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PINE BEETLE POPULATIONS: A LONG-TERM ANALYSIS

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INTRODUCTION

Through the years, discussion has persisted about the value of mortality factors as regulators and/or controlling factors within populations, particularly insect populations. The possibility of manipulating mortality factors to biologically control insect populations has had an appeal that has given direction to thought of integrated pest management proposals.

This paper deals with the probabilities of loss caused by a single mortality factor acting alone or in combination with other factors. In any population study, there remains "unknown" mortality that is not readily definable or measurable simply because measurement techniques are inadequate. Previous work by COLE (1962, 1973a, 1973b, 1974 and 1975) dealt with measurement and evaluation of selected mortality factors or with effects of these factors over a short period of time. The study reported here deals with known factors over three infestation levels for 13 years. The approach was to determine the probability of death, using competing risks analysis of life tables (CHIANG, 1968) to evaluate the effects of these factors of mortality—singly and in combination. In the end, it will be important to note the variability (or lack of it) in the amount of mortality caused by these factors over time.

DATA SOURCE

All known or suspected mortality factors were recorded by life stages of the mountain pine beetle for each generation year between 1964 through 1977, and by tree diameter and stage of infestation; i. e., preepidemic (1964-70), epidemic (1971-73) and postepidemic (1974-77). This was done in concurrence with the model developed by COLE *et al.* (1976). The infested tree was the sampling unit and, to minimize between-tree variance, trees were stratified by diameter classes; i. e., 23 cm d. b. h. and less, 28 to 36 cm d. b. h., and 38 cm d. b. h. and greater. The random sampling technique described by CARLSON and COLE (1965) focused on critical within-tree measurements and sampling efforts. The objective of the within-tree measurement was to characterize mortality by cause and life stages of the mountain pine beetle.

Two 15.2×15.2-cm samples were taken at breast height per tree and the insect population was recorded as individuals living and dead (by cause of death) within

developmental stages of the beetle. Previous life table work indicated that observations at five developmental intervals within a generation were sufficient to detect population mortality by cause of death within the beetle's developmental stages. Pertinent developmental intervals within the life cycle for observations of mortality are as follows:

0. Base population: The total number of eggs laid in starting population.
1. Late fall: Sample includes eggs and 1st and 2nd instar larvae that will enter winter.
2. Early spring: Sample establishes the number of larvae that survived the winter.
3. Summer: Sample determines the late larval and pupal populations.
4. Late summer: The final count of emerging adult population, obtained by caging the sample area.

Data were taken from infestations on three national forests: Wasatch, Teton, and Targhee. Periods of infestations by intensity were determined from the mountain pine beetle model (COLE *et al.*, 1976) and spanned years as follows:

- Preepidemic (0-10% of trees killed annually) 7 years (1964-1970)
- Epidemic (10-45% of trees killed annually) 3 years (1971-1973)
- Postepidemic (0-10% of trees killed annually) 4 years (1974-1977)

A special case occurred on the Cache National Forest in northern Utah. The mountain pine beetle has been active in this particular area from 1971 to the present time, or longer. The population has remained as a "high endemic" level over this period of time, as will be discussed later in this paper, and shows some particularly interesting relationships between the causes of mortality and the host populations.

DATA ANALYSES

The competing risks analysis (CHIANG, 1968) was used in the majority of analyses because death is not a repetitive event and is usually attributable to a single cause. Various risks, however, compete for the life of an individual and must be considered in cause-specific mortality studies. This analysis is well reported in the literature and was used by this author in previous publications (COLE, 1974, 1975). Specifics of the analysis will not be described here, except to state a few definitions:

- Risk of dying—a mortality factor present in a population prior to death of an individual within that population.
- Cause of dying—a mortality factor that actually resulted in the death of an individual in that population.
- Crude probability—the probability of death from a specific cause in the presence of all other risks acting in a population. It is also that mortality witnessed in the uncontrolled insect population and that which we measured during sampling for construction of the life table for the mountain pine beetle.

General probability—probability of death (or survival) when the cause of death is not specified.

The abridged cohort life table, in which a generation of beetles is sampled at particular points in time, was used throughout our study of mortality factors within the mountain pine beetle populations. The abridged cohort life table was not followed in its strictest sense because of destructive sampling. Death of the last individual was not recorded. Instead, the emergence of the adult beetle was equated with the end of life for that particular cohort. Consequently, flight mortality was not considered. In addition, we assumed that all individuals within the sample were subject to the same forces of mortality (risks) and that the survival of one individual was independent of the survival of any other group. By making this assumption, we avoided unnecessary complications (CHIANG, 1968).

RESULTS AND DISCUSSION

The basic data for the construction of life tables and competing risk analysis for the mountain pine beetle are shown in Table 1 and graphically in Figure 1. These data were stratified by tree diameter class and by period of infestation. Population numbers shown in both table and figure are on a sample basis; i. e., 15.2×15.2 cm of bark area.

Probabilities of survival and life expectations

Beetle populations were greater numerically in the largest diameter tree class. The population change among tree diameter classes in the preepidemic stage showed a slight reversal; i. e., the starting population was greatest in the 30-cm trees, but survival was greatest in the 38-cm trees. Epidemic populations followed expectation,

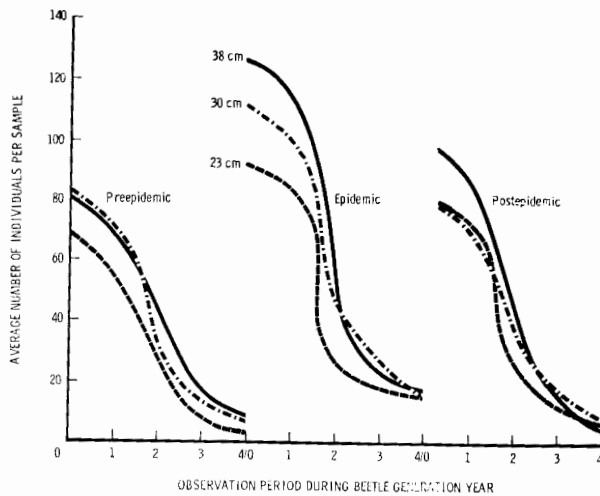


Fig. 1. Mountain pine beetle brood survival by observation, by tree diameter class, by stage of infestation.

Table 1. Population survival and mortality by cause by tree diameter class and stage of infestation for the mountain pine beetle, based on sample.

