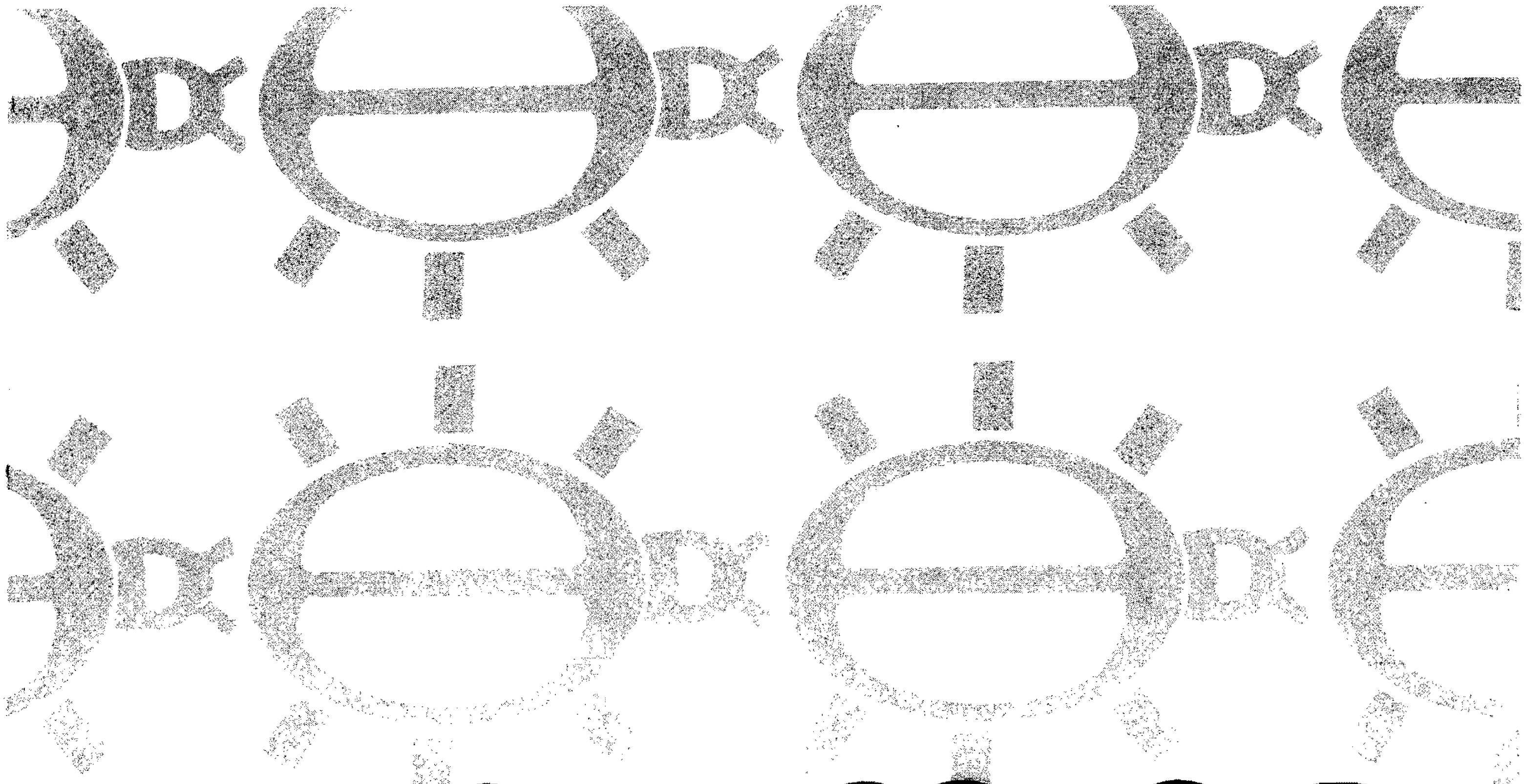
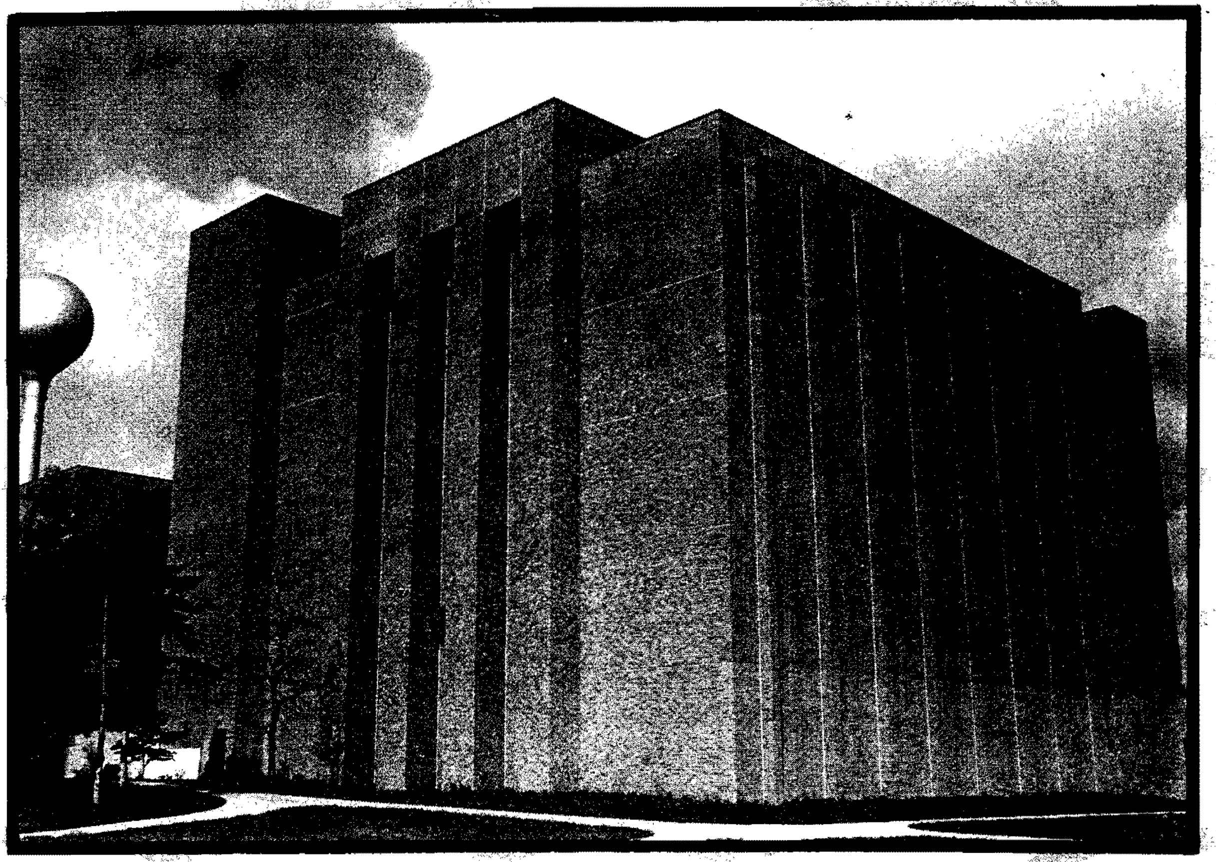


INSECT ECOLOGY

PAPERS PRESENTED IN THE A. C. HODSON ECOLOGY LECTURES



AGRICULTURAL EXPERIMENT STATION · UNIVERSITY OF MINNESOTA · TECHNICAL BULLETIN 310 -1977

Contents

ERRATA SHEET

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In late June each year estimates of the severity of defoliation were obtained and recorded as none, light, medium, and heavy. The criteria used in making these distinctions are:

None — No leaves removed, terminal branches with normal foliage. (Caterpillars may be present, but no conspicuous signs of feeding.)

Light — No trees showing complete defoliation. Feeding damage confined to tops of aspen and oak crowns. Little or no feeding on other tree or brush species.

Moderate — Occasional aspen and oak completely stripped of foliage, most with tops thin. Little feeding on birch and brush.

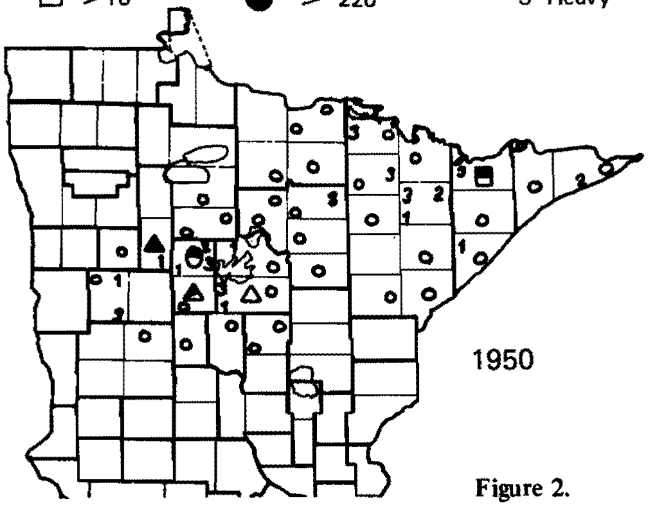
Heavy — Most aspen and oak trees completely stripped and conspicuous feeding damage on other species such as birch and brush. No cocoons formed in leaves on trees.

After the peak of the moth flight in late July or early August, cocoons were sampled to determine success of moth emergence and causes of pupal mortality. The abundance of cocoons was estimated by collecting them for a 3-minute period. Where the population was low, the sampling time was extended to obtain enough cocoons for pupal mortality inspection.

In the following recapitulation of the 1948-59 forest tent-caterpillar outbreak, the numerical and distribution changes will be reviewed, with special emphasis on egg band abundance and size, defoliation intensity, and pupal mortality. To avoid the confusion of all data being mapped for all of the several hundred collection points, the counties were divided into compartments of from 14 to 20 square miles. The estimates of egg band number and size were averaged for samples taken within each compartment. For example, St. Louis County, north of Duluth, has nine such compartments (figure 2).

Figures 2-11. Egg band numbers and size and defoliation estimates from 1950 to 1959.

Bands/Tree	**Eggs/Band**	**Defoliation**
X None	○<100-140	0 None
○ 1-5	⊙ 141-180	1 Light
△ 6-15	◓ 181-220	2 Medium
□ >16	● > 220	3 Heavy



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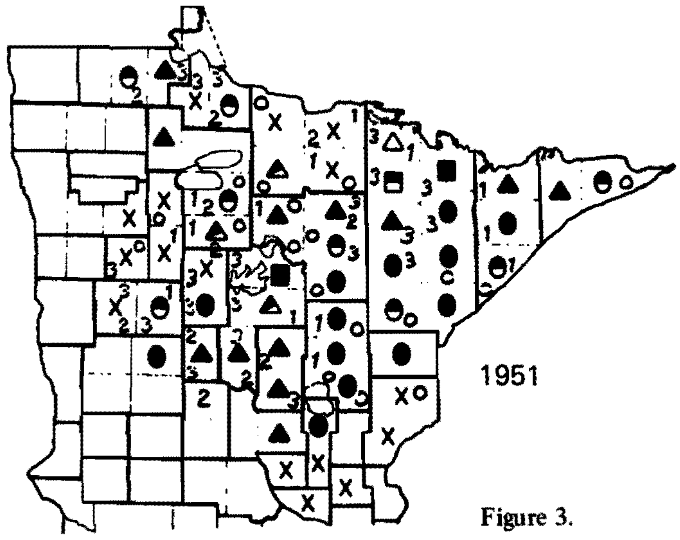

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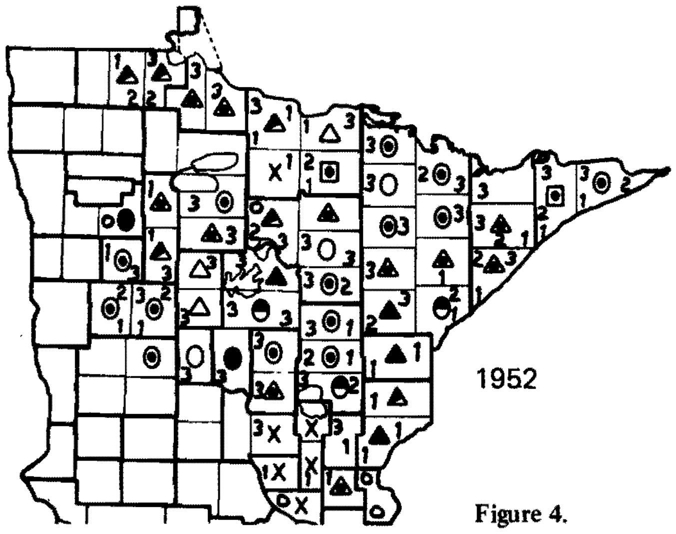

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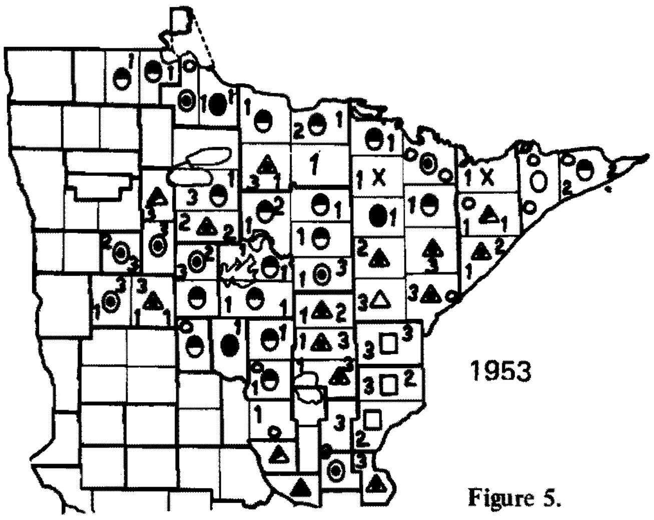
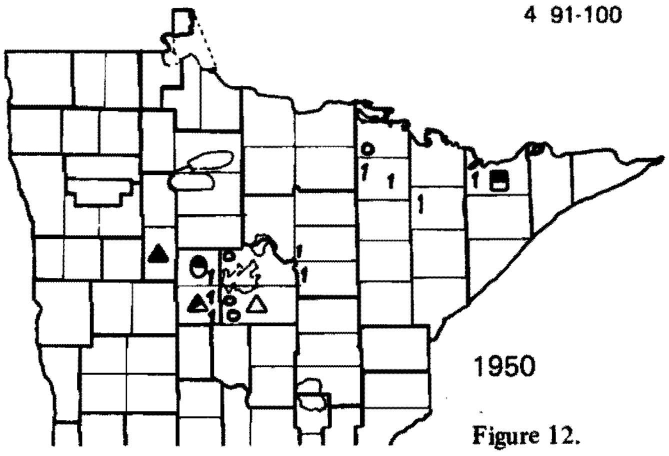


Figure 5.

Figures 12-20. Egg band numbers and size and estimates of pupal mortality.

Bands/Tree	**Eggs/Band**	**Pupal Mortality**
X None	○ <100-140	0 <30%
○ 1-5	⊙ 141-180	1 30-55
△ 6-15	◒ 181-220	2 56-75
□ >16	● > 220	3 76-90
		4 91-100



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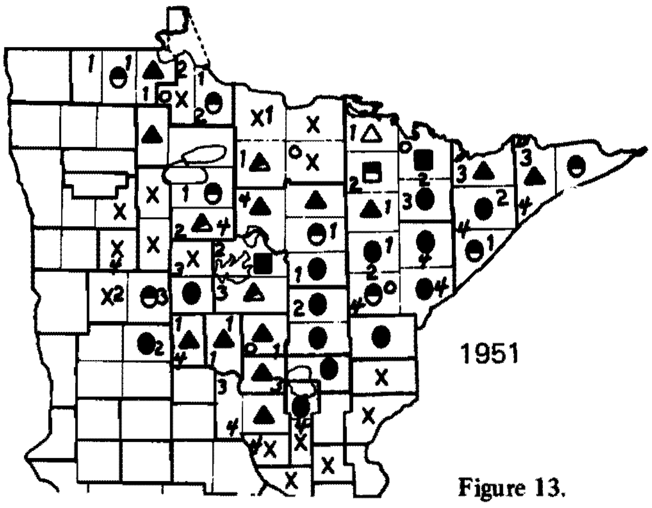

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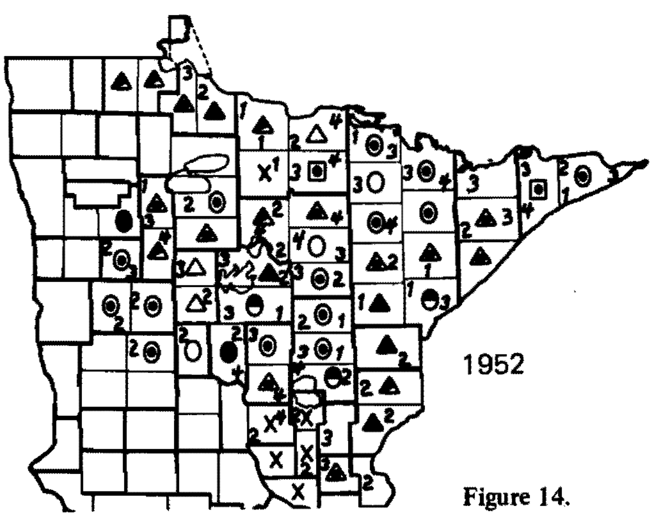

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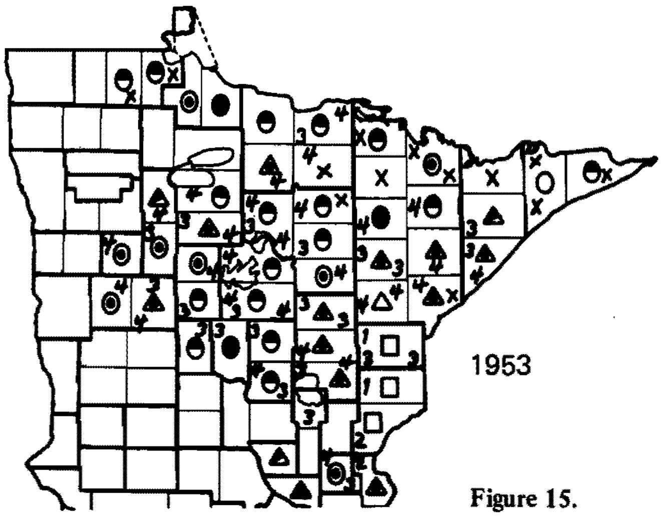

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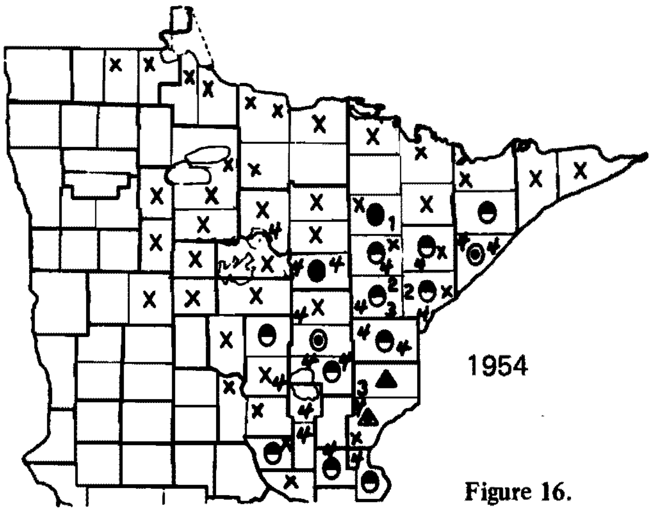

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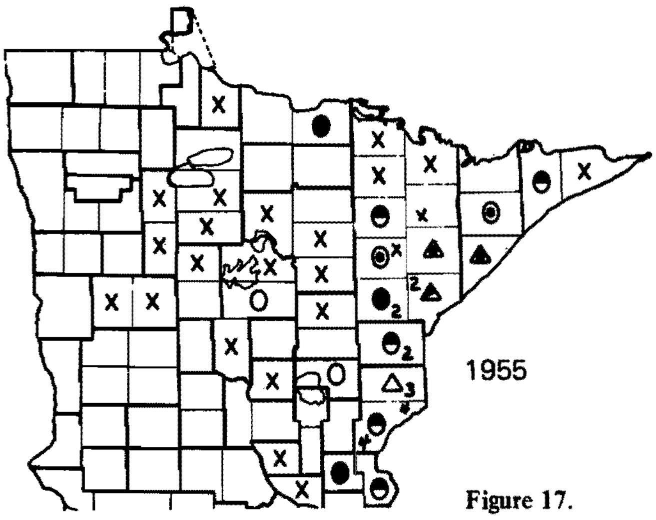


Figure 17.

INTRODUCTION

Dr. A.C. Hodson retired from the position of head and professor of the Department of Entomology, Fisheries and Wildlife, University of Minnesota, June 30, 1974. During his active service, he did significant research in ecology of forest, fruit, field crop, and stored grain insects as well as on basic aspects of population dynamics, diapause, and other aspects of physiological ecology. During his tenure as head, he increased the faculty and enhanced the already excellent reputation of the departmental programs. He was also instrumental in bringing about the new building, pictured on the cover, that bears his name.

Dr. Hodson's most enduring and enjoyed activity at the University was, however, his teaching and working with undergraduate and graduate students beginning with his days as teaching assistant through his tenure as head. Because these activities were interwoven so closely with his research, we selected several of Dr. Hodson's former students to present lectures in a special A.C. Hodson Ecology Lecture series from February to June 1975 to celebrate this benchmark in his continuing career. The selection was made to reflect as many of the diverse areas of insect ecology as possible. Because of this, we had to bypass many of Dr. Hodson's excellent students. All of these speakers were invited to publish their papers in this technical bulletin.

To testify that Dr. Hodson has been busy and active as professor emeritus, we present his lecture as the lead article. The others are arranged in an alphabetical order. Dr. A. Okubo, co-author with Dr. H.C. Chiang, is not a Hodson student.

More than 75 students completed graduate degrees under Dr. Hodson's tutelage. We take pleasure in quoting expressions from some of them which reflect their high esteem of Dr. Hodson as scientist, teacher, adviser, and friend. We think this collage expresses their sentiments eloquently.

"Outstanding is my remembrance of the classes and especially the field trips with you. You subtly made me realize how much I had been missing in the observations of the vegetative and animal life about me. Somewhat smugly I have a deeper appreciation for ecology than is commonly attributed to the term today, thanks to you. You enriched my life, for which I'm eternally grateful."

"Among the many things I have enjoyed most during my association with you and of which I still reminisce with pleasant memories are those brief coffee breaks at the Student Center (when we used to surface from Coffey Hall basement). Those moments were not only relaxing, but brought much of the needed better understanding and added extra meaningful dimensions to the life within the academe. It was your understanding and help to your students, especially those from other lands, that made things much easier and more enjoyable."

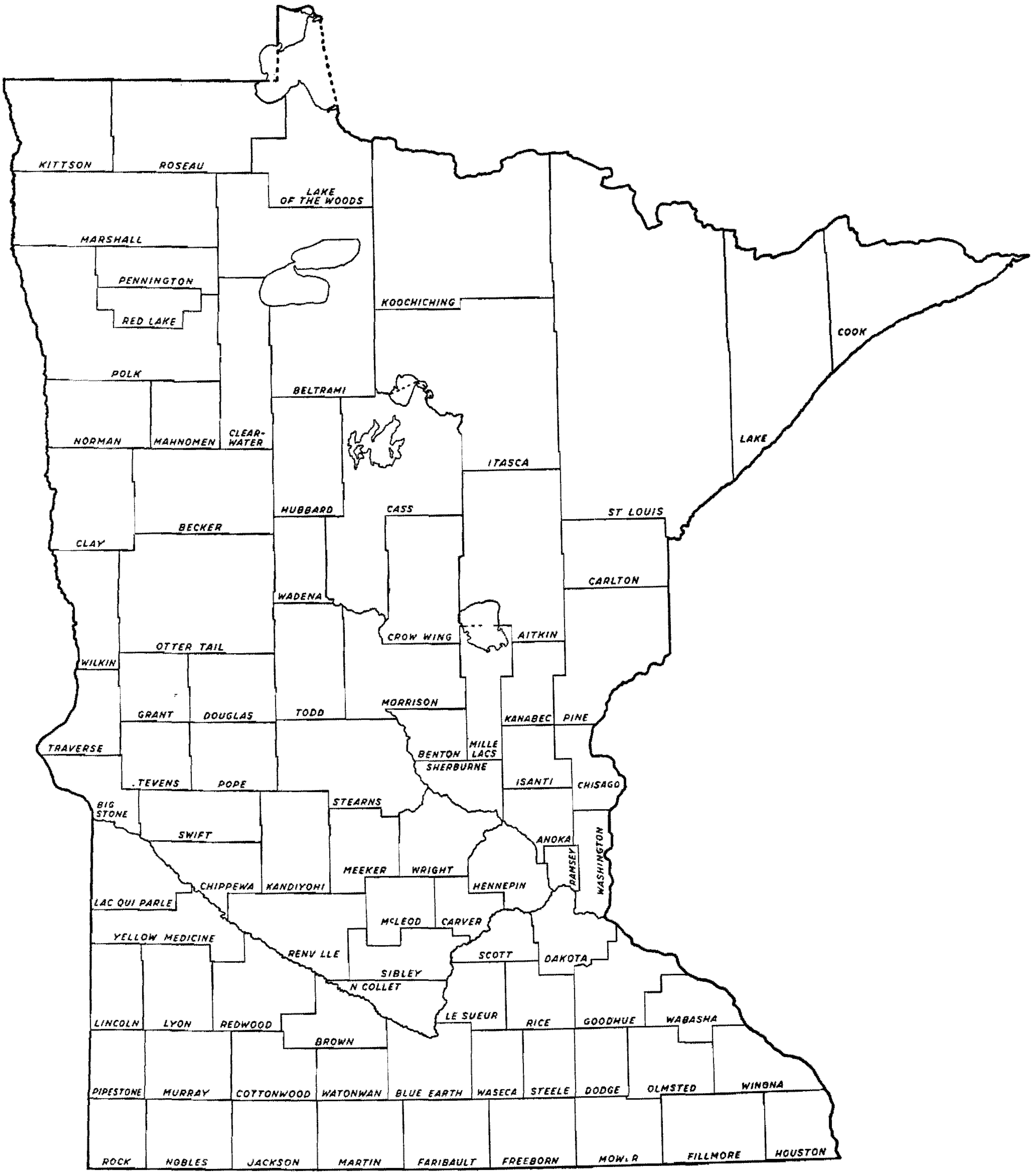
"Perhaps the quality that most students remember and admire you for the most was not your research or teaching, which were excellent, but your willingness to take the time (even when you didn't have it) to discuss with them their problems, their research, and a multitude of other things in your encouraging and enthusiastic way, yet with sincerity and honesty. Many people have one or the other of these qualities, but in my experience the combination is a rarity."

