A PRELIMINARY ANALYSIS OF MORTALITY IN EXPERIMENTAL POPULATIONS OF THE SPRUCE BUDWORM

by

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1. INTRODUCTION

The severe spruce budworm outbreak that developed during the late 1940's in northern New Brunswick subsided in the late 1950's and population density approached the endemic level by 1959. Endemic budworm populations have not been studied intensively in the past and therefore the investigation of the population dynamics of this forest pest at the outbreak level that was initiated in 1945 in northern New Brunswick as part of the Green River Project are being continued during the present endemic period in order to establish the factors and mechanisms that determine budworm density in place and fluctuations about the 'mean density' in time.

One of the main problems in studying an endemic population is the time and effort required to establish mean density on a plot within acceptable error limits and the effort required to collect sufficient numbers of insects to assess the effects of predation, parasitism, disease, inherent weakness and other mortality factors. Low budworm densities have thus necessitated a change in study techniques. Rather than attempt to determine survival at different stages within a generation (the life-table approach) our general aim is (1) to obtain a single population fix each year in terms of third- and fourth-instar larvae, (2) to describe and explain the factors that cause larval and pupal mortality and attempt to relate these factors to yearly changes in the third-instar larval density. The validity of this general approach, which largely ignores the egg, small larval, and adult stages, is partly justified by the analysis of epidemic budworm populations where it has been shown that the survival of large larvae is one of the major processes determining survival within the generation.

Experimental data that may supplement the findings and conclusions derived from natural populations are of special significance when studying natural populations at the endemic level. For this reason a continuing program was initiated in 1959 to assess budworm survival during the third-instar to adult age interval using partially 'controlled' populations in the field. This report deals with a preliminary analysis of the results of this study obtained in the period 1959-62. The main objectives of this study are to investigate the effects of climate, parasitism, and predation on the budworm using the 'exclusion' technique and to obtain an index of large-larval survival in any one year to check against the trend of natural populations in the Green River area. The exclusion technique (sleeve cages, insecticides, biological control agents such as ants) is a common method of assessing the efficiency of certain mortality factors. Dowden et al. (1953) caged small trees (10 to 12 feet high) with cloth and wire and left some trees exposed and checked budworm survival in each treatment. They concluded that 20 to 40 per cent more budworm disappeared from exposed trees than from trees protected with wire screening and that these figures upheld their theory that birds are important predators of the budworm. Exclusion techniques have certain disadvantages since cages may produce a major change in the microclimate and may also confine individuals that normally disperse within or between host plants.

2. METHODS

Each year a stock of budworm was obtained by forcing first-instar larvae to spin hibernacula on balsam fir twigs covered with old staminate flower cups. These twigs were taken to the field and pinned to the branches of balsam fir reproduction in late August and early September in order to overwinter the stock under natural conditions. Approximately 2,000 second-instar larvae were overwintered in this manner. In early May of the following year samples of these twigs were brought into the laboratory and checked every two days until it became apparent that emergence from hibernacula was imminent. All twigs were then collected, placed in vials, and housed in an open insectary. As the second-instar larvae emerged they were taken to the study plot and placed on the branch tips of balsam fir reproduction at a stocking density of one larva per tree. One study plot (G2) consisted of a moderately dense stand of balsam fir approximately 15 to 25 feet in height that had developed after clear-cutting of the mature over-story in 1945 and this plot was used in 1959 and 1960. In 1961 and 1962 experimental populations were set out in a new plot (G17) with stand characteristics and history similar to G2. In 1962 populations were also established on plot I3 (14 air miles south of G17) in an attempt to relate changes in local climate to possible changes in budworm survival.

The second-instar larvae were placed on branch tips between 3 and 5 feet from the ground and the branch tips were covered with a perforated plastic bag. This minimized dispersal from the branches before the larvae started to mine needles or buds. The bags were removed within a period of three days, depending on weather conditions. Approximately 500 second-instar larvae were established on the study plot each year on trees where cutting-trails (from previous pulpwood operations) permitted the use of relatively exposed branches with vigorous growth near ground level. The 500 larvae were therefore scattered over an area of approximately 2 acres, and were, in effect, added to a resident population of approximately 5,000 larvae (a rough estimate of the study density on G17). After the larvae started to spin feeding sites either between needles or adjacent to vegetative buds they were arbitrarily divided in separate experimental populations. In the period 1959-1962 six series of experimental populations (A, A1, B, C, D, and E) were studied but only three series (B, C, and D) were studied during each of the four years. A description of each population series follows:

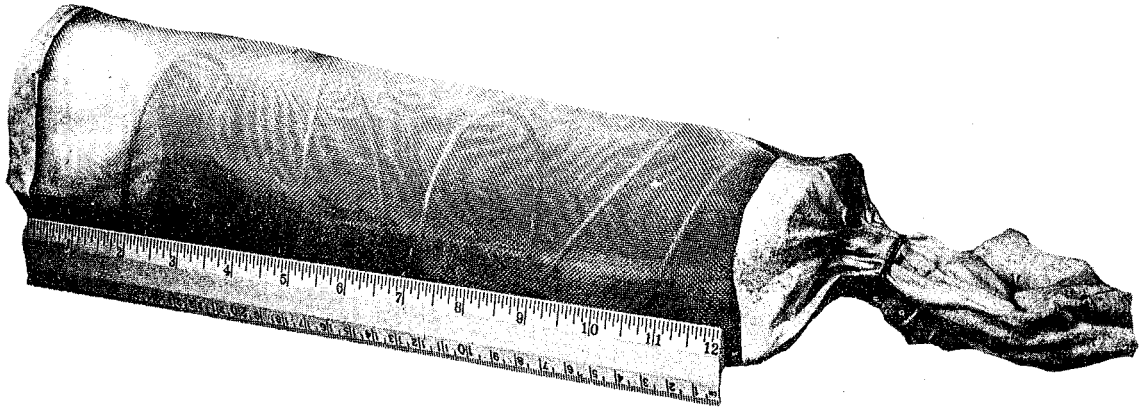
Series B.--This series consisted of approximately 100 larvae set up on balsam fir and caged with a cylindrical cage about 12 inches long, 5 inches in diameter, and constructed of fine mesh plastic screening (Plate 1, Fig. 1). Strips of cotton cloth about 6 inches wide were used to close the ends of the cage, and a coil of wire was inserted to support and shape the plastic screening. It was assumed that the cage would exclude parasites and invertebrate and vertebrate predators, and that disease, inherent population 'vigor' and weather (plus the interaction of these factors) would be the principal source of mortality.

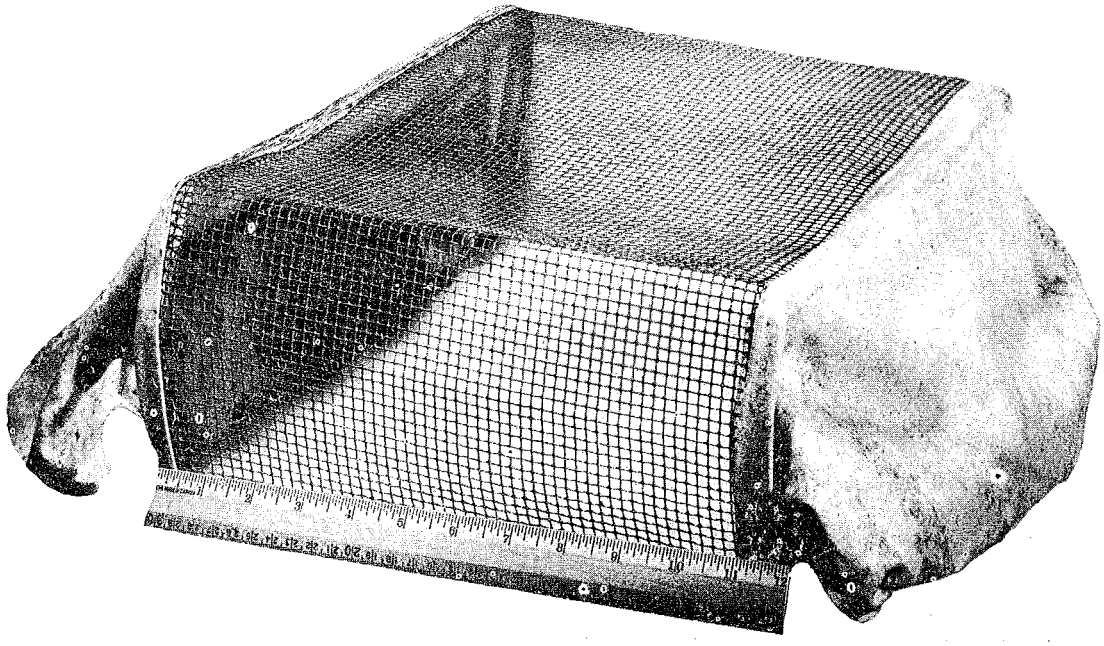
Series C.--This series consisted of approximately 100 larvae set up on balsam fir and caged with galvanized screening of 1/4-inch mesh size. A cylindrical cage 12 inches long and approximately 6 inches in diameter was used in 1959 but replaced in 1960 with a 10-inch diameter cage as birds and invertebrate predators were potentially able to remove larvae while resting on the outside of the smaller cage. In 1961 a square cage was designed (12" x 12" x 7" deep) and proved to be the most

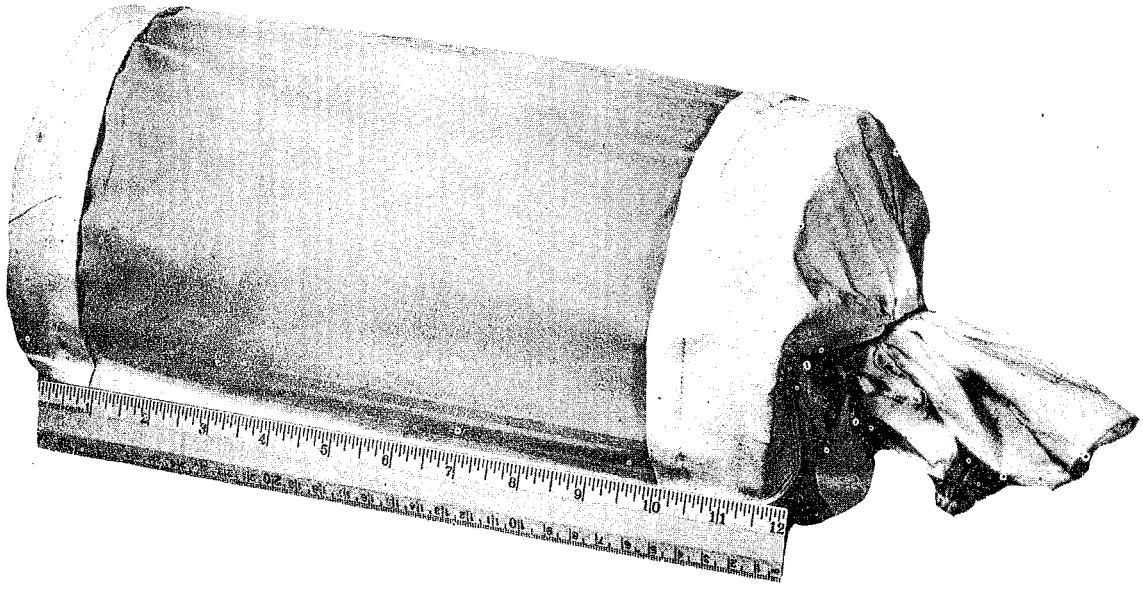
Plate 1. Fig. 1.--B Series Cage

Fig. 2.--C Series Cage

Fig. 3.--E Series Cage







satisfactory (Fig. 2). Strips of cloth were used to enclose the ends of the cage. It was assumed that parasites and invertebrate predators would have access to the caged larvae while birds would be excluded and that this experiment would consequently provide an index of budworm survival in the absence of predation by birds. However, it was soon apparent that sixth-instar larvae tended to move about on the foliage just before pupation and in so doing were able to pass through the 1/4-inch mesh of the cage and were lost; larval dispersal thus confounded the survival data. In 1960 and 1961 a sheet of waterproof paper was therefore placed on the bottom of the cage to trap dispersing larvae. In 1962 half of the cages in this series were modified to trap dispersing larvae (C1) while the remainder (C2) permitted dispersal. The modification consisted of a strip of nylon 'mesh' (mesh size approximately 1/16th of an inch) completely covering the bottom of the cage but, unlike the paper, possibly allowing small parasites and spiders access through the bottom as well as the top and sides of the cage.

