noted for other gymnosperms by Feret (1971) and by Rudin and Rasmuson (1973). That the complicated inheritance occurs more frequently in forest trees than in cultivated crops is expected since wild heterozygous organisms carry more modifying genes than do inbred ones that have been cultivated longer.

Further research on the problem of excessive segregates in supposedly nonsegregating families would be worthwhile. Also, future sampling should compare geographic sources to determine the generality of our findings.

The gene actions underlying band patterns were not obscured even though appearance of some bands was complicated or marred. None of the 84 chi-square tests indicated poor fits. We attribute this result to the resolving power of the diallel mating design. Too few unrelated crosses would probably have resulted in failure to reach working genetic hypotheses.

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Inheritance of glutamate oxalo-acetate transaminase isozymes in virginia pine megagametophytes[1]

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Summary

Polyacrylamide gel electrophoresis was used to examine inheritance of GOT isozymes in megagametophytes of Virginia pine. Two unlinked loci were found to code for GOT: Locus A with 5 alleles, and Locus B with 3 alleles. Irregular segregation patterns were found among megagametophyte populations of some trees. These results suggest the possibility of non-random degeneration of 3 of 4 megaspores produced in meiosis.

Four populations of Virginia pine were compared on the basis of allelic frequency and occurrence. Little or no significant differences were found.

Key words: Isozymes, Virginia pine, megagametophyte, electrophoresis, glutamate oxalo-acetate transaminase.

Zusammenfassung

In Megagametophyten von *Pinus virginiana* Mill. wurde die Vererbung von GOT Isoenzymen elektrophoretisch untersucht. Zwei nicht gekoppelte Loci codieren für GOT: Locus A mit 5 Allelen und Locus B mit 3 Allelen. Bei Megagametophytenpopulationen einiger Bäume wurden unregelmäßige Segregationsmuster gefunden. Diese Ergebnisse sprechen für die Möglichkeit nicht zufälliger Degeneration von 3 der 4 Megasporen der Meiose.

Vier Populationen von *Pinus virginiana* Mill. wurden hinsichtlich Vorkommen und Frequenz von Allelen verglichen. Unterschiede waren gering oder nicht signifikant.

Introduction

The development of seed orchards is an established aspect of forest tree improvement programs. The direct determination of genetic diversity in domesticated populations may become mandatory as breeding programs progoss. In particular, the significant decrease or increase in the genetic base of selected seed orchard populations relative to that of natural populations of a given species begs exploration. This problem is relevant for several reasons. Drastic decreases in population size can lead to allelic losses creating largely monomorphic populations (Bonnell and Selander, 1974). Populations with disproportionately fewer alleles per locus may be more susceptible to insect and disease epidemics than populations composed of widely divergent genotypes (NAS, 1972). The dangers of a narrow genetic base have been clearly demonstrated with inbred crop species and could be even more pronounced in a long-lived tree species. Of long term importance is the possibility

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that the permanent loss of existent genetic variation could mean the irreversible loss of potentially valuable characteristics.

The quantitative genetic measurements generally applied to seed orchard populations and their progeny do not provide assessment of the genetic structure of populations. Quantitative measurements are essentially gross population indicators, are sensitive to genotype-environment interactions, are based on multiple locus characteristics and do not delimit allelic heterozygosity of individuals. Electrophoresis, however, is capable of separating enzymatic and non-enzymatic proteins, the products of individual alleles. Consequently, analysis of isozyme variation provides a relatively precise estimation of genetic variation to compare genetic variation in different populations (Lewontin and Hubby, 1966; Hubby and Lewontin, 1966).

The application of electrophoresis to conifer species was first described by Bergmann (1971) and Bartels (1971). Conifers are unique in that genetic control of specific isozymes can be determined in a single generation without extensive breeding experiments. The haploid megagametophyte tissue of each seed is the product of one of the four megaspores produced in meiosis. Because the degeneration of three of the daughter cells is presumably random, different segregational genotypes of the megagametophyte should be randomly distributed among the seed from a single parent tree. Thus, in a diploid tree heterozygous for a particular gene locus, one would predict a 1 : 1 segregation ratio of alleles among megagametophytes collected from a single tree.

