Population Changes of the Mountain Pine Beetle in Relation to Elevation[1]

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ABSTRACT

Dendroctonus ponderosae Hopkins was studied in lodgepole pine, *Pinus contorta* Douglas, at 4 elevations between 1923 and 2750 m in northwestern Wyoming. The beetle had a 1-year life cycle at 1923 and 2130 m. At 2450 m, part of the population completed a generation in one year, but the remainder required two years. Two years usually were required to complete a generation at 2573–2750 m. Life tables showed high mortality rates and declining populations at the 3 highest elevations, in contrast to high survival rates and increasing populations at the lowest elevation. Cool temperatures at high elevations delayed development, so the beetle overwintered in stages that were particularly vulnerable to winter temperatures. The conclusion is that mountain pine beetle populations are regulated by weather at high elevations.

Mountain pine beetle (*Dendroctonus ponderosae* Hopkins) populations in lodgepole pine, *Pinus contorta* Douglas, in Grand Teton National Park and in the Togwotee Pass area of the Teton National Forest, northwestern Wyoming, were sampled in early spring 1968. Many beetles entered the previous winter as 3rd and 4th instars, pupae, or teneral adults. This indicated that more than one year was required for a generation at high elevations, in contrast to the one-year cycle found previously at lower elevations (unpublished data, Research Work Unit 2201, Ogden, Utah).

In eastern Montana and central Idaho the mountain pine beetle has one generation/year in lodgepole pine, but 2 years may be required at high elevations (Evenden et al. 1943, Gibson 1943).

Reid (1962a) observed that the mountain pine beetle usually has one generation/year in lodgepole pine at Invermere, B.C. However, in 3 of 6 years, parent mountain pine beetles established 2 broods in a single season; only one brood/year was established during the other 3 years. In 1956, he found that the beetle required 2 years to complete a generation in Banff National Park, Alberta, where a generation had been completed previously in a single year. He concluded that the life cycle of the beetle may differ from year to year within and between regions because of weather differences.

Although the mountain pine beetle has been studied in several geographic areas, no study of life cycle variations, specifically in relation to elevation and population, dynamics in lodgepole pine has been made. This study was initiated to determine these relations.

Methods

Trees were selected in September 1968 at 4 elevations—1923 m near the S end of Grand Teton National Park; 2130 m in Turpin Meadows near the Buffalo River; 2450 m about 3 km below Togwotee Mountain Lodge; and 2573–2750 m 1.5–16 km above Togwotee Mountain Lodge, all in the Teton National Forest. At elevations of 1923 and 2130 m,

only trees infested in the fall of 1968 could be identified as containing mountain pine beetles; broods had emerged from trees infested in previous years. However, at elevations of 2450–2750 m, 2 groups of infested trees containing mountain pine beetles were identified—one group, infested the fall of 1967, contained brood in early May 1968; a 2nd group had been infested the fall of 1968. Twelve trees—four, 20–28 cm dbh; four, 30–36 cm dbh, and four, 38 cm dbh and larger—infested in each year were selected for sampling mountain pine beetle populations at each elevation. To verify previous observations, a few trees infested in the fall of 1969 also were sampled. Beetle populations were sampled according to the method described by Carlson and Cole (1965). Two 15.2-cm² samples of bark were taken at random within ±1 ft of breast height from each tree. Mountain pine beetles and associated insects were counted in each sample; causes of beetle mortality were recorded. Samples were taken 4 times/year—September, October, May, and June. During the summers, plastic cages were stapled over two 15.2-cm² areas of bark on each tree. A plastic test tube, 28×103 mm, was attached to the cage to catch emerging beetles.

Beetles in all stages (except the egg stage) were placed in alcohol each time the population was sampled. These were taken to the laboratory where larval head capsules were measured and the proportion of the population in each stage was determined. Emerging adults were sexed by means of differences in the morphology of the 7th abdominal tergum (Lyon 1958).

A developmental index was used to compare rates of development at different elevations. Values assigned to the stages were 1, eggs; 2, 1st instar; 3, 2nd instar; 4, 3rd instar; 5, 4th instar; 6, pupa; 7, teneral adult; 8, new adult and 9, emerged adult. The proportion of the population in each stage was multiplied by the numerical value for that stage. The values for all stages present on a given date were added to obtain the developmental index.

