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Host effects on the genetic structure of mountain pine beetle, Dendroctonus ponderosae, populations[1]

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Abstract

To evaluate the effects of host tree species and phloem thickness on the genetic structure of mountain pine beetle populations, electrophoretic analyses were conducted on beetles from both lodgepole pine and ponderosa pine from a single stand in northeastern Utah. Stratification of the population by host tree species accounted for a significant portion of the differences among beetles. Beetles from ponderosa pine were more genetically diverse than those from lodgepole pine. Males were, in general, more genetically diverse than females. Male mountain pine beetles also varied more from tree to tree than did females. Beetles in thin-phloem lodgepole pine were more diverse than beetles in thick-phloem lodgepole pine. Males were more diverse than females in all thin-phloem lodgepole pine but not in thick-phloem lodgepole pine. We suggest direct relationship between levels of stress and genetic diversity in mountain pine beetles. Monitoring shifts in genetic diversity in a mountain pine beetle population from year to year might permit estimation of levels of stress being encountered by the population and could aid prediction of population levels in subsequent years.

Résumé

Afin d'évaluer les effets des essences hôtes et de l'épaisseur du phloème sur la structure génétique des populations du dendroctone du pin ponderosa, on a analysé, par électrophorèse, des dendroctones capturés sur des pins tordus et des pins ponderosa dans un peuplement du nord-est de l'Utah. La stratification de la population selon l'essence expliquait de façon significative les différences observées parmi les dendroctones dans le peuplement. Ceux des pins ponderosas étaient génétiquement plus diversifiés que ceux des pins tordus. Les mâles étaient en général plus diversifiés que les femelles. Les mâles variaient aussi plus d'un arbre à l'autre que les femelles. Les dendroctones capturés sur des pins tordus à phloème mince variaient aussi plus que ceux des pins tordus à phloème épais. Les mâles

étaient plus diversifiés que les femelles, dans le cas de tous les pins tordus à phloème mince, mais non dans le cas des pins tordus à phloème épais. Une corrélation directe entre les contraintes subies par les dendroctones et leur diversité génétique est proposée. En contrôlant les fluctuations de la diversité génétique d'une population de dendroctones du pin ponderosa, d'une année à l'autre, on pourrait estimer les contraintes subies par cette population et prévoir les taux d'augmentation ou de diminution des effectifs dans les années ultérieures.

Introduction

Electrophoretic studies of isoenzymes in mountain pine beetles suggest that environmental variables affect genetic differentiation of beetles both among and within sites. A few years ago, we made a preliminary study of genetic relationships among four mountain pine beetle populations in northeastern Utah (Stock and Amman 1980). Results of the preiminary study indicated that genetic differentiation of local mountain pine beetle groups is more closely related to host tree species than to geographic distance among sites. The greatest differences were found between beetles from ponderosa pine and lodgepole pine, not between populations farthest apart. That study also suggested that male mountain pine beetles varied more among sites than did females, and that beetles from ponderosa pine were more variable than those from lodgepole pine.

More recently, we focused on an epidemic of mountain pine beetles infesting both ponderosa pine and lodgepole pine in a single stand in Utah. Because of the close link between genotype and environment, we believed that this approach would provide useful information and raise new questions about the interactions of mountain pine beetles with their host trees.

Host tree species can influence survival and, consequently, the genetic makeup of invading beetles (e.g., Sturgeon 1980). Smith (1963, 1965) demonstrated that monoterpene vapors from pine oleoresin can be toxic to invading bark beetles and that beetles tend to be most tolerant of vapors of their natural hosts. Our work (Stock and Amman 1980) also suggested that genetic differentiation of beetles between sites was related, at least in part, to host species. Therefore, one objective of this study was to determine if genetic differentiation occurs among mountain pine beetles within a single stand and, if so, if this differentiation is related to host tree species.

