Genetic Differentiation Among Mountain Pine Beetle Populations from Lodgepole Pine and Ponderosa Pine in Northeast Utah[1]

M. W. STOCK AND G. D. AMMAN

Department of Forest Resources, University of Idaho, Moscow, Idaho 83843

and

U.S. Forest Service, Intermountain Forest and Range Expt. Station, Ogden, Utah 84401

ABSTRACT

Ann. Entomol. Soc. Am. 73: 472–478 (1980)

Isozyme comparisons were made among mountain pine beetles (*Dendroctonus ponderosae* Hopkins) from 4 sites in NE Utah. Genetic differentiation was more closely associated with host tree species—lodgepole pine (*Pinus contorta* var. *latifolia* Engelmann) vs. ponderosa pine (*P. ponderosa* Lawson)—than with geographic distances among sites. Differences in average heterozygosity and frequencies at certain gene loci may be related to stage in the infestation cycle or environmental stress related to food quantity. Differences were small between males and females at any one site but among sites males showed greater differences than did females. A difference in gene frequencies between early- and late-emerging beetles was found at one site.

Mountain pine beetles (*Dendroctonus ponderosae* Hopkins) show considerable intraspecific variation over their range of distribution in the western U.S. For example, while preferred hosts of this pest include lodgepole pine (*Pinus contorta* Douglas), ponderosa pine (*P. ponderosa* Lawson), western white pine (*P. monticola* Douglas), limber pine (*P. flexilis* James), sugar pine (*P. lambertiana* Douglas), and whitebark pine (*P. albicaulis* Engelmann) (Blackman 1931), local endemic beetle populations in mixed pine stands may prefer to attack only one pine species (Baker et al. 1971, Craighead 1921, Hopkins 1916, Wood 1963). Within a single host species, beetles may show differences in tree diameter preference (Amman 1977, Cole and Amman 1969, McCambridge 1967, Sartwell and Stevens 1975, Stark et al. 1968). In stands of different host species, beetles respond differently to steroisomers of host volatiles and beetle-produced pheromones (McKnight 1979). Effective regional management programs for the mountain pine beetle require a fuller understanding of the genetic basis for such differences among beetle subgroups.

Isozyme studies have provided empirical evidence that while geographic isolation between populations may lead to species differentiation (Stock et al. 1978, 1979), factors such as local host plant preferences may also result in differentiation among sympatric insect populations (Bush 1975). Recent work suggests that genetic differentiation among mountain pine beetle populations may be at least partly related to host species preferences; small but significant genetic differences occur between sympatric beetle groups attacking different hosts in mixed stands (Sturgeon 1980). These studies provide a groundwork for more detailed examination of genetic differentiation among mountain pine beetle populations. The purpose of our study was to assess genetic variation associated with host tree species, stage of outbreak, available food (phloem thickness), geographic proximity, and beetle sex. We examined mountain pine beetles from 4 sites in NE Utah. Over the past 25 years, mountain pine beetle epidemics have caused heavy tree losses in lodgepole pine forests of this region. On the N slope of the Uinta Mts. in Utah, where 3 of our collection sites were located, the large beetle infestation in the late 1950s and early 1960s resulted in loss of 36% of lodgepole pines of commercial size at low elevations (Amman et al. 1973). Since then, beetle populations have been at low levels in the Uinta Mts. except for a few localized epidemic infestations.

Methods

Site Selection

Mountain pine beetle collection sites (Fig. 1) were selected to represent areas of differing host tree species, geographic proximity, and infestation status. Beetles from Logan Canyon, Bear River, and Hoop Lake were collected from lodgepole pine; beetles from Ashley were collected from ponderosa pine. The Logan Canyon site was located about 60 km N of Logan, Utah, in a stand of lodgepole pines isolated from surrounding lodgepole stands by sagebrush flats and by stands of aspen, Douglas-fir, and subalpine fir. The Bear River and Hoop Lake sites were located in a continuous lodgepole pine forest on the N slope of the Uinta Mts., approximately 65 km apart from one another. Bear River was 145 km from the Logan Canyon site. Some limber pine, another mountain pine beetle host, occurred between the two areas but approximately 75 km distant from the Bear River infestation. The Ashley plot was about 62 km E of Hoop Lake in the extreme NE corner of Utah. There the continuous lodgepole pine forests of the N slope of the Uinta Mts. are replaced by ponderosa pines.

