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WITHIN-GENERATION MORTALITY OF THE JACK PINE TIP BEETLE, *CONOPHTHORUS BANKSIANAE* MCPHERSON, IN MICHIGAN[1]

David J. Hall[2] and Louis F. Wilson[3]

The jack pine tip beetle (*Conophthorus banksianae* McPherson) is a shoot-infesting scolytid that primarily attacks jack pine (*Pinus banksiana* Lamb.) in Michigan. The insect was previously thought to be a variant of *C. resinosae* Hopkins, which attacks cones and shoot tips of red pine. McPherson described *C. banksianae* as a new species, following life cycle and behavioral studies (McPherson, Wilson, and Stehr 1970; McPherson, Stehr, and Wilson 1970). Separating them by morphological features has been unsuccessful (Herdy 1963).

Because jack pine is a major forest resource in Michigan and the jack pine tip beetle (JPTB) is capable of reducing the value of this resource, a study was begun to examine means for its control. The objective here was to determine the influence of natural mortality on the total within-generation mortality of the jack pine tip beetle in Michigan so that biological or cultural control methods might be sought. This necessitated examining a range of population densities at several locations within the beetle's known range.

LIFE CYCLE IN BRIEF

Details of the JPTB life cycle appear in McPherson, Wilson, and Stehr (1970). In brief, the beetle attacks and kills the apical portion of the new shoot. If the beetle only feeds in the tip the damage is called a feeding attack, but if oviposition occurs it is called a reproductive attack. A reproductive attack begins when the beetle bores into the side of the shoot tip just below the bud and excavates a nuptial chamber. From 1 to 5 eggs are laid in niches along the gallery. Oviposition occurs from early July to early August. The larvae pass through two instars during the summer. Pupation begins in early August and the first adults eclose in Mid-August. Adults overwinter within the dead shoot tips, which break off and fall to the ground in late summer and early autumn.

STUDY AREAS

Four areas planted to jack pine between 1954 and 1962 were selected for study. The plantings were located in Wexford, Manistee, and Grand Traverse Counties. The trees were planted in rows; the spacing averaged 6 by 6 ft. Tree height averaged 12 to 16 ft. at the end of the study. The crowns closed several years before the beginning of the study. Beetle densities throughout the study ranged from moderate to high, according to the degree of shoot attack.

The soils ranged from coarse to medium sand, and all four sites were abandoned farmland. Three of the plantations had been subjected to severe water erosion.

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SAMPLING SYSTEM

A sampling system for the study of any insect population must provide a reasonably precise estimate of the mean absolute density. (Absolute density is the number of insects per unit area.) But most insect populations are aggregated, making precision difficult to achieve, and characteristics of the habitat or life cycle add to the time and expense of sampling.

A sampling system requires determination of a sampling universe, an adequate sample unit, sufficient sample size, and proper timing. The degree of precision generally aimed for is a standard error within 10% of the sample mean (Morris 1955, Southwood 1966). However, this level is not often realized because the sample size needed to attain it becomes impractical. Instead, the feasible approach is to calculate the optimum sample unit and sample size within required economic constraints (Lyons 1964, Morris 1955, Morris 1960, Southwood 1966), and then test the system to determine if the precision is adequate.

SAMPLE UNIT SIZE AND SAMPLE SIZE

Because the immature stages of the JPTB occur exclusively in the shoot tip, it would seem reasonable to use one or several tips as a sample unit. Then, by knowing the number of shoot tips per acre, the absolute population density could be calculated. The difficulty, however, is that not all tips are equally susceptible to attack by the adult. Upper crown tips and exposed tips are preferred (Hall and Wilson 1974). Therefore, the part of the crown over a unit area of the ground was chosen as the sample unit—a unit that requires no conversion to estimate absolute density.

