

Mountain Pine Beetle (Coleoptera: Scolytidae) Mortality in Three Types of Infestations

GENE D. AMMAN

Intermountain Forest and Range Experiment Station,
U.S. Department of Agriculture Forest Service,
Ogden, Utah 84401

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ABSTRACT Populations of mountain pine beetles, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae), in lodgepole pine, *Pinus contorta* var. *latifolia* Engelmann, were sampled at three heights within trees in endemic, epidemic, and postepidemic infestations. Eight mortality factors were evaluated: competition within and between broods, parasites, predators, pathogens, winter temperature, drying of the phloem, pitch, and unexplained mortality. Beetle survival was significantly greater ($P < 0.01$) in endemic (3.7%) than in epidemic (1.4%) and postepidemic (0.5%) infestations. Survival did not differ ($P > 0.05$) by height in trees. Parasites and predators accounted for 8, 33, and 4% of total mountain pine beetle losses in endemic, epidemic, and postepidemic infestations, respectively. *Medetera* (13%) and woodpeckers (15%) accounted for the greatest amount of predation, and this occurred during epidemic infestations. Most parasites and predators showed the typical density-dependent response. Clerids were the single exception, taking a greater proportion of beetles in endemic infestations, thus suggesting a role by clerids in keeping mountain pine beetle populations at an endemic level. However, clerids accounted for only 0.9% of beetle losses.

THE MOUNTAIN PINE BEETLE (MPB), *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae), continues to cause heavy losses of lodgepole pine throughout much of the western United States and western Canada. Forest characteristics identified as conducive to MPB outbreaks are significant numbers of trees 80 years or older that are greater than 20 cm in diameter at breast height (1.4 m above ground), and locations where temperatures are optimal for beetle development (Amman et al. 1977, Safranyik et al. 1974). However, the factor or factors responsible for the start of outbreaks are unknown.

A variety of factors are known to cause mortality of MPB during the span of almost a year that the beetles are developing to maturity within the inner bark of lodgepole pine, *Pinus contorta* var. *latifolia* Engelmann (Berryman 1976, Cole 1975, 1981, Reid 1963). Many parasites and predators have been identified, starting with the work of DeLeon (1934). Most past work in lodgepole pine, with the exception of that of Berryman (1976) and Cole (1981), was done during epidemic infestations of MPB. Only Cole (1981) evaluated the effect of individual parasites and predators in field studies; he took population samples at breast height (1.4 m) on infested trees.

In 1973 and 1974, factors causing mortality of beetles in lodgepole pines were assessed in three types of infestations—endemic, epidemic, and postepidemic. This study differs from previous studies in that all three types of infestations, although widely separated geographically, were

sampled in the same years and at three heights in infested trees. The principal objectives of the study were (1) to determine beetle survival in the three infestation types, and (2) to assess mortality factors, particularly parasites and predators, that may be responsible for keeping beetle populations at low levels during endemic periods.

Materials and Methods

In the fall of 1973, two study areas were selected in each of three MPB infestation types—endemic, epidemic, and postepidemic. These designations reflect biological and behavioral differences occurring among the beetle populations; however, the only current method of classifying infestation types is by numbers of trees killed per ha by MPB.

Monitoring single infestations over time would have required many years. For example, one of the endemic infestations used in this study has not developed into an epidemic after 9 years, even though forest conditions are considered conducive to buildup in the beetle population. In this study, the assumption was made that, had the endemic types developed into outbreaks, populations would have been affected by the same mortality factors and in the same ways as populations studied in the epidemic and postepidemic types. All infestations were in pure lodgepole pine forests.