"I always appreciated your relaxed, efficient method of administration. It seemed to me that you greatly facilitated problem solving in our department and that we could always count on some sensible, creative, constructive conversation when we came to discuss departmental problems. You also always made it pleasant just to drop by for a friendly chat."

"Perhaps it's an old cliche, but it just won't seem right without you at the helm of the Department. Others can recall your many contributions and achievements — scientific, academic, and otherwise — but I remember you best as a warm, interested, highly capable Department Head and friend."

We appreciate the support of the Institute of Agriculture, Forestry and Home Economics through the organization and presentation of the lecture series, and especially the Agricultural Experiment Station and its administrative and editorial staff, for producing this publication as a technical bulletin.

H.M. Kulman and H.C. Chiang, co-editors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CLEARWATER
LAKE
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HUBBARD
CASS
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BECKER
CLAY
CARLTON
WADENA
CROW WING
AITKIN
OTTER TAIL
WILKIN
GRANT
DOUGLAS
TODD
MORRISON
KANABEC
PINE
TRAVERSE
BENTON
MILLE LACS
SHERBURNE
.TEVENS
POPE
ISANTI
CHISAGO
BIG STONE
STEARNS
SWIFT
ANOKA
WASHINGTON
RAMSEY
CHIPPEWA
KANDIYOHI
MEEKER
WRIGHT
HENNEPIN
LAC QUI PARLE
McLEOD
CARVER
YELLOW MEDICINE
RENV LLE
SCOTT
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WABASHA
PIPESTONE
MURRAY
COTTONWOOD
WATONWAN
BLUE EARTH
WASECA
STEELE
DODGE
OLMSTED
WINONA
ROCK
NOBLES
JACKSON
MARTIN
FARIBAULT
FREEBORN
MOW.R
FILLMORE
HOUSTON

Some Aspects of Forest Tent Caterpillar Population Dynamics

A.C. Hodson
Department of Entomology, Fisheries, and Wildlife
University of Minnesota, St. Paul, MN

ABSTRACT

The course of a forest tent caterpillar outbreak from its inception in 1948 to its termination in 1959 is followed with special attention given to a number of geographical and temporal changes. The important aspects covered are shifts in population numbers, changes in fecundity as represented by egg band size, defoliation history, pupal parasitism, and weather-induced mortality. Light trap records were taken at 19 sites in the infested area to follow adult population trends.

In 1938 an outbreak of the forest tent caterpillar, *Malacosoma disstria* Hbn., in Minnesota terminated when the remaining population along the North Shore of Lake Superior was decimated, primarily because of bad weather and parasitism by the flesh fly, *Sarcophaga aldrichi* Parker (Hodson, 1941). For 10 years little evidence of the forest tent caterpillar was found anywhere in Minnesota. Then in 1948 the first heavy defoliation was observed at Basswood Lake in Lake County on the Canadian border and in a small stand of aspen on the west shore of Leach Lake in Cass County. The acreage infested at these two sites increased in 1949, and an additional defoliated area was reported on Lake Vermillion near Tower, Minnesota. During the following summer more heavily infested stands were found in the vicinity of the original sites and near Detroit Lakes, about 70 miles southwest of Leach Lake in Becker County. Figure 1 shows the further development and decline of the outbreak, which continued in Minnesota until 1959.

Intensive annual surveys and population sampling were initiated to record the course of the outbreak and predict defoliation to be expected in subsequent years. Egg bands were sampled by state and federal forest rangers and University personnel throughout the northern forested area of the state. At each of several hundred sites, three condominant aspen trees were felled in the fall and all new egg bands were examined at the University to obtain an estimate of the number of eggs per band. This was done by removing the spumaline to expose the eggs, and then counting the number of eggs around the circumference and multiplying by the number of rows. This method gave sufficiently reliable estimates of egg band size, but has been improved upon by Witter and Kulman, 1969.

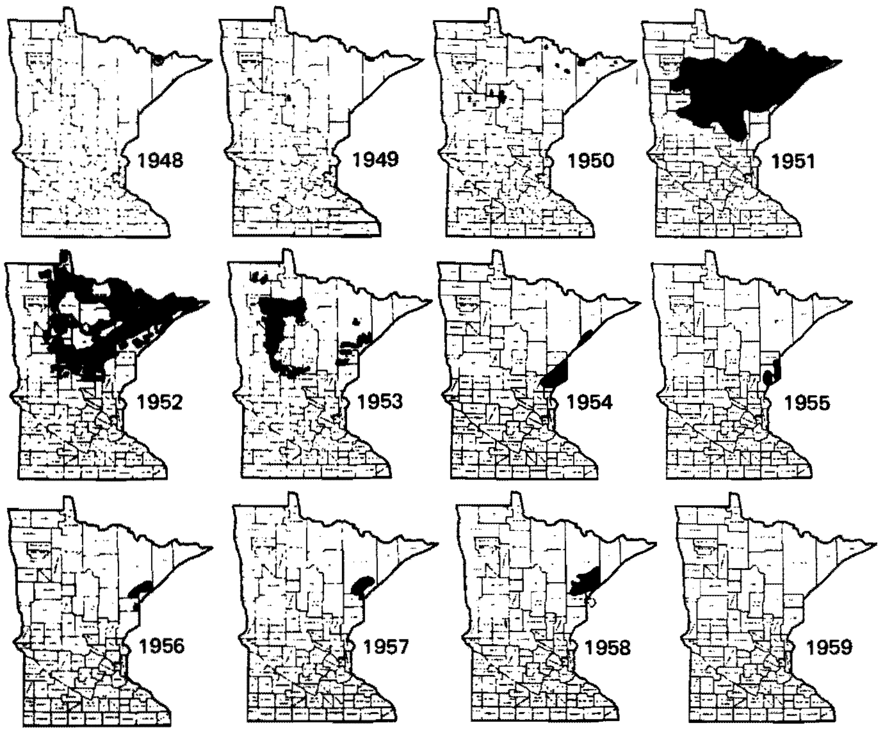

Figure 1. Defoliation record based on aerial mapping and ground surveys, 1948-1959.

In late June each year estimates of the severity of defoliation were obtained and recorded as none, light, medium, and heavy. The criteria used in making these distinctions are:

None – No leaves removed, terminal branches with normal foliage. (Caterpillars may be present, but no conspicuous signs of feeding.)

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After the peak of the moth flight in late July or early August, cocoons were sampled to determine success of moth emergence and causes of pupal mortality. The abundance of cocoons was estimated by collecting them for a 3-minute period. Where the population was low, the sampling time was extended to obtain enough cocoons for pupal mortality inspection.

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Bands/Tree	**Eggs/Band**	**Pupal Mortality**
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○ 1-5	⦿ 141-180	1 30-55
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□ 16	● 220	3 76-90
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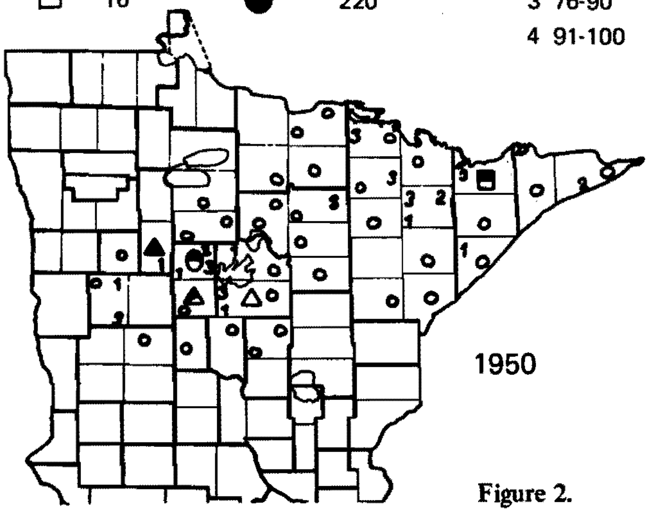

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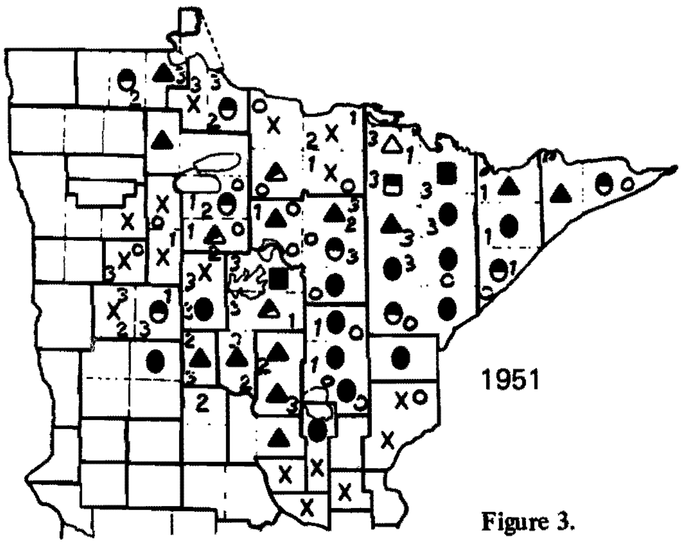

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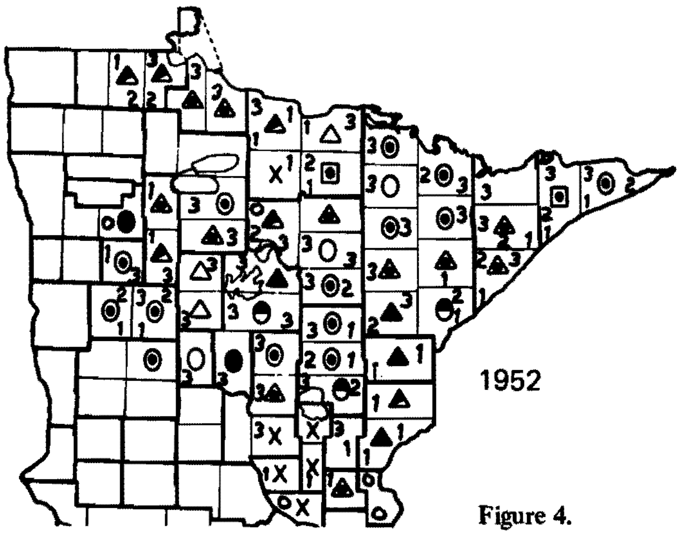

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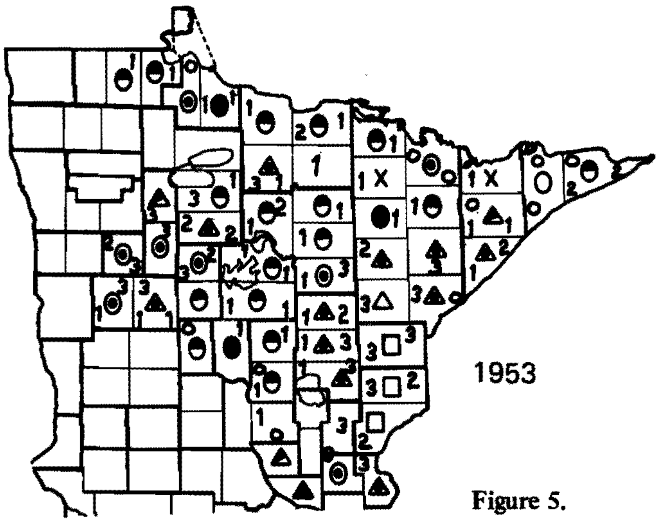

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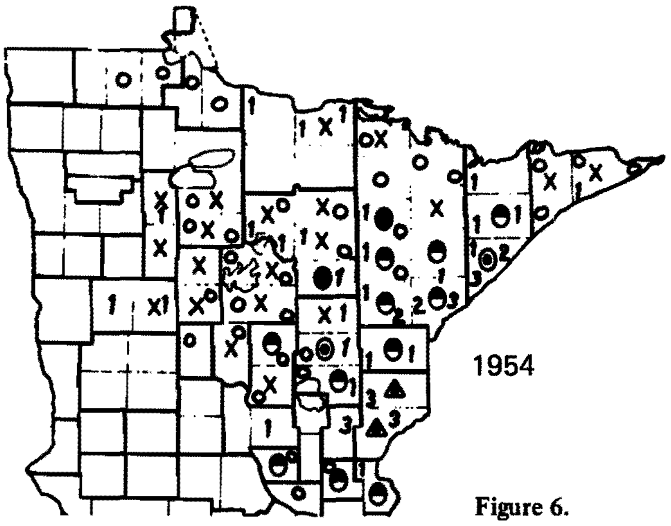

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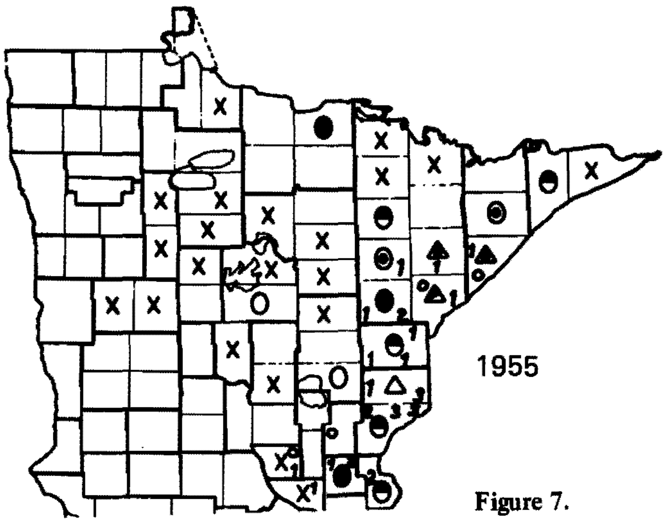

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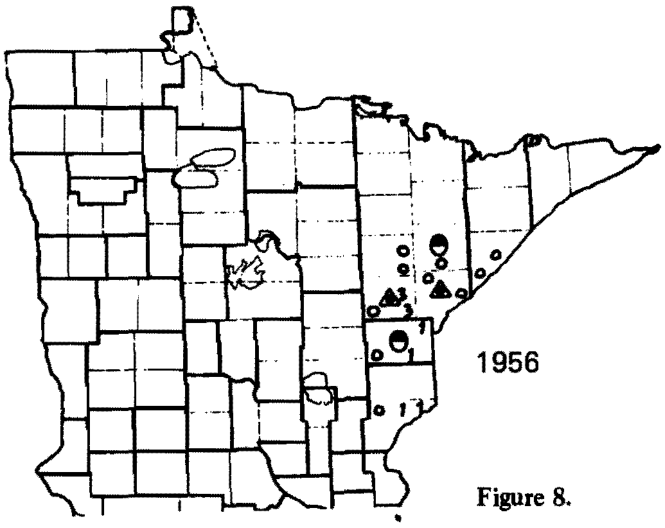

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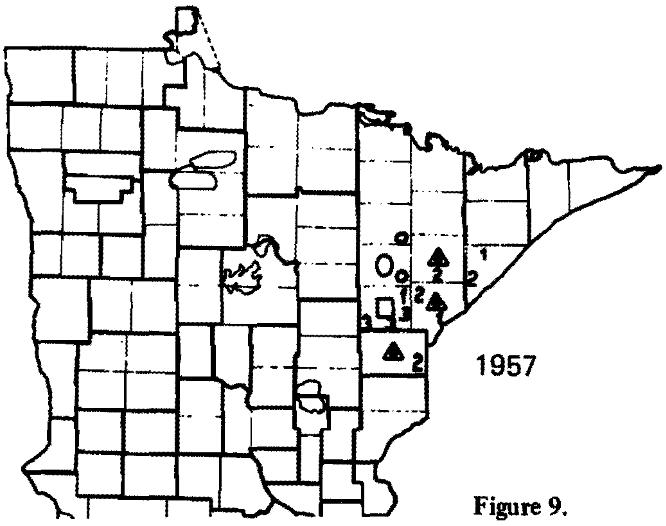

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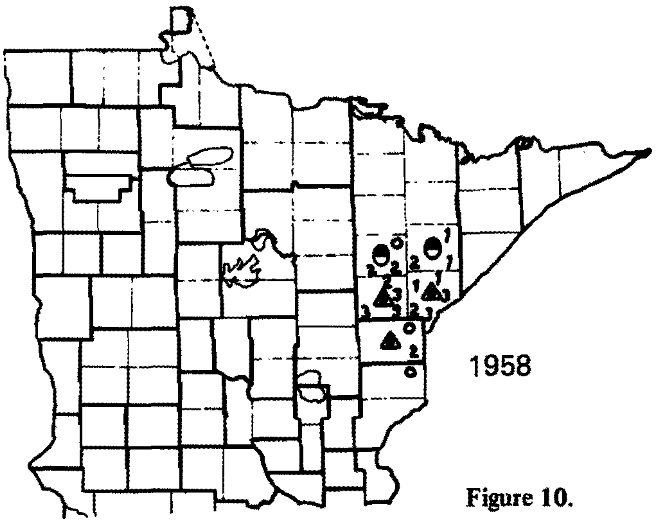

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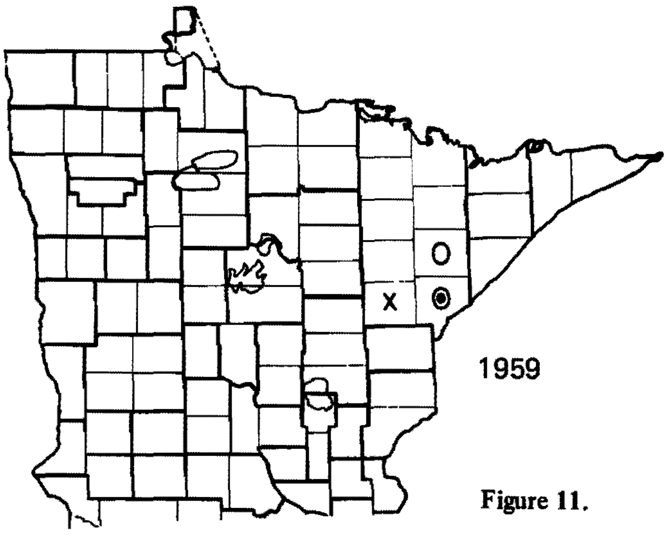

Figure 11.

The first estimates of the population parameters indicated above were made in 1950. Only a few egg band samples were taken along the Canadian border near Basswood Lake, and on the west side of Leach Lake (near center of the map) where heavy defoliation had been reported first in 1948 and 1949 (figure 2). At this time the egg bands were quite large and numerous. Heavy defoliation indicated by the numeral 3 was reported from two additional areas where bands had not been sampled – near Tower along Lake Vermillion, and southwest of Leach Lake near Detroit Lakes in Becker County.

Figure 3 shows a dramatic change from what was shown in figure 2. This is due both to the much more extensive sampling by state and federal forest rangers and the upsurge of the forest tent caterpillar population. In 1951 egg band sampling was initiated on a large scale and defoliation estimates were made at all the same sites. Egg bands were collected in at least small numbers throughout most of the northeast and central portions of the forested area. The exceptions were northcentral, near International Falls, and the most western and southeastern areas.

The preponderance of solid black elliptical symbols shows the character of early stage of population build-up, i.e. small numbers of large bands per tree. At this stage of the outbreak there had been little competition for food in the newly infested areas. The greater number of triangles and squares along the Canadian border, along the Iron Range, and near Leach Lake indicates an increase in population density where the heavy infestation had been present the longest. The X and open elliptical symbols just west of Leach Lake represent the early decline of the population where defoliation had been observed the longest.

To the east and southeast the infestation was just getting underway with either few or no large egg bands being found. The egg bands were collected in the fall each year; consequently, their number and size reflects population change and the effects of feeding competition during the summer of the same year.

The defoliation records taken in late June, 1951, by aerial mapping and ranger evaluations show the same trend. Generally very heavy defoliation was observed along the Canadian border, the Iron Range, and near Leach Lake, with some small hot spots in the west near Detroit Lakes. The failure of the rangers to report egg bands in the west where some heavy defoliation occurred may be due to the very spotty nature of the infestation. The tendency for the heavily defoliated areas to extend south and southeast of the original sites can be seen by comparing defoliation estimates for 1950 and 1951. It is probable that the northwesterly prevailing winds may account for this phenomenon.

Figure 4 shows that in 1952, there were generally fewer and smaller egg bands in the center of the large infested area and along the Canadian border. There had, by now, been 3 years of heavy defoliation in these areas, with a large percentage of the population dying from starvation, particularly just south and west of Leach Lake. The frequency of the numeral 3 in figure 4, designating heavy defoliation in 1952, shows the extent to which the caterpillar population had increased over what is shown for 1951 in figure 3. Exception can be seen along the shore of Lake Superior and in the southwest where the egg band abundance had been low in the fall of 1951.

On the basis of egg band collections made in the fall of 1952, it had been predicted that heavy defoliation of the aspen would occur again 1953, except in the oldest infestations in the northeast and central areas. Figure 5 shows another dramatic change. Light defoliation was reported in all but the more recently infested areas in the west and southeast. The nearly complete collapse of the outbreak over the most northern part of the state was caused by very unfavorable weather during the 3 weeks following egg hatching. Consequently, there was much less defoliation than had been predicted.

The egg band picture in figure 5 also shows the effect of the drastic population reduction. The preponderance of elliptical symbols in all but the eastern and southeastern areas illustrates the generally low egg band abundance and the presence of moderate size egg bands. On the other hand, in the compartments south of Duluth, very large numbers of small egg bands resulted from a population build up followed by competition for food. This is illustrated by the presence of open squares in Carlton and Pine Counties.

In 1954 the population reduction continued with medium to heavy defoliation observed only along the north shore of Lake Superior and in Kanabec, Pine, and Carlton Counties south of Duluth (figure 6). Where there had been small numbers of egg bands per tree in 1953, none were found in 1954 in those areas where heavy infestations had persisted the longest. This condition is illustrated by the number of X symbols on the map in nearly all but the east and southeast sites. However, small populations of moderate size egg bands commonly were found north and a little west of Duluth.

Figure 7 shows a continued contraction of the forest tent-caterpillar population for 1955. The heaviest defoliation again was found south of Duluth in Pine County with mostly light and some medium defoliation along the eastern fringe of the forested area. The 1955 fall egg collections indicated that most sites had small populations with medium size egg bands. Triangle symbols north of Duluth suggested that some heavy defoliation could be expected in 1956 which, as shown in figure 8, was reported in southern St. Louis County, west of Duluth. It was also only in this general area that enough egg bands were collected to predict continued medium to heavy defoliation in 1957.

The prediction for continued heavy defoliation was realized in 1957 as shown by the frequency of the numeral 3 in southern St. Louis County in figure 9. The open square in the compartment west of Duluth indicates a large number of small egg bands caused by extensive starvation in the defoliated areas. In spite of the reduced number of moths emerging in 1957, the large numbers of egg bands produced sufficiently large numbers of caterpillars to cause heavy defoliation in many sites for a 3rd year (figure 10). There also were enough egg bands collected in the fall of 1958 to suggest that the same sites would be defoliated for a 4th year in 1959. Figure 11 shows that no defoliation was reported in 1959. Weather conditions just before and after the eggs hatched were so unfavorable that the population crashed and the state outbreak which began in 1948 was terminated. A fall survey showed a very few egg bands in scattered sites but no indication of further defoliation. In fact, no defoliation was observed until the most recent outbreak began along the Canadian border in 1964 in an area where the population had crashed earlier in 1953.

During this account of the ebb and flow of the forest tent caterpillar population and its defoliation history, two factors responsible for population decline have been mentioned: severe competition for food and unfavorable spring weather after the eggs had hatched. Another cause of population decline was pupal mortality, primarily from very high levels of insect parasitism. Figures 12-20 illustrate the character of this biological population suppressor as it expressed itself

Figures 12-20. Egg band numbers and size and estimates of pupal mortality.