The Logan Canyon population was classified as a low level epidemic. Mountain pine beetle epidemics were reported in this area in the early 1960s. (Washburn

[1] Work leading to this publication was funded by the U.S. Forest Service on a cooperative agreement between the Intermountain Forest and Range Experiment Station, Ogden, Utah, and the University of Idaho, Moscow. Received for publication March 7, 1980.

[2] Washburn, R. I. 1961. Bark beetle conditions in the coniferous forests of Forest Service Region 4. USDA Forest Service, Division of Timber Mgmt., Branch of Forest Insect and Disease Prevention and Control, Ogden, Utah. 20 pp mimeographed.

[3] Washburn, R. I. 1964. Black Hills beetle conditions, Forest Service Region 4. USDA Forest Service, Division of Timber Mgmt., Ogden, Utah. 23 pp. mimeographed.

[4] Washburn, R. I. 1957. Mountain pine beetle infestations, Wasatch National Forest Utah Appraisal Survey. USDA Forest Service, Division of Forest Insect Research, 4 pp mimeographed.

0013-8746/80/0404-7207$00.75/0

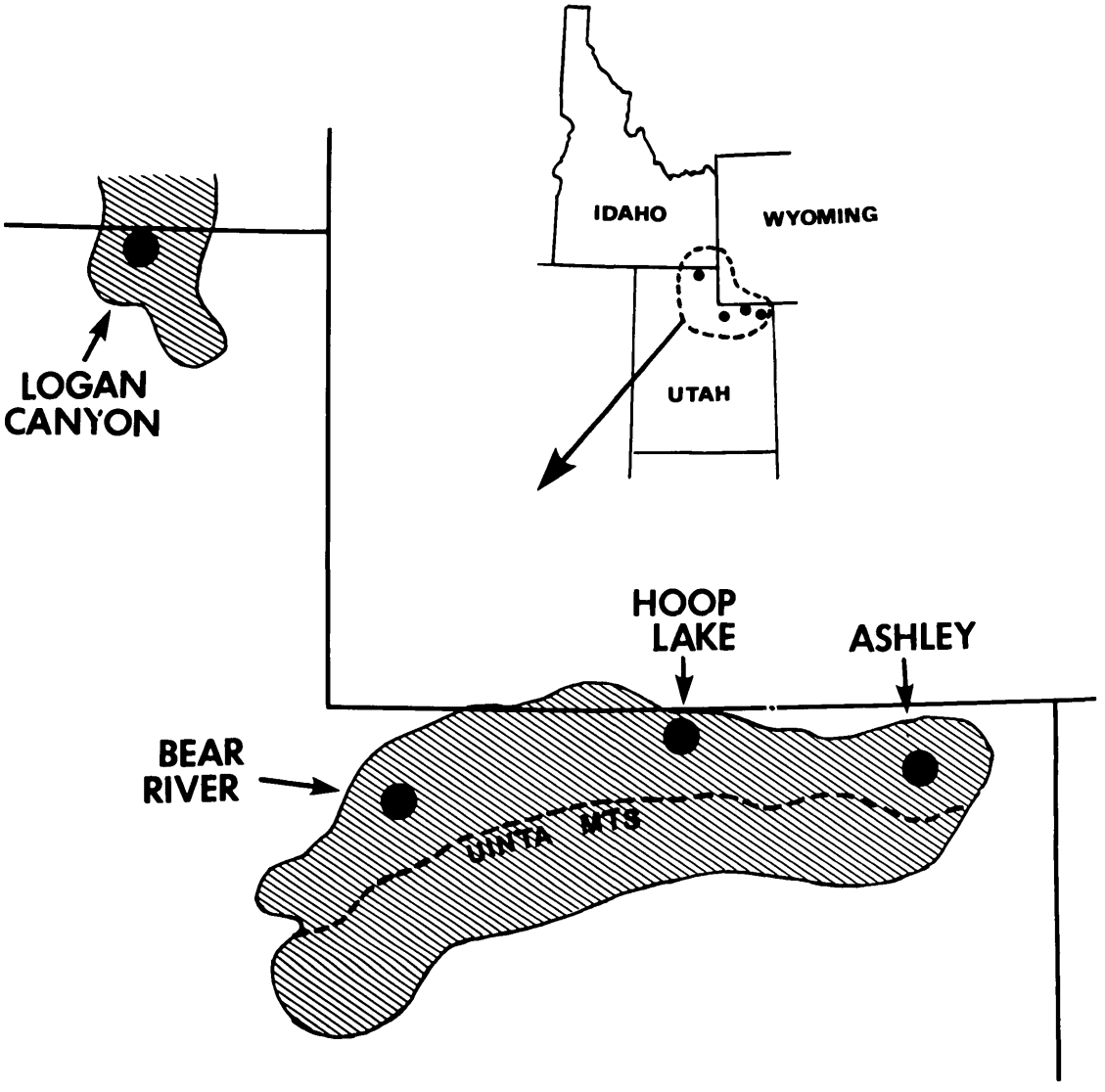

FIG. 1.—Sites where mountain pine beetles were obtained for this study. Shaded regions show the range of lodgepole pine over the area. Ponderosa pine is found in the Ashley area and along the south slope of the Uinta Mts.