Populations were considered endemic when less than 1 tree in 40.5 ha was infested; epidemic when tree losses had exceeded 12/ha and were showing an increasing trend; and postepidemic when tree losses had peaked and then declined to a level of

about 1 tree in 4 ha. Endemic populations were sampled in the Sawtooth National Forest near the upper end of the Salmon River in southcentral Idaho, and in Hyalite Canyon in the Gallatin National Forest south of Bozeman, Mont. Epidemic populations were sampled in the Targhee National Forest in southeastern Idaho near Ashton, and in the Wasatch-Cache National Forest north of Logan, Utah. Postepidemic populations were sampled in northwestern Wyoming in the Bridger-Teton National Forest at Turpin Meadows on the Buffalo River east of Moran, and at Elkhart Park northeast of Pinedale. Within each area, four to six infested trees were selected for sampling of beetle populations. All the infested trees that could be found within about 2.6 km² in endemic and postepidemic areas, and four and six trees in the two epidemic areas, were sampled. In all, 8, 10, and 12 trees were sampled in the endemic, epidemic, and postepidemic areas, respectively. The study was limited to this number of trees to conserve sampling time.

Two bark samples, 232 cm², were removed within ± 30.5 cm of the 1.4-, 3.7-, and 6.1-m levels on each sample tree by the method of Carlson and Cole (1965) for sampling MPB. Hot paraffin was painted over bare wood to slow the rate of drying where bark was removed.

Populations were sampled four times on the same trees—in October, May, late June, and late July to early August. All MPB and associated insects were counted. Numbers of beetle attacks and amounts of egg gallery also were recorded. The base MPB population was established by adding all live (all stages) and dead beetles counted in the first (October) sample. Dead insects were assigned to specific causes of mortality.

Within-brood competition occurs when progeny from the same female encounter one another as they feed away from the egg gallery. When larval feeding galleries coalesce, one larva usually is killed by the other (entomocide [Cole 1973]) and may be consumed (cannibalism). Therefore, when two larval feeding galleries joined and one larva was missing, death by within-brood competition was inferred. Between-brood competition was diagnosed the same as within-brood competition, except that encounters occurred between larvae from different egg galleries.

Larvae killed by subfreezing temperatures turn black. They were soft and only partially black if death was recent, or dry and shriveled if death occurred several weeks or even months previously.

Death due to drying was diagnosed by the drying and shriveling of larvae that remained cream color, even when very dry and brittle.

Larvae killed by pitch were found in portions of the bark inundated by pitch. This almost always occurred on trees or portions of trees that sustained low attack densities by parent beetles, or had low amounts of egg galleries.

Death attributed to parasites, predators, and disease was diagnosed as follows.

Coeloides rufovariegatus (Provancher) (Hymenoptera: Braconidae) larvae were attached to beetle larvae, and during the final sample *Coeloides* cocoons of the parasite were observed in the bark.

Medetera aldrichii Wheeler (Diptera: Dolichopodidae) larvae were usually seen in the sample. A characteristic staining occurred in the larval gallery where *Medetera* had killed a beetle larva. The staining was probably caused by a fungus growing on some of the beetle fluids that flowed into the bark as *Medetera* fed.

Thanasimus undatulus Say and *Enoclerus spehegeus* F. (Coleoptera: Cleridae) larvae were always present, and phloem tissue was usually chewed into fine pieces by the clerids in their search for MPB larvae. MPB larval galleries terminating in the area where clerids had chewed away the phloem tissue were considered killed by the clerids.

Woodpecker, *Picoides tridactylus* (L.) and *P. villosus* (L.), predation was measured by counting the number of holes pecked through the bark that ended in larval galleries. Occasionally a small piece of bark was chipped from the tree. In these cases, the number of larvae lost to woodpecker feeding was estimated by determining the area of bark removed and multiplying it by the density of larvae found in undisturbed bark nearby.

Death was attributed to pathogens (possibly *Beauveria bassiana* [Balsamo] Vuillemin) when the larva appeared normal but was moribund, or was flaccid, or had fungi growing over the larval surface.

Most unspecified mortality was recorded when the number of live plus dead individuals was subtracted from the number of live individuals observed the previous sample date. A very small amount was due to inability to determine cause of death when the larva, or place where the larva had been, was observed.

Plastic screen cages (12.5 mesh per cm) that covered 930 cm² of bark surface each with a collecting tube attached, were stapled to the trees—two per sample height—after the June sample. The July-August sample consisted of new adults in the cages as they emerged to infest green trees. Emerging insects were collected several times during the emergence period. After the emergence period, cages were removed and a 232-cm² sample of bark was removed from the center of the area previously covered by the cage. The bark was examined for dead beetles and for cocoons of parasites. All insects were taken to our laboratory in Ogden, where they were identified and counted. MPB were sexed, using characteristics of the seventh abdominal tergite (Lyon 1958).