Series D.--This series consisted of approximately 200 larvae set out on balsam fir and left exposed until the survivors reached the late pupal stage.

Series A.--Series A consisted of approximately 100 second-instar larvae established on balsam fir and left 'exposed' on the branch. An open tray about 20 inches square and 6 inches deep with wooden sides and a cotton bottom was placed under each branch. The sides of the tray were ringed with tanglefoot in order to trap larvae that dropped from the branch. This treatment was only used in 1959 and then discontinued, since 'missing' larvae were not found in the trays and the trays may have unduly influenced predation by birds.

Series A1.--This series consisted of approximately 100 larvae established on white spruce and left 'exposed' on the branch. The objective was to check relative survival on white spruce and balsam fir. The experiment was set up in 1960 but discontinued since the population survival curves on the two host plans were almost identical.

Series E.--This series was very similar to Series B except that the cage was constructed of fine mesh nylon (Fig. 3) rather than plastic screening. Series E was first used in 1962 to check the potential variation in budworm survival resulting from the characteristics of the cage.

In any one year the series of populations were intermixed so that, for example, the exposed larvae of Series D were not clumped together in one part of the study area. The larvae were examined every three days (series C and D) with a minimum disturbance of the feeding site, and movement to new feeding sites was noted on a diagram of the branch. Dead and missing larvae were recorded under four headings; parasitism, predation, dead and diseased, and missing. Parasitized larvae were taken to the laboratory and reared. Difficulty was experienced in classifying other dead larvae. If the integument was broken or scarred death was attributed to predation. If the integument was not broken, or if the larva appeared flaccid, it was recorded under 'dead and diseased'. These dead larvae, when possible, were frozen and later examined for the presence of pathogens. The subjective analysis of disease and predation is discouragingly evident. Dead larvae were also recorded by instar. In some instances the date of larval death was not listed as the date when the dead larva was found but was adjusted to a previous date on the basis of larval development and degree of feeding on the shoot. Mortality was necessarily

recorded as the actual number of budworm killed by a particular factor on a particular date. This differs from the usual assessment of mortality where, for example, a sample of the host population is collected and dissected for parasites and the number of hosts with parasites is, in effect, the apparent number that would be killed by parasites in the absence of all other mortality factors. The assessment of mortality in terms of 'actual' rather than 'apparent' proportions caused certain difficulties in the interpretation of the data.

The periodic recording of living larvae gave a series of population fixes for each experimental series from the beginning of the third instar to the late pupal or adult stage and these have, for comparative purposes, been plotted as survivorship curves (Figs. 4, 5, 6 and 7). Survivorship curves and estimates of early larval mortality were based on third-instar density rather than on the number of second-instar larvae established in feeding sites since no attempt was made to find second-instar larvae that dispersed or were 'missed' from the tagged branch. An estimate of the 'loss' between second-instar larvae in mines and third-instar larvae in new shoots (on the same branch) for the period 1959-62 is as follows:

	Second-instar larvae in mines	Third-instar larvae in shoots	Per cent loss
1959	462	367	21
1960	477	325	32
1961	422	369	36
1962	486	410	16

This loss appears to be a function of current shoot development when newly moulted third-instar larvae begin to attack the current shoots.

3. PROBLEMS IN ANALYSIS

The problems of analysing and interpreting mortality data obtained from experimental population studies may be briefly stated as follows:

1. Mortality factors are measured in terms of their effects on the budworm and not their presence or density in the ecosystem. The relationship between a particular mortality factor and budworm survival must therefore be interpreted with caution, particularly if regression techniques are used.

2. The method of collecting mortality data from experimental populations is such that the actual number of budworm killed by a particular factor is observed and recorded. Data are therefore presented as the actual proportion killed and the interaction between factors is accounted for in the data collection technique. This differs from the usual circumstances where a sample of hosts are examined and the apparent mortality is measured.

The remainder of this discussion deals with the problems arising from statement (2) above and the discussion may be illustrated by using the hypothetical example recorded in Table I. This table shows a population of 80 third-instar

Fig. 4.--Survivorship curves for series B, C, and D in 1959. Survival rate based on third-instar density.

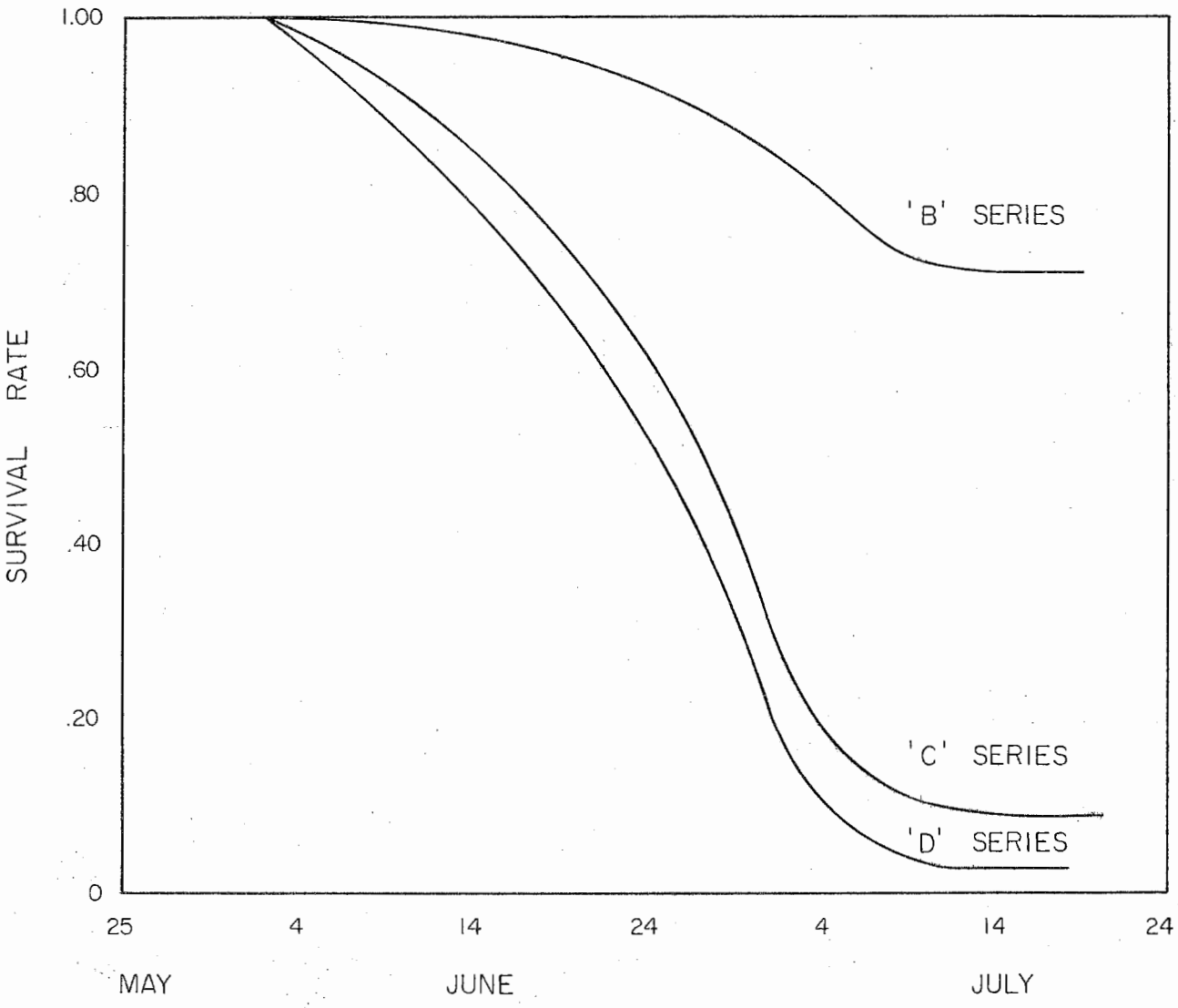

1.00
.80
.60
.40
.20
0
SURVIVAL RATE
'B' SERIES
'C' SERIES
'D' SERIES
25
4
14
24
4
14
24
MAY
JUNE
JULY

Fig. 5.--Survivorship curves for series B, C, and D in 1960. Survival rate based on third-instar density.

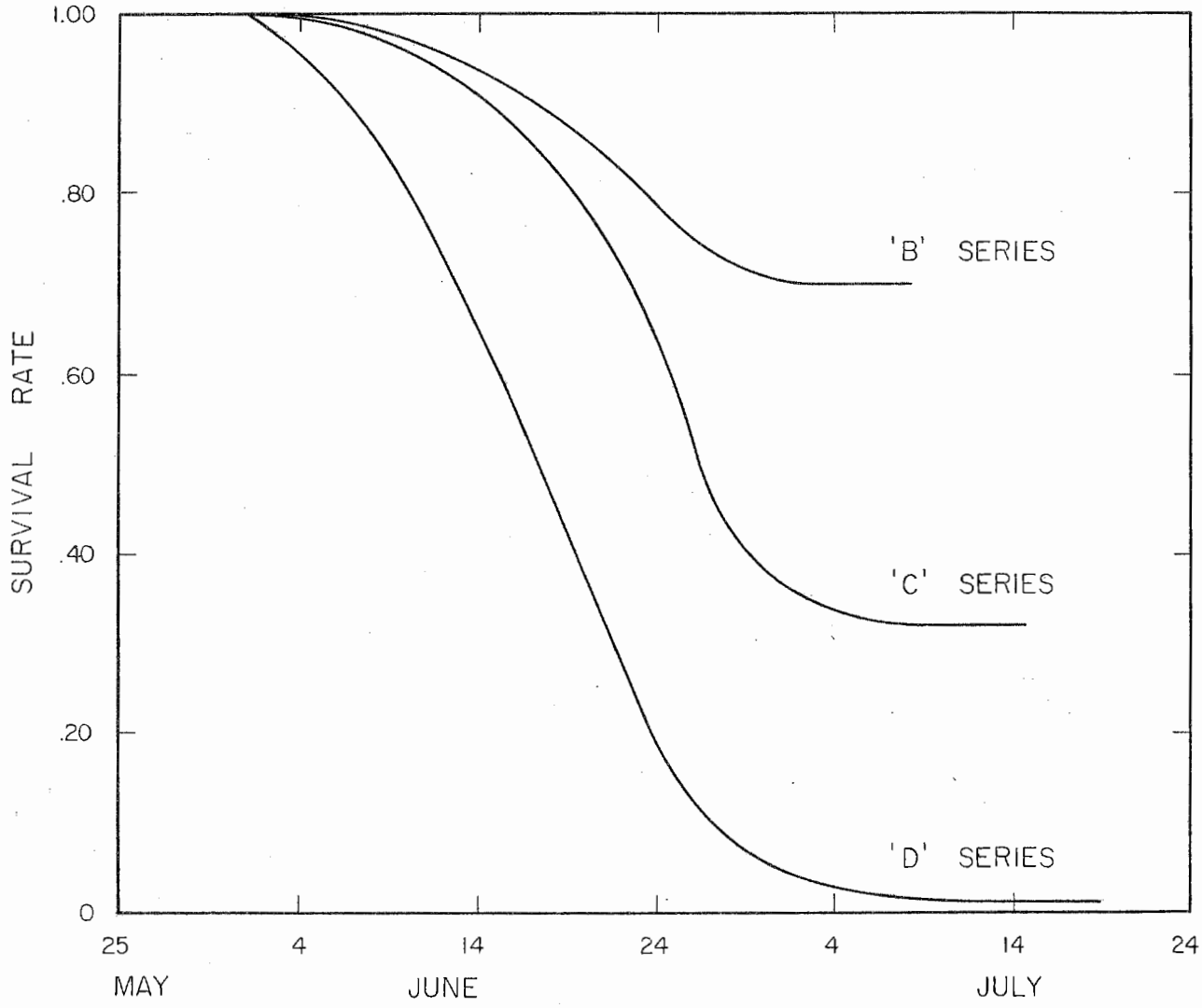

1.00
.80
.60
.40
.20
0
SURVIVAL RATE
'B' SERIES
'C' SERIES
'D' SERIES
25
4
14
24
4
14
24
MAY
JUNE
JULY

Fig. 6.--Survivorship curves for series B, C, and D on Plot G17 in 1961. Survival rate based on third-instar density.