Bands/Tree		Eggs/Band		Pupal Mortality	
X	None	○	100-140	0	30%
○	1-5	⊙	141-180	1	30-55
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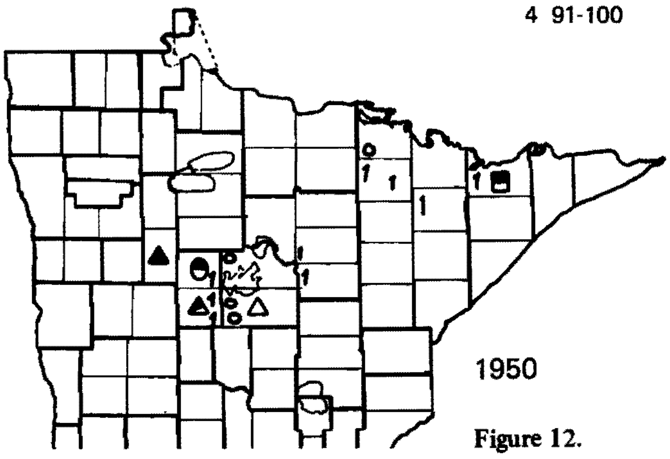

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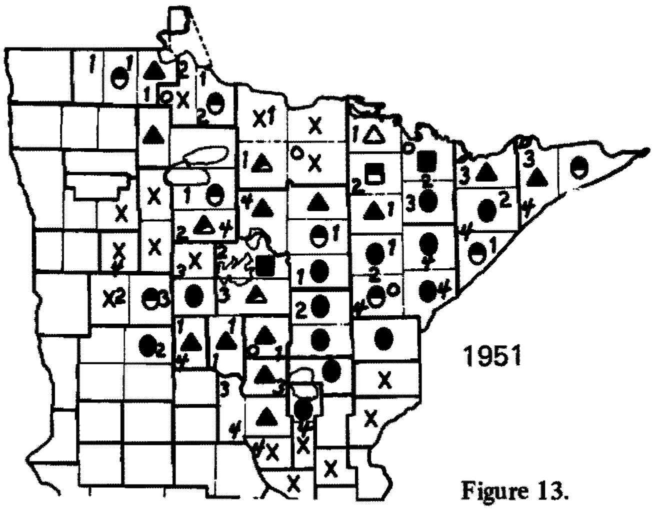

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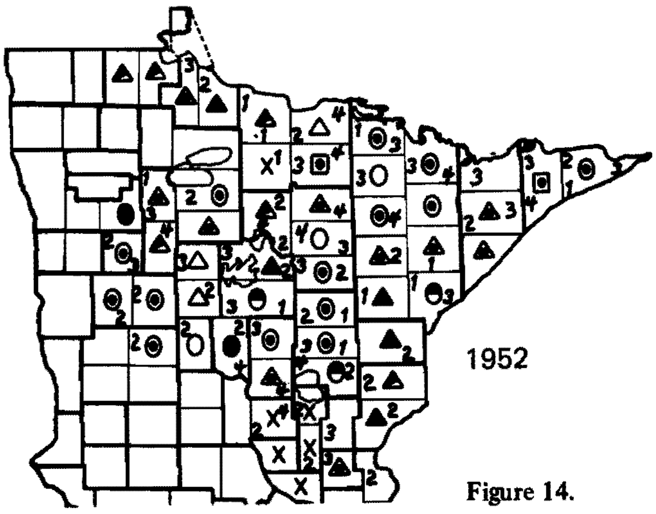

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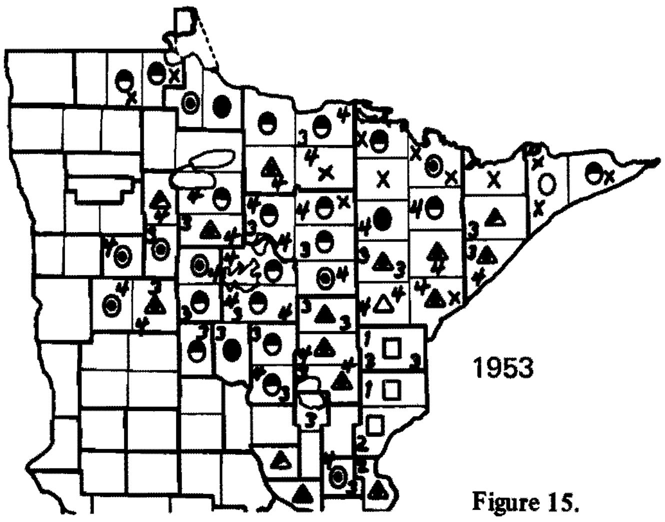

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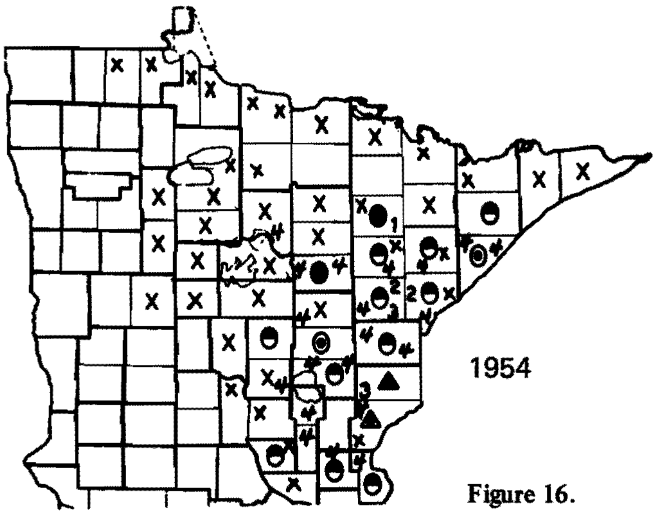

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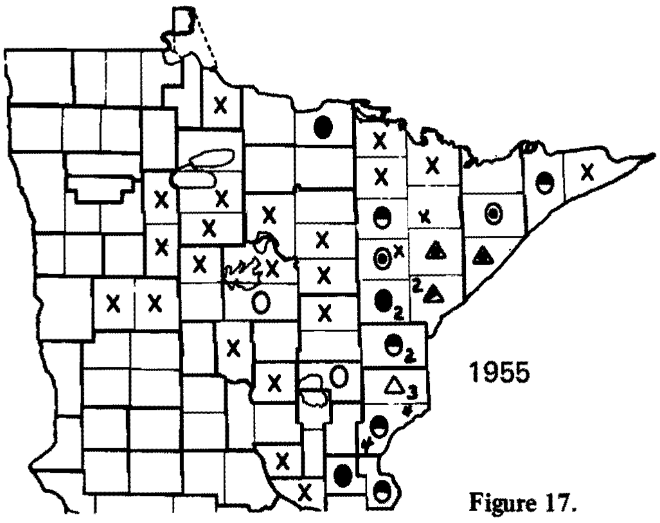

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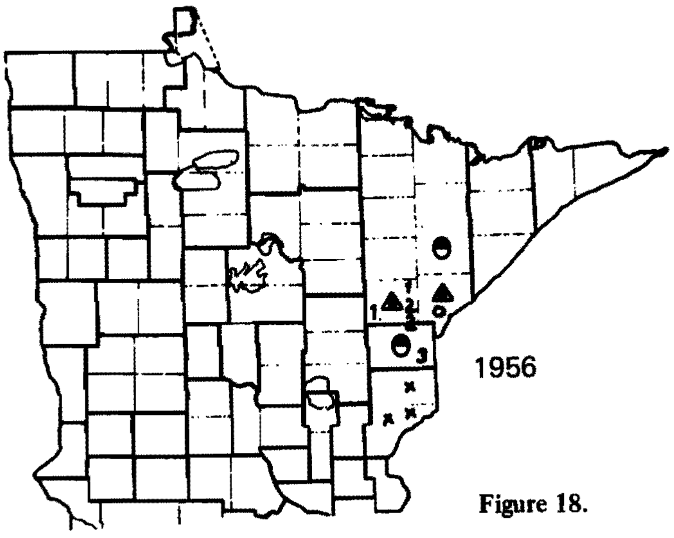


Figure 18.

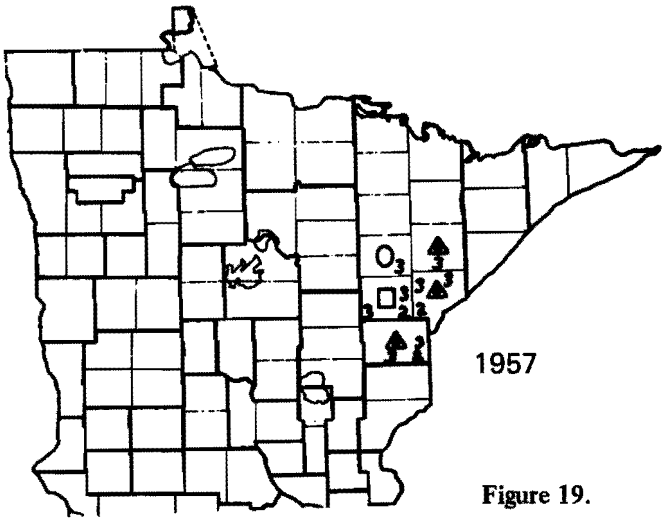


Figure 19.

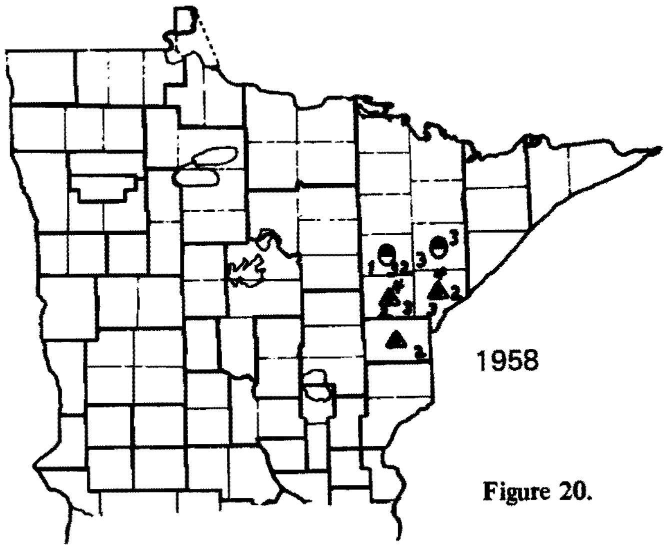


Figure 20.

during the outbreak. During the early stages, as seen in figure 12 for 1950, pupal mortality was uniformly low, usually less than 30 percent. As the host population increased, the pupal mortality also became more significant. For example, the mortality of pupae near Leach Lake, about in the center of the map, was 23 percent in 1950, 68 percent in 1951, 82 percent in 1952, and 94 percent in 1953. This sequence is typical of most areas where data were obtained for early to late stages of outbreak behavior, as will be evident from a review of pupal mortality throughout the state outbreak history.

Figure 13 shows that pupal mortality in 1951 was highest in two situations: either where the forest tent-caterpillar infestation had persisted for 2 or more years or where the infestation was spreading from nearby high population sites. The first of these situations was found along the Canadian border near Basswood Lake and along the Iron Range. The second can be seen in the western, eastern, and southern areas where the infestation was spreading. Figure 14, the 1952 data, shows that again the areas with the longest history of heavy defoliation have increased pupal mortality. In contrast, some of the areas with the first noticeable defoliation in 1951 show some reduction in pupal mortality because the rapid increase of the caterpillar population was much greater than that of their natural enemies. This increase is indicated by the large number of egg bands found in the fall of 1952. The high level of pupal mortality reported for the oldest infestation sites, such as at Leach Lake, was due to two successive events. The high caterpillar mortality due to starvation reduced the number of cocooning caterpillars to the extent that insect parasites were able to kill a larger percentage of pupae than might have been expected without prior severe larval competition for food. For example, it was estimated that about 98 percent pupal parasitism in some sites represented mortality of only about 5 percent of the total population present earlier in the season in these areas.

As we move on to 1953, pupal mortality was very high with more than 90 percent recorded from many sites. The presence of the numeral 4 in most of the compartments illustrates this situation. The marked increase in mortality was caused by weather-induced spring mortality of small larvae resulting in small numbers of pupae at the peak of insect parasite activity and by a disproportionate increase in the parasite population. As noted before, the egg band numbers and size were both smaller in the fall of 1953 than in 1952.

Figure 16 shows the results of the 1953 population crash. Spring mortality, larval starvation, and a high percentage of parasitism had reduced the infested area to about 1/3 of its size in 1952. Again the frequency of the numeral 4, indicating high pupal mortality, describes the situation in 1954. But in spite of the high percentage of pupal mortality, enough eggs were present in the fall to make it necessary to predict continued defoliation in 1955. In many sites the caterpillar population was so large that more than 98 percent mortality would have had to occur just to keep the population from increasing.

As expected there was heavy defoliation in 1955, confined to the southeast infested area. The high percentages of pupal mortality shown in Figure 17 were reported only from Kanabec and Pine Counties, south of Duluth. North and west of Duluth only moderate parasitism was observed. This situation may be explained by a fungus epizootic that reduced the population of *Sarcophaga aldrichi*, the principal parasite.

The effects of the high pupal mortality in 1955 south of Duluth are shown in the 1956 map (figure 18). Only small numbers of egg bands were found, and by 1956 the population had crashed in this area. The percentage of pupal mortality north and west of Duluth continued to be lower than would have been expected at the stage of the outbreak. Again, as in 1955, the parasitism by the sarcophagid fly was much less than had occurred in other areas after 3 or 4 years of moderate to heavy defoliation. Egg bands were numerous enough in the fall to foretell more defoliation in 1957. In 1957 pupal mortality ranged commonly between 76 and 90 percent but was not high enough to terminate the outbreak (figure 19). Other factors such as spring weather and only moderate caterpillar competition did little to reduce the caterpillar numbers. Consequently, heavy defoliation occurred in 1958. Figure 20 shows that the pupal mortality was somewhat higher than in 1957 but not high enough, except in two sites north of Duluth, to prevent deposition of enough egg bands to cause defoliation for yet another year. However, two factors caused the population to crash in 1959: Hatching occurred several days before the aspen leave buds opened and very unfavorable weather followed egg hatching.

During this account of some aspects of population changes during a forest tent-caterpillar outbreak, reference has been made to natural control factors that have been responsible for often precipitous declines in population numbers. One of them, starvation, occurred wherever the caterpillars were so numerous that they consumed all available tree and brush foliage. The result of this severe competition for food was either the death of millions of larvae or the production of smaller moths that produced small egg bands. Very commonly both events occurred on the same sites.

A second cause of heavy mortality was produced by insect parasites (frequently augmented by the prior reduction in the caterpillar population by starvation). Of these parasites the flesh fly, *Sarcophaga aldrichi*, was the most common and important. This species can breed in carrion as well as destroy pupae in their cocoons (Hodson, 1939). Table 1 shows its important role as a natural cause of pupal mortality.

Table 1. Percent total pupal mortality (A) and mortality caused by *Sarcophaga aldrichi* parasitism (B).

Area	Year	A	B
Pelican L.	1951	30	10
	1952	97	63
	1953	98	81
	1954	No cocoons	
Brainerd	1951	60	25
	1952	89	75
	1953	85	87
	1954	100	100
Leach L.	1950	23	19
	1951	68	45
	1952	81	73
	1953	94	87

From the data in Table 1, it can be seen that in early stages of outbreak development pupal mortality was low and the contribution of *S. aldrichi* to the mortality was not very significant. By the 3rd or 4th year the total mortality of pupae had increased significantly and the sarcophagids provided the major contribution to pupal death.

As mentioned earlier in the text pupal mortality near Duluth (1956-1958) did not reach the high levels recorded for other infested areas and lower parasitism by *S. aldrichi* probably was a contributing factor. This contention is supported by the data in table 2.

Table 2. Total pupal mortality (A) and mortality caused by *S. aldrichi* parasitism (B) (average for six areas in the vicinity of Duluth)

Year	A	B
1956	62	55
1957	83	68
1958	80	52

A comparison of tables 1 and 2 shows how comparatively little pupal mortality, and particularly sarcophagid parasitism, contributed to population reduction in the years 1956-58. This helps to explain the longer persistence of heavy defoliation in the east than farther west and north.

A third suggested cause of high mortality was unfavorable weather before or during the few weeks following the hatching of forest tent-caterpillar eggs. As mentioned earlier, an extensive weather induced population crash occurred in 1953, and weather was primarily responsible for the termination of the outbreak in the remaining infested areas in 1959. In the spring of 1953 the death of young larvae rather than unhatched pharate larvae was involved. In 1959 in some areas there was a very high mortality in pharate larvae, about 95 percent, while in others there was about 90 percent favorable hatch but very poor survival of the young larvae. We have no explanation for why these two very different conditions were observed as little as 6 miles apart.

The history of the relation of weather conditions to the onset and/or termination of outbreaks has been described by Hodson (1941), Wellington (1952), Blais et al. (1953), Prentice (1954), Witter and Kulman (1972), and Ives (1973). In my investigations of weather's role in regulating populations of the forest tent-caterpillar, the temperatures before, during, and after egg hatching were examined over the span of two outbreaks (1933-38 and 1948-59).

Figure 21 shows the results of this study. The absolute minimum temperatures and the number of *negative* day-degrees by which the maximum temperature failed to reach 59°C for 3 weeks following hatching are presented. The broken line on the minimum temperature graph is located at 26°C, the temperature below which the aspen leaves would be expected to freeze. The maximum temperature of 59°C was selected because Hodson (1941) had shown that little caterpillar feeding takes place below that temperature. The histograms portray the relative caterpillar abundance during the course of the two outbreaks. The dates for egg hatching were obtained by field observation during the outbreaks, but were estimated during those years when the population was very low. The estimated dates were calculated by summing the amounts by which the average daily temperatures for March, April, and early May exceeded 46°C. It was found that the summation of 80 day-degrees fit known hatching dates within about ± 2 days, sometimes the exact day.

The significant points in the temperature records for both Bemidji and Brainerd are first the relatively high minimum temperatures and a low value for the accumulated negative day-degrees below 59°C. for 2 to 3 years prior to and during the course of the two outbreaks. A low negative day-degree accumulation suggests favorable temperature due to either generally high maxima or very few days with low maxima or both during the 3 weeks following egg hatching. Secondly, at the termination of the outbreaks in 1938 and 1953 the minimum temperatures probably were much less important than the prolonged cool weather as indicated by the high value shown for the negative day-degree accumulation during the 3 weeks following hatching. For example, at Bemidji the mini-

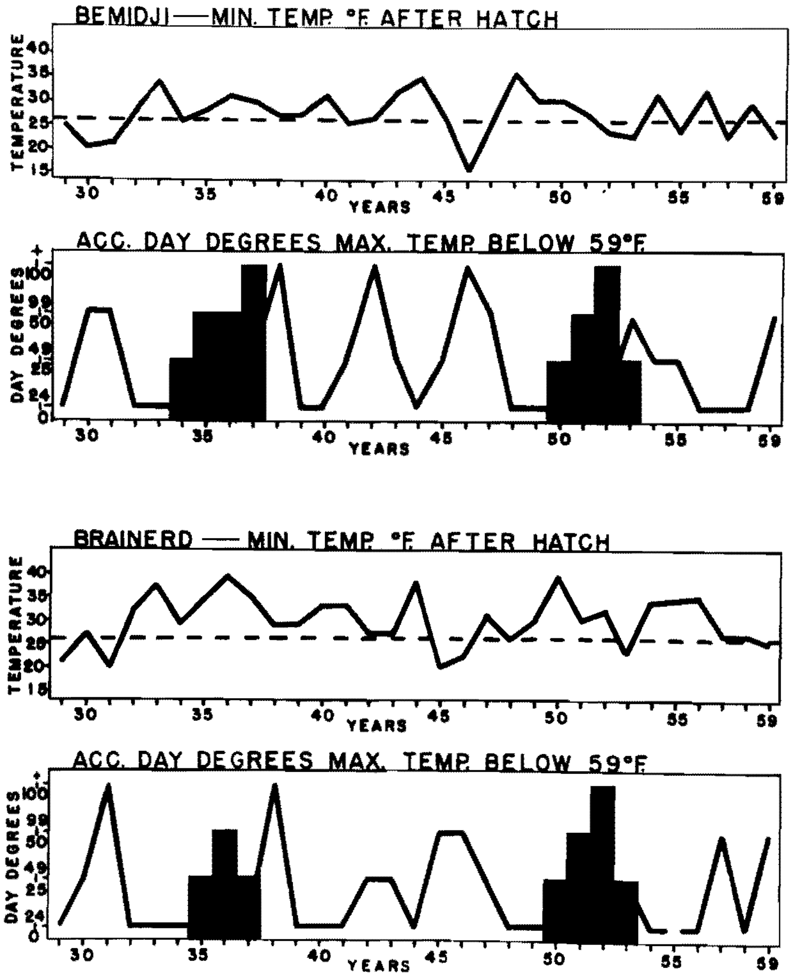


Figure 21. Temperative records during the 3 weeks following forest tent caterpillar egg hatching as related to caterpillar abundance during two outbreaks.

mum was only 26°C, a temperature not fatal to the newly hatched larvae (Raske, 1975). In contrast, the day-degree accumulation of maximum temperatures below 59°C was 116. Moreover, there were 12 days when the maximum temperature failed to reach 59°C with as many as 5 consecutive days when this condition prevailed. The result was a spectacular crash of the population. The same situation is shown for Brainerd in 1938. There was a less striking increase in the negative day-degree temperature accumulation at Brainerd in 1953. While the data suggest less than favorable temperature after hatching, other factors such as starvation and parasitism played a more important role in terminating the outbreak in that locality. Again in 1959 a marked upward trend in the day-degree accumulation of maximum temperatures below 59°C was accompanied by a population crash in the last area to be heavily infested north and west of Duluth.

As a final item in this lengthy discourse on forest tent-caterpillar population dynamics, I will report the results of light trap collections of the moths. A number of people had asked whether the populations surviving a major crash persisted at low endemic levels throughout the previously infested area or in more discrete units that might serve as epicenters for another outbreak. As can be seen in figure 21, there is no indication of measurable populations between outbreaks. Furthermore, there were no periods of 2 or 3 years of favorable weather during those years until just before the next outbreak. As a matter of fact only occasional individual larvae were seen by this observer between 1938 and 1948. Consequently, light traps (the so-called Minnesota trap) were placed in localities that represented different stages of the 1948-59 outbreak to see whether the presence or absence of moths would answer the question raised above.

Nineteen light traps, serviced through the cooperation of state and federal forest rangers were set up in 1956 (figure 22). These traps were operated in July from 1956 to 1967. The results, shown in table 3 and figures 23-33, indicate that with one or two exceptions at least small numbers of moths were caught indicating a low level population throughout most of the area trapped. The much larger number of moths in traps 2 and 3 in 1956-58 (figures 23-25) were caught in traps located north and west of Duluth where figure 10 shows heavy defoliation still occurring. The picture changes abruptly in 1959 (figure 26) with 16 of the traps showing a reduction in moth numbers and a total catch of only 5 percent of that in 1958. The widespread reduction in moths caught suggests that unfavorable weather conditions prevailed generally and were not limited to the area near Duluth when the population crash could be observed. Without the light trap records, the effect of unfavorable weather would have gone unnoticed in most localities because there were far too few caterpillars to obtain reliable population reduction data.