To determine the optimum sample unit size and sample size, data were collected in April 1970 in a heavily attacked jack pine stand. A 12- by 12-ft. grid consisting of 144, 1-ft.^{2} units was marked off on the ground and the number of beetle attacks from the previous year was counted in the crown above each square. Also, the vertical distance of each attack from the top of the trees was measured. These data were then further sampled on the computer (CDC 6500)[4] by simulation. Simulation is accomplished by placing the data in the memory of the computer and randomly sampling them for different size units and sample sizes. The sample unit sizes examined were 1, 2, and 4 ft.^{2} and sample size was varied from 20 to 50 sample units. A cutoff level (the distance from the ground below which attacks were discounted) was varied from 69 to 95 in. The variance and standard error of the means of each simulated sample were computed.

The 1-ft.^{2} samples gave the lowest standard errors. Standard error was high when all tips were considered, that is, when the cutoff level was 60 in. (Fig. 1). There were no attacked tips below 60 in. so the true mean of the 144-ft.^{2} sample area was obtained. The standard error was somewhat lower when the cutoff level was 70 or more in., so some of the attacks in the lower part of the crown were eliminated from sampling. To stay within 10% of the mean, a sample size of about thirty-four 1-ft.^{2} sample units was needed.

The 2-ft.^{2} sample unit was used in 1970 to reduce the excessive number of zeros in the samples. In both years, 30 sample units were taken in each of the 3 areas with high-density populations and 45 sample units were taken in the area with a low-density population. Within each plantation, the 30 or 45 sample units were divided evenly among 3 plots. Each plot was 60 by 60 ft. and included about 100 trees. The lower limbs of all the plot trees were pruned from the base up to 70-in. cutoff level for ease of movement in the plot. At most, this eliminated only a few tips susceptible to beetle attack.

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[4] Mention of trade names does not constitute endorsement of the products by the USDA Forest Service.

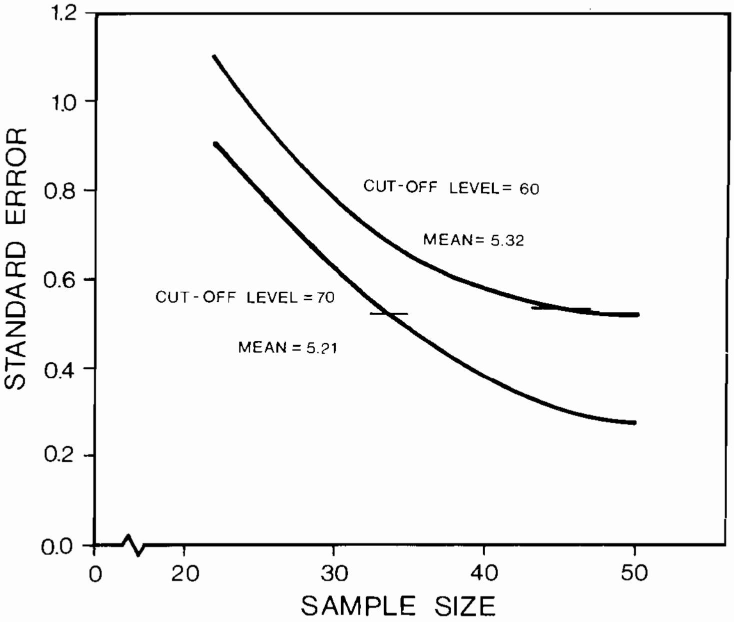

Fig. 1. Standard error of mean number of JPTB attacks per 1 ft.^{2} on number of sample units per sample. The cutoff level refers to distance from the ground below which attacks were discounted.

PROCEDURES

In 1970 the sample units were selected by throwing a marker into the plot. In 1971, a grid was marked off on the ground, each square was numbered, and numbers for each sampling date were drawn from a random number table. The marker in 1970 and a stake in the ground in 1971 located the center of a sample unit. A 12-ft. aluminum pole was held vertically in the center of the sample unit so that it projected through the crown surface. A length of heavy aluminum wire was bent around the pole so that it could slide up and down the pole and maintain a right angle to the pole. Its length was such that when revolved around the pole it circumscribed a circle with an area of the desired sample unit size. The wire was moved up or down the pole in the area of the crown surface, so that attacked tips inside a cylinder described by the device were collected. An 8-ft. aluminum stepladder was used to reach the tips.