Differences between areas and heights in trees were analyzed for significance by using *t* tests.

Table 1. Lodgepole pine and MPB characteristics in three classes of infestations (endemic, epidemic, and postepidemic)

Item	Height above ground and infestation class											
	1.4 m			3.7 m			6.1 m			Heights combined		
	En- demic	Epi- demic	Post- epi- demic	En- demic	Epi- demic	Post- epi- demic	En- demic	Epi- demic	Post- epi- demic	En- demic	Epi- demic	Post- epi- demic
No. of trees sampled	8	10	12	8	10	12	4	7	4	8	10	12
No. of samples (232 cm ²)/ sample date	16	20	24	16	20	24	8	14	8	40	54	56
Tree diam (cm)												
\bar{x}	34.5	32.8	26.2									
SD	8.6	9.4	7.9									
Tree age	—	73.5	64.0									
Beetle brood/232 cm ²	101.3	84.7	107.1	65.5	73.4	78.8	62.6	80.3	83.5	79.3	79.3	91.6
New adults/232 cm ²	3.5	1.5	0.6	2.9	0.8	0.3	1.8	1.1	0.6	2.9	1.1	0.5
Beetle survival (%)	3.5	1.8	0.6	4.4	1.1	0.4	2.9	1.4	0.7	3.7	1.4	0.5
% Female	57.2	62.8	72.1	59.9	72.4	63.2	72.9	57.1	85.7	60.6	63.8	69.9
Beetle attacks/232 cm ²	2.2	3.1	2.8	1.7	1.9	2.1	1.4	2.8	2.1	1.8	2.6	2.4
Beetle egg gallery cm/ 232 cm ²	54.4	80.5	77.7	43.4	60.2	59.7	38.6	58.2	62.7	46.7	67.3	67.8

Percents were transformed to arc sine before analyses. Data presented in tables and figures are not transformed, except as noted.

Results and Discussion

Mountain Pine Beetle Survival. MPB survival was expected to be greater in epidemic than in either endemic or postepidemic infestations. However, this did not occur in this study. Survival from egg to adult was significantly different among infestation types ($P < 0.01$). Average survival was 3.7% for endemic plots, 1.4% for epidemic plots, and 0.5% for postepidemic plots. Numbers of beetles emerging per 232 cm² showed the same relation (Table 1). One of the endemic plots (Gallatin), which had survival of only 1.6%, became epidemic 3 years later, but the other plot (Sawtooth), which had survival of 4.6%, has remained endemic. Epidemic plots (Wasatch-Cache and Targhee), with survival of 1.4%, remained at epidemic or near-epidemic levels until about 1980. Postepidemic plots (Bridger-Teton), with survival of 0.5%, have remained at the low postepidemic level, with infested trees difficult to find. Survival did not differ significantly by height in trees.

The number of attacking female beetles per 232 cm² of bark surface differed significantly ($P < 0.001$) by infestation type, being lowest in endemics (1.8) and highest in epidemics (2.6), with post-epidemics being intermediate (2.4). The amount of egg gallery per 232 cm² also differed significantly ($P < 0.001$) by infestation type (Table 1).

The percentage of emerging new adults that was female differed significantly ($P < 0.01$) between the endemic (60.6%) and the other two infestation types (epidemic, 63.8; postepidemic, 69.9%). Percentage of females in epidemic and postepidemic

broods did not differ significantly ($P > 0.05$) in this study.

Any factor that stresses the beetle population causes reduced male survival, with excessive drying of the trees considered a primary factor (Cole et al. 1976). The increased gallery density in epidemic and postepidemic infestations coupled with the smaller tree diameters, particularly in postepidemic infestations, would promote drying and is probably responsible for reduced male survival in these populations (Table 1).