Infestation	Developmental interval	No. alive	No. dead	WC	BC	CL	CD	MD	PA	WP	T	D	PI	UNK	Numbers per sample ¹									
															WC	BC	CL	CD	MD	PA	WP	T	D	PI
Tree diameter class: 23 cm																								
Preepidemic	0	69.64	0	0	0	0	0	0	0	0	0	0	0	0	0									
	1	55.37	14.27	1.10	1.08	0	0	0.25	0	0	0.26	0	0	0	11.58									
	2	30.36	25.01	1.23	1.25	0.03	0	0.70	0	0.58	13.78	1.00	0	0	6.44									
	3	8.21	22.15	0.71	1.11	0.01	0.35	0.26	0.39	0.63	7.07	0.31	0.11	0.11	11.20									
	4	3.33	4.88	0	0	0	0	0	0	0	0	0	0	0	4.88									
Sum		66.31	3.04	3.44	0.04	0.35	1.21	0.39	1.21	21.11	1.31	0.11	0.11	34.10										
Epidemic	0	93.60	0	0	0	0	0	0	0	0	0	0	0	0										
	1	85.78	7.82	0.75	0.73	0	0	0.48	0	0.10	1.03	0	0.20	4.53										
	2	27.38	58.40	1.30	2.33	0	0	0.38	0.05	1.15	37.02	8.61	0	7.56										
	3	19.35	8.03	0.15	0.35	0.03	0.30	0.13	0.18	0.20	0.17	0.67	0.03	5.82										
	4	15.21	4.14	0	0	0	0	0	0	0	0	0	0	4.14										
Sum		78.39	2.20	3.41	0.03	0.30	0.99	0.23	1.45	38.22	9.28	0.23	0.23	22.05										
Postepidemic	0	80.43	0	0	0	0	0	0	0	0	0	0	0	0										
	1	69.96	10.47	1.97	2.95	0.15	0.03	1.84	0.20	0.03	2.12	0.11	0.32	0.75										
	2	26.84	43.12	0.20	0.86	0.04	0.01	0.85	0.14	1.65	12.39	4.80	0.45	21.73										
	3	13.24	13.60	0	0	0.08	1.08	0.06	0.08	0.62	0.46	4.34	0.02	6.86										
	4	6.00	7.24	0	0	0	0.02	0	0.02	0	0	0.07	0	7.13										
Sum		74.43	2.17	3.81	0.27	1.14	2.75	0.44	2.30	14.97	9.32	0.79	0.79	36.47										

Table 1. (2)

Infestation	Developmental interval	No. alive	No. dead	WC	BC	CL	CD	Numbers per sample ¹						
								MD	PA	WP	T	D	PI	UNK
Tree diameter class: 30 cm														
Preepidemic	0	83.68	0	0	0	0	0	0	0	0	0	0	0	0
	1	70.78	12.90	0.33	0.58	0	0.02	1.11	0.84	0	0.03	0	0	9.99
	2	32.70	38.08	0.51	2.00	0	0	1.35	0.27	2.33	15.33	0.35	0.14	15.80
	3	15.46	17.24	0.55	0.41	0.03	0.36	0.86	1.01	1.58	6.15	0.07	0	6.22
	4	7.42	8.04	0	0	0	0	0	0	0	0	0	0	8.04
Sum		76.26	1.39	2.99	0.03	0.38	3.32	2.12	3.91	21.51	0.42	0.14	40.05	
Epidemic	0	113.48	0	0	0	0	0	0	0	0	0	0	0	0
	1	103.65	9.83	1.63	2.10	0	0	1.65	0	0.23	1.27	0	0.15	2.80
	2	49.48	54.17	0	3.25	0	0	0.43	0.70	1.38	29.80	6.70	0	11.91
	3	30.04	19.44	0	0	0.10	0.48	0.15	0.05	0.68	0.10	0.93	0	16.95
	4	15.14	14.90	0	0	0	0	0	0	0	0	0	0	14.90
Sum		98.34	1.63	5.35	0.10	0.48	2.23	0.75	2.29	31.17	7.63	0.15	46.56	
Postepidemic	0	80.15	0	0	0	0	0	0	0	0	0	0	0	0
	1	66.99	13.16	2.50	1.54	0.03	0.08	2.10	0.10	0.18	3.10	0	0	3.53
	2	34.21	32.78	0.40	0.69	0.03	0.17	1.68	0.28	0.72	12.15	3.01	0.11	13.54
	3	16.78	17.43	0	0	0.21	0.35	0.07	0.78	0.64	0.41	3.52	0	11.45
	4	8.33	8.45	0	0	0	0	0	0	0	0	0.03	0	8.42
Sum		71.82	2.90	2.23	0.27	0.60	3.85	1.16	1.54	15.66	6.56	0.11	36.94	

with population density directly related to tree diameter. During the postepidemic infestation period, an inverse trend compared to the endemic period occurred. The 38-cm diameter class trees contained not only the largest starting populations, but showed the greatest proportional mortality. The trend between the 23- and 30-cm diameter classes was similar. This could be since the few 38-cm diameter trees remaining after the epidemic simply could not support and/or produce much beetle population because of excessive drying resulting from the increased attack density (COLE *et al.*, 1976).

The general survival trend within each stage of infestation for each diameter class was approximately of like magnitude with the greatest mortality occurring between the late fall and spring periods; i.e., winter kill.

The probability of an individual surviving the entire growth period (egg to adult) was determined for each diameter class within each stage of infestation (Table 2 and Figure 2), i.e., when the cause of death is not specified, $P_{ij} = Pr$ (an individual alive at age x_i will survive to age x_j), $i \leq j$; $i, j = 0, 1, \dots$. The probability increased

Table 2. General probabilities of an individual surviving the entire growth period from egg to adult stages by tree diameter class and stage of infestation.

Stage of infestation	Tree diameter class		
	23 cm	30 cm	38 cm
Preepidemic	0.00196	0.00551	0.00850
Epidemic	0.00900	0.01403	0.00850
Postepidemic	0.00360	0.00776	0.00223

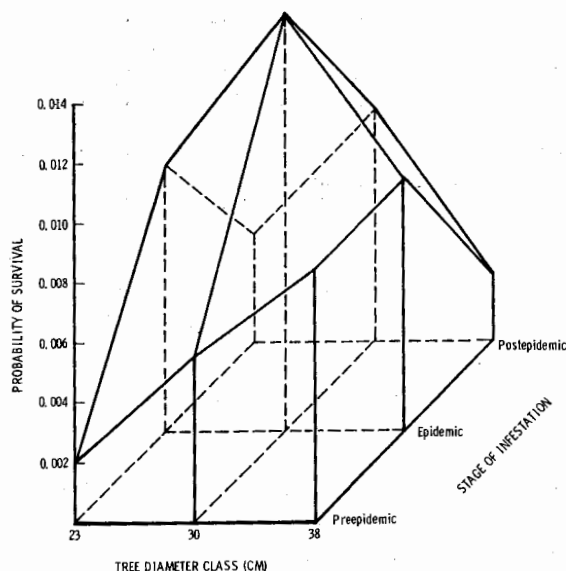


Fig. 2. Probability of any one egg surviving to the adult stage by tree diameter class over stage of infestation.

from the 23- to the 38-cm trees within the preepidemic period; during the epidemic and postepidemic periods, the probability peaked within the 30-cm diameter class and was approximately equal in the 23- and 38-cm diameter classes. If we consider the habitat and food supply only, then these trends are not unusual and relate well to the expected survival by phloem thickness within diameter class distributions within a stand structure (AMMAN, 1969; COLE and AMMAN, 1969). As the infestation progresses, these probability-of-survival trends reflect the change in tree distribution and characteristics. One might interpret this to mean that if the probability of survival increases over diameter class during the preepidemic stage of infestation then an epidemic is likely to develop.

The peaks within the 30-cm diameter class during the epidemic and postepidemic periods of infestation probably occur because the larger diameter trees have been killed, leaving either fewer trees in each case to contribute to the survival data or residual trees within this diameter class are slower growing and therefore provide less food (thinner phloem) for beetle survival. These assumptions will be carried further as we develop the influence and role of the mortality factors.