Samples were taken every 6 days while eggs were present from about July 1 to August 10 and every 7 or 8 days thereafter until nearly all the insects reached the adult stage. The attacked tips from each sample unit were placed in a plastic bag with a label and sealed. They were held in a freezer at 5° F until they could be dissected.

In the laboratory each tip was sliced in half lengthwise and first classified as either a feeding attack or reproductive attack, depending upon the date collected and the presence or absence of immature stages of the insect. When present, the number of each stage of the insect was recorded. Mortality before freezing was also recorded and cause of death diagnosed whenever possible. Previously dead larvae could be distinguished from normal frozen, "healthy" larvae by color and physical appearance. The number of parasites and other organisms were also recorded.

AGE-SPECIFIC DENSITY ESTIMATES

To estimate the mortality of the JPTB it was necessary to estimate absolute density of the insects in each stage. However, no one sample mean will accurately estimate the density of any stage because the eggs are laid over a period of about 40 days and there is no one time when all the immature insects are present in one stage.

Several methods of analyzing data of this type are discussed by Southwood (1966). The most straightforward of these methods is the total incidence method, which has been used successfully on several insects. In this method, successive sample means are plotted on graph paper over sampling day. When all the means for one stage (say the eggs) are plotted, a curve is drawn through the points (Fig. 2). The total area under the curve (the total incidence) represents the total number of egg-days. The area can be determined by counting squares under the curve or by using a planimeter. This area divided by the mean developmental time gives an estimate of the average egg density throughout the generation.

Density estimates derived from the total incidence curves gave negative mortality estimates in two instances. Therefore, in order to arrive at more accurate age-specific density estimates, another method of estimation was used which we call the "accumulation method." The densities are calculated by: (1) plotting the numbers of dead plus living callow adults in the sample over sampling date; (2) adding the numbers of dead plus living pupae in the sample to the previously calculated callow adult densities and plotting these numbers; (3) calculating and plotting the numbers of second instar, first instar, and egg numbers for each sampling date; and (4) plotting the number of reproductive attacks in each sample.

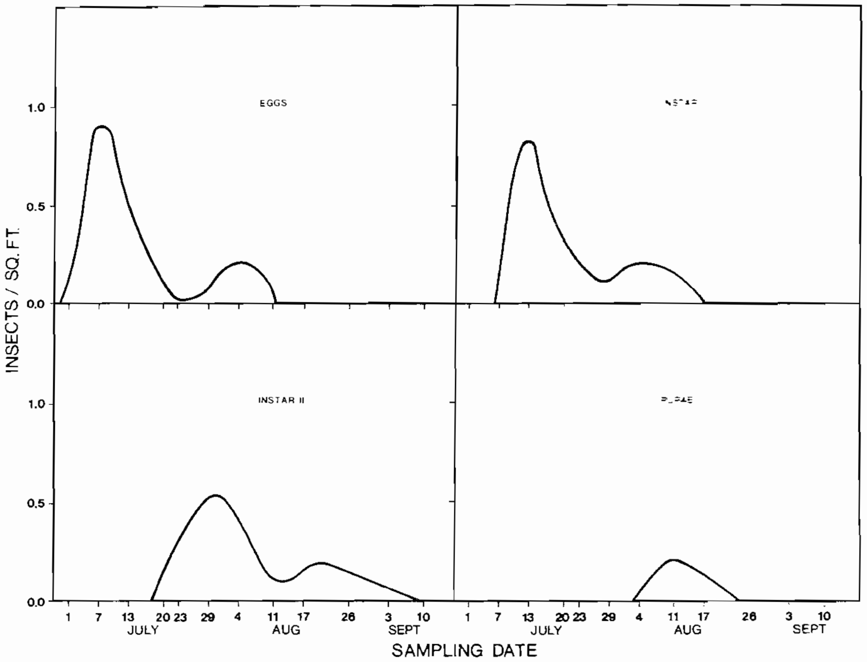

Fig. 2. Total incidence curves for the eggs, larvae, and pupae of the JPTB for plantation No. 1 in 1971.