Whether the rates of MPB survival, highest in endemic areas, are consistent from year to year is unknown, but considerable year-to-year variation probably occurs. The few infested trees in endemic areas, although having beetle survival higher than in epidemic populations, still results in a small total population. Large losses of new adults probably occur during dispersion after emergence. Significant losses to any mortality factor could prevent endemic infestations from increasing, or could even drive a local population to extinction.

In contrast, epidemic populations can have low survival per tree for a year or more but still have a large total population because of the large numbers of infested trees. When survival is low, the small numbers of beetles per tree concentrate on fewer trees than the previous year. When survival improves, resulting in large numbers of beetles, the epidemic expands again, with greater numbers of trees infested than in the previous year. Because of the large total population in epidemics, the beetle population can go through these expansion-concentration phases without reaching the level of extinction within a given area.

Mortality Factors. The same mortality factors operated within all three types of infestations. Those of most interest were the parasites and pred-

Table 2. Largest numbers of clerid, *Coeloides*, and *Medetera* larvae observed on any one sample date

Species and height (m)	Endemic				Epidemic				Postepidemic			
	Sawtooth		Gallatin		Targhee		Wasatch-Cache		Turpin		Elkhart	
	\bar{x}	SEM	\bar{x}	SEM	\bar{x}	SEM	\bar{x}	SEM	\bar{x}	SEM	\bar{x}	SEM
Clerids												
1.4	2.13	0.69	0.25	0.25	0.00	—	0.33	0.23	0.00	—	0.33	0.26
3.1	0.75	0.37	0.25	0.25	0.13	0.13	0.08	0.08	0.08	0.08	0.75	0.46
6.1	1.00	0.71	0.00	—	0.13	0.13	0.17	0.17	0.08	0.08	0.00	—
<i>Coeloides</i>												
1.4	0.63	0.50	1.37	0.89	0.50	0.50	1.33	0.91	0.00	—	0.08	0.08
3.1	0.50	0.50	0.08	0.13	0.00	—	0.25	0.18	0.00	—	0.00	—
6.1	0.00	—	0.00	—	0.00	—	2.00	1.48	0.00	—	0.00	—
<i>Medetera</i>												
1.4	1.00	0.63	1.75	0.94	4.13	0.64	4.67	1.69	0.08	0.08	0.25	0.18
3.1	0.08	0.13	2.50	1.13	6.75	2.20	4.42	2.98	0.08	0.08	0.08	0.08
6.1	0.25	0.25	1.25	0.63	1.13	0.48	3.17	2.32	0.00	—	0.00	—

Values represent number of larvae per 232 cm². *Medetera* were most abundant in the fall; clerids and *Coeloides* were most abundant in early summer. SEM, Standard error of the mean.

ators because of their potential to regulate beetle populations. The most abundant—*Coeloides*, clerids, and *Medetera*—were nevertheless present in small numbers and unevenly distributed in relation to size of the sample (232 cm²), as indicated by large standard errors of the mean (Table 2). Parasites were about as numerous as reported by Reid (1963), but predators were considerably more abundant than observed by Reid except in the postepidemic infestations. Losses of MPB to *Coeloides*, *Medetera*, clerids, and woodpeckers differed significantly among infestation types ($P < 0.01$).

Parasitism by *Coeloides*, considered the most important insect parasite of MPB (DeLeon 1935a), was at a low level in all infestation types, ranging from 0.02% in postepidemic infestations to 1.7% in epidemic infestations (Table 3). The low densities in endemic and postepidemic infestations may be related to the very mobile beetle populations. Beetles tend to disperse widely, and therefore are probably difficult for the more fragile *Coeloides* to find, because a large proportion of the parasites stay in the trees for almost a year after the beetles have emerged (DeLeon 1935a). In epidemic infestations, infested trees generally are spaced closer to trees infested the previous year, thus making it easier for *Coeloides* to find the newly infested trees, lessening the chance of inflight mortality, and enhancing mating.