The primary objective of this study was to determine the genetics and inheritance patterns of glutamate oxalo-acetate transaminase (GOT) isozymes for population analysis of Virginia pine. Concurrently, the enzyme system was used to study the distribution of genetic variation in a natural population and a seed orchard population of Virginia pine (*Pinus virginana* Mill.).

Materials and Methods

Unopened cones were collected from individuals in four populations of Virginia pine. Trees selected were samples of two natural populations, one located at Blacksburg, Virginia (n = 7), and the other at the Reynolds Homestead Research Center at Critz, Virginia (n = 20). The third population was a sample from a clearcut area at Critz, Virginia planted with nursery-run stock obtained from the Virginia Division of Forestry (n = 29). Individual trees from these populations were chosen on the basis of their accessibility and fruitfulness. Cones were also collected from each of the twenty-six clones in a "first generation" seed orchard population at Appomattox, Virginia (n = 26). All cones were oven-dried at 37° C. Seed was collected and stored at 4° C until used.

Each electrophoretic sample was a crude protein extract of the gametophyte from a single seed. The gametophyte of a single seed was excised and placed in a 1 ml. centrifuge tube containing .075 ml., 0.1 N Tris (2 amino 2-hydroxymethyl 1, 3 propanediol)-HCl buffer, pH 8.0 (Firenzuoli *et al.*, 1968). The tissue was ground with a glass rod and then centrifuged at 3,500 xG for 10 minutes to remove cell debris. Electrophoresis was performed using discontinuous, vertical polyacrylamide slab gel electrophoresis according to the method of Daivis (1964). The procedure employed a 3.3 percent spacer gel and a 7.5 percent running gel. Samples were run initially at 50 V for 105 minutes followed by 175 V for 130 minutes. GOT activity was localized in the gels by the staining technique of Schwartz (1963).

A minimum of five seed samples from each tree were analyzed. Assuming heterozygous individuals were segregating in a 1 : 1 ratio this would give a 1/16 chance of misidentifying heterozygous individuals as homozygotes. When a single tree had two mutually-exclusive band patterns among its seeds, larger sample sizes were run. The occurrence of two bands in a 1 : 1 ratio was tested using Chi square analysis.

Results

Eight isozymes of GOT were identified in Virginia pine (*Figure 1*). Two isozymes, $A3_1$ and $A3_2$, were not reliably distinguishable from each other and were combined and considered together as A3. From study of the segregation patterns exhibited by individual trees, it was determined that the isozymes represented the products of two gene loci coding for GOT in Virginia pine: Locus A and Locus B. Locus A had four alleles (isozymes A1—A4, *Figure 1)* and Locus B, three alleles (isozymes B1—B3, *Figure 1)*. Isozymes A1, B2, and B3 were unique alleles, each occurring in only one heterozygous tree among the four sample populations.

The experimental segregation ratios among megagameto-

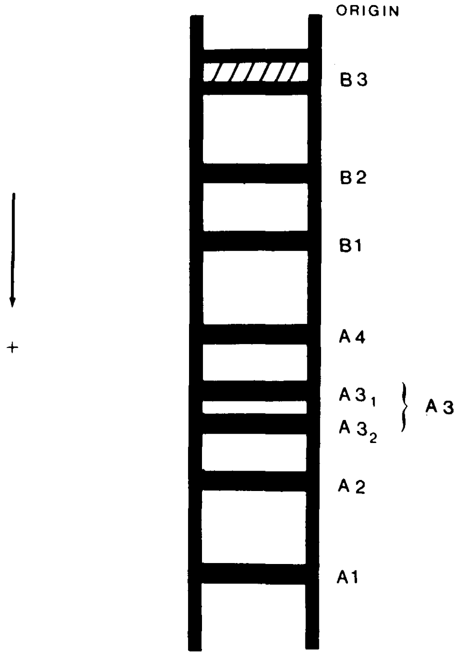

Figure 1. — Schematic representation of the total banding pattern of GOT isoenzymes in Virginia pine.