1961[2], 1964[3]). Beetles were detected at the study site in 1970. In subsequent years the beetle population remained at a moderate level but the rate of tree killing never reached the high level reported at the other lodgepole pine sites. Most of the remaining large diameter trees (i.e., suitable mountain pine beetle hosts) in the Logan Canyon stand were killed in 1979 so the beetle population is expected to decline within the next year or two.

The Bear River population was similar to the Logan Canyon population in that it has approached the end of the epidemic cycle. Populations were at low levels in this area until 1970, at which time an epidemic developed. Most large diameter trees have now been killed and the beetle population is beginning to decline.

The Hoop Lake population was chosen for its apparent endemic status. This area had a large mountain pine beetle population in 1957 (Washburn 1957[4]) and was part of the extensive infestation that occurred across the Uinta Mts. in the late 1950s and early 1960s. By 1964, most beetle activity in the Hoop Lake area had subsided. A few widely scattered beetle killed trees were noted when this area was visited in 1975 and this low level of tree mortality has continued to the present.

Based on current tree losses, the Ashley population is at a high endemic level. The infestation is in ponderosa pine and is located near Flaming Gorge National Recreation Area. Widely scattered killing of ponderosa pine by the beetles has been reported for this area since 1968 (Baker 1969) with a reported increase in number of trees killed in 1976 (Moyer 1976).

Beetle Collection

Several billets (i.e., short logs) ca 46 cm long were cut from infested ponderosa pine trees at Ashley in November 1978. In June 1979, billets were cut from two infested lodgepole pine trees—one with thin phloem (<2.5 mm) and one with thick phloem (>3.0 mm)—at

the Logan Canyon, Bear River, and Hoop Lake sites. Billets collected in November 1978 were maintained in the Ogden laboratory for two months, then transferred to temperatures of 21–24°C. Billets obtained in June 1979 were placed immediately at 21–24°C. Emerging adult beetles were collected, sexed using the technique described by Lyon (1958), and placed in ventilated plastic petri dishes with moist sawdust for mailing to the University of Idaho for electrophoretic analysis.

Electrophoretic Analysis

Enzyme products of 15 gene loci were examined using starch gel electrophoresis (Fig. 2). A buffer system described by Ridgway et al. (1970) was used to resolve esterase (EST), peptidase (PEP), and leucineaminopeptidase (LAP). For aspartate aminotransferase (AAT), malate dehydrogenase (MDH), phosphoglucose isomerase (PGI), alpha-glycerophosphate dehydrogenase (AGP), and tetrazolium oxidase (TO), a buffer system described by Clayton and Tretiak (1972) was used. In all cases, a migration distance of 6 cm in the anodal direction for a dye marker provided adequate resolution of banding patterns. Staining techniques used were those described by Guenther (1978).

Observed genotype frequencies were compared to values derived from random-mating (Hardy-Weinberg) expectations. Deviations from Hardy-Weinberg expectations provide clues that factors such as inbreeding, linkage, inadequate sample size, the Wahlund effect (pooling of genetically different groups), selection, or the presence of a silent allele may be upsetting the theoretical equilibrium. Contingency chi-square tests, based on the observed numbers of each allele at a single locus, were used to compare gene frequencies among

