1960) opined that reproductive and vegetative parts in *Nicotiana glauca* are not correlated phenotypically with each other, showing the presence of "correlation pleiades". SAKAI and SHIMAMOTO (1965a) have shown that foliar and floral characters are each correlated amongst themselves. The present investigation is in agreement with these find-

ings and, further, foliar instabilities are interrelated amongst themselves. The next step is to determine the extent of independency of the four indices of instabilities and how each one is affecting the other.

The developmental character right-handedness and left-handedness as has been observed by KOJIMA *et al.* (1955) and SUEOKA and MUKAI (1956) in wheat and *Aegilops* species was found to be species-specific or genotype dependent. In coconut palm DAVIS (1962, 1963) found the trait to be non-heritable. However, the phenomenon seems to be different from the present asymmetry and can not be compared with it. Van valen categorised asymmetrical development in organisms into three categories: 1) directional asymmetry, 2) antisymmetry, and 3) fluctuating asymmetry. It has been demonstrated in the present study that in clones and zones of *Tectona grandis* bilateral asymmetry of leaves is not directional and the sum total of individual directionality of trees makes a clone non-directional, leading to fluctuating asymmetry or antisymmetry, which means that either side of a leaf growing bigger than the other side is only by chance. The asymmetry of leaves in teak is determined most probably individually, because asymmetry among clones and zones is independent. Increased instability at the middle growth stages of a genotype is common, and genotypes with decreased instability at the middle stage are more stable. A similar overall result was obtained in the present experiment. It seems therefore, that the state of the maximum growth of a leaf need not necessarily coincide with the development of maximum intra-plant variation when buffering action is supposed to be highly active.

Higher bole-length, as we found, or higher Cigar yield, as found by SAKAI and SHIMAMOTO (1965a) with lower instability indicates that, whether by natural or by artificial selection, genes must have been accumulated through ages for better buffering against the occurrence of errors. Whether this is true for forestry species is yet to be determined but we conclude that the developmental procedure is governed by stochastic rather than by deterministic rule.

#### Conclusion

From our results and discussions the following conclusions are drawn. (1) The developmental instability measured by bilateral asymmetry, vein-distance variability and vein-deviation index varies among teak clones. From the asymmetry index the Kurseong (clone M) teak is the most unstable, whereas all other clones are moderately unstable. The vein-distance variability is high in Laos (clone N) and Nilambur (clone A) teaks compared to Dandeli (clone G), Kurseong (clone M) and Dhansingh teak (clone K). The vein-deviation index is high in Nilambur (clone A) and Dhansingh (clone K) trees. In consolidated grouping, Dan-

deli (clone G), falls in the lower group of instability indices constantly, whereas no other clone performs similarly. (2) The sum total of random individual directionality makes for non-directional clones, except for the Laos (clone N) teak which shows significant right-sidedness. Within a clone, at least one tree out of three in every clone has positive (left sided directionality) and at least one has negative directionality. (3) The study of instability indices at different height (3 zones) shows that vein-distance variability is higher in top and lower zones than in the middle zone. The Nilambur (clone A) teak gives an increasing order of vein distance variabilities from the top to the bottom zone, and in Kurseong (clone M) teak, the variability is relatively uniform over all zones. (4) Indices of developmental instabilities are positively interrelated. (5) Indices of developmental instability is correlated with other vegetative characters like leaf length, leaf breadth and bole-length.

#### Literature Cited

BAGCHI, S. and IYAMA, S.: Radiation induced developmental instability in *Arabidopsis thaliana*. *Theor. Appl. Genet.* 65: 85–92