A curve was first drawn through the points (r) representing the sample means of the reproductive attacks (Fig. 3). Because the number of reproductive attacks remains constant after oviposition has ceased, a horizontal line was drawn through the points from early August to the end of the season. Deviations from this line were considered sampling error. Curves were then drawn through points for the various stages of the insect. The deviation of a point (r) above or below the curve for reproductive attacks was taken into account when deciding where to draw the curves for the individual stages. If the r-point was far above the reproductive attack curve, the r-point was considered to be an overestimate and the curve for the egg density was placed below the point e. The curve was drawn horizontally from where the point leveled off and began to decrease to the end of the sampling season. The density estimate for each stage was read off the end of its curve (Table 1).

The rationale is that at any one time during the period when immatures are present the number of insects that entered the egg stage is equal to the sum of the living and dead insects in all the stages.

This method is roughly equivalent to removing the bark covering a bark beetle gallery after the brood has matured. One can count the egg niches, the number of exit holes of the new adults, and determine the age at death of the remainder of the brood.

The method requires that the individual insect remain within the original host during its entire immature life and the remains of the dead insects must not be lost or destroyed. The first requirement is fully met by the tip beetle, but the second requirement may not always be met for the following reasons. Infertile or nonviable eggs are difficult to distinguish when present with other eggs, and later they may be consumed by larvae and lost. Also, a few of the first instars die and may disintegrate, but usually the head capsule can be detected and recorded. A few dead pupae and some callow

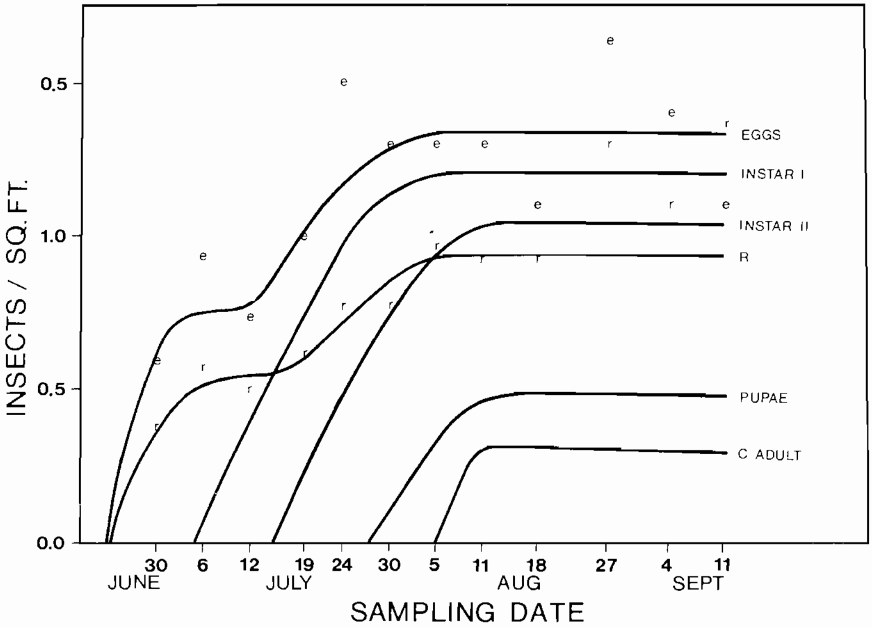

Fig. 3. Accumulation curves for all stages of the JPTB and reproductive attacks for plantation No. 3 in 1971.

Table 1. Age-specific density estimates represented as insects/ft.^{2} based on the accumulation method for JPTB data in 1970, 1971.

