

that trees less than 10 years old are capable of producing substantial seed crops. Of the fruiting trees in 1976, 53% had 100 to 200 seeds per catkin and 3% had more than 300 seeds per catkin. Thus, a tree with 100 catkins can easily produce between 10,000 and 30,000 seeds. Because certain families and trees tend to flower earlier and more prolifically than others, excellent opportunities exist for selecting for high seed production at an early stage in an improvement program.

Selection for early flowering in *Betula* should, however, be approached with caution. Thus, STERN (1963) found the correlation between growth and early, prolific flowering in *Betula verrucosa* EHRH. to be positive in some families but negative in others. For this reason, 265 flowering trees in this study were each compared with a non-flowering tree from the same plot. A t-test showed that the flowering trees tended to be taller and to have bigger crowns than the non-flowering ones (CLAUSEN, 1979). Thus, early and

prolific flowering did not have an adverse effect on growth of these yellow birch families.

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Genetic Heterozygosity and Radial Growth Variability in *Pinus contorta*

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Summary

The relationship between heterozygosity level and stability in the phenotypic character, annual radial growth, was examined within a population of *Pinus contorta*. Needle tissue was sampled from 152 lodgepole pines in the subalpine region of the Front Range in Colorado. Heterozygosity levels were determined from four electrophoretically detectable enzymes from the needle tissue. Each tree was cored, ages were estimated, and ring widths were measured. The coefficient of variation, a measure of dispersion in growth increment, was calculated for each tree and related to the level of heterozygosity. The results indicate that trees with overall high levels of heterozygosity have significantly less growth variability than trees with low levels of heterozygosity. When the loci are examined separately, however, there are no significant differences between the genotypic groups. This suggests a complex interaction among the four loci involved. Although the mechanism linking overall heterozygosity level to phenotypic variability remains unknown, these results add to the increasing evidence that a strong relationship exists between heterozygosity and phenotypic variability.

Key words: heterozygosity, lodgepole pine, developmental homeostasis, growth variability, isozyme variation

Zusammenfassung

In der Population von *Pinus contorta* wurde die Beziehung zwischen Heterozygotiegrad und der Stabilität

des phänotypischen Merkmals Jahrringbreite untersucht. Stichproben des Nadelgewebes wurden von 152 Kiefern in der subalpinen Zone des Front Range Gebietes in Colorado (U. S. A.) entnommen. Der Heterozygotiegrad wurde jeweils an 4 elektrophoretisch nachweisbaren Enzymen des Nadelgewebes bestimmt. An Bohrproben jedes Baumes wurde das Alter geschätzt und die Jahrringbreite gemessen.

Der Variationskoeffizient wurde als Maß für die Streuung des Zuwachses für jeden Baum berechnet und zum Heterozygotiegrad in Beziehung gesetzt. Die Ergebnisse zeigen, daß Bäume mit insgesamt hohem Heterozygotiegrad eine signifikant geringere Variabilität des Wachstums aufweisen als Bäume mit geringerem Heterozygotiegrad. Werden die Loci jedoch getrennt untersucht, ergeben sich keine signifikanten Unterschiede zwischen den Genotypgruppen. Dies deutet auf eine komplexe Interaktion zwischen den vier betreffenden Loci hin. Obwohl der Mechanismus des Zusammenhangs zwischen Gesamtheterozygotiegrad und phänotypischer Variation unbekannt bleibt, tragen die Ergebnisse zur steigenden Evidenz einer engen Beziehung zwischen Heterozygotie und phänotypischer Variation bei.

Introduction

The relationship between protein variation and morphological variation in natural populations is poorly understood. One aspect of this issue which has received some em-

pirical attention is the association between genetic heterozygosity and phenotypic variation. Such interest focuses on the general questions "Is there an association between heterozygosity and levels of morphological variation and if so, what is the direction of that relationship?"

It has been proposed (LERNER, 1954; LEWONTIN, 1956) that increased levels of heterozygosity are related to decreased levels of phenotypic variation or enhanced levels of "developmental homeostasis." Such an association would have obvious implications for the explanation of many developmental strategies as well as the maintenance of genetic variation within populations. Empirical evidence has supported this homeostasis/heterozygosity association in both laboratory and domesticated populations (ROBERTSON and REEVE, 1952; MATHER, 1953; DOBZHANSKY and WALLACE, 1953; LERNER, 1954), most of which were animal species.