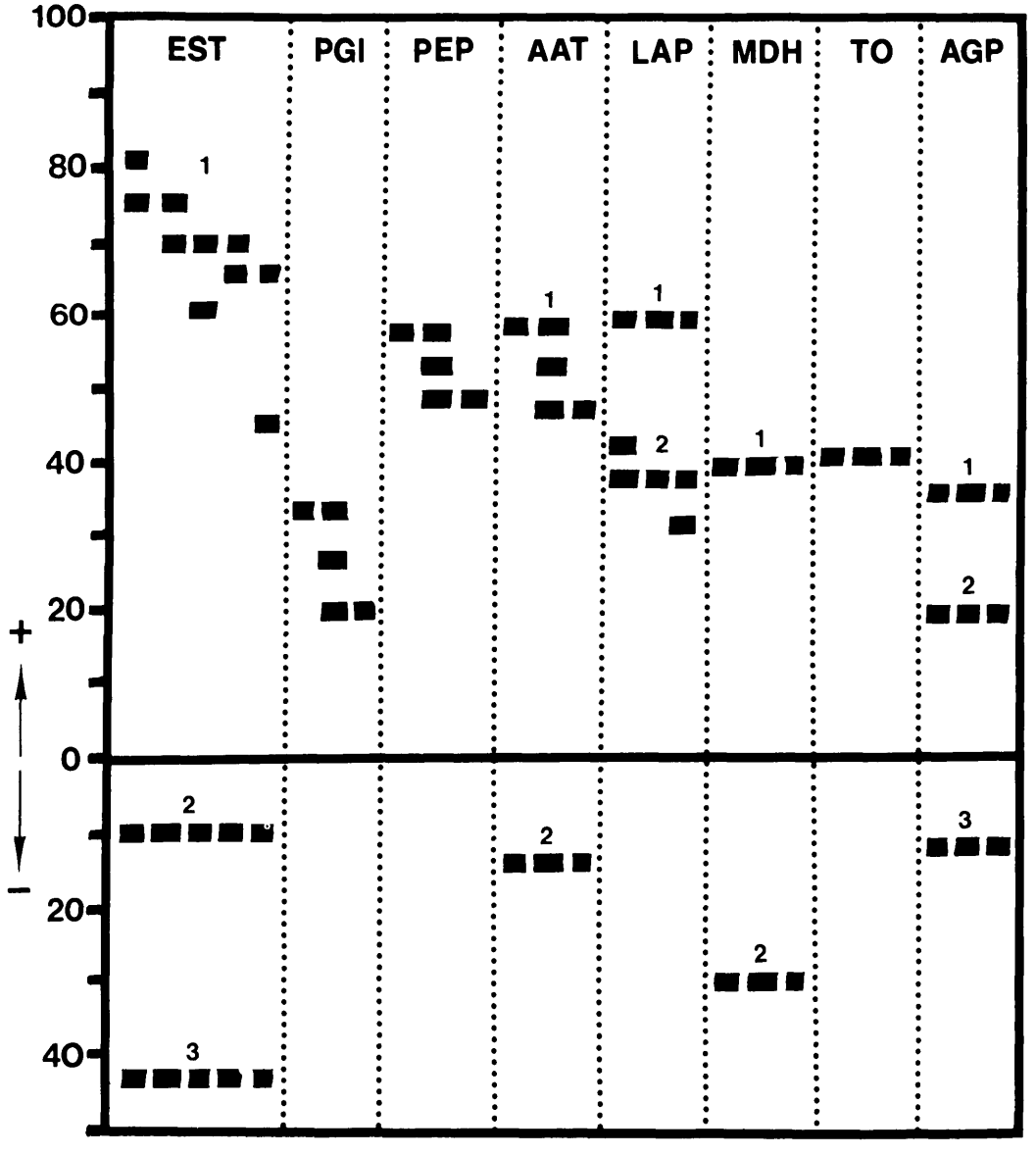

FIG. 2.—Mobilities of mountain pine beetle isozymes relative to the mobility of a red food dye marker (designated as 100). Representative genotypes are shown. When more than one locus was present, loci were numbered in an anodal/cathodal direction.

the sites, between the sexes, etc. To compare overall genetic composition of populations, Nei's (1972) genetic identity and genetic distance values were calculated using data from all loci examined. Two-tailed t-tests were used to determine if differences in average heterozygosity occurred between groups. F-tests were used to compare variances among male and female mountain pine beetles.

Results

A total of 3,434 mountain pine beetles were obtained from the Logan Canyon site, 979 from Bear River, 202 from Hoop Lake, and 82 from Ashley.

Of the 15 loci examined, 4 (AAT1, EST1, LAP2, PEP) were polymorphic (i.e., the frequency of the common allozyme was less than 0.98), one (PGI) showed slight variation, and 10 (AAT2, AGP1, AGP2, AGP3, EST2, EST3, LAP1, MDH1, MDH2, T0) were monomorphic in all groups (Table 1). In most cases, genotype frequencies for each locus fell within expected values for random-mating populations. In 5 cases, however, deviation from expected proportions occurred. Beetles from Logan Canyon (for AAT1 and EST1 loci) and Hoop Lake (PEP locus) showed significant deficiencies of heterozygotes and excesses of homozygotes. The deviation of EST1 genotypes in the Logan Canyon sample was most striking. Separation of the Logan Canyon sample into early- and late-emerging groups revealed a significant shift in EST1 allozyme frequencies with time and a closer conformance to random-mating expectations than when all Logan Canyon beetles were pooled. At all other loci from Logan Canyon and at EST1 in Bear River, no differences were seen between early- and late-emerging beetles.