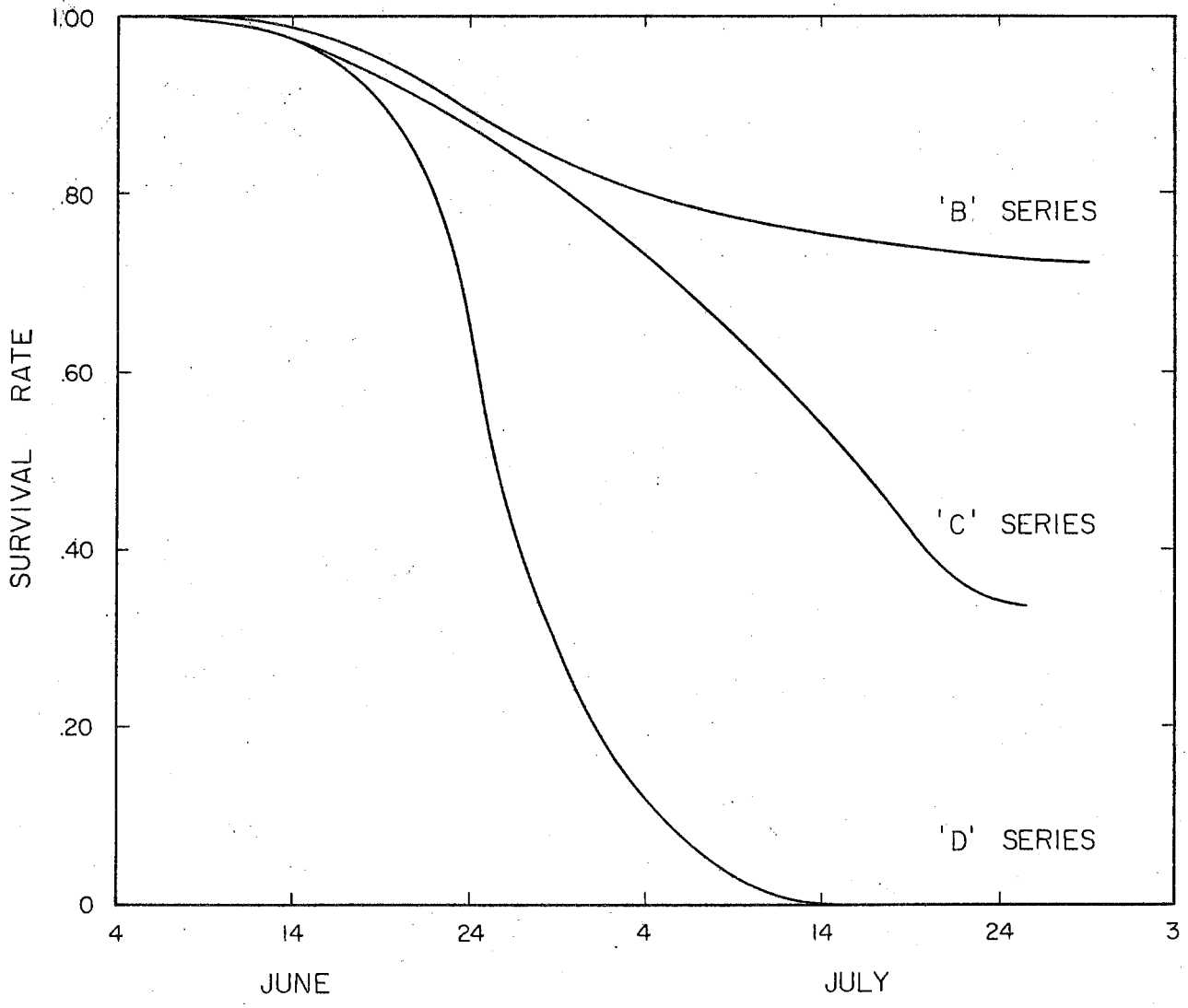
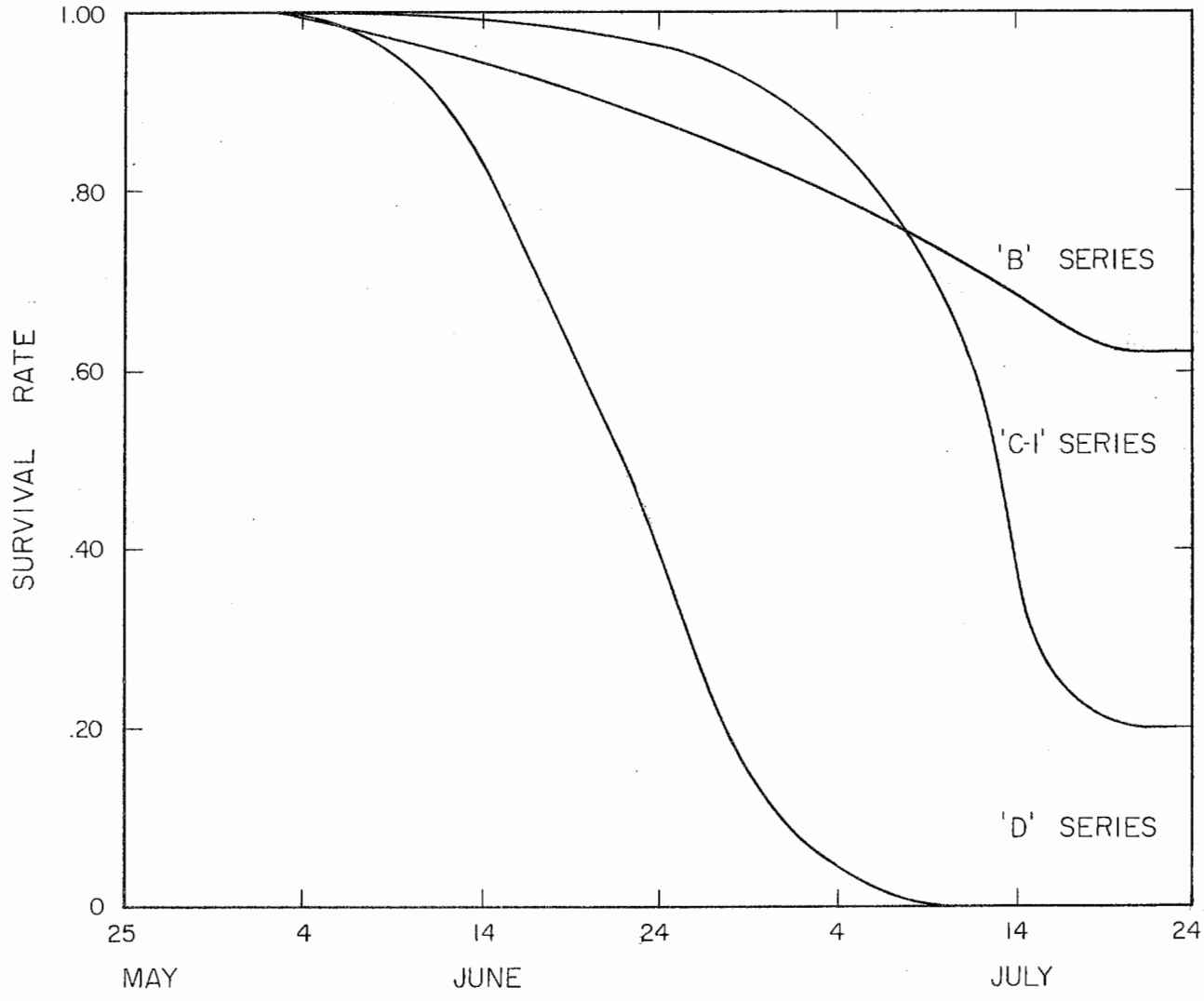

1.00
.80
.60
.40
.20
0
SURVIVAL RATE
'B' SERIES
'C' SERIES
'D' SERIES
4
14
24
4
14
24
3
JUNE
JULY

Fig. 7.--Survivorship curves for series B, C1, and D on plot G17 in 1961. Survival rate based on third-instar density.


1.00
.80
.60
.40
.20
0
SURVIVAL RATE
'B' SERIES
'C-I' SERIES
'D' SERIES
25
4
14
24
4
14
24
MAY
JUNE
JULY

larvae reduced to two adults as the result of parasitism and disease. It is assumed that the population was counted at successive intervals in its development and the actual numbers of larvae killed by parasites and disease recorded. The proportion of hosts killed by a particular factor at a particular stage is therefore based on the number of hosts present at the beginning of that developmental stage.

Contemporaneous mortalities. Table I shows that, as a result of measuring mortality in terms of the actual proportion killed, contemporaneous mortalities are additive. Thus, 40 per cent of the third-instar larvae are killed by parasites and 10 per cent by disease and total mortality equals 50 per cent. (Note that if the apparent proportion of hosts killed by these factors had been measured, the apparent mortalities could only have been summed if no interaction occurred.)

Sequential mortalities. Sequential mortalities are not additive, and Table I shows that sequential survivals (1 - mortality rate) are not multiplicative, again because the data are based on the actual rather than apparent proportion of hosts killed. For example, sequential mortalities caused by parasites in Table I are 40%, 30%, 25%, and 40%. If these data are converted to survivals and multiplied,

$$(1 - .40)(1 - .30)(1 - .25)(1 - .40) = .189$$

mortality due to parasites

the result shows a survival rate of .189, or conversely, 81.1 per cent. Similarly, 67.6% of the hosts were killed by disease, but these data, 81.1% and 67.6%, can in no way be combined to show a total mortality of 97.5% (78/80) which was the observed mortality. Therefore, 81.1% is not a realistic estimate of mortality caused by parasites. However, if one wishes to compare the effect of parasites on budworm survival in relation to other factors, a means of combining sequential mortalities is required. This can be accomplished by summing the total number of hosts killed by a factor and presenting this as a proportion of initial or third-instar density. For example, in Table I total parasitism would be 53/80 or 66.25 per cent, and total disease would be 25/80 or 31.25 per cent. The combined mortality would be additive (66.25% + 31.25%) and equal 97.50 per cent, as observed. This is the correct means of interpreting total parasitism in terms of the third-instar population, but in an intuitive sense it fails to assess the potential impact of parasitism on the host population. For example, in Table I if six rather than four pupae had been killed by parasites, total parasitism in terms of third-instar density would equal 55/80 or 68.75 per cent, an increase of 2.5 per cent (68.75 - 66.25). In terms of the pupal period, however, an increase of two pupae killed would represent 60 per cent rather than 40 per cent parasitism. In both instances the population would become extinct;

(1) 68.75% parasitism + 31.25% disease = 100% mortality of the population

(2) 60% parasitism (of pupae) + 40% disease (of pupae) = 100% mortality of pupae

but it would appear to be more appropriate to discuss the impact of parasitism on the population in terms of an increase from 40 to 60 per cent than from an increase of 66.25 to 68.75 per cent.

