AN ABSTRACT OF THE THESIS OF

THOMAS EVAN NEBEKER for the DOCTOR OF PHILOSOPHY
(Name) (Degree)

in ENTOMOLOGY presented on August 29, 1973
(Major) (Date)

Title: POPULATION DYNAMICS OF THE DOUGLAS-FIR CONE MOTH *BARBARA COLFAXIANA* (KFT.) (LEPIDOPTERA: OLETHREUTIDAE)

Redacted for Privacy

Abstract approved: William P. Nagel

A population of the Douglas-fir cone moth, *Barbara colfaxiana* (Kft.), was studied on the Buckhead Seed Production Area, Oakridge, Oregon, during 1971 and 1972. A method of estimating cone and insect populations is presented. Factors contributing to the mortality of *B. colfaxiana* are discussed, with resinosis being the critical factor. Larval food consumption is discussed with reference to calories of cone tissue consumed through time. An average of 761 calories are consumed through the four larval stages. Amounts consumed of each structure (bracts, scales, seeds) are presented. A structural model is presented that depicts the role of *B. colfaxiana* in a natural stand.

Population Dynamics of the Douglas-fir Cone Moth, *Barbara colfaxiana* (Kft.) (Lepidoptera: Olethreutidae)

by

Thomas Evan Nebeker

A THESIS

submitted to

Oregon State University

in partial fulfillment of the
requirements for the
degree of

Doctor of Philosophy

Completed (August 29, 1973)

Commencement June 1974

APPROVED:

Redacted for Privacy

Associate Professor of Entomology
in charge of major

Redacted for Privacy

Department Chairman, Department of Entomology

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Dean of Graduate School

Date thesis is presented August 29, 1973

Typed by Mildred N. Israelsen for Thomas Evan Nebeker

ACKNOWLEDGMENTS

My endeavors have been enhanced by the advice, criticism, and encouragement of my committee and friends. I have been fortunate and happy in having Dr. W. P. Nagel (Major Professor), Dr. N. H. Anderson, Dr. J. Rudinsky, Dr. S. Overton and Dr. K. E. Rowe on my committee. Their advice and criticism throughout this study has been invaluable. I wish to express my sincere thanks to them for the freedom they afforded me in the selection and completion of this problem.

To the following I am particularly grateful for their advice and help: Mr. F. H. Schmidt, U. S. Forest Service, Forest Sciences Laboratory, Corvallis, Oregon, for his suggestions regarding the diapause problem encountered during this study and artifical media for use in rearing *Barbara colfaxiana*. Mr. S. W. Meso, U. S. Forest Service, Regional Office, Portland, Oregon, for making available past data and supplying a portion of the photos used in the text. Ms. Diana Kerns and Mr. M. H. Russell, Department of Entomology, Oregon State University, Corvallis, Oregon, a special thanks for their assistance in the field and laboratory. Mr. D. L. Isaacson, Department of Entomology, Oregon State University, Corvallis, Oregon, for hours of conversation, thought and friendship that is priceless. Dr. R. Waring, Department of Forestry, Oregon State University, Corvallis, Oregon, for agreeing to serve on my committee in the absense of Dr. Anderson during the preliminary examination. Dr. D. McIntire, Department of Botany, Oregon State University, Corvallis, Oregon, for comments regarding the thesis during the final examination and serving as graduate representative in the absense of Dr. Rowe. Dr. Mary Ann Strand, Coniferous Forest Biome, School of Forestry, Oregon State University, Corvallis, Oregon, for her comments and suggestions regarding the structural model and modeling processes.

I wish to thank Dr. Foote and members of the U.S.D.A. Agricultural Research Service, Entomology Research Division, Beltsville, Maryland, for their identification of specimens sent to them.

This work was supported by a National Science Foundation Grant, GZ-1372, in "Pest Population Ecology: An Inter-University Training Program".

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POPULATION DYNAMICS OF THE DOUGLAS-FIR CONE MOTH, *BARBARA COLFAXIANA* (KFT.) (LEPIDOPTERA: OLETHREUTIDAE)

I. INTRODUCTION

The Douglas-fir cone moth, *Barbara colfaxiana* (Kft.), is one of the many consumer populations associated with the cone system of Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco. The moth was described by Kearfott (1907) as *Evetria colfaxiana*. Heinrich (1923) revised the family Olethreutidae and created a new genus, *Barbara*, for which *E. colfaxiana* was the type species. He divided the genus into three varieties of the type and a species considered to be an aberrant form of *colfaxiana* (Hedlin, 1960). All feed on Douglas-fir cones except the variety *B. colfaxiana siskiyouana* (Kft.), which feeds on cones of several species of *Abies*. Another species, *B. mappana* Freeman, feeds on cones of Engelmann spruce (*Picea engelmannii*). *B. colfaxiana* occurs throughout the range of Douglas-fir in British Columbia, the Pacific Coast States, and the Rocky Mountains.

Since the early 1900's and the systematic work of Kearfott and Heinrich, life history studies, insect associations, and attempts at control of *B. colfaxiana* populations have been emphasized (Keen, 1952, 1953, and 1958; Radcliffe, 1952; Hedlin, 1958, 1960a, 1960b, and 1968; Hedlin, et. al. 1960; Johnson, 1958; Johnson, et al., 1960, 1966, and 1967; Koerber, 1960 and 1962; Clark, et. al., 1963; Dewey, 1965 and 1969; Dewey and Honing, 1968; Ruth and Hedlin, 1969). Little detailed analysis of field data has been done concerning cone and seed insect population dynamics in the Pacific Northwest except for Kozak (1963) who analyzed some of the factors associated with the distribution and intensity of attack by cone and seed insects in Douglas-fir. Also, Hedlin (1964) followed cone production, insect-caused damage to cones, and cone-insect populations in four plots of Douglas-fir on Vancouver Island, British Columbia, from 1957 to 1962. Recently, Barcie and Merkel (1972) compiled a bibliography about insects destructive to flowers, cones, and seeds of North American conifers.

Life tables have been used for the development of realistic population models that provide a view of insect life systems and processes that regulate population numbers (Deevy, 1947; Morris, 1954; Stark, 1958; Caughley, 1966; Blank, et. al., 1967; Varely and Gradwell, 1968; and Harcourt, 1970). Harcourt (1969) reviewed the development and use of life tables in the study of insect populations. Methods of life table analysis were proposed by both Morris (Morris, 1963; Nielson and Morris, 1964) and Varely and Gradwell (1960) (both methods are outlined in detail by Southwood, 1966), and Luck

(1971) compared the two methods. Ives (1964) pointed out some of the problems in the development of life tables for insects.

Nothing has been reported concerning the bioenergetics of Douglas-fir cone and seed insects. However, such an approach can be a valuable method of reducing the parameters of the system to a common unit, the calorie, and possibly as a means of assessing the importance of consumers. Davis and Warren (1965) and others have suggested that through this approach the functional components and their relationships can be analyzed.

Attempts to control _B. colfaxiana_ have been generally unsuccessful. Little is known of its population dynamics largely because the basis for sound investigations of the population dynamics, an accurate sampling method, has not been developed. Hence, if Douglas-fir cone moth populations are to be managed, a thorough understanding of factors regulating its numbers is necessary.

Thus, the main emphasis of this study was to work with a population of _B. colfaxiana_ to obtain information concerning its dynamics. The objectives of this study were: (1) to develop a sampling technique for the construction of a partial life table of a population of _B. colfaxiana_; (2) to determine the critical age interval and possibly identify critical factors regulating this population; (3) to determine the amount of Douglas-fir cone and seed tissue consumed by _B. colfaxiana_ through time; and (4) to develop a structural model to assess the function of _B. colfaxiana_ in a natural stand.

II. STUDY AREA

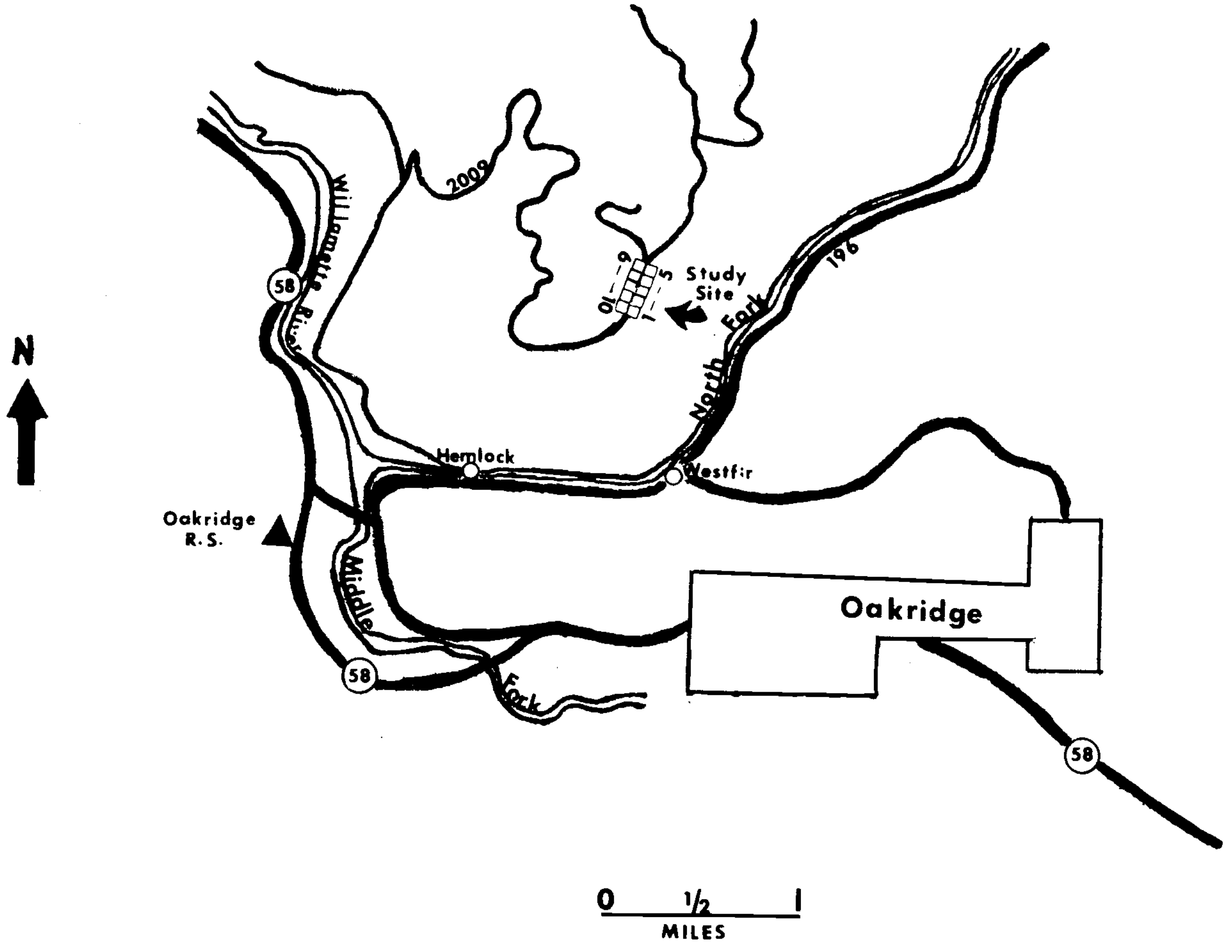
The area chosen for this study was the Buckhead Seed Production Area, Willamette National Forest, 6 miles northeast of the Oakridge Ranger Station, Oakridge, Oregon (Figure 1) at an elevation of 2,000 feet, more specifically:

> Oregon, Lane County, Sec. 6, R1E,
> T21S, W. M. on federal lands administered
> by the U. S. Forest Service, Lowell
> Ranger District.

During 1964, the area was thinned of all hardwoods, true fir and some Douglas-fir. During 1965, the area was sprayed with Cygon by helicopter in an attempt to control cone and seed insects. During 1966, no sprays were used, while in 1967 a hydraulic sprayer was used to apply Cygon. During 1968, the area was treated in the same manner as in 1965. From 1965 to 1968 the area was fertilized with urea. Since 1968, attempts at control have been with systemics, Cygon 267, Bidrin, and Meta-Systox-R. The last insecticide tests were made during 1970.

Within the area ten one-acre plots were established. The number of trees per plot varied. The area was bordered on the north mainly by Douglas-fir and some true fir, on the east and west by rather dense mixed hard- and soft-woods, and on the south with hardwoods and Douglas-fir. The area was surrounded by a buffer strip.

Figure 1. Location of the Buckhead Seed Production Area (=Study Site) northwest of Oakridge, Oregon.


N
2009
Study Site
10
9
5
1
North Fork
196
Willamette River
58
58
58
Hemlock
Westfir
Oakridge R.S.
Middle Fork
Oakridge
0 1/2 1
MILES

III. LIFE HISTORY

Adult emergence began in late April and continued through mid-May. The first adult in 1971 was observed on 7 May, in 1972 on 12 May. Oviposition began approximately 14 May 1971, and 20 May 1972, and continued for 30-40 days. The behavior of B. colfaxiana during oviposition agreed with that described by Hedlin (1960). The insect hovers around the extremities of the branches and settles on the foilage (only twice were adults observed lighting directly on the cone). After settling, the moth walks over the foliage, feeling continually with the ovipositor until a cone is reached; oviposition may or may not begin immediately. The insect stands on the bract (Figure 2), usually facing the tip of the cone, and from this position eggs are deposited on the abaxial surface of the bract. Occasionally an egg is found on the axial surface of the bract. Figure 3 illustrates the various areas of oviposition on the bract and Figure 4 the frequencies of oviposition on the various areas. Koerber (1960) reported that there were no significant differences between the numbers of eggs deposited on the basal, middle, or terminal third of a cone.

The most eggs found on one cone was 5, with 2 on a single bract. The egg when first laid is pearly white (Figure 5) and attached to the bract by a sticky substance, which can be seen around the margin of the egg (Figure 6).

Figure 2. Barbara colfaxiana during oviposition.

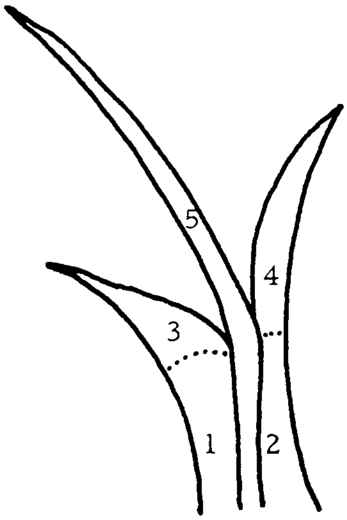


Figure 3. Areas of oviposition by B. colfaxiana on a Douglas-fir bract (abaxial view).