When populations were compared at each locus, major differences were found. Ashley beetles showed a highly significant difference from those of the other sites at AAT1, EST1, and LAP2. At EST1, differences also occurred between beetles from Logan Canyon and Bear River and between beetles from Bear River and Hoop Lake. Allozyme frequencies at the PEP locus fell into two groups; Logan Canyon and Ashley beetles were nearly monomorphic for allozyme PEP(58) while Bear River and Hoop Lake beetles had a significantly higher frequency of allozyme PEP(48).

Nei's genetic identity values (Table 2) showed that high levels of overall genetic similarity occurred among all groups but that Ashley beetles were less similar to beetles from the 3 lodgepole pine sites. Beetles from lodgepole pine were similar to each other at the .998-.999 level but similar to Ashley beetles from ponderosa pine at the .992-.993 level. Nei's genetic distance values (Table 2) show again that the greatest distance between groups was between the Ashley beetles and all other groups. Ashley beetles also had a significantly higher ($P < 0.05$) average heterozygosity (14.4%) than did beetles from the other sites (Logan Canyon 10.4%, Bear River 11.2%, Hoop Lake 10.8%).

When data from males and females at each site were compared (Table 3), only one difference was found. Males and females from Bear River differed significantly at the LAP2 locus. Females showed a higher frequency of allozyme LAP2 (38) and a lower frequency of allozyme LAP2(32) than did males. No significant differences in average heterozygosity occurred between males and females from any site. Preliminary examination of data suggested that males showed a wider range of variation from site to site than did females, a situation reported earlier in mountain pine beetle populations from Oregon, Idaho, and Montana (Stock and Guenther 1979). For example, the frequency of allozyme AAT1(58) varied from .51–.64 in females and from .35–.69 in males. Allozyme LAP2(38) varied from .48–.63 in females and from .21–.83 in males. However, F-tests and contingency tests for each locus failed to reveal any significant differences. Once larger samples of males are obtained for comparison at these sites, more definitive conclusions concerning relative variability may be drawn.

When beetles collected from trees with thick and thin phloem were compared, Logan Canyon beetles showed a significant difference in gene frequencies at LAP2 and PGI, Bear River beetles were different at EST1, and Hoop Lake beetles were different at AAT1, LAP2, and PEP. However, no consistent differences could be identified between beetles collected from trees with thick and thin phloem across populations at any single locus. No significant difference in average heterozygosity occurred between beetles from thick and thin phloem at any of the 3 lodgepole pine sites.

Discussion

The mountain pine beetle groups we examined show high levels of overall genetic similarity, a condition that is to be expected among conspecific populations in such close geographic proximity (Avise 1974). In several cases, significant differences in gene frequency occurred between populations but at no locus was one population fixed for a different allozyme than another. Fixation for different allozymes is commonly found in more clearly differentiated populations and is a good index of genetic divergence among species subgroups (Ayala 1975, Stock et al. 1979).

The genetic differences between groups may be related to differences in relative geographic proximity, host tree species, or stage of outbreak. If geographic barriers to gene flow have lead to genetic divergence between populations of mountain pine beetle in NE Utah, one would expect that the Logan Canyon beetles, being the most geographically separated (in terms of host tree distribution), would show the largest differences from those at other sites. However, Logan Canyon beetles appeared very similar to beetles at other lodgepole pine sites and the major divergence appears to have occurred between beetles from Ashley (in ponderosa pine) and beetles from the 3 lodgepole sites. Several explanations might be advanced for observed differences between Ashley beetles and the others, and the similarity of Logan Canyon beetles to beetles from other lodgepole pine sites. Difference in time of collecting infested billets—November for Ashley and June for other areas—could be a factor. While preliminary evidence (Stock and Higby, unpublished data) suggest that this is not a major factor, further tests are needed before time of collection can be discounted. Also, movement of beetles across the wide distance separating Logan Canyon bee-

Table 1.—Allozyme frequencies in mountain pine beetles from 4 sites in Utah. Below the dotted line, numbers of beetles tested are given for the 10 monomorphic loci. Data from males and females and from beetles from thick and thin phloem are pooled.