A possible solution to this problem would be to combine the sequential mortalities caused by parasites to give an estimate of total parasitism, but it has already been pointed out that the sequential mortality data obtained in experi-

TABLE I

A hypothetical population of 80 budworm reduced to two adults as the result of parasitism and disease. Proportion of host killed expressed in terms of the number of living larvae in each instar.

	No. larvae	No. killed by parasites and disease	Proportion killed by parasites and disease	Proportion surviving	Cumulative[1] proportion surviving	No. larvae killed by Parasites Number	Parasites Proportion	Disease Number	Disease Proportion
III-instar	80	40	.50	.50	.50	32	.40	8	.10
V-instar	40	20	.50	.50	.25	12	.30	8	.20
VI-instar	20	10	.50	.50	.125	5	.25	5	.25
Pupae	10	8	.80	.20	.025	4	.40	4	.40
Adults	2								
Totals		78				53		25	

Actual survival = 2/80 = .025

[1](.50) (.50) = .25
(.50) (.50) (.50) = .125 etc.

mental populations cannot be combined. Further, this is essentially Thompson's approach and Miller has pointed out (1955) that it must be used with caution since it tends to ignore other mortality factors acting on the population. This latter objection may not be too serious in experimental populations because a number of mortality factors are measured and one would analyse the variation in parasitism in relation to the variation of other mortality factors before attempting to relate it to host survival.

The first objection to combining sequential mortalities, that actual rather than apparent proportions of hosts killed are measured in experimental populations, can be nullified in the following manner. The hypothetical example in Table I shows that among third-instar larvae, disease and parasites cause an actual mortality of 10 per cent and 40 per cent, respectively. But it is reasonable to assume that these factors interact and that some hosts are attacked by both. Consequently, the apparent mortality caused by disease would equal 10 per cent plus an unknown proportion X, and the apparent mortality caused by parasites would equal 40 per cent plus Y; since disease and parasites are present in the ratio of 4 to 1, the apparent mortalities could be transformed to 10 + X per cent and 40 + 4X per cent. It can also be assumed that the interaction between parasites and disease is such that the presence of one in the host has a minimum effect on the attack of the other. If both attack the host, the probability of host survival thus equals:

(1 - apparent proportion attacked by disease)(1 - apparent proportion attacked by parasites)

Host survival in the example = .50, and therefore

$$1 - (.10 + X)\ \ (1 - (.40 + 4X)\ = .50$$

$$X = .01$$

If the above assumptions are correct, the apparent mortalities caused by disease and parasites equal 11 per cent and 44 per cent, respectively. Apparent mortalities were computed for the other host stages in Table I and the following example shows the results obtained for parasitism:

	III	V	VI	Pupae
Actual mortality by parasites	40%	30%	25%	40%
Apparent mortality by parasites	44%	35%	29%	55%

The apparent mortalities by parasites can be converted to survival rates:

	III	V	VI	Pupae
Survival rate	.56	.65	.71	.45

and, since parasites are acting in sequence, the survival rates can be multiplied to give a cumulative survival rate of .116. In other words, 11.6 per cent of the hosts survived parasite attack. In the same manner, the proportion of hosts sur-

viving attack by disease equals .214 and the proportion of hosts surviving both factors is (.116)(.214) or .025 as compared to the observed in Table I of .025. This technique may be an acceptable means of combining sequential mortalities obtained in experimental populations. It does provide a total estimate of mortality caused by a factor as well as giving due weight to mortality that occurs late in a sequence of events.

This discussion on the interpretation of mortality data may be summarized as follows:

(1) Mortality data in experimental populations are measured in terms of the actual rather than apparent proportion of hosts killed.

(2) As the result of (1), contemporaneous mortalities are additive.

(3) As the result of (1), sequential mortalities cannot be converted to survival rates and multiplied.

(4) An estimate of the total effect of a factor acting in sequence can be obtained by relating mortality to the initial or third-instar density, but this procedure tends to minimize the effect of a factor acting late in the sequence.

(5) A possible solution to (4) is to convert actual proportions killed to apparent proportions. Sequential survival values then become multiplicative and an estimate of the total effect of a factor can be obtained.

(6) Significant changes in apparent versus actual mortality are not only dependent on the level of the actual mortality but also on the level of other contemporaneous mortalities associated with it. This has been analysed by Morris (1957) in his interpretation of mortality data.

(7) The procedure in (5) can only be attempted when one has a sound understanding of the interaction between factors.

It is now anti-climatic, but necessary, to inform the reader that the use of cumulative survival rates has not been adopted in the following analysis since a number of assumptions must be tested before the procedure may be eventually adopted. Instead, in the preliminary analyses to be discussed below the age-interval from third-instar larvae to pupae has been divided into two age intervals: (1) from the third instar to the appearance of the first sixth instar in the population, and (2) from the first sixth instar to the adult stage. These are termed the early larval and late larval age intervals. The number of hosts killed by a particular factor is consequently presented as a proportion of either early larval density (third instar) or late larval density (density at the beginning of the sixth instar). This, in effect, is a compromise between computing the effect of a factor solely in terms of third-instar density and attempting to compute a cumulative survival rate.

4. GENERAL INDEX OF CLIMATE

The importance of climate in governing changes in budworm density is well known, although the relative importance of various climatic factors and their interaction with the budworm has yet to be established. Some index of climate is necessary for the following discussion of mortality in experimental populations and rather than use the measurement of a specific climatic factor such as temperature, an attempt has been made to designate only whether climate was favorable or unfavorable in 1959, 1960, 1961, and 1962.

Budworm development provides an index of general climate, and the following data on the appearance of the first sixth-instar larva and first pupa in the experimental populations during the period 1959-62 suggest that climate was favorable in 1960:

Year	First sixth-instar larva	First pupa
1959	June 20	July 2
1960	June 12	June 25
1961	June 28	July 8
1962	June 26	July 5

The rate of balsam fir shoot growth also suggests that climate was favorable in 1960:

Year	25% Shoot growth	50% growth	75% growth
1959	June 7	June 21	July 2
1960	May 31	June 12	June 21
1961	June 16	June 27	July 6

If 1960 is accepted as a computation base, the deviations (in days) in budworm development and balsam fir shoot development are as follows for 1959, 1961, and 1962:

	Deviations in days from 1960				
Year	First sixth-instar larva	First pupa	25% shoot growth	50%	75%
1959	+ 8	+ 7	+ 7	+ 9	+11
1961	+16	+13	+16	+15	+15
1962	+14	+10	+14	+15	+19

These data show that phenological events were approximately one week later in 1959 than in 1960, and two weeks later in 1961 and 1962 than in 1960. Further analyses of balsam fir shoot growth have shown that the rate of growth in 1959 was comparable to the 1952-58 mean. It is therefore concluded that climate was favorable in 1960, about average in 1959, and unfavorable in 1961 and 1962.

The analysis of temperature data for the period 1959-62 has not been completed. In a preliminary abstraction, maximum daytime temperatures were averaged for seven-day periods beginning on May 15 (about the time budworm emerge from hibernacula). The following table records the deviations in these averages from a mean computed for the 1959-62 period:

Deviations in maximum temperature (mean daily maximum over a seven-day period) from an average computed for the period 1959-62

	May			June				July	
Year	15	22	29	5	12	19	26	3	10
1959	+ .6	+ 5.1	-1.8	-3.3	-5.0	-2.1	-5.1	+6.6	+6.4
1960	+3.3	+12.7	+9.4	+2.0	-1.7	+ .6	+5.0	- .9	0
1961	-6.7	-11.9	-4.5	-1.2	0	+3.0	- .2	-2.2	+1.5
1962	+2.6	- 5.9	-3.1	+2.7	+6.6	-1.5	+ .1	-3.7	-8.0

These data show that the rapid budworm development rate in 1960 could be associated with high temperatures in late May and early June. In 1959 temperature was high during the first two weeks of July when large larvae were developing to pupae and this doubtless had a favorable effect on survival.

June precipitation records for 1959, 1960, 1961 and 1962 are as follows:

	1959	1960	1961	1962
Total rain for June	8.43	3.72	3.54	4.33
8.00 a.m. to 6.00 p.m. data:				
(1) Max. rate for 1 hour	1.40	.38	.27	.20
(2) Max. duration of 1 storm	6 hrs.	4 hrs.	4 hrs.	5 hrs.
(3) Total hrs. with rain	43	16	24	32
(4) Total rain	4.94	1.06	.87	1.42
(5) Mean rainfall per hr.	.49	.11	.09	.44

The critical attributes of precipitation in relation to budworm survival have not been established. The above data show a high rainfall in 1959 as compared with 1960 and 1961. In the arbitrary period of 8.00 a.m. to 6.00 p.m. it rained for a total of 16 hours in 1960 as compared with 24 and 43 hours in 1961 and 1959, and this may have contributed to the rapid budworm development rate in 1960.

In 1962 preliminary tests using a recording potentiometer were carried out to compare maximum daily temperature, minimum temperature and relative humidity in the various cages with ambient conditions. However, difficulties were experienced with radiation even on small thermocouples and the tests must be repeated.

5. RESULTS FOR EACH SERIES

B. Series.--This series of experiments was carried out yearly during the period 1959-62 with little or no change in cage design. In 1962 a new cage material (Series E) was used but both types of cages were supposed to measure the same mortality factors. Figure 8 shows the survival curves and Tables II-VII record mortality data from these experiments. Survival rates from the third instar to the adult stage were as follows:

1959	1960	1961	1962
.71	.70	.73	.62 (Series B) .49 (Plot I3) .70 (Series E)

These data show a very high survival rate of the budworm for the third instar age interval. The mean of approximately .70 for field rearing in cages compares favorably with results reported by Stehr (1954) for laboratory rearings in which he obtained survival rates ranging from .60 to .80 during the second instar to adult age interval. The above results were also supplemented by experiments carried out in 1962 where small trees (about 5 feet in height) were caged with cotton and nylon cloth fastened to a wooden frame. Second-instar larvae were placed on the trees and then counted when 50 per cent of the adults had emerged and the remainder were living pupae. The survival rates on three trees where 21, 23, and 21 larvae had been set out, were .86, .70, and .81, respectively. However, the uniformity in survival rates in Series B and during the four-year period was not expected. It was assumed that changes in local climate would result in real changes in the proportion of hosts killed by disease and other intrinsic mortality factors, although it was also recognized that the tightly woven screen cage could modify the microclimate within the cage. The low survival of .49 on plot I3 in 1962 did result from a high intrinsic mortality rate, but sufficient data are not available to relate this to local climatic conditions.

C. Series.--Changes in cage design and other influences tends to confound any attempt to compare survival rates in this series during the period 1959-62. In 1959 larvae could easily disperse from the small cage, while in 1960 the foliage in some cages was limited to such an extent that partial starvation occurred and an increase in dispersal was noted. In 1961 and 1962 two different methods of placing a 'floor' in the cage to limit dispersal probably confounded the results to some extent. Figure 9 shows the survival curves for this series and Tables VIII-XII record the mortality data. Survival rates were as follows:

Fig. 8.--Survivorship curves for the B series in the period 1959-62. Plotted over the common base of the appearance of the first sixth-instar larva and first pupa in the population.