Stage	1970 Plantation No.				1971 Plantation No.			
	1	2	3	4	1	2	3	4
Egg	2.20	1.21	2.26	2.02	1.08	1.12	1.33	1.71
Larva I	1.92	1.07	2.11	1.81	.92	1.05	1.20	1.49
Larva II	1.72	.93	1.86	1.68	.67	.83	1.03	1.04
Pupa	.82	.52	1.16	1.17	.25	.37	.47	.45
Callow adult	.67	.36	.84	.96	.15	.32	.31	.31

adults may be destroyed by other callow adults. All of these losses cause some underestimation of densities of the immature stages when using the accumulation method. The method is fairly accurate in estimating second instar through callow adults, but the underestimate of the egg and first instar densities can be large. Thus the egg and first instar densities listed are large underestimates (Table 1).

To improve upon the egg density estimates, egg *intensities* were determined. This was done by using the estimated number of eggs per reproductive attack (egg intensity) and the density of reproductive attacks. The raw data from each population were scanned for reproductive attacks that contained eggs. Then, the mean number of eggs per reproductive attack (egg intensity) and the standard error were computed. The egg intensity for each population was multiplied by that population's reproductive attack density to arrive at the egg density estimate. Thus, the formula used was:

$$\text{Egg density} = \text{egg intensity} \times \text{reproductive attack density}$$

or

$$\text{Eggs/ft.}^2 = \text{eggs/reproductive attack} \times \text{reproductive attacks/ft.}^2$$

These egg density estimates are higher than those calculated by the accumulation method, as expected (Table 2). The egg intensities show little variation within years as well as between years. Most of the differences in egg densities are accounted for by density of reproductive attacks.

For mortality analysis, egg densities were used from Table 2 and densities for remaining stages of the insect were used from Table 1. Inspection reveals that the density estimates were higher in 1970 than in 1971 with the exception of plantation 2. However, the densities in plantation 4 as well as 2 increased in 1971, as was evident from field observation. The density estimates, however, do not reflect these increases. This discrepancy is probably due to the different sampling systems used each year.

MORTALITY ANALYSIS

Southwood (1966) defines *apparent mortality* as "the numbers dying as a percentage of the numbers entering that stage" and *real mortality* as "the numbers of a stage dying as a percentage of the numbers entering the generation." The *apparent mortality* is normally used in analysis of mortality data.

Table 2. Egg intensities, egg density estimates, and reproductive attack densities of the JPTB in 1970, 1971.

Parameter	1970 Plantation No.				1971 Plantation No.			
	1	2	3	4	1	2	3	4
Egg intensity	1.89	2.00	1.77	1.97	2.15	1.83	1.88	1.85
Standard error	.09	.13	.12	.11	.23	.15	.13	.17
Reproductive attack density	1.41	.70	1.51	1.33	.78	.80	.93	1.04
Egg density	2.66	1.40	2.67	2.62	1.68	1.46	1.76	1.92

The apparent mortality was calculated using the age-specific density estimates from the previous section. Thus:

$$M_n = \frac{D_n - D_{n+1}}{D_n}$$

where M_n is the apparent mortality of stage n and D_n and D_{n+1} are the absolute densities of stage n and the succeeding stage (n+1), respectively. Total generation mortality was calculated by dividing the difference between the egg and callow adult density by the egg density.

The mortality due to each factor was first calculated as a proportion of the number of dead insects recorded in each stage. Each of the proportions was multiplied by the apparent mortality of the stage to arrive at the estimated apparent mortality due to each factor.

The apparent mortality figures are useful for comparing the percent dead larvae with the percent dead eggs or pupae; they show the relative "killing power" of age-specific mortality or actual mortality factors. The greatest apparent mortality occurred in the second instar with an overall mean of 49.2% (Table 3). Egg mortality was slightly lower with a mean of 31.0.

Recall that the first instar densities used in calculating the mortalities were underestimates, which would cause an overestimation of egg mortality as well as an underestimation of first instar mortality. Therefore, the egg mortality is actually smaller than it appears in the Table and the first instar mortality is larger.