Enzyme	Allozyme	Logan Canyon	Bear River	Hoop Lake	Ashley
		Polymorphic			
AAT1	58	.66	.64	.64	.48
	47	.34	.36	.36	.52
	N	377	309	108	48
EST1	80	.02	.03	.02	0
	75	.40	.30	.44	.25
	71	.25	.33	.20	.20
	66	.09	.10	.09	.25
	60	.24	.23	.25	.24
	45	.01	.01	0	.04
	N	660	354	115	79
LAP2	43	.03	.05	.05	.23
	38	.54	.60	.64	.41
	32	.42	.35	.31	.36
	N	145	176	48	37
PEP	58	.99	.92	.90	.98
	48	.01	.08	.10	.02
	N	523	342	106	80
		Slightly Polymorphic			
PGI	28	.99	1.0	1.0	.99
	19	.01	0	0	.01
	N	456	337	116	72
		Monomorphic			
AAT2	N	378	298	107	48
AGP1	N	504	291	92	65
AGP2	N	492	295	94	63
AGP3	N	499	302	94	65
EST2	N	618	350	114	79
EST3	N	617	351	110	60
LAP1	N	145	176	48	37
MDH1	N	616	346	113	79
MDH2	N	615	349	112	79
TO	N	528	289	110	59

tles from other populations might have occurred, perhaps influenced by a climatic event such as high winds, but it is unlikely that sufficient gene exchange could have occurred, or is occurring, to explain the high level of overall similarity between these groups.

An alternative explanation is genetic differentiation related to beetle invasion of different host species—lodgepole pine at Logan Canyon, Bear River, and Hoop Lake; ponderosa pine at Ashley. Ponderosa pine and lodgepole pine present very different habitats to invading beetles. For example, the microenvironment, as affected by volatiles from host oleoresin, is different in important ways in the two tree species. Smith (1963, 1965) demonstrated that monoterpene vapors from pine oleoresin can have a toxic effect on invading bark beetles and that there is a close association between vapor toxicity of pine resins and host relationships. Host volatiles differ markedly between lodgepole pine and ponderosa pine. The primary lodgepole pine volatile is beta-phellandrene; in ponderosa pine the primary volatile is delta-3-carene (Mirov 1961). These differences could affect beetle survival differentially in the two tree species.

Genetic differences among areas might also be related to stage in the infestation cycle. Ashley beetles had higher levels of average heterozygosity which have, in other insect groups, been associated with the logarithmic phase of a population increase (e.g., Turner 1960, Carson 1961). In contrast to beetles at other sites, Ashley beetles appear genetically to be in the increase phase of an outbreak cycle.

Table 2.—Nei's indices of genetic identity (lower left) and genetic distance (upper right) for mountain pine beetles from 4 sites in Utah. Data from 15 gene loci (4 polymorphic, 11 monomorphic) were used (see Table 1).

	Logan Canyon	Bear River	Hoop Lake	Ashley
Logan Canyon	—	.001	.002	.007
Bear River	.999	—	.002	.007
Hoop Lake	.998	.998	—	.008
Ashley	.993	.993	.992	—

Table 3.—Comparison of allozyme frequencies between male and female mountain pine beetles from 4 sites in Utah. Differences at the 95% level are indicated by *.

		Logan Canyon		Bear River		Hoop Lake		Ashley	
Enzyme	Allozyme	F	M	F	M	F	M	F	M
AAT1	58	.64	.69	.65	.65	.64	.57	.51	.35
	47	.36	.31	.35	.35	.36	.53	.49	.65
	N	188	189	242	67	101	7	38	10
	X^2	1.85		0		.30		1.69	
EST1	80	.02	.02	.02	.05	.02	0	0	0
	75	.40	.41	.30	.29	.44	.36	.23	.29
	71	.24	.28	.34	.30	.20	.21	.21	.17
	66	.09	.08	.09	.13	.08	.21	.23	.29
	60	.25	.20	.23	.22	.25	.21	.30	.19
	45	0	.01	.01	.01	0	0	.03	.07
	N	335	325	267	87	108	7	58	21
	X^2	9.69		5.70		3.08		4.04	
LAP2	43	.02	.05	.06	.03	.06	0	.20	.36
	38	.59	.50	.63	.54	.61	.83	.48	.21
	32	.39	.45	.30	.44	.33	.17	.32	.43
						42			
	N	69	76	119	57		6	30	7
	X^2	2.92		7.41*		2.49		3.54	
PEP	58	.99	.98	.91	.95	.90	.86	.98	1.0
	48	.01	.02	.09	.02	.10	.14	.02	0
	N	258	265	268	74	99	7	60	20
	X^2	2.16		3.48		.25		1.04	
PGI	28	.99	.99	1.0	1.0	1.0	1.0	.99	.98
	19	.01	.01	0	0	0	0	.01	.02
	N	225	231	259	78	104	12	50	22
	X^2	0		.30		0		.37	