Mini-max thermometers were attached 12 dm aboveground to shaded tree trunks at the 3 highest elevations. Temperatures were recorded each time

personnel were in the area. U.S. Weather Bureau climatological data (1968–69) collected at Moose, Wyo., near the lowest plot were used as temperature indicators for the lowest plot. In addition, U.S. Weather Bureau climatological data (1966–70) collected at Moran, Wyo., the nearest weather station to Togwotee Pass, were used to determine year-to-year changes in avg monthly temperatures.

Results and Discussion

Length of Life Cycles

One year was required for the mountain pine beetle to complete its life cycle at 1923- and 2130-m elevations. A portion of the population completed a

generation in one year at 2450 m, but the remainder stayed in the trees and survivors emerged the 2nd year. Most beetles required 2 years to complete a generation at 2573–2750 m. Temperatures at high elevations were consistently cooler than those at lower elevations during the summer, when beetles would be developing (Fig. 1).

Collected data suggest the following sequence of events. At elevations as low as 1923 m, beetles generally complete development and emerge by September (Fig. 2). The brood adults make fresh attacks and usually have adequate time to construct egg galleries before cold fall temperatures stop activity. Avg egg gallery length was 27.3 cm in October
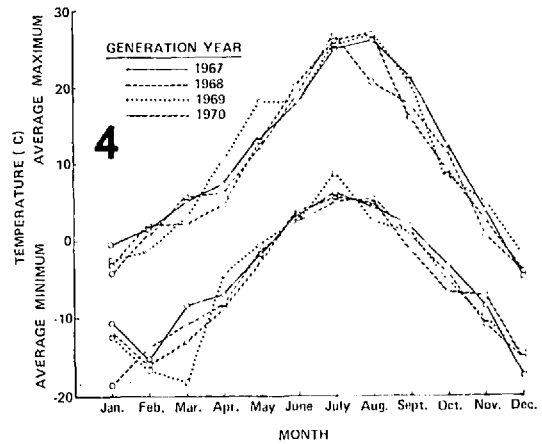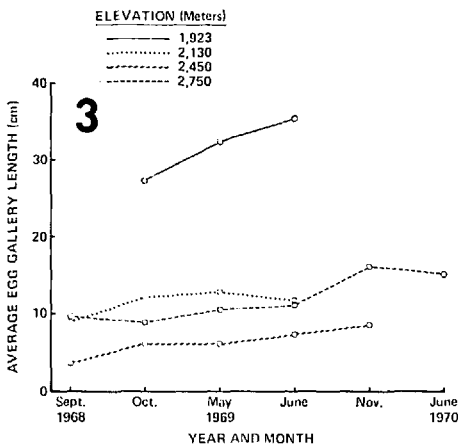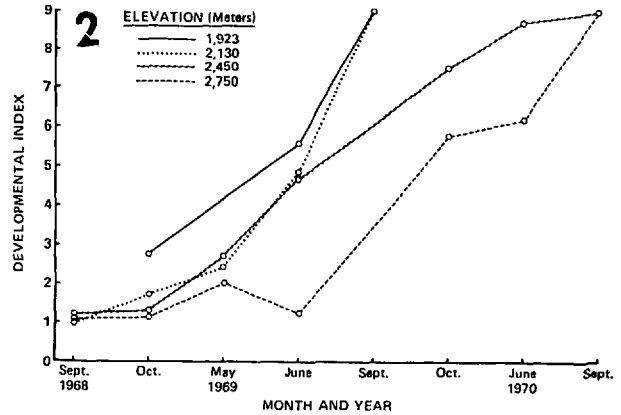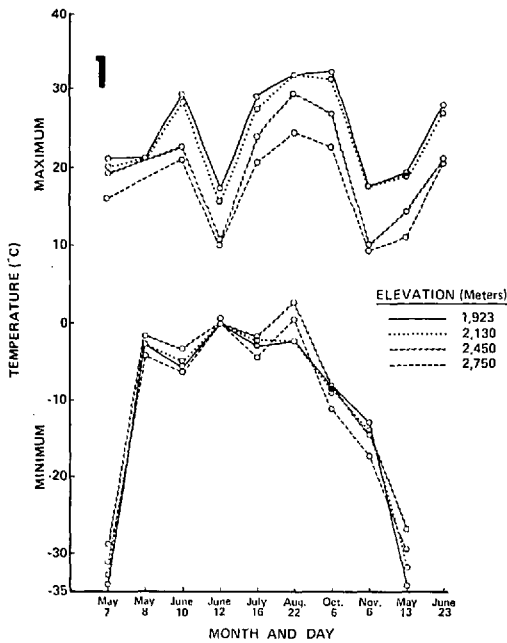

FIG. 1.—Temperatures observed on mini-max thermometers placed at 2130, 2450, and 2750 m elevation and temperatures obtained from U.S. Weather Bureau monthly summaries for 1968–69 at Moose, Wyo., near the lowest plot (ca. 1923 m).