Most of the known factors had little apparent effect upon the populations (Table 4). The one that appeared important was parasitism in the second instar and pupa, accounting for a mean percent of 27.0 and 13.8, respectively.

Two parasitoid species (both Hymenoptera) were encountered. Over 95% of the parasitism was by *Cecidostiba dendroctoni* Ashmead (Pteromalidae).[5] The other parasitoid was not reared to adulthood and, therefore, not identified. The numbers of dead insects due to the two parasitoids were combined for calculation of apparent mortality.

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[5] Determined by B. D. Burks of the Systematic Entomology Laboratory, USDA, U.S. National Museum.

Table 3. Age-specific and total-generation mortality (percent) for all stages and generations of JPTB in 1970, 1971.

Stage	1970 Plantation No.				1971 Plantation No.				Mean
	1	2	3	4	1	2	3	4	
Egg	27.8	23.6	21.0	30.9	45.2	28.1	31.8	22.4	31.0
Larva I	10.4	13.1	11.8	7.2	27.2	20.9	14.2	30.2	16.9
Larva II	52.4	44.1	37.6	30.2	62.7	55.4	54.3	56.7	49.2
Pupa	18.3	30.8	27.6	17.9	40.0	13.5	34.0	31.1	26.6
Total Generation mortality	74.8	74.3	68.5	63.3	91.1	78.1	82.4	83.9	77.0

C. dendroctoni was easily recognized by its distinctive egg chorion, which is very durable. The adult parasitoid apparently works from outside the attacked tip, paralyzes the host with its ovipositor, and deposits the egg next to the host within the tip. The parasitoid larva feeds externally on the host. when it matures, it chews an exit hole through the side of the tip. Inasmuch as adults have been collected in early June. there must be at least one more generation per year on an alternate host. Most of the known hosts are scolytids (Muesebeck *et al.* 1951, Peck 1963), and this is the first record of the parasitoid upon the JPTB.

To examine the relative contribution of age-specific mortality to variance of total-generation mortality, the apparent mortality of each of the immature stages plus the apparent mortality due to parasitism in the second instar were plotted over total generation mortality. Also the coefficient of determination (r^2) of each relation was calculated (Fig. 4). Mortality in the second instar was the largest contributor to variance in the total generation mortality with an r^2 of 0.90. Most of this variation is contributed by parasitism with an r^2 of 0.83.

Relative mortality can be assessed by comparing the positions of the points on the graph as well as by examining Table 4. The egg stage has the second highest mean mortality rate but the lowest r^2. The first instar and pupal stages showed lower mean mortality rates but had higher correlations than the egg mortality. High apparent mortality in the second instar means high generation mortality; the same cannot be said of mortality in the remaining stages.

The apparent mortality was examined also to determine if there was an apparent density-dependent relation. To do this, the egg, larval, and pupal mortalities plus the mortality of the second instar due to parasitism, plus the total generation mortalities were plotted over egg density. A density-dependent relation was not observed.

IMPORTANCE OF MORTALITY FACTORS

Parasitism, the chief mortality factor in this study, accounted for 15 to 40% of the second instars and up to 25% of the pupae. It was the only mortality factor observed that contributed strongly to total generation mortality and the only factor that appeared to affect it. The parasitoid, *Cecidostiba dendroctoni,* exerted the most influence on the within-generation mortality but did not exhibit density-dependence. This parasitoid has more than one generation per year and necessarily depends upon other scolytids besides