Comparisons of male and female mountain pine beetles gave results similar to those obtained by Stock and Guenther (1979) in a study of Pacific Northwest populations. Minimal differences were seen between males and females at any one site but greater differences occurred among males across sites than among females. These differences between males and females are believed related to the greater ability of the homogametic mountain pine beetle females to withstand environmental stress (Amman and Pace 1976).

Trees with thin phloem are less suitable hosts for mountain pine beetles than trees with thick phloem because they provide less food for brood production. Although differences between beetles from thin and thick phloem occurred at some gene loci, the differences were not consistent in the 3 groups in which such comparisons were made.

These isozyme analyses suggest how sampling methods for genetic characterization of mountain pine beetle populations might be improved. A condition of excess homozygotes and insufficient heterozygotes, which was most marked in the Logan Canyon population for the EST1 locus, is usually attributable to sex linkage, the presence of a silent allele, or the Wahlund effect (Crow and Kimura 1970). Both sex linkage and silent alleles at this locus have been ruled out for the populations examined in this study. Pooling of progeny from a limited number of parental pairs would create the Wahlund effect, however, and the observed excess of homozygotes. Thus it is possible that while taking a mountain pine beetle population sample from only one or two infested trees might be adequate in many cases, a sample biased for the brood of too few beetles could occur. This bias in the Logan Canyon sample may have produced the observed deviation from Hardy-Weinberg proportions at the EST1 and AAT1 loci. Supporting evidence is obtained from comparison of early- and late-emerging beetles which revealed a genetic change in EST1 allozyme frequencies over time. Such stratification of genotypes based on time of emergence may be related to slight differences in life histories (e.g., time of oviposition, duration of development) of the few broods that were sampled.

Acknowledgment

We thank Mari Hoffman, Candace Harring, and Marcia Tomaszek for assistance in rearing beetles and Pamela Higby for assistance in the genetic analyses. We also thank R. W. Stark, University of Idaho; W. F. McCambridge, U.S. Forest Service, Fort Collins, CO; W. E. Cole, U.S. Forest Service, Ogden, UT; R. H. Smith, U.S. Forest Service, Berkeley, CA; and K. B. Sturgeon, University of Colorado, for their reviews of the manuscript.

REFERENCES CITED

Amman, G. D. 1977. The role of the mountain pine beetle in lodgepole pine ecosystems: impact on succession. Pp. 1–18 *in* The role of arthropods in forest ecosystems, W. J. Mattson (ed.). Springer-Verlag, New York.

Amman, G. D., B. H. Baker, and L. E. Stipe, 1973. Lodgepole pine losses to mountain pine beetle related to elevation. USDA Forest Serv. Res. Note INT-171, 8 pp.

Amman, G. D., and V. E. Pace. 1976. Optimum egg gallery densities for the mountain pine beetle in relation to lodgepole pine phloem thickness. USDA Forest Serv. Res. Note INT-209, 8 pp.

Avise, J. C. 1974. Systematic value of electrophoretic data. Syst. Zool. 23: 465–81.

Ayala, F. J. 1975. Genetic differentiation during the speciation process. Evol. Biol. 8: 1–78.

Baker, B. H. 1969. Forest insect and disease conditions in the Intermountain states during 1968. USDA Forest Serv., Region 4, Branch of Forest Insect and Disease Prevention and Control, Div. Timb. Mgmt., Ogden, UT. 18 pp.

Baker, B. H., G. D. Amman, and G. C. Trostle. 1971. Does the mountain pine beetle change hosts in mixed lodgepole pine and whitebark pine stands? USDA Forest Serv. Res. Note INT-151, 7 pp.

Blackman, M. W. 1931. The Black Hills beetle (*Dendroctonus ponderosae* Hopkins) New York State College of Forestry Tech. Publ. no. 36, 97 pp.

Bush, G. L. 1975. Sympatric speciation in phytophagous insects. Pp. 187–206 *in* Evolutionary strategies of parasitic insects and mites, P. W. Price (ed.). Plenum Press, New York.

Carson, H. L. 1961. Heterosis and fitness in experimental populations of *Drosophila melanogaster*. Evolution. 15: 495–509.