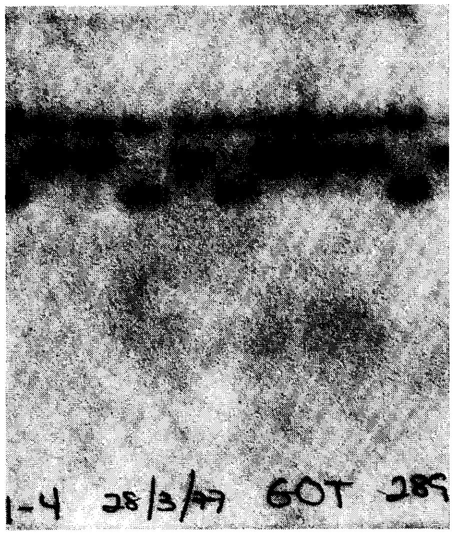

Figure 2. — Photograph of a polyacrylamide slab gel satined for GOT activity. Zymogram illustrates the segregation of the A2 and A4 alleles among gametophytes from Tree 289. There is no segregation for the B1 allele at the B locus.

Table 1. — Female gametophyte segregation patterns at the GOT A locus of Virginia pine.

Segregant genotype	Tree I.D.	$n^{1/}$	Segregation ratio	χ^2	P
A2:A4	88	50	Observed: 33:17 Expected: 25:25	5.12	< .05
A2:A4	62	42	Observed: 24:18 Expected: 21:21	.86	.3-.5
A2:A4	410	21	Observed: 12:9 Expected: 10.5:10.5	.43	.5-.7
A2:A4	568	17	Observed: 10:7 Expected: 8.5:8.5	.53	.3-.5
A2:A4	21	16	Observed: 10:6 Expected: 8:8	1.00	.3-.5
A2:A4	466	12	Observed: 8:4 Expected: 6:6	1.33	.2-.3
A2:A4	452	100	Observed: 42:58 Expected: 50:50	2.56	.1-.2
A2:A4	289	29	Observed: 6:23 Expected: 14.5:14.5	9.97	< .05
A2:A4	353	19	Observed: 8:11 Expected: 9.5:9.5	.47	.3-.5
A2:A4	332	16	Observed: 7:9 Expected: 8:8	.25	.5-.7
A2:A4	541	12	Observed: 5:7 Expected: 6:6	.33	.5-.7
A2:A4	306	10	Observed: 4:6 Expected: 5:5	.40	.5-.7
A3:A4	94	8	Observed: 6:2 Expected: 4:4	2.0	.1-.2
A3:A4	495	53	Observed: 33:20 Expected: 26.5:26.5	3.19	.05-.1
A3:A4	416	23	Observed: 10:13 Expected: 11.5:11.5	.39	.5-.7
A3:A4	F	23	Observed: 10:13 Expected: 11.5:11.5	.39	.5-.7
A3:A4	T	17	Observed: 7:10 Expected: 8.5:8.5	.53	.3-.5
A3:A4	M	16	Observed: 7:9 Expected: 8:8	.25	.5-.7
A2:A3	29	13	Observed: 6:7 Expected: 6.5:6.5	.077	.7-.8
A2:A3	398	12	Observed: 6:6 Expected: 6:6	0	> .9
A2:A3	7	43	Observed: 26:17 Expected: 21.5:21.5	1.883	.1-.2
A2:A3	14	14	Observed: 8:6 Expected: 7:7	.286	.5-.7
A1:A2	L	20	Observed: 10:10 Expected: 10:10	0	> .9

1) n = sample size.

Table 2. — Female gametophyte segregation patterns at the GOT B locus of Virginia pine.