Life expectations

Life table studies focus centrally upon life expectation and survival rates. By comparing these, we can evaluate the intensity of risks measured during the stages of population growth. The rate of survival (or conversely, mortality) can more or less govern life expectation. For the mountain pine beetle, the total life interval from egg to egg can be assumed to be approximately 365 days. High mortality rates can lessen life expectation, whereas low mortality rates could lengthen life expectation. Table 3 shows an abridged life table for determining proportions of death and survival, life expectation, and the variances for both.

Life expectations for the mountain pine beetle populations fluctuate somewhat within diameter classes among stages of infestations and among diameter classes within each stage of infestation, but generally increase from the smallest to the largest diameter class and peak over time during the epidemic stage (Figure 3). Exceptions are within observation times of brood development. Life expectation within the 30-cm diameter tree class appears to be consistent. Less change would indicate that the 30-cm diameter class could well be the carrying habitat for the mountain pine beetle. A strong positive trend over diameter occurred in the preepidemic stage. This trend disappears in the epidemic and postepidemic stages with survival being higher in the 30-cm class. Survival peaks during the epidemic stage in all diameter classes. These data suggest that the high survival in the 38-cm trees during the preepidemic stage triggers the epidemic. The increased survival in the 30-cm trees during the epidemic and postepidemic stages suggests that once the epidemic starts this diameter class is the most important contributor to beetle population increases.

The greatest life expectations occur within the epidemic stage of infestation and

Table 3. The abridged cohort life table and life expectations for mountain pine beetle populations by tree diameter class within stage of infestation.

Infestation/tree diameter class	Interval length (days) x_i to x_{i+1}	Number live at start of x_i (l_i)	Number dying during x_i to x_{i+1} (d_i)	General Surviving x_i to x_{i+1} (p_i)	Dying x_i to x_{i+1} (q_i)	Variance ($Vp_i = Vq_i$)	Fraction of last interval of life (a_i)	Life expectations at age x_i (e_i)	Life expectations observed at age x_i (Ve_i)	Standard error (SEe_i)
Preepidemic	30	69.64	14.27	0.795	0.205	0.00234	0.50	158.26	137.58	11.73
	180	55.37	25.01	0.436	0.564	0.00444	0.50	165.18	124.33	11.15
	60	30.36	22.15	0.118	0.882	0.00343	0.50	47.10	8.24	2.87
	30	8.21	4.88	0.048	0.952	0.00557	0.50	33.25	6.34	2.52
	60	3.33	3.33	0	1.000	—	—	30.00	—	—
	30	83.68	12.90	0.856	0.154	0.00158	0.50	163.01	107.11	10.35
30 cm	180	70.78	38.08	0.391	0.609	0.00336	0.50	159.99	90.67	9.52
	60	32.70	17.24	0.185	0.815	0.00461	0.50	61.49	19.33	4.40
	30	15.46	8.04	0.089	0.911	0.00524	0.50	36.60	7.21	2.69
	60	7.42	7.42	0	1.000	—	—	30.00	—	—
	30	82.56	12.58	0.848	0.152	0.00156	0.50	176.40	131.83	11.48
	180	69.98	29.62	0.489	0.511	0.00357	0.50	175.42	115.54	10.75
38 cm	60	40.36	23.40	0.205	0.795	0.00404	0.50	58.11	15.19	3.90
	30	16.96	8.71	0.100	0.900	0.00531	0.50	36.89	7.42	2.72
	60	8.25	8.25	0	1.000	—	—	30.00	—	—

Table 3. (2)

Infestation/tree diameter class	Interval length (days) x_i to x_{i+1}	Number live at start of x_i (f_i)	Number dying during x_i to x_{i+1} (d_i)	General probability Surviving x_i to x_{i+1} (p_i)	Dying x_i to x_{i+1} (q_i)	Variance ($Vp_i = Vq_i$)	Fraction of last interval of life (a_i)	Life expectations at age x_i (e_i)	Life expectations observed (Ve_i)	(SEe _i)
Epidemic	30	93.60	7.82	0.916	0.084	0.00082	0.50	169.95	72.21	8.50
	180	85.78	58.40	0.293	0.707	0.00241	0.50	146.43	57.61	7.59
	60	27.38	8.03	0.207	0.793	0.00600	0.50	86.80	54.80	7.40
	30	19.35	4.14	0.162	0.838	0.00702	0.50	50.37	18.17	4.26
	60	15.21	15.21	0	1.000	—	—	30.00	—	—
	30	113.48	9.83	0.913	0.087	0.00070	0.50	181.14	82.90	9.10
30 cm	180	103.65	54.17	0.436	0.564	0.00237	0.50	166.90	71.68	8.47
	60	49.48	19.44	0.265	0.735	0.00394	0.50	71.09	22.26	4.72
	30	30.04	14.90	0.133	0.867	0.00384	0.50	37.68	5.60	2.37
	60	15.14	15.14	0	1.000	—	—	30.00	—	—
	30	128.88	11.65	0.848	0.152	0.00100	0.50	173.31	77.71	8.82
	180	117.23	66.05	0.489	0.511	0.00213	0.50	159.04	57.41	7.58
38 cm	60	51.18	24.88	0.205	0.795	0.00318	0.50	68.14	16.79	4.10
	30	26.30	9.22	0.100	0.900	0.00342	0.50	44.22	6.84	2.62
	60	17.08	17.08	0	1.000	—	—	30.00	—	—

Table 3. (3)

Infestation/tree diameter class	Interval length (days) x_i to x_{i+1}	Number live at start of x_i (l_i)	Number dying during x_i to x_{i+1} (d_i)	General probability surviving x_i to x_{i+1} (p_i)	Dying probability x_i to x_{i+1} (q_i)	Variance ($Vp_i = Vq_i$)	Fraction of last interval of life (a_i)	Life expectations at age x_i (e_i)	Life expectations observed at age x_i (Ve_i)	(SE e_i)
Postepidemic	30	80.43	10.47	0.870	0.130	0.00141	0.50	159.01	93.76	9.68
	180	69.96	43.12	0.334	0.666	0.00318	0.50	150.56	76.51	8.75
	60	26.84	13.60	0.165	0.835	0.00513	0.50	67.85	26.81	5.18
	30	13.24	17.24	0.075	0.925	0.00524	0.50	46.72	11.68	3.42
	60	6.00	6.00	0	1.000	—	—	30.00	—	—
	30	80.15	13.16	0.836	0.164	0.00171	0.50	168.08	125.01	11.18
30 cm	180	66.99	32.78	0.427	0.573	0.00365	0.50	168.14	109.39	10.46
	60	34.21	17.43	0.209	0.791	0.00483	0.50	63.03	21.41	4.63
	30	16.78	8.45	0.104	0.896	0.00555	0.50	37.34	7.95	2.82
	60	8.33	8.33	0	1.000	—	—	30.00	—	—
	30	100.20	17.71	0.823	0.177	0.00145	0.50	152.18	77.16	8.78
	180	82.49	47.65	0.348	0.652	0.00275	0.50	151.63	63.64	7.98
38 cm	60	34.84	20.10	0.147	0.853	0.00360	0.50	55.92	12.08	3.47
	30	14.74	9.40	0.053	0.947	0.00341	0.50	31.26	3.44	1.85
	60	5.33	5.33	0	1.000	—	—	30.00	—	—