The moth catch increase recorded from trap numbers 10 and 11 beginning in 1962 (figures 29 and 30) forecast a new outbreak along the Canadian border near International Falls and Crane Lake. The first heavy defoliation was reported in 1964 (figure 31), and the moth catch reflects the rapid popu-

Table 3. Forest tent caterpillar light trap collections, 1956-1967

No.	Township range	1956	1957	1958	1959	1960	1961	1962	1963	1964	1965	1966	1967
1	42-20	77	134 +	84 -	11 -	27 +	4 -	13 +	8 -	0 -	34 +	65 +	33 -
2	52-18	3,525	3,329 -	6,260 +	121 -	31 -	12 -	23 +	69 +	192 +	133 -	202 +	150 -
3	54-17	670	1,126 +	623 -	40 -	23 +	20 -	11 -	43 +	161 +	123 -	28 -	11 -
4	45-28	0	99 +	65 -	1 -	0 -	0 -	2 +	0 -	0	1 +	0 -	0
5	139-26	8	1 -	3 +	2 -	0 -	2 +	4 +	2 -	0 -	1 +	1	3 +
6	61-26	21	89 +	44 -	21 -	14 -	38 +	8 -	32 +	55 +	10 -	15 +	76 +
7	60-21	26	10 -	13 +	3 -	22 +	5 -	4 -	21 +	61 +	23 -	8 -	12 +
8	48-23	9	5 -	30 +	4 -	7 +	6 -	4 -	1 -	1	2 +	2	0 -
9	144-32	1	6 +	23 +	21 -	9 -	30 +	10 -	23 +	45 +	15 -	12 -	22 +
10	68-22	21	18 -	87 +	28 -	24 -	15 -	91 +	146 +	1,267 +	3,955 +	2,078 -	1,678 -
11	67-17	30	17 -	8 -	2 -	2 -	11 +	20 +	19 -	440 +	1,942 +	418 -	797 +
12	62-15	13	47 +	27 -	11 -	12 +	1 -	2 +	17 +	5 -	42 +	49 +	46 -
13	57-7	1	142 +	25 -	3 -	1 -	0 -	0	28 +	4 -	62 +	346 +	6 -
14	62-3E	3	6 +	15 +	36 +	16 -	5 -	5	69 +	8 -	223 +	14 -	19 +
15	142-31	0	9 +	2 -	2 -	6 +	1 -	1	0 -	20 +	2 -	1 -	0 -
16	151-28	3	5 +	6 +	21 +	12 -	17 +	—	19 +	57 +	43 -	17 -	—
17	149-31	0	0	0	0	1 +	0 -	0	1 +	0 -	20 +	6	5 -
18	59-8	3	—	101 +	52 -	12 -	1 -	8 +	97 +	—	58	—	—
19	49-17	56	598 +	60 -	3 -	4 +	2-	4 +	7 +	6 -	0 -	0	0
	TOTAL	4,510	5,687	7,544	386	249	289	284	643	3,037	3,465	3,262	1,858
	Percent of previous year		126	133	5	65	116	98	226	473	114	94	87
	Increase		+11	+9	+2	+8	+5	+9	+13	+9	+10	+5	+6
	Decrease		-6	-9	-16	-11	-13	-5	-6	-7	-8	-10	-9
	No change		1	1	1	0	1	4	0	2	1	3	2

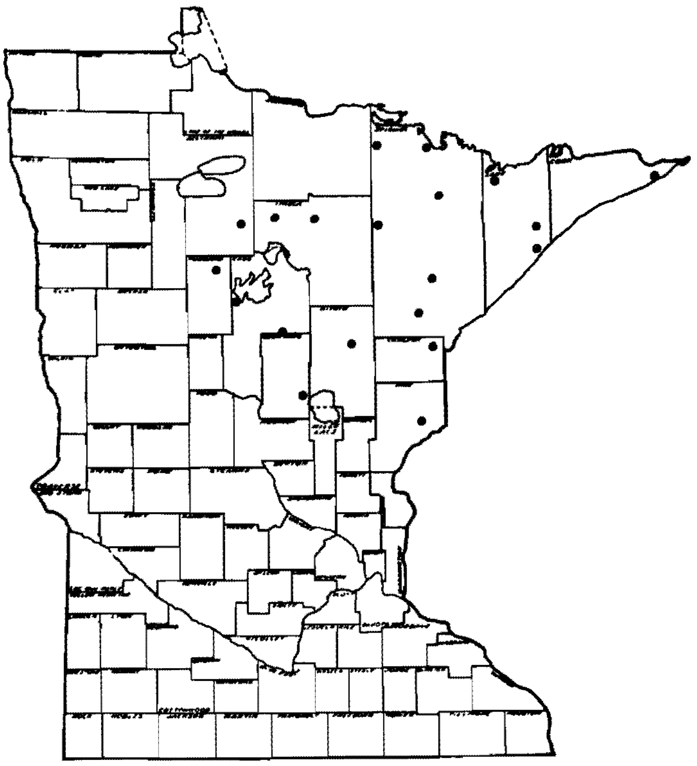
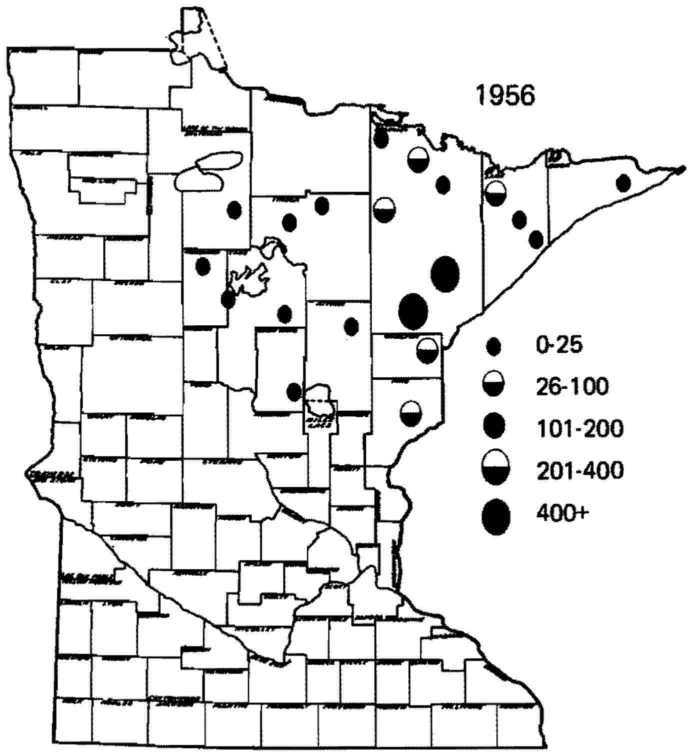


Figure 22. Geographical location of forest tent caterpillar light traps.



Figures 23-33. Pictorial record of numbers of moths caught in light traps, 1956-66.

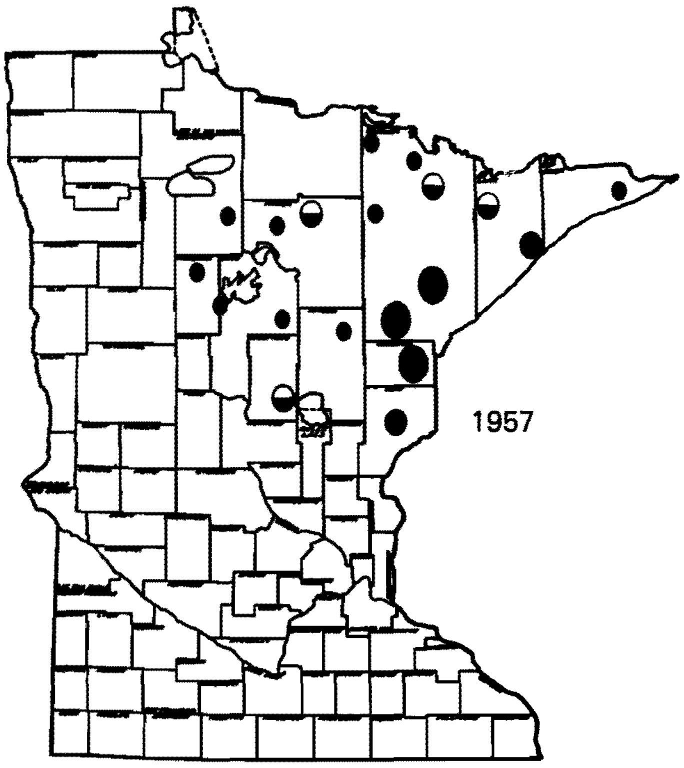


Figure 24.

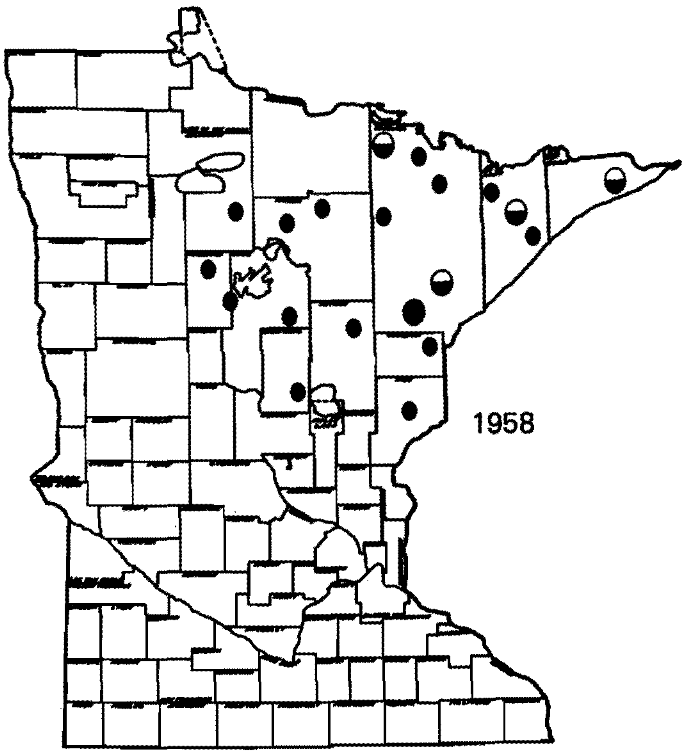


Figure 26.

- ● 0-25
- ◒ 26-100
- ● 101-200
- ◒ 201-400
- ● 400+

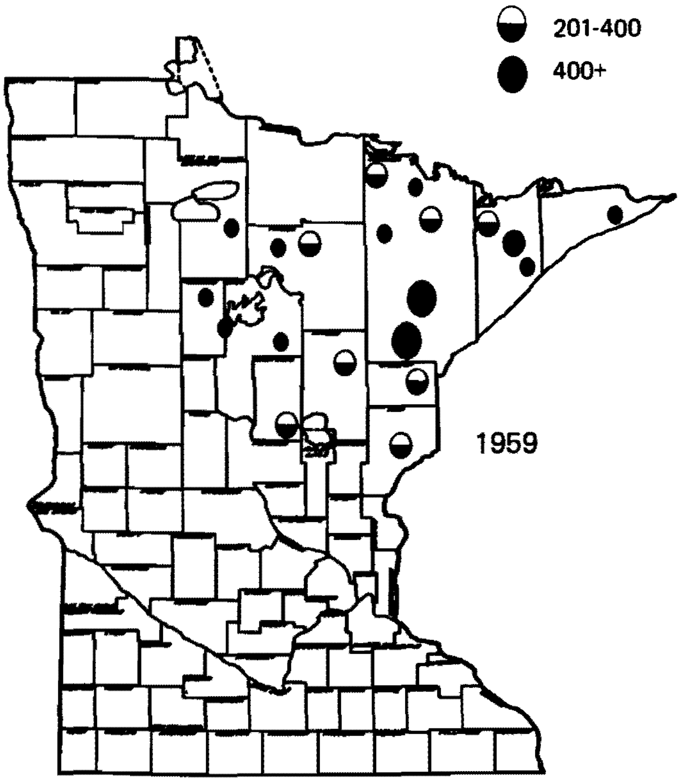


Figure 25.

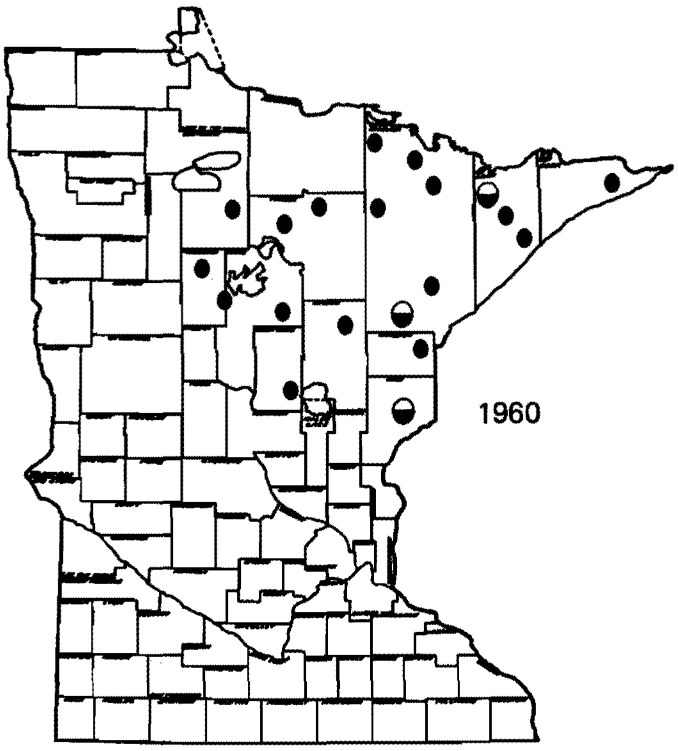


Figure 27.

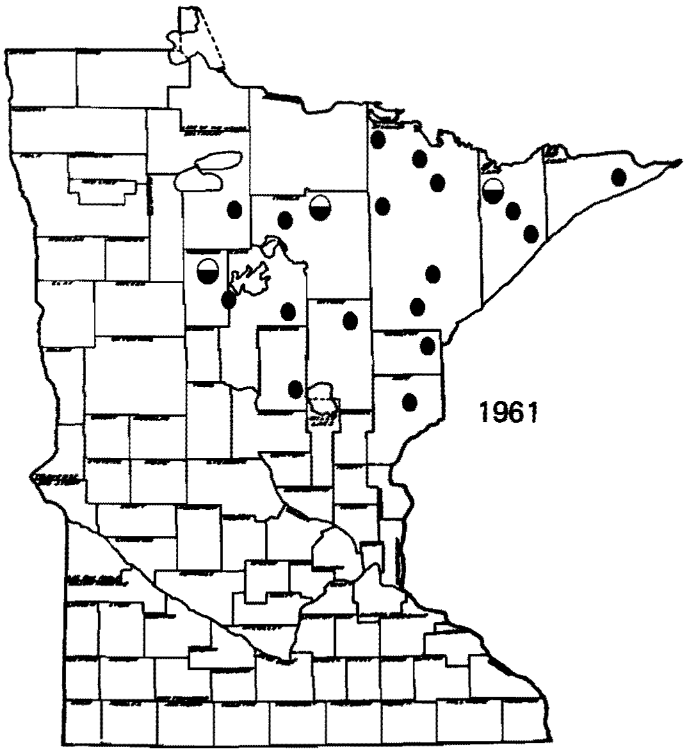


Figure 28.

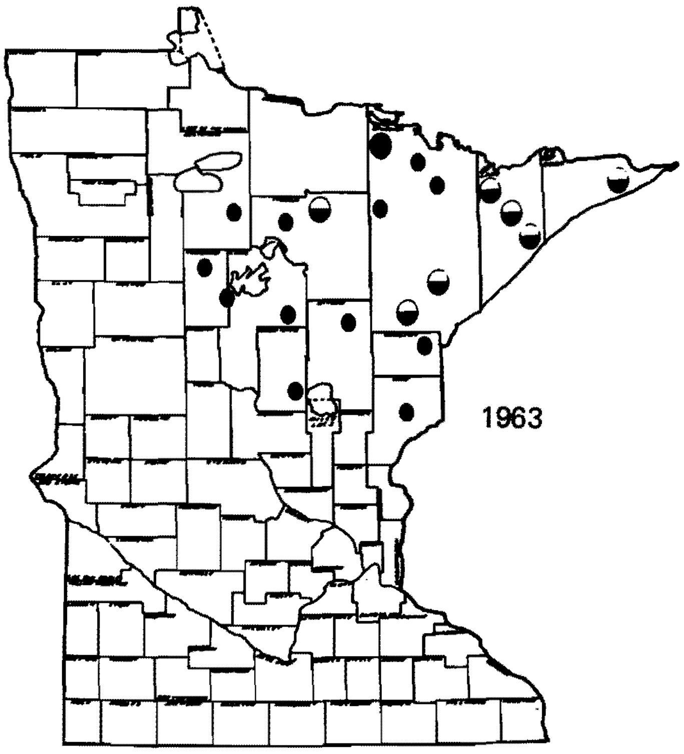


Figure 30.

● 0-25
◒ 26-100
● 101-200
◒ 201-400
● 400+

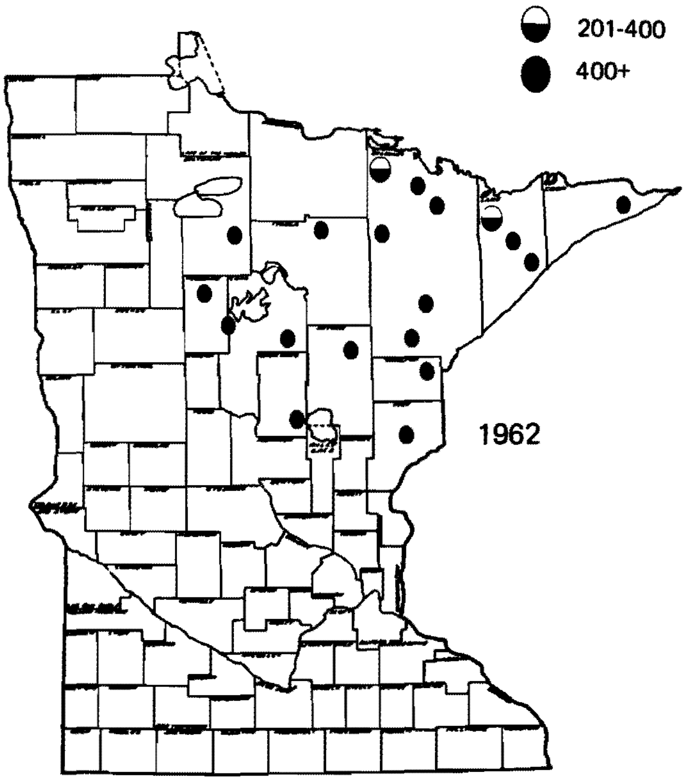


Figure 29.

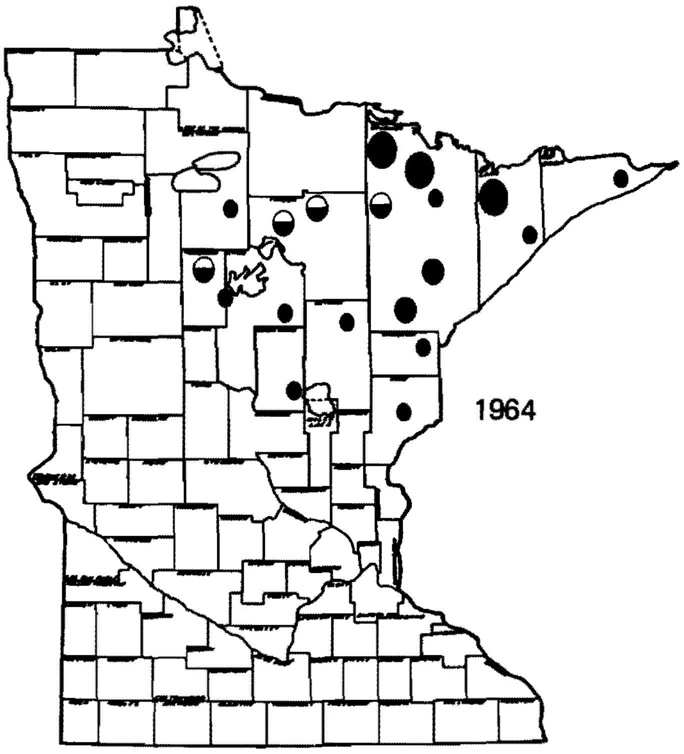


Figure 31.

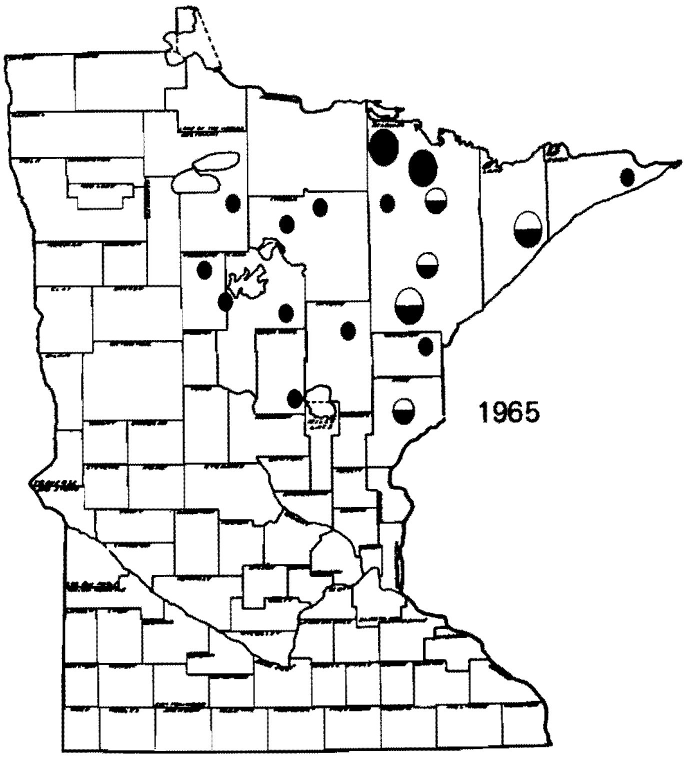


Figure 32.

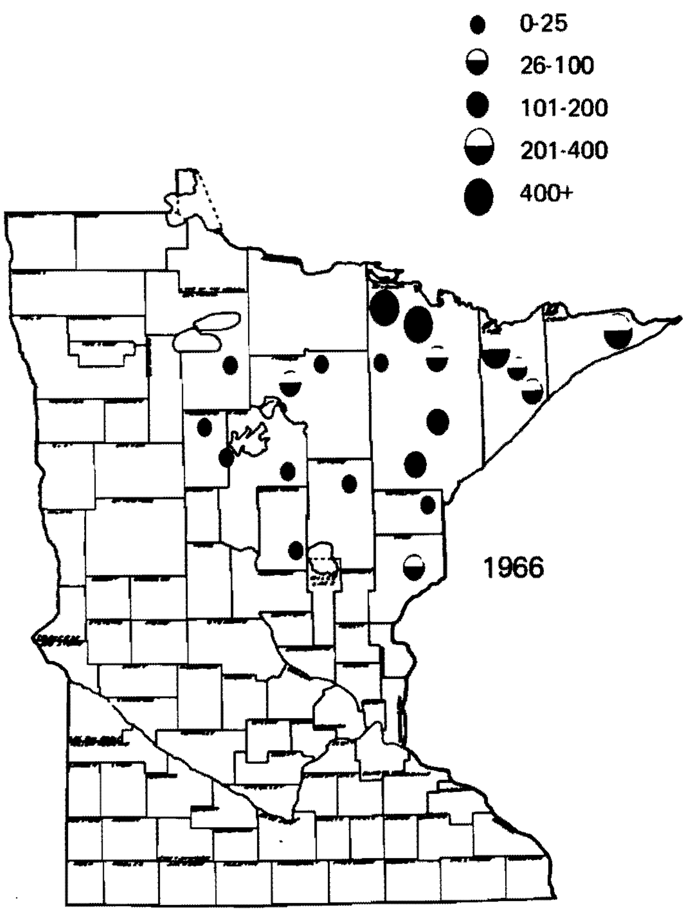


Figure 33.

lation increase in these areas. This outbreak persisted for 8 years with a quite different history than the one described in this account. But that is another story (Witter et al., 1975).

A summary of the population dynamics for the 1948-59 outbreak follows: The first evidence of heavy defoliation was reported along the Canadian border and along the west shore of Leach Lake. The previous outbreak also began along the Canadian border. The spread during both outbreaks was generally south and east of the original infestations. Except at a few sites near Lake Superior, heavy defoliation occurred for no more than 3 years. In the early stages the egg bands were few in number and contained large numbers of eggs. As competition for food resulted from a rapid population increase, the size of the egg bands became much smaller. Where severe starvation occurred, both the number and size of the bands were much reduced. The local termination of high populations was caused by starvation, frequently followed by a high percentage of pupal parasitism. The population crash over large areas was due to mortality of small larvae associated with unfavorable spring weather. The most important parasite, *Sarcophaga aldrichi* required 2 to 3 years to become most effective. In all these respects the outbreak followed the course of the previous one, 1933-38 (Hodson, 1941), except that it lasted longer and encompassed a much larger area.

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Dispersal and Attack Behavior of the Southern Pine Engraver, Ips grandicollis Eichh., Coleoptera, Scolytidae

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ABSTRACT

Results of several field experiments show that odors emanating from pine logs were the stimuli that attracted initially attacking pioneer beetles and that these odors were effective in attracting dispersing beetles before they alighted on the logs. It was also shown that wounded resinous pine wood, several kinds of tree foliage, and a number of odoriferous chemicals increased the attractiveness of pine logs to the pioneer beetles that first found and initiated attacks. Some of the chemicals that increased the attractiveness of the pine logs were compounds that might not be expected as being produced in the logs. These included materials such as anisole, piperonal, citral, carbon disulfide, and acetone.

Various meteorological factors that were significantly related to the abundance of beetles that responded to pine logs containing fresh attacks were temperature, wind speed, and humidity. There was a highly significant relationship for "time of day" and the attraction of dispersing beetles during the evening period when the observations were made; however, the factor of light intensity, which was a condition that changed rapidly during these crepuscular periods, was not related to beetle abundance.

The most injurious insect pests of forests in the South are bark beetles. Both the adults and larvae bore extensive galleries through the succulent inner-bark and in so doing destroy the vital cambial and phloem tissues. The species that attack pines concentrate their attacks in certain trees rather than lightly infesting many; therefore, these attacks usually cause rapid death of infested trees. The most injurious species in the South now is the southern pine beetle, *Dendroctonus frontalis* Zimm. During the past year (1975), 79,607,000 cubic feet of pine timber have been salvaged from forests in 10 southern states due to outbreaks of this bark beetle (U.S. Forest Service, 1975). At other times, however, pine engraver beetles (*Ips* spp.) have been more injurious but the *Ips* outbreaks are never as prolonged nor as devastating as those caused by the southern pine beetle.

Anderson (1948) first experimentally demonstrated that attacking *Ips pini* beetles produced an attractant that initiated a rapid colonization of the infested hosts. Since then numerous investigators have shown that this same mechanism occurs for many other species of bark beetles. Before and even after Anderson's report, many forest entomologists considered Person's (1931) theory of inner-bark fermentation a tenable explanation for the concentrating attraction (Gordon, 1938 and Miller and Keen, p. 47, 1960). Since the early 1960's, however, the greatest interest in bark beetle behavior has been concentrated on the pheromone phenomenon but this secondary attraction does not explain how the initial pioneer beetles select suitable host trees.

It has been well known from the earliest times that many species of bark beetles prefer to attack weakened or recently felled trees. This behavior of selecting and attacking hosts that are definitely physiologically weakened indicates that the pioneer beetles can differentiate the more suitable breeding medium, but it does not explain the nature of the stimulus(i) nor the efficiency of the response. It is possible that the initial host selection behavior is at least partially a random phenomenon. For example, it could be that the beetles that first find suitable trees are stimulated only after alighting or, possibly, only after boring a trial entrance.