FIG. 2.—Avg mountain pine beetle development at 4 elevations (1968 generation year).

FIG. 3.—Avg egg gallery length at 4 elevations.

FIG. 4.—Avg minimum and average maximum monthly temperatures at Moran, Wyo. (U.S. Weather Bureau, 1966–70).

Table 1.—Percent of mountain pine beetle populations occurring in each stage at 4 elevations.

Month	Insect[a] stage	1923 m 1968	1923 m 1969	2130 m 1968	2450 m 1967	2450 m 1968	2450 m 1969	2750 m 1967	2750 m 1968	2750 m 1969
					First year					
Sept.	E	[b]—	—	100	—	81	—	—	95	—
	I	—	—	0	—	19	—	—	5	—
Oct.	E	12	0	45	—	74	23	—	90	6
	I	39	0	41	—	18	49	—	10	35
	II	32	21	13	—	8	28	—	0	37
	III	16	25	1	—	0	0	—	0	19
	IV	1	54	0	—	0	0	—	0	3
May	I	—	20	59	—	63	20	—	100	26
	II	—	37	38	—	7	68	—	0	40
	III	—	39	3	—	23	12	—	0	33
	IV	—	4	0	—	7	0	—	0	1
June	E	0	0	0	—	0	0	—	80	0
	I	4	0	0	—	0	0	—	20	2
	II	1	0	0	—	0	8	—	0	10
	III	1	0	25	—	29	31	—	0	47
	IV	39	86	68	—	71	61	—	0	41
	P	39	14	7	—	0	0	—	0	0
	TA	16	0	0	—	0	0	—	0	0
					Second year					
Sept.	III	0	0	0	6	—	0	33	—	—
	IV	0	0	0	38	—	0	34	—	—
	P	0	0	0	27	—	0	7	—	—
	TA	0	0	0	21	—	0	25	—	—
	NA	0	0	0	8	—	0	1	—	—
	EA	100	100	100	0	59	100	0	11	24
Oct.	III				4	20		35	18	0
	IV				38	3		35	38	46
	P				0	3		5	12	6
	TA				31	15		23	21	19
	NA				19	0		2	0	5
	EA				8	59		0	11	24
May	III				0	—		27	—	6
	IV				29	—		40	—	12
	P				0	—		0	—	0
	TA				26	—		33	—	26
	NA				0	—		0	—	14
	EA[c]				45	—		0	—	42
June	III				0	0		0	31	—
	IV				10	2		63	25	—
	P				.0	0		0	0	—
	TA	NA			40	9		37	11	—
	NA				10	2		0	6	—
	EA[c]				40	87		0	27	—
Sept.	EA				100	100		100	100	—

[a] E = egg; I, II, III, IV = larval instars; P = pupa; TA = teneral adult; NA = new adult; EA = emerged adult.
[b] — = not sampled.
[c] Increase in % emergence over October figures is due to mortality of other stages, not to emergence of additional beetles.

(Fig. 3). Laboratory studies have demonstrated that rate of gallery construction is highly dependent upon temperature (Amman 1972); therefore, egg-gallery length is a good indicator of temperatures that prevail after trees are infested. At 1923 m, most eggs hatched, and over 50% of the larvae reached the 2nd or 3rd instar by late October or early November (Table 1). These larvae completed development the following spring and probably emerged in July and August to complete the cycle. Collections were not made frequently enough to determine precise time of emergence.

In 1968, maximum temperatures were lower than usual during August and September (Fig. 4), and emergence of adults and start of the next generation were delayed at elevations as low as 2130 m. Consequently, much of the population at this and at higher elevations entered the winter as eggs or 1st instars (Table 1); most died during the winter. Larvae that survived at 2130 m were able to complete development and to emerge as adults by September (Fig. 2).

At 2450-m elevation, beetle development appeared to be more dependent upon weather of a given year; part of the population completed a generation in one year, but the remainder required 2 years (Table 1;

Fig. 2). Beetles usually completed a generation in a single year in tree trunks that received some direct sunlight. However, many beetles in well-shaded trunks did not complete development in one year.