Clayton, J. W., and D. N. Tretiak. 1971. Amino citrate buffers for pH control in starch gel electrophoresis. J. Fish. Res. Board Canada 29: 1169–72.

Cole, W. E., and G. D. Amman. 1969. Mountain pine beetle infestations in relation to lodgepole pine diameters. USDA Forest Serv. Res. Note INT-95, 7 pp.

Craighead, F. C. 1921. Hopkins' host-selection principle as related to certain cerambycid beetles. J. Agric. Research 22: 189–220.

Crow, J. F., and K. Kimura. 1970. An introduction to population genetics theory. Burgess Publ. Co., Minneapolis. 591 pp.

Guenther, J. D. 1978. Genetic diversity among mountain pine beetle (*Dendroctonus ponderosae* Hopkins) populations attacking lodgepole pine and white pine in the Pacific Northwest (Coleoptera: Scolytidae). M.S. thesis, University of Idaho, Moscow. 65 pp.

Hopkins, A. D. 1916. Economic investigations of the scolytid bark and timber beetles of North America. U.S. Dept. Agric. Program of Work, 1917. p. 353.

Lyon, R. L. 1958. A useful secondary sex character in *Dendroctonus* bark beetles. Can. Entomol. 90: 582–4.

McCambridge, W. F. 1967. Nature of induced attacks by the Black Hills beetle, *Dendroctonus ponderosae* (Coleoptera: Scolytidae). Ann. Entomol. Soc. Amer. 60: 920–8.

McKnight, R. C. 1979. Differences in response among populations of *Dendroctonus ponderosae* Hopkins to its pheromone complex. M.S. thesis, Univ. of Washington, Seattle. 77 pp.

Mirov, N. T. 1961. Composition of gum turpentines of pines. USDA Tech. Bull. 1239. 158 pp.

Moyer, M. 1976. Forest insect and disease conditions, Intermountain Region 1976. USDA Forest Service, Forest Insect and Disease Control, State and Private Forestry, Ogden, UT. 10 pp.

Nei, M. 1972. Genetic distance between populations. Amer. Nat. 106: 283–92.

Ridgway, G. J., S. U. Sherburne, and R. D. Lewis. 1970. Polymorphism in the esterases of Atlantic herring. Trans. Amer. Fish. Soc. 99: 147–51.

Sartwell, C., and R. E. Stevens. 1975. Mountain pine beetle in ponderosa pine with prospects for silvicultural control in second growth stands. J. For. 73: 136–40.

Smith, R. H. 1963. Toxicity of pine resin vapors to three species of *Dendroctonus* bark beetles. J. Econ. Entomol. 56: 827–31.

Smith, R. H. 1965. A physiological difference among beetles of *Dendroctonus ponderosae* (=*D. monticolae*) and *D. ponderosae* (=*D. jeffreyi*). Ann. Entomol. Soc. Amer. 58: 440–2.

Stark, R. W., P. R. Miller, E. W. Cobb, D. L. Wood, J. R. Parmeter, Jr. 1968. Incidence of bark beetle infestation in injured trees. *In* Photochemical oxidant injury and bark beetle (Coleoptera: Scolytidae) infestation of ponderosa pine. Hilgardia 39: 121–34.

Stock, M. W., and J. D. Guenther. 1979. Isozyme variation among mountain pine beetle (*Dendroctonus ponderosae*) populations in the Pacific Northwest. Environ Entomol. 8: 889–93.

Stock, M. W., J. D. Guenther, and G. B. Pitman. 1978. Implications of genetic differences between mountain pine beetle populations to integrated pest management. *In* Theory and practice of mountain pine beetle management in lodgepole pine forests. Univ. of Idaho Press, Moscow. pp. 197–201.

Stock, M. W., G. B. Pitman, and J. D. Guenther. 1979. Genetic differences between Douglas-fir beetles (*Dendroctonus pseudotsugae*) from Idaho and coastal Oregon. Ann. Entomol. Soc. Amer. 72: 394–7.

Sturgeon, K. B. 1980. Evolutionary interactions between mountain pine beetle, *Dendroctonus ponderosae* Hopkins, and host trees in the Colorado Rocky Mountains. Ph.D. thesis, University of Colorado, Boulder, 160 pp.

Turner, N. 1960. The effect of inbreeding and crossbreeding on numbers of insects. Ann. Entomol. Soc. Am. 53: 686–8.

Wood, S. L. 1963. A revision of the bark beetle genus *Dendroctonus* Erichson (Coleoptera: Scolytidae). Great Basin Naturalist 23: 1–117.