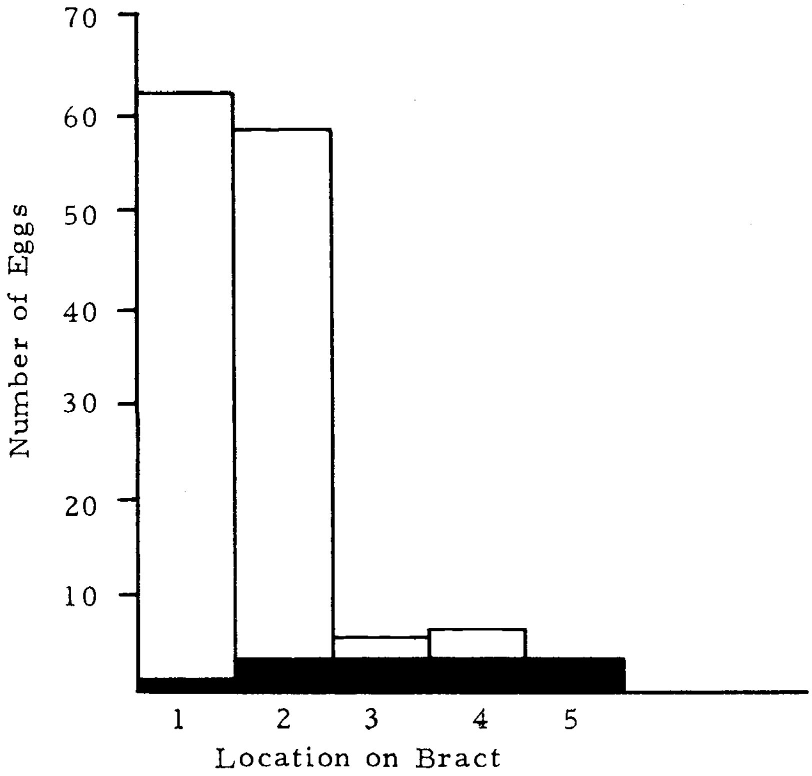


Figure 4. Number of B. colfaxiana eggs found on the axial surface of the bract (shaded) and abaxial surface (unshaded).

Figure 5. Egg of *B. colfaxiana* just after being laid.

Figure 6. *B. colfaxiana* egg with cementing material visible around the margin.

Four to six days after the egg is laid the outline of the developing larva becomes visible and is orange in color. Gradually, with the development of the larval head capsule, the egg appears to turn black. The egg stage lasted approximately 15 days.

After hatching the larva searches for a feeding site. The first larvae were observed on 14 May 1971 and 25 May 1972. The behavior of the first instar concurred with the observations of Radcliffe (1951), Keen (1958), and Hedlin (1960). The larva crawls up the bract toward the base of the cone, until it reaches a suitable feeding site between a bract and scale (Figure 7). The cone scale is very pubescent during this stage of development and unless the larva can wedge itself between a bract and scale and penetrate the pubescent layer it is unable to start feeding on scale tissue (Hedlin, 1960). Once established, the larva feed on the scale or bract tissue. The first instar lasts approximately 11 days, after which the larva spins a protective barrier within the feeding area behind which it molts. This is true for each molt. The larva continues to feed on scale tissue and burrows into the cone during the next two instars. Instar II lasts approximately 9 days and instar III approximately 14 days. By the time the larva reaches the fourth instar, which lasts approximately 29 or 30 days, the feeding is concentrated around the central axis; it consumes mainly seeds and some scale tissue. Periods of larval development and head capsule measurements are shown on Table 1.

Figure 7. Initial feeding site of B. colfaxiana first instar larva.

Table 1. _B._ _colfaxiana_ larval developmental periods and head capsule widths at the Buckhead Site, 1971.

Instar	Period	Head-Capsule Width (mm) $\bar{x} \pm$ S.D.	Head-Capsule Width (mm) Range	No. Measured
1	14 May - 25 June	0.26 ± 0.04	0.18 - 0.30	100
2	4 June - 9 July	0.42 ± 0.03	0.35 - 0.50	95
3	25 June - 23 July	0.71 ± 0.04	0.57 - 0.80	135
4	2 July - 6 August	1.18 ± 0.07	0.86 - 1.36	347

Figure 8 is a histogram of the distribution of the head capsule widths. A summary of the seasonal life history of _B._ _colfaxiana_ is presented in Figure 9.

The fourth instar larva spins a tough resinous cocoon in which to pupate, near the central axis. The first pupae were observed on 6 August 1971. _B._ _colfaxiana_ overwinters as a pupa.

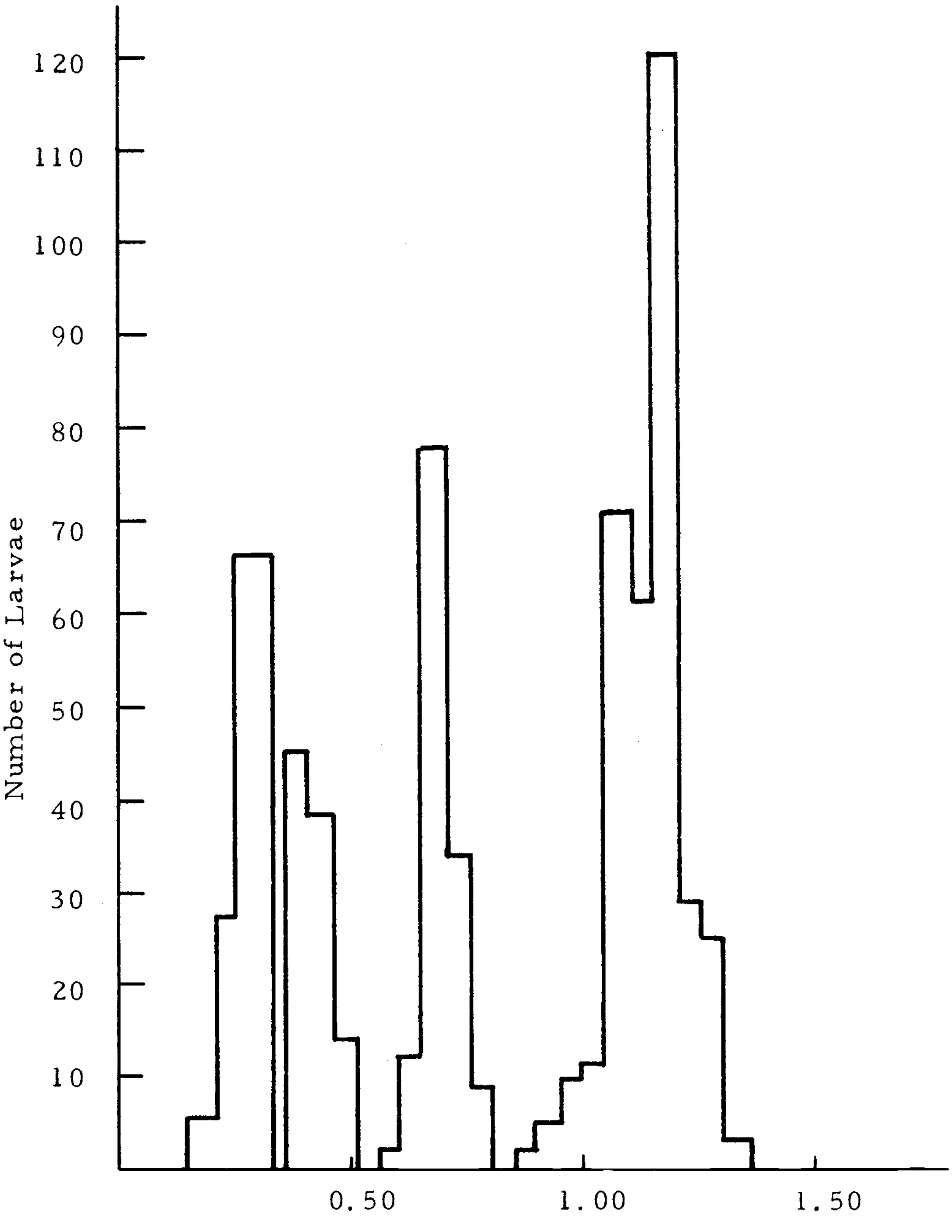


Figure 8. Histogram of B. colfaxiana head capsule widths.

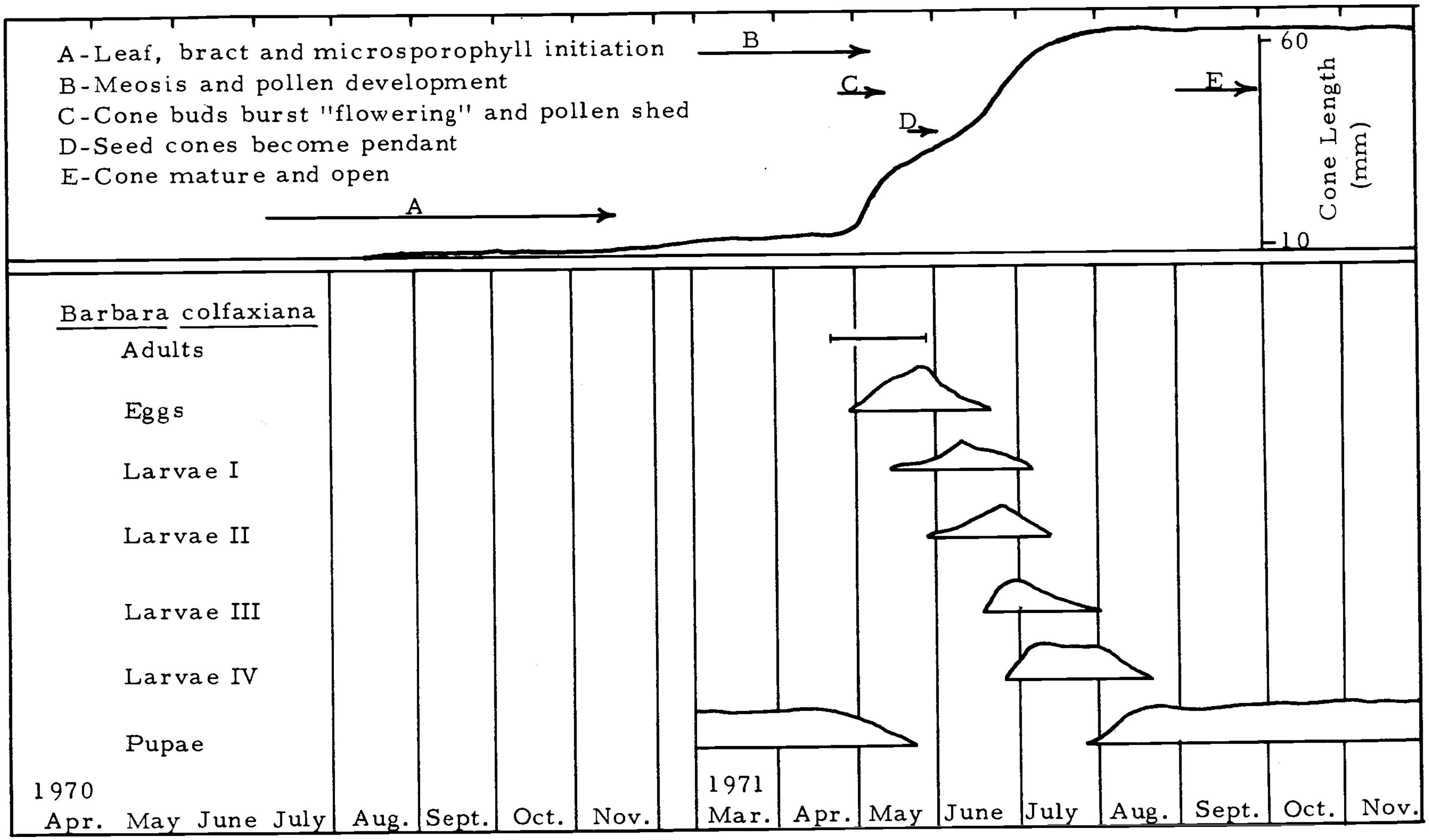


Figure 9. Seasonal development of B. colfaxiana compared with phenology of Douglas-fir cones, Buckhead Seed Production Area 1971. Curves are relative estimates to shown peaks of each stage.

IV. SAMPLING

Sample Unit

The sample unit upon which the partial life table was based was 600 cones. This unit contained all immature stages of _B. colfaxiana_. It was obtained by dividing the crown into two sections, designated N (north) and S(south), with 10 cones collected from the mid-crown in each section from 30 trees. Originally, it was intended to divide the crown into four sections, according to the four cardinal directions, with 5 cones from each section, but due to the additional amount of time required to do this, it was discontinued after the first sample. The use of this unit permitted estimates of absolute population per tree or unit area.

Sampling Procedure

Due to limited manpower and the considerable distance to the study area, it was decided that one day per week would be devoted to collecting field samples. This interval provided sufficient time for the samples to be examined before additional samples were taken.

At each sampling, 14 May 1971 through 4 June 1971, and on 13 August 1971, 3 trees were selected at random from each plot, a sample total of 30 trees. The reason for switching back to 3 trees per plot on 13 August 1971 was to compare percentage infestation within plots. From each tree 10 cones were collected from the mid-crown in each N and S section by using a sectional aluminum pole pruner, a total of 600 cones per week. If cones from the mid-crown of a tree could not be collected by using the pole pruner the tree was climbed. To collect a sample from 30 trees took 16 man hours. From 11 June 1971 through 6 August 1971, the number of trees per plot sampled (n_h), was based on the total number of trees per plot (N_h), total number of trees on the area (N), and the desired sample size of 30 trees. The number of trees sampled from each plot was calculated using the following:

$$n_h = \frac{N_h}{N} \times 30$$

The reason for stratifying in this manner was to reduce the number of times a sample would have to be taken from any one tree in a plot with few trees. This was not based on the assumption that the more trees per plot the greater the number of sample units necessary, but to reduce the amount of destructive sampling. Weekly sampling of the trees was with replacement, that is a tree could have, theoretically, been sampled each week.