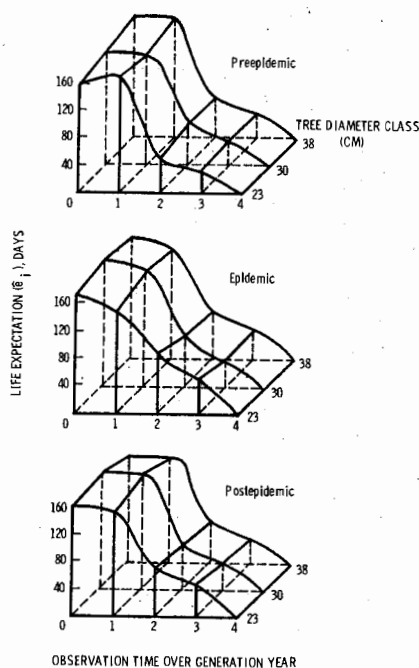


Fig. 3. Life expectations (days) at each observed time over generation year by diameter class within stage of infestation.

tend to equalize among diameter classes during the early brood developmental stages, but shift in favor of the smaller diameter class in the late brood development stage. There is a direct reversal between life expectations during the preepidemic and postepidemic stages of infestation. During the preepidemic stage, the greatest life expectations occur in broods within the larger diameters; during the postepidemic stage, they occur within the 30-cm diameter class. This may be a reflection of the diameter-phloem distributions within the stand before and after a mountain pine beetle infestation or, as recent observations indicate, an effect of beetle quality generated in large diameter trees.

We consider life expectation (\hat{e}_i) for discussion purposes because some interpretation can be made of its value based on *a priori* knowledge of the beetle. The increases of life expectation, when they do occur, are probably associated with decreased attack density of the beetle by diameter from the preepidemic to the epidemic stage (COLE *et al.*, 1976). During the postepidemic period in particular, a minimal number of large diameter trees remain, however, and these are usually not conducive to brood production. Associated with this lack of large trees is an increase in attack density (COLE *et al.*, 1976). Increased attack density increases the rate of tree drying and beetle mortality due to this drying.

General probability of survival

The general probability of survival from one growth interval to the next follows

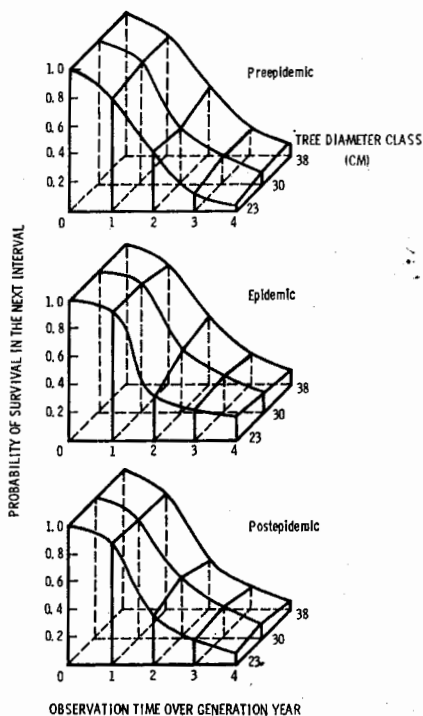


Fig. 4. Probability of survival in the next interval by tree diameter class during stage of infestation.

the configuration of life expectations (Figure 4). During the preepidemic period of infestation, the general probability of survival increases over diameter class within each brood developmental period. The chance of survival shifts slightly in favor of the 30-cm diameter class during the epidemic and continues to strengthen in this diameter class during the postepidemic stage of infestation over each brood developmental period.

Within diameter class, over stage of infestation, the probability of survival generally peaks during the epidemic. This probability is greater during the postepidemic stage than during the preepidemic stage in the 23- and 30-cm diameter classes, but the reverse is true within the 38-cm diameter class (Figure 5). This again may be due to the pattern of tree killing during the epidemic, i. e., the beetle progressively destroys its preferred food supply (large diameters) over the life of the infestation.

The data and analyses to this point support the theory that the 30-cm diameter trees are supporting the beetle population in the main. The 38-cm trees may in fact supply the impetus for starting epidemics, but, because of their fewer numbers and early elimination from the stand, these trees quickly lose their commanding position. Consequently, the 30-cm diameter trees, which are still more than sufficient for beetle population growth, carry the bulk of population growth through the epidemic and into the postepidemic stage of infestation. The beetle produces less brood in these

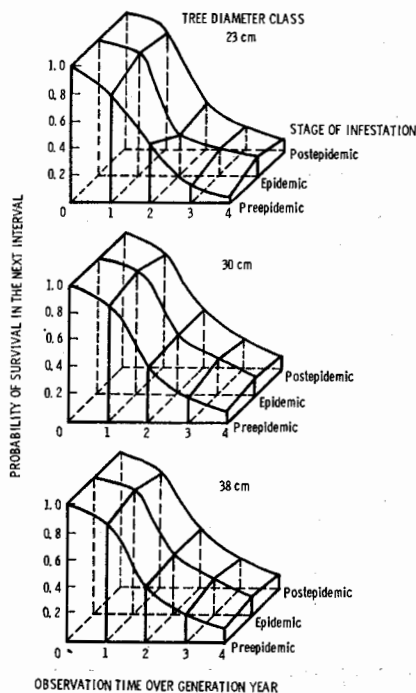


Fig. 5. Probability of survival in the next interval by stage of infestation within tree diameter class.

23-cm trees, probably through the lack of adequate habitat for the beetle and increased rate of drying. The chance-of-survival increase in these trees during the peak of the epidemic is probably due to the greater number of these trees being infested, the reduced attack density, and possibly to an artifact of population sampling.

Crude probability of death

The general mortality is the total mortality for a particular point in time. The component probabilities of death (crude probabilities) caused by the specific mortality factors are additive to and constitute the general mortality. As in most cases, the greatest cause of mortality is shown as "unknown." This "unknown" category accounted for approximately 50% of the mortality that occurred during any generation of beetles, within any diameter class of trees, and during any one stage of infestation (Figure 6). We believe, however, it quite reasonable and proper to assume by reason of sampling theory, that if this cause was known, it would be proportionally distributed among the other causes of mortality in respect to their occurrence. Thus, in the interpretation of the following analyses, we will be concerned with the factors as they were recorded and evaluated.

The crude probabilities of death due to specific mortality factors are shown in Table 4 and Figure 7. The general probability of death is the rear profile in each case (Figure 7). Smoothed curves have been drawn through mortality estimates for

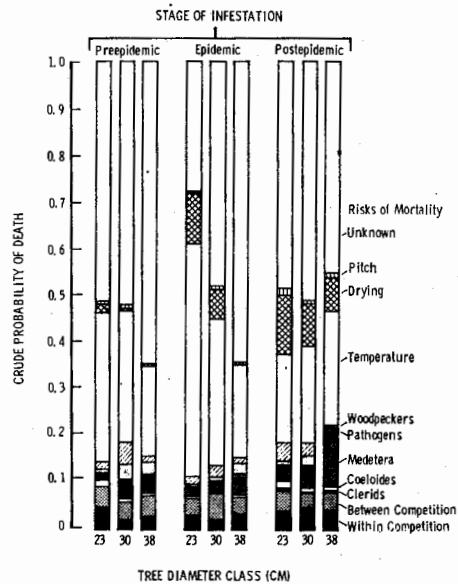


Fig. 6. Crude probability of death by specific mortality factors.

discrete points in time to facilitate visual appraisal of mortality trends over time. Mortality read from these graphs, however, is only pertinent at that particular point in time.

