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THE RELATION OF GROWTH TO HETEROZYGOSITY IN PITCH PINE

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The connection between fitness and heterozygosity has eluded geneticists for decades. The classic form of the Neo-Darwinian argument hypothesizes that heterozygosity confers genetic homeostasis (Lerner, 1954); i.e., multiple molecular forms of the same enzyme endow the organism with a broader range of tolerance to environmental variation because different forms may differ in their optima for temperature, pH, and other factors (Johnson, 1976). In maize (*Zea mays* L.), inbred lines and their hybrids are similar in growth rate when raised under constant conditions at optimal temperatures, but hybrid superiority becomes progressively more obvious as conditions deviate from the optimum (McWilliam and Griffing, 1965). Apparently, homozygotes in maize can only deal successfully with a narrow range of conditions as compared to heterozygotes.

In a variety of organisms, including butterflies, fish, and oysters, variance for morphological traits decreased with increasing heterozygosity at enzyme loci (Eanes, 1978; Mitton, 1978; Zouros et al., 1980), and bilateral symmetry, a measure of developmental homeostasis, increased with heterozygosity in lizards and bivalves (Soulé, 1979; Kat, 1982). Growth rate increased with heterozygosity in oysters and salamanders (Singh and Zouros, 1978; Zouros et al., 1980; Pierce and Mitton, 1982). The perennial herb, cylindric blazing star (*Liatris cylindracea* Michx.), can be roughly aged by counting rings in the corm, the subterranean perennating organ. In natural populations, heterozygosity was higher among older than among younger individuals, suggesting poor survival for homozygotes (Schaal and Levin, 1976). Grown in a uniform environment, biomass production and reproductive potential of the herb were weakly, but positively, related to the level of enzyme heterozygosity. However, Mitton and colleagues (Mitton and Grant, 1980; Knowles and Grant, 1981; Mitton et al., 1981) noted conflicting results in forest trees, which are among the most polymorphic of organisms (Hamrick, 1979; Hamrick et al., 1979). In only one of three tree species was there a positive association between mean width of the annual ring, taken as a measure of growth and fitness, and heterozygosity. In two of the species, variance in ring width increased with increasing heterozygosity and in the third, it decreased.

The relationship between growth and heterozygosity in trees is confusing, and more data are needed to draw firm conclusions. Our objective was to relate growth to heterozygosity in pitch pine (*Pinus rigida* Mill.), for which we had information on 21 enzyme loci in several populations. We were also interested in whether heterozygotes had greater longevity and whether annual growth was more or less well-buffered in heterozygotes than in homozygotes. A positive association be-

tween growth and heterozygosity might be used to suggest a functional significance for the extensive enzyme polymorphisms found in natural populations, but lack of single locus overdominance would point to alternative hypotheses.

Materials and Methods

Sampling

Cones were collected from eight natural populations of pitch pine during the autumn of 1976. The sites were among those described by Guries and Ledig (1982), and represented nearly the entire range of pitch pine. Stands varied in age and character (Table 1). Cone-bearing trees represented roughly 33 to 51% of the total population.

A plot center was established, and trees sampled in concentric circles to include approximately 50 to 60 cone-bearing individuals. The Blue Ridge, NC population was an exception. It was strung out linearly along the Blue Ridge Parkway, and apparently had established on the disturbed bank, following road construction. Not all trees yielded sufficient viable seed for analysis and for various reasons it was impossible to determine the age of others. Therefore, final sample sizes were less than 60 trees.

Starch Gel Electrophoresis

Seed was extracted from cones, germinated in petri dishes and the haploid megagametophytes excised for electrophoresis. Each tree was genotyped for 21 loci using at least six to eight megagametophytes per individual. Detailed procedures, gene frequencies, and inheritance for each of the loci were previously reported (Guries and Ledig, 1978, 1982; Guries et al., 1978). None of the loci deviated significantly from Hardy-Weinberg expectations in any of the populations investigated. For the present study, individuals were grouped into heterozygosity classes according to the number of heterozygous loci, from 0 to 9. Because some variants are not electrophoretically detectable, some heterozygotes will be mis-

Table 1. *Sample means for age, density, heterozygosity, and other characteristics.*