Our second point of investigation was the effect of phloem thickness on the genetic structure of the beetle population. We had noted in our preliminary study that male mountain pine beetles were more variable from site to site than were females. This occurrence is believed to be related to the males' greater vulnerability to conditions of cold, drought, and crowding (Amman and Pace 1976). Trees with thin phloem are considered less suitable, i.e., more stressful, hosts for mountain pine beetle because they provide less food and less space for brood production. Number of emerging males varied more from tree to tree than number of emerging females in both thick and thin-phloem lodgepole pine, also suggesting that males are more sensitive to individual tree differences. However, number of

emerging males was significantly more variable in thin-phloem trees than thick-phloem trees. The coefficient of variation (100 s/$\bar{x}$) of beetles emerging per square foot of lodgepole pine bark surface was 54 for females in both thick and thin phloem, but 90 for males from thick phloem and 148 for males from thin phloem (calculated from data used by Amman and Pace (1976)). We therefore expected that genetic comparisons of males and females in individual trees and between trees of different phloem thickness might give us clues as to the effect of this variable on the beetle population. Thus, our next objectives were to determine if genetic differences occur between male and female mountain pine beetles from individual trees in a stand; if males vary more from tree to tree than females; and if genetic differences occur between mountain pine beetles reared in thick and thin phloem.

Methods

In summer 1980, mountain pine beetles were sampled at a site in the Ashley National Forest in northeastern Utah (fig. 1). The stand was located at 7500 ft (2286 m) elevation and was about 75% lodgepole pine and 25% ponderosa pine, with a few Douglas-fir, subalpine fir, and aspen. At higher elevations, the forest was almost pure lodgepole pine and, at lower elevations, almost pure ponderosa pine. The beetle population in this area started to increase around 1976 and reached epidemic levels in 1980. By 1982, 44% of the lodgepole pine and 15% of the ponderosa pine had been killed, and a large number of freshly infested trees suggested that the infestation would continue for several more years.

A total of eight beetle-infested lodgepole pine trees (four thick-phloem, four thin-phloem), and five ponderosa pine (three thick-phloem, two thin-phloem) were felled and cut into billets. Thick-phloem trees had phloem more than 2.2 mm thick; thin-phloem trees had phloem less than 1.8 mm thick. The billets were stored in the Ogden laboratory for two months at 3°C, and then transferred to individual cages at 21-24°C. Emerging adult beetles were collected daily, sexed using the technique described by Lyon (1958), and placed in ventilated petri dishes with moist sawdust for mailing to the University of Idaho for electrophoretic analysis.

Nearly 900 beetles in a stratified series of samples were thus obtained for comparison of males and females from lodgepole pine and ponderosa pine, and from trees of differing phloem thickness (fig. 2). The genetic makeup of these samples was assessed using techniques of starch gel electrophoresis to identify enzymes produced by different alleles at multiple gene loci. Methods for electrophoresis of mountain pine beetles are described by Higby and Stock (1982). Genotype frequencies at individual loci were compared, within samples, to Hardy-Weinberg (random mating) expectations and, between samples, using a contingency chi-square test. Levels of overall genetic diversity were estimated and compared using Nei's (1975) average heterozygosity.