Many foresters and entomologists have observed bark beetle attacks that were unsuccessful (Anderson, 1948; Wood and Vite, 1961). These failures suggest that the pioneer attacking beetles were not always adept in selecting suitable breeding material.

Specific conditions that have been correlated with initial host selection have been abnormal amounts of water in the innerbark (Anderson, 1948) and various odors (Buchanen, 1941; Heikkenen & Hrutfiord, 1965; Rudensky, 1966; Moeck, 1970; Werner, 1972). Vite and Wood (1961) reported that oleoresin pressure was related to whether or not the attacks of *Dendroctonus monticolae* Hopk. were successful but their data indicate that the pioneer beetles initiated attacks irrespective of the resin pressure.

Rudensky (1966), using field trapping methods, found that tree resins and certain terpenes attracted dispersing *Dendroctonus pseudotsugae* Hopk. beetles. More recently Werner (1972) found that *I. grandicollis* Eichh. beetles responded to several terpenes and that the quantity of these compounds present in the inner-bark of girdled and felled trees increased greatly. He also indicated that trapping tests were conducted in the field but did not present any quantitative data regarding the results of this part of the work.

In the study discussed here the southern pine engraver, *Ips grandicollis*, was used. Of the several reasons for this choice, the main one is that the southern pine beetle is so greatly feared that any known infestations are destroyed as soon as possible; therefore, it was unlikely that a field study using this species could be carried out satisfactorily. Several species of *Ips*, on the other hand, are always present in some numbers in southern stands of pine, and these insects are not fought as vigorously by the governmental agencies concerned with controlling forest pests.

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[1] Parts of the work reported on here were supported by grants from the Forest Service, U.S. Dept. of Agriculture and from the Southern Forest Disease and Insect Research Council. The students who did the field work included G.D. Hertel, F.P. Hain, E.W. Elliott, and J.N. All.

OBJECTIVES

The various studies undertaken dealt with several aspects of the dispersal and attack behavior of the southern pine engraver. These were (1) to determine how the pioneer beetles first reach suitable hosts, (2) to determine the efficiency of the naturally produced pheromone produced by attacking beetles in attracting other beetles; and (3) to determine what effect various meteorological factors have on the activity of the dispersing beetles.

1. Mechanism of Host Selection by Pioneer Beetles

Several experiments were used to determine how the first beetles (the pioneers) find suitable host trees or logs in which they initiate attacks. The first studies were designed to determine whether initial host selection was a random phenomenon or whether some sensory stimuli aided the beetles in locating suitable hosts before they actually landed on the logs.

One experiment consisted of exposing a large number of loblolly pine logs, *Pinus taeda* L., in areas where the beetles were known to be present. The logs were 1 foot long, and the cut ends were sealed with paraffin. These logs were then evenly distributed by placing them on the ground over a circular area of 2.33 acres. Two logs were placed at each location. The places where the logs were exposed were chosen by marking six concentric circles 30 ft. apart extending out from the center. On each of these circles the logs were spaced 30 ft. apart. With minor modifications this experiment was replicated twice in stands of pine and tested once in a stand of hardwoods. The 40-year-old pine stands were checked carefully to be sure that no trees within the experimental area were infested with *Ips* or other bark beetles.

The rationale of these experiments was that any dispersing pioneer beetles that attacked the exposed logs had to move into the area from somewhere outside. If the beetles were able to detect these logs, all of which were equally suitable to be attacked, from some distance before they alighted on them, the logs in the outer rows would be attacked sooner and more frequently than those nearer the center. On the other hand, if finding the logs was a completely random phenomenon, all the logs wherever located should be attacked as frequently and quickly.

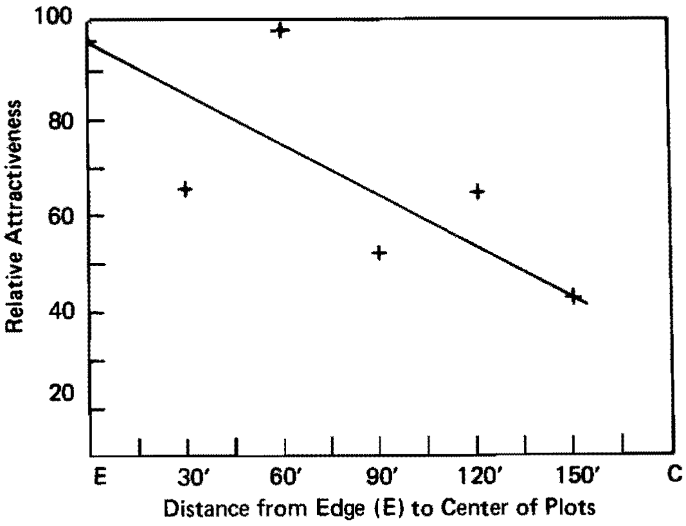

Figure 1. Relationship of the attractiveness of suitable pine logs to attacking pioneer beetles dispersing into areas where the logs were placed (r = -0.65, n = 18).

After these experiments had been established, the logs at each station were checked carefully each morning to determine whether any had been attacked. All infested logs were immediately removed and replaced with fresh logs.

Results: The results (figure 1) show that the outer three rows of logs were attacked more than two times as often as those in the inner three rows. There were 0.09 versus 0.04 attacks per day per station for the three outer rows and three inner rows respectively. In addition, the outer rows of logs also had a larger proportion attacked one or more times than did the inner rows — 68 percent versus 36 percent. These differences were highly significant. For this relationship between the number of attacks per log per day the correlation coefficient was -0.65. The number of rows of logs for the three replicates was 18; therefore, the relationship is highly significant. In this experiment there were 378 locations where the logs had been exposed to attack.

Conclusions: The results suggest that the pioneer beetles moving into the area had some ability to find suitable host material before they actually came in contact with it. If the logs had been attacked in a random manner, those at all locations, whether in the outer periphery or near the center, would have been attacked at about the same rate irrespective of where they had been placed. It is obvious, however, that if the attractiveness of the exposed logs had been extremely great, those logs placed in the outer periphery would have been attacked even more frequently than they were.

2. Kinds of Stimuli Involved in Attracting Pioneer Beetles to Suitable Host Material

It is possible that one or even two or more kinds of sensory receptors were involved in attracting the beetles to suitable host material. The most obvious of these are visual, olfactory, and tactile; therefore, these relationships were investigated in some depth.

A controlled paired experiment was used for determining the nature of each of the stimuli studied. The dispersing beetles were offered a choice of two conditions so that if one of these was more attractive than the other it would be attacked first. Logs for each pair were cut from adjacent parts of the same tree bole to eliminate any variability that might occur between different trees. Two 1-foot long pine logs were used at each location, and the cut ends were sealed with hot paraffin. The four logs for each test were then exposed in the field by placing them on the ground but separating each pair by 8 to 15 feet. Two of the logs at one of the stations were then treated in some way while the other two logs 8 to 15 feet away were the untreated controls. This experimental method was also used for many of the other experiments discussed later.

Camouflage Tests: Although it seemed unlikely that visual stimuli were involved in helping the beetles find the logs, this factor was checked first. This type of stimulus was not thought to be of much importance because the area the susceptible logs occupied was only about 1/10 of 1 percent of the total plot areas. In addition, the boles of the numerous standing pine trees also were of the same appearance and texture as the logs although the trees were vertical rather than horizontal. In a preliminary test, logs oriented in either the vertical or horizontal position were attacked with equal frequency. For the 127 pairs of logs placed in the two positions the number of attacks by pioneer beetles per log per day was exactly the same (0.004).

In one of the camouflage tests one pair of logs for each replicate was covered with old dead and decaying ground litter while the adjacent "check" logs were left exposed. The results for the 13 replicates were that the beetles attacked the covered logs as quickly as the exposed logs. The chi-square value was 54 percent. This result supported the hypothesis that visual stimulus was not very important in attracting pioneer beetles.

Other tests consisted of camouflaging the pine logs with various kinds of foliage-bearing branches including pine, red cedar, and sweetgum. In addition, the attractiveness of the natural pheromone produced by male beetles attacking pine logs was also measured to compare with the varous other treatments tested. The results of these paired tests (table 1) showed that several kinds of tree foliages exposed along with the logs were more attractive than the logs exposed alone. The most attractive of these was the pine foliage with the end-sealed logs, but logs with the ends left uncoated and various kinds of other foliage, even that of a deciduous hardwood and red cedar, attracted more pioneer beetles than did the pine logs that had the cut ends sealed. These studies suggest that odors emanating from the foliage were responsible for the attraction of the pioneer beetles.

3. Attractiveness of Various Kinds of Odors to the Dispersing Pioneer Beetles

Inasmuch as the previous experiments suggested that odors from nonhost sources such as cedar and hardwood foliage were somewhat attractive to the pioneer beetles, other types of odors were tested.

The paired type of experimental procedure described previously was used again. In this case each odoriferous material tested was applied to the bark on the top side of one set of logs of each pair while the untreated pair was used for comparison.

The chemicals tested were selected to produce various types of odors that could be classified as resinous, spicy, fruity, flowery, foul, burnt, and acidic. Table 2 lists those that were significantly more attractive to the pioneer beetles that first initiated attacks and table 3 lists those that were not significantly more attractive or even repellent. Of these, ammonia was the only one that was significantly repellent.

In one experiment several chemicals appeared to be repellent when applied in more concentrated solutions but became more attractive when diluted (table 4).

Contradictory results occurred with one of the chemicals. In two series of tests with acetone there was no increase in the attractiveness of the treated logs (table 3), but in the third test the treated logs were very attractive. Possible reasons for this difference are unknown.

Nevertheless, from the general results it appears that logs treated with a number of diverse chemicals, if used in appropriate concentrations, the odors attracted more dispersing pioneer beetles than did similar untreated logs placed nearby (table 2).

These results indicated that the pioneer beetles did not limit their response to only one specific odor emanating from suitable host material but that several different types of odors increased the attractiveness of the logs.

Table 1. Attractiveness of various materials to dispersing pioneer beetles of *Ips grandicollis*

Host material	Relative attractiveness*	Treat. logs attacked first†	Logs tested
		percent	*no.*
1. Recently attacked logs, end sealed	100	100	4
2. Pine logs, end sealed; + fresh pine foliage	30.4	100	235
3. Pine logs, cut ends, not sealed	7.0	80	191
4. Pine logs, end sealed; + dry pine foliage	5.6	67	81
5. Pine logs, ends sealed; + fresh hardwood foliage	5.6	67	72
6. Pine logs, ends sealed; + fresh cedar foliage	2.3	62	72
7. Pine logs, cut ends, sealed with wax	1.5	–	301

*Probabilities using Chi Square tests indicate that the differences between the various treatments are repeatable under the same experimental methods as follows:

No. 1 and all the other treatments, 99.9%; 2 & 3, 99.7%; 2 & 4, 90.7%; 2 & 5, 95%; 2 & 6, 95%; 2 & 7, 99.5%; 3 & 4, 50%; 3 & 5, 90%; 3 & 6, 50%; 3 & 7, 99.8%; 4 & 7, 78.6%; 5 & 7, 98%; 6 & 7, 99.5%. Paired tests of treatments were not made for treatments 4 & 5, 4 & 6, and 5 & 6.

†For each test the logs were exposed in the field simultaneously with the treated and untreated logs of each pair spaced 15 feet apart. The pairs of pine logs for each comparison were always cut from adjacent parts of the same tree boles and, unless indicated otherwise, the severed ends were sealed with paraffin.

Table 2. Loblolly pine logs treated with various chemicals that increased the attractiveness of the logs to the dispersing attacking pioneer *Ips grandicollis* beetles

Chemicals	Pairs tested	Treat. logs attacked first	Probabilities differences are significant
	number	*percent*	*percent*
d, α pinene 2% + acetone	22	91	99.5
Pinene (tech.) + acetone	20	85	99.5
β pinene 2% + acetone	22	81	99.0
Turpentine 100%	25	80	97.5
Anisole 2% + acetone	22	76	97.0
Piperonal 2% + ethanol	21	74	95.0
Amyl acetate 2% + acetone	21	71	95.0
Citral 0.5% + acetone	20	78	97.5
Carbon disulfide 100%	20	83	99.0
Acetone 100%	22	81	99.0

*The severed ends of the logs were sealed with paraffin, the logs for each test paired were cut from adjacent parts of the same tree bole, and the treated logs were separated from the untreated check logs by 15 feet.

4. Influence of Meteorological Conditions on the Dispersal of Ips Beetles

The effects of various atmospheric conditions such as temperature, humidity, air movement, light intensity, and

Table 3. **Loblolly pine logs treated with chemicals that either repelled or did not make the logs significantly more attractive to the dispersing initially attacking pioneer *Ips grandicollis* beetles***

Chemicals	Pairs tested	Treat. logs attacked first	Probabilities differences are significant
	number	*percent*	*percent*
Ammonia 20%	21	33	95
o-methoxyphenol 2% + ethanol	17	29	90
Eugenol 2% + acetone	24	37	75
Acetic acid 100%	26	37	50
Geraniol 2% + acetone	38	47	25
Ethanol 95%	21	50	0
α terpineol 1% + ethanol	20	56	50
Pyridine 33%	20	62	75
Methyl salicilate 0.1% + acetone	19	67	75

*The severed ends of the logs were sealed with paraffin, the logs for each paired test were cut from the adjacent parts of the same tree bole, and the treated logs separated from those untreated by 15 feet.

Table 4. **Relationship of initial attacks by *Ips grandicollis* to the concentrations of several chemicals applied to loblolly pine logs**

Chemical	Concentration	Treat. logs attacked heaviest	Pairs tested
	percent	*percent*	*no.*
Acetic acid	100	0	11
	50	0	10
	25	0	11
	2	27	11
	0.5	60	10
Turpentine	100	0	11
	25	0	12
	2	36	11
	0.5	50	14
	0.25	50	10
Pinene (tech.)	100	50	10
	25	67	9
	2	80	10

time of day on the dispersing beetles were also studied, and the data obtained correlated with the relative abundance of responding beetles. These dispersing beetles were those drawn to "attraction centers" consisting of cages containing logs being attacked by male *Ips* beetles. The beetles that had been attracted were removed and the number recorded during 15-minute periods from 5:30 to 8:30 P.M. E.S.T. During each of these 15-minute periods, the various atmospheric conditions were also measured.

Because this field study was conducted over a period of several summer months, the various atmospheric conditions were not uniformly interrelated, but the values often varied considerably at the same time on different days. In addition, because each of the factors measured had some influence on the numbers of beetles attracted, the values for each of the four conditions other than the specific one being evaluated were first standardized before being used for analyzing the effect of any single factor.

The data were analyzed by using programs contained in the Statistical Analysis System (SAS) (1972) and the computations were made on an IBM Computer 370-165.

Data for each of the variables studied were separated into classes with respect to the independent variables and the analysis made of the numbers of beetles attracted for each class. Because our interest was primarily to determine the general relationships of beetle activity with the different atmospheric conditions, the analysis was not extended to determine the degree of significance for the individual classes of the independent variables for each of the factors studied.

The results are presented in figures 2 through 5 and table 5. As can be seen in table 5, the only condition measured for which the number of beetles attracted was not significant was light intensity. This result was unexpected because the dispersal activity of the beetles appeared to be strongly related to time of day (figure 2) when the light conditions were changing greatly during the evening period when the observations were made.

For all the other conditions studied maximum beetle attraction always occurred in the mid-range and never at the extremely high or low conditions. This also was somewhat unexpected at least for some of the factors. For example, it was thought that high humidity might be favored by the

Table 5. **Probabilities that repeatable differences occur in the numbers of *Ips grandicollis* beetles attracted when the data were analyzed for various intensities of seven environmental factors**

Condition	F value	Degrees of freedom: Greater mean sq.	Degrees of freedom: Lesser mean sq.	Probability that differences are significant*
		no.	*no.*	*percent*
Time of evening	3.450	9	311	99.83
Light intensity	0.809	9	336	39.12
Temperature	3.696	5	340	99.68
Wind speed	3.823	5	340	99.74
Relative humidity	8.808	6	339	99.99
Saturation deficity	7.193	6	339	99.99
Rate of evaporation	3.479	6	339	99.73

*Probability that the differences between some of the means for the various classes are significant.

Table 6. **Presence of dispersing beetles of *Ips grandicollis* in several types of plant communities**

Habitat	Experiment no. #1	#2	#3	#4
	relative abundance			
Pine forest	1.00	1.00	1.00	1.00
Mixed hardwood	2.00	0.74	0.55	0.25
Opening in pine stand	1.25	0.66	0.26	–
Field away from pine stand	0.75	–	–	–

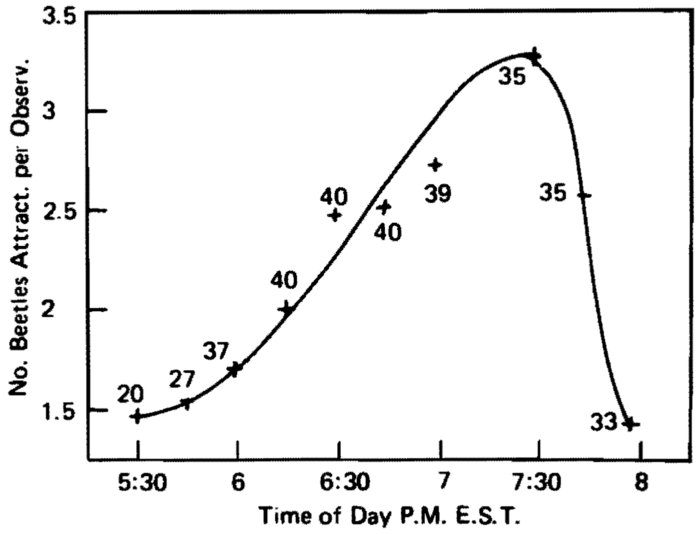

Figure 2. Abundance of responding *Ips grandicollis* beetles at various times during the evening period.

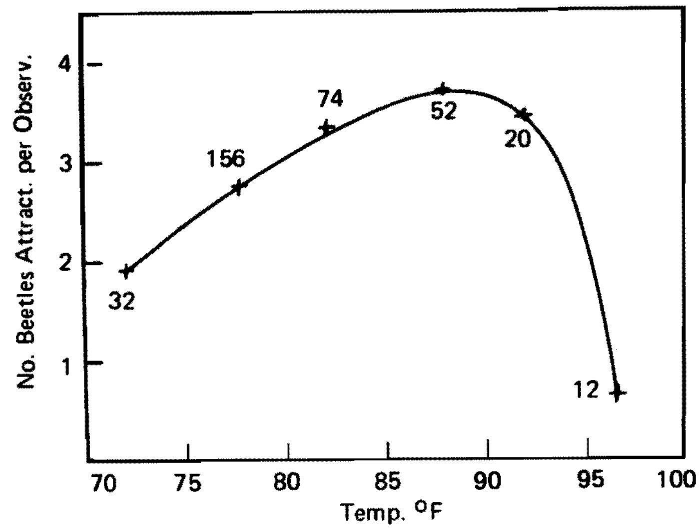

Figure 3. Abundance of responding *Ips grandicollis* beetles at various temperatures.

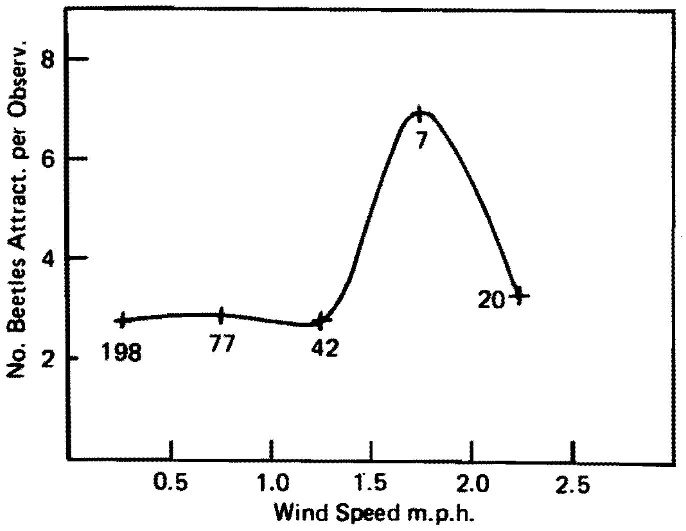

Figure 4. Abundance of responding *Ips grandicollis* beetles at various rates of air movement.

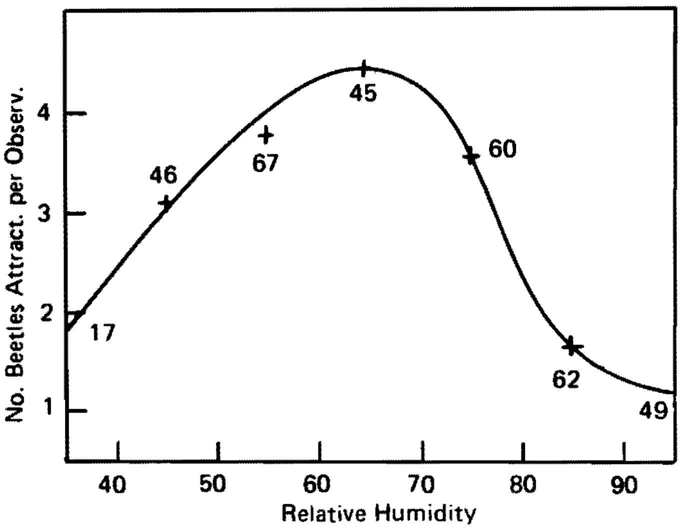

Figure 5. Abundance of responding *Ips grandicollis* beetles at various humidities.

beetles because these insects develop and live much of their lives in the moist inner-bark of the trees.

In addition to the data relating beetle activity to relative humidity (figure 5) similar analyses considering evaporation were also studied. These relationships were also significant (table 5), but because the curves were very similar to that for relative humidity, graphic presentations will not be included here.

5. Efficiency of the Aggregating Pheromone Produced by Attacking Male Beetles

The last study to be discussed here dealt with the attracting efficiency of the pheromone odors produced by the attacking male beetles combined with those of the host being attacked. To do this the relative abundance of the beetles moving to the new host trees was measured by attracting these dispersing beetles to "attraction centers" as described previously.

The dispersing beetles used in this experiment were obtained from two sources. Some were reared in pine logs in an insectary, and the others were field reared insects that were collected when they came to the "attraction centers." For identification purposes the beetles were marked by placing small spots of enamel on their pronotums before using them. The marked beetles were then released at varous distances and in different directions from the "attraction centers." Those that flew to and landed on the cages were collected, identified, and the data recorded.

Figure 6 shows that the beetles were not very strongly attracted to the combined stimuli of the naturally produced pheromone plus the host odors under the conditions studied. Beetles that had already responded by flying once to an "attraction center" returned more readily to the source of the

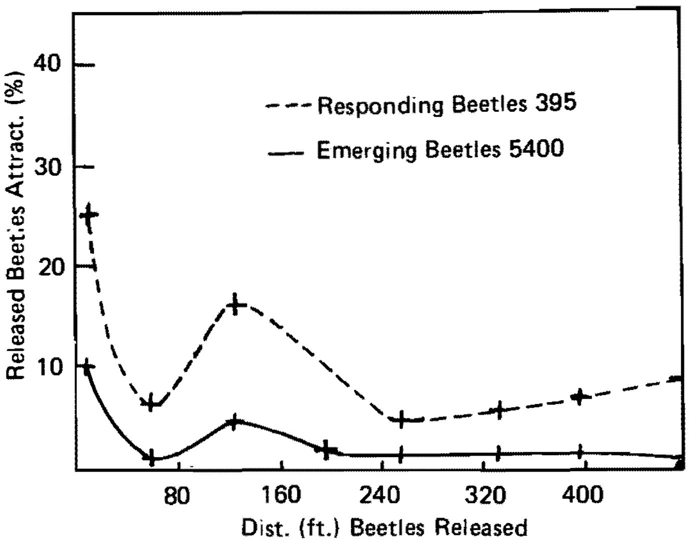

Figure 6. Efficiency of the naturally produced pheromone of *Ips grandicollis* in attracting recently emerged and field-reared beetles from various distances.

attractant than did the younger beetles that had recently emerged and had never flown previously. Nevertheless, a sizable proportion of these field-reared beetles also did not return to the "attraction centers."

The results in figure 6 are only for those beetles released downwind from the sources of the attractant. In this direction the odors should be carried to the beetles in larger quantities than if they had been located upwind or to the side from where the odors emanated. This expectation was substantiated by finding that beetles released upwind and crosswind were recovered only 14 and 37 percent respectively as often as those released downwind. Wind velocities varied from 0.8 to 2.0 mph during the times the tests were made. See also Hertel et al. (1969).

Additional evidence that dispersing beetles were not very strongly attracted by either the beetle produced pheromone or suitable host material alone was obtained by measuring the populations of dispersing beetles in areas where the host pine trees were absent and comparing these results with beetle populations within stands of pine. The results of four replications are presented in table 6. In #1, beetles attacking pine logs were used to attract the responding beetles present, but in the remaining three observations only pine logs were used to attract the dispersing pioneer beetles. For the observations made in the hardwood stands and the open areas, the presence of the pine logs and, in one case, the beetles producing the pheromone might be attracting the beetles from distant pine stands. However, the low recovery of beetles reported previously on the study of releasing marked beetles supports the contention that these attractants were not very effective even when the dispersing beetles were rather close to the sources where the odors originated.