Segregant genotype	Tree I.D.	$n^{1/}$	Segregation ratio	χ^2	P
B1:B2	495	53	Observed: 25:28 Expected: 26.5:26.5	.17	.5-.7
B1:B3	452	100	Observed: 52:48 Expected: 50:50	.16	.5-.7

1) n = sample size.

phytes from individual trees and the Chi-square analysis testing conformance to an expected 1 : 1 ratio are given in *Table 1*. The segregation of isozymes at Locus A in trees 88 and 289 did not conform statistically to a 1 :1 segregation ratio. Several other heterozygous trees, while conforming statistically to a 1 : 1 ratio at the .05 level of probability, had very low P values. The unequal segregation ratios observed were not associated with a particular allelic type: tree 88 had an excess of megagametophytes with the A2 allele, while tree 289 had an excess of the A4 allele. Locus B, unlike Locus A, did conform well to a 1 : 1 segregation ratio (*Table 2*).

Two of the sample trees were heterozygous at both Locus A and Locus B and it was therefore possible to test for linkage between the two loci. The results of the linkage analysis are given in *Table 3*. The two loci were not linked. However, there did appear to be an interactive effect between the two loci. In both heterozygotes the observed genotypic frequencies did not conform well to the 1 : 1 : 1 : 1 ratio of the four genotype classes expected under the assumption of independent assortment. An analysis of the source of deviation showed that unequal segregation oc-

Table 3. — Analysis of the linkage relationship between the GOT A locus and the GOT B locus in two individuals of Virginia pine.

Example 1: Tree 495

Segregation assuming independent assortment of Locus A and Locus B

$n^{1/}$	Presumed genotype		Segregating genotypes and segregation ratios				χ^2	P
			A3/B1	A3/B2	A4/B1	A4/B2		
53	A3/A4	Observed: Expected:	19 13.25	14 13.25	6 13.25	14 13.25	6.55	.05-.10

Segregation at Locus A and Locus B

$n^{1/}$	Presumed genotype		Segregating genotypes and segregation ratios			χ^2	P
			A3/A4		B1/B2		
53	A3/A4	Observed: Expected:	33.20 26.5:26.5			3.19	.05-.1
53	B1/B2			Observed: Expected:	25:28 26.5:26.5	.170	.5-.7

Segregation at Locus A in association with each Locus B allelic type

$n^{1/}$	Presumed genotype		Segregating genotypes and segregation ratios			χ^2	P
			A3/B1:A4/B1		A3/B2:A4/B2		
25	A3/A4	Observed: Expected:	19:6 12.5:12.5			6.80	< .01
28	A3/A4			Observed:	14:14	0.00	> .9

Example 2: Tree 452

Segregation assuming independent assortment of Locus A and Locus B

$n^{1/}$	Presumed genotype		Segregating genotypes and segregation ratios				χ^2	P
			A2/B1	A2/B3	A4/B1	A4/B3		
100	A2/A4 B1/B3	Observed: Expected:	25 25	17 25	27 25	31 25	4.16	.2-.3

Segregation at Locus A and Locus B

$n^{1/}$	Presumed genotype		Segregating genotypes and segregation ratios			χ^2	P
			A2:A4		B1:B3		
100	A2/A4	Observed: Expected:	42:58 50:50			2.56	.1-.2
100	B1/B3			Observed: Expected:	52:48 50:50	.16	.5-.7

Segregation at Locus A in association with each Locus B allelic type

$n^{1/}$	Presumed genotype		Segregating genotypes and segregation ratios			χ^2	P
			A2/B1:A4/B1		A2/B3:A4/B3		
52	A2/A4	Observed: Expected:	25:27 26:26			.16	.5-.7
48	A2/A4			Observed: Expected:	17:31 24:24	4.00	.02-.05

1) n = sample size.

Table 4. — Allelic frequencies at the GOT A and GOT B loci in four populations of Virginia pine.

Population	n[1]	Frequency of heterozygous individuals Parental population	 Progeny
Critz: Natural population	20	.650	.534
Blacksburg: Natural population	7	.715	.600
Critz Clearcut: Planted population	28	.630	.584
Seed Orchard: "First generation"	25	.40	.545

[1]) n = sample size.

Table 5. — Genotypic frequencies at the GOT A and GOT B loci in four populations of Virginia pine.