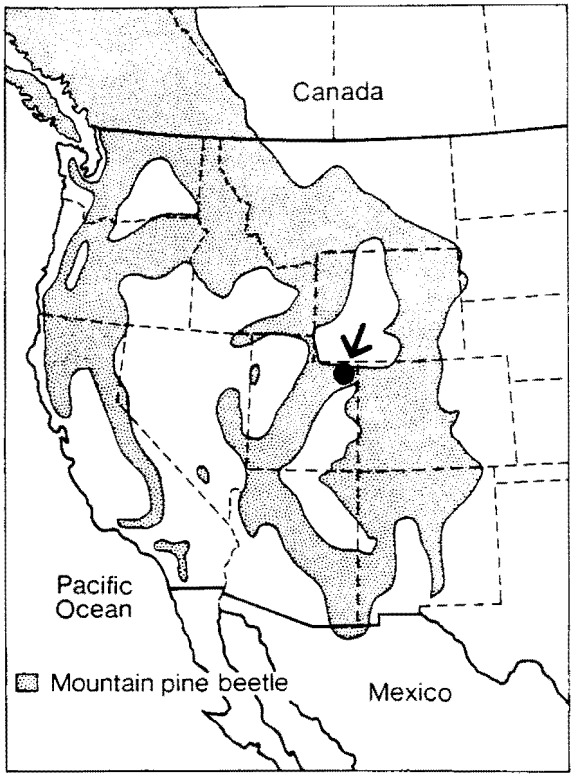

Fig. 1. Location of study site in northeastern Utah.

Results and discussion

Of the 17 gene loci examined, six (AAT1, AcP, EST1, LAP2, PEP and PGI) were polymorphic, i.e., the frequency of the common allozyme at the locus was less than 0.98 in at least one group, and 11 (CK, AGP1, AGP2, AGP3, EST2, EST3, IDH, LAP1, MDH1, MDH2, and TO) were monomorphic.

Genetic differentiation did occur among mountain pine beetles within the stand and this differentiation was related to host tree species. Stratification of the population by host tree species accounts for a significant portion of the differences among beetles in the stand. When data from all beetles at the Ashley site were pooled, proportions of genotypes deviated significantly from random-mating expectations (Table I). At several polymorphic loci, there was a much greater than expected number of homozygotes and a deficiency of heterozygotes, evidence that genetically different groups had been pooled. Separate analysis of beetles from lodgepole pine and ponderosa pine resulted in genotype proportions much closer

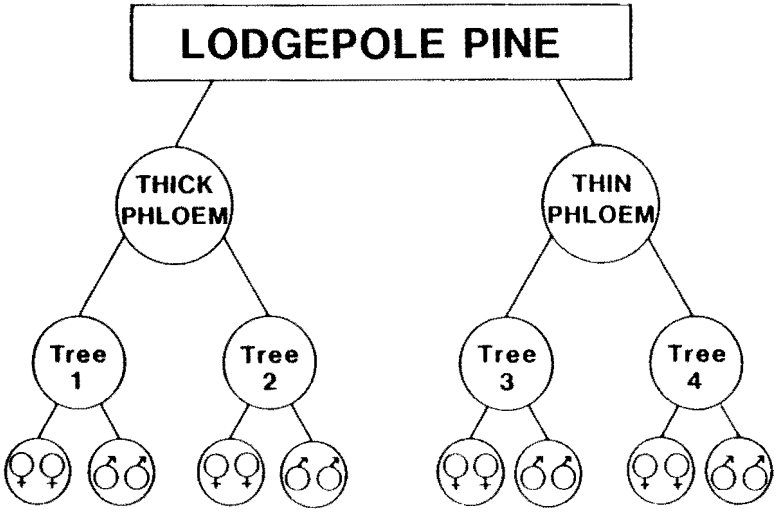

Fig. 2. Sampling scheme for mountain pine beetles used in this study. An identical scheme was used for beetles from ponderosa pine at the site.

to those expected within a randomly mating population.

Beetles from ponderosa pine were more genetically diverse than those from lodgepole pine (13.1% compared to 12.6% average heterozygosity, Table I). This difference is consistent with earlier work. Three mountain pine beetle populations from lodgepole pine in this same geographic area had an average heterozygosity of 11.5 to 12.4%, while a group from ponderosa pine at the same site had an average heterozygosity of 13.3% (Stock and Amman 1980). Similar calculations with Sturgeon's (1980) data for Colorado mountain pine beetles give an average heterozygosity of 12.3% for beetles from lodgepole pine and 13.5% for beetles from ponderosa pine.

Our results also show that there are genetic differences between male and female mountain pine beetles from individual trees in the stand. In 13 of 65 (20%) locus-by-locus comparisons of male and female beetles in both lodgepole pine and ponderosa pine, males were significantly different from females (Tables II and III). In most of these cases, males were more genetically diverse than females and, over all loci, males were slightly more genetically diverse than females (12.3% compared to 12.0% average heterozygosity).