DISCUSSION

The results of this study differ from past work in that (1) the attractants produced by susceptible host material emanated from the intact host logs and not from exposed wounds, (2) the pioneer beetles were able to detect the suitable host material from some unknown distance before alighting, and (3) the pioneer beetles responded to a number of different types of odors some of which were not the kinds that would be expected to be produced by the susceptible host pines. From these results it appears that the behavior of *Ips grandicollis* beetles in moving from the trees in which reared to fresh breeding material is a combination of a general dispersal phenomenon, probably consisting of a random type of movement, and when the flying beetles get close enough to a source of suitable attractants they respond to olfactory stimuli.

The intensity of attractiveness of the combined odors of the pheromone produced by the attacking beetles and the host odors was much stronger than the odors emanating from suitable host material by itself. Nevertheless, none of the attractants – even the pheromone – were very efficient in drawing a very large proportion of the dispersing beetles present in the immediate vicinity of the attractants.

From these findings it appears that emerging southern pine engraver beetles either had the inherent behavior to first disperse and/or their sensory receptors were not sufficiently sensitive to detect any of the attracting odors from any appreciable distance.

This general type of behavior probably is advantageous for the beetle populations as a whole, because it would help prevent the excessive concentration of the insects in localized areas where the odors were strongest. If they did concentrate excessively and then some unfavorable conditions occurred, a large proportion of the beetle population in the area might be destroyed. Wider, less concentrated distributions of the beetles might insure better overall success of the species.

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Some Studies on Side Effects of Pesticides Used in Agricultural and Forest Pest Protection Situations

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ABSTRACT

In attempting to ascertain the consequences of persistent pesticides on nontarget soil arthropods, literature reports of induced resistance suggested both laboratory and field experiments. As a consequence, it was possible to document high levels of resistance to DDT in the Collembolan, *Folsomia candida*, and in *Caloglyphus krameri*, a mite. In the case of *Folsomia*, metabolites were described as well as effects of DDT ingestion on longevity, mortality, instar duration, egg production, and egg viability. The ability of *Folsomia* to serve as biological carriers of DDT resulted in field experiments in which they provided a source of contamination for food chain studies. DDT degradation pathways in a variety of litter arthropods is described.

INTRODUCTION

As my contribution to the Hodson recognition lectures I have chosen to deal with subject matter that evolved because of the nature of responsibilities I assumed subsequent to leaving Minnesota. In Minnesota my research commitments, and indeed my early employment elsewhere, focused on forest insect problems. Fortunately, Dr. Hodson's philosophy of graduate training did not require a student to confine himself to a particular problem area. He did engender in me an ecological mind set that has since conditioned my approach to problem solving, but I never felt constrained to limit myself to forest protection research. Fortunately we did not have such constraints built into our research training, because no one at that time could anticipate that our investigative priorities would shift so dramatically from production forestry and agriculture to an equally important one of evaluating the practices that we recommended. In my case, an early assignment was finding ways to protect conifers from such pests as the European Pine Shoot Moth, Zimmerman Pine Moth, Pine Rootcollar Weevil and Spruce Gall Aphid.

Approximately 10 years ago, concerns about pesticide side effects forced us to seek alternatives to accepted control practices or at least to prove that our former recommendations were compatible with the newly articulated environmental ethic. Much of what we did 10 years ago had to be rethought, a good deal of it abandoned or modified, and substitute approaches had to be developed. Ecologists, who before 1965 had not yet achieved scientific respectability in the minds of those who routinely subjected their hypotheses to controlled experimentation, had to monitor the consequences of agricultural, industrial, and even wildlife management practices. Credible impact statements had to be devised, virtually without precedent. If it were needed, one could find in these experiences compelling justification for graduate training that equips a student with sound training in fundamentals as opposed to "problem solving" expertise. It conditions my attitude toward the education of the graduate students we now train.

The work that I shall describe evolved from the following beginnings. Asked to monitor the effects of Japanese Beetle and Cereal Leaf Beetle eradication efforts, we found ourselves without accepted techniques. New questions presented themselves, for which satisfactory answers had to be found through specific and often very basic investigations. A few of these will be dealt with here, some with an obligatory focus on arthropod biology; others with equally essential analytical techniques, most of which were previously alien to an ecologically oriented research expertise. Questions relating to the specificity of pesticide action, pesticide persistence, and food chain magnification had to be addressed if credible answers were to be published. Although traditional survey techniques proved useful in documenting catastrophic numerical abundance declines, these usually focused on major taxa. More subtle ecosystem perturbations are seldom identified by such techniques, because the labor involved in identifying to a species level for more than a few selected groups is too formidable. Only two aspects of the work that was carried out to answer these questions will be summarized here. These include laboratory studies on pesticide resistance in easily reared species and litter food chain transfer studies.

PESTICIDE DEGRADATION AND FOOD CHAIN TRANSFER

Laboratory studies

Published results of studies on the consequences of pesticide applications to nontarget organisms suggest that beneficial soil fauna should not be ignored in assessing environmental impact of pesticide usage. Our curiosity about soil detritus feeders, while not unique, represents one of only a few American efforts to illuminate the taxonomy and biology of soil and litter arthropods other than those known to feed on crop plants. Studies on the taxonomy and biology of soil Collembola and oribatid mites provide a point of departure (Snider, R.J., et al., 1969; Snider, R.J., 1967; Snider, R.M., 1973; Snider, R.M., and Butcher, J.W., 1973). The work of Edwards and Jeffs, 1964; Karg, 1965 and 1967; and Scopes and Lichtenstein, 1967, among others, describe differential response of soil arthropod fauna to chlorinated hydrocarbon insecticides. These studies establish the susceptibility of mite predators as a partial explanation of post spray increases of certain Collembola species and also provide direct evidence that *Folsomia fimetaria (candida)* was quite resistant to DDT. The extent of this resistance was readily demonstrated through laboratory experiments in which inoculum of *Pencillium frequentans* Westing and *Verticillium albo-atrium* Reinke and Berthold were placed on PDA agar to which acetone dissolved pp' DDT was added at the rates of 10 to 20 ppm in the final solution. After vaporizing the acetone, collembola were added and permitted to feed on the mycelium. At intervals of 8, 26, and 69 days after collembola were introduced, 50 mg live weight of these insects were removed and macerated in hexane. After the solids had sedimented, the clear supernatant liquid was decanted and injected without cleanup into a GLC colum (Butcher et al., 1969). Levels of DDE found in the supernatant increased with time, and detectable levels were noted within 24 hours after collembola began feeding. Within 38 days DDE had increased to a figure exceeding 30 percent of the DDT present. These and subsequent experiments established clearly that DDT ingested by *Folsomia* was metabolized rather spectacularly to DDE.

In a second set of experiments (Aucamp and Butcher, 1971), a mite, *Caloglyphus krameri* (Berlese), also made this conversion. More interesting, however, was the discovery that only a trace of DDE (0.01 ppm) could be found in macerated *Rhizoglyphus robini* after 24 hours exposure to yeast treated with 1000 ppm DDT, although levels of DDE in similarly fed *C. Krameri* approached 30 ppm. To what extent these differences can be accounted for by physiological processes, as contrasted with prior exposure induced resistance, is unknown. It is apparent, however, that dissimilarities do exist, and these may be significant in soil arthropod species complex changes and, ultimately, altered soil fertility and humification processes.

In part because the preoccupations of our group were in a different research area, these possible consequences were not studied in field situations. Instead it was decided to investigate the remarkable tolerance of *F. candida* to DDT and attempt to ascertain to what extent massive dosages of the insecticide affected longevity and mortality, instar duration, egg production, and egg viability (Butcher and Snider, 1975). Figure 1 (reproduced from the 1975 paper) illustrates the survival time in days of isolated *Folosomia* individuals that were fed on brewers yeast contaminated with pp' DDT (all individuals were introduced into rearing vials as first instar juveniles and incubated at 15°C, 21°C, or 26°C). Clearly the addition of DDT did not significantly alter the temperature effects on longevity or survival. These studies did confirm earlier observations that duration of stadia increased as temperature decreased and as the insect aged. Statistically significant lessening of instar duration could be correlated with DDT concentration at 15°C, but not at the 21°C and 26°C temperatures. Egg production studies earlier had shown that lower temperatures induce increased egg production and that higher temperatures produced erratic egg laying patterns. Average fecundity per instar in the DDT feeding studies proved to be higher in DDT-fed individuals as compared with the controls, and the same was true of the mean number of eggs laid per lifetime. Hatching success of DDT-fed individuals was similar to that observed in the controls. These studies demonstrate conclusively that *Folsomia candida* is not affected adversely by massive dosages of DDT.

Individuals reared at 26°C were all fed upon brewers yeast contaminated at the rate of 150,000 ppm DDT. The 21°C and 15°C data are survival days for animals fed at the rate of 100 ppm, 10,000 ppm, 100,000 ppm, and 150,000 ppm (average survival time for all individuals). Progressively higher DDT concentrations did not materially change the survival pattern, and the time required to reach a particular percentage mortality varied little between the four DDT series.

LITTER FOOD CHAIN STUDIES

It was decided that the resistance phenomenon might be employed to identify food relationships by setting up litter arthropods studies, and a possible byproduct might yield information establishing DDT metabolism for those arthropods that had not or could not be studied in the laboratory. By loading *Folsomia* with DDT and then releasing them in a circumscribed forest litter universe, it was hoped that at least some links in the food chain could be detected. It was thought that, by introducing the compound through the medium of an insect likely to be fed upon by other arthropods, it would be possible to exclude the possibility that the insecticide would kill anything except the predators that ingested the carrier.

Accordingly for each study 15-20 g of Collembola that had been loaded with (a) technical grade DDT (principally 65-73 percent pp' DDT and 19-20 percent op' DDT), (b) op'

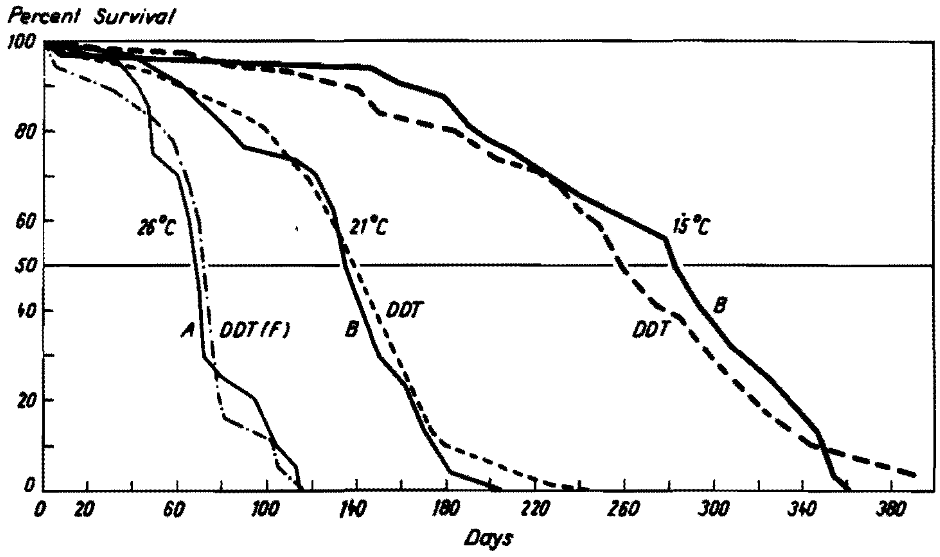

Figure 1. Survival of DDT-fed and control individuals of *Folsomia candida* at three temperatures. Data for Series A, 26° C, from Snider and Butcher (1973).

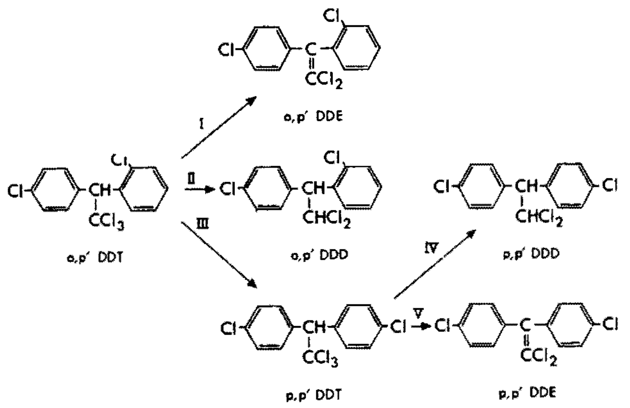

Figure 2. Major routes of DDT metabolism in a forest litter arthropod food chain from Klee et al. (1973).

DDT, (c) pp' DDT, and (d) pp' DDE at the rates of 1000 ppm of each compound were released in separate 5 x 5 M^2 plots established in a central Michigan beech maple forest floor site. Each plot was fenced by a 45 cm high window screen frame. Collembola loaded with only one of the above compounds were released in one of two such plots on each occasion. An equivalent quantity of untreated Collembola was released in the second or 'control' plot in each instance.

Over a sequence of six collection periods macro- and micro-arthropods were collected and identified to a taxonomic level that provided sufficient biomass for insecticide analysis in each instance. Detection of metabolites was done by means of GLC (Klee et al., 1973).

Ten major groups of cryptozoan macro fauna were catalogued in the forest plots under study (Manley, 1971). These included Araneae, Chilopods, Coleoptera, Diplopods, Diptera, Hymenoptera, Lepidoptera (larvae), Orthoptera, Pulmonata, and Oligochaeta. The first three taxa comprised the majority of litter food chain predators, with Araneae the most important. The two predominant micro-arthropod groups found were collembola and oribatid mites.

Results of samplings and analysis over a 50-day period elucidated the major routes of DDT metabolism shown in figure 2 (Klee et al., 1973).

Although it cannot be detailed here, the works of Klee et al. (1973) and Manley (1971) describe metabolic breakdown pathways for each of the taxonomic groups that could be analyzed by the methods available.

What is reported here are several examples of research that derived from concerns generated by the consequences of previously accepted agricultural and forest protection practices. If it were not necessary to respond to new concerns generated by new problems, it would be profitable to explore these in more depth. Currently, the experience gained is being applied to fresh problem situations. Two of the programs now being investigated at MSU involve the effects of waste water irrigation on beneficial soil fauna in crop and forest litter situations and on the movement and degradation of short-lived pesticides in terrestrial and aquatic environments. In the first instance information should emerge on the ultimate importance of detritus feeders to soil fertility, and in the second it is hoped that a model can be described that will enable us to systematically analyze the side effects of pesticide applications.

In whatever degree I am personally able to provide answers to these questions, a large share of the credit belongs to Dr. Hodson for his enlightened approach to research training. His mature counsel and philosophy of graduate instruction is reflected in the achievements of each of those who were privileged to be associated with him.

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Quantitative Analysis and Mathematical Model of Horizontal Orientation of Midges, Anarete pritchardi Kim, in a swarm (Diptera: Cecidomyiidae)

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ABSTRACT

The early observations on the swarming of species of *Anarete* included its relation to (1) the direction and intensity of light, (2) air temperature and day hour, (3) movement and mating of individual midges within the swarm, and (4) reproductive isolation and speciation. Early kinematical analyses dealt with characteristics such as the mean, variance, standard deviation, skewness, and kurtosis of the insect coordinates; insect number-density distribution in space, frequency distribution of insect velocity; velocity autocorrelation coefficients; effective advective velocity and diffusivity for swarming.

Recent observations dealt with the horizontal orientation of midges. From photographs taken at 1/1000 sec exposure, the distribution of frequency of individuals heading in different angles with the sun was determined. The results suggested that the midges yawed from 30° right of the sun to 30° left of the sun, or between alignment of the front of the two compound eyes with the sun. Mathematical analyses suggested that the oscillation is around the equilibrium body axis in a simple harmonic, or pendulum, fashion with some damping, superimposed by a random motion.

EARLY OBSERVATIONS AND ANALYSES ON THE SWARMING OF THE SPECIES

One noon in the summer of 1958 while working in a cornfield on the University of Minnesota Agricultural Experiment Station at Waseca, Minnesota, one of us (Chiang) noticed a discarded Winston cigarette pack at the edge of the field and some shadowy movement 4-5 cm above the white area of the pack. Upon closer examination, it became clear that these shadows were small dipterous insects (2 mm long) displaying a swarming movement. The swarm followed the white area when the pack was moved. Due to pressure for other work, no further observations were made but specimens were collected for identification. That winter, the insect was identified by Dr. E.F. Cook of the University of Minnesota as *Anarete*, possibly an undescribed species.

We knew that if the species were new, observatons on its biology should be significant. Literature was searched and little was found on the behavior of diurnal swarming of insects. In the summer of 1959, systematic observations were made on the same species using a white board as a swarm marker. Observations were made also with markers of different colors. Another species of midge that swarms 40-50 cm above a dark marker was collected. Both types were sent to Dr. E.A. Pritchard of University of California for identification. Both were identified as *A. johnsoni*. Dr. Pritchard then was informed of the difference in their swarming behavior, one at 4-5 cm above a white marker and the other 40-50 cm above a dark marker. Upon reexamination of the specimens, he indicated that the high swarming form is *A. johnsoni*, but the low swarming form is undescribed. The latter confirmed Dr. Cook's assessment. This incidence illustrates vividly the importance of ecological data to systematicists. As Dr. Pritchard could not find the time to describe the new species, he suggested that the interim name of *A.* near *felti* be used. This name was used in publications until Dr. K.C. Kim named it *A. pritchardi* in 1968 (Kim, 1968) honoring the contribution to Cecidomyiidae by Dr. Pritchard who was then deceased. From 1959 to 1968, quantitative observations were made of *A. pritchardi* swarming in relation to the direction and intensity of light (Chiang, 1961, 1965) to air temperature and day hour (Chiang and Stenroos, 1963) and to movement (Chiang, 1968) and mating (Chiang, 1962) of individual midges within the swarm. In addition, comparative studies of swarming of several other *Anarete* species were made (Chiang, 1963).

The development of the studies was quite by accident. Chiang had worked in the very field and nearby ones for 10 summers, yet never noted the insect until a particular kind of cigarette pack was there at near noon on a sunny day. As discovered later, the species swarms mainly near noon on warm sunny days and over a white surface. There is a threshold size of the marker to induce swarming, and this size increases with lowered light. The size of the white area of the cigarette package happened to be about the minimal size and effective only under maximal lighting.

Because of its small size and unique habit, this insect never came to the attention of systematicists. This contention is supported by the fact that Dr. Pritchard worked on the taxonomy of a group of Cecidomyiid in Minnesota for his Ph.D. and collected extensively in the state (Pritchard, 1942). Even if collected without knowledge on its swarming behavior, the specimens probably would have been identified as a known species. Dr. Kim, always thorough in approach, revised all North American species of the genus *Anarete* when he described the new species. The information gathered helped in developing a comparison of morphology and swarming behavior of four closely related *Anarete* species (Chiang, 1971). This comparative study produced the conclusion that differences in responses to swarm markers resulted in a reproductive isolation mechanism and enhanced speciation. This comparative study would not have been possible had it not been for the thoroughness in Dr. Kim's approach.

Equally unexpected results evolved from a photographic study of wing beat of midges in a swarm. Enlarged photo-

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[1] Contribution no. 168 from the Marine Sciences Research Center, State University of New York, Stony Brook, New York.

graphs brought out details of body movement. Significant interpretations were made on the different kinds of vertical movement and speed of horizontal movement. That report caught the attention of Okubo who was interested in dispersal of small organisms as a physical phenomenon (Okubo, 1972).

In 1964 and 1966, movie films were taken with the objective of determining how long a midge stays in a swarm. The film speed proved to be too slow to follow the individuals from one frame to the next. The project was thus discontinued.

During the AIBS meetings in Minneapolis in 1972, Okubo visited Chiang. During the visit, the films were mentioned. Okubo saw the possibility of studying the kinematics of the midge swarming by analyzing the movie film. He took the film which had been gathering dust for 6-8 years in Chiang's office. Though with some difficulty, midges in several segments were tracked and analyzed. A number of statistical characteristics of swarming individuals were calculated, including the mean, variance, standard deviation, skewness, and kurtosis of the insect coordinates; insect number-density distribution in space, frequency distribution of insect velocities; velocity autocorrelation coefficients; effective advective velocity and diffusivity for swarming (Okubo and Chiang, 1974). The results are enlightening not only in the mathematical and physical aspects of swarming, but also in the biological interpretations. The same basic data have been analyzed for the acceleration and force fields of each midge in the swarm (Okubo, Chiang, and Ebbesmeyer, 1976).

RENEWED INTEREST IN PHOTOGRAPHIC STUDIES

Our association renewed the interest in photographic studies of motions of midges in a swarm. To determine the camera speed that will freeze the motion of the midges, photographs of swarms were taken with a range of shutter speeds. At 1/1000 sec the motion was frozen, and the resolution was so good that the body orientation of all individuals can be determined. Analysis of the photographs enabled us to speculate on the mechanism of orientation of midges in a swarm. We must consider the study a surprise because we had no idea what the photographs may show when they were taken. Because the data are presented here for the first time, some technical details will be given.

On August 7, 1973, at the edge of a cornfield on the University of Minnesota Agricultural Experiment Station at Rosemount, Minnesota, a swarm was induced over a large rectangular white marker that was placed with its front edge perpendicular to the incidence of the sun's rays. A camera was set up facing down toward the midges against the white marker as a background. The front edge of the marker that was toward the sun was on top of the photograph.

The enlargement of photographs taken with 1/1000 sec exposure showed midges in frozen motion and sharp focus. There were 119 images, indicating a very large swarm. Of these the body orientation of 115 can be determined. Four others were flying directly toward (or away from) the lens, and their images were simply dots. In analyzing the orientation of the midges, the direction of the sun was designated as 0°, and the angle of the orientation of each midge right or left of the sun was determined. The numbers of midges in different orientations were then plotted (figure 1 A). The midges predominantly headed toward the general direction of the sun, and in decreasing numbers faced greater angles from the sun. Midges swarm over the edge of the marker nearest to the sun, and it has been suspected that to maintain this orientation the midges probably face the sun while swarming. The present photographs and analysis provide a definite answer.

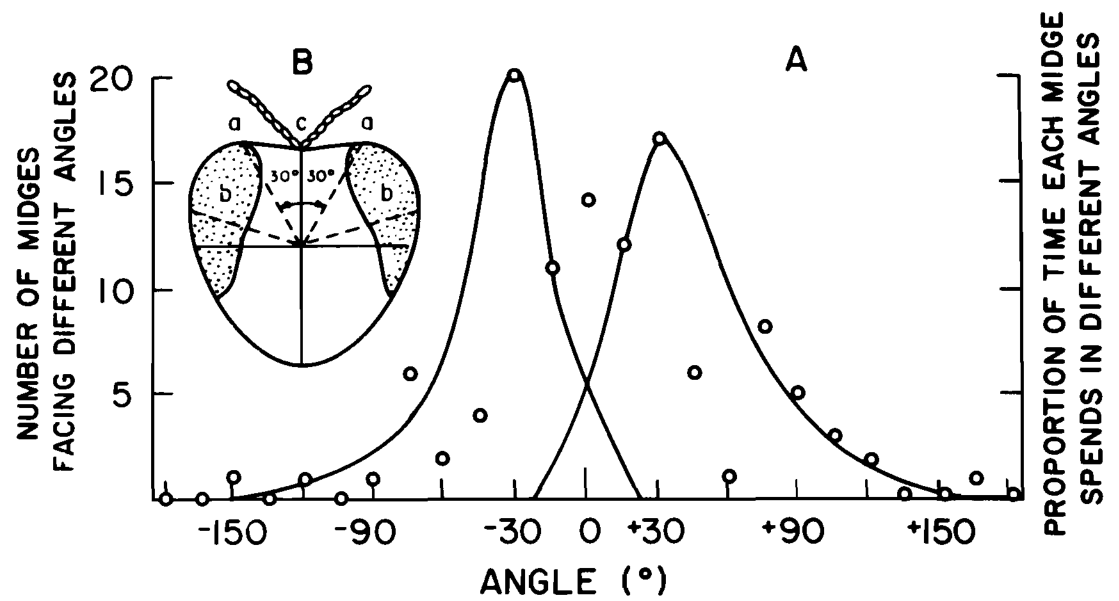

Figure 1A. The distribution of number of midges at different angles to the sun and the distribution of percent of time a given midge spent at different angles to the sun, showing two peaks at 30° right and 30° left of the sun.

Figure 1B. The top view of the head of a midge, showing the front (a) of compound eyes (b) which form 30° angle with the front of head (c).

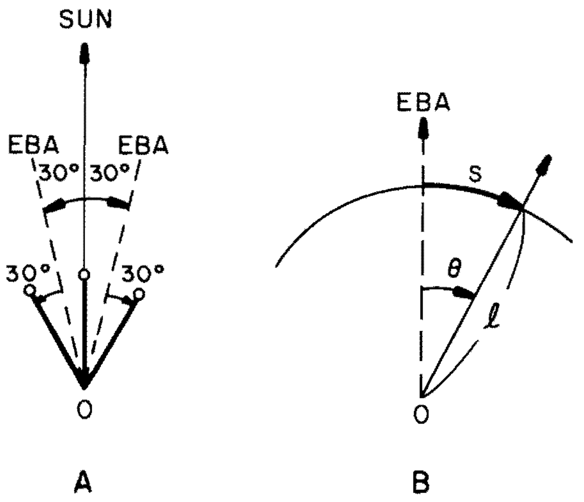

Figure 2 A. Idealized model of the "equilibrium body axes" (EBA) with respect to the direction of the sun.