Samples were collected periodically from August 1971 through April 1972 to assess further morphological development, parasitism, and predation. Sampling during 1972 was the same as 1971 but less frequently and with only 2 trees per plot since it was an extremely poor year for cone production; a total of 24 cones were produced on the Buckhead Seed Production Area in 1972.

Estimation of Cone Population

A means of estimating the total number of cones was required to estimate absolute population densities of the various immature stages of *B. colfaxiana*. Since all of these stages were found on or in the cone, a common technique could be used. A total census of the population would be disadvantageous, as in most population studies, when the same information could be obtained at a reduced effort through sampling. Therefore, a method of sampling to obtain reasonably precise estimates of the total number of cones, as efficiently as possible, was of prime interest.

To do this, a systematic sample with a quasi- or pseudo- index was used to estimate the total number of cones on the Buckhead Seed Production Area. This technique uses probability proportional to size (pps). Hartley and Rao (1962) developed the theory (for large N) associated with this procedure, which was developed for the case when the order of the listed index (size) units is random. Hartley (1966) utilized the fact that with systematic sampling the total number of different samples is N, rather than $\binom{N}{n}$ as with completely random sampling. Stage (1971) described the method for pps sampling developed by Hartley (1966), and to facilitate drawing samples using this method Stage provided a computer subroutine, PPSORT in FORTRAN IV, that identifies the units in the sample, calculates their sampling probability, and summarizes the distribution of this probability over the entire population for use in subsequent estimates of the population total and its variance. Stage's program was not used during this study. Jack Colby of the US/IBP Coniferous Biome, Corvallis, Oregon, developed a similar program, using data obtained during this study. Colby's program provided the probabilities used in making the various estimations.

Stage (1971) also indicated that selecting a sample unit with pps frequently can result in increased efficiency in estimating population totals. The procedure requires that each unit in the population be characterized by an index variable that is correlated with the variable of real interest to be measured for that unit. If a list of the index variable can be obtained cheaply for all units in the population, then sampling with pps according to the method developed by Hartley (1966) can be more efficient than pps sampling by other methods. How much more efficiently depends on the character of the functional relation between the index and the variable of real interest.

The index is based on the amount of information (approximate number of cones) on a tree in comparison to the number on a tree with the greatest number of cones on the area. The comparisons were made visually.

Each tree in each of the 10 plots was given an index $\underline{I}$ according to the criteria outlined in Table 2. After indexing each tree, they were

Table 2. Summary of indexing system and criteria for each index.

INDEX (I)	RANGE	CRITERIA
1.00 .90 .80	.75 - 1.00	Heavy - cones throughout the crown, dense
.70 .60 .50	.50 - 74	Medium - cones throughout the crown, sparse, or mid- and upper- crown, dense
.40 .30	.25 - 49	Light - cones in mid- and upper- crown, sparse to dense
.20 .10 .00	.00 - .24	Very light - cones only in upper crown or scattered very sparsely

ranked in order of index, from the highest to the lowest in each plot and the accumulative total T_I was calculated for all 10 plots.

With the time available for sampling, it was decided that a sample of $\underline{n} = 12$ of the $\underline{N} = 364$ cone bearing trees, with pps, were to be selected as units to estimate the total number of cones on the area. To select a sample of $\underline{n} = 12$ a sample interval $\underline{S}$ had to be computed:

$$S = \frac{1}{n} \times T_I$$

and a random number $\underline{r}$ between 1 and $\underline{S}$ (inclusive) selected. The trees with

$$T_{I-1} < r + (t-1)\,S \leq T_I; \quad t = 1, 2, \ldots, 12$$

were selected for sampling.

After the sample trees were selected, the same procedure was again followed in selecting the whorls to be sampled. Four whorls per tree were selected with pps. Within each selected whorl one branch was selected at random, with equal probabilities on which to count the cones. The sample selection can be summarized in the following steps:

Step 1. Assign an index $\underline{I}$ to each tree $\underline{j}$ in the area.

Step 2. Arrange the indices from highest to lowest in each plot and sum indices over all trees in the area.

$$\sum_{j=1}^{N} I_j = T_I$$

Step 3. Select $\underline{n}$ trees of the total $\underline{N}$ cone bearing trees systematically with probability proportional to I_j.

Step 4. Assign an index $\underline{W_i}$ to each whorl $\underline{i}$ on a selected tree.

Step 5. Arrange the whorl indices W_i from highest to lowest for this tree and sum the indices.

$$\sum_{i=1}^{K} W_i = W$$

Step 6. Select $\underline{k}$ whorls of the total $\underline{K}$ whorls per tree systematically with probability proportional to $\underline{W_i}$.

Step 7. From the selected whorls select one branch at random (numbering the $\underline{m_i}$ branches clockwise with the one pointing most northerly as number one) with equal probability.

Step 8. Count all live cones $\underline{y}$ on the branch selected.

The sample unit estimations for whorl, tree, plot, and area can be summarized as follows:

Step 1. Estimation of the number of cones on the $\underline{i^{th}}$ whorl is:

$$\hat{t}_{yi} = m_i \cdot y$$

where: $\underline{m_i}$ = number of branches in the $\underline{i^{th}}$ whorl.

Step 2. Estimation of the number of cones on the $\underline{j^{th}}$ tree is:

$$\hat{t}_{yj} = \sum_{i=1}^{k} \frac{\hat{t}_{yi}}{\pi_i}$$

where:

$$\pi_i = \frac{kW_i}{W}$$

and

π_i = inclusion probability of the $\underline{i^{th}}$ whorl.

Step 3. Estimation of the number of cones on the area is:

$$\hat{T}_y = \sum_{j=1}^{n} \frac{\hat{t}_{yi}}{\pi_j}$$

where:

$$\pi_j = \frac{nI_j}{T_I}, \quad \underline{n} = \text{number of sample trees.}$$

Step 4. Estimation of the number of cones per plot requires identification of the conditional inclusion probabilities for these plots.

$$\hat{T}_{ya} = \sum_{j=1}^{n_a} \frac{\hat{t}_{yi}}{\pi_{ca}}$$

where:

$$\pi_{ca} = \frac{n_a I_j}{T_I} = \text{conditional inclusion probability of the tree in plot } \underline{a} \text{ being sampled.}$$

Considering the entire area with a sample of $\underline{n} = 12$ an estimate of the variance of $\hat{T}_y$ is given by:

$$\hat{V}(\hat{T}_y) \doteq N\left(\frac{N-n}{n}\right)\left(\frac{1}{n-1}\right)\left\{\sum_{j=1}^{n} \hat{t}_{yj}^{\,2} - \frac{(\Sigma\hat{t}_{yj})^2}{n}\right\}$$

This accounts for most of the variance between trees, but not within trees. Table 3 summarizes the estimates for each of the 12 trees sampled and then projects an estimate of the total cones on the area. As mentioned before, the precision of the estimates depends on how well correlated the index was with the actual number of cones. Theoretically, if the index was absolute, there would be a perfect

Table 3. Area ($\hat{T}_y$), Plot ($\hat{T}_{ya}$) and Tree ($\hat{t}_{yj}$) cone estimates along with indices for the Buckhead Seed Production Area, September 1971.

Plot No.	No. of Cone Bearing Trees	Mean Index	Tree No. Sampled	Index	$\hat{t}_{yj}$	$\hat{T}_{ya}$
I	36	.60	24	.85	523	34,744
			31	.30	791	
II	22	.43	—	—	—	—
III	43	.45	14	.90	3209	43,877
			42	.50	615	
IV	34	.44	29	.70	1355	27,597
V	57	.34	3	.80	2977	45,570
			5	.20	252	
VI	61	.29	6	.40	385	16,245
VII	47	.31	36	.70	4778	49,354
			29	.05	20	
VIII	19	.39	—	—	—	—
IX	11	.39	—	—	—	—
X	35	.45	8	.90	3505	90,290
			11	.35	2924	

$\hat{T}_y = 424,523$

$\hat{V}(\hat{T}_y) = 27,082,463,044$

$\sqrt{\hat{V}(\hat{T}_y)} = 164,567$

positive linear relationship between the index and the actual number of cones with a variance of zero. However, with the high numbers of cones per tree and the sizes of the trees, it would be almost impossible to count every cone on a tree to check the accuracy of the estimates. It can be seen (Figure 10) that the indices are fairly well correlated with the estimates. Also, there was a significant relationship ($P < 0.05$) between the two variables.

The precision of the estimates could have been increased by indexing the branches in each selected whorl. It can be seen in Table 4 that due to the random selection of the branch within a whorl, a number of trees with high indices had low cone estimates and vice versa when compared with other trees with different indices.

The indices were inversely correlated with the number of cone bearing trees (Figure 11). The only conclusion that can be drawn is that there appeared to be a trend for less information (number of cones) on plots with more cone bearing trees, given that the indices were significantly correlated with the number of cones (Figure 10).

Cone Survival

Cone survival was monitored on the Buckhead Site during 1971 to estimate absolute population densities of Douglas-fir cones through time. Branches were tagged mainly on the north and south aspects, occasionally on the east and west aspects, in the lower- and mid-crown. Because of the high density of cones and the size and shape of the

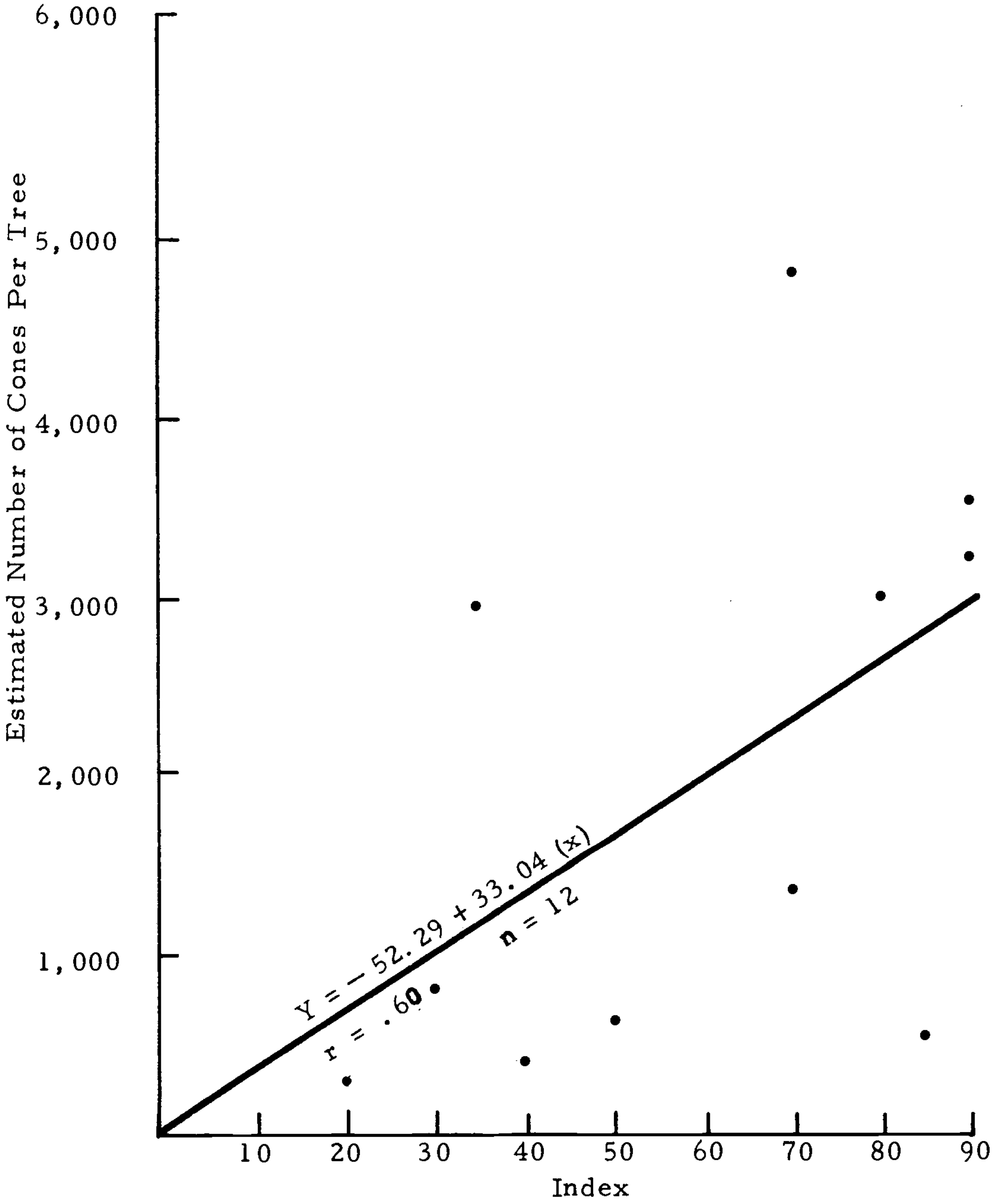


Figure 10. Relationship between indices and estimated cones per tree on the Buckhead Seed Production Area 1971.

Table 4. Summary of the tree ($\hat{t}_{yj}$) and the whorl ($\hat{t}_{yi}$) cone estimates for the Buckhead Seed Production Area in September 1971.