Males vary more from tree to tree than females. At two of the six polymorphic loci (AAT1 and AcP), males varied much more from tree to tree than did females. At AAT1, the range of frequency of the common allele was .29 to .83 for males and .55 to .71 for females. At the AcP locus, the range of frequency of the common allele was .43 to .83 for males and .60 to .79 for females. Little or no dif-

Table I. Allele frequencies at six polymorphic loci for all beetles collected at the Ashley National Forest site, and for separate collections from lodgepole pine and ponderosa pine. Hardy-Weinberg chi-square values for each data set (HW) and contingency chi-square values (Cont) for comparison of beetles in lodgepole and ponderosa pine are also shown. (* = p < .05, ** = p < .01)

Enzyme	Allele	All beetles	Lodgepole pine only		Ponderosa pine only
AAT1	1	.62	.61		.63
	2	.38	.39		.37
	N	706	543		163
	HW	7.4**	2.8		.1
	Cont			1.65	
AcP	0	—	—		.01
	1	.65	.64		.67
	2	.35	.36		.32
	N	722	540		182
	HW	.1	0		.2
	Cont			10.5**	
EST1	1	.01	.01		.01
	2	.40	.41		.39
	3	.24	.23		.24
	4	.12	.13		.10
	5	.23	.22		.24
	6	.01	—		.01
	N	868	586		282
	HW	20.5	9.5		5.6
	Cont			4.8	
LAP2	1	.05	.05		.06
	2	.69	.74		.60
	3	.26	.21		.34
	N	586	348		238
	HW	24.6**	14.4*		9.9*
	Cont			26.9**	
PEP	1	.97	.97		.97
	2	.03	.03		.03
	N	864	584		280
	HW	4.7	1.9		3.3
	Cont			0	
PGI	1	.99	.99		1.0
	2	.01	.01		—
	N	887	598		289
	HW	5.3*	2.0		0
	Cont			2.3	
Average heterozygosity (%)		12.6			13.1

Table II. Allele frequencies at six polymorphic loci for males (M) and females (F) from individual lodgepole pine trees at the Ashley National site. Eleven additional loci were monomorphic. Hardy-Weinberg chi-square values (HW), contingency chi-square values (Cont) for comparison of males and females, and average heterozygosity for each sample are also shown. (* = p < .05, ** = p < .01)