(1983). — BERG, R. L.: The ecological significance of correlation pleiades. *Evolution* 14: 171–180 (1960). — DAVIS, T. A.: The non-inheritance of asymmetry in *Cocos nucifera*. *J. Genet.* 58: 42–50 (1962). — DAVIS, T. A.: The dependence of yield on asymmetry in coconut palms. *J. Genet.* 58: 186–215 (1963). — JINKS, J. K. and MATHER, K.: Stability in development of heterozygotes and homozygotes. *Proc. Roy. Soc. London B143*: 561–578 (1955). — KOJIMA, K., MUKAI, T., SUBMOTO, H., SUEOKA, N. and ONO, H.: Studies on the right and left handedness of spikelets in Einkorn wheats. VI. Polygenic analysis in a species cross. *Proc. Japan Acad.* 31: 228–233 (1955). — LEVIN, D. A.: Developmental instability in species and hybrids of *Liatris*. *Evolution* 24: 613–624 (1970a). — LEVIN, D. A.: Developmental instability and evolution in peripheral isolates. *Amer. Nat.* 104: 343–353 (1970b). — PAXMAN, G. J.: Differentiation and stability in the development of *Nicotiana rustica*. *Ann. Botany (London)* 20: 331–347 (1956). — ROY, S. K.: The variation of organs of individual plants. *J. Genet.* 58: 147–176 (1963). — SAKAI, K. I. and SHIMAMOTO, Y.: Developmental instability in leaves and flowers of *Nicotiana tabacum*. *Genetics* 51: 801–813 (1956a). — SAKAI, K. I. and SHIMAMOTO, Y.: A developmental genetic study on panicle characters in rice, *Oryza sativa* L. *Genet. Res.* 6: 172–182 (1965b). — SUEOKA, N. and MUKAI, T.: Studies on the right — and left-handedness of spikelets in Einkorn wheats. VII. The C-value of the species of *Triticum* and *Aegilops*. *Proc. Japan Acad.* 32: 191–196 (1956). — VAN VALEN, L.: A study of fluctuating asymmetry. *Evolution* 16: 125–142 (1962).

## The Genetic Consequences of Mass Selection for Growth Rate in Engelmann Spruce

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#### Summary

The genetic consequences of mass selection for growth rate in Engelmann spruce, *Picea engelmannii*, were studied with 4 enzyme polymorphisms. Super seedlings and their controls were chosen from a nursery and established in two plantings in the Rio Grande National Forest in Colorado. Super seedlings differed from controls in allelic frequencies at 1 of the 4 loci, and at one of the plantings, super seedlings had a higher proportion of highly heterozygous genotypes. The mass selection may have favored highly heterozygous genotypes, but the genetic consequences of this selection were slight.

Selection has been reported to produce excesses of heterozygotes in the mature stands of several species of conifers. The excesses in heterozygotes are relevant to both the controversy concerning the form of selection in conifers, and the question of the utility of protein genotypes in artificial breeding programs.

*Key words:* Protein polymorphism, heterozygosity, growth rate, Engelmann spruce.

#### Introduction

Natural populations of coniferous forest trees have moderate levels of heritability for growth rate. For example, the broad sense heritabilities of growth rates in southern pines are typically 40% to 80%, and the narrow sense heritabilities typically 10% to 50% (DORMAN, 1976). Foresters may capitalize on these high levels of genetic variation

by realizing substantial genetic gains with just a single round of mass selection. In these selection programs, plus trees are chosen on the basis of form and growth rate, and these selected trees are utilized as the parents for the next generation. This relatively simple program of selection has achieved excellent genetic gains in loblolly pine (ZOBEL, 1971), slash pine (GODDARD *et al.*, 1973), and Monterey pine (SHELBOURNE, 1974), but there has been little or no response to selection in Scots pine (NILSSON, 1968) and jack pine (CANAVERA, 1969, 1975).

In addition to describing patterns of variation at polygenic characters in provenance studies, forest geneticists use electrophoretic analyses to estimate levels of genetic variation and to describe patterns of geographic variation of protein loci (MITTON, 1983; GURIES, 1984). These studies have demonstrated that conifers are the most genetically variable group of species (HAMRICK *et al.*, 1979).

The consequences of mass selection upon the variability of proteins are unknown, yet mass selection for growth may influence protein variability, for several recent studies have reported relationships within populations between protein heterozygosity and components of growth. Growth rate is positively correlated with individual heterozygosity in quaking aspen (MITTON and GRANT, 1980), pitch pine (LEDIG *et al.*, 1983; BUSH, SMOUSE and LEDIG, 1987), and knobcone pine (STRAUSS, 1986), but not in Douglas-fir (BONGARTEN *et al.*, 1985). The variability of growth rate is associated with individual heterozygosity in lodgepole pine (KNOWLES and GRANT, 1981; LINHART and MITTON, 1985), and Douglas-fir (BONGARTEN *et al.*, 1985). For consideration of genetic conservation and response to selection, we need to know

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