Considerable year-to-year variation in the life cycle can occur (Fig. 5), but temperatures during the August to September flight period appear to be critical. In 1968, few brood adults emerged from trees infested the previous year (Table 1), and egg galleries made by them in newly infested trees at 2450 m were shorter than at other elevations (Fig. 3). Gallery lengths averaging only 6.1 cm in October were probably related to cool temperatures that delayed both emergence of new adults and egg-gallery construction. In 1969, when temperatures were higher during the flight period than in 1968, about 50% of the population reached the adult stage and emerged in one year at 2450 m elevation. In 1970, all beetles emerged in a single year (Table 1).

At 2573–2750-m elevation, the 2-year cycle appears to be the rule regardless of year-to-year temperature fluctuations (Table 1; Fig. 6). However, a warm August and September the year following infestation would enable a greater proportion of the population to complete development and emerge in a single year. For example, in 1970 ca. 25% of the brood from 1969 fall attacks completed development and emerged; August 1970 was warmer than the average. Additional beetles probably would have emerged from the trees in September if temperatures had not dropped well below those recorded for other years (Fig. 4). Survivors could be expected to emerge in 1971; however, winter mortality among pupae, teneral adults, and mature adults would likely be large.

At 2573–2750 m, egg-gallery length averaged 9 cm in October 1968—longer than the avg length at 2450 m. Because the beetles had a 2-year cycle, they probably emerged earlier the 2nd summer than those completing a generation in one year at 2450 m. Therefore, the beetles would have had more time to construct galleries than those at 2450 m before low temperatures stopped activity. Increases in avg gallery lengths the spring of 1969 indicate extensions
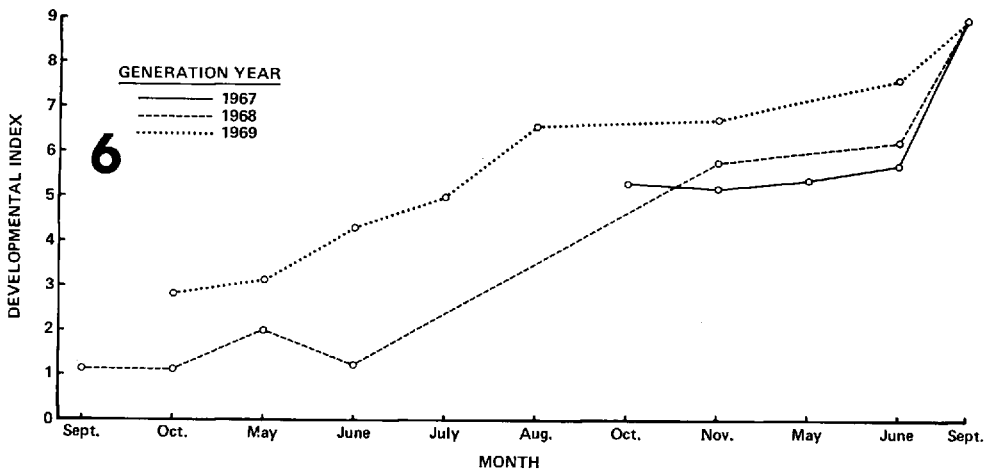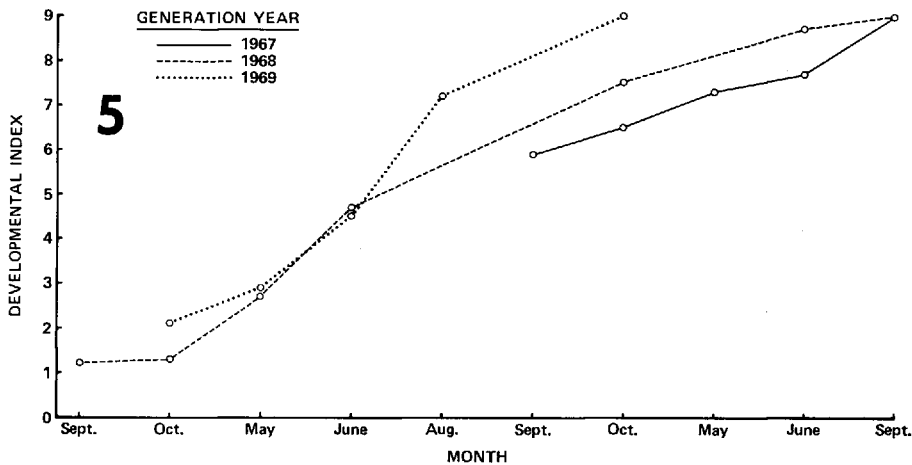

Fig. 5.—Avg mountain pine beetle development at 2450-m elevation during generation years 1967–69.
Fig. 6.—Avg mountain pine beetle development at 2573–2750-m elevation during generation years 1967–69.