		Lodgepole pine (thick phloem)									
Enzyme	Allele	1		2		3		4		Total	
		F	M	F	M	F	M	F	M	F	M
AAT1	1	.68	.69	.61	.61	.63	.66	.57	.62	.62	.63
	2	.32	.31	.39	.39	.37	.34	.43	.38	.38	.37
	N	60	37	48	44	53	46	49	49	213	176
	HW	.1	1.2	.3	.1	1.2	.1	.3	.4	2.0	.3
	Cont	0		0		.2		.5		.1	
AcP	0	—	—	—	.01	—	—	—	—	—	—
	1	.67	.69	.65	.63	.68	.69	.60	.56	.65	.66
	2	.33	.31	.35	.36	.32	.31	.40	.44	.35	.34
	3	—	—	—	—	—	—	—	—	—	—
	H	63	44	48	45	54	45	54	39	220	171
	HW	.3	1.7	3.7	1.4	1.1	3.4	.1	5.4*	2.1	4.1*
	Cont	.2		1.1		0		.3		1.5	
EST 1	1	.02	—	.02	.01	.02	.01	—	.01	.01	.01
	2	.45	.37	.30	.48	.45	.42	.42	.37	.42	.41
	3	.21	.26	.26	.25	.20	.21	.20	.34	.22	.26
	4	.14	.16	.16	.06	.13	.18	.12	.11	.13	.13
	5	.18	.21	.27	.21	.20	.17	.26	.17	.21	.19
	6	—	—	—	—	—	.01	—	.01	—	—
	N	64	49	47	51	52	50	58	52	218	202
	HW	7.6	15.9*	4.8	6.4	2.3	5.8	1.8	2.4	22.6*	5.8
	Cont	3.5		10.0*		2.0		8.6*		5.6	
LAP2	1	—	.08	.01	—	.02	.15	.02	—	.01	.05
	2	.83	.77	.90	1.0	.80	.75	.80	.92	.83	.86
	3	.17	.15	.09	—	.19	.10	.17	.08	.15	.09
	N	39	13	40	10	32	10	43	18	154	51
	HW	.4	.4	0	0	.3	.1	.7	0	4.5	.3
	Cont	6.1*		2.2		6.5*		2.7		6.9*	
PEP	1	.96	.96	1.0	.99	.98	.99	.96	.99	.97	.98
	2	.04	.04	—	.01	.02	.01	.04	.01	.03	.02
	N	64	50	50	50	56	44	59	50	229	195
	HW	0	0	0	0	0	0	.5	0	.9	.1
	Cont	0		1.0		.1		2.1		.1	
PGI	1	.99	1.0	.99	1.0	.99	.98	.99	1.0	.99	.99
	2	.01	—	.01	—	.01	.02	.01	—	.01	.01
	N	64	50	50	50	56	49	60	50	230	199
	HW	0	0	0	0	0	0	0	0	0	0
	Cont	0		0		.0		0		0	
Average heterozygosity (%)		11.5	12.0	11.0	9.6	11.7	12.1	12.3	10.8	11.8	11.4

Table II. (Cont'd)

Enzyme	Allele	Lodgepole pine (thin phloem)									
		5		6		7		8		Total	
		F	M	F	M	F	M	F	M	F	M
AAT1	1	.55	.71	.63	.52	.60	.61	.63	.60	.60	.58
	2	.45	.29	.37	.48	.40	.39	.37	.40	.40	.42
	N	20	7	27	27	20	18	20	15	87	67
	HW	0	.1	.3	1.8	0	.1	.8	.3	0	1.3
	Cont	1.2		1.4		0		0		.1	
AcP	0	—	—	—	—	—	—	—	—	—	—
	1	.79	.50	.65	.68	.68	.74	.74	.55	.71	.66
	2	.21	.50	.35	.32	.32	.26	.26	.45	.29	.34
	3	—	—	—	—	—	—	—	—	—	—
	H	17	5	24	30	19	19	17	10	77	64
	HW	1.4	0	0	6.3*	.4	.3	0	1.1	.1	7.1**
	Cont	6.0*		1.0		.7		2.5		1.1	
EST 1	1	—	—	—	.03	—	—	.03	.03	.01	.02
	2	.26	.43	.52	.30	.40	.50	.60	.26	.46	.36
	3	.29	.29	.21	.25	.20	.23	.07	.18	.19	.23
	4	.13	.14	.08	.17	.15	.08	.08	.18	.11	.14
	5	.32	.14	.19	.22	.25	.20	.23	.34	.24	.24
	6	—	—	—	.03	—	—	—	—	—	.01
	N	19	7	31	30	20	20	20	19	90	76
	HW	.5	0	.3	1.6	.5	1.3	0	.8	4.2	1.8
	Cont	2.1		9.8		1.7		9.6*		7.3*	
LAP2	1	.04	—	.37	.05	—	.08	.05	.03	.13	.05
	2	.39	.71	.47	.57	.79	.50	.80	.63	.62	.58
	3	.57	.29	.16	.38	.21	.43	.15	.34	.25	.37
	N	14	7	19	29	12	20	20	19	65	75
	HW	.2	.1	2.7	.2	.3	.1	.3	0	5.4	1.0
	Cont	7.7*		17.3**		5.9		4.0		9.0*	
PEP	1	.98	.93	.98	.95	1.0	.90	.95	.88	.98	.92
	2	.02.	.07	.02	.05	—	.10	.05	.12	.02	.08
	N	20	7	23	30	20	20	20	20	83	77
	HW	0	0	0	0	0	.7	0	.6	.5	1.7
	Cont	.6		.6		4.2*		1.4		5.8	
PGI	1	1.0	1.0	1.0	1.0	.98	1.0	1.0	1.0	.99	1.0
	2	—	—	—	—	.02	—	—	—	.01	—
	N	20	7	33	30	20	20	20	20	93	77
	HW	0	0	0	0	0	0	0	0	0	0
	Cont	0		0		0		0		0	
Average heterozygosity (%)		12.4	12.6	13.0	13.7	11.8	13.2	10.9	14.2	12.8	13.8