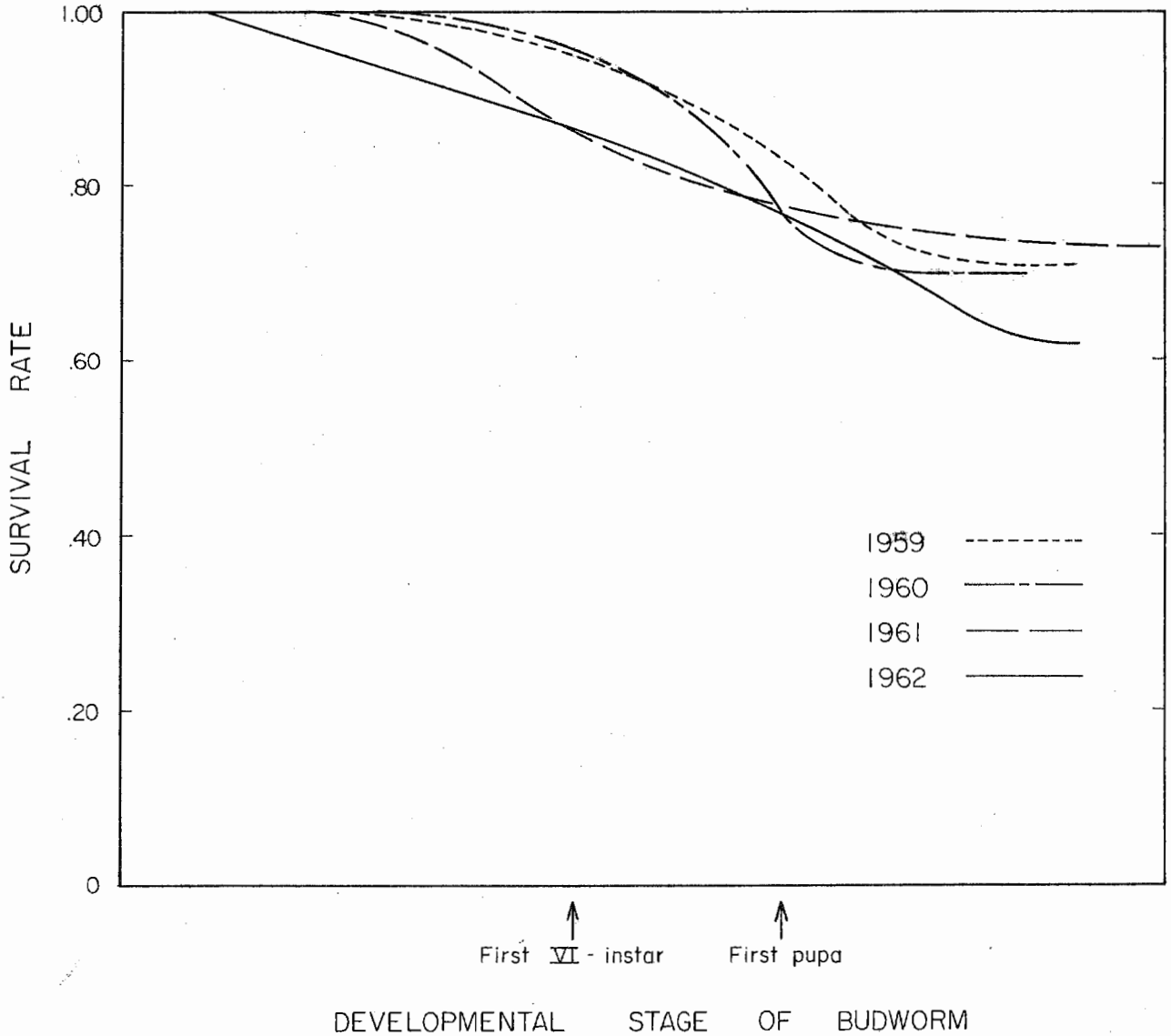

1.00
.80
.60
.40
.20
0
SURVIVAL RATE
1959
1960
1961
1962
First VI - instar
First pupa
DEVELOPMENTAL STAGE OF BUDWORM

TABLE II

B Series, 1959

Date	No. living larvae	Total loss	Missing	Predation	Dead	Disease	Dead + disease	Parasitism
May 19	92	17						
June 4	75	3	3					
18	72	5	4	1				
24	67	2	2					
July 3	65	12	2	1	3		3	6
8	53	0						
22	53							
Total		22	11	2	3		3	6

Adults: 53 = 32 females, 21 males

No dead larvae examined for disease.

TABLE III

B Series, 1960

Date	No. living larvae	Total loss	Missing	Predation	Dead	Disease	Dead + disease	Parasitism
May 18	92	21	19		2		2	
June 1	71	1		1				
8	70	5		3	1		1	1
16	65	4		2				2
20	61	10		4	2	2	4	2
27	51	1		1[1]				
July 4	50							
Total		21	0	11	3	2	5	5

Adults: 50 = 25 males, 25 females

[1]Prepupae

TABLE IV

B Series, 1961

Date	No. larvae	Total loss	Missing	Predation	Dead	Disease	Dead + disease	Parasitism
May 31	103	30	30					
June 7	73	1			1		1	
16	72	5	1	3		1	1	
21	67	6	3		2	1	3	
29	61	3	2					1
July 7	58	2	1		1[1]		1	
13	56	0						
17	56	0						
20	56	3			3[1]		3	
24	53	0						
27	53							
Total		20	7	3	7	2	9	1

Adults: 53 = 29 males, 24 females

[1]Pupae

TABLE V

B Series, 1962, G17

Date	No. larvae	Total loss	Missing	Predation	Dead	Disease	Dead + disease	Parasitism
May 31	43	6	6					
June 3	37	2			2		2	
7	35	1		1				
14	34	2	1		1		1	
19	32	0						
21	32	1	1					
26	31	0						
30	31	2				1	1	1
July 2	29	1		1				
9	28	2	1	1				
12	26	1	1					
16	25	2			2[1]		2	
19	23							
Total		14	4	3	5	1	6	1

Adults: 23 = 15 males, 6 females, 2 undetermined

[1]Pupae

TABLE VI

E Series, 1962, G17

Date	No. larvae	Total loss	Missing	Predation	Dead	Disease	Dead + disease	Parasitism
May 31	53	6	6					
June 3	47	3		2	1		1	
14	44	0						
19	44	0						
21	44	2	1		1		1	
26	42	0						
30	42	1	1					
July 2	41	1			1		1	
9	40	1		1				
12	39	3	2	1				
16	36	3			3[1]		3	
23	33							
Total		14	4	4	6	0	6	0

Adults: 33 = 18 males, 15 females

[1]Pupae

TABLE VII

B Series, 1962, I3

Date	No. larvae	Total loss	Missing	Predation	Dead	Disease	Dead + disease	Parasitism
May 29	41	2	2					
June 3	39	2			1	1	2	
11	37	2		1	1		1	
14	35	4	1		3		3	
19	31	1			1	0	1	
21	30	1	1					
26	29	2		1	1		1	
30	27	3	1			2	2	
July 2	24	1		1				
9	23	4	1	1	2		2	
12	19							
23	19							
Total		20	4	4	9	3	12	0

Adults: 19 = 9 males, 9 females, 1 undetermined

1959	1960	1961	1962
.086[1]	.33[2]	.33[2]	.20 (C1)[3] .088 (C2)[4]

1. Small cage with no 'floor'
2. Cage with waterproof paper as a 'floor'
3. Cage with nylon mesh as a 'floor'
4. Cage without floor

One interesting result noted in these experiments was the behavior of sixth-instar larvae before pupation. The examination of foliage for pupae while sampling natural populations has suggested that some larvae tend to move from the sixth-instar feeding site and pupate on other parts of the branch. This dispersal was quite evident in the C cages since a number of pupae were found on the cotton ends (toward the tree trunk) of the cage. In 1960 and 1961 only 38 per cent and 27 per cent, respectively, of the larvae that pupated did so in the sixth-instar feeding site. Preliminary data from a recording potentiometer did not show a temperature increase in these cages under full sunlight which would result in an abnormal behavioral pattern. The full impact of this dispersal pattern in natural populations and the vulnerability of larvae during this period has received little attention.

D. Series.--The methods used in setting up this series of experiments were similar in all years. The larvae were left exposed on the branch. Small, healthy larvae usually staged near the branch tip where they had originally established feeding sites. Large larvae (sixth instar) tended to move about on the branch just before spinning a pupation site, and it was therefore necessary to examine the tree very carefully during this period. Survival curves for these experiments are shown in Figure 10, and mortality data are recorded in Tables XIII-XVII. Survival rates were as follows:

1959	1960	1961	1962
.036	.017 .015[1]	.000	.000 (G17) .000 (I3)

1. Population on white spruce

In setting up these experiments it was realized that few individuals would survive to the late pupal or adult stage and further that the loss of very few individuals during the late larval and pupal stage would result in a geometric variation in the survival rate. However, it was hoped that a sufficient number might survive to the early pupal stage to permit the calculation of a survival rate for the third instar to the early pupal stage. Such a survival rate might be a realistic index of events occurring in any one year and permit inter-year comparisons. In 1961 and 1962 no individuals reached the pupal stage, but some large larvae did survive to that point in time (early June) when pupae started to develop in the B and C cages. Consequently, survival in the D series has been analysed in terms of the third instar to the 'first pupa' age interval although it is realized that inter-year comparisons must be carefully interpreted.

Fig. 9.--Survivorship curves for the C series in the period 1959-62. Plotted over the common base of the appearance of the first sixth-instar larva and first pupa in the population.