Stand	Latitude (N)	Longitude (W)	Elevation (m)	Sample size	Age (yrs)		Site[1] index	Density[2] (trees/ha)	MAI[3] (cm^2)	Heterozygosity[4]	
					Mean	St dev				Mean	Range
St. Chrysostôme, Quebec	45°15′	73°30′	75	50	38	9.4	30	3,597	2.7	2.4	0-5
Bradley Field, CT	41°45′	72°45′	50	42	22	3.2	50	3,639	6.9	3.0	0-6
Marconi Station, MA	42°00′	70°00′	5	56	40	17.8	30	7,318	2.5	3.6	0-7
Michaux State Forest, PA	40°00′	77°45′	150	35	47	13.3	35	2,493	6.9	2.2	0-8
Helmetta, NJ	40°30′	74°30′	95	57	40	6.8	40	4,571	3.5	3.4	0-9
Lebanon State Forest, NJ	40°00′	74°15′	45	52	53	11.6	35	3,199	3.1	2.9	0-6
Shawnee State Forest, OH	38°30′	83°00′	250	28	71	13.1	—	—	4.1	2.3	0-5
Blue Ridge, NC	36°30′	81°45′	915	36	29	6.6	55	—	12.6	2.9	0-6

[1] Height at 50 years, estimated from site index curves in Hampf (1965)
[2] Calculated as $(10{,}000 \text{ m ha}^{-1})/(0.8) \times (\text{mean distance between nearest neighbors})^2$
[3] Mean annual basal area increment adjusted to age 25
[4] Observed number of heterozygous loci per individual among 21 loci

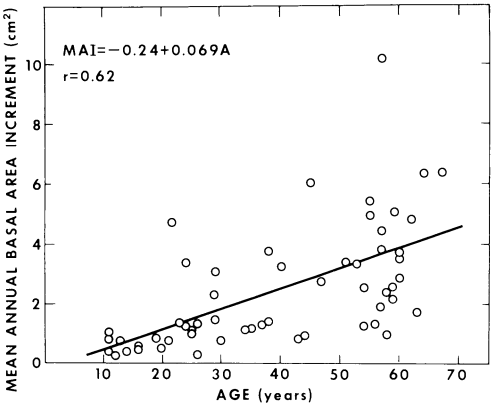

FIG. 1. Mean annual basal area increment and its variance generally increase with age, as illustrated for pitch pine at Marconi Station, MA. Each point represents a single tree.

classified as homozygotes, creating a bias in favor of the lower classes.

Mensurational

Measurements were made of tree height and diameter at breast height (4.5 feet above ground level). Each tree was bored and an 11 mm diameter core, from the bark to the center, removed at ca. breast height. The position of each tree, including those not bearing cones, was mapped using a plane table, telescopic alidade, and surveyor's tape. Distance from each tree to its nearest neighbor was calculated and used to estimate stand density from a formula developed for the random pairs method of vegetation analysis (Cox, 1972).

The width, or radial dimension, of each annual growth ring, from pith to bark, was measured on the core samples using the electronic Addo-x system (Graham, 1980). Age was determined by the total ring count.

Previous studies that sought to relate vigor to heterozygosity analyzed radial growth. However, we used basal area growth (i.e., growth in cross-sectional area) as an index. Comparisons of mean annual radial growth are biased in favor of younger trees, because the radial growth of a tree usually slows from year two onward. As a tree grows, growth must be distributed around a greater circumference each year, the circumference increasing 2π times as fast as the radius. In a stand with several age classes, comparisons of mean annual radial growth between older trees and younger trees will make it more difficult to detect relationships between growth rate and heterozygosity. Covariance adjustment for age will help, but a linear adjustment is not equivalent to the non-linear conversion of radial growth to basal area growth.

Mean annual basal area increment (MAI), the sum of the annual basal area increments divided by the ring count, generally increases with age for several decades, peaks, and then declines during senescence. All of the sampled stands were apparently on the ascending portion of the curve (e.g., Fig. 1). Yearly variation in climate and the degree of competition will affect the pattern; the variance in annual increment increases with age because older trees have been exposed to a greater range of climatic variation than younger trees. Although pitch pine stands are predominantly even-aged, there was enough variation to cloud comparisons among trees. To enable comparison of trees of different age, MAI was adjusted to stand mean age by regression analysis within each population. Although the relationship is probably semi-logarithmic during this phase, linear regression was used because the age dispersion was too limited and the scatter too great to justify more complex adjustments. Because of the limited age distribution, the regression of MAI on age was statistically significant for only two of the eight stands, Marconi Station, MA and Blue Ridge, NC. Nevertheless, for consistency, adjustments were made for each stand.