		Genotype											
Population	n[1]	A2/A2	A3/A3	A4/A4	A2/A4	A2/A3	A3/A4	A1/A2	B1/B1	B1/B2	B1/B3	B2/B3	B3/B3
Critz: Natural population	20	.200	.000	.150	.600	.000	.050	-----	.950	-----	.050	-----	-----
Blacksburg: Natural population	7	.143	.000	.143	.429	.286	.000	-----	1.00	-----	-----	-----	-----
Critz Clearcut: Planted population	28	.214	.036	.107	.500	.072	.072	-----	.960	.040	-----	-----	-----
Seed Orchard: "First generation"	25	.200	.000	.400	.240	.000	.120	.040	1.00	-----	-----	-----	-----

[1]) n = sample size.

Table 6. — Frequency of GOT A heterozygotes in four populations of Virginia pine and frequencies of heterozygous progeny after one generation of random mating.

			Locus A				Locus B	
Population	n[1]	A1	A2	A3	A4	B1	B2	B3
Critz: Natural population	20	----	.500	.025	.475	.975	----	.025
Blacksburg: Natural population	7	----	.500	.143	.357	1.00	----	----
Critz Clearcut: Planted population	28	----	.500	.107	.393	.982	.018	----
Seed Orchard: "First generation"	25	.020	.340	.060	.580	1.00	----	----

[1]) n = sample size.

curred at the A locus and that unequal segregation occurred at the A locus only in association with one of the two B alleles. In the first case, tree 495, alleles A3 and A4 segregated unequally only in the gametophytes of the genotype A3/A4 and B1/B1 while A3/A4 and B2/B2 segregated equally. In the second case, tree 452, alleles A2 and A4 segregated unequally only in the gametophytes of the genotype A2/A4 and B3/B3 while A2/A4 and B1/B1 segregated equally.

The observed deviations from expected segregation ratios are not associated with a single allelic type at either the A locus or the B locus. Tree 495 had an excess of seeds with the A3 allele over the A4 allele in association with B1, the common allelic form at the B locus. Tree 452 had an excess of the A4 allele over A2 in association with B3, an unusual B allele *(Table 3)*.

GOT allelic frequencies are listed in *Table 4* by population. The GOT A locus was polymorphic with several allelic types present in intermediate frequencies. The GOT B locus was essentially monomorphic with one allelic type predominating in all four populations. All four populations possessed the three common Locus A allelic forms. The seed orchard population possessed a unique allele at the A locus (A1) while the Critz natural and planted stands each possessed a unique allele at the B locus (B2 and B3, respectively). The four populations analyzed here were not significantly different from each other in terms of allelic frequencies according to the arcsin transformation t-test of SOKAL and ROHLF (1969). Genotypic frequencies *(Table 5)* show a similar amount of homogeneity among the four populations analyzed. The only statistically significant differences in genotype frequencies were between the frequency of A4/A4 genotypes in the Virginia Division of Forestry seed orchard and the Critz planted stand and between the frequency of A2/A4 seed orchard genotypes and both Critz stands.

Both natural populations, Blacksburg and Critz, were analyzed for conformance to Hardy-Weinberg equilibrium. Both populations were found to be in equilibrium.

The frequency of individuals heterozygous at Locus A among the four populations is given in *Table 6*. The data showed that the seed orchard population was the most homozygous, heterozygosity occuring in only 40% of the trees. The differences between the four populations were not statistically significant. The percent heterozygosity in the progeny of the analyzed populations under the assumption of panmixia was also calculated *(Table 6);* heterozygosity of the seed orchard population progeny was estimated at 54 percent, a value within the range of values found for the other three populations.

Discussion and Conclusions

Comparing the genetic composition of populations involves examination of (1) statistically significant differences in allelic and genotypic frequencies, and (2) the presence or absence of different allelic types. The first gives an estimate of the degree of differentiation between populations as a result of random or selective forces in natural populations. The second gives an estimate of the representation of the total genetic variation of a species in any given population.

The different organization at the two GOT loci is an important consideration when evaluating the presence or absence of allelic types. Locus A is highly polymorphic while Locus B is close to fixation for one allelic form. The seed orchard population of select trees carried all common Locus A alleles as well as one unusual A allelic type. At the B locus, however, only the common B1 allele was found in the seed orchard population while both Critz populations possessed one unusual allelic type. The Blacksburg population cannot really be considered comparable because of the very small sample size. It is not known if the decreased genetic variation at a locus which shows little natural variation represents a significant loss of variation.