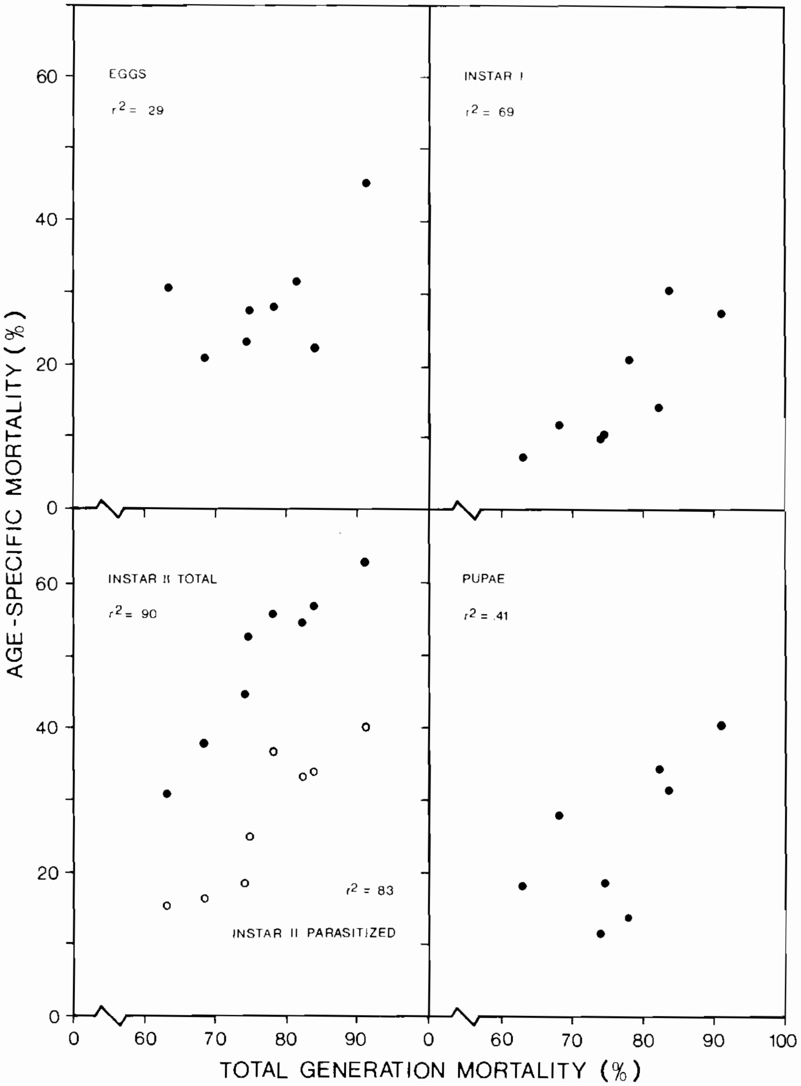

Fig. 4. The contribution of age-specific mortality to total-generation mortality for eggs, larvae, and pupae of the JPTB.

the JPTB, and thus should not necessarily be expected to respond to densities of the JPTB alone. Density-dependence was not observed in the within-generation mortality for any other factor affecting the JPTB either, but that does not mean that the JPTB is free of density-dependent influences altogether. For instance, mortality from adult dispersal might increase as population density rises. Perhaps, density-dependence was not found because the insect densities studied were within a range so narrow that density-dependence was not discernible.

Table 4. Factors causing mortality (percent) of the various stages of the JPTB in 1970, 1971.

Stage	Cause of mortality	1970 Plantation No.				1971 Plantation No.				Mean	Range
		1	2	3	4	1	2	3	4		
Egg	Desiccation	3.1	4.3	0.0	0.0	0.0	0.0	5.3	2.6	1.9	0.0- 5.3
	Pityophthorus	.0	.0	3.8	.0	.0	.0	.0	.0	.5	.0- 3.8
	Misc. and unknown	24.7	19.3	17.2	30.9	45.2	28.1	26.5	19.8	25.8	17.2-45.2
	Total	27.8	23.6	21.0	30.9	45.2	28.1	31.8	22.4	31.0	21.0-45.2
Larva I	Desiccation	0.3	0.0	0.0	0.3	1.5	3.5	0.0	0.6	0.8	0.0- 3.5
	Pitched	.9	.6	.2	.2	.8	.0	.0	.6	.4	.0- .9
	Chewed	.8	.9	.6	.2	2.3	.0	3.4	1.1	1.2	.0- 3.4
	Pityophthorus	.4	.0	.2	.2	.8	.0	.0	.0	.2	.0- .8
	Parasitism	.4	2.7	.4	.5	3.0	3.5	1.3	6.3	2.7	.4- 6.3
	Misc. and unknown	7.6	8.9	10.3	5.8	18.9	13.9	9.5	21.6	12.1	5.8-21.6
	Total	10.4	13.1	11.8	7.2	27.2	20.9	14.2	30.2	16.9	10.4-30.2