Table 2.—Changes in mountain pine beetle populations occurring in the 1968 generation at 4 elevations.

Item	Elevation (meters)			
	1923	2130	2450	2573–2750
Generation survival, %	17.6	2.6	7.4	4.0
Emerging adults[a]	36.0	5.0	6.0	6.0
Females per male	1.31	1.89	2.5	1.42
Population change[b], %	+172	−411	−326	−372

[a] Numbers/30.4 cm² of bark surface.
[b] Based on ratio of emerging brood to attacking parents.

by surviving beetles (Fig. 3). However, these extensions would be dependent upon moisture content and rate of bark deterioration (Reid 1962b).

Survival

Population changes were determined for the 1968 generation year at 4 elevations (Table 2). Numbers of surviving beetles at the 3 highest elevations were 3–4 times less than the numbers of beetles that originally infested the trees, an indication of declining populations. However, at the lowest elevation, the number of surviving beetles was ca. 3 times the number of beetles that originally infested the trees. Therefore, an increase in the number of newly attacked trees was expected at the lowest elevation. Population trends indicated by these studies are substantiated by surveys conducted by Klein (Klein and Tegethoff 1970).

In preliminary models for the mountain pine beetle, Cole[3, 4] found that survival in late larval stages explained the largest amount of variance in proportions of beetles that survived from egg to adult. My observation showed that similar numbers of larvae were alive at the start of the 3rd and 4th stages at 1923 and 2130-m elevations. However, 71% completed larval development at 1923 m, but only 13% at 2130 m. The lower survival appeared to be largely related to competition for phloem (food) and to drying of phloem. Larvae that died had hard, shriveled, cream-colored bodies. Death of larvae having these characteristics was attributed to lack of phloem, which either had been completely utilized or could not be utilized because it had dried.

At the 2 highest elevations, most mortality occurred in the winter when beetles were in early stages of development; consequently, competition did not occur among the small numbers of larvae that reached the 3rd and 4th stadia.

Samples were analyzed to determine which stages were most likely to be affected by winter temperatures. Eggs, larvae, and pupae killed by cold turned brown to black. All eggs were killed by winter temperatures (Table 3). Eggs constituted 12% of the population at the lowest elevation and 90% at the

[3] W. E. Cole. The mountain pine beetle in lodgepole pine, *Dendroctonus monticolae* Hopk. (Coleoptera: Scolytidae). A systematic random sampling plan for life tables and their analysis. Intermt. For. and Range Exp. Stn. Undated, unpubl. rep. 12 p. On file in Research Work Unit 2201, Ogden, Utah 84401.
[4] W. E. Cole. Mountain beetle dynamics in lodgepole pine forests: an approach and its analysis. Invitational paper given at IUFRO Congr., Gainesville, Florida, March 1971.

highest elevation in 1968 (Table 1). The 1st instar also appeared to be fairly susceptible to winter temperatures; approximately 50% of the beetles at this stage were killed. Larger larvae (3rd and 4th instars) are more cold hardy. Yuill (1941) studied cold-hardiness of 4th-stage mountain pine beetles, because overwintering usually occurs in this stage in California. He found that cold-hardiness varied with locality and host. He concluded that larvae of the mountain pine beetle could develop sufficient cold-hardiness to survive winter temperatures likely to occur in California. Sômme (1964) did not examine the 4th instar of *D. ponderosae,* but he found no difference in glycerol content among the first 3 instars; therefore, there is no adequate explanation for the large loss of 1st and 2nd instars observed in this study. In my study, most of the beetles that completed their life cycle in one year survived the winter well as late larvae. In contrast, beetles that completed a cycle in 2 years appeared to be vulnerable to winter temperatures when in the late larval stage. Possibly this could be attributed to lack of moisture in hibernacula. The tree was dry after being dead for more than one year; thus, larvae probably become desiccated after giving up moisture during the winter. The importance of moisture in hibernacula to the survival of insects was described by Hodson (1937). By extrapolation, when temperatures are below −18°C, the mountain pine beetle should survive best in a moderately damp environment.