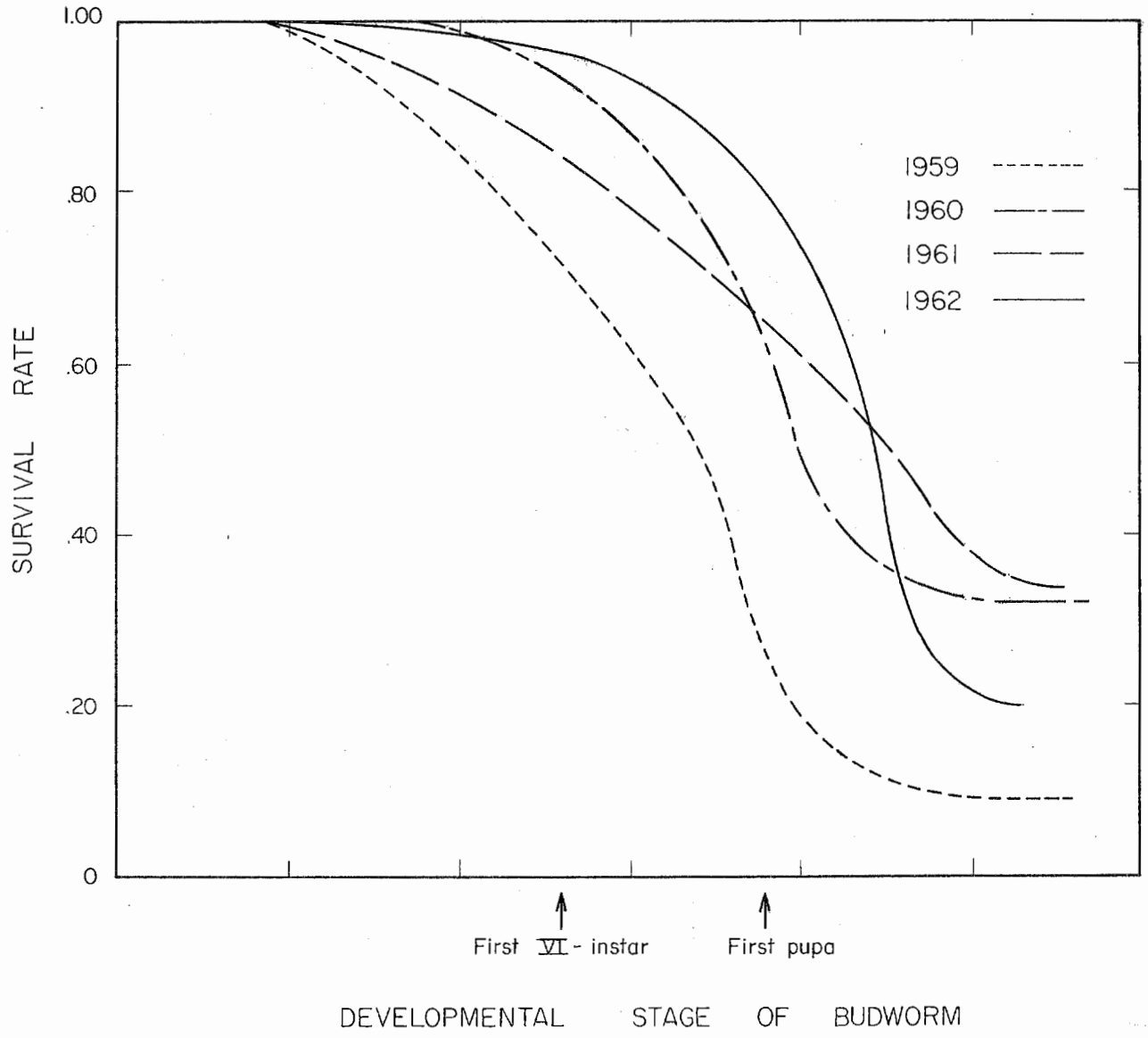

1.00
.80
.60
.40
.20
0
SURVIVAL RATE
1959
1960
1961
1962
First VI - instar
First pupa
DEVELOPMENTAL STAGE OF BUDWORM

TABLE VIII

C Series, 1959

Date	No. larvae	Total loss	Missing	Predation	Dead	Disease	Dead + disease	Parasi-tism
May 19	96	26	26					
June 2	70	7	3	2	2		2	
11	63	8	7	1				
16	55	12	11	1				
23	43	5	3	1	1		1	
30	38	27	13	3	2		2	9
July 5	11	4			1		1	3
8	7	1	1					
14	6							
22	6							
Total		64	38	8	6		6	12

Adults: 6 = 3 males, 3 females

TABLE IX

C Series, 1960

Date	No. larvae	Total loss	Missing	Predation	Dead	Disease	Dead + disease	Parasitism
May 18	102	30	30					
June 2	72	0	-					
8	72	11	1	8	1		1	1
17	61	9	6	2	1		1	
22	52	22	7	4	1		1	7
28	30	6	5		1	3	4	
July 6	24							
Total		48	19	14	4	3	7	8

Adults: 24 = 19 males, 5 females

TABLE X

C Series, 1961

Date	No. larvae	Total loss	Missing	Predation	Dead	Disease	Dead + disease	Parasitism
May 31	86	19	19					
June 6	67	0						
9	67	3			3		3	
15	64	3		2				1
20	61	3		1				2
22	58	2		1				1
27	56	3	2	1				
30	53	8	6	1				1
July 6	45	5	5					
10	40	1	1					
13	39	5	1	2[1]		1	1	1
17	34	12	2[1]	3[1]	7[1]		7	
20	22							
Total		44	17	11	10	1	11	6

Adults: 22 = 13 males, 9 females

[1]Pupae

TABLE XI

C1 Series, 1962

Date	No. larvae	Total loss	Missing	Predation	Dead	Disease	Dead + disease	Parasitism
May 31	54	9	9					
June 3	45	1			1		1	
7	44	1				1	1	
26	43	1						1
30	42	5	4			1	1	
July 2	37	2	1					1
9	35	12	7	1	4		4	
12	23	10	9		1		1	
16	13	4	1		1[1]		1	2
19	9							
23	9							
Total		36	22	1	7	2	9	4

Adults: 9 = 6 males, 2 females, 1 undetermined

[1]Pupae

TABLE XII

C2 Series, 1962

Date	No. larvae	Total loss	Missing	Predation	Dead	Disease	Dead + disease	Parasitism
May 31	62	5	5					
June 3	57	2		1	1		1	
14	55	1	1					
21	54	4	1		1	2	3	
26	50	4	4					
30	46	6	5			1	1	
July 2	40	1				1	1	
5	39	3	1	1				1
9	36	21	13	1	4		4	3
12	15	6	5		1[1]		1	
16	9	0						
19	9	4	1	1[1]	2[1]		2	
23	5							
25	5							
Total		52	31	4	9	4	13	4

Adults: 5 = 3 males, 2 females

[1]Pupae

Fig. 10.--Survivorship curves for the D series in the period 1959-62. Plotted over the common base of the appearance of the first sixth-instar larva and first pupa in the population.

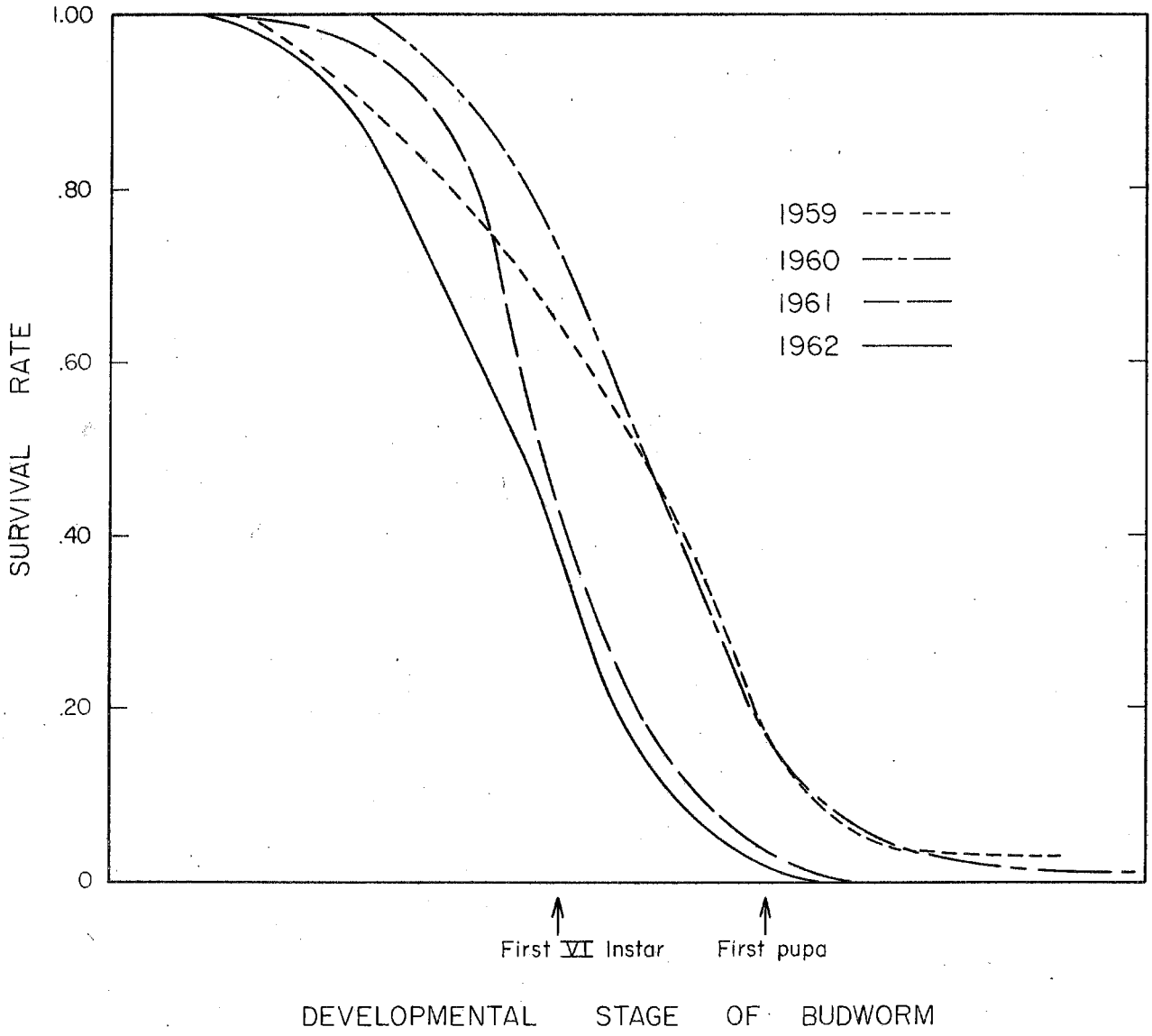

1.00
.80
.60
.40
.20
0
SURVIVAL RATE
1959
1960
1961
1962
First VI Instar
First pupa
DEVELOPMENTAL STAGE OF BUDWORM

TABLE XIII

D Series, 1959

Dead	No. larvae	Total loss	Missing	Predation	Dead	Disease	Dead + disease	Parasi-tism
May 19	176	38	38					
June 2	138	18	7	7	4		4	
10	118	12	7	5				
16	108	32	20	6	3	2	5	1
23	76	35	18	5	8	2	10	2
30	41	32	14		1		1	17
July 5	9	2	2					
8	7	2	2[1]					
10	5	0						
22	5							
Total		133	70	23	16	4	20	20

Adults: 5 = 5 males

[1] Pupae

TABLE XIV

D Series, 1960

Date	No. larvae	Total loss	Missing	Predation	Dead	Disease	Dead + disease	Parasitism
May 25	186	69	69					
June 1	117	7	3	2	2		2	
7	110	47	20	12	4	1	5	10
14	63	17	4	6	2	2	4	3
21	46	38	8	11	3	6	9	10
27	8	2	1			1	1	
July 6	6	4	4					
11	2							
Total		115	40	31	11	10	21	23

Adults: 2 = 2 females

TABLE XV

D Series, 1961

Date	No. larvae	Total loss	Missing	Predation	Dead	Disease	Dead + disease	Parasitism
May 30	180	60	60					
June 6	120	1			1		1	
9	119	2				2	2	
15	117	10	1	6		2	2	1
20	107	29	5	15		6	6	3
23	78	26	4	8		6	6	8
27	52	19	6	4		5	5	4
30	33	22	10	2		3	3	7
July 6	11	9	6			1	1	2
10	2	1	1					
13	1	1	1					
15	0							
Total		120	34	35	1	25	26	25

TABLE XVI

D SERIES, 1962, G17

Date	No. larvae	Total loss	Missing	Predation	Dead	Disease	Dead + disease	Parasi-tism
May 31	178	34	34					
June 3	144	4			4		4	
7	140	0						
9	140	3	1		2		2	
11	137	26	9	10	4	2	6	1
14	111	16	10	3	1		1	2
19	95	20	6	4	1	3	4	6
21	75	38	15	9	2	5	7	7
26	37	16	7	2	1	2	3	4
30	21	11	4	1	3	2	5	1
July 2	10	5	1		1	2	3	1
5	5	5	5					
9	0							
Total		144	58	29	19	16	35	22

TABLE XVII

D SERIES, 1962, I3

Date	No. larvae	Total loss	Missing	Predation	Dead	Disease	Dead + disease	Parasi-tism
May 31	149	22	22					
June 3	127	2		1	1		1	
7	125	5	3		2		2	
11	120	16	7	7	2		2	
14	104	16	9	4		3	3	
19	88	15	6	7		1	1	1
21	73	23	13	2		1	1	7
26	50	18	8	1	1	2	3	6
30	32	11	8	1		2	2	
July 2	21	17	12	3		2	2	
9	4	3	2			1	1	
12	1	1			1	0	1	
16	0							
Total		127	68	26	7	12	19	14