Among the four populations sampled, no significant differences in allelic frequencies were evident. Absence of differences may be a function of the conservative statistical test which is very sensitive to small sample size. The seed orchard population showed a lower, but non-significant, degree of heterozygosity. This is consistent with the only statistically significant differences found between populations. The seed orchard population showed an increase in the homozygous A4/A4 genotype compared to the natural population at Critz and conversely, a decrease in the heterozygous A2/A4 genotype. In the case of the GOT system elucidated here, the genetic information in the seed orchard population and the natural population is statistically equivalent. Selection seems to affect the manner in which information is distributed among individuals within the two types of populations.

The unequal inheritance patterns of GOT isozymes in Virginia pine has also been observed among megagametophytes and in diploid progeny from controlled crosses in loblolly pine *(Pinus taeda* L.) (Adams and Coutinho, 1977) and Scotch pine *(Pinus sylvestris* L.) (Rudin, 1975). These reports were based on very small sample sizes and in both cases unusual inheritance was assumed to be associated with a particular allelic type at one of the GOT loci. The data presented here and a reassessment of the data presented by Rudin (1975) and Adams and Coutinho (1977) indicate that the situation may not be quite so straightforward.

Rudin found that two of eight trees were heterozygous at the GOT A locus in Scotch pine (A1/A2 and A2/A22). The gametophytic segregation for alleles A1 and A2 did not conform well to a 1 : 1 segregation ratio. In controlled crosses between the heterozygote and three homozygous (A2/A2) individuals he found progeny from one cross had a significant decrease in the number of expected heterozygotes, while the progeny of the other two crosses conformed statistically to a 1 : 1 segregation ratio between the heterozygous and homozygous genotypes, although there were slightly fewer heterozygotes in both crosses. Rudin's hypothesis assumed an inviability associated with the A1 allele and according to his hypothesis the A1/A2 genotype should have been less fit than the A2/A2 genotype. However, if decreased viability in the progeny were associated only with the GOT A locus, then the progeny from the three crosses, genetically equivalent at the A locus, should all have had significantly fewer A1/A2 genotypes. Thus, rather than suggest that a specific allelic type resulted in decreased viability in both the gametophyte and diploid individuals, Rudin's results suggest that the A2/A2 parents were not genetically equivalent in some factor which affects the viability of individuals associated with particular locus A genotypes.

The existence of an additional factor, other than a specific A allelic type affecting viability, is also suggested by the analysis of a controlled cross of the second heterozygous genotype. The A2/A22 genotype segregated equally among the megagametophytes, yet in a cross with a homozygous A2/A2 individual the progeny did not conform to expected frequencies. In this case, either a specific A allele affected viability only at the diploid level or there is an additional genetic factor capable of affecting viability present in the homozygous tree but not the heterozygous tree.

The unequl inheritance patterns described by Adams and Coutinho (1977) were found only in the diploid progeny from three controlled crosses between one heterozygous individual and three homozygous individuals. The heterozygous individual did produce megagametophytes exhibiting equal segregation ratios. Unlike Rudin's data, the progeny from each cross did not vary significantly from expected values and only by pooling the data from the three crosses did there appear to be a deficiency in the progeny of the heterozygous genotype. Because this observation was based on both pooled data and a very small sample size it is not possible to determine whether the heterozygous genotype is less common in general and what possible mechanisms could cause a decrease in the occurrence of heterozygotes.

The inheritance patterns of GOT isozymes in Virginia pine presented in this paper have shown that degeneration of three of the four megaspores produced in meiosis may not always be a random process. Because there is no direct experimental evidence of the events following meiosis which produce a single functional megaspore, unusual meiotic events cannot be completely eliminated as a hypothesis for the patterns seen here. However, the consistency of the genotypic patterns found in the linkage analysis would suggest a genetic mechanism producing decreased viability.