We also calculated the periodic annual basal area increment (PAI) for the decade 1969–1979 and a relative mean annual volume increment (MAV), as MAV = $\text{dbh}^2 \times \text{height/age}$. Developmental variability was examined as the standard deviation of ring width, to make results

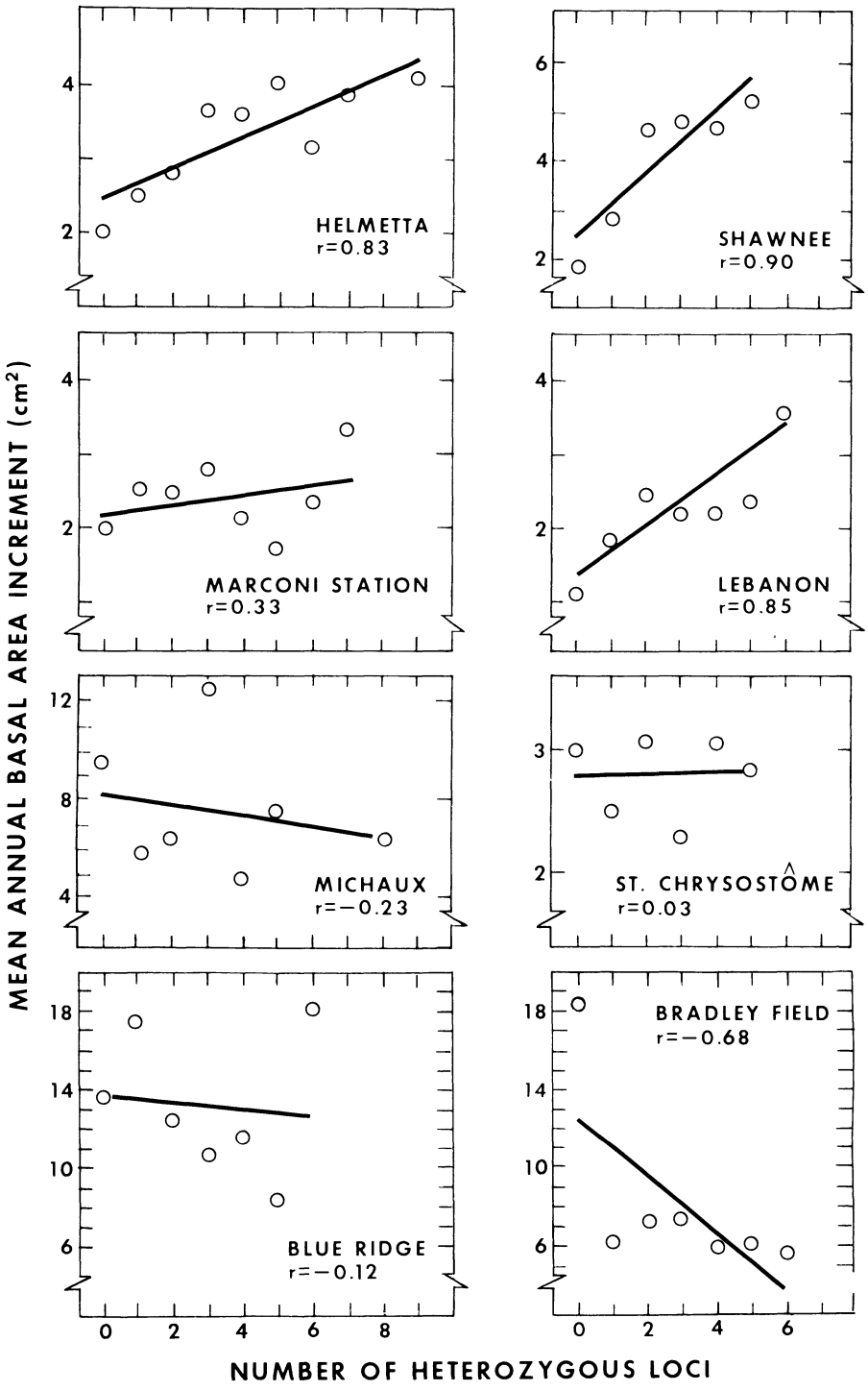

FIG. 2. Relationships between average mean annual basal area increment within a heterozygosity class and number of heterozygous loci in eight stands of pitch pine. Note the difference in scale of the ordinate.