6. MORTALITY FACTORS

6.1 Missing

The unaccountable loss of larvae from feeding sites tends to confound any attempt to interpret mortality data drawn from experimental population studies. In the B series approximately 10 per cent of the larvae (based on third-instar density) could not be accounted for during the examination of the foliage and it was assumed that this loss was primarily sampling error. In the C series, 25 to 54 per cent could not be found primarily as the result of the dispersal of sixth-instar larvae from feeding sites and eventual drop from the cage. In the D series, 28 to 53 per cent of the larvae (also based on third-instar density) was 'missed'. The proportions of hosts 'missed' in the C and D series are comparable although it is evident that the 'missing' category is measuring two different patterns of events in these series. For example, if the number of larvae 'missed' are accumulated from one sampling period to the next and expressed as a proportion of the third-instar density, the following results are obtained for the 1962 C and D series data:

	D series		C1 series		C2 series		
	Missed		Missed		Missed		
Date	No.	Proportion[1]	No.	Proportion	No.	Proportion	Development
June 3							III-instar
7							
9	1	.01					
11	10	.07					
14	20	.14			1	.02	
19	26	.18			2	.04	
21	41	.28			2	.04	
26	48	.33			6	.11	First sixth-instar
30	52	.36	4	.09	11	.19	
July 2	53	.37	5	.11	11	.19	
5	58	.40	5	.11	12	.21	First pupa
9			12	.27	25	.44	
12			21	.47	30	.53	
16			22	.49	30	.53	
19					31	.54	

1. Proportion based on third-instar density

These data show that by the time the first sixth-instar larva appeared in the population, approximately 33 per cent of the D series were missing, while only zero to 11 per cent of the C series had dispersed from the cages. Some mortality factor apparently removed small larvae from the foliage in the D series and it is assumed that invertebrate predators are largely responsible. This topic is discussed in the following section.

Table XVIII records the proportions of early larvae, late larvae, and early plus late larvae 'missing' for all experiments for the 1959-62 period.

TABLE XVIII

Proportion of larvae 'missing' in all experiments, 1959-62

	1959			1960			1961			1962		
	Early[1] larvae	Late[2] larvae	Early + late[3] larvae	Early larvae	Late larvae	Early + late larvae	Early larvae	Late larvae	Early + late larvae	Early larvae	Late larvae	Early + late larvae
Series B (G17)	.09	.06	.15	.00	.00	.00	.05	.05	.10	.05	.07	.11
B (I3)										.05	.07	.10
E										.02	.07	.09
Series C or C1	.30	.40	.54	.01	.30	.26	.00	.30	.25	.00	.51	.49
C2										.04	.58	.54
Series D (Gn)	.25	.47	.51	.20	.27	.34	.08	.46	.28	.28	.46	.40
D (I3)										.30	.60	.54

[1]Proportion of early larvae based on third-instar density

[2]Proportion of late larvae based on large-larval density

[3]Proportion of early + late larvae based on third-instar density

6.2 Predation

The assessment of mortality caused by invertebrate predators where larval cadavers were left on the foliage proved to be quite arbitrary. Dead larvae were classified under 'predation' if the integument was broken, or scarred, or if the body contents appeared to have been sucked out. It was recognized that some larvae classified as 'dead and disease' may have actually succumbed to predator attack and the reverse could also have been true where sucking arthropods attacked but did little feeding. Table XIX records the proportion of hosts killed by invertebrate predators where cadavers were left on the foliage. Predation of early larvae was higher on the exposed branches (D series) than in the C cages although it had been hoped in setting up these experiments that little or no difference would occur. Table XIX shows no accountable trends in predation during the period 1959-62 but the data, particularly for the D series in 1959, 1961, and 1962, do show that the proportion of early larvae killed by invertebrate predators was considerably greater than the proportion of late larvae. This trend was reversed in 1960 when a higher proportion of late larvae were killed. The same conclusion can be drawn from the following table which records the proportion of hosts killed in various instars for the period 1959-62:

Year	No. budworm examined	Proportion killed by invertebrate predators in various instars				
		II	III	IV	V	VI
1959	35		.26	.23	.31	.20
1960	63		.08	.14	.25	.52
1961	45		.29	.49	.11	.11
1962	53	.02	.30	.40	.17	.11

These data suggest that if budworm development rate is rapid (1960) predation tends to occur among late larvae, while a larger proportion of early larvae are attacked if development is slow. This could be a function of the length of time that the host is vulnerable to attack, or a lack of synchronization with some of the more important invertebrate predators.

Table XIX shows that invertebrate predation of late larvae in the C series was comparable to predation on the exposed branches (as contrasted to early larval predation), and, with the exception of 1960, predation of late larvae varied from 9 to 12 per cent. It is therefore concluded that a complex of invertebrate predators other than spiders generally attack about 10 per cent of the late larval population.

The discussion of invertebrate predation to this point is based on a count of larval cadavers found on the foliage. However, it was recognized that some larvae could have been completely devoured or removed by invertebrate predators, and that large larvae and pupae were doubtless removed by birds. Thus a proportion of the larvae 'missing' in the D series could reasonably be assumed to have been removed by invertebrate predators and birds and the following analysis is an attempt to assess total predation based on this assumption. In considering total predation of early larvae it was further assumed that (1) birds do not attack small larvae (and gizzard analyses support this conclusion), and (2) early larvae

TABLE XIX

Proportion of larvae killed by invertebrate predators where larval remains were left on the foliage, 1959-62

	1959			1960			1961			1962		
	Early[1] larvae	Late[2] larvae	Early + late[3] larvae	Early larvae	Late larvae	Early + late larvae	Early larvae	Late larvae	Early + late larvae	Early larvae	Late larvae	Early + late larvae
Series B (G17)	.01	.01	.03	.06	.11	.15	.04	.00	.00	.03	.07	.08
B (I3)										.03	.10	.10
E										.04	.05	.09
Series C or C1	.06	.09	.11	.11	.10	.19	.06	.12	.16	.00	.02	.02
C2										.02	.06	.07
Series D (G17)	.13	.07	.17	.12	.27	.26	.24	.12	.29	.18	.08	.20
D (I3)										.17	.10	.20

[1]Proportion of early larvae based on third-instar density

[2]Proportion of late larvae based on large-larval density

[3]Proportion of early + late larvae based on third-instar density

missing in the B series were, in effect, the result of sampling error. This 'error' was then applied to early larvae 'missing' in the D series and the remainder were treated as larvae actually removed from the foliage by invertebrate predators. For example, in 1959, 9 per cent of the early larvae in the B series were classified as missing, or as sampling error. This was equal to 12 larvae (9 per cent of 138) in the D series. A total of 34 small larvae were missed in the D series and thus the assumed proportion taken by invertebrate predators was (34-13)/138 or 16 per cent. Total predation was therefore equal to

16% removed by invertebrate predators
13% cadavers left on the foliage

29%

On this assumption, total predation of early larvae during the period 1959-62 was as follows:

	1959	1960	1961	1962
Removed	16%	20%	3%	15%
Cadavers	13	12	24	18
Total	29%	32%	27%	33%

The speculative aspects of these results are quite evident, but the hypothesis that up to 30 per cent of the early larvae in an endemic population are taken by invertebrate predators could serve as a basis for further research of the predation problem.

Unfortunately, the analysis of predation of late larvae is also speculative. It has already been pointed out that invertebrate predation of late larvae (where the cadavers were left on the foliage) averaged about 10 per cent. But attempts to assess the proportion of late larvae removed from the foliage (primarily by birds) were confounded by the unexpected loss from the C cages. It was hoped that parasites, invertebrate predators, and intrinsic mortality would be the only factors causing mortality in the C series and thus a survival rate in the absence of bird predation could be obtained and compared with the D series to give an index of the effect of birds on the population. Dispersal from the C cages nullified this assumption. However, an attempt has been made to assess predation of large larvae by birds on the following hypotheses;

(1) that the proportion of late larvae 'missing' in the B series was essentially sampling error,

(2) that the number of late larvae 'missing' plus the number that survived in the C series was, in effect, a count of larvae that escaped attack by invertebrate predators, parasites, and disease, and that these larvae would be vulnerable to attack by birds in an exposed population,

(3) that the proportion of late larvae vulnerable to bird predation (as calculated from the C series) could be compared to the proportion of

larvae 'missing' in the D series in an attempt to assess bird predation in the D series.

The following example from the 1959 data shows how these assumptions were used in the assessment of bird predation. In 1959, 6 per cent of the late larvae in the B series were 'missed' and therefore classified as sampling error. In the C series, 17 late larvae were 'missed', 6 survived and, correcting for sampling error, this means (23-3)/43 or 47 per cent of the late larvae escaped attack by invertebrate predators, disease and parasites and would have been vulnerable to attack by birds. If the interaction of invertebrate predators, disease, and parasites on the host were similar in the C and D series, then 47 per cent of the late larvae in the D series were vulnerable to bird predation. Thus, 36 larvae (47 per cent of 76) were vulnerable to birds, as compared to 31 larvae (41 per cent) that were actually classified as 'missing' in the D series. Similar interpretations for 1960-62 data give the following results:

		1959	1960	1961	1962
1.	Sampling error	.06	.00	.05	.07
2.	Proportion of late larvae in C series classified as healthy and vulnerable to bird predation	.47	.85	.64	.65
3.	Population density of late larvae in D series	76	63	52	37
4.	Calculated number of larvae in D series vulnerable to bird predation. Based on (2) above.	36	54	33	24
5.	Observed number of 'missing' larvae in D series	31	17	21	14
6.	Proportion of larvae 'missing' in D series	.41	.27	.40	.38

In 1959 and 1961 the calculated number of larvae vulnerable to birds and the observed number of 'missing' larvae are roughly comparable, and these data suggest that birds could removed up to 40 per cent of the late larval population. No relationship is evident in the 1960 data primarily because the mortality caused by parasites, predators, and disease largely occurred during the late larval period and the attack rate was much higher in the D series than in the C cages.

6.3 Dead and Disease

In the field, diseased larvae were classified under 'disease' on their flaccid appearance, while dead larve with no apparent break in the integument were classified as 'dead'. Some of the latter group were later examined by M. M. Neilson, but since it was not possible to examine all dead larvae microscopically and define

TABLE XX

Proportion of budworm dying as the result of 'dead and disease', 1959-62.

	1959			1960			1961			1962		
	Early[1] larvae	Late[2] larvae	Early + late[3] larvae	Early larvae	Late larvae	Early + late larvae	Early larvae	Late larvae	Early + late larvae	Early larvae	Late larvae	Early + late larvae
Series B (G17)	.00	.04	.04	.01	.06	.07	.07	.07	.12	.08	.10	.16
B (I3)										.18	.17	.31
E										.14	.10	.13
Series C or C1	.03	.09	.09	.01	.10	.10	.04	.14	.16	.04	.16	.20
C2										.07	.18	.23
Series D (G17)	.07	.14	.14	.06	.22	.18	.14	.17	.22	.17	.30	.24
D (I3)										.08	.18	.15

[1]Proportion of early larvae based on third-instar density

[2]Proportion of late larvae based on large-larval density

[3]Proportion of early + late larvae based on third-instar density

the intrinsic cause of mortality, the 'dead' and 'disease' categories were necessarily combined for analysis purposes. Table XX records the proportion of budworm killed as the result of 'dead and disease'. These data suggest that (1) the mortality rate is generally higher among late larvae than early larvae, (2) if budworm development rate is rapid as in 1960, the higher mortality rate among late larvae is more pronounced, and (3) the mortality rate was generally higher in the unfavorable climatic years of 1961 and 1962 than in 1959 and 1960. The differential mortality rate between late larvae and early larvae in 1960 and its possible relationship to the rate of host development are also evident in the following data:

	Proportion of hosts dying in various stadia					
Year	II	III	IV	V	VI	Pupa
1959			.08	.41	.36	.15
1960	.02	.02	.05	.21	.58	.12
1961	.02	.16	.26	.16	.13	.27
1962	.10	.16	.23	.09	.33	.07

Table XX also points out one of the many problems in collecting, analysing and interpreting mortality data from experimental populations. For example, the proportion of budworm killed as the result of 'dead and disease' on plots G2 and G17 is as follows (taken from Table XX):

	1959	1960	1961	1962
Series B	.04	.07	.12	.16, .13
C	.09	.10	.16	.20, .23
D	.14	.18	.22	.24

In any one year the progressive increase in mortality in the three series of experiments is obvious, although one could assume on biological grounds that this type of mortality would be comparable in all experiments regardless of whether the larvae were caged or exposed. This is particularly true in comparing C cages and exposed branches in the D series. At this point in the study one can only assume that the B cages do have some effect on this type of mortality, but that the variations in the C and D series could result from chance alone.