During this study, no pupae survived the winter. Of the teneral adults, 12%–55% survived. New adults apparently are more susceptible to cold than tenerals, possibly because new adults may have fed before winter. Insects generally freeze more readily when food is in the gut. The life-table sample showed no survivors among new adults (Table 3); however, supplemental examinations disclosed a few. These were always found below the snow level, insulated against very cold temperatures. In addition, moisture levels may have been higher in this portion of the tree. Reid (1963) also observed that most pupae and teneral adults entering the winter were killed by cold temperatures.

The proportion of parent adults that survived the first winter after infesting the trees in 1968 was strongly related to elevation; none lived through the 2nd winter. At the lowest elevation, 67% of the parents survived the winter compared with only 12% at the highest elevation (Table 3). Although the mortality rate among parent adults seemed related to temperature, woodpeckers also took many parents (the downy woodpecker, *Dendrocopos pubescens,* and the hairy woodpecker, *D. villosus,* were observed). Predation of parent adults was indicated when the hole made by the woodpecker terminated in an egg gallery.

Woodpeckers consumed 54% of the parent adults at the highest elevation, 2573–2750 m (only 12% of parents survived), 37% at 2450 m (39% survived), and 27% at 2130 m (36% survived). Woodpecker predation was not determined at 1923 m, but 67%

Table 3. — Percent winter survival of mountain pine beetle stages at 4 elevations.

Stage	Generation year 1967		Generation year 1968			
			Elevation			
	2450 m	2573–2750 m	1923 m	2130 m	2450 m	2573–2750 m
Egg	[a]—	—	0	0	0	0
Small larvae	—	—	[c]39	61	75	44
I	—	—	—	45	58	55
II	—	—	—	95	35	—
Large larvae	[b]29	[b]31	—	67	[b]14	[b]89
III	—	13	—	67	8	100
IV	29	20	—	—	50	59
Pupae	0	0	—	—	0	0
Teneral adult	12	38	—	—	55	45
New adult	0	0	—	—	0	0
Parent adult	—	—	67	36	39	12

[a] — = None represented in the sample.
[b] Present 2nd winter, but not the 1st.
[c] Larval collection was not obtained in spring for determining proportions in each instar.

of parent adults survived. Assuming that unknown causes of mortality accounted for 20%–25%, as at the other elevations, woodpeckers could have taken only a small number of parents at 1923 m elevation.

A possible explanation for the apparent small amount of predation by woodpeckers at the lowest elevation is that larvae were larger and more numerous than at higher elevations (Table 1, 1968 generation) and were preferred. Woodpecker preference for parent adults rather than larvae at higher elevations was probably related to the small size of larvae; most were in the 1st stage (Table 1). Observations by Koplin and Baldwin (1970) support this observation. They found that woodpeckers, including the hairy woodpecker, ignored larvae of the Engelmann spruce beetle, *D. rufipennis* Kirby, that were less than 3½–4 months old.

Reid (1963) reported that almost all adults above snow level and about 50% of those below snow level were killed by low temperatures at Invermere, B.C., and that 100% mortality above and below snow level occurred at Banff, Alberta.

Significance in Mountain Pine Beetle Dynamics

Amman (1969) observed that fewer beetles emerged from trees of similar bark thickness as elevation increased. It now appears that poor synchrony of the life cycle with weather conditions is largely responsible for low beetle survival at high elevations. As a result of reduced emergence at high elevations, fewer lodgepole pines were attacked and killed at high elevations than at low elevations. Amman and Baker (1972) found that 74% of the trees 23 cm dbh and larger survived a mountain pine beetle infestation at 2662 m elevation on Togwotee Pass (the area used for this study), but only 43% survived at 2189 m near the W foot of Togwotee Pass. Subsequently, the same phenomenon was demonstrated for the north slope of the Uinta Mountains in Utah.[5] In both cases, the important factors of diam-

[5] G. D. Amman, B. H. Baker, and L. E. Stipe. Lodgepole pine losses to mountain pine beetle related to elevation on Utah's North Slope. USDA For. Serv. Res. Pap. INT (in preparation).

eter distribution (Cole and Amman 1969) and phloem thickness of trees (Amman 1969) that regulate mountain pine beetle populations at lower elevations were found to be more favorable for buildup in beetle populations as elevation increased. Therefore, food, which regulates populations at low elevations was not a limiting factor at high elevations.

Conclusions

The data show that mountain pine beetle populations are regulated by weather conditions at high elevations. Cool temperatures delay development, so a large proportion of the population enters the winter as eggs, and 1st and 2nd instars. In these stages, mortality is abnormally high under subfreezing conditions.

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