TABLE 2. *Correlation coefficients for the standard deviation of annual basal area increment and standard deviation of annual ring width with heterozygosity in eight pitch pine stands.*[1]

Stand	Ring width	Basal area increment
St. Chrysostôme, Quebec	.79*	−.13
Bradley Field, CT	−.15	−.71*
Marconi Station, MA	.52	.48
Michaux State Forest, PA	−.93***	−.38
Helmetta, NJ	−.41	.43
Lebanon State Forest, NJ	.28	.71*
Shawnee State Forest, OH	.75*	.84**
Blue Ridge, NC	−.25	−.03

[1] Statistically significant at $.05 < P < .10$, *, $.01 < P < .05$, **, $P < .01$, ***

comparable to those of previous studies, and as the standard deviation of annual basal area increment for each core.

RESULTS

The correlations of mean MAI on heterozygosity class varied among stands (Fig. 2). In five of the eight stands the correlation was positive, and in three negative. The relationship was strongly positive and statistically significant in three instances and significantly negative only at Bradley Field, CT. Results were similar for both age-adjusted and nonadjusted values. In fact, the positive regression for nonadjusted MAI at Marconi Station, MA reached statistical significance. Patterns for MAV and PAI were similar to those for MAI.

Correlations between heterozygosity and either the within-tree standard deviation of annual basal area increment or the standard deviation of ring width, the latter measure being the same as that used by Mitton et al. (1981), were inconclusive. Few of the correlations were statistically significant, and the sign of the correlation was positive in only half the cases (Table 2). The variance of MAI within heterozygosity classes was closely related to the mean, apparently a scale effect. Therefore, the correlation between the standard deviation of MAI and heterozygosity was positive in most cases and negative in the Bradley Field, CT population. Because of scale effects, a better comparison is the coefficient of variation. In no population was there a statistically significant relationship between the coefficient of variation for MAI and number of heterozygous loci.

F-tests for differences among genotypes at individual loci failed to reveal any convincing patterns. Given the possible number of *F*-tests (96), the number of differences reaching statistical significance (7) at the 5% probability level was hardly greater than the number expected by chance alone. There was no consistency from stand to stand. For example, there were significant differences ($.01 > P > .05$) in MAI and in the standard deviation of ring width for genotypes at the *Mdh-2* locus in the population from Shawnee State Forest, OH, but in no other population.

We compared performance of heterozygotes to corresponding homozygotes at individual loci where possible. At most polymorphic loci in pitch pine the common allele exceeds 90% in frequency (Guries and Ledig, 1982), so homozygotes for the rare allele are often missing in samples as small as ours. For 57 cases (individual loci within populations), heterozygotes and both homozygotes were present. In these 57 possible comparisons, MAI of heterozygotes exceeded that of homozygotes less than half the time, in 25 comparisons; i.e., there was no convincing evidence of overdominance at allozyme loci in any population. Heterozygotes were often intermediate to homozygotes (14 comparisons) or inferior to either homozygote (20 comparisons).

The limited age distribution within stands made it difficult to detect any tendency of heterozygotes for greater longevity. Correlations of age with heterozygosity were positive in six of eight stands, but nonsignificant, varying only from $r = -.20$ to .22.

DISCUSSION

The results suggest that growth may be positively associated with heterozygosity. That does not mean heterozygosity per se is advantageous; there was no evidence of

overdominance associated with any of the loci tested. We will discuss the positive relationship between growth and heterozygosity, a new observation in forest trees, and propose explanations to explain variation in the relationship among populations. Secondly, we will argue that the apparent superiority of heterozygotes is really a measure of inbreeding depression in homozygotes due to recessive deleterious alleles on chromosome segments marked by allozyme loci.

Growth rate is a trait of low heritability in forest trees, a characteristic usually associated with fitness traits. Growth rate should affect fitness directly, because fitness depends, in part, upon survival. In the development of a plant community, self-thinning occurs, such that dominant individuals suppress and eventually eliminate the slow-growing ones. One avenue of suppression is through crown competition for light, and diameter and crown surface area are closely related to stem diameter or basal area in forest trees (Stout, 1964). MAI may affect fitness in a second way because a greater MAI results in a larger diameter which means a larger crown and more sites for cone and seed production.