Figure 2 B. Mathematical model for the yawing of midge.

The frequency suggests a bimodal distribution. The special significance of this pattern follows. This frequency distribution of individuals, if it were typical for the species, can also be interpreted as the percent of time a given midge spends in the different angles to the sun. The two modes corresponded to 30° right and 30° left of the sun. If a midge yaws right and left of the direction of the sun, the speed of movement will decrease as the midge reverses its orientation. This would result in a bimodal distribution as described.

To see if this yawing is related to the visual perception of the insect, photographs of the head with the configuration of the compound eyes were taken. The front edge of the compound eye is ca 30° from the front center of the head (figure 1 B). This suggests that the amplitude of the yaw was between the points of alignment of the two eyes with the sun. These facts describe the behavioral mechanism with which the midge maintains its general orientation to the sun. This is similar to the orientation of insects moving toward a point stimulus.

As indicated earlier, the frequency of distribution of individuals is also the distribution of percent of time a given midge spent at different angles to the sun. The distribution shows that a midge could find itself heading directly away from the sun but only very briefly. This could mean that a midge, once yawed beyond 90° from the sun, would turn completely about very quickly. This is consistent with the early observation (Chiang, 1968) that midge made a complete turnabout in 1/50 sec and without a measurable reduction in the speed of movement. Another possibility is that the midges fly sideways and backwards while maintaining the orientation toward the sun.[2]

MATHEMATICAL MODEL FOR THE ORIENTATION

Because the above explanation makes sense in the biology of the insect, we became interested in developing a mathematical model.

Consider two positions of the body axis each being 30° right or left of the sun, as with the "equilibrium" position of yawing (figure 2 A). An angular deviation of the body axis from each position produces the motion of yawing referred to as the equilibrium position (figure 2 B).

Assume that the oscillation around the equilibrium body axis is simple harmonic (or pendulum) type with some damping, superimposed by a random motion. The equation of motion for the arc length, s, is expressed by:

$$\frac{d^2s}{dt^2} + \beta\frac{ds}{dt} + \omega^2 s = A(t) \qquad (1)$$

where t = time, β = frictional coefficient, ω = frequency, A(t) = random forcing function.

Let $P(s, t; s_o)$ be the probability density function of the displacement s at t $[s_o = s(t{=}o)]$.

The function P is assumed to obey the following Fokker-Planck equation (Wang and Uhlenbeck, 1945):

$$\frac{\partial P}{\partial t} = -\frac{\partial}{\partial s}(m_1 P) + ½\frac{\partial^2}{\partial s^2}(m_2 P) \qquad (2)$$

where

$$m_1 = \lim_{\Delta t \to o} \frac{1}{\Delta t} \int_{-\infty}^{\infty} (y-s)\, P\,(y,\Delta t;s)dy \qquad (3)$$

$$m_2 = \lim_{\Delta t \to o} \frac{1}{\Delta t} \int_{-\infty}^{\infty} (y-s)^2\, P\,(y,\Delta t;s)dy \qquad (4)$$

For our purpose it may be relevant to consider only a steady-state distribution, P(s). From (2) we have:

$$O = -\frac{d}{ds}(m_1 P) + ½\frac{d^2}{ds^2}(m_2 P) \qquad (5)$$

When t is large compared with β^{-1}, equation (1) is reduced to:

$$\frac{ds}{dt} + \beta^{-1}\omega^2 s = \beta^{-1} A(t) \qquad (6)$$

This assumption is consistent with the fact that we are concerned with the steady-state.

The two moments m_1 and m_2 can easily be calculated from (6). Thus we obtain:

$$m_1 = \lim_{\Delta t \to o} \frac{\overline{\Delta s}}{\Delta t} = -\beta^{-1}\omega^2 s \qquad (7)$$

$$m^2 = \lim_{\Delta t \to o} \frac{\overline{\Delta s^2}}{\Delta t} = 2\beta^{-2}\lambda^2 \qquad (8)$$

where the random function is assumed to be a "white noise" with zero average, so that:

$$\overline{A} = o$$

$$\overline{A(t)A(t+\tau)} = 2\lambda^2\,\delta\,(\tau)$$

$\delta(\tau)$ being a Dirac function and λ being constant.

Substituting (7) and (8) into (5) and integrating twice with respect to s subject to dP/ds=o, $P = P_o$ at s = o, we obtain:

$$P(s) = P_o \exp\left(-\frac{\omega^2\beta}{2\lambda^2}s^2\right) = P_o \exp\left(-\frac{s^2}{2\sigma^2}\right) \qquad (9)$$

where $\sigma^2 \equiv \lambda^2/\omega^2\beta$. Since $\int_{-\infty}^{\infty} P(s)ds = 1$,

$$P_o = (2\pi)^{-½}\,\sigma^{-1} \qquad (10)$$

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[2] This possibility was verified in movie films taken at 100 fps in the summer of 1976 as part of research under NSF Grant BNS75-23059, "Ecology and Kinematics of Swarm Maintenance" to the University of Minnesota and the State University of New York, Stony Brook.

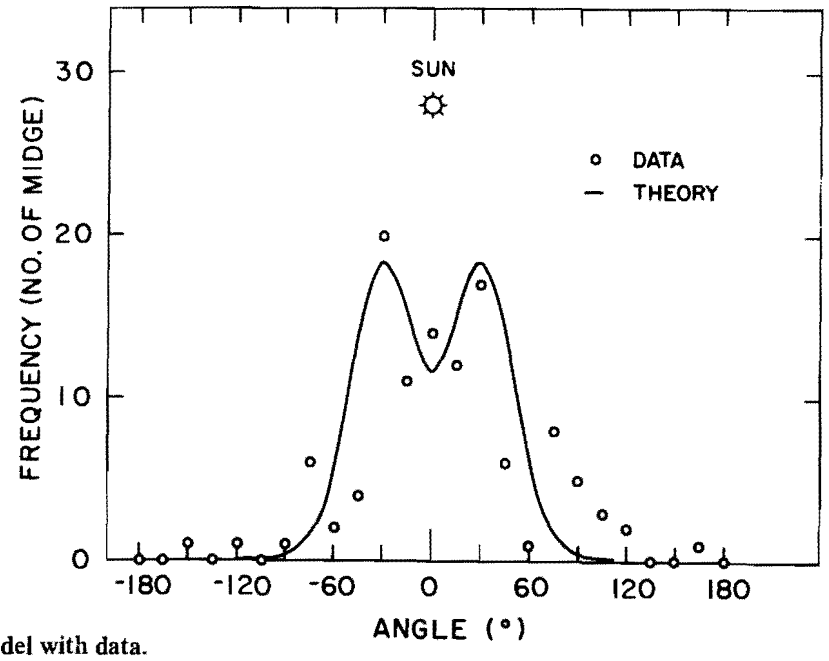

Figure 3. Comparison of the mathematical model with data.

Equation (9) is rewritten in terms of the angular density function $P(\theta) = P(s)\, ds/d\theta$:

$$P(\theta) = (2\pi)^{-1/2}\, \ell\sigma^{-1} \exp\left(-\,\theta^2/2\,(\sigma/\ell)^2\right) \tag{11}$$

Note that $s = \theta\ell$, θ = angle, ℓ = length between O and C.

Because there are two equilibrium positions in the model, we add two density functions, each around one equilibrium position. Thus, if ϕ denotes the angle deviated from the direction of the sun, the probability density function for the body axis orientation, $P(\phi)$, reads:

$$P(\phi) = 2^{-1}\,(2\pi)^{-1/2}\,\ell\sigma^{-1}\left[\text{expi}\left\{-(\phi-\pi/6)^2/2(\sigma/\ell)^2\right\} + \exp\left\{-(\phi+\pi/6)^2/2(\sigma/\ell)^2\right\}\right] \tag{12}$$

For the comparison of (12) with data, we will use the frequency distribution, i.e. the number of midges, against ϕ.

Figure 3 shows the comparison of the theoretical frequency with the data. In the figure we take $\sigma/\ell = \pi/9 = 20^\circ$.

The theory fits reasonably well with the data, although the theoretical curve appears to taper faster than the data towards the larger angles where the frequencies are smaller. If the fit were improved by increasing the equilibrium from 30 to a greater angle, the modification would suggest that the alignment is not at the front edge but at a point closer to the center of the eye. Of course, to bring about this type of refinement in the biological explanation is a unique capability of mathematical modeling. Unfortunately in the present case, if the angle is increased, though tapering will better fit the data, the peaks would be off the actual data. Thus, we explain the discrepancy on the basis of sampling error, until new facts become known.

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Stored Product Insects and Microorganisms in Grain Ecosystems

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ABSTRACT

The need for stored grain scientists to integrate efforts in developing a multidisciplinary approach to reduce food losses, especially for people suffering from food shortages, is evident. Maximum effort has been directed to increase agricultural production. It is time to consider saving what has been harvested from deterioration. Most efforts to date have not been entirely satisfactory.

The most important organism in stored grain is the grain itself. Many other micro- and macro-organisms also interact with the grain at various storage stages. All interact with several chemical and physical characteristics of a grain mass. Some interactions may even begin in the field before harvest.

Because the deterioration of grain results from ecological relationships among several biotic and abiotic variables, it can be fully understood only by adapting a multidisciplinary approach. Collecting information from stored grain scientists on the many single facets of the problem is also mandatory in devising an effective pest management program.

Many of us have been involved in international assignments during which we have seen the stress of people suffering from food shortages. World leaders demand that one of the goals for the next 10 years must be to remove the great affliction of starvation from every man, woman, and child. Dollars alone, at least in developing countries, are not going to solve the problem. I feel, as do many others, that we should devote and integrate our efforts to help developing nations increase their own capabilities for food production and conservation. Maybe the initiation of a world food system is the answer.

Consequently, we need to compile all the ecological knowledge on stored food and their pests that is not limited to national boundaries. This knowledge could form the basis for an international strategy for the solution of stored food problems (Sinha, 1973b). In other words, stored food scientists from all over the world need to adapt a multidisciplinary approach.

I believe that we should have started this type of approach years ago; however, it was only in October 1974 that we took the initial steps toward this goal at the first International Working Conference on Stored Product Entomology held at Savannah, Georgia (anonymous, 1974). The conference objective was to provide a forum on current research and future needs. The program consisted of more than 50 symposia and panel presentations with the participation of 214 agricultural scientists, marketing specialists, and agricultural administrators from 27 nations.

Among the accomplishments was the organization of a permanent committee for arranging future conferences on stored product entomology. The following resolution was adopted by all participants:

> "This conference, being cognizant of the urgent need for action to provide and preserve a food supply to all mankind, confirms the great importance of losses during storage and transportation — representing wastage of human endeavor, natural resources and energy which could be greatly reduced by implementation of methods currently known in our applied science."

It was also decided that (1) the above resolution would be presented to leaders of nations who are interested in world food problems and (2) future contact would be maintained among the conference participants to establish a working framework for holding future international stored product conferences.

There are not many stored-product entomologists in this world nor are there many institutions for producing researchers with a wide knowledge of stored-product entomology.

Man, however, has been storing grains and their products since he began to cultivate plants and raise domesticated animals. Considerable effort has been directed toward increasing agricultural production through efficient cultivation of marginal land, improved varieties, and high yielding crop husbandry. Unfortunately, only recently has it been recognized that it is common sense to emphasize saving from deterioration what has been harvested.

Man is deprived of the fruits of his investments through both money and labor in agriculture because of the loss of stored produce. Although modern man has used various measures (such as grain drying, use of pesticides, etc.) to reduce agricultural losses, most have been stop-gap measures. Satisfactory control of organisms in stored grain is seldom achieved. However, preventing the waste of agricultural produce during handling, storage, and transportation can be achieved in part by putting into practice what is already technically known about storage and conservation of grain (Bailey, 1974; Hyde and Burrell, 1973).

In grain storage, the most important organism is the grain itself. Although stored grain appears dormant, it has all the properties of a living organism. Many other organisms, from microorganisms to small mammals, also interact with the grain at various stages of storage. All interact with many chemical and physical variables, such as temperature, moisture, and storage structure. In fact, interactions may begin in the field before the grain is even harvested.

To understand the ecology of storage, one should consider a grain bulk as an ecological system or ecosystem in which the abiotic physical-chemical environment and the biotic assemblage of flora and fauna interact (Wallace, 1973). The major biotic variables, other than the grain, in a grain bulk include microorganisms, such as fungi, actinomycetes, and bacteria; arthropods, such as insects and mites; and vertebrates, such as rodents and birds. These pests rarely act alone; their ecological associations develop, in time, with the grain and with other organisms.

Because spoilage of grain results from ecological relationships among several biotic and abiotic variables over a period of time, it can be understood and prevented only by adapting a multidisciplinary approach. Unfortunately, it has not often been the practice among scientists, economists, and grain management personnel to work in multidisciplinary teams. Stored-grain scientists do not usually study the whole ecosystem, share data immediately and effectively, or make a proper synthesis of the interaction of variables before making their individual management decisions. Gathering information on as many single facets of the problem as possible is very important for the most accurate final synthesis of the data (Sinha, 1973a).

Grain deterioration usually is measured by weight losses; chemical changes in protein, carbohydrates, and oils; and contamination by chemicals and biological toxins (Hall, 1970). This deterioration occurs at different stages in the marketing channel. Once contamination of grain takes place, it becomes a part of the grain mass. To try to completely remove it is an impossible task. For instance, once the grain is infested by insects it can never be thoroughly cleaned during the flour making process. In addition to total insects, insect fragments, and excrement, there is also a threat to the public health (Gorham, 1975) from potentially dangerous contamination by bacteria and molds, yeast, protozoa, viruses, and their metabolic byproducts. The importance of all these to the cereal grain industry is well documentated (anonymous, 1968). New facts of importance, such as the true significance of the protozoa and viruses to the cereal industry, are being discovered.

Most of the bacteriological studies of grains such as wheat and corn were made during the first four decades of this century. Renewed interest in the bacteriology of these grains in recent years has come mainly from an expanding market for flour in refrigerated and frozen foods. Because flour is a major raw ingredient in many of these non-sterile foods, an evaluation of the number and kinds of microorganisms is important to the milling and refrigerated food industry. In fact, processors are beginning to request that the miller guarantee the suitability of his flours with a maximum bacterial count of 5,000 per gram. In some cases counts are being specified as 14,000 per gram for use in canned biscuits, 10,000 per gram for frozen fruit pies, and 5,000 per gram for TV dinners and frozen meat pies (Doty, 1961).

Bacteria that are important to the cereal industry cause infectious diseases and food poisoning; for example, *Salmonella* spp. inhabit the intestinal tract of man and animals. More than 1,200 serotypes are known, and all are considered pathogenic. This bacterium induces gastrointestinal disorders ranging from discomfort to death (Kelterborn, 1967). Birds, rodents, and insects may contaminate the grain in the field with Salmonella or other pathogenic bacteria. The use of machinery containing bird droppings or rodent pellets may contaminate the grain before loading vehicles for shipment. Cattle trucks often are used during harvesting periods. These trucks may have hauled hogs or cattle the day before with little effective sanitation before reloading with grain. The country elevators or transporting vehicles may also cause similar contamination. Even in the terminal elevator, birds, rodents, or humans may defeat the product.

The survival of Salmonella on grain has been ascertained (Crumrine and Foltz, 1969). *Salmonella montevideo* survived storage for 28 weeks on wheat samples held at relative humidities that resulted in equilibrium moisture contents between 9 and 13 percent. At these levels of moisture content, no bacterial multiplication can occur. However, the survival of viable pathogenic bacteria in any food or feed is a potential disease source.

The molds are another group of microorganisms that are a problem for the cereal industry. Substantial literature has been accumulated on fungi and their activities in stored grain. However, relatively little is known about the number, kinds, and taxonomic distribution of these organisms in commercial flours. Considerably less is known about their incidence in new refrigerated flour products such as canned bisuits, dinner rolls, pizza dough, etc. (Graves and Hesseltine, 1966).

That foods might become toxic by certain fungi growing in them or in the ingredients from which they were made is a relatively recent discovery. Compounds called mycotoxins are suddenly a very exciting and popular field of study. Unfortunately they are another problem for the grain and cereal industry. Toxic metabolites produced by certain molds under specific conditions can cause great economic losses in animals. The symptoms may be a decrease in growth rate, production of diseases, or death (Christensen et al., 1968). The means of detecting mycotoxins involves specialized laboratory testing. Unfortunately, no simple test or device is available to use in country elevators or storage terminals to determine whether mycotoxins are or are not present in grain being handled.

It is well documentated that mycotoxins such as aflatoxin have carcinogenic properties. Many of us who ate peanuts and peanut products during the 1960's must at times have been ingesting considerable amounts of aflatoxin. It is reasonable to assume that some human cancers must have resulted from aflatoxin ingestion. In many countries this may constitute a large public health problem that only research can evaluate. With all the complexities in this new field, it seems conservative to say that mycotoxin research is still in its infancy as far as the identification and solution of the actual field problems (Christensen, 1971).

Physical-chemical interactions in stored products have been studied extensively while biological interactions are still virtually unknown. It is very difficult to determine cause-effect relationships among different kinds of organisms, but we know that such data are necessary for solving food storage problems.

Studies on the relationship between stored-grain insects and fungi were initiated at the University of Minnesota in the 1950's (Agrawal, 1957). Since then, much has been learned about the associations of these two contaminants. We know that some insects reject certain fungal diets. Some fed on a few fungi, although these fungi are incapable of supporting pest populations. Still other insects are capable of feeding and reproducing exclusively on fungi (Sikorowski, 1964; Sinha, 1968).

Because insects are associated directly with storage fungi and some storage fungi are known to produce mycotoxins, research on insect-mycotoxin interrelationships was continued as part of the original project at the University of Minnesota. Several metabolites of different storage fungi belonging to the genera *Aspergillus, Alternaria, Penicillium, Fusarium,* and *Chaetomium* have been or are being screened to determine their effects on the survival and reproduction of stored grain insects (Eugenio et al., 1970; Rao et al. 1971).

Some of the results indicate a wide range of insect responses: mortality, inhibition of growth, and reduced fecundity and fertility (Wright et al., 1976). In other cases the insects obtain nutritional benefit that enhance reproduction, growth, and development. Some species are being investigated for long-range effects, genetic changes, and sublethal physiological effects. Additional studies are being conducted to elucidate these new and complex relationships.

The potential of stored grain insects as a source and as possible disseminators of pathogenic bacteria to man or animals has not been investigated until recently. In general, the association between bacteria and some stored grain insects is different from the association of these insects with storage fungi. Fungi contribute, at least in some cases, the vitamins necessary for normal growth and reproduction of the insects. Bacteria, such as *Pseudomonas*, members of the *Bacillus* group, and others commonly associated with decayed stored products, have adverse effects on some stored-grain insects (Sinha and Harasymek, 1974).

Experiments with the granary weevil [*Sitophilus granarius* (L.)] illustrated that if this insect is grown under sterile conditions, the weevils do not contain any detectable number of microorganisms and can go on for several generations with no apparent effect (Harein and De Las Casas, 1968). However, bacterial counts in these insects increase greatly after death. This may explain the variable results obtained with samples of grain or flour from storehouses or mills where the presence of several dead insects significantly changes the total bacterial counts. Removing dead insects may be an important part of clean up after fumigation of a mill.

Studies have indicated that the hide beetle *Dermestes maculatus* De Geer requires large numbers of *Salmonella* before even a few can be detected in its feces. It also requires multiple doses to become a good carrier (Julseth et al., 1969). This insect probably would not encounter high numbers of *Salmonella* cells in one feeding in its natural environment. This serves to cast doubt on any intestinal transmission and dissemination of *Salmonella* by this beetle.

The rice weevil *Sitophilus oryzae* (L.) has been implicated in some transmission studies. Results have indicated that it is capable of contaminating clean wheat with *Salmonella montevideo*, and the chances for contamination were greater after exposure to *Salmonella* contaminated wheat for 2 weeks (Husted et al., 1969). However, the *Salmonella* dissemination capacity of this insect from an infection site was limited to 30 to 270 cm (Schuster, 1972). Therefore, the rice weevil probably plays a relatively small role on the cycle of Salmonellosis, yet its vector potential should not be overlooked.

Five different species of Salmonella were isolated from field infestations of the lesser mealworm *Alphitobius diaperinus* Panzer (Harein et al., 1970). This indicates that this insect should be considered a potential source of pathogenic bacteria. However, the data to date have failed to demonstrate that the lesser mealworm is a significant contributor of microorganisms in its environment (Harein et al., 1972).

In summary, stored product entomology, like all other branches of economic entomology, uses knowledge obtained from the practice of many disciplines. The basic problem was described by Charles Darwin more than 100 years ago:

> "It is good thus to try in imagination to give to any one species an advantage over another. Probably in no single instance should we know what to do. This ought to convince us of our ignorance on the mutual relations of all organic beings; a conviction as necessary, as it is difficult to acquire." (Darwin, 1859)

I have discussed some of the research and emphasized the necessity for study of the interrelationships between stored-grain insects and associated microorganisms. They seem to interact in mutual dissemination. I have also mentioned the necessity of integrating professional disciplines in the handling and storage of the fruits of our harvest. A multidisciplinary approach is the only sound basis for devising effective preventive methods along with better pest management programs for the storage and conservation of foods and feeds.

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Biological Control—A Form of Applied Ecology

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ABSTRACT

The selection of target insect pests and exotic natural enemies for biological control introductions is discussed. Criteria used to designate suitable target species are reviewed and until there is more documented evidence, it is concluded that no pest should be excluded from biological control attempts. The lack of mathematical modeling is noted, i.e. studies to describe the attributes of a biological control agent most likely to be effective. The question of multiple versus single species introductions is examined as well as the r- and K-strategists concept and genetic considerations.

Biological control, in a restricted sense, makes use of parasites, predators, and pathogens to control pest organisms. This can be done by introducing natural enemies into new areas, conserving and augmenting those that already exist, or inundating biotic agents in much the same manner as an insecticide is applied. My special concern during the past 15 years has been biological control introductions, as a service to agriculture and forestry research workers in Canada. Initially I had intended to discuss the whole broad topic, but after some thought I decided to concentrate my presentation to aspects with which I am most familiar: the selection of target insect pests and the selection of candidates from the species of natural enemies available. In doing so, I will also tend to limit my remarks to insect parasites and predators of plant pests.

A biological control introduction program can involve several groups of people: (1) those who request information and collections of living material, (2) those overseas who respond to the requests, (3) those who receive collections in quarantine for screening, and (4) those who release the entomophagous species and subsequently evaluate the results, and are usually the same as those mentioned in (1). My responsibilities have been to solicit requests from Canadian establishments, to help prepare an annual program in consultation with overseas collaborators and domestic program coordinators, and to receive reports on overseas research, and collections of insects for rearing in quarantine from which to obtain the desired species. Except for weed-feeding insects, virtually all imported biological control collections, both for forest and agricultural pests, are received at our Ottawa Biocontrol Laboratory.

One of our most influential executives in Canadian agricultural research has been quoted as saying that programs are established on the basis of politics, money, and need, and in that order. I would hesitate to mention that here if I didn't think it to be more or less true elsewhere. However, I will be more concerned with the biological aspects of programs knowing that priorities are often changed by other considerations.

Under the broader aspect of pest management, Huffaker and Smith (1972) have developed a set of guidelines to be followed in developing a pest management program:

"1. Separate the real pests from those induced by insecticides in the different regions involved.

2. Establish realistic economic injury levels for the real pests with appropriate attention to the hidden costs of controls.

3. Separate the real pests into those causing intolerable losses, the key pests, and those causing light or sporadic damage controllable by occasional use of insecticides.

4. Identify the key factors controlling, or of great potential value for controlling, populations of the key pests and measure their effects. Such key factors would include a key resistant variety, a natural enemy, or a cultural measure.

5. Design and test control systems based on these guidelines in each of the areas where the key pests and/or factors are different.

6. Modify control systems according to time and area conditions and new inputs as the program develops."

Recently the U.S.D.A. has assigned priorities for research on pest species in their overseas biological control laboratories. These are based on: (1) economic importance of the target pest(s), (2) potential for success, (3) availability and interest of research workers for conducting domestic phases of the research, and (4) current and potential resources required and/or available for overseas and domestic quarantine activities. Some of these items are related to finances and perhaps politics which indicates how difficult it is to ignore other considerations.

Most authors have given similar criteria with different emphasis or detail. For example, Bennett (1974) gave the following reasons for initiating biological control programs: "(1) a recently introduced pest is discovered; (2) other methods of control have been tried and failed; (3) other methods of control are too costly or produce detrimental side effects; (4) a pest is under partial biological control or natural control but an improved level of control is necessary; (5) one species (sometimes more than one) amongst a group of pests is considered a key species which if taken out by biological control should permit the relaxation of pesticide treatments and allow natural enemies to bring the other species of the complex under control."

The foregoing statements are not likely to be seriously challenged by most workers. It is more interesting to consider the more controversial or novel suggestions. For example, Turnbull and Chant (1961) stated: "Indirect pests are suitable subjects for biological control; direct pests are not." The main difference between these categories is based on the populations of pests that could be tolerated. Direct pests cause damage to the marketable product, e.g., fruit, or presumably are vectors of disease organisms. Hence, they must be reduced to the verge of extinction before satisfactory control is achieved. This statement was made at a time when insecticides could be and were used to give a "cosmetic" appearance to marketed produce; under the present atmosphere we might expect that control standards would be less stringent. In any event, the hypothesis was vigourously rebutted by others (e.g., Huffaker et al., 1961). In my own opinion it seems axiomatic that there is less chance to reduce a direct pest to a satisfactory level than an indirect one. Nevertheless, in view of the extreme scarcity of some pests after biotic agents have been introduced, I would not omit direct pests from consideration entirely, especially if it is relatively easy to select and collect a good candidate natural enemy. And even if only partial control is obtained, it may be possible to reduce the pesticide load in an otherwise impossible situation.

