

Interpreting Some Mortality Factor Interactions Within Mountain Pine Beetle Broods¹

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ABSTRACT

The mix of mortality factors within *Dendroctonus ponderosae* Hopkins populations was analyzed by using crude and general probabilities of death from specific causes and from all causes, within specified life stages and for the generation as a whole. These analyses provide the basis for discussion of actual results and some hypothetical cases. Control efforts should accentuate one or more of the controllable causes of mortality or, perhaps eliminate one or more causes, if those remaining would be accentuated. The effect on total mortality of such action may depend heavily on the nature of the interactions among the causes. Knowledge of how mortality factors operate singly and particularly in mix will permit additional characterization of the population dynamics of the mountain pine beetle.

The mountain pine beetle, *Dendroctonus ponderosae* Hopkins, is a native pest that has a substantial impact upon the lodgepole pine, *Pinus contorta* Douglas, ecosystem. Historically, the beetle has infested large areas of lodgepole pine, depleting stands by periodically killing the largest, most vigorous trees. The extent of such losses, in large part, is a function of diameter distribution of the green stand, elevation, phloem thickness (food supply within trees), current insect population density, and the mix of mortality factors operating on the insect population. The last variable, mortality mix, is the focal point of interest here, since it may have a bearing on the potential for population controls.

Attack density of the mountain pine beetle is related to tree diameter and provides the basis for brood production. Amman (1969, 1973) found that brood production in phloem of a given thickness is inversely related to elevation, which in turn is associated with temperature, particularly winter temperature. Mountain pine beetle brood production is relatively low at elevations above 2,400 m; consequently survival of lodgepole pine is much higher. Throughout the elevation zones sampled, the probability of lodgepole pine being attacked by the mountain pine beetle is a linear function of the elevation of the stand (Amman and Baker 1972, Amman et al. 1973). This finding held even in the presence of an ample food supply (thick phloem in trees of large diameter) at high elevations. However, at low elevations, where growing conditions are optimal for the beetle, brood production was directly related to food quantity. Thus, the foregoing information substantiates the hypothesis that food is limiting to population growth at low elevations and temperature is limiting at high elevations.

As stated in an earlier report (Cole 1973), crowding can have either a direct or an indirect effect on mortality. As crowding increases, relative food supply decreases; as a result, brood mortality increases. Within a given food supply (thin phloem), crowding shortens the developmental period of the surviving

larvae and decreases the reproductive capacity of the female adult beetle. Conversely, within a given large quantity of food, the developmental period lengthens, resulting in greater female survival.

Temperature also has a direct effect upon larval (brood) survival, particularly during the winter. This effect is tempered by the amount of insulation provided the beetle brood by the depth of bark, which is related to tree diameter. Trees of small diameter usually have thin bark that provides less insulation and results in greater brood mortality than occurs in trees of large diameter. An increased attack density by the beetle could decrease life expectation during the 2nd and 3rd life stages by accelerating growth and causing larvae to overwinter in a stage not in synchrony with winter survival ability (Cole 1973). For example, winter-hardiness of larvae is dependent upon life stage at the onset of winter. Should larvae enter winter out of synchrony, they would be unprepared to survive low temperatures.

Parasites and predators as regulators, controlling factors, or both of the mountain pine beetle have been studied for many years. In the past, however, inability to evaluate the effects of parasites and predators upon the mountain pine beetle has been an obstacle to biological control efforts.

Other mortality factors relative to mountain pine beetle population dynamics are rate of drying of phloem (again correlated with thickness), age of tree, woodpeckers, resin flow (pitching), and pathogens. Main effects of these and other factors have been determined independently and, in a few studies, interactions have been identified.

Methods

All mortality factors, known or suspected, were sampled by life stages of the 1971-72 beetle generation and by tree diameter and phloem thickness strata. The infested tree was assumed to be the sampling unit. To minimize between-tree variance, trees were stratified by diameter. The random sampling technique described by Carlson and Cole (1965) focuses on critical within-tree measurements

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and sampling efforts. Objective of within-tree measurement, was to characterize mortality by cause and, for reasons discussed later, life stages.