These data continue to substantiate previous studies (COLE, 1974, 1975) showing that temperature (winter-kill) followed by drying of phloem in the early summer remain the two greatest causes of mortality of mountain pine beetle broods. These factors generally decreased as diameter increased, and they varied with the stage of infestation, with drying showing a steady increase in the 23-cm diameter class.

Specific mortality factors

Individual mortality factors (risks) measured were: within competition, i. e., mortality from crowding of larvae within a single brood or egg gallery; between competition, i. e., mortality from crowding of larvae from two or more separate or different broods or egg galleries; the insect predators, *Medetera aldrichii* (Diptera: Dolichopodidae); *Thanasimus undatulus* and *Enoclerus sphegeus* (Coleoptera: Cleridae); the insect parasite, *Coeloides dendroctoni* (Hymenoptera: Braconidae); woodpeckers; low winter temperatures; drying of the phloem; pitch; and pathogens.

The probability of death due to a mortality factor is the proportion that factor contributes to the total loss from all mortality factors. Interpretations are in the context of *probability of death* occurring and not in numerical occurrence of the mortality factor.

Within competition decreased over diameter during the preepidemic stage of infestation, fluctuated during the epidemic stage, and decreased with diameter during the postepidemic stage (Figure 8). *Between competition* followed somewhat the same

Table 4. (2)

Stage of infestation	Develop-mental interval	Survival	General probability		WC	BC	CL	CD	MD	PA	Crude probabilities ¹					UNK
			Death	0							WP	T	D	PI		
Epidemic	0	1.000	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	1	0.916	0.084	0.096	0.093	0	0	0	0.061	0	0.013	0.132	0	0	0.026	0.579
	2	0.293	0.707	0.022	0.040	0	0	0	0.007	0.001	0.020	0.634	0.147	0	0	0.129
	3	0.207	0.793	0.019	0.044	0.004	0.037	0.016	0.022	0.022	0.025	0.021	0.083	0.004	0.004	0.725
	4	0.162	0.838	0	0	0	0	0	0	0	0	0	0	0	1.000	
Crude probability per generation				0.028	0.044	0.001	0.004	0.013	0.003	0.003	0.018	0.448	0.118	0.003	0.281	
30 cm	0	1.000	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	1	0.913	0.087	0.166	0.214	0	0	0	0.168	0	0.023	0.129	0	0	0.015	0.285
	2	0.436	0.564	0	0.060	0	0	0	0.008	0.013	0.025	0.550	0.124	0	0	0.220
	3	0.265	0.735	0	0	0.005	0.024	0.008	0.008	0.003	0.035	0.005	0.048	0	0	0.872
	4	0.133	0.867	0	0	0	0	0	0	0	0	0	0	0	1.000	
Crude probability per generation				0.017	0.055	0.001	0.005	0.023	0.008	0.008	0.023	0.317	0.078	0.001	0.472	
38 cm	0	1.000	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	1	0.848	0.152	0.033	0.040	0.002	0	0	0.091	0.137	0	0.019	0	0	0	0.678
	2	0.489	0.511	0.044	0.003	0	0	0	0.064	0	0.008	0.333	0.002	0	0	0.546
	3	0.205	0.795	0.013	0.105	0.001	0.006	0.018	0	0.013	0.013	0.209	0.003	0	0	0.633
	4	0.100	0.900	0	0	0	0	0	0	0	0	0	0	0	1.000	
Crude probability per generation				0.027	0.041	0.001	0.002	0.047	0.023	0.007	0.202	0.002	0	0	0.649	

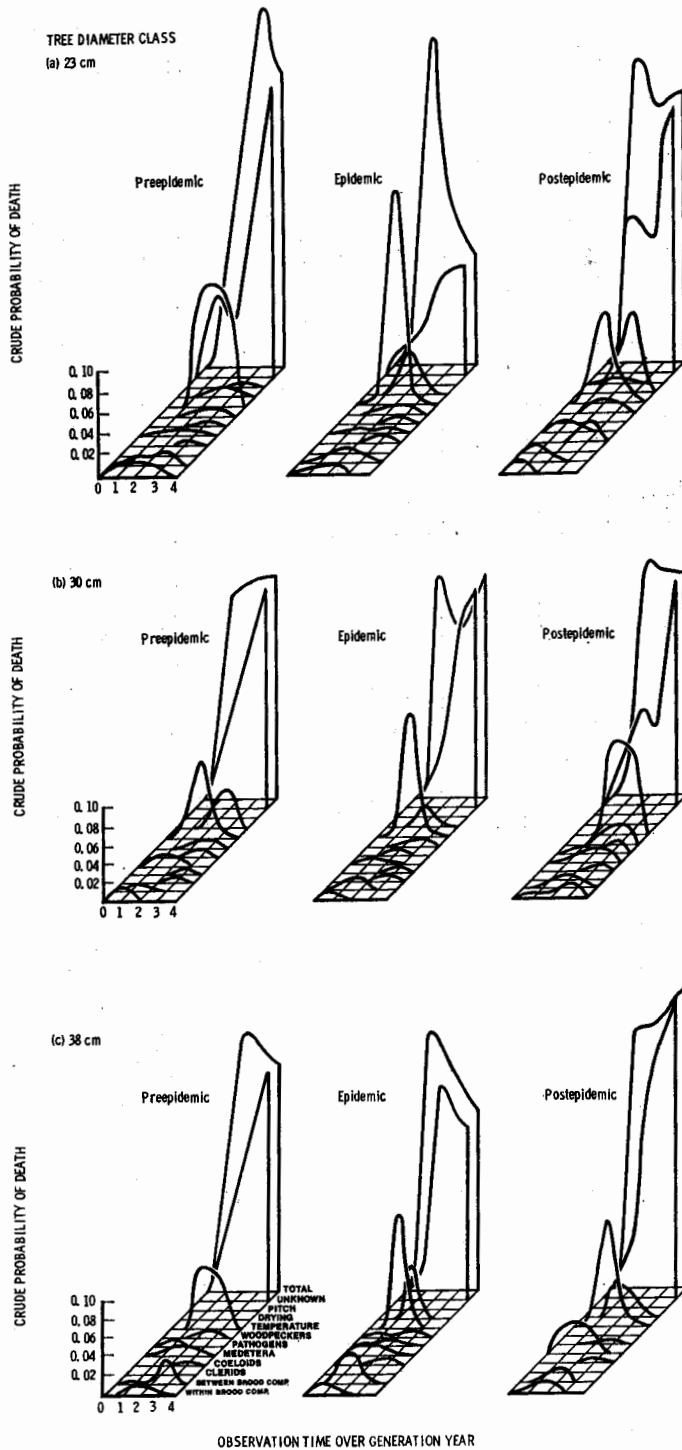


Fig. 7. Graphic display of crude probability of death from specific mortality factors by tree diameter class within stage of infestation over observation during generation year.

pattern as *within competition* (Figure 9). Combining the effects of these two forms of competition, or crowding, we find some minor fluctuations of these patterns during the preepidemic and epidemic stages of infestation over diameter, but a definite decrease of mortality due to these factors during the postepidemic stage (Figure 10). Competition had the least influence within the 38-cm diameter class trees. Mortality from both within and between competition was the same during the preepidemic and

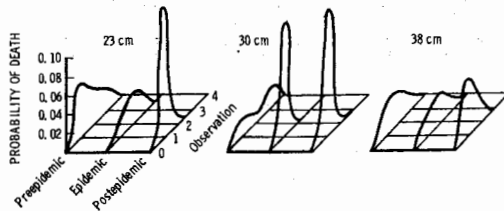


Fig. 8. Crude probability of death due to within brood competition by tree diameter class.