Parasitism differed significantly ($P < 0.001$) by height in tree. Although *Coeloides* densities have been reported to increase with height in sugar pine, *P. lambertiana* Douglas (Dahlsten and Stephen 1974), this occurred only in epidemic infestations in my study. In endemic and postepidemic infestations, *Coeloides* was most numerous at the 1.4-m height. The greater *Coeloides* densities in the lower samples in endemic and postepidemic infesta-

tions was surprising, because others reported greater parasitism with increased height and associated it with bark thickness. Thinner bark occurring higher in the tree allows *Coeloides* to reach beetle broods with its relatively short ovipositor. Apparently, the moderately thin bark of most lodgepole pine in my study allowed *Coeloides* to reach its hosts over most of the trunk.

Medetera was by far the most numerous of the insect predators of MPB, as observed earlier by DeLeon (1935b). Predation by *Medetera* was greatest in the epidemic infestations, accounting for 13% of the beetles (Table 3). However, predation was low in the endemic (4%) and postepidemic (0.08%) infestations. Predation by *Medetera* differed significantly by height ($P < 0.001$) only between the 1.4- and 6.1-m samples in epidemic infestations. Schmid (1971) also reported greater predation by *Medetera* in the lower part of ponderosa pine during epidemic infestations. The lack of significance by height for predation by *Medetera* in endemic and postepidemic infestations is probably related to the generally low amount of predation and consequently much larger sample size needed to show significant differences.

Predation by clerids ranged from 0.2% in postepidemic areas to 0.9% in endemic areas (Fig. 1). The clerids did not show the typical density-dependent response; predation was highest in endemic rather than epidemic areas. The clerids, operating in an inverse density-dependent manner, could not bring a beetle population under control once an epidemic had started. However, the clerids may be important in keeping beetle populations at low levels during the endemic period, thus delaying the start of an epidemic, particularly since the difference in MPB survival between endemic and epidemic populations was only 2.3% (Table

Table 3. MPB survival and mortality by specific causes in three classes of infestation (preepidemic, epidemic, and postepidemic) and three heights in lodgepole pine

Item	Height above ground, and infestation class														
	1.4 m				3.7 m				6.1 m				Heights combined		
	Endemic	Epidemic	Post-epidemic		Endemic	Epidemic	Post-epidemic		Endemic	Epidemic	Post-epidemic		Endemic	Epidemic	Post-epidemic
Starting populations	No.	1,621	1,693	2,371	1,048	1,467	1,891	501	1,124	1,124	668	3,170	4,284	5,130	
Emerging adults	No.	56	29	15	47	16	8	14	15	15	5	117	60	28	
	%	3.5	1.7	0.6	4.5	1.1	0.4	2.8	1.3	1.3	0.7	3.7	1.4	0.5	
Mortality factors															
Within	No.	48	72	1	64	17	10	0	112	112	0	112	201	11	
competitors ^a	%	3.0	4.3	0.05	6.1	1.2	0.5	0	10.0	10.0	0	3.5	4.7	0.2	
Between	No.	13	110	15	28	0	27	0	128	128	16	41	238	58	
competition ^b	%	0.8	6.5	0.6	2.7	0	1.4	0	11.4	11.4	2.4	1.3	5.6	1.1	
Clcid	No.	19	6	4	9	4	4	1	7	7	0	29	17	8	
	%	1.2	0.4	0.2	0.9	0.3	0.2	0.2	0.6	0.6	0	0.9	0.4	0.2	
<i>Coelotides</i>	No.	17	26	1	5	17	0	0	31	31	0	22	74	1	
	%	1.0	1.5	0.05	0.5	1.2	0	0	2.8	2.8	0	0.7	1.7	0.02	
<i>Medetera</i>	No.	58	246	2	49	219	2	20	94	94	0	127	559	4	
	%	3.6	14.5	0.1	4.7	14.9	0.1	4.0	8.4	8.4	0	4.0	13.0	0.08	
Pathogen	No.	0	35	5	15	88	0	0	0	0	0	15	123	5	
	%	0	2.1	0.2	1.4	6.0	0	0	0	0	0	0.5	2.9	0.1	
Woodpecker	No.	35	142	33	25	354	88	0	153	153	75	60	649	196	
	%	2.2	8.4	1.3	2.4	24.1	4.7	0	13.6	13.6	11.2	1.9	15.2	3.8	
Temperature	No.	454	574	803	189	291	599	81	212	212	131	724	1,077	1,533	
	%	28.0	33.9	31.2	18.0	19.8	31.7	16.2	18.9	18.9	19.6	22.8	25.1	29.9	
Drying	No.	306	158	564	308	275	167	84	144	144	106	698	577	837	
	%	18.9	9.3	21.9	29.4	18.7	8.8	16.8	12.8	12.8	15.9	22.0	13.5	16.3	
Pitch	No.	0	12	11	0	35	24	0	2	2	3	0	49	38	
	%	0	0.7	0.4	0	2.4	1.3	0	0.2	0.2	0.4	0	1.1	0.7	
Unknown	No.	615	283	1,117	309	151	962	301	226	226	332	1,225	660	2,411	
	%	37.8	16.7	43.4	29.4	10.3	50.9	60.0	20.1	20.1	49.8	38.7	15.4	47.1	