In spite of the desirability of the nondestructive X-ray sampling technique (Amman and Rasmussen 1974), it was necessary to find and count insects in their bark environment by destructive sampling. In taking subsamples of infested bark, the following stratification was used:

Two 15.2x15.2-cm samples were taken per tree^a and the insect population was recorded as individuals living or dead (by cause of death) within developmental stages of the beetle. Five trees were sampled from each of 2 phloem thickness strata: less than and greater than 0.28 mm, within each of 3 diameter strata; less than 22.9 cm, 25.4-35.6 cm, and greater than 38.1 cm, within each of 3 habitat strata, *Calamagrostis*, *Pachistima*, and *Vaccinium*. These habitat types can be generally related to elevational zones of 1,800 m, 2,250 m, and 2,550 m. A total of 180 samples were taken per sample date. Thus, a

^aThese were actually restricted to the bark area near breast height. However, they would have more appropriately represented the insect population within the tree had they been better distributed over the attacked area of the bole in proportion to surface area. Further, total bark area in subsamples should have been sufficient to provide a relatively large insect count in the early stages, say 500 eggs, larvae, or both. Here, actual counts were relatively small, averaging about 60 per sample. A large insect count would have permitted estimation of percent mortality within binomial confidence intervals of ca. ± 80% about the estimated percentage for mortality cause, when the percentage was either very low (5%) or high (95%). The interval would shrink to about ± 12% when the percentage for a cause approached 50%.

total of 900 samples were taken during one generation of the beetle.

Previous life-table work indicates that observations at 5 developmental intervals within a generation are enough to detect population mortality by cause within the beetle's developmental stages. Pertinent developmental intervals within the life cycle for observations of mortality are as follows:

Late fall.—Sample fixes the base population and includes eggs and 1st and 2nd instars.

Early spring.—Sample establishes the number of larvae that survived the winter.

Late spring.—Sample determines the late larval and pupal populations.

Early summer.—Accounts for callow adults and new adults.

Late summer.—The final count for emerging adult population, obtained by caging the sample area.

Survival and mortality estimates within the 3 diameter strata were first based on brood-per-attack and then adjusted linearly to a common attack density; 4 attacks per 0.09 m².

Results

The following example deals only with crude and general probabilities of death and offers some insight into population control potential.

Crude probability is that probability of death from a specific risk in the presence of all other risks acting in a population and is that mortality witnessed

Table 1.—Population survival and mortality by cause for a generation of mountain pine beetle.^a

Tree dbh (cm)	Observation	Number surviving	No. dead	Number of dead larvae by mortality cause							
				Crowding	Parasites and predators	Temperature	Drying	Pitch	Pathogens	Woodpeckers	Unknown
22.86	0	68	0	0	0	0	0	0	0	0	0
	1	63	5.00	1.00	0.70	0	0	2.70	0	0	0.60
	2	14	49.00	.98	0	34.79	5.88	0	0	7.35	0
	3	10	4.00	.11	.27	0	3.62	0	0	0	0
	4	9	1.00	.05	.39	0	.52	0	0.05	0	0
	5	8	1.00	0	.63	0	.13	0	0	0	.25
Total			60.00	2.14	1.99	34.79	10.15	2.70	0.05	7.35	0.85
30.48	0	70	0	0	0	0	0	0	0	0	0
	1	63	7.00	0	0	0	0	1.61	0	0	5.39
	2	18	45.00	11.25	0	32.85	0	.90	0	0	0
	3	12	6.00	0	5.00	0	0	0	0	0	1.00
	4	10	2.00	.50	1.50	0	0	0	0	0	0
	5	9	1.00	0	1.00	0	0	0	0	0	0
Total			61.00	11.75	7.50	32.85	0	2.51	0	0	6.39
38.10	0	72	0	0	0	0	0	0	0	0	0
	1	62	10.00	3.80	2.20	0	0	0	1.10	0	2.90
	2	24	38.00	9.50	3.04	21.28	0	0	0	4.18	0
	3	15	9.00	1.50	0.58	0	6.46	0	0	0.46	0
	4	13	2.00	0	1.37	0	0.23	0	0	0.27	0.13
	5	12	1.00	0	1.00	0	0	0	0	0	
Total			60.00	14.80	8.19	21.28	6.69	0	1.10	4.91	3.03

^a Adjusted to equal attack density.