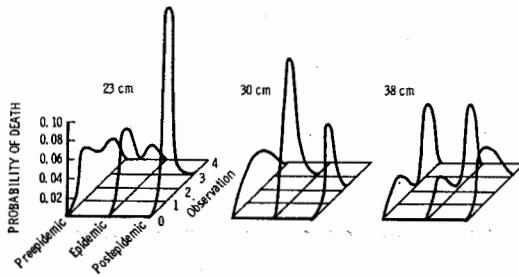


Fig. 9. Crude probability of death due to between brood competition by tree diameter class.

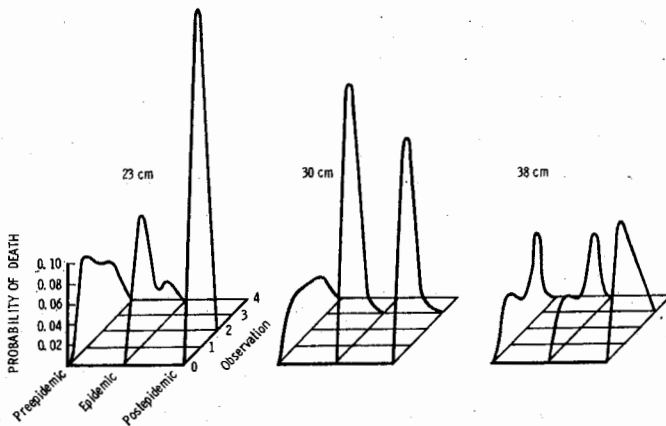


Fig. 10. Combined crude probability of death from within and between brood competition by tree diameter class.

epidemic stages and peaked slightly during the postepidemic stage. Even though populations can be expected to be greater within the 38-cm diameter tree class, mortality from competition was probably offset by the better habitat and survival conditions. Competition offers the greatest influence within the 23-cm diameter tree class for the opposite reasons. The peak mortality from competition occurred in the 30-cm trees during the epidemic stage and again probably reflects population density, which occurred under these conditions.

Medetera aldrichii showed a density dependence over time (Figure 11). Not only did *Medetera* show preference for the greater beetle populations by diameter class,

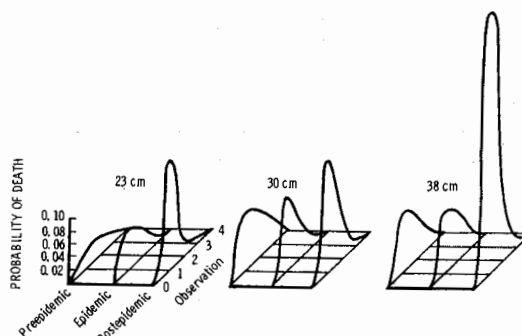


Fig. 11. Crude probability of death from *Medetera* by tree diameter class.

but preference increased by stage of infestation. This could be a proportional increase since populations were decreasing. Because of this tendency, *Medetera* was the principal insect predator/parasite that could warrant further investigation as a biological control agent of the mountain pine beetle. Further, NAGEL and FITZGERALD (1975) have shown that *M. aldrichii* has a rather voracious appetite. SCHMID (1971) attributed a major share of beetle mortality to *M. aldrichii*, but one should remember these past studies refer to numbers of prey consumed by the predator. This current study deals with *probability* of loss.

Thanasimus undatulus and *Enoclerus sphegeus* were recorded together as Clerids. The probability of death by these Clerids was extremely minor and generally can be (at least in this case) disregarded as exerting any real influence on reducing mountain pine beetle populations (Figure 12).

Any appreciable probability of death by *Coeloides dendroctoni* was restricted to the 23-cm diameter trees and showed some increase over stages of infestation (Figure 13). This restriction to the smaller diameter trees is probably due to the thinner bark—thicker bark restricts egg deposition by *Coeloides*, which has a rather short ovipositor.

Probability of death due to *woodpeckers* generally occurred in the 23- and 30-cm

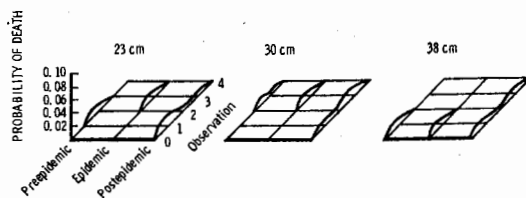


Fig. 12. Crude probability of death from Clerids by tree diameter class.

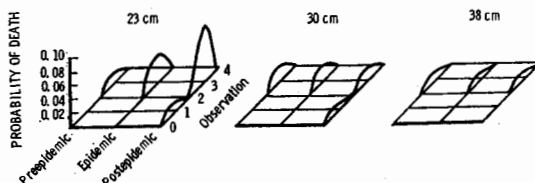


Fig. 13. Crude probability of death from *Coeloides dendroctoni* by tree diameter class.

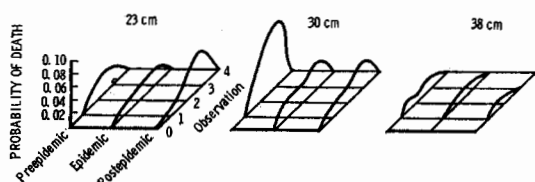


Fig. 14. Crude probability of death from woodpeckers by tree diameter class.

diameter trees and showed an increase over stage of infestation in the 23-cm diameter trees and a decrease in the 30-cm diameter tree classes. Little woodpecker-caused mortality occurred in the 38-cm diameter tree class during any stage of the infestation (Figure 14). This is partly a reflection of sampling at breast height, i. e., snow depths prevented woodpecker activity during much of the winter. In addition, thick bark tends to discourage woodpeckers, and generally woodpeckers do not normally seek food in the lower bole when food is readily available higher in a tree.

Temperature alone presented the greatest influence of all mortality factors measured (Figure 15). The evident peaks of probability of death during the epidemic stage of infestation are probably due to unusually low temperatures during that stage rather than to the beetle population level. Probability of death due to temperature over diameter class by stage of infestation, however, decreased (as would be expected) by diameter class. The exception, surprisingly, was the increased probability by diameter class within the postepidemic stage. Mortality from drying could have well preceded the mortality from temperature in the flow of events. Also, mortality from cold, dry

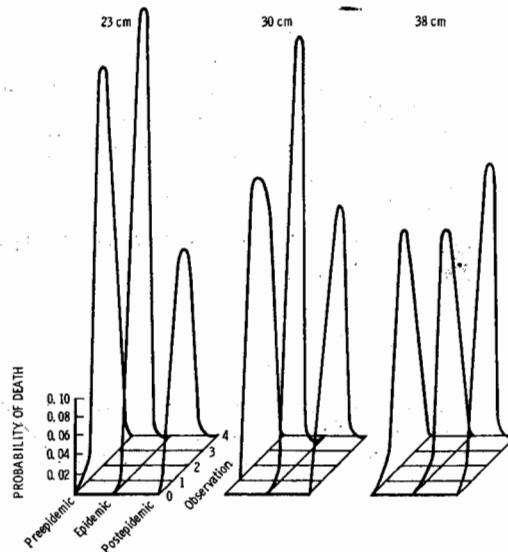


Fig. 15. Crude probability of death from low winter temperatures by tree diameter class.