Table III. Allele frequencies at six polymorphic loci for males (M) and females (F) from individual ponderosa pine trees at the Ashley National Forest site. Eleven additional loci were monomorphic. Hardy-Weinberg chi-square values (HW), contingency chi-square values (Cont) for comparison of males and females, and average heterozygosity for each sample are also shown. (* = p < .05, ** = p < .01)

		Ponderosa pine (thick phloem)								Ponderosa pine (thin phloem)					
Enzyme	Allele	1		2		3		Total		4		5		Total	
		F	M	F	M	F	M	F	M	F	M	F	M	F	M
AAT1	1	.71	.58	.62	.83	.55	.73	.62	.71	.63	.72	.62	.46	.62	.62
	2	.29	.42	.38	.17	.45	.27	.38	.29	.38	.28	.38	.54	.38	.38
	N	24	6	21	3	33	22	78	31	8	18	13	12	21	30
	HW	.6	0	.8	0	.3	.1	.1	.1	1.7	1.8	0	.2	.9	4.0*
	Cont	.7		1.0		3.7		1.7		.5		1.2		0	
AcP	0	—	—	—	—	.02	—	.01	—	—	.04	—	—	—	.02
	1	.77	.43	.71	.83	.70	.68	.73	.63	.76	.52	.65	.67	.72	.57
	2	.23	.57	.29	.17	.25	.33	.25	.37	.24	.44	.35	.33	.28	.40
	3	—	—	—	—	.03	—	.01	—	—	—	—	—	—	—
	N	24	7	21	3	32	20	77	30	19	27	13	15	32	42
	HW	.8	.1	.1	0	0	.6	.5	.7	.7	3.4	.2	.1	.1	3.4
	Cont	6.0*		.4		2.4		3.7		6.2*		0		4.3	
EST1	1	.02	.07	.03	—	—	—	.01	.02	—	.03	—	—	—	.02
	2	.41	.57	.50	.50	.33	.30	.40	.38	.28	.33	.41	.41	.34	.37
	3	.15	.07	.13	—	.37	.09	.24	.08	.32	.37	.21	.25	.27	.31
	4	.11	—	.13	.17	.14	.20	.13	.16	.12	.05	.07	.05	.09	.05
	5	.30	.29	.23	.33	.14	.39	.21	.36	.23	.22	.30	.29	.27	.25
	6	—	—	—	—	.01	.02	.01	.02	.05	—	—	—	.03	—
	N	23	7	20	3	35	22	78	32	30	30	28	28	58	58
	HW	0	0	.6	0	5.6	2.8	8.9	4.2	1.7	2.5	1.7	1.4	2.1	.6
	Cont	3.4		1.2		15.7**		11.0*		7.1		.3		7.0	
	1	—	—	.13	—	.06	—	.09	—	.07	.02	—	—	.04	.01
	2	—	—	.69	—	.63	—	.66	—	.64	.57	.46	.74	.56	.65
	3	—	—	.19	—	.31	—	.25	—	.29	.41	.54	.26	.40	.34
	N	—	—	8	—	8	—	16	—	28	23	24	21	52	44
	HW	—	—	.2	—	1.6	—	2.0	—	0	0	2.6	.1	3.3	0
	Cont	—		—		—		—		2.7		7.2*		2.5	
PEP	1	.98	.86	.98	.67	.96	.96	.97	.91	.97	1.0	1.0	1.0	.98	1.0
	2	.02	.14	.02	.33	.04	.04	.03	.09	.03	—	—	—	.02	—
	N	24	7	21	3	35	23	80	33	30	30	30	30	60	60
	HW	0	.1	0	0	0	0	0	.4	0	0	0	0	0	0
	Cont	3.5		8.6*		0		3.6		2.0		0		2.0	
PGI	1	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	N	24	7	21	3	35	23	80	33	30	30	30	30	60	60
Average heterozygosity (%)		—		—		12.1		—		13.1		—		12.6	
		—		12.6		12.6		12.9		11.8		12.7		12.6	