The individual tree segregation data rejects the hypothesis that any genetic mechanism is due to a single GOT A allelic type. Even particular combinations of GOT A and GOT B allelic types is not a sufficient explanation in that identical parental genotypes at the A and B loci have both normal and abnormal segregation of alleles among the gametophytes. A reasonable hypothesis must explain the patterns of the double heterozygotes: both the equal segregation at the B locus and the unequal segregation at the A locus in conjunction with only one of the B allelic types. Both conditions are met if one postulates a third locus, linked to locus B, the products of which interact with those of locus A such that particular combinations produce decreased viability in the development of the megagametophyte. This, the simplest hypothesis to explain the patterns of inheritance in Virginia pine, cannot be accepted or rejected without further experimentation.

The presence of lethal and semi-lethal recessive alleles has long been hypothesized to partially explain the large percentage of empty seed in the seed crop of pines (e.g. Sarvas, 1962). Johnsson (1967) was able to demonstrate that empty seed does have a strong, though unspecified, genetic component by using controlled crosses of the tester, partial diallele and complete diallele designs. Based on results from the reciprocal crosses he postulated the presence of lethal alleles affecting the development of both the female gametophyte and the embryo.

The GOT system described here is a potential example of a specific semi-lethal allelic system in which specific, as yet nonpredictable, genotypes have reduced viability in the development of a mature megagametophyte from a megaspore.

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Simulation of populations with fluctuating fitness values. Two-locus case

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Summary

The effect of fluctuating fitness values on the genotypic composition of two-locus populations is investigated in this paper. A comparison to the results of one-locus populations is attempted. The interaction of epistasis and recombination is studied in more detail. Selection pressures are assumed to fluctuate independently, neither with autocorrelation between genotypes nor between generations. Whereas the expectation of fitnesses follow simple additive or multiplicative selection schemes, actual values of genotypic fitness in any generation do not exhibit a simple relationship. This is due to independent fluctuations of selection intensities. The following results are obtained.

1) Fluctuating fitness values introduce less amounts of fluctuations of zygote frequencies in two-locus populations as compared to one-locus populations.

2) Recombination fractions may be assigned in their effect to three regions. In the first region with no or loose linkage, gene frequencies fluctuate independently and account completely for the fluctuations of gamete frequencies. In the second region with intermediate recombination, there are additional fluctuations of linkage disequilibrium resulting in increased fluctuations of gamete frequencies. In the third region with tight linkage, only fluctuations of gene frequencies are left. Fluctuations of gamete frequencies are consequently reduced again. It is not possible to demonstrate a systematic effect of recombination on gene frequency fluctuations. Range and location of the different regions of recombination fractions are determined by the amount of conditional epistasis present in the selection scheme applied.

The results are discussed with respect to the evolutionary advantage of recombination.

Key words: Simulation, fluctuating fitness, two-locus model, linkage disequilibrium, recombination, epistasis.

Zusammenfassung

In der vorliegenden Arbeit wurde der Einfluß fluktuierender Fitnesswerte auf die genotypische Zusammensetzung digener Populationen untersucht. Ein Vergleich mit den Ergebnissen monogener Populationen wurde angestrebt, Wechselwirkungen zwischen Epistasie und Rekombination näher untersucht. Die Fluktuationen der Selektionskräfte wurden als unabhängig angesehen, d. h. ohne Autokorrelation zwischen Genotypen und zwischen Generationen. Während die Erwartungswerte der Fitness einfachen additiven oder multiplikativen Selektionsmustern folgen, sind die aktuellen Werte der genotypischen Fitness als Folge der unabhängigen Fluktuationen der Selektionswerte in keiner Generation nach einer einfachen Beziehung zusammengesetzt. Im einzelnen wurden die folgenden Ergebnisse erhalten.

1) In digenen Populationen sind die Fluktuationen der Zygotenfrequenzen, die durch variable Fitnesswerte induziert werden, kleiner als in monogenen Populationen.

2) Die Rekombinationsfrequenzen können ihrem Einfluß nach drei Regionen zugeordnet werden. In der ersten Re-

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