Plot No.	Tree No.	Tree Index	Whorl No.	Whorl Index	m_i	y	$\hat{t}_{yi}$	π_i	$\hat{t}_{yj}$
I	31	.30	15	.6	3	12	36	.32000	791
			14	.9	6	17	102	.48000	
			12	.9	5	15	75	.48000	
			10	.8	6	22	132	.42667	
	24	.85	15	.8	5	19	95	.31068	523
			11	.9	4	19	76	.34955	
			7	.8	5	0	0	.31068	
			4	.4	4	0	0	.15534	
III	14	.90	15	.9	5	39	195	.29032	3209
			12	.9	5	67	335	.29032	
			10	.8	7	51	357	.25807	
			7	.6	5	0	0	.19355	
	42	.50	10	.7	6	9	54	.47458	615
			9	.4	5	16	80	.27119	
			8	.4	4	14	56	.27119	
			7	.5	6	0	0	.33898	
IV	29	.70	17	.9	3	19	57	.39130	1355
			15	.9	5	28	140	.39130	
			14	.8	4	26	104	.34783	
			11	.5	4	30	120	.21739	

Table 4. (Continued)

Plot No.	Tree No.	Tree Index	Whorl No.	Whorl Index	m_i	y	$\hat{t}_{yi}$	π_i	$\hat{t}_{yj}$
V	5	.20	8	.8	3	9	27	.50000	252
			7	.9	4	16	64	.56250	
			6	.9	4	6	24	.56250	
			4	.7	6	3	18	.43750	
	3	.80	12	.9	6	76	456	.26471	2977
			9	.8	5	37	185	.23529	
			6	.8	5	22	110	.23529	
			1	.2	6	0	0	.05882	
VI	6	.40	13	.7	6	7	42	.29474	385
			11	.9	7	4	28	.37895	
			9	.9	4	16	64	.37895	
			6	.5	6	0	0	.21053	
VII	36	.70	13	.9	4	173	692	.34952	4778
			10	.9	6	152	912	.34952	
			6	.7	6	0	0	.27185	
			4	.6	4	11	44	.23310	
	29	.05	7	.5	3	1	3	.62500	20
			6	.5	5	1	5	.62500	
			5	.7	3	2	6	.87500	
			3	.6	3	0	0	.75000	
X	8	.90	18	.7	3	113	339	.22764	3505
			16	.9	5	73	365	.29268	
			13	.9	9	3	27	.29268	
			7	.7	7	22	154	.22764	
	11	.35	10	.9	6	22	132	.43374	2924
			7	.8	9	4	36	.38554	
			9	.7	4	19	96	.33735	
			6	.4	8	54	432	.19277	

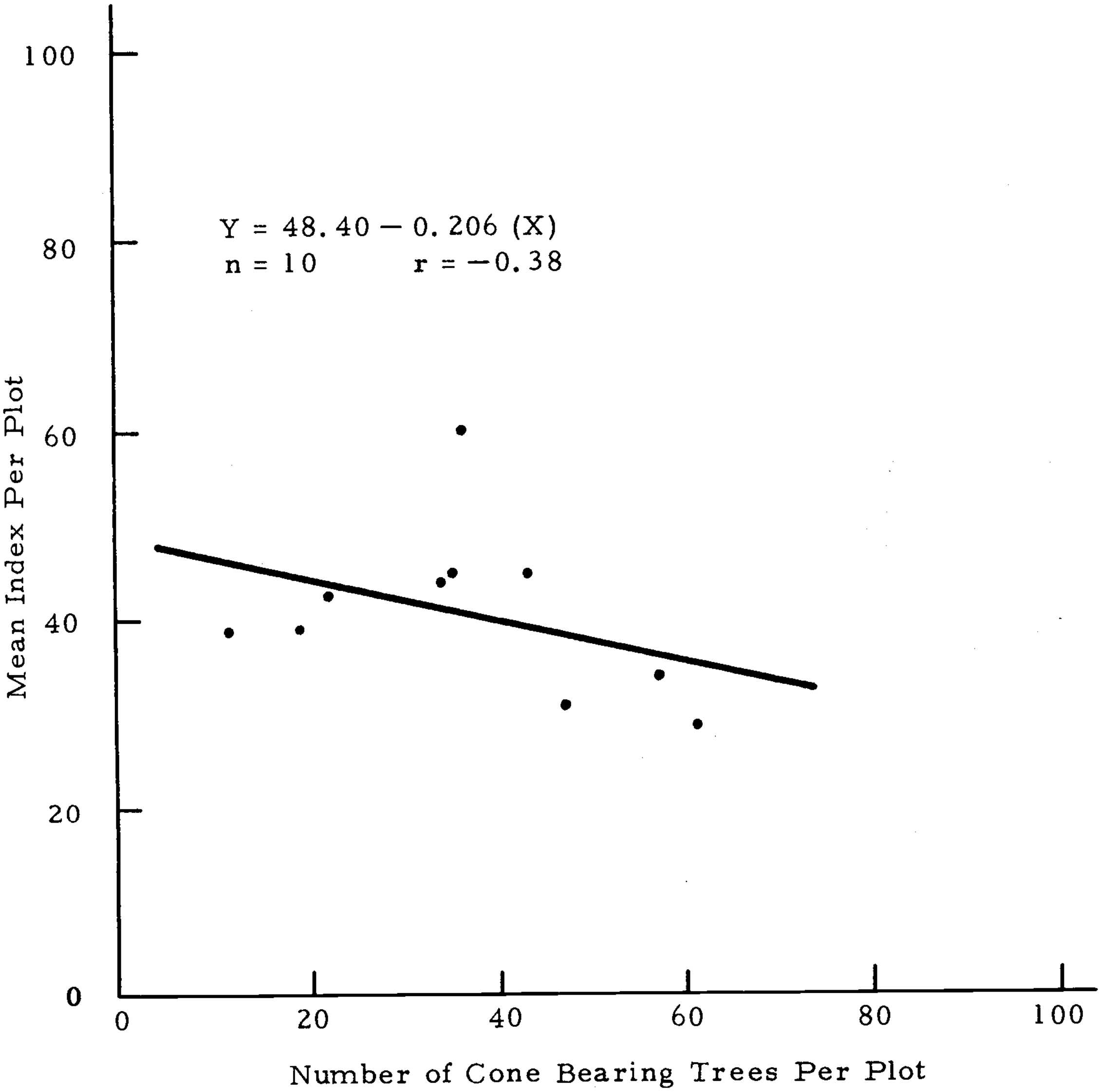


Figure 11. Relationship of the mean index and number of cone bearing trees over all 10 plots at the Buckhead Site, 1971.

branches, it was impossible to obtain a reliable estimate of cone survival in the mid-crown without distructive sampling. Hence, the survivorship curve (Figure 12) was based on information from the lower-crown (Table 5). The following assumptions were made at this point: (1) the percentage mortality is equal throughout the crown, and the information obtained from the lower crown was applicable to the remaining portions of the crown, and (2) there was no differential mortality between plots. The survivorship curves for plots I, III, IV, V, VI, VII, X were developed using the same percentages as for the entire area and summarized in Table 6. The cause of cone mortality in the early stages of development was not identified. All cones failing to develop were classed as aborted cones. As can be seen in Table 5, the abortion rate was high during 1971 with 56.5 percent of the cone population failing to survive.

Distribution of *B. colfaxiana*

The dispersion of a population, the description of the pattern of distribution of the animals in space, is of considerable ecological significance. Not only does it affect the sampling program and method of analysis of the data, but it may be used to give a measure of population size and, in its own right, is a description of the condition of the population (Southwood, 1966). The individuals may have three basic or more types of spatial distribution: (1) a random distribution, (2) a contagious

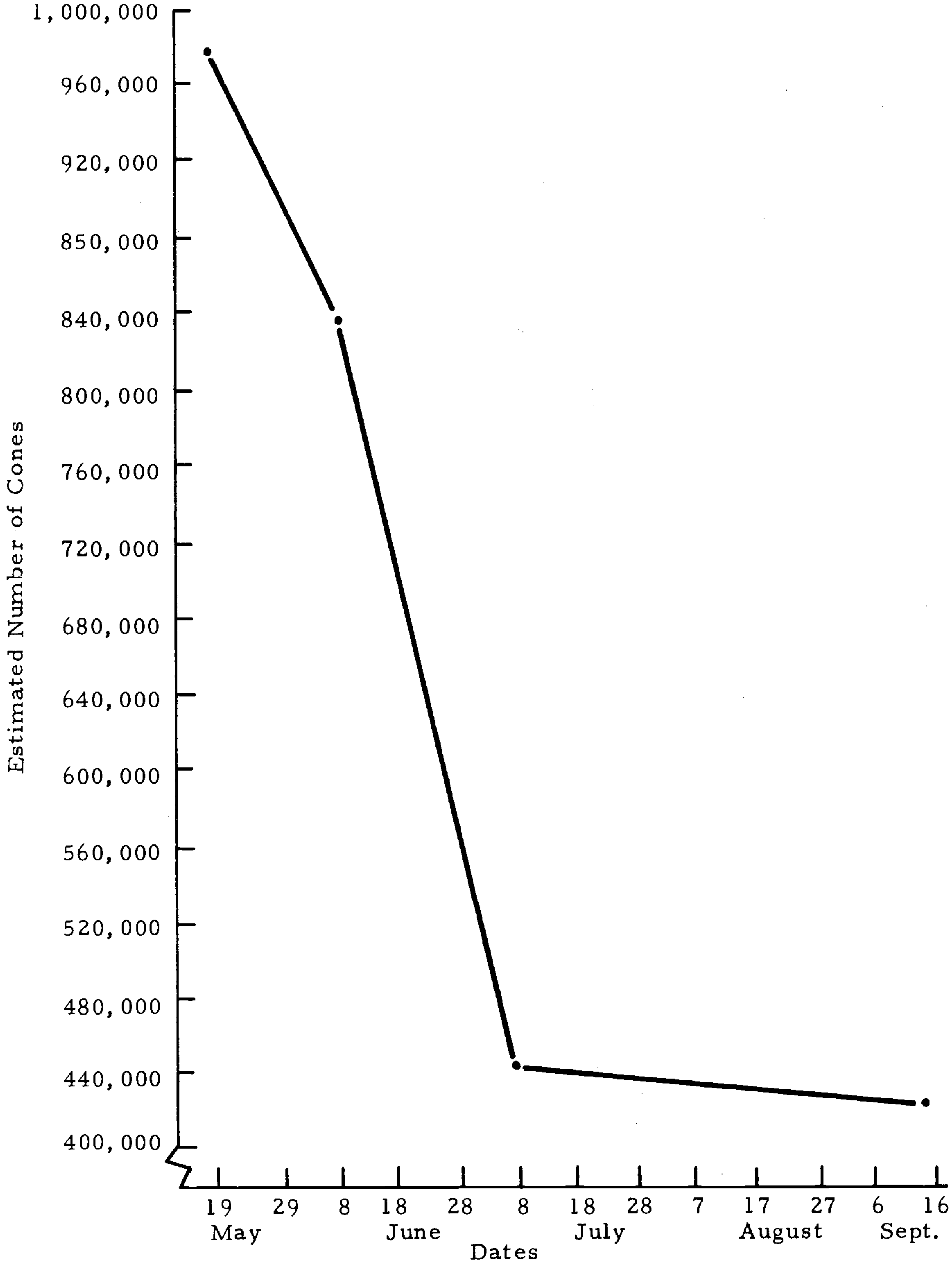


Figure 12. Survivorship curve for Douglas-fir cones on the Buckhead Seed Production Area, 1971.

Table 5. The number of cones alive on selected branches through 1971 on the Buckhead Seed Production Area.

	Lower North (LN)					Lower South (LS)			
Branch	Date				Branch	Date			
Number	May 19	June 10	July 7	Sept. 15	Number	May 19	June 10	July 7	Sept. 15
5	32	32	8	7	3	25	9	9	8
12	24	24	17	14	6	17	16	2	2
13	25	21	9	9	17	25	15	15	14
16	9	9	7	7	18	14	13	13	13
28	42	42	10	10	27	23	22	2	1
33	17	15	15	15	34	30	25	25	23
Total	149	143	65	62		134	100	66	61
Percentage Mortality	0	4.0	56.4	58.4		0	25.4	50.8	54.5
Percentage Mortality	LOWER NORTH & LOWER SOUTH					0	14.1	53.7	56.5

Table 6. Estimated number of cones per plot for four dates in 1971.

	DATE			
Plot No.	May 19	June 10	July 7	September 15
I	79,871	68,609	36,980	34,744
III	100,867	86,645	46,701	43,877
IV	63,441	54,496	29,373	27,597
V	104,759	89,988	48,503	45,570
VI	37,344	32,079	17,290	16,245
VII	113,458	97,460	52,531	49,354
X	207,563	118,297	96,102	90,290

distribution (clumped, over-dispersion, or aggregated distribution), (3) a regular distribution (uniform, under-dispersion, or even dispersion).

There are few examples of randomly distributed population-members within a given area. Even though the distribution of host food may be random, the dispersion of the population is still usually one of groups (Elton, 1949). However, it can be seen in Table 7 that, by using the Chi-Square goodness of fit test, the egg distribution of _B_. _colfaxiana_ agrees with the Poisson (random) distribution ($P < 0.10$). This suggests but does not prove that the eggs were randomly distributed on the study area during 1971. The class intervals were obtained from counts on 20 cones taken from the mid-crown of each of 30 trees selected at random. Similar results would be obtained for the larvae and pupae since the larvae attack the cone the egg was laid on and subsequent development takes place within the same cone.

In subsequent analysis, clumping was not suggested when analyzed as above. However, greater densities were observed in the center of the study area, with densities decreasing to the north and south of the central plots (III + VIII) (Table 8). A further difference in densities of _B_. _colfaxiana_ was suggested (Table 9) by Russell (1972).

Table 7. Frequency distribution of 14 May 1971 egg data.

CLASS INTERVAL	OBSERVED FREQUENCY	EXPECTED FREQUENCY (BASED ON POISSON DISTRIBUTION)	$\frac{(0-E)^2}{E}$
0	7	3.7982	2.6991
1	7	7.8496	0.0920
2	4	8.1113	2.0839
3	6	5.5878	0.0304
4	3	2.8870	0.0044
5	1	1.1933	0.0313
6	2	0.5727	3.5572

Where: Class Interval = number of eggs per 20 cones

Frequency = number of observations that fall into that class interval

Chi Square = Summation of $\frac{(0-E)^2}{E}$

Chi Square = 8.4983 is not significant at $(P < 0.10)$

Table value at 0.10 = 9.236

Table 8. Densities of B. colfaxiana eggs on the Buckhead Seed Production Area, 1971.

Plot	$\bar{X} \pm$ S. E.	Plot	$\bar{X} \pm$ S. E.	Plots	$\bar{\bar{X}} \pm$ S. E.
I	8.80 ± 3.44	X	3.20 ± 2.46	I+X	5.55 ± 4.21
II	6.60 ± 1.75	IX	3.60 ± 0.87	II+IX	5.10 ± 1.95
III	11.60 ± 1.94	VIII	11.00 ± 5.56	III+VIII	11.30 ± 5.89
IV	4.80 ± 1.83	VII	7.80 ± 2.08	IV+VII	6.30 ± 2.77
V	6.60 ± 1.86	VI	2.40 ± 1.03	V+VI	4.50 ± 2.13

Plots I - V on the east side of the study area.
Plots VI - X on the west side of the study area.
Plots I + X on the south end of the study area.
Plots V + VI on the north end of the study area.

$\bar{X}$ = mean number of eggs/60 cones over all sample dates.

$\bar{\bar{X}}$ = mean for plots pooled.