^a Competition within brood of an individual egg gallery.

^b Competition among brood of several egg galleries.

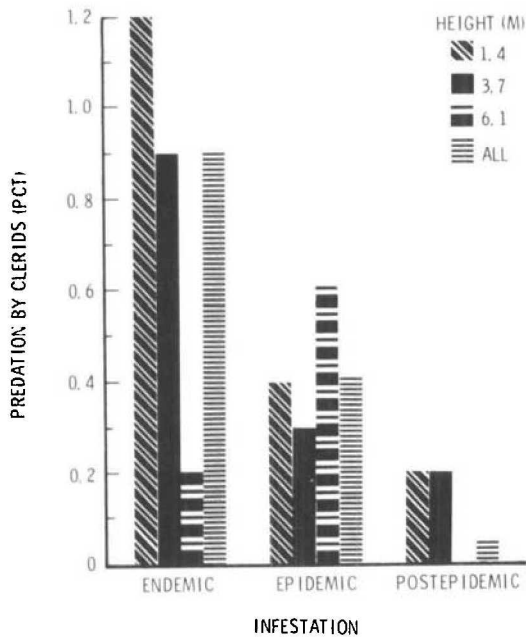


Fig. 1. Percent predation of MPB by clerid beetles (*T. undatulus* Say and *E. sphegeus* F.) in endemic, epidemic, and postepidemic infestations.

1). Predation by clerids differed significantly by height only for endemic areas, being greatest in the base of the tree, where MPB density also was greatest (Table 3).

Among the parasites and predators, woodpeckers were responsible for the greatest losses of MPB, ranging from 1.9% in endemic areas to 15.2% in epidemics (Fig. 2). Predation by height differed only between the 1.4- and 3.7-m levels in epidemic areas where woodpeckers took 8.4 and 24.1% of the beetles, respectively. Predation at 1.4 m probably was restricted by deep snow. Woodpeckers do most of their feeding on MPB during the winter; therefore, the 1.4-m level would usually be covered by snow.

Losses of larvae to a pathogen, possibly *Beauveria bassiana* (Balsamo) Vuillemin, were significantly different between endemic (0.5%) and the other two types of infestations, but not between epidemic (2.9%) and postepidemic (0.1%) infestations. Losses to pathogens did not differ significantly by height in trees within any of the infestation types.

Overall, parasites and predators accounted for only 8 and 4% of total MPB losses in endemic and postepidemic infestations, respectively, compared with 33% in epidemic infestations (Fig. 3).

Intraspecific competition has long been regarded as one of the principal density-dependent mortality factors affecting insect populations. Losses of MPB to competition differed significantly among all infestation classes ($P < 0.01$). These losses ranged from 1.3% in postepidemic infestations to