Furthermore, a molecular mechanism explaining the relationship has been recently proposed (FINCHAM, 1972; HOCHACHKA and SOMERO, 1973; JOHNSON, 1976) and supported by a significant amount of empirical evidence in vitro kinetic studies (KOEHN, 1969; GIBSON, 1972; MERRITT, 1972; VIGUE and JOHNSON, 1973; DAY *et al.*, 1974; MILLER *et al.*, 1975). In these studies enzymes extracted from an individual heterozygous at a particular locus were found to operate under a greater range of conditions as compared to those extracted from an individual homozygous at that locus.

Does this homeostasis/heterozygosity association exist in populations of organisms outside of the laboratory? Among the few studies attending to natural populations, MITTON (1978) found decreased morphological variation in highly heterozygous marine fish (*Fundulus heteroclitus*), and EANES (1978) found a similar association in the monarch butterfly (*Danaus plexippus*). A related study (SOULE, 1979) indicated a negative correlation between morphological bilateral asymmetry and heterozygosity in lizards. In plant studies a strong association between heterozygosity and phenotypic variability has been found in natural populations of aspen (MITTON and GRANT, 1980) and in ponderosa pine (KNOWLES and GRANT, 1980). This association however, was opposite in direction to that found in the animal studies; heterozygous individuals were more variable in the phenotypic character than the homozygous individuals.

In the present study, this heterozygosity/homeostasis relationship is examined in another long-lived perennial plant species, lodgepole pine (*Pinus contorta*). Heterozygosity was assessed by horizontal starch gel electrophoretic techniques and the phenotypic character examined was annual radial growth increment as determined by ring width measurements.

Materials and Methods

The general distribution of lodgepole pine extends from the Yukon territory and south-eastern Alaska southward to northern Baja, California. Its range includes the Black Hills of South Dakota and the Front Range of Colorado. The present study site is located in the southeastern area of this distribution on a southeasterly facing slope at an elevation of 2800 meters, approximately six miles north of Nederland, Colorado. The stand is generally characterized by a dense overstory of lodgepole pine with much needle-covered bare soil and a few rocky outcroppings. One hundred and fifty-two trees were randomly sampled along eight fifty meter transects located within two closely spaced fifty meter by fifty meter quadrats. A small sample of needle tissue was removed from each tree and prepared for electrophoretic analysis using the procedures described in MITTON *et al.* (1979 a). Four loci were resolved:

peroxidase (PER), phosphohexose isomerase (PHI), fluorescent esterase (EST), and alcohol dehydrogenase (ADH). The inheritance pattern for three of the four enzymes (PER, PHI, ADH) was examined by resolving progeny needle tissue from open-pollinated maternal trees with heterozygous genotype. A homozygous genotype provided the seed source for examining the fourth enzyme (EST). In all cases the progeny enzyme variation behaved as proper Mendelian units. The heterozygous trees produced all expected genotypes and the homozygous genotype produced offspring like itself. This was anticipated because the allele homozygous in this individual had a high frequency in the population.

Genotypes were scored directly from the banding pattern on the gel. For each locus an individual was scored as either a heterozygote or a homozygote regardless of exactly which alleles comprised that genotype. Therefore, each individual was characterized by four heterozygosity scores, one for each of four loci. These four scores were collapsed into a single overall heterozygosity score for each individual as follows: all those trees with zero or one loci heterozygous of the four loci scored were categorized as predominantly homozygous trees and all those trees with two, three or four heterozygous loci of the four loci scored were categorized as predominantly heterozygous trees.

Each tree was cored on the upslope side at knee height and the ring widths of each core were measured with the aid of a binocular stereoscope fitted with an ocular micrometer gauged measure ten units per millimeter. To examine variability in growth the single measure of dispersion, the coefficient of variation in annual radial growth, was calculated for each tree. This particular measure was chosen because of the great between-tree variation in annual growth. Variation in ecologically suppressed lodgepole pine trees with their strikingly small mean annual growth increment could only be compared to ecologically dominant trees in a meaningful way by adjusting for these differences in mean growth. The use of the coefficient of variation accomplishes this adjustment.