$s_1^2 = s_2^2 = \ldots = s_{10}^2$ at $(P < 0.01)$ using Bartletts test for homogeneity of variances.

Table 9. Densities of *B. colfaxiana* pupae in the canopy on the Buckhead Site 1971 (Russell, 1972).

Section	Mean/20 Cones	S. E.	T-test
Lower crown	2.90	0.78	
			N.S.
Mid crown	1.58	0.46	
			*
Upper crown	0.52	0.08	
			**
Lower crown	2.90	0.78	

N.S. = non significant at $P < 0.05$

* = significant at $P < 0.05$

** = significant at $P < 0.01$

V. LIFE TABLE FOR BARBARA COLFAXIANA

It was the intent of this study to develop two life tables for B. colfaxiana representing the 1971 and 1972 generations. However, due to the unexpected high percentage (97.34%) of the 1971 population remaining in diapause during 1972 and the cone crop failure (only 24 cones were produced on the Buckhead Site during 1972 compared to the estimated 424,523 cones that were produced during 1971) only a partial life table was developed. The limited information concerning the 1972 population will be presented in the section dealing with second generation mortality.

Life tables, originally devised by students of human demography, have been adopted in recent years to studies of natural populations for a wide range of animals and plants (Harcourt, 1970; Hawksworth, 1965; Hett and Louks, 1968; Waters, 1969). They provide a convenient method of tabulating numeric changes within a generation, along with the measurable mortality factors contributing to these changes. The usefulness of the life table is a function of the number of age intervals that can be monitored quantitatively. Ives (1964) pointed out that the compilation of life tables for an insect population requires reliable sampling techniques for estimating the number of individuals in these different age intervals. Hence, it was the intent of this study (having developed such a sampling technique for the cone and indirectly for the immature stages of *B. colfaxiana*) to construct a partial life table for *B. colfaxiana* to meet the second part of the first objective of this study. Further, in this chapter the suspected critical age interval for *B. colfaxiana* will be identified and the critical factor(s) contributing to the mortality in this interval, as well as the other age intervals will be discussed.

Preparation of the Partial Life Table

In constructing the partial life table for *B. colfaxiana* seven age intervals were used: egg through instar I; instar II; instar III; instar IV; non-diapausing pupae; diapausing pupae; and adults. The egg and instar I were combined because the small larvae (those alive) were hard to find prior to a successful entrance into the cone. Hence, reliable estimates for the number entering instar I were not obtained and to develop the partial life table as realistically as possible the egg and instar I were combined.

To determine the number entering a given age interval a graphical integration technique was used. This is the crudest and simplest method (Southwood, 1966), but proved most practical for these estimations. The number of eggs, larvae (of various stages), and/or pupae were counted on each sample date. The percentage infestation of each stage was determined for each sample date, along with the estimated number of cones $\underline{\hat{T}_y}$ (Table 10). The percentage infestation per age interval and $\underline{\hat{T}_y}$ (per sample date) were multiplied together to obtain an absolute estimate of the number of individuals per age interval per sample date. These successive estimates were plotted. The points were joined and the area under the curve was calculated with a compensating polar planimeter. The number of individuals entering a given age interval were computed by:

$$l_x = \frac{A}{d_i}$$

Where:

l_x = number entering the interval

A = area under the curve, expressed as number of individuals

d_i = mean time spent in a particular age interval (= developmental time).

The number of pupae was determined by taking the mean number found per sample date ($\bar{X} \pm$ S. E. = 90.00 ± 24.36), between 6 August 1971 and July 1972, and multiplying by the number of sample units (708). Pupae were considered in diapause if they hadn't emerged by 1 July 1972. The number of adults was estimated from the number of cast pupal skins found per sample date.

The column headings for the partial life table are:

x = age interval;

l_x = number alive at the beginning of x;

d_xF = factor responsible for d_x;

d_x = number dying during x;

$100d_x/l_x$ = d_x as a per cent of l_x;

S_x = survival rate within x (Table 11).

To determine viability, eggs from the first three samples were reared individually in small vials, to prevent cannibalism, and percentage hatching was determined (95.40%). All other mortality factors were obtained from direct observations, except the unknown factors. The unknown mortality was derived from the difference between the number entering the next age interval and the number unaccounted for when all mortality factors were summed and subtracted from the number entering the previous age interval. As can be seen in Table 11, this factor is rather large for some age intervals. The factors contributing to this "unknown" were: (1) sampling error; (2) error in determination of the area under the curve (lack of accuracy in operation of the planimeter and possible plotting error); (3) larval movement (especially during instar I prior to the establishment of a feeding site).

The mortality factors dxF were treated as though they operated randomly, except in the egg and instar I interval. In that interval the

Sample Date	Eggs[1]	%[2]	Eggs[3]	Instar I[1]	%[2]	Instar I[3]	Instar II[1]	%[2]	Instar II[3]	Instar III[1]	%[2]	Instar III[3]	Instar IV[1]	%[2]	Instar IV[3]	$\hat{T}_y$
14 May	62	10.33	100,812	1	0.17	1,659										975,915
21 May	80	13.33	128,235	0	0.00	0										962,000
28 May	93	15.50	142,290	8	1.33	12,209										918,000
4 June	57	9.50	83,030	25	4.17	36,446	1	0.17	1,486							874,000
11 June	37	6.17	50,964	58	9.67	79,874	10	1.67	13,794							826,000
18 June	1	0.17	1,234	20	3.33	24,276	40	6.67	48,424							726,000
25 June				6	1.00	6,240	55	9.17	57,221	65	10.83	67,579				624,000
2 July				2	0.33	1,716	10	1.67	8,684	62	10.33	53,716	36	6.00	31,200	520,000
9 July				1	0.17	768	2	0.33	1,491	25	4.17	18,842	109	18.17	82,101	451,849
16 July							0	0.00	0	7	1.17	5,242	81	13.50	60,480	448,000
23 July							1	0.17	768	2	0.33	1,469	71	11.83	52,644	445,000
30 July													78	13.22	58,565	443,000
6 Aug.													18	3.00	13,200	440,000
													4	0.67	2,928	437,000

[1] Number found per sample date

[2] Percentage infestation per 600 cones

[3] Estimated number of individuals per sample date

Example calculation (14 May 1971)

No. of eggs found in sample = 62
Percent infestation (62/600) = 10.33%
Estimated cone crop (Figure 12) = 975,915
Absolute estimate of eggs (10.33% x 975,915) = 100,812

Table 10. A comparison of the number, percentage infestation (of a particular stage/600 cones) and estimated number of individuals per state per sample date on the Buckhead Seed Production Area, 1971.

Table 11. A partial life table for *B. colfaxiana* on the Buckhead Seed Production Area 14 May 1971 through 2 August 1972 (l_x per 10 acres).

x	l_x	d_xF	d_x	$100d_x/l_x$	S_x
Egg-instar I	239,200	Infertility	11,003	4.60	
		Trichogramma sp.	4,114	1.72	
		Resinosis (Larvae)	37,041	16.53	
		Miscellaneous (Larvae)	21,641	11.57	
		Unknown	62,845	26.27	
		Total	136,644	57.13	42.87
Instar II	102,556	Resinosis	1,723	1.68	
		Miscellaneous	2,584	2.52	
		Unknown	25,201	24.57	
		Total	29,508	28.77	71.23
Instar III	73,048	Resinosis	453	0.62	
		Miscellaneous	906	1.24	
		Unknown	936	1.28	
		Total	2,295	3.14	96.86

Table 11. (Continued)

x	l_x	d_xF	d_x	$100d_x/l_x$	S_x
Instar IV	70,753	Resinosis	1,068	1.51	
		Disease	354	0.50	
		Glypta evetriae	2,384	3.37	
		Predators	354	0.50	
		Miscellaneous	1,606	2.27	
		Unknown	1,308	1.85	
		Total	7,074	10.00	90.00
Non-diapausing Pupae	63,679	*Gaurax* sp.	1,827	2.87	
		Other parasites	3,248	5.10	
		Predators	1,013	1.59	
		Miscellaneous	5,680	8.92	
		Total	11,768	18.48	81.52
Diapausing Pupae	51,911				100.00
Adults	1,382	(Sex 46.51% ♀♀)	**		

** Adult mortality was not assessed.

mortality factors operating on the eggs were subtracted first and the number surviving were treated as instar I. This also contributed to the large unknown mortality factor in the first age interval, because the unknown mortality of both stages is combined. If an accurate estimate of the number entering instar I could have been obtained, then the unknown mortality factor for this interval would have been separated. Resinosis was treated as occurring before the miscellaneous mortality factors, because the mortality due to this factor was observed before the other factors in the first age interval. The miscellaneous mortality factors are unexplained deaths; the individuals were found but the cause of death could not be determined.

First Generation Mortality

It is not possible to determine the key factor(s), e.g. the mortality factor largely responsible for the changes in population density from year to year (Morris, 1959) from the studies of a single generation. However, it is possible to identify the possible critical factor(s) responsible for within generation density changes. It is also possible within the generation to determine a possible critical (key) interval (Population Dynamic Group, 1964), or, for species in which stages overlap considerably, the key stage of development (Beaver, 1966). The critical age interval or stage of development is the age interval in which generation survival is largely determined.

The critical age interval for B. colfaxiana was the first age interval (egg-instar I). Figure 13 illustrates that most of the change in the 1971 generation occurs in this interval, and that the size of this generation, at least, is determined by the mortality occurring in this stage.

The possible critical factor for this partial generation appears to be resinosis. It must be stressed that this is not the key factor for prediction, the factor that accounts for the main fluctuations in population size and not the principal regulating factor as defined by Morris (1959). It is the factor that caused the greatest numerical change (other than the unknown) in the partial generation. The contributing factors to the large unknown are explained previously (page 41). Resinosis occurs when the larva becomes trapped in the resin (pitch) and is unable to free itself. Of the estimated 187,289 dying between 14 May 1971 through 2 August 1972, 40,285 died from the excessive pitch flow.

Egg - instar I. Egg parasitism by Trichogramma sp., not minutum Riley, was the only natural enemy observed causing mortality (1.70%) to the egg stage. Attempts were made to observe other natural enemies, e.g. predators, in the field but none were observed consuming B. colfaxiana eggs. However, numerous earwigs (Forficula auricularia L.) were observed on cones with eggs of B. colfaxiana. Isaacson (1973) reports that earwigs were observed on Tyria jacobaeae L. (Lepidoptera: Arctiidae) eggs clusters in the field and are known to take eggs in the laboratory. Earwigs are highly suspect in contributing to the unknown

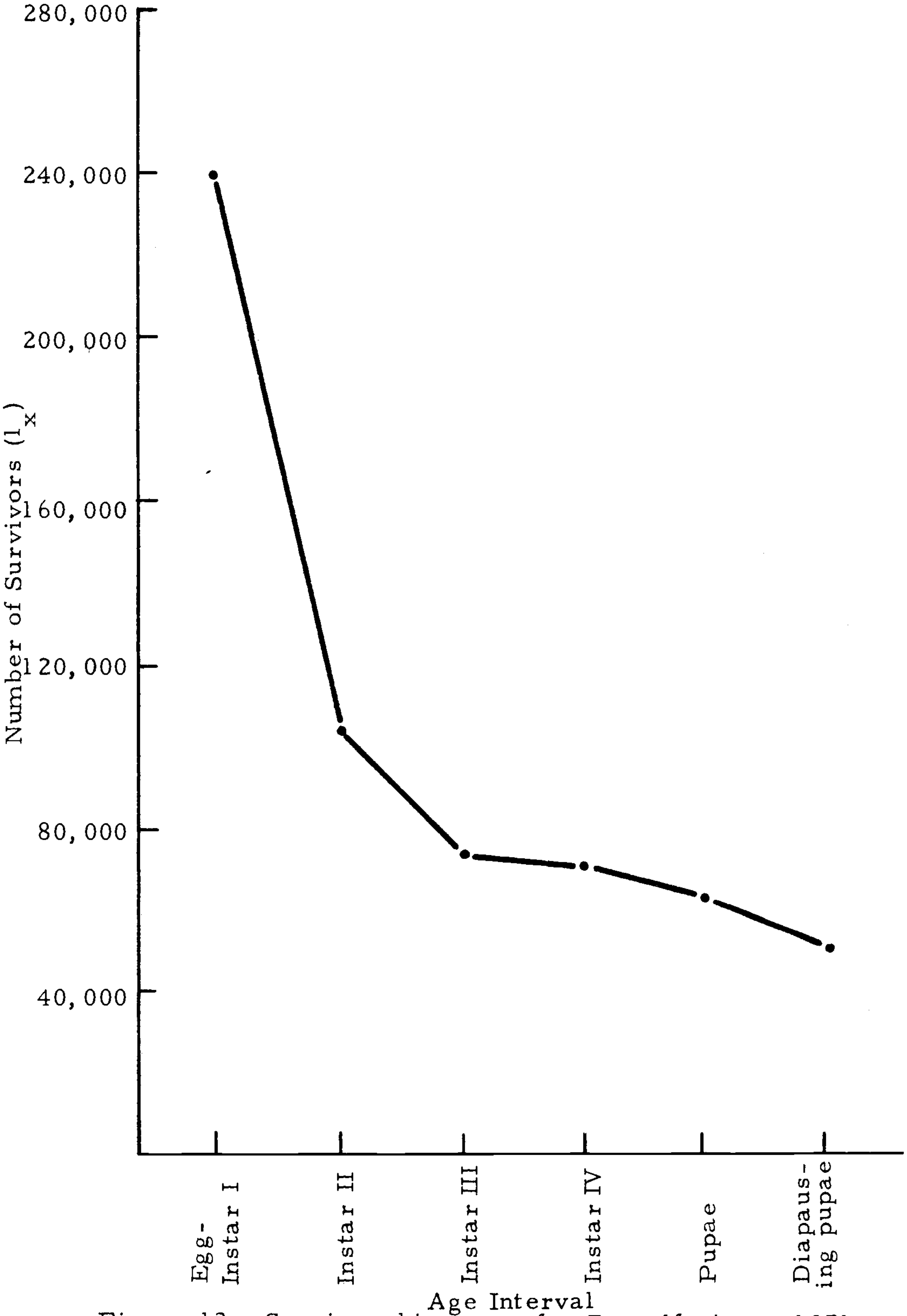


Figure 13. Survivorship curve for B. colfaxiana, 1971.

mortality that occurred during this stage. Infertility was the only other factor that was found to contribute to the mortality during the egg stage (4.60%).