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 13.7% 8.4% 42.3 8.0% 2.5% .5% 5.8% 5.9%

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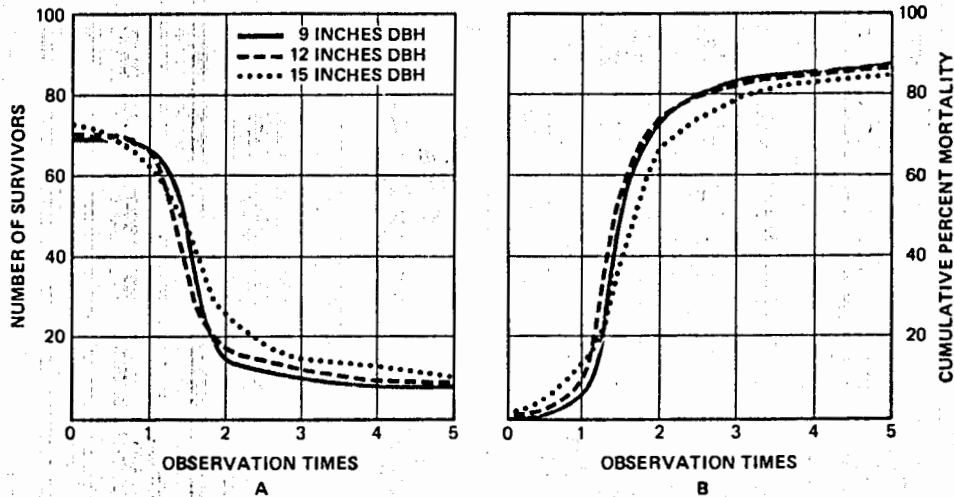


FIG. 1.—Number of survivors and cumulative percent mortality within mountain pine beetle generation. (9 in. = 22.86 cm; 12 in. = 30.48 cm; and 15 in. = 38.10 cm.)

in the uncontrolled insect population. *General probability* is that probability of death from all causes determined either within a specified life stage or for the generation as a whole (Chiang 1968).

Survival increased with diameter, which reflects expectation. In spite of the fact that these populations entered winter at practically the same level, more beetles finally emerged from trees of larger diameters than smaller (Table 1).

The general survival trend over 1 generation shows that the greatest change in beetle populations occurred during the winter and early summer. The population fell at approximately equal rates and magnitude between sample periods 1 and 2, and again between 3 and 4, and 4 and 5, when population survival curves approached a lower asymptote (Fig. 1). With this background on population levels, let us look to the general probabilities of an insect surviving the growth periods (Table 2).

In populations within the 22.86- and 30.48-cm trees, an insect had an 0.13 probability of reaching the adult stage. In populations within 38.10-cm trees, an insect had an 0.16 probability of maturing. These probabilities are rather high compared to past life tables, but this report deals with high populations. This trend of greater probability of survival within the larger tree diameters is reflected over each life stage of the population. Simply stated, a beetle has a better chance to survive in trees of larger diameter, even when the phloem is thin, as in this case.

In Fig. 2, general probabilities of death are shown in the rear profile.³ Those in the foreground are crude probabilities of death (by cause). In the 5th life stage, for example, general mortality was 13%

³Smoothed trends have been drawn through mortality estimates for discrete points in time to facilitate visual appraisal of mortality trends over time. Mortality read from these graphs, however, is only pertinent at the observation points in time.

within the 9-in. tree population. Of this 13%, the probability that death was caused by parasites and predators was 0.63; by drying of phloem, 0.13; and from unknown causes, 0.125. If graphs are interpreted in this manner, some points of general interest are evident. Temperature when followed by drying dominates the mortality picture. If a cold winter effect is accompanied by severe drying of the phloem, the combinatorial effect drastically reduces the population. Also, the effects of crowding and of parasites and predators are reduced as a result of winterkill. Woodpeckers apparently respond to greater beetle population density during the winter and, in addition, may be responsible for increased drying and associated mortality.

Control efforts should accentuate one or more of the controllable causes of mortality or, perhaps, eliminate one or more causes, if those remaining would be accentuated. The effect on total mortality (per-unit-bark area) of such alternative action may depend heavily on the nature of the interactions between the causes.

For example, if high mortality from winter temperatures occurs, it might be expected that mortality from crowding, along with mortality from parasites and predators, would be minimal, but that mortality from, or in the presence of, drying of phloem could increase. In the absence of such cold weather, mortality from crowding and from parasites and predators would be expected to increase. The interaction pattern between these two competing risks is without expectation; consequently, mortality from drying might be reduced.