Larva II	Pitched	4.2	2.6	1.8	0.6	3.0	0.0	0.6	0.7	1.7	0.0- 4.2
	Chewed	4.9	2.9	2.0	3.1	.0	5.0	2.5	2.0	2.8	.0- 5.0
	Pityophthorus	.6	.0	.0	.4	.0	.6	.0	.0	.2	.0- .6
	Lep. larvae	.0	.0	.0	.4	.0	.0	.6	.7	.2	.0- .7
	Parasitism	24.6	18.3	15.9	15.0	39.8	36.1	32.8	33.6	27.0	15.0-39.8
	Misc. and unknown	18.0	20.3	17.9	10.6	19.9	13.7	17.7	19.8	17.2	10.6-20.3
	Total	52.4	44.1	37.6	30.2	62.7	55.4	54.3	56.7	49.2	30.2-62.7
Pupa	Pitched	4.3	2.6	5.3	3.3	5.0	0.0	0.0	0.0	2.6	0.0- 5.3
	Chewed	2.1	5.1	3.2	2.7	10.0	.0	.0	.0	2.9	.0-10.0
	Pityophthorus	3.2	.0	2.1	.0	.0	.0	.0	.0	.7	.0- 3.2
	Lep. larvae	.0	.0	1.1	.7	.0	.0	2.8	.0	.6	.0- 2.8
	Parasitism	2.1	12.8	6.4	6.6	25.0	13.5	25.5	18.7	13.8	2.1-25.5
	Misc. and unknown	6.5	10.3	9.5	4.6	.0	.0	5.7	12.4	6.1	.0-12.4
	Total	18.3	30.8	27.6	17.9	40.0	13.5	34.0	31.1	26.6	13.5-40.0

Other mortality factors contributed little to total generation mortality in any stage of the insect, but contributed up to 45% mortality within any one stage. In some instances the actual mortality factors were not determined. Desiccation, indicated by a shriveled appearance of the insect and a dried internal appearance of the tip, was noted during the egg period and first larval stadium. Some of the other undetermined mortality may also have been due to desiccation. The significance of desiccation is not certain. Perhaps the size of the shoot tips or stresses in the tree may contribute to water losses and premature wilting of the tissues.

Sometimes the larvae and pupae were engulfed in resin ("pitched") within the shoots. This was encountered most often after rainy weather. Apparently the resin within the dead tip absorbs water and expands or turgor pressure increases and enhances resin flow. Whatever the cause, the insect is unable to cope with the excess resin.

Occasionally larvae and pupae were disfigured ("chewed") by some other inhabitant of the shoot. Most mortality in this category was probably the result of sibling cannibalism. The larvae particularly exhibit aggressive and antagonistic behavior to siblings. Many dead insects were encountered when larval feeding galleries intersected. Callow adults may also have killed some of the less developed insects in the shoots as well. Adult bark beetles, *Pityophthorus* sp., and an unidentified larval lepidopteran may also have killed some larvae as they were present with disfigured larvae or pupae.

Mites, which were occasionally observed in the galleries, may have caused a small amount of mortality. Their size made them difficult to spot amoung the debris and difficult to relate to dead insects.

In conclusion, only one factor is known to be important in influencing total generation mortality of the JPTB–parasitism by *C. dendroctoni*. Other factors such as desiccation and sibling cannibalism in the egg and first instar may be important but their impact is presently too small to evaluate.

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