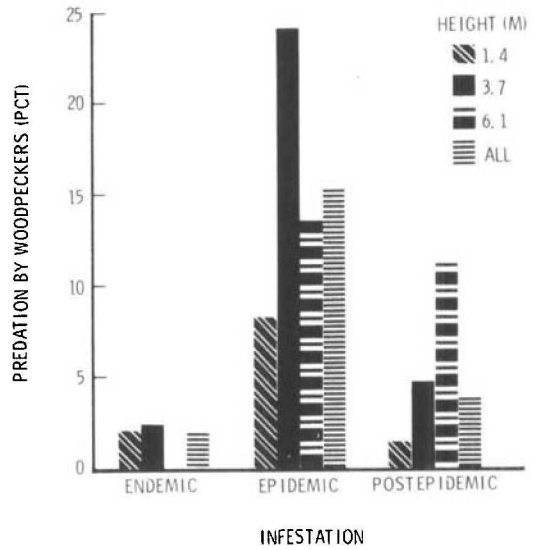


Fig. 2. Percent predation of MPB by woodpeckers in endemic, epidemic, and postepidemic infestations.

10.3% in epidemic infestations (Table 3), although egg gallery density was similar in these two infestation types. The lower loss to competition in postepidemic than in epidemic infestations may be related to the large number of beetle eggs present in late fall (23.4% in postepidemic areas versus 0.4% in epidemic areas). Local weather determines when new adult beetles will emerge and infest green trees, and how many eggs will hatch before cold temperatures prevent additional hatching. All eggs that have not hatched by the onset of winter are killed by subfreezing temperatures, and thus competition among larvae could be reduced substantially. Losses to competition in endemic infestations were also less than in epidemics. Mean egg gallery density in endemic infestations (46.7 cm/232 cm²) was significantly less than in epidemics (67.3 cm) ($P < 0.01$).

Losses to intraspecific competition by height in trees for endemic infestations were significantly lower at 1.4 m than at 3.7 m ($P < 0.01$), but no loss was attributed to this factor at 6.1 m. Significant differences occurred among all heights in epidemic infestations ($P < 0.01$), being least at 3.7 m and greatest at 6.1 m. Losses to competition were least at 1.4 m and greatest at 6.1 m in postepidemic infestations ($P < 0.01$). Differences in competition are probably related to the amount of egg gallery, which differed significantly among heights.

Losses to pitch (resinosity) did not occur in trees sampled for endemic populations; this suggests that the trees selected were the poorer specimens not capable of much resin production. Losses to resinosis differed significantly between epidemic (1.1%) and postepidemic (0.7%) infestations ($P < 0.01$). During epidemics, the best trees are infest-

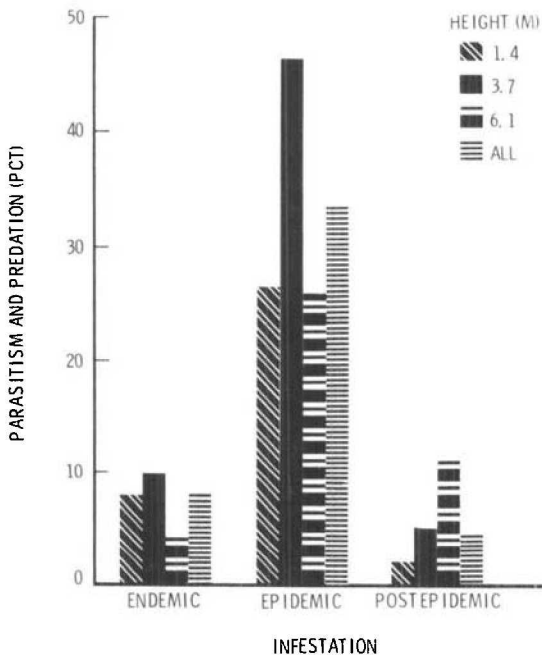


Fig. 3. Percent loss of MPB to all parasites and predators combined in endemic, epidemic, and postepidemic infestations.

ed, and these are capable of producing considerable pitch. Trees infested in postepidemic infestations generally are not as vigorous as those infested during epidemics, but may be better than those infested during endemic periods. Losses to pitch did not differ significantly by height in trees within any of the infestation classes. Losses were light, ranging from none in endemic to 2.4% at 3.7 m in epidemic infestations (Table 3). Reid (1963) found an average of 15% of egg gallery rendered nonproductive by resin, but attack densities were lighter than reported here. In my study, the low losses of MPB brood to resinosis were at least partly related to sampling only trees that had attack densities high enough to kill the trees.