Discussion

If the rather coarse expectations outlined here have any basis in fact, there is little hope that any theoretical model would represent these interactions

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2 examples

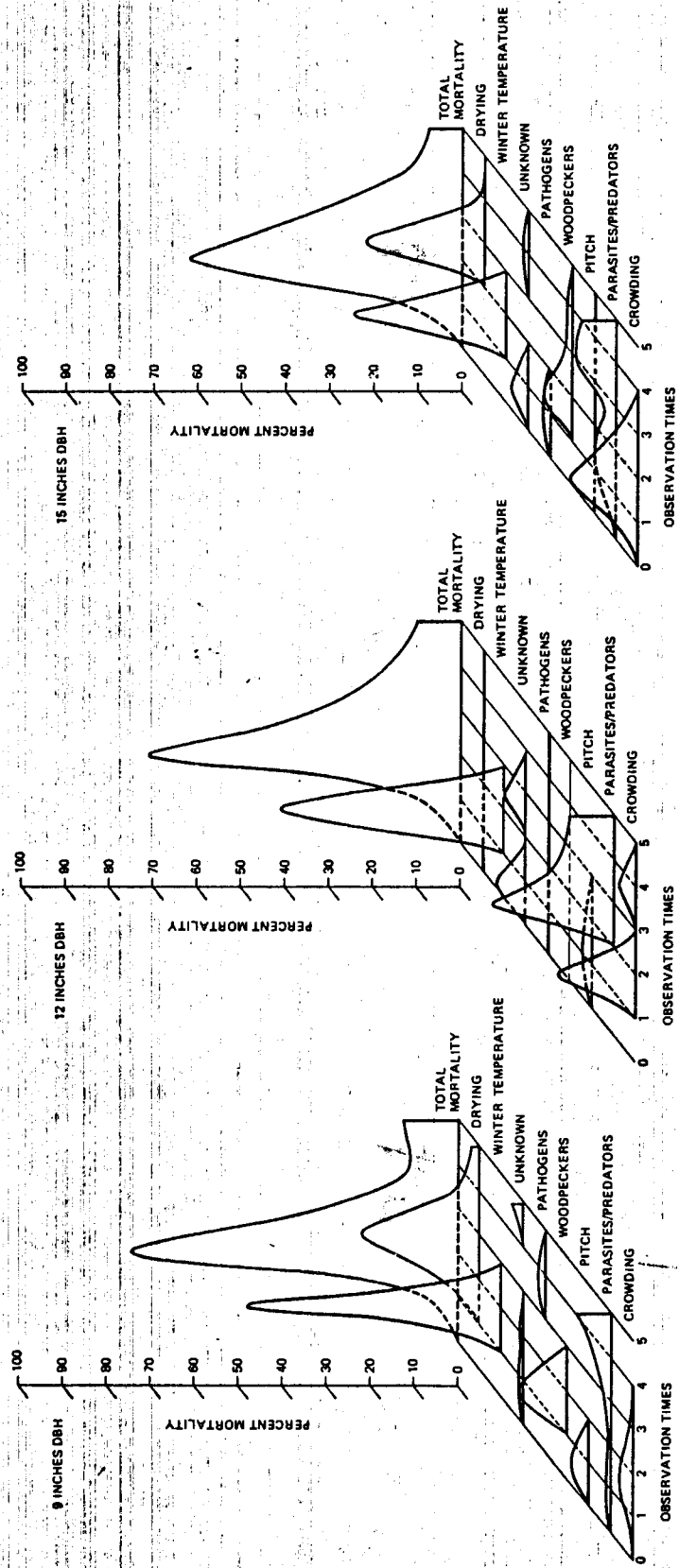


FIG. 2.—Proportional mortality by factor and life stage within a mountain pine beetle generation. (9 in. = 22.86 cm; 12 in. = 30.48 cm; and 15 in. = 38.10 cm.)

Table 2.—Crude probabilities of death due to a specific mortality factor in the presence of all other factors over one generation of the mountain pine beetle.