It has already been pointed out that some dead larvae were examined for disease symptoms, but such a biased sample could not be used to obtain a realistic estimate of the incidence of disease. But it is of interest to note that 4 out of 12 dead larvae (33 per cent) examined in 1959, 20 out of 42 (48 per cent) in 1960, and 45 out of 55 (82 per cent) in 1962 were diseased.

6.4 Parasitism

A small chalcid, Elachertus cacoeciae Howard, and Apanteles sp. (very rare) are the only parasitic species recovered from experimental populations. This is an extremely simple complex since approximately 10 species have been recovered from natural populations in the area. E. cacoeciae is an external parasite which lays two or more eggs per host and has been recovered from a variety of lepidopterous

hosts. Table XXI records the proportion of hosts killed by parasites. In the D series parasitism (based on third-instar density) ranged from 11 to 21 per cent. Parasitism was higher in the D series than the C series indicating that the open mesh cages did, unfortunately, have an adverse effect on parasite attack.

The proportion of hosts killed in the various instars by E. cacoeciae is given in the following table:

	Proportion of hosts killed in various instars				
Year	III	IV	V	VI	Undetermined
1959	.03		.19	.78	
1960	.04	.06	.28	.62	
1961	.14	.31	.24	.31	
1962	.03	.20	.45	.30	.02

These data suggest that E. cacoeciae generally kills fifth- and sixth-instar larvae, but if host development rate is slow (1961 and 1962), a considerable number of third- and fourth-instar larvae may also be killed. Table XXI shows no specific trends in parasitism during the period 1959-62. A rather constant per cent parasitism would be expected since E. cacoeciae overwinters in an alternate host and it is quite probable that it has more than one generation per year.

6.5 Total Mortality

The section on various mortality factors is briefly summarized in the following table, in which is recorded the mortality of early larvae and late larvae in the D series:

	Early larvae	Late larvae			
	Mortality caused by:	Mortality caused by:			
	Total predation	Disease	Parasitism	Birds	Invertebrate predators
1959	.29	.14	.25	.41	.10
1960	.32	.22	.21	.27	.10
1961	.27	.17	.25	.40	.10
1962	.33	.24	.16	.38	.10

These data suggest the following survival rates for the period 1959-62:

1959 - (.71)(.10) = .071
1960 - (.68)(.20) = .136
1961 - (.73)(.08) = .058
1962 - (.67)(.12) = .080

but it must be noted that these survival rates are overestimates, since (1) they are based on actual rather than apparent mortalities, and (2) some early larvae were killed by parasites and disease as well as predators.

TABLE XXI

Proportion of budworm killed by parasites, 1959-62

	1959			1960			1961			1962		
	Early[1] larvae	Late[2] larvae	Early + large[3] larvae	Early larvae	Late larvae	Early + late larvae	Early larvae	Late larvae	Early + late larvae	Early larvae	Late larvae	Early + late larvae
Series B (G17)	.00	.09	.08	.01	.06	.07	.00	.02	.01	.00	.03	.03
B (I3)										.00	.00	.00
E										.00	.00	.00
Series C or C1	.00	.28	.17	.01	.11	.11	.06	.04	.09	.00	.07	.09
C2										.00	.08	.07
Series D (G17)	.01	.25	.14	.09	.21	.20	.10	.25	.21	.11	.16	.15
D (I3)										.06	.12	.11

[1]Proportion of early larvae based on third-instar density

[2]Proportion of late larvae based on large-larval density

[3]Proportion of early + late larvae based on third-instar density

7. THE KEY PERIOD IN LARVAL SURVIVAL

If the survival rate from the third instar to adult age interval is denoted as S_{III-A} and,

S_{III-VI} = survival rate from the third instar to the time when the first sixth-instar larva is found in the population,

S_{VI-P} = survival rate from the first sixth instar to the appearance of the first pupa,

S_{P-A} = survival rate from the first pupa to the appearance of adults,

then the following generalization is true:

$$S_{III-A} = (S_{III-VI})(S_{VI-P})(S_{P-A}).$$

This generalization was used in an attempt to find the key period that largely determines survival during the third instar to adult age interval. No detailed analysis was attempted since only four years' data for any one experimental population were available. Further difficulties were experienced in the analysis since in 1961 and 1962 the D populations became extinct before the adult stage and it was therefore necessary to assume a survival rate of $.001(S_{III-A})$ for analysis purposes. The following results, which show regressions coefficients derived from the regression of S_{III-A} on S_{III-VI}, S_{VI-P}, and S_{P-A}, are presented but no conclusions can be drawn until more data become available:

	S_{III-A} on S_{III-VI}	S_{III-A} on S_{VI-P}	S_{III-A} on S_{P-A}
B	.84	.38	.50
C	.41	.34	.86
D	.81	.62	

The apparent importance of the survival of small larvae in the B and D series requires corroborating evidence.

8. RELATIVE IMPORTANCE OF MORTALITY FACTORS

The difficulty of interpreting mortality data and assigning degrees of importance to various factors in population regulation has already been discussed. I have yet to establish a satisfactory method of expressing the proportion of hosts killed by a factor so that the following discussion of results is only tentative and subject to change pending the acquisition of more data and modification of study techniques. Such an analysis is also hampered by the fact that mortality or survival data are based on the effect of a factor and not on an independent measurement of the presence of the factor in the ecosystem.

In attempting to assess the importance of a factor each experimental series was examined separately. The relationship between survival from the

third instar to the adult stage (S_{III-A}) and the following variables were investigated by graphical and regression methods:

(1) Proportion of early larvae killed by a particular factor, with the proportion based on third-instar density.

(2) Proportion of late larvae killed by the factor and based on late larval density.

(3) Proportion of early plus late larvae killed by the factor and based on third-instar density.

The relationship between S_{III-A} to cumulative survival rates (as discussed in a previous section) was also investigated but will not be reported.

In the tabular data to follow the observed survival rates in a particular experimental series are ranked from high to low. The proportion of larvae killed by a particular factor are also listed and the importance of a factor is only inferred through its apparent rank correlation. In the B series, where the larvae were screened, the few parasites and predators that did enter the cage could be classed as random mortality and would not be expected to be related to survival. The proportion of hosts dying as the result of 'dead and disease', however, appear to be related to S_{III-A}:

Year	Observed survival in B series	Ranked survivals	Proportion of budworm killed by 'dead and disease'		
			Early larvae	Late larvae	Early + late larvae
1959	.70	.73	.07	.07	.12
1960	.70	.71	.00	.04	.04
1961	.73	.70	.01	.06	.07
1962 G17	.62	.70	.04	.10	.13
I3	.49	.62	.08	.10	.16
Series E	.70	.49	.18	.17	.31

In the C series the proportion of small plus large larvae, and the proportion of large larvae that were 'missed', appear to be related to S_{III-A}; except that in 1959, the proportion of small plus large larvae dying as the result of 'dead and disease' also appear to be related to S_{III-A}:

Year	Observed survival in C series	Ranked survivals	Proportion 'missing'		Proportion 'dead and disease'
			Late larvae	Early late larvae	Early + late larvae
1959	.086	.33	.30	.25	.16
1960	.33	.328	.30	.26	.10
1961	.328	.20	.51	.49	.20
1962 C1	.20	.088	.58	.54	.23
C2	.088	.086	.40	.54	.09

In 1959 the interaction of 'dead and disease' and parasites confounded the results since the proportion of hosts killed by parasites in 1959 was high in relation to other years and this may have resulted from the design of the cage in that year.

In the D series the survival rate for the third instar to the pupal stage (S_{III-P}) rather than S_{III-A} was used as the dependent variable. The following data suggest that the proportion of early plus late larvae dying as the result of 'dead and disease' and possibly the proportion of early larvae attacked by predators are related to S_{III-P}:

Year	Observed survival in D series	Ranked survivals	Proportion 'dead and disease' Late larvae	Proportion 'predation' Early larvae
1959	.18	.18	.14	.13
1959	.15	.15	.18	.12
1960	.04	.10	.15	.17
1961	.03	.04	.22	.24
1962 G17	.10	.03	.24	.18
I3				

No conclusions can be drawn from the above data on mortality in the B, C, and D series. However, it is of interest to consider that the proportion of budworm dying as a result of 'dead and disease' has some effect on survival, since it would fit the generally accepted hypothesis of the importance of weather.

9. SURVIVAL IN EXPERIMENTAL AND NATURAL POPULATIONS

The analysis of data obtained from life tables during the period 1950-58 showed that generation survival of the budworm is largely determined by survival from the third instar to pupal age interval (Morris, 1963). Therefore, one aim in establishing experimental population studies was to relate the survival rates determined from exposed branches to the yearly changes in density in natural populations of the spruce budworm. Unfortunately, zero survival rates in the D series in 1961 and 1962 have nullified this approach but, as more data become available, it may be possible to determine a key period in the third instar to adult age interval and carry out the proposed analysis. For example, it may be assumed that the early larval period (third instar to the beginning of the sixth instar) is the key period in the third instar to adult age interval and, consequently, survival in this period largely determines population density in the following generation. In 1960, survival in the D series during this period was .73 and the 1960 to 1961 rate of change in a natural population in the area was a 5-fold increase. In 1961, early larval survival in the D series was .36 and the 1961 to 1962 rate of change in a natural population was .34. In 1962, early larval survival in the D series was .28 and one would therefore suspect another decline in density in 1963.

10. FUTURE PLANS

The four years' study of experimental populations of the spruce budworm has produced limited results, but these warrant continuation of the program. The scope of future work, however, depends largely on designing a cage that will allow free access of parasites and invertebrate predators, limited dispersal but no loss of larvae larvae, and exclude birds. The results from this cage might permit an indirect but realistic appraisal of the 'missing' group on the exposed branches. Other lines of research might develop from the following comments and assumptions:

(1) With additional data it may be possible to relate intrinsic mortality in the B series to local climatic conditions. In any event, survival in the B series and fecundity in the B and C series (to be presented in a separate Interim Report) provide an index of population 'vigor' that may prove valuable in analysing changes in natural populations.

(2) It may be possible to obtain some index of invertebrate predation to analyse the 'loss' of small larvae in the D series by introducing a known number of predators on to caged trees. Results in 1962 suggested that budworm survival is high in small caged trees where DDT is carefully used to sterilize the environment.

(3) Survival in the D series was discouragingly low although it may be possible to study mortality on exposed branches with two 'populations'. In one the mortality of small larvae would be assessed. The 'second' population could be caged until the appearance of the first sixth instar and then exposed in order to assess large larval mortality, although the density of the experimental population in comparison to the resident population would have to be carefully considered. In any event, it is hoped that the D series will eventually suggest a key period in larval survival and the relative importance of the mortality factors under investigation.

11. REFERENCES

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