Losses to the physical factors of cold temperature and drying of phloem tissue accounted for the greatest specified mortality of MPB, an observation also made by Cole (1981). However, these losses did not differ significantly ($P > 0.05$) among infestation types. Losses to cold temperatures ranged from 22.8% in endemic to 29.9% in postepidemic infestations. Losses to cold were significantly greater ($P < 0.05$) at 1.4 m in both endemic and epidemic infestations than in higher samples (endemic 28% at 1.4 m and 18% at 3.7 m; epidemic 33.9% at 1.4 m and 19.8% at 3.7 m). In postepidemic infestations, losses were slightly higher at 3.7 m (31.7%) than at 1.4 m (31.2%). Greater losses to cold in the lower samples were surprising, because the bottom portion of the tree trunk has thicker bark than the upper portion and is usually

protected by snow. However, considerable death occurs in the spring when cold temperatures follow resumption of feeding by larvae.

Losses of beetle brood as a result of drying of phloem tissue ranged from 13.5% in epidemic to 22.0% in endemic infestations. However, losses differed significantly by height in trees. Drying caused significantly more mortality only between 1.4 m (21.9%) and 3.7 m (8.8%) in postepidemic infestations ($P < 0.05$). Although differences in losses to drying were not significant among infestation types in this study, Cole (1981) shows an increase in losses to drying in all diameter classes from beginning to end of an infestation. Increases in attack and egg gallery densities probably are responsible for increased drying (Cole et al. 1976).

Unspecified mortality, the category that continually plagues the sampler in population dynamics studies, was assigned the greatest losses in endemic (38.7%) and postepidemic (47.1%) infestations, but not in epidemic infestations (15.4%). Why the samplers did so much better in assigning mortality to specific factors in epidemic infestations than in the other two types is unknown. Possibly, some different and very subtle mortality factors operate in endemic and postepidemic infestations. The same trend is shown by Cole (1981) in trees of the 23-cm-diameter class, and to a lesser extent in the 38-cm-diameter class.

None of the mortality factors stood out as an obvious regulator of MPB populations. However, a mortality factor that is regulatory could not be determined in a short study of this type. Most mortality factors appear to be operating in similar magnitudes to those reported by Cole (1981), whose study covered a much longer time.

Parasites and predators showed the typical density-dependent response, taking the greatest percentage of beetles during epidemics. The lowest amount of parasitism and predation occurred in postepidemics, which suggests that the parasites and predators may be selecting other species of Scolytidae, which probably are more numerous during such periods. Evenden and Gibson (1940) found large numbers of lodgepole pine killed by *Ips* and *Pityogenes* after the main mountain pine beetle infestation.

The single exception was the clerids, which caused greatest losses of beetles during endemic infestations, resulting in one of the main differences between the results of this and Cole's (1981) study. My observations (endemic) occurred earlier in the beetle infestation cycle than Cole's (pre-epidemic). The clerids caused significantly greater losses of beetles in endemic than other infestation types, whereas in Cole's study predation by clerids was about equal throughout the infestation cycle. The higher rate of predation in endemic than in the other two infestation types suggests that additional studies of endemic populations are needed to define the role of clerids.

In addition to the possible role of clerids, a sig-

nificant mortality factor may be present within the unknown category where greater losses occurred during endemic and postepidemic than during epidemic infestations. It seems unlikely that any obvious mortality factor was overlooked in this and previous studies, but the less obvious could be operating, for example, nematodes, infertility, or a lethal genetic factor.

In any case, lodgepole pine stand structure appears to be the overriding factor for an outbreak of beetles to occur. Although lodgepole pine stand structure (trees of large diameter and having thick phloem [Cole et al. 1976]) conducive to a beetle outbreak is attained, several years may pass before an outbreak actually occurs. Once an outbreak starts, it continues until the large diameter trees of a stand are killed; then the population gradually returns to the endemic level (Cole et al. 1976). How the epidemic is triggered remains unknown, but important clues probably will be found in studies of endemic infestations.

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