Results

The electrophoretic analysis indicated that among the four polymorphic loci, three loci (PER, EST, ADH) consisted of three alleles each and the fourth locus (PHI) was comprised of three common and one very rare allele. The percentage of individuals heterozygous at each locus varied from 12 to 50 percent. Among the four loci two were comprised of a single allele which was very common in frequency ($> .9$) and two consisted of a single allele which was predominant but less common. *Table 1* summarizes these aspects of the genetic data distributions. Of the four loci assessed, only PER deviates significantly from a genotypic distribution as expected from the HARDY-WEINBERG equilibrium law. This deviation results from a deficiency of heterozygotes.

The age distribution of the sample trees is presented in *Figure 1*. This distribution, truncated at the higher age classes, agrees well with the general ecology of lodgepole pine and the specific historical events affecting the study sample. Lodgepole pine generally grows in even aged stands (SCHUBERT, 1974) as this distribution indicates and is adapted to colonize fire-destroyed regions. Fire evidence and written accounts (DOUGLASS, 1954) indicate a single fire burned the entire site in approximately 1891 resulting in a period of high germination and sapling recruitment near the turn of the 20th century with lower

Table 1. — Description of genetic data distributions for four loci in lodgepole pine.

Locus	Number of Alleles Present	Frequency of Most Common Allele	Percent of Individuals Heterozygous	Genotypic Fit to HARDY-WEINBERG Equilibrium (Significance of χ^2)
PER	3	.62	34	<.05
PHI	4	.94	13	n.s.
EST	3	.91	18	n.s.
ADH	3	.62	53	n.s.

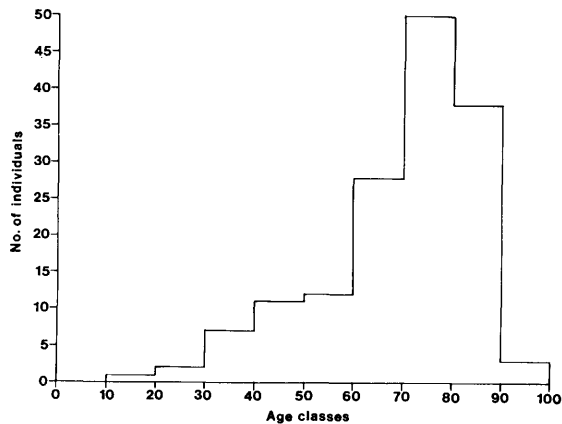


Figure 1. — Age distribution of the lodgepole pine sample in ten year age classes.

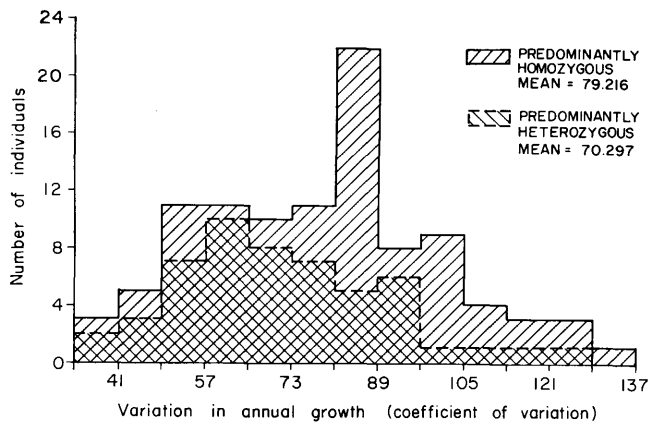


Figure 2. — Distribution of variation in annual radial growth as measured by the coefficient of variation for the predominantly homozygous and the predominantly heterozygous lodgepole pine trees.

frequencies of recruitment in recent years as the stand matured.

Two analyses were conducted to address the association between heterozygosity and growth variability. First, growth variabilities were compared with a t-test between heterozygotes and homozygotes for the four loci separately (Table 2). Although there are no significant differences in growth variabilities between heterozygotes and homozygotes, it is noteworthy that the directional trend is consistent. For each locus the homozygotes have slightly greater growth variability than the heterozygotes. Next, growth variabilities were compared between the predominantly homozygous and predominantly heterozygous individuals using the composite heterozygosity score. The results are illustrated in Figure 2. Growth variability shows sub-

stantial scatter in the trees of both heterozygosity categories. The average growth variability in the homozygous trees, however, exceeds that of the heterozygous trees. A t-test indicated that the difference in growth variabilities between these two heterozygosity categories is statistically significant ($t = 2.52, p < .025$). It is noteworthy that the mean annual growth of the trees in the two heterozygosity categories are not significantly different ($t = 0.65, p > .50$). The variabilities in growth, however, indicate a striking contrast. The predominantly homozygous trees have significantly greater growth variability, as measured by the coefficient of variation, than the predominantly heterozygous trees. Even though the two types of trees grow at the same average rate, the predominantly homozygous trees vary around the rate much more markedly than the predominantly heterozygous trees.