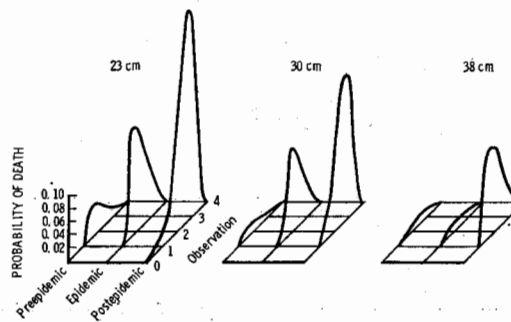


Fig. 16. Crude probability of death from drying of phloem by tree diameter class.

trees is usually greater than from cold, wet trees.

Probability of death due to *drying of the phloem* increased over stage of infestation within each diameter class, but decreased over diameter class within stage of infestation (Figure 16). These observations reflect the general trend of phloem and sapwood (an indicator of tree moisture) being thinner in trees remaining after each stage of an infestation. Within each stage of infestation, drying in small diameter trees is greater than in large diameter trees. This is consistent with both phloem and sapwood thickness being directly related to tree diameter (AMMAN, 1978). The large increase in drying in the postepidemic stage is probably influenced by increased attack and gallery densities that occur in this stage of infestation (COLE *et al.*, 1976). Drying of the phloem and the resulting mortality are also related to woodpecker feeding and

mountain pine beetle population level.

At the most, we experienced only 1.4 percent chance of an egg surviving to an adult within the 30-cm diameter tree class, and then only during the epidemic stage of infestation—all other stages were less than 1. Does this mean we are dealing with an approximate difference of 0.5 probability of survival between epidemics and endemics? One must remember first, that these probabilities do not reflect population numbers per se. The probability of any one individual surviving from the egg to the adult stage is interesting from a statistical point of view and useful as an indicator of infestation growth. From an entomological point of view, the percent survival from egg to adult is probably more descriptive. In this case, percent survival varied from an 11% increase from preepidemic to epidemic stage in the 23-cm trees, and only 4% over the same period of time in the 30-cm trees. Again, we are dealing with a rather small increase in survival between preepidemics and epidemics. In both cases, probability of survival and percent survival, the trends reflected are approximately the same; only the magnitude of index has changed. The mountain pine beetle is synchronized so closely with stand development and growth that increased food supply, as a contributor to population explosion, probably far outweighs the influence of population reduction by biological and physical factors of mortality.

A special case

We have maintained one particular study plot on the Cache National Forest in northeastern Utah that may best illustrate some of these points of interest. The mountain pine beetle has been active in this particular area for 7 years or longer (10-15% of trees killed annually). The population has remained at a constant "high endemic" level over this period. If certain factors (risks) of mortality were to be density dependent or independent, or if a steady mountain pine beetle population was to provide an opportunity for these factors to increase, then certainly this situation should have provided such an opportunity.

In this case, the probability of any one egg reaching the adult stage was 0.00358 for the populations within the 23-cm diameter class; 0.00639 for the 30-cm diameter class; and 0.00560 for the 38-cm diameter class. These probabilities and the percent survival for the Cache were comparable to, but greater than, survival recorded for the postepidemic populations in the other plots (10.4% in the 23-cm, 10.5% for the 30-cm, and 9.9% for the 38-cm diameter classes).

The crude probabilities for each mortality factor recorded are shown in Table 5 and Figure 17. Once again, these curves are comparable to the postepidemic population levels found in the other study plots. *Within competition* mortality is greatest within the 23-cm diameter tree class, while *between competition* mortality is greatest within the 38-cm diameter tree class. Combined, these two mortality factors show the greatest effect on population reduction in the smallest and largest diameter classes (Figure 18).

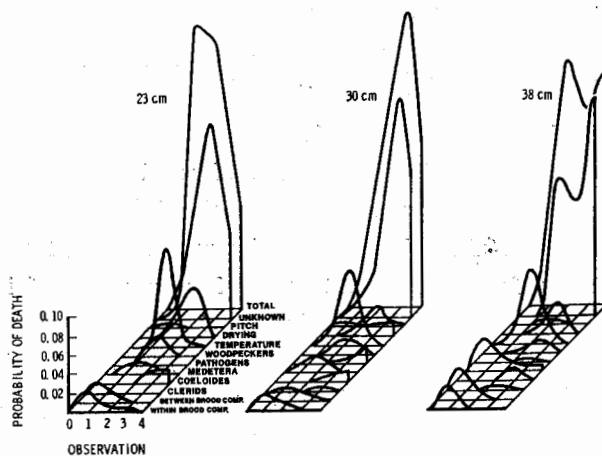


Fig. 17. Crude probabilities of death from specific factors by tree diameter class for the special case, Cache National Forest.

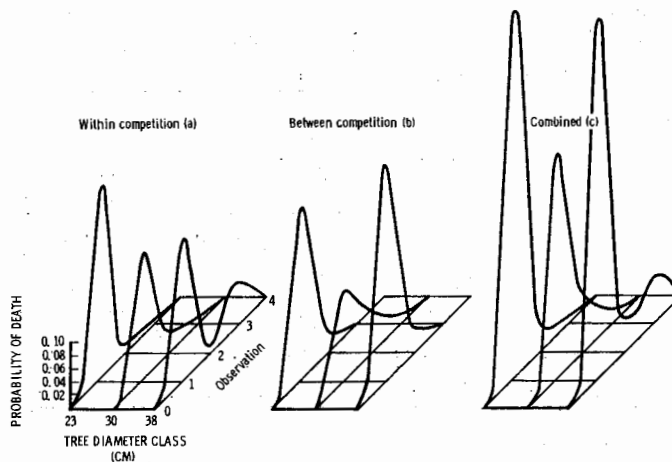


Fig. 18. Crude probability of death from within (a), between (b) and combined within-between competition (c) for a special case, Cache National Forest.

From the measured losses caused by parasites, predators, pathogens, and pitch, about the same picture found in the other data sets emerged. That is, *Clerids* had a minor influence on the amount of mortality (Figure 19a); *Coeloides* activity was greatest in the smallest diameter class and least in the largest diameter class (Figure 19b); *Medetera* showed some density dependence with the greatest predation occurring in the largest diameter class and least in the smallest (Figure 19c); probability of death caused by *woodpeckers* was rather evenly distributed among diameter classes, peaking in the spring within the 23-cm and in midsummer within the 30- and 38-cm diameter classes (Figure 19d); mortalities caused by *pathogens* and *pitch* were highest

Table 5. Crude probability of death due to a specific mortality factor in the presence of all other factors by tree diameter class for the special case, Cache National Forest.