The correlation between growth rate (i.e., MAI) and heterozygosity are clearly positive and meaningful in three stands (Fig. 2). The result apparently agrees with Lerner's (1954) classic hypothesis of heterozygote superiority. Growth rate has been related to heterozygosity in molluscs, salamanders, and herbaceous plants (Schaal and Levin, 1976; Singh and Zouros, 1978; Zouros et al., 1980; Pierce and Mitton, 1982). But what is the explanation for lack of correlation or a negative correlation in the other five stands? Apparently, the answer is that the relation of MAI to heterozygosity is related to stand age (Fig. 3); MAI becomes more dependent on the number of heterozygous loci with increasing age ($r = .85$). The pattern strikingly calls to mind age-dependent trends for genetic variance in plantation-grown forest trees (Franklin, 1979). Additive genetic variance seems to be fully

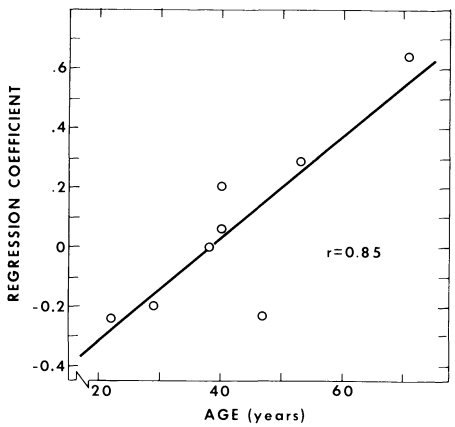

FIG. 3. Relationship between stand mean age and the regression coefficients of mean annual basal area increment on number of heterozygous loci for eight stands of pitch pine. (Regression coefficient for Bradley Field, CT calculated without the "O" heterozygosity class, an apparently aberrant point based on only a single individual.)

expressed only after the onset of competition, a situation analogous to the expression of genetic heterozygosity in the present case.

We hypothesize that heterozygote superiority is expressed most strongly in fluctuating environments. A one-year-old stand has encountered only a limited range of conditions, and preadapted homozygotes are likely to be as successful as heterozygotes. But, the older the stand, the greater the range of climatic conditions to which it has been exposed. In addition, older trees have interacted with more competitors than younger trees during the process of natural thinning. Competition accentuates differences in growth, slowly-growing individuals being further suppressed by the rapidly-growing. Additive genetic variance for growth traits in forest trees increases markedly as crowns close and they enter a phase of close competition (Franklin, 1979).

We can use these hypotheses to predict situations in which the MAI-heterozygosity relationship will be strongest. If climatic fluctuation is important, heterozygote superiority should be most strongly expressed where the variance of climatic

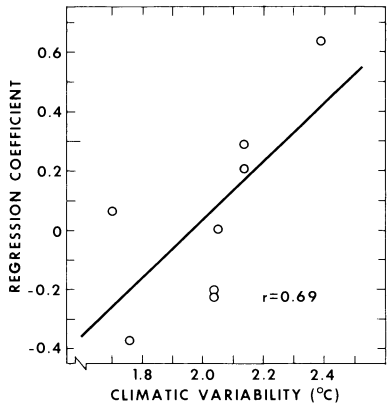

FIG. 4. Relationship between climatic variability and the regression coefficients of mean annual basal area increment on the number of heterozygous loci for eight stands of pitch pine. Climatic variability is the standard deviation of mean monthly maximum temperature for each month, calculated across years of record and pooled across the 12 months.

parameters is greatest. We correlated the regression coefficient between MAI and heterozygosity with the standard deviations of mean monthly maximum temperature and precipitation over the years of record, pooled over months; statistics which express the unpredictable component of climatic variation. We also ran correlations against the seasonality index, which is the standard deviation of the average mean maximum temperature from January through December, and the diurnal index, which is the difference between mean monthly maximum and minimum temperatures. These latter are repeatable, and therefore predictable, aspects of climatic variability. The only statistically significant relationship ($r = .69$; $.10 > P > .05$) was with year-to-year climatic variation; i.e., climatic unpredictability (Fig. 4). As hypothesized, the more unpredictable the monthly temperature, the stronger is the relationship between MAI and heterozygosity.

If competition is important, we can also predict that the relationship between MAI and heterozygosity will depend on stand density. We expressed stand density as the number of stems per hectare. Unfortunately, data were not available for Shawnee State Forest, OH or Blue Ridge, NC, two of the more extreme stands. The relationship was weak and nonsignificant ($r = .28$), but positive, as predicted. A better measure of competition might yield more significant results, because competition is not measured only by the number of stems. Young stands can have many more stems than older stands but experience less competition because their crowns are smaller.