The possibility existed that age structure differences between predominantly heterozygous and predominantly homozygous trees had statistical implications for the heterozygosity/growth variability association. A strong correlation between age and mean annual growth is common in tree species. If predominantly heterozygous trees were older or younger than predominantly homozygous trees, then mean radial growth difference between the heterozygosity levels would be expected. And if age differences between heterozygosity classes produced differences in mean growth rates, we might expect to see differences in growth variability also, since the mean and variance of radial growth can be correlated. The results of a t-test comparing the ages of the two heterozygosity categories ruled out the possibility of differences in age structure dictating differences in variability of radial growth. The mean ages of the predominantly homozygous trees and the predominantly heterozygous trees are 69.11 and 69.25 respectively ($t = .05, p > .90$). Thus, the growth variability differences between trees of the different heterozygosity levels cannot be attributed to age structure differences between predominantly heterozygous and predominantly homozygous trees.

Discussion

These results indicate a statistically significant relationship between overall levels of heterozygosity and radial growth variability in lodgepole pine. This evidence of a strong heterozygosity/phenotypic variability association is consistent with the findings in other natural populations of both plant and animal species (MITTON, 1978; EANES, 1978; SOULÉ, 1979; MITTON and GRANT, 1980; KNOWLES and GRANT, 1980). Furthermore, the direction of this association is consistent with the findings in other natural populations of both plant and animal species (MITTON, 1978; EANES, 1978; SOULÉ, 1979; MITTON and GRANT, 1980; KNOWLES and GRANT, 1980). Furthermore, the direction of this asso-

Table 2. — Comparison of radial growth variabilities between heterozygotes and homozygotes for individual loci in lodgepole pine (1 = homozygote, 2 = heterozygote)

Locus	Heterozygosity Level	Number of Individuals	Mean radial growth Variability (Coefficient of Variation)	T-value	Significance Level
PER	1	99	77.71	1.20	n.s.
	2	53	73.45		
PHI	1	133	76.73	.79	n.s.
	2	19	72.68		
EST	1	125	76.94	.91	n.s.
	2	27	72.90		
ADH	1	71	77.82	.88	n.s.
	2	81	74.82		

ciation supports the empirical and theoretical proposals of LERNER (1954) and may be considered an extension of LERNER's hypothesis to smaller segments of the genome. Developmental homeostasis has been associated with heterozygosity or hybrid vigor as obtained from progeny of between-strain crosses (LERNER, 1954 for review), the finer scale of chromosomal heterozygosity obtained from manipulated *Drosophila* genomes (DOBZHANSKY and WALLACE, 1953) and finally heterozygosity as measured at the level of individual loci by electrophoretic techniques (MITTON, 1978; EANES, 1978; MITTON and GRANT, 1979; KNOWLES and GRANT 1980). These observations support the proposal that phenotypic constancy is associated with heterozygosity as measured even at the level of a small number of randomly selected individual loci.

Furthermore, it may be biologically significant that growth variability in lodgepole pine is associated most strongly with an overall level of homozygosity as opposed to homozygosity at any single locus. This would suggest an interaction among the loci involved resulting in an enhancement of growth variability with decreasing overall levels of heterozygosity.

The direction of these results, however, is inconsistent with the findings in other tree species including aspen and ponderosa pine (see MITTON et al., 1979b for review). Why are high levels of heterozygosity associated with growth variability in populations of ponderosa pine and aspen but with growth constancy in lodgepole pine? Although an explanation for this inconsistency is not obvious, speculations will be presented.

LEWONTIN (1956) proposed that heterozygosity would be associated with phenotypic constancy only when the phenotypic character under consideration contributes directly to the fitness of the organism. It is doubtful that annual radial growth increment is directly related to fitness for any of the tree species examined but it may have a different indirect relationship according to the ecological strategies of each species. For example, viable seed output would be a character more directly related to fitness than growth increment. If seed production is inversely related to annual growth increment as has been shown (FRITTS, 1976), we would speculate that the differential reproductive strategies between ponderosa pine and aspen taken as a group and lodgepole pine could account for the different directional trends in the homeostasis/ heterozygosity findings. Both ponderosa pine and aspen are well known for their sporadic reproductive output during mast years (MARR, 1961; SCHUBERT, 1974; LINHART et al., 1979).