ferences were seen at the other four loci.

Beetles from thin-phloem lodgepole pine were more diverse (13.2% average heterozygosity) than beetles from thick-phloem lodgepole pine (11.5% average heterozygosity) (Table IV). Males were more diverse than females in all thin-phloem lodgepole pine, but not in thick-phloem lodgepole pine (Tables II and III). No similar differences in average heterozygosity were seen in beetles from ponderosa pine.

We had expected that males would vary more from tree to tree than would females, since male mountain pine beetles are more sensitive to microenvironmental variation. The ratio of males to females emerged per unit area of lodgepole pine bark surface was 1:2 from thick phloem and 1:3 from thin phloem. These ratios suggest that thin-phloem conditions are, indeed, more stressful to the developing beetles. The greater genetic diversity observed among mountain pine beetles, especially the males, reared in thin-phloem lodgepole pine suggests that an *increase* in genetic diversity resulted from stress. Many years ago, Ford and Ford (1930) postulated the reverse—that genetic diversity increases when selection pressures relax and permit a greater diversity of genotypes to survive. Conversely, they suggested that increased selection pressures, such as those precipitating a population decline, would result in decreased genetic diversity. Ford and Ford's ideas were based on a study of phenotypic variation in a butterfly population over a period of 55 years. Field workers in British Columbia, however, observed phenotypic variation to increase during the 1976 population crash of Douglas-fir tussock moth; at that time, an unusually high number of previously rare pale forms of larvae were seen (Rod Carrow, personal communication).

There are several possible mechanisms whereby genetic diversity may increase with stress. The relationship between environmental heterogeneity and species or population heterogeneity is well-documented (e.g., MacArthur 1972). Less uniformity in the environment of beetles in thin phloem could result in a more heterogeneous beetle population. Also, the advantage of heterozygosity (heterosis) may be expressed more readily under severe environmental conditions (e.g., Smith *et al.* 1975). Finally, extreme stresses may activate previously unexpressed gene forms (e.g., Schlesinger *et al.* 1982).

From a more practical standpoint, the apparently direct relationship between stress on mountain pine beetles and genetic diversity might be used to advantage by forest managers. Shifts in genetic diversity in a population from year to year might permit estimation of levels of stress being encountered by the population and could aid prediction of population levels in subsequent years.

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Table IV. Allele frequencies at six polymorphic loci for mountain pine beetles in individual lodgepole pine (LPP) and ponderosa pine (PP) trees at the Ashley National Forest site. Hardy-Weinberg chi-square values (HW) and average heterozygosity are also shown for each sample. (* = p < .05, ** = p < .01)