With tree species, a further prediction can be tested. Because the record of each annual increment is preserved in the pattern of wood rings, MAI can be calculated for each tree when it was 10, 20, . . . , n years old, up to the age of the tree when sampled. If the relationship between MAI and heterozygosity does become stronger with age, this should be apparent from the historical pattern as recorded in the growth rings. Results partially verify predictions (Fig. 5). In five stands, heterozygote superiority did increase with age, but in three it did not. Two of the latter might be explained by site conditions. At St. Chrysostôme, Quebec, trees grow on an impervious sandstone cap which supports a maximum soil depth of less than .5 m, and in most places, much less (Grandtner, 1961). Trees reach a maximum height of only ca. 10 m before being windthrown. At Marconi Station on Cape Cod, wind and salt spray prune the crowns of trees that emerge from the canopy. Therefore, in both stands, height is restricted by physical limitations, so heterozygotes may be unable to express their advantage through biotic competition. We have no explanation for the negative relationship between MAI and heterozygosity at Bradley Field, CT, but it was the youngest stand sampled (ca. 22-years-old), and in time, competition may result in a positive relationship.

Previously, positive relationships between growth and heterozygosity in trees have been found only in aspen (*Populus tremuloides* Michx.; Mitton and Grant, 1980), and not in lodgepole (*Pinus contorta* Dougl. ex Loud.) or ponderosa pine (*P. ponderosa* Dougl. ex Laws; Knowles

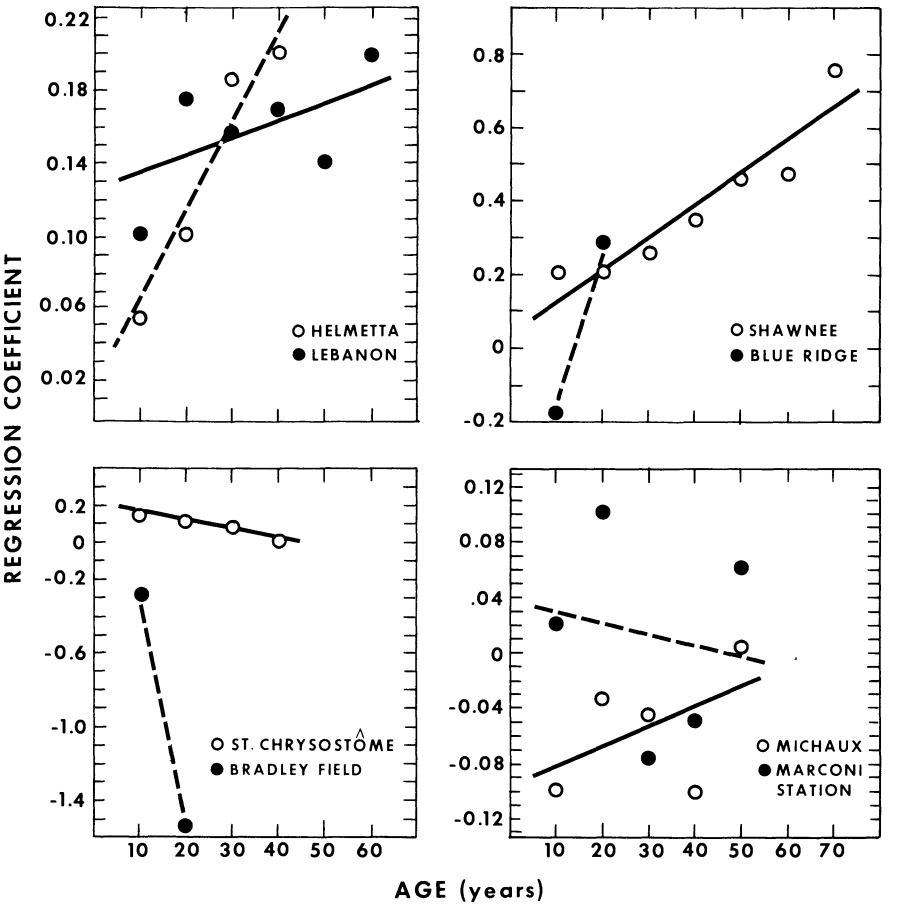

FIG. 5. Graphs for each of eight pitch pine stands, showing the change with age in the regression coefficients between mean annual basal increment at 10-year intervals and the number of heterozygous loci. Note the difference in scale of the ordinate.

and Grant, 1981; Mitton et al., 1981). For those species, estimates of heterozygosity were based on only three or four loci, compared to 21 for pitch pine, and the fewer the loci, the greater the probability of misclassification if it is intended to characterize average heterozygosity for the entire genome (Mitton and Pierce, 1980). If more loci had been scored or more populations analyzed, a positive relationship might be found in lodgepole and ponderosa pine. Inevitably, there are so many sources of random variation within natural stands, such as differences between trees in age of establishment, local density, and microsite conditions, that the relationship between vigor and heterozygosity may be hopelessly concealed.