Lodgepole pine, on the other hand, is mainly serotinous in this geographic area of study and produces cones regularly every year. Ponderosa pine and aspen may be storing and shunting energy into reproductive effort with the concomitant annual variation of growth increment. This strategy of varying year to year radial growth increment may enable the organism to optimize or stabilize reproductive output during mast years. In contrast, the regular annual cone production habit of lodgepole pine may be stabilized by a consistent annual energy allocation to radial growth increment. These possibilities are as yet speculations and would be clarified by future empirical investigations.

Whatever the explanation, these results add to the increasing evidence of a strong relationship between heterozygosity levels and phenotypic variability. It is noteworthy that regardless of the level of heterozygosity measured (hybrid progeny, heterozygous chromosomes, or heterozygosity at individual loci), and regardless of whether the study organism is a plant or animal, a strong relationship between homeostasis and heterozygosity obtains. Although the mechanism underlying this relationship remains unknown at present the amassing evidence suggests that there does exist a biologically meaningful phenomena linking genetic heterozygosity to phenotypic variability.

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Regulation of flowering in Scots pine (*Pinus sylvestris* L.) grafts by gibberellins

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Summary

Spraying shoots of Scots pine grafts with gibberellins from the end of May to mid August caused significant changes in flowering. The GA_{4/7} mixture tripled the intensity of female flowering and GA₃ had a negative effect on male flowering. The gibberellins used did not affect significantly the length and girth increments of shoots. There were no interactions between the less polar GA_{4/7} and the more polar GA₃. It is suggested that earlier treatment with GA_{4/7} favours the formation of male flowers and later treatment stimulates female flowers.

Key words: *Pinus sylvestris* L., flowering, gibberellins, sexual differentiation.

Zusammenfassung

Besprühen von Zweigen in der Krone von Kiefernpropflingen (*Pinus sylvestris* L.) mit Gibberellinlösungen in der Zeit von Ende Mai bis Mitte August hatte eine signifikante Änderung der Blütenbildung zur Folge. Durch GA_{4/7} wurde die Zahl der weiblichen Blüten verdreifacht, GA₃ wirkte sich auf die Bildung männlicher Blüten negativ aus. Die genannten Gibberelline haben den Durchmesser- und Längenzuwachs der behandelten Zweige nicht signifikant beeinflusst. Eine Interaktion der Wirkung der schwach polaren GA_{4/7} mit der stärker polaren GA₃ wurde nicht festgestellt.

Auf Grund der bisherigen Ergebnisse darf man annehmen, daß die Behandlung mit GA_{4/7} am Anfang der Vegetationsperiode die Bildung der männlichen Blüten fördert,

während eine wiederholte Behandlung während der gesamten Periode die Bildung der weiblichen Blüten stimuliert.

Introduction

Since the last literature review on the physiology of flowering in conifers (PHARIS and KUO, 1977) several papers have been published on the effect of gibberellins on flowering in Pinaceae. These reports confirmed the positive effect of mixed GA_{4/7} either alone or in combination with other factors on the stimulation of male flowering (CHALUPKA, 1978; LUUKKANEN and JOHANSSON, 1980), female flowering (GREENWOOD, 1979; ROSS and GREENWOOD, 1979) or both (TOMPSETT, 1977; TOMPSETT and FLETCHER, 1979; HARE *et al.*, 1979; PURITCH *et al.*, 1979; ROSS 1979). It turned out also that GA₃ may under certain conditions stimulate flowering in *Picea abies* (BLEYMÜLLER, 1976, 1978; CHALUPKA, 1979).

The paper presented here reports further data on the hormonal stimulation of flowering in Scots pine from the Institute of Dendrology in Kórnik.

Materials and Methods

The experiment was set up in the spring of 1978 on 17 year old Scots pine grafts growing in a seed orchard in Kórnik. Each of the selected clones was represented by 12 grafts on which 3 branches were chosen from successive whorls. These branches were designated as upper, middle and lower and shoots of the previous (1977) year, and new