		LPP (thick phloem)					LPP (thin phloem)					PP (thick phloem)				PP (thin phloem)		
Enzyme	Allele	1	2	3	4	Total	5	6	7	8	Total	1	2	3	Total	4	5	Total
AAT1	1	.68	.61	.64	.60	.62	.59	.57	.61	.61	.59	.68	.65	.62	.64	.69	.54	.62
	2	.32	.39	.36	.40	.38	.41	.43	.39	.39	.41	.32	.35	.38	.36	.31	.46	.38
	N	97	92	99	98	389	27	54	38	35	154	30	24	55	109	26	25	51
	HW	.3	0	.4	.8	1.9	.2	.5	0	1.6	.8	.7	.4	0	0	.1	.3	.8
AcP	0	—	—	—	—	—	—	—	—	—	—	—	—	.01	—	.02	—	.01
	1	.68	.64	.68	.59	.65	.73	.67	.71	.67	.69	.69	.73	.69	.70	.62	.66	.64
	2	.32	.36	.32	.41	.35	.27	.33	.29	.33	.31	.31	.27	.28	.29	.36	.34	.35
	3	—	—	—	—	—	—	—	—	—	—	—	—	.02	.01	—	—	—
	N	107	92	99	93	390	22	54	38	27	141	31	24	51	106	46	28	74
	HW	.2	4.8*	2.0	3.1	.1	1.0	3.4	0	.4	4.3*	.3	0	.8	.8	1.4	.4	1.8
EST1	1	.01	.02	.01	—	.01	—	.02	—	.03	.01	.03	.02	—	.01	.02	—	.01
	2	.42	.39	.44	.40	.41	.31	.41	.45	.44	.41	.45	.50	.32	.39	.31	.41	.36
	3	.23	.25	.21	.26	.24	.29	.23	.21	.13	.21	.13	.11	.26	.20	.34	.23	.29
	4	.15	.11	.15	.11	.13	.13	.12	.11	.13	.12	.08	.13	.17	.14	.08	.06	.07
	5	.19	.23	.19	.22	.21	.27	.20	.23	.28	.24	.30	.24	.24	.25	.23	.29	.26
	6	—	.01	—	—	—	—	.02	—	—	.01	—	—	.02	.01	.03	—	.01
	N	113	98	102	110	420	26	61	40	39	166	30	23	57	110	60	56	116
	HW	11.0	8.1	9.4	2.7	14.7	.7	3.3	2.0	3.5	3.4	.1	.7	9.9	11.1	5.5	4.7	3.8
LAP2	1	.02	.01	.05	.02	.02	.02	.18	.05	.04	.09	—	.13	.06	.09	.05	—	.03
	2	.82	.92	.79	.84	.84	.50	.53	.61	.72	.60	—	.69	.63	.66	.61	.59	.60
	3	.16	.07	.17	.15	.14	.48	.29	.34	.24	.32	—	.19	.31	.25	.34	.41	.38
	N	52	50	42	61	205	21	48	32	39	140	—	8	8	16	51	45	96
	HW	0	0	.3	.8	3.7	.2	7.5	.9	0	7.2	—	.2	1.6	2.0	.2	2.2	1.7

(Cont'd)

Table IV. Cont'd

Enzyme	Allele	LPP (thick phloem) 1	2	3	4	Total	LPP (thin phloem) 5	6	7	8	Total	PP (thick phloem) 1	2	3	Total	PP (thin phloem) 4	5	Total
PEP	1	.96	.99	.99	.97	.98	.96	.96	.95	.91	.95	.95	.94	.96	.95	.98	1.0	.99
	2	.04	.01	.01	.03	.02	.04	.04	.05	.09	.05	.05	.06	.04	.05	.02	—	.01
	N	114	100	100	109	424	27	53	40	40	160	31	24	58	113	60	60	120
	HW	0	0	.2	.9	0	0	1.1	.9	2.0	2.6	0	0	.1	.3	0	0	0
PGI	1	1.0	.99	.98	1.0	.99	1.0	1.0	.99	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
	2	—	.01	.02	—	.01	—	—	.01	—	—	—	—	—	—	—	—	—
	N	114	100	105	110	429	27	63	40	40	170	31	24	58	113	60	60	120
	HW	0	0	.3	0	.7	0	0	0	0	0	0	0	0	0	0	0	0
Average heterozygosity (%)		11.5	10.8	11.8	11.8	11.5	13.0	13.7	12.9	12.9	13.2	12.3	13.1	12.9	12.9	12.9	12.5	12.7

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