There are at least two explanations for a positive relationship between growth and heterozygosity. The first is that heterozygosity per se is advantageous irrespective of locus. Heterozygotes at a locus may be able to achieve optimal performance in a greater range of environments than homozygotes because they have two (monomers) or more (multimers) forms of an enzyme, each perhaps exhibiting different optima for temperature, pH, hydration, or other factors. Homozygotes would have only a single form. In contrast to our results, overdominance is associated with

single allozyme loci in guppies and oysters (Beardmore and Shami, 1979; Zouros et al., 1980; Koehn and Shumway, 1982). Our failure to reveal heterosis at allozyme loci in pitch pine does not support a hypothesis of overdominance at allozyme loci, but it does not rule out overdominance at associated loci.

A second explanation is that heterozygosity is merely an index of inbreeding. The proportion of progeny resulting from selfing or mating among near relatives will be higher in our relatively homozygous classes and progressively lower in heterozygous classes. Inbreeding in most conifers results in a pronounced and predictable depression of growth. In seedlings from self-pollination, height growth is depressed about 10 to 30% on the average (Franklin, 1970). The magnitude of the difference increases with time (Eriksson et al., 1973; Libby et al., 1981). There is also evidence that the number of embryonic lethal equivalents is high in conifers, ranging from 1.8 in noble fir (*Abies procera* Rehd.) to 8.0 in lodgepole pine, 8.5 in loblolly pine (*Pinus taeda* L.), and 11.2 in Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), which indicates that the total frequency of deleterious recessive genes may be quite high (Sorensen, 1969; Franklin, 1972; Sorensen et al., 1976; Sorensen, pers. comm.). Homozygosity at the enzyme loci assayed in pitch pine could be an index of homozygosity as a result of coancestry.

Much of the observed variation in growth rate among forest trees could be the result of variation in the level of outcrossing. Variation among progeny of white pine (*Pinus strobus* L.) was attributed to silvicultural modifications of the breeding system that affected the degree of inbreeding (Ledig and Smith, 1981). In other species, enforced outcrossing compared to natural wind-pollination results in progeny with comparatively rapid growth (Coles and Fowler, 1976; E. B. Snyder, pers. comm.). The observed increase in additive genetic variance with the onset of crown closure in plantation culture (Franklin, 1979) may also result from competition among trees homozygous for larger or smaller numbers of recessive deleterious alleles.

The failure to find any evidence of greater longevity for heterozygotes may reflect the pattern of regeneration and stand development in pitch pine. Stands of pitch pine are regenerated in the wake of catastrophe, usually fire, and could represent the offspring of a few chance survivors. Homozygotes may be more frequent because of the population bottleneck. Though inbreds have slow growth and could normally be suppressed, their survival may be enhanced in the absence of competition, an example of Wright's (1931) classic case of drift, with homozygotes occupying low adaptive peaks when selection is relaxed. Eventually, gaps will be filled by crossing among the original colonizers. The younger age class would become established under conditions of increased competition from parents and siblings, and heterozygotes may occur in higher frequency than they did among the original colonizers. Under such circumstances, a weak negative correlation between heterozygosity and age might develop, even if heterozygotes were longer-lived.

It is still open to question whether heterozygotes in forest trees are homeostatically adjusted to environmental fluctuation relative to homozygotes. Mitton et al. (1981) found a weak, negative correlation between heterozygosity and the variance in ring width in lodgepole pine. The relationship was weakly positive in aspen (Mitton and Grant, 1980) and ponderosa pine (Knowles and Grant, 1981). Knowles and Grant (1981) suggested that ring width variability was greater in heterozygotes because heterozygotes were capable of utilizing good years to better advantage in cone and seed production than homozygotes. Radial and even terminal growth is reduced in heavy mast years or in the succeeding year (e.g., Morris, 1951; Eis et al., 1965). Because lodgepole pine is serotinous, Mitton et al. (1981) assumed that its annual cone production was relatively constant, and therefore, a negative relationship was apparent between variation

in annual radial increment and heterozygosity. While we have no direct comparision of serotinous-coned trees and open-coned trees, the Lebanon State Forest and Helmetta, NJ populations are polymorphic, with 60% and 20% serotinous-coned trees, respectively (Ledig and Fryer, 1972), and the other stands are essentially open-coned. Mitton et al.'s (1981) hypothesis would predict a negative relationship between the standard deviation of annual basal area increment and heterozygosity in Lebanon State Forest and Helmetta, but in fact, the relationship is positive. It will be difficult to demonstrate any consistent relationship in natural stands, because variability will increase with age as a result of exposure to climatic extremes and competitors.