Tree diameter class	Observation	General Survival	Death	Crude probabilities ¹															
				WC	BC	CL	CD	MD	PA	WP	T	D	PI	UNK					
23 cm	0	1.000	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	1	0.829	0.171	0.276	0.251	0.006	0	0.103	0.025	0.011	0.109	0.002	0.037	0.180					
	2	0.315	0.685	0.006	0.020	0	0.001	0.041	0.001	0.076	0.387	0.089	0.001	0.380					
	3	0.132	0.868	0.003	0	0.003	0.044	0.010	0.004	0.001	0.009	0.189	0.002	0.735					
30 cm	4	0.104	0.896	0	0	0	0.117	0	0	0.006	0.008	0.059	0	0.810					
	Crude probability per generation		0.057	0.059	0.002	0.013	0.045	0.006	0.056	0.244	0.092	0.007	0.419						
	0	1.000	0	0	0	0	0	0	0	0	0	0	0						
	1	0.832	0.168	0.187	0.131	0	0	0.133	0.037	0.008	0.187	0.010	0.031	0.276					
38 cm	2	0.457	0.543	0.023	0.055	0	0.001	0.078	0.005	0.077	0.372	0.056	0.004	0.330					
	3	0.160	0.840	0.004	0.012	0.007	0.023	0.012	0.007	0.039	0.030	0.108	0.007	0.751					
	4	0.105	0.895	0	0	0.004	0.054	0.004	0	0	0	0.065	0	0.873					
	Crude probability per generation		0.046	0.052	0.002	0.011	0.062	0.011	0.047	0.201	0.065	0.010	0.493						
38 cm	0	1.000	0	0	0	0	0	0	0	0	0	0	0						
	1	0.778	0.222	0.205	0.308	0	0	0.317	0.009	0	0.086	0	0.011	0.064					
	2	0.356	0.644	0.006	0.033	0	0	0.050	0.001	0.007	0.307	0.029	0.012	0.554					
	3	0.204	0.796	0.066	0	0.006	0.058	0.036	0.010	0.038	0.070	0.149	0	0.567					
Crude probability per generation	4	0.099	0.901	0	0	0	0.001	0.019	0	0	0	0.009	0	0.972					
			0.065	0.091	0.001	0.010	0.110	0.004	0.010	0.176	0.040	0.009	0.484						

¹ WC—Competition within a single brood
 BC—Competition between broods
 CL—Cleridae
 CD—*Coeloides dendroctoni*
 MD—*Medetera aldrichi*
 PA—pathogens
 WP—woodpeckers
 T—winter temperature
 D—drying of the phloem
 PI—pitch
 UNK—unknown

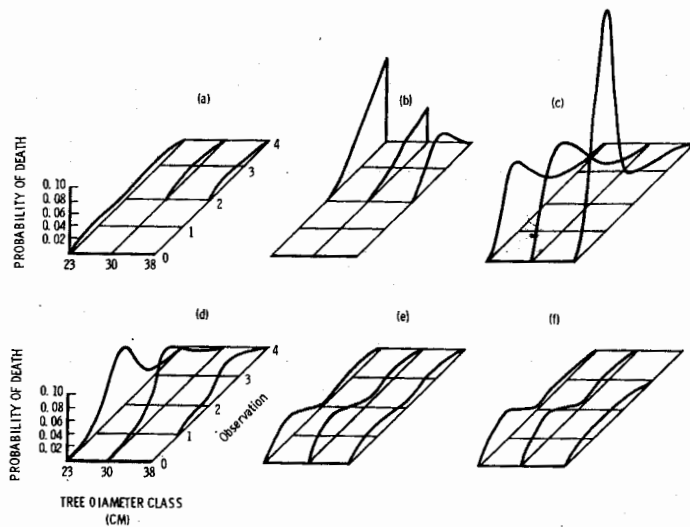


Fig. 19. Crude probabilities of death from Clerids (a), *Coeloides* (b), *Medetera* (c), woodpeckers (d), pathogens (e), and pitch (f) for a special case, Cache National Forest.

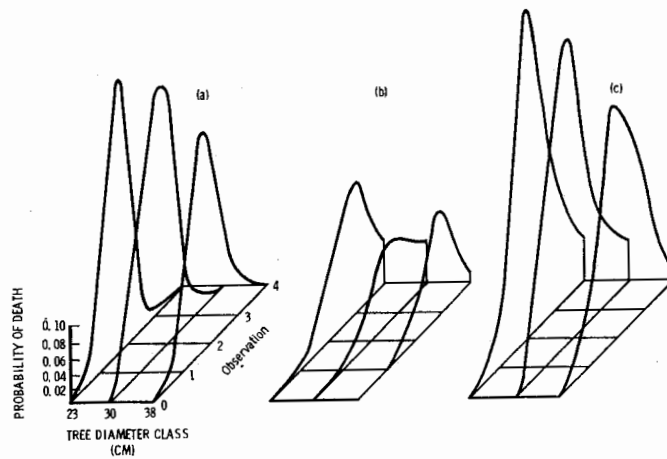


Fig. 20. Crude probabilities of death from low winter temperatures (a), drying of phloem (b) and combined temperature-drying (c) for a special case, Cache National Forest.

within the 23- and 30-cm diameter classes and during the fall (Figures 19e and f).

Temperature, again, had the greatest influence in the smallest diameter class. The influence of *drying* followed a like pattern. Together, for any generation, these two mortality factors caused the greatest reduction of mountain pine beetle populations (Figures 20a, b, and c).

The interpretation of the probabilities presented here is that none of these risks acting in the presence of other risks offers much, if any, regulatory influence upon a

mountain pine beetle population. This agrees with REID (1963) that predators occurred in too low numbers to be considered important control factors. Consequently, because no single risk or combination of these risks offer much regulatory influence, the contention that mountain pine beetle populations are food regulated is further strengthened (COLE and AMMAN, 1969). The evidence shows that the mountain pine beetle is food regulated at optimum temperature conditions and temperature regulated at high elevations where optimum food conditions prevail. Reducing and/or minimizing tree loss to the mountain pine beetle is thus dependent upon manipulating the food supply by management of the tree (stand) growth.

SUMMARY

The interpretation of the probabilities presented in this paper is that none of the competing biological risks, acting in the presence of other risks, offers much, if any, regulatory influence upon a mountain pine beetle population. Consequently, if no single risk, or combination of these risks, offers much help, then the contention that mountain pine beetle populations are food-regulated is once again strengthened (COLE and AMMAN, 1969). The evidence remains (or continues) that the mountain pine beetle is food-regulated at optimum temperature conditions and temperature-regulated at optimum food conditions. Reducing and/or minimizing tree loss to the mountain pine beetle is thus dependent upon manipulating the food supply or management of the tree (stand) growth.

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松の穿孔虫の個体群における死亡のリスクと要因—長期間データの分析

W. E. COLE

他のリスクが存在する下ではどんな生物的リスクも個体群調節に影響を及ぼさない。もし単一のリスクが役立たなければ(リスクが組合わさった場合も)、松の穿孔虫の個体群は食物によって調節されるということを再度主張することができた。松の穿孔虫は最適な気温では食物により調節され、最適食物条件の場合には気温によるといえた。本種による木の被害を少なくすることは、食物供給を操作するか、木(林分)の成長を管理するかいずれかに依存する。