Of the mortality factors occurring during the first instar, resinosis was the only one that was quantified and appears to be the most important factor in this stage. An estimated 37,041 first instar larvae died from resinosis, or 16.53% of the total larvae found.

It is within this interval that the greatest percentage of the mortality occurred (excluding the unknown factor), hence the decision to call it the critical age interval and the possible critical factor within this interval as resinosis. The possible critical factor here is one of the factors measured quantitatively. This does not rule out the possibility that factors other than resinosis are any less important. With the refinement of sampling techniques, the factors contributing to the large unknown may be definable and possibly other critical factors identified.

Larval instars. Of the several mortality factors operating on larval instars II-IV, resinosis was the most common. Resinosis accounted for 3,244 of the estimated 10,364 deaths occurring during these instars. It was also during these instars that larvae were found dead, but cause of death was not apparent and could not be explained. These unexplained (miscellaneous) deaths accounted for 49.17% of the total found dead in these instars. From the appearance of the larvae, a thermal-caused death is strongly suspect.

An estimated 354 fourth instar larvae were killed by an unidentified disease. The larvae were black and the body cavity was filled with a fluid-type material on which fungi later developed. Of the natural enemies (predators and parasites) found causing mortality, *Glypta evetriae* Cushman (Hymenoptera: Ichneumonidae) was the most common. It caused mortality near the end of the fourth instar, when the larva was ready to pupate. The parasite larva constructs a delicate semitransparent case within the cocoon constructed by the host larva and remains in this as a larva until spring of the following year. A few were observed to emerge in the fall shortly after killing the host; these observations agree with Hedlin (1960).

The final factor that contributed to the death of *B. colfaxiana* during the fourth instar was predation. Predators found in the feeding chamber of *B. colfaxiana* (near a dead larva) or evidence that suspected them of being predators and the cause of death were: *Agulla* sp, (Neuroptera: Raphidiidae); *Hemerobius* sp. (Neuroptera: Hemerobiidae); *Lestodiplosis* sp. (Diptera: Cecidomyiidae); *Enoclerus* spp. (Coleoptera: Cleridae); *Dioryctria abietella* sp. (Lepidoptera: Phycitidae). These predators accounted for an estimated 354 deaths.

D. abietella was the only predator that was not actually observed in a feeding gallery of *B. colfaxiana*. However, fragments of *B. colfaxiana* larvae and pupae were found in the feeding gallery of *D. abietella*. Hence, it was assumed that it was *D. abietella* larvae that consumed larvae and/or pupae of *B. colfaxiana*.

Pupae. Pupal mortality was mostly attributed to parasitism. An estimated 1,827 (2.87%) died as a result of assumed parasitism by Gaurax sp., a small dipteran. Because the larval habits are unknown, it can only be assumed that Gaurax sp. is parasitic. Sabrosky (1951) suggested that it seems likely that the larvae do not do any direct damage, but feed in the frass of other insects. Only pupae of Gaurax sp., two per B. colfaxiana pupa, were observed during this study. It is possible that Gaurax sp. larvae entered the cocoon after the larva or pupa had died.

All other parasites were lumped together because of the numerous B. colfaxiana pupae found dead that had been parasitized, but the parasite(s) had emerged and the exact parasitic species causing death could not be determined. The following hymenopterous parasites were reared from B. colfaxiana pupae collected during 1971 and 1972 from the Buckhead Seed Production Area: Tetrastichus barbarae Burks and Elachertus pini Gahan (Eulophidae); Perilampus fulvicornis Ashmeas (Perilamphidae); Itoplectis evetriae Vier. (Ichneumonidae); and Bracon sp. (Braconidae)[1]. They accounted for an estimated 3,248 (5.10%) of the dead B. colfaxiana pupae. The predators found in the cones with dead B. colfaxiana pupae were the same as those found when the larvae were present and again assumed to have been the cause of death.

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[1] Questionable determination, identification was based on 4 larvae and 2 pupae by A. S. Menke.

The final factor causing death, under the heading "miscellaneous," was not determined. The pupae had developed to a point where the scales on the body and wings were visible through the pupal skin and appeared ready to emerge but failed. Some of these pupae were dissected in an attempt to determine the cause of emergence failure. The dissections revealed nothing that would give an indication as to the cause of emergence failure. The pupae appeared normal except the organs within the body cavity were collapsed and appeared dehydrated.

Diapausing pupae. Keen (1958) reported that it is a peculiarity of this insect (*B. colfaxiana*) that not all of the overwintered pupae transform and emerge as adults the following spring. Some members of the population continue in diapause through spring, summer, and winter of the second year. The majority of these diapausing pupae emerge at the normal time during the second spring. Further, some of these diapausing pupae remained dormant during the second summer and winter and finally emerged the third spring, after a dormant period of 2 1/2 years nearly 3 years after the beginning of development. An estimated 51,911 pupae remained in diapause through 1972 on the Buckhead Study Site. The percentage diapausing was 97.34% during 1972. Radcliff (1952) found 6.8% of a 1950 population in diapause, of which more were in diapause in wet sites (11.0%) than dry sites (3.4%). He also found a higher percentage in diapause where pupae overwintered in cones on the ground (9.2%) than when they overwintered in cones on the trees (4.1%). The significance of diapause has been discussed in great length by numerous individuals and Danilevskii (1965) offers a text on the subject. The significance of the diapausing population on the Buckhead Seed Production Area will be discussed in the following chapter dealing with the effects of reduced cone crop.

Adults. During the spring of 1972, an estimated 1,382 adults emerged of which 46.51% were female. The female percentage was determined from the sex ratio of the pupae. Figure 14 illustrates the difference between a male and female pupae. Adult mortality was not assessed during this study. Since only 24 cones were produced on the study area during 1972 it was assumed that those that emerged emigrated.

Second Generation Mortality

On 25 May 1972, 7 cones and 18 eggs were brought into the laboratory. Of the 18 eggs, only 6 hatched. Upon examination of the remaining 17 cones on 2 August 1972, only 5 cones had been attacked by *B. colfaxiana*. On that date, 1 pupa and 2 dead larvae (instar undeterminable nor cause of death) were found.

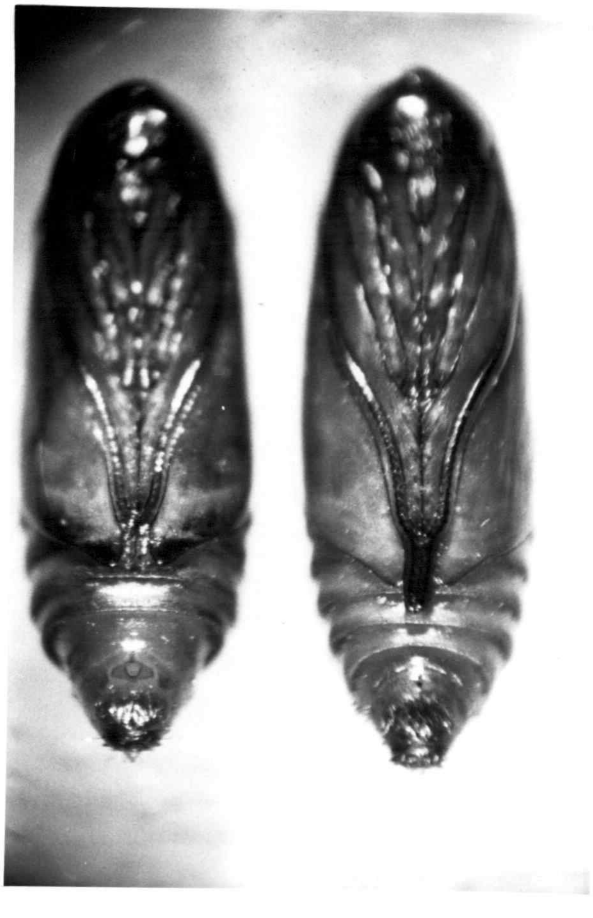

Figure 14. Pupae of B. colfaxiana, female on the left and male on the right.

VI. CAUSES AND EFFECTS OF A REDUCED CONE CROP

Food supply for *B. colfaxiana* can be a very important limiting factor, especially since *B. colfaxiana* is reportedly monophagous and dependent on cones for both food and shelter. It will be the intent of this chapter to discuss some of the suspected causes and effects of a fluctuating cone crop.

Fluctuations in cone crop from year to year are apparent and numerous theories have evolved from correlations of temperatures, rainfall and numerous other factors in trying to explain these fluctuations, however, few conclusive results have been obtained from these correlations. Some generalizations can be made, such as weather conditions appear to be very important for a good cone crop. For example, good cone crops in Douglas-fir are positively correlated with precipitation preceding and at the time of cone initiation by a warm, sunny summer during early cone bud development, and low temperature and sunshine in the spring and summer preceding cone initiation or 27-30 months before seed release (Lowry, 1967). This type of information is common but hard to interpret and one would assume the reverse to be true in years of a poor cone crop.

Other theories have been put forth, but few conclusive statements can be made regarding how many environmental, physiological and morphological factors influence cone development in Douglas-fir. The reason is that little is known of the physiological condition of the tree during cone development, so we cannot understand all the interactions that might occur (Allen and Owens, 1972). Studies have been made trying to understand the effects of hormones, juvenility, photoperiod, and nutrition on cone production. However, the question is still unanswered as to why abundant cone crops do not occur every second year. It is apparent from studies of Isaac (1943) and Lowry (1966) that the time between abundant or medium cone crops in a region is 2 to 7 years and is commonly 5 years.

Allen and Owens (1972) offer the following explanation as to why a 2 year cycle would actually seldom occur:

> Although it is not possible to relate all of the information pertaining to cone development in order to give a complete explanation of the cyclic nature of cone production in Douglas-fir, certain factors are related in an intelligible manner. Reproductive buds appear to have higher nutrient requirements than do vegetative buds. Vegetative buds in turn have higher requirements than partially developed latent buds or primordia that abort. Both carbohydrate, especially reserve starch, and certain amino acids appear to be required for cone-bud development. An elongating shoot on which primordia develop obtains most of its nutrients from the subjacent 1-year-old shoot. When the subjacent 1-year-old shoot bears expanding seed cones, the elongating shoot is usually chlorotic, not vigorous, and lateral bud development is poor. Few or no reproductive buds develop and the vegetative buds that do develop are neither large nor vigorous. Expansion of the vegetative buds the following spring usually results in shoots that are not vigorous. This does not provide optimal conditions for bud development during the year of the good cone crop, nor in the following year. The second spring after a good cone crop would likely be the first time when conditions within the tree would again be suitable for cone-bud development. This assumes that environmental factors are

> favorable. As a result, it would normally be at least 3 years between heavy cone crops in Douglas-fir. This unfortunately, does not take into consideration all the factors affecting the last 14 months of cone development, but simply the early development of cone buds. However, a cycle approaching 3 years should be possible under carefully managed seed orchard conditions where fertilizer application, pollination, frost and insect damage can be partially controlled. (Allen and Owens, 1972, p. 34-35).

Hence, it can be seen that the causes of an abundant cone crop are not well understood and effects of the reduced cone crop are less understood from the standpoint of its cause and further its effect on organisms (mammals, birds, insects, etc.) that depend on the cone and subsequent seeds for food. The following discussion will pertain only to the effect of the reduced cone crop on the Buckhead Seed Production Area.

Undoubtedly, the cyclic fluctuations of the cone crop are one of the most important factors limiting the size of the population of _B. colfaxiana_ and other cone and seed insect populations on the Buckhead Seed Production Area. With few exceptions, the insect complex attacking Douglas-fir cones is dependent on cone production. The fluctuation in cone production, as represented by the 1971 and 1972 cone crops, can be extreme and so abrupt as to preclude parasites and predators from becoming dominant regulatory factors. In years following a heavy cone crop, as would be expected, the mean number of individuals (_B. colfaxiana_) per 20 cones would increase (Figure 15).[2] However, the

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[2] The data previous to 1970 were obtained from S. Meso of the U. S. Forest Service, Region 6, Portland, Oregon.

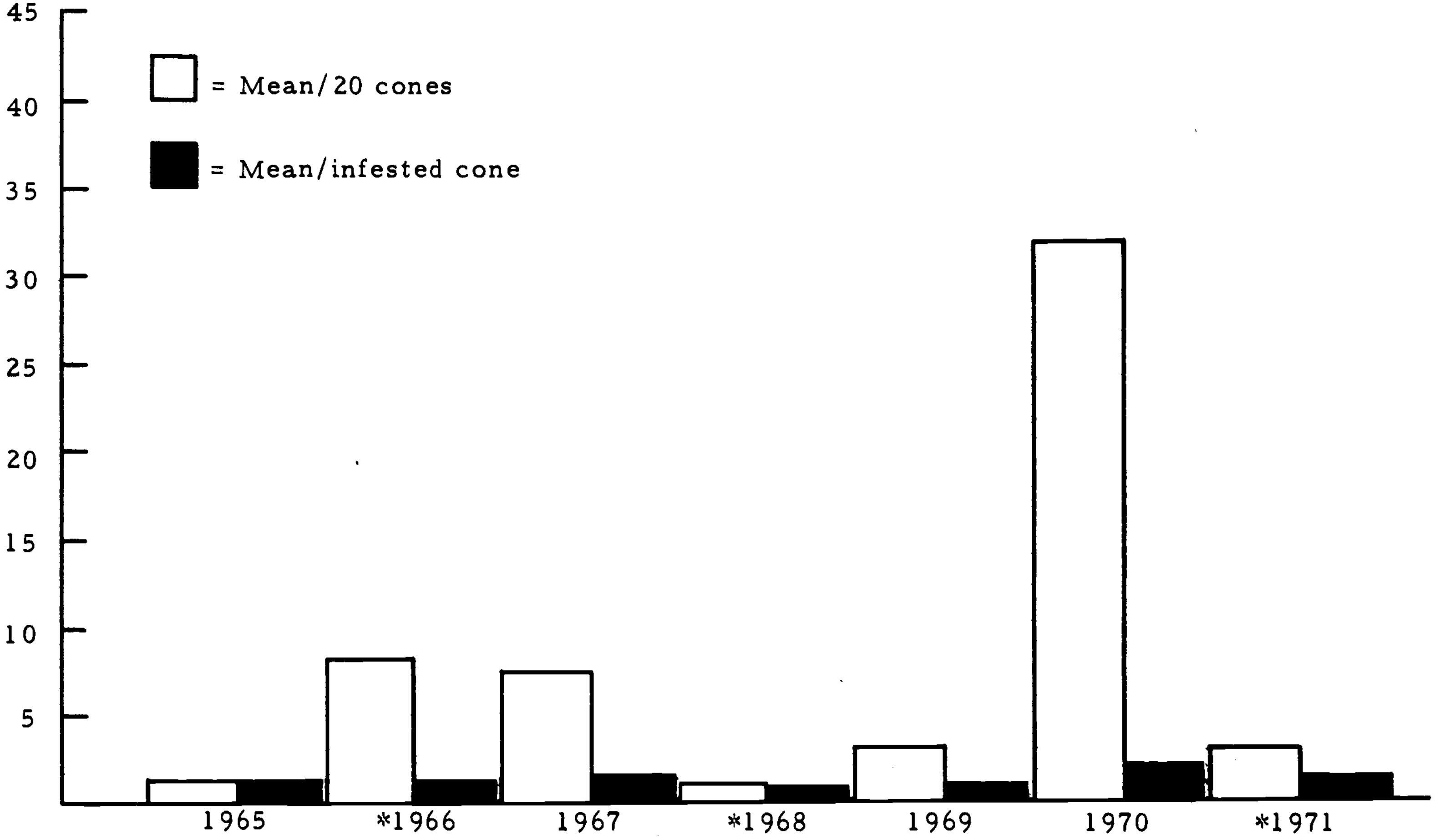

Figure 15. Mean number of B. colfaxiana per 20 cones and mean number per infested cone from 1965 through 1971 on the Buckhead Seed Production Area. (*) denotes years with heavy cone crops being produced on the area.

mean number per infested cone remains approximately the same from year to year (Figure 15). During 1966, 1968, and 1971, heavy cone crops were produced on the study site, with lighter crops being produced in between.