Summary

Within some populations, mean annual growth rate was greater for trees heterozygous at a high proportion of their isozyme loci than for relatively homozygous trees. The strength of the heterozygosity-growth relationship varied from strongly positive in the oldest stands to negative in the youngest. The regression coefficient relating growth to heterozygosity was strongly correlated with age ($r = .85$). Because of the record left by the annual rings, tree growth at various past ages can be related to heterozygosity, and within most stands the relationship between growth rate and heterozygosity increased as trees aged. Apparently, the superiority of heterozygotes is not expressed in young stands. The delayed expression of heterozygote superiority may reflect the greater homeostasis of heterozygotes in the face of year-to-year climatic variation, or the accentuation of differences by competition between heterozygotes and homozygotes as the canopy closes.

In fact, the heterozygosity-growth relationship was strongest in the least predictable environments ($r = .69$), as measured by the standard deviation of mean monthly maximum temperatures over years of record. But competition may also be involved because heterozygote superiority was most strongly expressed in the densest stands ($r = .28$). The failure of previous investigations to find correlations may result from scoring too few loci to adequately characterize heterozygosity, or to sampling populations in which competition was not strongly expressed. The relationship of growth to heterozygosity appears explicable with reference to age, stand structure, and climatic variability.

There was no heterosis associated with any single locus, suggesting that depression of growth in homozygotes is a result of linked deleterious recessives. Deleterious recessives are in high frequency in most conifers. Homozygosity in pitch pine probably identifies individuals carrying chromosome segments identical by descent from recent ancestors, and apparent heterozygote superiority may actually measure inbreeding depression in homozygotes.

Homeostasis in forest trees has been measured by the inverse of variability in ring width or annual increment. For pitch pine there was no consistent relationship of variability to heterozygosity, perhaps because of random error and because variability in annual increment is not a cumulative characteristic like mean annual increment.

Acknowledgments

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1983 THE THEODOSIUS DOBZHANSKY PRIZE RECIPIENT

Mr. Anthony J. Zera, winner of the 1983 prize, is currently a senior graduate student in the Department of Ecology and Evolution at the State University of New York, Stony Brook. Mr. Zera's research interests are in the fields of ecological and biochemical genetics. His doctoral work concerns the biochemical properties and population genetics of polymorphic enzyme systems in the wing-polymorphic waterstrider, *Limnoporus canaliculatus*. This work is being done under the direction of Dr. Richard K. Koehn.

The Dobzhansky prize monies will be used for the analysis of the hormonal basis of wing-polymorphism in waterstriders. This research will be carried out in the laboratory of Dr. Mary Ann Rankin at the University of Texas at Austin, where Mr. Zera will be a postdoctoral fellow.

THE THEODOSIUS DOBZHANSKY PRIZE

The Theodosius Dobzhansky Prize of the Society for the Study of Evolution is awarded to a young investigator in aid of research. Money for the prize was collected by a committee of Dobzhansky's friends and colleagues and turned over to the Society for administration. Because of his lifelong interest in young people and his efforts at helping them get started on a research career, it was decided that the proceeds should be used to help support the research of a young investigator. The prize is a maximum of $1000 and was awarded for the first time in 1981. The intent is that the prize is awarded for research that could not be performed without the financial aid.

Eligibility. Applicants should have received the Ph.D. degree no earlier than the summer of 1980. The prize may also be awarded to support research for the dissertation. Foreign applicants should be at an equivalent stage of their career.

Application. The candidate should apply in writing to

Dr. Jeffry B. Mitton
Department of EPO Biology
University of Colorado
Boulder, CO 80309

The application should include a 500 word summary of the proposed research, a curriculum vitae and bibliography, and a proposed budget showing any other sources of support. If the candidate has performed any previous research, a 500 word summary should be included. The candidate should also request that two letters of recommendation be sent. If the candidate has a dissertation or any papers published or submitted to journals, it would be helpful but not essential to send copies. Three copies of application materials must be sent. No material can be returned. The *deadline for receipt of all application materials is May 1, 1984.*

It is possible that the prize will be divided between two or more recipients. The recipient will be notified during the annual meeting of the Society.