Tree dbh (cm)	Observation	General probabilities		Crude probabilities							
		Survival	Death	Crowding	Parasites and predators	Temperature	Drying	Pitch	Pathogens	Woodpeckers	Unknown
22.86	1	0.93	0.07	0.20	0.14	0	0	0.54	0	0	0.12
	2	.24	.76	.02	0	0.71	0.12	0	0	0.15	0
	3	.16	.84	.03	.07	0	.91	0	0	0	0
	4	.15	.85	.05	.39	0	.52	0	0.05	0	0
	5	.13	.87	0	.63	0	.13	0	0	0	.25
Crude probability/generation				.03	.03	.58	.17	.05	<.01	.12	.02
30.48	1	.90	.10	0	0	0	0	.23	0	0	.77
	2	.26	.74	.25	0	.73	0	.02	0	0	0
	3	.17	.83	0	.83	0	0	0	0	0	.17
	4	.14	.86	.25	.75	0	0	0	0	0	0
	5	.13	.87	0	1.00	0	0	0	0	0	0
Crude probability/generation				.19	.12	.54	0	.04	0	0	.10
38.10	1	.86	.14	.39	.22	0	0	0	.11	0	.29
	2	.33	.67	.25	.08	.56	0	0	0	.11	0
	3	.21	.79	.16	.06	0	.71	0	0	.05	0
	4	.18	.82	0	.07	0	.12	0	0	.14	.07
	5	.16	.84	0	1.00	0	0	0	0	0	0
Crude probability/generation				.25	.14	.35	.11	0	.02	.08	.05

appropriately. It seems more likely that we will have to depend heavily upon empirical evidence. Controlled experiments do not seem to be an attainable source of interaction information at present. About the only practical alternative would involve data generated from large-sample, within-tree counts of insects-per-unit of bark area. The data set per tree, then, would consist of count-by-mortality cause at each sampling time. Given an array of such data sets, and mortality combinations that were sufficiently variable, an interaction-sensitive regression analysis might at least serve to establish 4- or 5-dimensional relations useful for structuring control strategies.

In the hypothetical graph (Fig. 3), it might be

that total mortality would be accentuated by high crowding of larvae after a cold winter. The use of pheromones to induce artificial clustering of attacks on the tree could intensify this effect.

Crude probabilities can be estimated directly, but net and partial crude probabilities (Chiang 1968) can only be estimated through their relations with the crude probabilities. This restriction does not necessarily negate the original objective, but illustrates the incompleteness of utilizing net and partial crude probabilities at this time. Only the second portion of net probability definition, "the probability of death if a specific risk is eliminated from the population," is oriented to a practical treatment alternative for insect control. Even then, the poten-

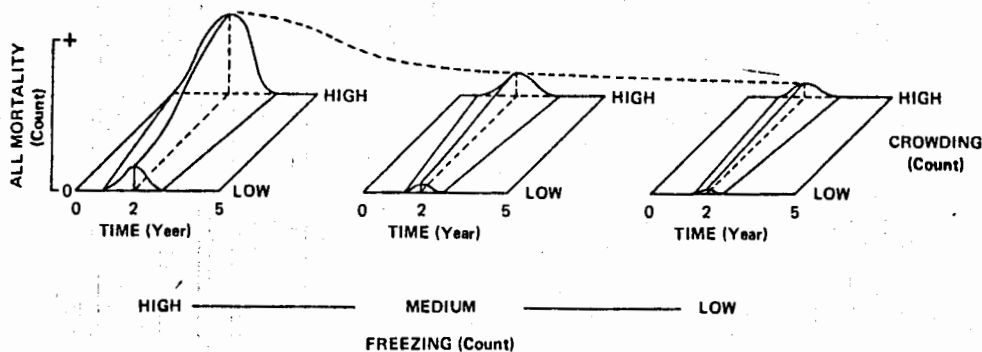


FIG. 3.—Hypothetical temperature/crowding relation as potential pheromone strategy.

tial for this alternative is low. Under field conditions, no risk of death can be completely eliminated. The same follows for partial crude probability (Chiang 1968). He assumed that increases in specified mortality causes are accompanied by proportionally distributed reductions in the remaining causes. I feel certain that interactions are likely to exist and may not be well represented by this assumption. To assume that a rise in any particular source of mortality results from exclusion of all but the source being evaluated is also intuitively inconsistent. However, this type of information might be useful for possible manipulation of a beetle population. For example, larval mortality might be increased by removal of a substantial portion of the food supply. On the other hand, given other factors at a known level, the probability of death from a specific cause or factor would appear to be more useful for both simulation and manipulation. Highly specialized experimentation is needed to provide empirical quantification of net and partial crude probabilities.

Once we know how mortality factors operate, we will know what is to be measured in order to characterize population dynamics. We then must be able to measure the entire population within an infested stand and to predict, by strata, the course of that infestation.

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