It would be suspected that in years of light crops there would be intensive inter- and intra-specific competition of seed and cone insects. Competition being defined, in this case, as the activity of two (or more) cone inhabitants to gain the same particular things or to gain the measure each wants from the supply of cones when that supply is not sufficient for all. The definition was abbreviated from one given by Milne (1961). If any competitive superiority is to be gained it would probably be to the insects which become established first. Of the insect complex attacking the Douglas-fir cones at the Buckhead Site, *B. colfaxiana*, *Contarinia oregonensis* Foote and *C. washingtonensis* Johnson (Diptera: Cecidomyiidae) are the first to begin consuming the tissue, followed by *Megastigmus spermatrophus* Wachtl (Hymenoptera: Chalcididae), *Dioryctria abietella* (D. & S.) (Lepidoptera: Phycitidae), *Henricus fuscodorsana* (Kearf.) (Lepidoptera: Phaloniidae), and *Leptoglossus occidentalis* Guer. Hence, it is suspected that *B. colfaxiana* is the superior competitor, interspecifically, principally from the standpoint that it attacks first and reduces the amount of resource available to the other cone and seed insects. There is cone partitioning, in that some feed on restricted parts of the cone (*M. spermatrophus* on seeds;

C. oregonensis within hard galls at the base of the scales, and some feeding on seeds; *C. washingtonesis* on scales; *L. occentalis* on seeds; *D. abietella* on the outer parts of the cone, generally outside the feeding area of *B. colfaxiana* which is concentrated mainly around the central axis on scale and seed tissues).

As mentioned earlier, some of these cone and seed insects can be classed as predators, e.g., *D. abietella* on *B. colfaxiana* and possibly others. The number of seeds and/or galls that *M. spermatrophus* and *C. oregonensis* are in and are consumed by *B. colfaxiana* and *D. abietella* is not known, but predation is suspected. *B. colfaxiana* is also suspected to be cannibalistic in the field, although not confirmed in this study. Cannibalism was demonstrated in the laboratory when 2 or more larvae were placed on artifical media (food not limited) during this study and by Ruth and Hedlin (1969). Frequency of predation of some cone and seed insects on other cone and seed insects, along with cannibalism in the case of *B. colfaxiana*, would undoubtedly increase as a result of a reduced cone crop.

Competition may be avoided by some cone inhabitants. In the case of *D. abietella*, feeding is later than that of *B. colfaxiana* and if there is insufficient cone material for development it will feed on other cones, foliage and/or bore into branches. It is a very mobile insect and can move readily to other food sources. Hence, the food supply (cones) available to *D. abietella* may be seriously reduced and the resultant mortality of *D. abietella* would depend on how successful the larvae were in finding another cone or another suitable food source. _B. colfaxiana_ apparently has the ability to avoid competition, through diapause, as evident with the 1972 population on the Buckhead Seed Production Area, when 97.34% of the population remained in diapause, hence avoiding the situation of extreme food shortage. However, factors stimulating diapause are not known but could be the same as those influencing cone production. Attempts to break diapause of _B. colfaxiana_ were made during this study, but with no success. The significance of diapause has direct bearing on subsequent generations, and if the percentage diapausing is correlated with cone crop, then an understanding of the causes of cone crop fluctuations would give insight to the fluctuations of the _B. colfaxiana_ population size on the Buckhead Seed Production Area, in addition to the influence of the other mortality factors. Further, this idea of diapause to avoid food shortage is similar to the idea that many animal populations have intrinsic mechanisms which prevent them from becoming so dense as to induce population crashes through shortage of resources (Monro, 1967).

Aside from the effects of reduced crop on the insect populations, it also has an effect on the other animal populations that utilize the seeds for a food source.

VII. SEED AND CONE CONSUMPTION BY BARBARA COLFAXIANA

It was not the intent of the third objective to develop a complete energy budget for B. colfaxiana, but to determine how much of the various cone structures (bracts, scales, and seeds) were consumed by an average member of the population. As a means of measuring the amount consumed, a measuring unit needed to be selected. The study of energy and energy transformation is limited without a means of measurement, hence, the calorie was selected as the common unit. The reasons for selecting this unit were first, to acquaint the author with a technique used in bioenergetic studies, and second, that the information might be useful in models dealing with energy transfer from one component to another in a forest ecosystem.

In order to obtain caloric values for the various parts of the cone a few mechanical operations, standardization of the oxygen bomb calorimeter and preparation of the material, needed to be completed before the actual measurements could be made.

Standardization of the Oxygen Bomb Calorimeter

The standardizing operation of the calorimeter was in reference to a standard reference (benzoid acid) from which the energy equivalent or water equivalent factor of the system can be selected. The factor represents the combined heat capacity of the water bucket, of the water itself, of the bomb and its contents, and of parts of the thermometer, stirred and supports for the bucket.[3]

Calculation of the energy equivalent of the calorimeter is exactly the same as for testing any sample fuel. A standard, in this case a benzoic acid pellet weighing not less than 0.9 nor more than 1.1 grams was used. The energy equivalent was computed by solving the following equation:

$$W = \frac{H_m + e_1 + e_2}{t}$$

Where:

W = energy equivalent of the calorimeter in calories per degree Fahrenheit

H = Heat of combustion of standard benzoic acid in calories per gram (6318 cal/gram)

m = mass of standard benzoic acid sample in grams

t = corrected temperature rise in degrees Fahrenheit

e_1 = correction for heat of formation of nitric acid in calories, and

e_2 = correction for heat of firing wire, in calories (2.3 cal/cm).

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[3] Parr Instrument Company, 1968. Test certificate for Parr 1411 oxygen bomb calorimeter, serial number 2834.

Original test data indicated that W was 1,346 calories for the calorimeter used in this study.[3] However, several tests using benzoic acid as a standard suggested W ($\bar{X} \pm$ S. E.) = 1332 ± 2.55 calories was a more realistic value. The new value for W was significantly different from the original ($P < 0.01$). The reason for the difference is not fully understood, most likely due to the procedure and physical changes in the equipment from continued use.

Caloric Determinations

Cones fed on by *B. colfaxiana* were collected at weekly intervals, 25 June 1971 through 13 August 1971. They were frozen until May 1972 when caloric determinations began. The cones were taken from the freezer and placed in a freeze drier until approximately 99% of the water was removed. After drying, the cones were placed in a desiccator for a week before cone-structure separation began. The desiccator had potassium pentoxide in it as a desiccant. The cones were then removed from the desiccator and the various parts (bracts, scales, and seeds) were excised. The following data were recorded: weight of whole cone (dry), weight of individual damaged tissue and its "twin", weight of larva (dry) if present, and number of damaged parts. A "twin" is a part (bract, scale, or seed) of the cone adjacent to the damaged part, that was assumed to be equal in all respects.

After separating and weighing the various parts, they were again placed in the desiccator. When enough material was available for each of the kinds of parts, they were pulverized and pellets made, approximately 1 gram each, and returned to the desiccator until the caloric determinations could be made. Only two caloric determinations were made per cone structure per date, if they were within 5 percent of each other. If the difference exceeded this limit, then a third determination was made and the two values that were within 5 percent used to represent the caloric value of that structure. The reason for making only two determinations, if within 5 percent of each other, was on the assumption that the variance was due to experimental error, given the samples were taken from the same homogeneous source. A small variance would be expected if the same material was being tested.

The method for operating the oxygen bomb calorimeter is outlined by the Parr Instrument Co. The caloric value is computed by the following equations for the Parr 1300:

$$Cg = \frac{tW - e_1 - e_2}{m}$$

$$t = TC - TTF - r_1(b - TF) - r_2(c - b)$$

Where:

Cg = calories per gram

t = net corrected temperature rise

W = energy equivalent of the calorimeter in calories per degree Fahrenheit

e_1 = millileters of Na CO_3, .0725N, solution used in the acid titration

e_2 = centimeters of fuse wire consumed in firing

m = weight of sample in grams

b = time when the temperature reached 60 percent of the total rise (to the nearest 0.1 min.)

TF = time of firing

c = time at beginning of period (after the temperature rise) in which the rate of temperature change becomes constant

TTF = temperature at time of firing

TC = temperature at time c, corrected for thermometer scale error

r_1 = rate (temperature units per minute) at which temperature rises during the 5 min. period before firing

r_2 = rate (temperature units per minute) at which the temperature falls during the 5 minute period after C.

The results of these determinations are presented in Table 12. Blank areas in the summary are due to the insufficient materials available from which to make a determination. The determinations under the column headed central axis are a result of burnings of those portions of the cone, terminal scales and bracts, basal scales and bracts, and the central axis that were inseparable.

It can be seen in Table 12 that little caloric change takes place in the various structures through the season. The greatest increase taking place in the seed as it matures, which would be expected.

Table 12. Caloric determinations (cal/gram) for the various structures of the Douglas-fir cone from the Buckhead Seed Production Area, 1971.

Date	Scale	Damaged Scale	Bracts	Seeds	Central Axis	Whole Cone
25 June	4,363	4,509	4,472	4,474*	4,585	4,650
2 July	4,472	4,490	4,544	4,320*	4,575	4,598
9 July	4,508	4,497*	4,596	4,470	4,660	4,480
16 July	4,484	4,605	4,563	4,626	4,664	4,698
23 July	4,528	4,849	4,656	4,864*	4,658	———
30 July	4,453	4,698	4,632	4,938	4,532	4,702
13 August	4,506	4,774	4,620	5,456	4,580	4,628

* Based on one determination, all others are averages of two determinations.

Consumption by B. colfaxiana

Because the cones were selected at random, and without reference to stage of development of B. colfaxiana larvae, on a given date, the following discussion will consider the consumption of an average member of the population that began feeding on about 26 May 1971. Given that this individual began feeding the latter part of May, the amount consumed thereafter is illustrated in Figure 16. The information from 26 May 1971 through 1 July 1971 was lacking and was the period when the early instars were present (Table 13). Hence the information from 2 July 1971 through

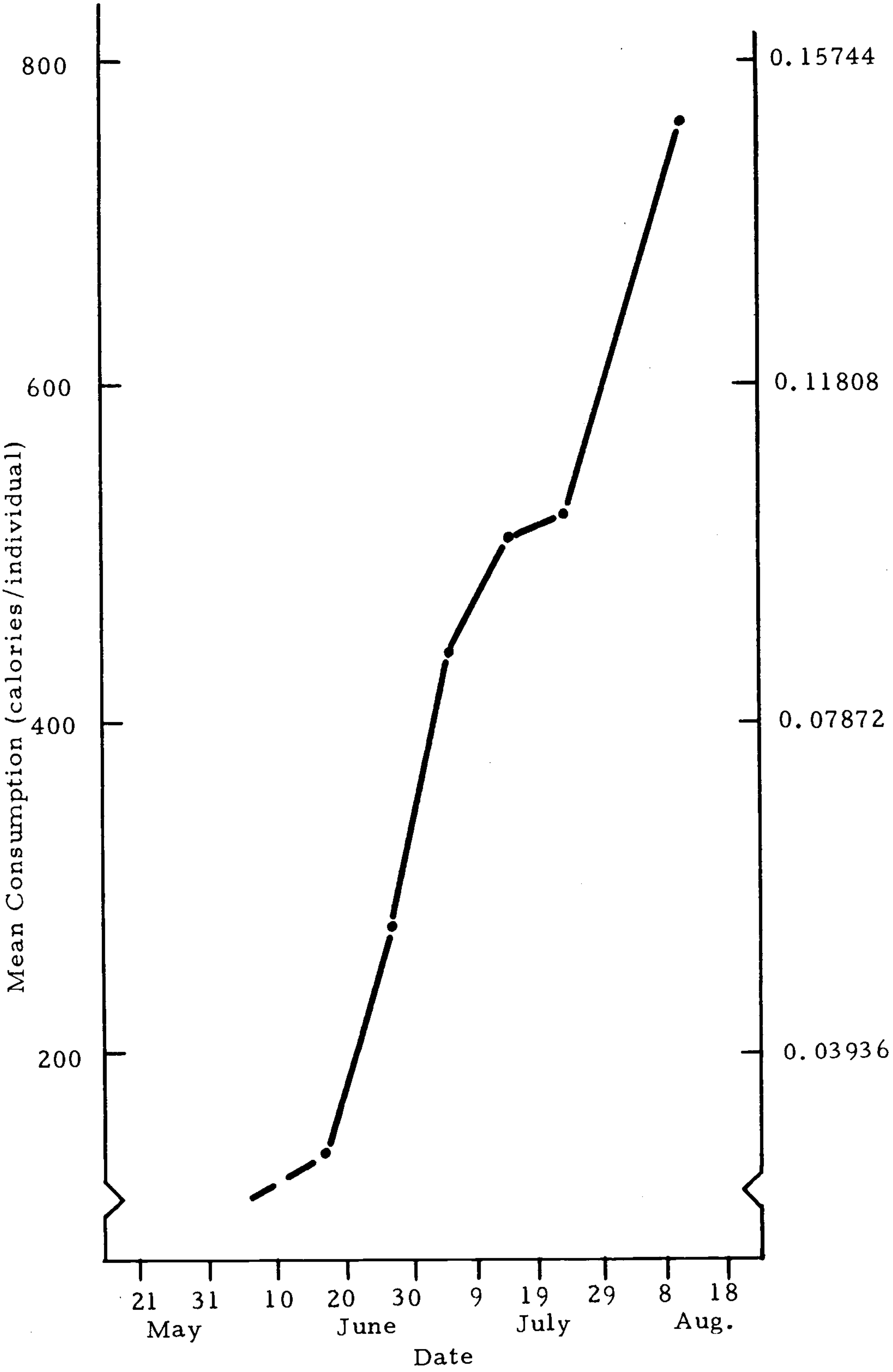


Figure 16. Cummulative consumption of Douglas-fir cone and seed tissue by _B. colfaxiana_ on the Buckhead Seed Production Area, 1971.

13 August 1971, presented in Figure 16, represents in essence the consumption of an average fourth instar larva. However, from these results it appears that 761.04 ± 426.03 calories is the average total amount consumed per individual to complete larval development and pupate. The female pupae weigh ($\bar{X} \pm$ S. E.) 0.01255 ± 0.00045 grams and the male ($\bar{X} \pm$ S. E.) 0.01198 ± 0.00027 grams.

The amount of the various cone structures (bracts, scales, and seeds)consumed is presented in Table 14, further illustrating the feeding behavior of *B. colfaxiana* previously discussed (page 11). In an attempt to determine the total calories of the various cone structures consumed, a simple linear regression model (Table 15) was used. Undoubtedly, the rate of comsumption is not linear, with lower rates of consumption at the beginning of a stage and then increasing until just before metamorphosis at which time consumption decreases. However, the sample interval was too long to detect these changes, and for predictive purposes a linear relationship was assumed. The data used to estimate the total consumption is presented in Table 14.

The 63,679 individuals that made it to the pupal stage consumed an estimated 48,464,266 calories. The way the data were obtained makes it difficult to estimate the total amount consumed by the entire population in a realistic manner. A rough approximation could be obtained by multiplying the total estimated larval population on a particular date by the $\bar{X} \pm$ S. E. consumed per individual for that date.

Table 13. Age distribution of the B. colfaxiana larval population on the Buckhead Seed Production Area 28 May 1971 through 30 July 1971.

Sample Date	Percentage of the larval population in			
	Instar I	Instar II	Instar III	Instar IV
28 May	100.00			
4 June	90.90	9.10		
11 June	81.48	18.52		
18 June	25.00	75.00		
25 June	3.28	44.26	52.46	
2 July		8.49	57.55	33.96
9 July			18.66	81.34
16 July			8.14	91.86
23 July			1.54	98.46
30 July				100.00

Table 14. Amount consumed (mean ± standard error) in calories, of the various cone structures per sample date by _B. colfaxiana_ on the Buckhead Seed Production Area, 1971.

Sample Date	Structure Bracts	 Scales	 Seeds	 Total
2 July	19.86 ± 7.41	117.88 ± 48.43	0	137.74 ± 53.99
9 July	49.64 ± *	210.70 ± 50.22	15.29 ± 4.43	275.63 ± 59.63
16 July	23.04 ± 12.32	306.53 ± 79.95	111.39 ± 33.59	440.96 ± 161.28
23 July	9.22 ± 11.50	226.72 ± 206.52	277.59 ± 65.23	513.53 ± 409.66
30 July	19.13 ± 14.17	401.44 ± 113.37	101.72 ± 35.26	522.29 ± 238.50
13 August	7.95 ± 6.42	289.60 ± 179.70	463.49 ± 116.38	761.04 ± 426.03

* Sample size = 1

Table 15. Estimated total amount consumed of the various structures per individual B. colfaxiana on the Buckhead Seed Production Area, 1971.

Structure	Regression Model	r^2	Estimated Total Amount Consumed in Calories
Bract	$Y = 58.604 + (-0.513) X$	0.333	7.304
Scale	$Y = -4.836 + 3.645 X$	0.408	359.664
Seed	$Y = -516.145 + 9.254 X$	0.829	409.255
Total	$Y = -458.237 + 12.444 X$	0.953	786.163

r^2 = coefficient of determination

Y = amount consumed

X = time

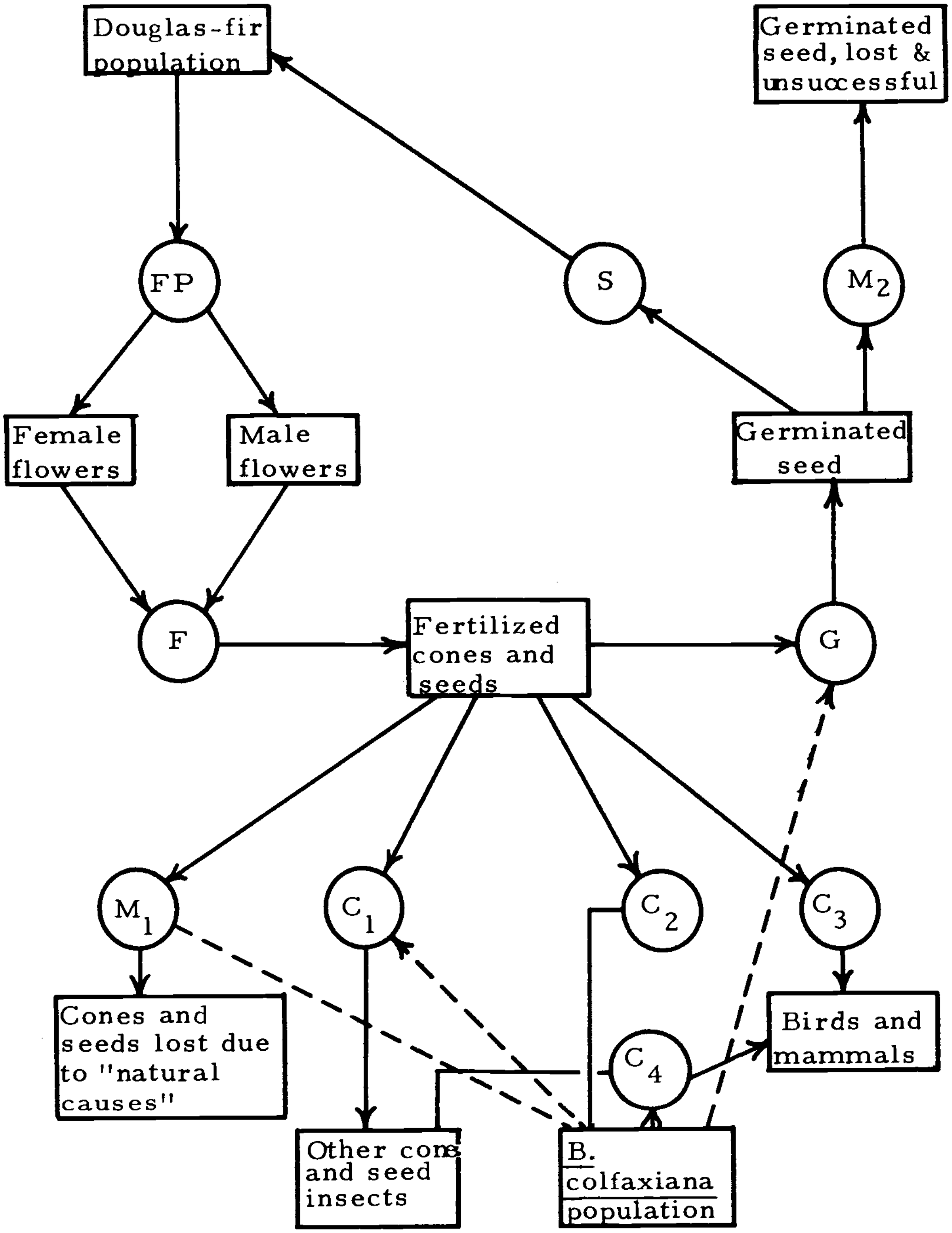
VIII. DISCUSSION

Douglas-fir is one of our most important timber trees, and in the Northwest it is the most important. Hence, a regular supply of seed has been and is in demand for reforestation purposes. For many years supplies of Douglas-fir seed have been obtained by collecting cones in natural stands when and where there were good crops of cones. But due to the cyclic nature of cone production the U. S. Forest Service and private companies have initiated programs of systematic seed production by the establishment of seed production areas and seed orchards. A seed production area, such as the Buckhead Seed Production Area, is a stand of natural trees of better than average form, specially treated to increase seed production. A seed orchard is defined as plantations consisting of grafts or seedlings from selected trees, isolated to prevent pollination from outside sources and specially treated for early and abundant seed production (Flowler, 1963). Many of the seed production areas, e. g. the Buckhead Seed Production Area, are no longer maintained as before. Emphasis is being placed on seed orchards and superior trees. Superior trees are being identified by the U. S. Forest Service and tagged for sources of seed in years when seed from that area is in demand.

The seed production areas, seed orchards, and superior trees represent a large investment of money and manpower and are operated to produce the maximum return of useable seed. It is under these situations that any organism decreasing the supply of seed is considered a "pest" and control measures are implemented to reduce the amount of seed lost or unavailable for collection and subsequent use in reforestation programs. It would be most desirable to implement a "management" program for mutual benefit.

However, it is not the intent of this chapter to develop an argument for or against classifying _B. colfaxiana_ as a "pest" in the various situations, nor management programs, but rather to look at _B. colfaxiana_ as a state variable in a very complex system and to take into consideration its function in the natural forest system. To do this a simple structural model was developed (Figure 17) in an attempt to visualize the relationship (possible function) _B. colfaxiana_ has to the Douglas-fir tree population. The model is of a natural stand, excluding seed production areas and seed orchards. In the latter two cases, _B. colfaxiana_ is viewed as a "pest" and with man's demand for seed is considered a major perturbation (when present) in these cases. In the natural forest system _B. colfaxiana_ can be viewed having an extremely different function and in some respects possibly even beneficial.

The model (Figure 17) is presented in a structural manner. The boxes are state variables, circles are control rate variables, solid lines indicate direct relationships, and broken lines indirect relationships. As the model is presented a temporal problem is



FP = Flower production
F = Fertilization
M_1, M_2 = Mortality
G = Germination
$C_1 - C_4$ = Consumption
S = Survival

Figure 17. A structural model of the relationship of *B. colfaxiana* to a Douglas-fir population.

evident. The annual cycle of the Douglas-fir population is different than the cycle of the consumers. To finalize this model the temporal problem will have to be dealt with but for purposes of this discussion will not be necessary.

For purposes of this discussion I will consider a Douglas-fir population to be bound spatially and the goal of the population is to reproduce sufficiently to replace those dying, thus maintaining a stable population. With this goal, the number of seeds required in a particular year is highly variable. It is forseeable that in years of high seed production few seeds are needed for regeneration purposes. The opposite condition, low seed production and high need, is also possible. It is the latter condition that will be of interest in this discussion.

As can be seen in Figure 17 the Douglas-fir population regeneration rate is influenced by a number of variables. The first and foremost requirement being that climatic conditions permit reproduction and secondly that the trees are physiologically capable of producing and supporting a developing cone crop. Some of the factors contributing to cone production and their periodicity have already been discussed (page 55). Further, both male and female cones need to be produced and their maturation synchronized. If the female cone is receptive before or after pollen is shed then it would be highly unlikely that any seed would be produced. Even if pollen is shed at the proper time this does not ensure fertilization will take place of all potential seed. Following fertilization and during the subsequent maturation of the seed, a number of factors (Figure 17), primarily consumers, are taking seed that may be needed for regeneration purposes. However, the first factor contributing to the loss of seed is abortion. In years of heavy cone production, such as 1971, this can be rather high (56.5%).

The biotic factors contributing to the loss of seeds are insects, birds and mammals. Consumption of cone and seed tissue and causal interactions are expressed simplistically in Figure 17. However, for purposes of the remaining discussion it is the indirect relationship of the Douglas-fir cone moth to M_1 (natural mortality) and G (germination) that I want to examine. This because of the resin flow that accompanies the feeding of _B. colfaxiana_ more so than any of the other biotic factors.

As was stated in earlier chapters (Chapters III and VII), initial feeding takes place on the bracts and then, upon entering the cone, the main portion of the diet is scale material. As the larva burrows through the cone tissues a resinous material is produced and causes the scales to stick together. Not all seeds are consumed in a cone by _B. colfaxiana_, and those not consumed are trapped between the scales when the resin dries and hardens with the maturation of the cone and the high temperatures in August and September. With man's current techniques of extraction, it is nearly impossible to extract these seeds. However, in nature this trapping of seeds can be seen as having two results as expressed in Figure 17. One being that the seed could be trapped in such a manner that it could not germinate because of the excessive resin on the seed coat. A second being, given only the scales are stuck together, beneficial in that this condition creates an ideal environment for germination. In order for this to be advantageous it also requires that the cone falls from the tree within the viable period of the seed. If the cone remains on the tree for several years this would be disadvantageous to the trapped seed.

However, for those seeds trapped in cones that have fallen to the ground germination could be enhanced from the following; (1) protection from extreme abiotic (climatic) and some biotic factors, (eg. ground feeding carabids), (2) moisture retention of the cone during the germination period, and (3) frass produced by B. colfaxiana in connection with the decomposition of the cone may further aid germination.

It can be seen that the above points are highly speculative and need experimental verification. However, through direct observations numerous seeds have been observed germinating in cones on the ground. Unfortunately, the number was not recorded in connection with the number having been infested with the Douglas-fir cone moth. If the above points are true, then in years when seed is necessary for natural regeneration and the other biotic and abiotic factors are taking unusually high numbers of seeds, then it is possible that the Douglas-fir cone moth is an asset to the system. Further, with the apparent synchrony of the Douglas-fir cone moth diapause and the cone crop fluctuations, a coevolution for a mutual benefit may be taking place.

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