Because of the large number of successes in islands either physically or ecologically delimited, Taylor (1955) suggested that biological control was most effective in such areas. From a statistical viewpoint this would seem to be so, but I am inclined to agree with DeBach (1964, 1971) that successes are more likely due to the proportion of efforts than to a geographical factor. For the same reason, analyses have shown that there have been more successes against scales and mealy bugs only because more introductions have been made to control these groups.

Other authors have proposed other hypotheses. Lloyd (1960) pointed out the greater number of biological control successes in perennial crop situations compared to those in annual crops. The importance of crop diversity (mixed crops), as compared to monocultures, in enhancing the effectiveness of natural enemies has been shown by Southwood (1971). Although these considerations should be noted, there is no evidence to preclude biological control attempts against pests of annuals grown in a monoculture.

To summarize, several writers have attempted to rationalize the uncertainties that are obviously present regarding suitable target pests for biological control. Despite these analyses, many of the hypotheses must await more documented evidence before they can be accepted conclusively. As DeBach (1971) states "no geographic area or crop or pest should be prejudged as being unsatisfactory for biological control attempts."

Having thus decided to introduce natural enemies against a particular target species, the next problem is to choose which ones to import. Of course this can only be done as the result of surveys and investigations in countries where the pest or allied species are endemic. In making the choice we have opinions that range from those who advocate the introduction of all primary parasites and potential predators available, to those who insist that only a single species should be imported and this only after careful observations and experimentation.

Usually it is only one or two of a group of introduced entomophagous species that provide the desired control. Several writers have noted that if a pest and its ecology were sufficiently known, then the attributes of the biological agent that would be most effective against it could be described. There appears to be only one instance when this has been done successfully, and that was in the 1930's against a native species in Fiji, the coconut leaf-mining beetle (Taylor, 1937). It is significant that the criteria were developed only after a deliberate and concerted effort could be made. Requirements for a new parasite included a more rapid rate of increase than native parasites, a specified time to complete one generation, survival when suitable hosts were not present, that all larval stages and pupae be suitable hosts, and other broad characteristics such as rapid dispersal and climatic suitability. The search for such a parasite then began, again in a concerted effort, and one was found to fit the requirements, even though it was considered to be of minor importance on another pest species in the same genus. Needless to say, the introduced parasite became established quickly, brought the pest under control in a short time, and still maintains that control today.

In recent reviews of books on biological control I have noted the criticism that mathematical modeling is absent in the application of biological control. In my view these criticisms are justified but much more effort would be required to obtain this type of information than is now expended. If even a limited amount of extra effort could be made then programs such as that against the coconut leaf-mining beetle would be more common.

In fact, many target species usually are being studied overseas at one time, limiting the amount of data that can be obtained on any one of them. As a result, those natural enemies that promise good probabilities are chosen. DeBach (1974) stresses the importance of a natural enemy with high searching ability but also considers three other desirable characteristics: host specificity, reproductive capacity, and environmental adaptability.

These can be readily accepted by most writers but the question of multiple versus single introductions has been controversial. Chant and Turnbull (1961) were concerned that competition between parasite species might reduce overall effectiveness in host population regulation and advocated introducing one selected agent at a time, followed by careful observations and other agents, if necessary, selected on the basis of these observations. This concern has also been expressed by others, e.g., to quote Pschorn-Walcher of the CIBC (gypsy moth report for 1974): "However, the establishment of the usually intrinsically superior, highly competitive parasite species attacking late larval or pupal stages may eventually reduce the chances for the well-adapted, but often intrinsically inferior species to become established."

Beirne (1975) noted that there was no evidence in Canada that total parasitism by interacting species was less than the parasitism of one of the species alone and advocated multiple introductions of parasites to avoid missing or delaying opportunities for pest control. Hassell and Varley (1969), using inductive population models, concluded that as long as hyperparasites and nonspecific parasites are excluded, there is little danger from successive introductions. They also noted that there were advantages to multiple introductions: a greater chance at least one species would become established, the possibility of better control by more species rather than one, and dominance of different species by competitive displacement in different climatic zones.

In Canada there is at times a curious blend of the single vs. multiple introduction practices. For example, seven species of parasites were introduced from Europe against the winter moth, and two of these became established and were shown to have reduced winter moth to extremely low levels in woodlands but not in orchards. Further work in Europe showed another parasite species that attacks prepupal stages in the soil and had gone undetected previously. But forestry workers expressed concern that this species might interfere with existing controls if it were introduced, and because of this no action has been taken.

Force (1972) used the concept of r- and K-strategists to describe the characteristics of parasites. r-strategists often exist in unstable environments, have high capacities for population increase but are poor competitors whereas K-strategists exist in fairly constant environments, have relatively low capacities for population increase, and are good competitors. Applying this to practical introductions of natural enemies, he suggests that r-strategists be introduced into the newly disturbed situation when a pest has recently invaded a new area. As he suggests, there is a tendency to collect the most numerous parasite in the endemic environment. But these undisturbed situations are likely to contain large numbers of K-strategists. K-strategists, however, are likely to be the poorest colonizers – lacking "toughness," adequate dispersal and searching abilities, and an adaptiveness to a variety of conditions. Those that are least dominant in a stable situation but are found consistently over a wide geographical or ecological range and are abundant in a disturbed situation should be introduced; these are the r-strategists.

Pschorn-Walcher (Birch casebearer report for 1976) has suggested the following criteria: (1) the species should be primary, relatively abundant, and constant, i.e., occurring in a wide variety of habitats that have different host populations (note the similarity to r-strategists), (2) the species should be synchronized with the host and well-adapted to it, i.e., not require an alternative host, (3) the species should be reasonably host-specific, (4) in the case of multiparasitism, an intrinsically inferior species, i.e., whose larvae succumb to other larval species occurring in the host at the same time, should be imported first because it has a better opportunity for establishment and build up.

Because of the large number of apparent failures of parasites and predators to become established after release, several writers have suggested that genetic factors may be responsible at times. Based on a genetic model, Remington (1968) gave two "rules of thumb:"

1) Introduce a large, wild sample from a large, central source population that has an environment most similar to that of intended establishment. Even better would be to introduce a closely spaced succession of wild samples from several source populations from various environments moderately like the area of intended colonization; this maximizes the relevant genetic variability on which selection can then act to produce an optimal genotype in the new environment.

2) Avoid introducing a few founders from a large source population or making mass releases from laboratory rearings bred for one or a few generations from one or a few individuals collected from a large source population.

With reference to numbers released, Beirne (1975), in an analyses of Canadian records, reported, "Of the species released in totals of under 5,000, 10% (9 of 98) became established; of the 5,000 to 31,200 group, 40% (13 of 33); but of the over 31,200 group, 78% (22 of 28)." He considered that "the greater the number of individuals, the greater the genetic diversity of the colony. Adequate genetic diversity is needed to produce the new genetic combinations that are essential to enable the colony to thrive, because of the probability that the phenotypes that prevailed in the endemic environment may be maladjusted to the colonial one. An additional reason could be that the larger numbers increase the probability that some individuals will find host or prey and mates sufficiently readily and quickly to enable the population to survive."

However, Force (1967) referred to some *Drosophila* experiments and warned that fitness characteristics might be affected adversely by incorporating different strains or populations just before or during the time of their release.

Regarding the second point, several authors have promoted mass rearing as a method to acclimatize the natural enemies before release in the field. In fact it is common policy in California to carry an importation over at least one generation before attempting colonization. On the other hand Simmonds (1963) considered it more expeditious to introduce the maximum possible genetic variability directly into the field from which by natural selection the most suitable strain would develop.

In the view of Mackauer (1972) the genetic-diversity of laboratory-propagated material is no larger than that of the field collected material from which it originated and indeed may be smaller. Although numbers are increased, the possibility of colonization is not necessarily enhanced.

When we consider all the uncertainties and the "ad-hoc" approach to biological control introductions, there is little wonder that some critics term the practice more an art than a science. Because of the emotional attitudes of some biocontrol experts I sometimes regard it as a religion in the dictionary sense of an "action that one is bound to do." This frequently occurs when the worker has been involved in a highly successful introduction program. And "success breeds success" so that one California worker told me recently that he expects one success in every 5 years to justify his existence. The phrase "publish or perish" seems to have been replaced by "succeed or sink." No doubt this is due to a great deal of effort.

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Butterfly Production Management

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ABSTRACT

A speculative overview of butterfly production management is presented which includes manipulation of habitats to enhance larval and adult food plants, accessibility and longevity of adults, early season introduction of migrants, and use of exotic butterflies and larval host plants.

Concentration and accessibility of butterfly adults for viewing and collecting may be influenced by adult longevity, adult food sources, larval host plant odors, and other factors. Dangers to butterflies and their host plants by concentrating adults are discussed. Production management opportunities by manipulation of larval host plants appears to be much greater for expansion of the local and regional range of butterflies than for increasing butterfly density. The paucity of the literature does not permit general conclusions concerning population regulating factors, carrying capacity concepts, etc. However, there is sufficient observational data to guide experimental production management studies. Migratory species are considered for management although the carryover from management inputs are lower than with resident butterflies. Introduction of exotic species is limited mainly to butterflies useful in weed control programs.

Speculative production research possibilities are given for the Pipevine Swallowtail, *Battus philenor* (L.); Black Swallowtail, *Papilio polyxenes asterius* Stoll; Giant Swallowtail, *Papilio cresphontes* Cramer; Little Sulphur, *Eurema lisa* (Boisduval and Le Conte); Dainty Sulphur, *Nathalis iole* Boisduval; Baltimore, *Euphydryas phaeton* (Drury); and Monarch, *Danaus plexippus* (L.).

INTRODUCTION

In his *Interlude in the Elysian Meadows*, Evans (1968) lamented the apparent decline in butterflies around the world. He despaired at finding butterflyless, house-filled suburbs in meadows where he chased butterflies as a child. In the following article, I will not promise that we can return his meadows, but I will suggest that with the use of applied research procedures, we can develop management methods to provide productive havens for butterflies in suburbs, other disturbed areas, and possibly in some natural areas.

Butterflies have fascinated man since the dawn of history, having been portrayed in the arts of man as symbols of mysticism, beauty, and grace. Macy and Shepard (1941) reviewed the mystic association between man and butterflies. Among the earliest are Chinese literature from the sixth century B.C. where white butterflies were the bearers of the souls of man and later the Psyche of ancient Egypt where the soul flew away after death on butterfly wings.

Butterflies also have been objects of natural history and scientific interest since early times; Aristotle (384-322 B.C.) described the life history of the Cabbage Butterfly, *Pieris rapae* (L.). Many people developed their first interest in natural history and biology through butterflies because they are attractive, abundant, and accessible. For the same reasons they have become effective vehicles for conservation education in recent years (Pyle, 1976).

Although larvae of several butterflies feed on desirable plants and trees, very few are important economic pests (Macy and Shepard, 1941). A few species are beneficial to man by feeding on undesirable plants, pollinating flowers and preying on harmful insects (Ford, 1945; Holloway, 1964; Owen, 1971). The economic value of butterflies as objects of scientific, natural history, and artistic interest is mostly from sale of adults, ova, and pupae to hobbyists and educators (see Newman, 1967; Owen, 1971; Carvalho and Mielke, 1972). Indirect monetary value accrues from butterfly parks and gardens, equipment, books, collection and study expenses, museum support, and tourists. The apparent lack of interest among applied entomologists in nonpestiferous butterflies is probably related to institutional indifference to aesthetic values of insects and prominence of wild tropical butterflies in the specimen trade.

Purpose, definition, and scope.

The purpose of this paper is to define butterfly production management, relate it to applied entomology, discuss its aesthetic and biological requirements, identify research needs, and consider a few candidate species for management in the upper Midwest.

I have defined butterfly production management as (1) manipulation of habitats to enhance larval and adult food plants, hibernation sites, voltinism, fecundity, adult longevity, and accessibility of butterflies, (2) introduction of species that are scarce or absent early in the season because of winter mortality and/or slowness of immigration in the spring from the South, and (3) introduction of exotic butterflies and larval host plants.

Butterfly production management, unlike conservation, selects candidate species on the basis of their (1) likelihood to respond to management, (2) viewing potential, (3) aesthetic qualities, and (4) insignificant pest potential – without reference to their natural rarity or endangered status.

Management could be considered for a wide range of habitats such as botanical conservatories, nature centers, parks, private yards, vacant urban land, railroad and power line rights-of-way, fence rows, and managed and unmanaged lands of all categories. Depending on the species and potential use of the resource, properties of various sizes, diversity, and stability could be employed making butterfly production management fit into the magazoo concepts, at least for the intensively managed reserves (see Sullivan and Schaffer, 1975; Miller, 1975).

GENERAL LITERATURE REVIEW

Since this is only an overview of butterfly production management, current literature reviews will be used whenever possible for the supporting data base in butterfly conservation, biology, and ecology.

Butterfly conservation has been summarized by Duffey and Morris (1965), Newman (1967), Gilbert and Singer (1975), and Pyle (1976). Most developed programs for butterfly conservation are for endangered species in England (e.g. Duffey, 1968; Howarth, 1973; Dempster, 1974). Programs in the United States (Pyle, 1976) and elsewhere are only starting. Although there is a wide public interest in endangered species, these efforts probably are limited in their relevance to the natural history activities of the general public because most of the butterflies are likely to be found only in small areas, remain somewhat scarce, and occur in fragile habitats needing protection from the public. They will be valuable for their biological data and for showing how butterflies and host plants respond to management. However, these programs will be different from production management because the species to be managed were selected for their endangered status rather than their ability to respond to management. Furthermore, these programs usually do not employ quasi-agricultural methods, exotic plants and butterflies, and the extensive use of man-altered habitats used in butterfly production management.

Another valuable resource is literature on "negative" management of pestiferous butterflies (e.g. Watanabe, 1976) and moths, the mirror image of which could be used for "positive" management of desirable butterflies. While familiarity with this literature is indispensable to the efficiency of butterfly production management, adult feeding and the relatively lower population density constitute major differences between most desirable butterflies and most pestiferous Lepidoptera. Furthermore, agriculturalists often need 90 percent or more control. In butterfly production management, increases of 25 to 50 percent probably would be considered very successful.

A fundamental base of data on butterfly biology and ecology is critical to management programs. This literature has been summarized by Ford (1945), Gilbert and Singer (1975), and Pyle (1976), and extensive bibliographies have been prepared by Tietz (1972). In the interest of brevity, extensive reference will be made of Gilbert and Singer's review of butterfly ecology covering 274 papers.

There is a vast quantity of important observations on life histories and general ecology in Howe (1975) and other books on butterflies of individual states or other geographical units. Most of these are listed in Tietz (1972) and Field et al. (1974). Only a few are cited, but references to the "general literature" refer to these sources.

Developing basic data is essential to the efficiency and broader application of management research. However, the careful practice of "things that work" for reasons we do not understand should not be disregarded. Therefore, one must evaluate the fragments of information and develop management research proposals that test basic assumptions in concert with production goals. Gilbert and Singer (1975) state: "In view of the paucity of data, statements in the literature about factors that limit or regulate butterfly populations usually are guesses based on circumstantial evidence."

Except for general coverage in books (e.g. Newman 1967, 1969, and Stone and Midwinter, 1975), rearing butterflies in outdoor cages, botanical conservatories or insect zoos has received little attention. Care must be taken to exclude parasites and maintain healthy populations as diseases prosper in weakened insects. Periodic harvesting of adults will keep a balance between larvae and food plants. It might be practical for some zoos and botanical conservatories to rear larvae on artificial diets (see Vanderzant, 1974). Continuous rearing of butterflies in enclosures may be limited only to certain genera (e.g. *Heliconius*) that can learn to orient to landmarks rather than orient to the sun like most other butterflies. The latter often destroy themselves flying against the walls (Gilbert, 1975).

Butterfly parks and nature centers (e.g. Heal, 1973; Jackson, 1976; Pyle, 1974), although their primary goals are natural history observation, conservation, and education, also can serve as practical testing grounds for butterfly management procedures.

Methods

The methods will be similar to those used in applied and basic ecology (e.g. Southwood, 1966). One of the most difficult problems will be the monitoring and adult population response to management practices (see Owen, 1975; Pollard et al., 1975; Ekholm, 1975).

AESTHETIC QUALITY OF ADULT BUTTERFLIES

Beauty is a highly personal thing, but the following are components that most people probably would consider among the principal factors for butterflies.

Color, pattern, and size

While these need no elaboration, gaudy and subtle and large and small all deserve attention.

Commonness

Common butterflies do not fail to impress us with their beauty (e.g. Spring Azure, *Celastrina argiolus* L.), and we could delight in their increased abundance. However, butterflies with aesthetic qualities not commonly encountered would add an element of newness.

Behavioral properties

Flower, puddle and carrion visiting, territoriality, migration, hilltopping, and flight pattern and speed are interesting phenomena to butterfly observers and collectors. Slow flying butterflies that visit flowers should be favored in production programs for the general public.

Freedom and ephemerality

Butterflies have a freedom and ephemeral aesthetic quality similar to birds and other wildlife animals and somewhat akin to the movement of grass in the wind. They must be experienced when they appear as they quickly move or change.

Desirability of the habitat

The beauty of butterflies usually can be best appreciated in pleasant surroundings. Since many butterflies visit flowers and are active during warm periods, few locations could be considered undesirable. Heal (1973) and Jackson (1976) have developed special butterfly habitats in public gardens.

ACCESSIBILITY FOR VIEWING AND COLLECTING

This section deals with factors affecting the opportunity to view and collect presently available adult butterflies by using management procedures that concentrate adults, but do not necessarily increase population size. Longevity, oviposition preference, and voltinism are also relevant to subsequent sections on production. Fecundity is covered in this section because of its close relationship to adult butterfly behavior.

Concentration and longevity of adult butterflies relative to food sources

The longevity and gregariousness of butterflies varies among species. Some tropical forms are active for 6 months (Gilbert and Singer, 1975) but most northern species are active for less than 1 month (Newman, 1969). Both factors can be influenced by food, shelter, and climate.

Adult butterfly food preferences can differ with season, sex, age, and biotype. The extensive observations on food preference by adult butterflies by Clark (1932), Saunders (1932), Norris (1936), Arms et al. (1974), Gilbert and Singer (1975), and the general literature include flower nectar, pollen, honeydew, tree sap, spittlebug foam, decaying fruit, fermenting baits, perspiration, urine, dung, carrion, sodium salts, stagnant water (mud puddles etc.), and moisture on the surface of soil, rocks, and mortar. Some of the studies show that adult feeding on nectar increases adult longevity. Gilbert and Singer report on unpublished work by Labine and Turk showing that 56 percent of the energy budget of the Cabbage Butterfly, *Pieris rapae* (L.), comes from adult feeding. Although little experimental data are available, most authors consider nectar and other foods important energy sources for adult activities. Gilbert and Singer report that butterflies are attracted to flowers for pollen and nectar also as a nitrogen source important for longevity and fecundity. Gilbert (1975) reports that *Heliconius* spp. that are fed pollen and nectar have a five fold greater egg production than those fed only nectar. He further points out that many species of butterflies are not capable of feeding on pollen.

Butterfly weed, *Asclepias tuberosa* L., and many other flowers are known to attract adult butterflies. The observations of Saunders (1932), Norris (1936), Newman (1967 and 1969), Heal (1973), Donahue (1976), and Jackson (1976), and the general literature reports should be examined for likely candidates and subjected to quantitative studies. Flower color, pollen, and nectar quality and quantity can be important factors.

Butterflies' attraction to dung, urine, damp soil, etc., is related to sodium salts (possibly for its association with a nitrogen source, Gilbert and Singer, 1975), but they also obtain other nourishment from these sources (Arms et al., 1974). It is not known why sodium attraction is restricted largely to males unless it is related to their greater flight activity (Gilbert and Singer, 1975). However, for the attraction and concentration of adult males, Arms et al. (1974) have shown that the active ingredient is sodium at concentrations of 10^{-3} to 10^{-2} mole. Sodium occurs in such low concentrations in most plants that it could be a limiting element for terrestrial herbivores.

The attraction of butterflies to the larval host plants has been noted in the general literature and recently analyzed in relation to the coevolution of butterflies and their host plants (Ehrlich and Raven, 1965). The culture and expansion of larval host plant material, discussed later, could also serve to concentrate butterfly adults. Macy and Shepard (1941) reported that dill, *Anethum graveolens* L., was unusually attractive to the Black Swallowtail, *Papilio polyxenes asterius* Stoll. Possibly certain host plants having strongly attractive odors could be used to concentrate adults. The best candidates are probably exotic plants (e.g., dill) that have not been exposed to evolutionary pressures against their "special" attraction to particular species of butterflies.

If carefully used, extracts from food plants might be effective for concentrating butterflies in areas with a high viewing potential. Crushed fresh plant material is also useful (Owen, 1971). Identification of the active ingredient would enable us to employ similar materials that are easier to obtain, and to identify exotic plants that are good candidates for additional host plants.

In summary, there is sufficient information to consider studies on flowers, larval host plants, their extracts, and various materials high in sodium for concentrating butterflies. Longevity and fecundity probably can be improved with floral nectar and possibly other nutrients added to environments where these are in short supply.

Flight habits in relation to accessibility

Flight pattern and speed, mobility, and migratory, seasonal, and daily habits affect the viewing and collection of butterflies and should be considered in management decisions.

Species that do not stray far from their larval host plant [e.g. the Baltimore, *Euphydryas phaeton* (Drury)] are excellent candidates for management because the rewards for local efforts will be concentrated in the area. Species that disperse rapidly will contribute little to local projects.

The swarming of male butterflies on hilltops or around other large conspicuous units above the general landscape is called hilltopping. According to Shields (1967) and Tyler (1975), females fly into the swarm for mating and then leave the area. Although Shields has shown that butterflies are able to fly considerable distances from their host plants to engage in hilltopping, it may be possible to utilize hilltopping in butterfly management by providing food plants for adults and larvae in the vicinity of the appropriate hills. With food plants nearby, females might not disperse as far for oviposition and thereby increase the local density of butterflies.

Information on flight habits are covered in the general literature and by Gilbert and Singer (1975). The latter refer to some of their work showing that mobility can vary within a species due to the proximity of larval and adult food plants. Although too little information is available to apply this finding to management research, it is difficult not to speculate on restricting species prone to disperse by providing adult food in breeding areas presently deficient in these resources. However, genetics or maternal nutrition may be involved also (genetics section).

Other factors affecting accessibility

Sex pheromones produced by caged virgin females possibly could be used to concentrate males. It is unlikely that synthetic pheromones will be developed for nonpestiferous butterflies unless development costs are reduced greatly by new technology. However, some pheromones have a rather wide spectrum and may be useful for nonpestiferous relatives of pestiferous species (Birch, 1974).

The communal roosting habits of butterflies often have been reported (Urquhart, 1960; Gilbert and Singer, 1975), but the controlling factors are not understood nor are we able to encourage the habit. The latter authors suggest that both home ranges and gregarious roosting might be influenced by learning in butterflies in some wet tropical areas where there is no complete seasonal break in the presence of adults. However, communal roosting of temperate grassland butterflies (Turner, 1975) and swallowtails (Klots, 1951) also has been reported. Congregating and trail-marking pheromones known for some beetles and ants, have not been reported for butterflies (Birch, 1974). Jones (1930) demonstrated that *Heliconius charitonius* (L.) locate the position of their communal roosts without the aid of chemical markers.

Traplining, the repeated use of feeding sites by adult butterflies on a regular time schedule, has been observed in both temperate and tropical butterflies. The regularity of visitation observed with *Heliconius* spp. by Gilbert (1975) suggests that it might be possible to guide butterflies through observation areas by establishing a "trapline" of attractive adult food plants.

Large butterflies usually live longer than small ones and, like those that are brightly colored, are easier to see. Butterflies attracted to desirable and/or inhabited locations are more likely to be viewed and/or collected. Butterflies with more than one generation per season, that hibernate as adults, that oviposit singly, that breed on herbs and bushes rather than trees, generally would be more accessible. Because of the ephemeral nature and small areas involved (Owen, 1971), butterfly territoriality probably would have only a minimal effect on viewing opportunities.

A few of these factors could be managed. The Alfalfa Butterfly, *Colias eurytheme* Boisduval, is able to breed all year in irrigated legume fields (Smith and Allen, 1954). Irrigation, staggered plantings, and cutting or trampling plant stems (e.g., nettles, *Urtica* spp., Newman, 1967 and 1969) in midsummer to stimulate new shoot growth may attract adults for oviposition, thus extending the oviposition period and possibly increasing the number of generations in some specific localities. Slansky (1974) has reviewed the relationship between voltinism and food plants in butterflies (also see section on introduction of exotic butterflies).

If it could be demonstrated that sun, shade, or hibernation sites were limiting to attraction or longevity, they could be adjusted simply and cheaply. There are extensive comments on butterfly preferences for these factors in the general literature, but there is little quantitative data. Heal (1973) and Jackson (1976) discuss adult hibernation shelters, but data are not yet available on their effectiveness.

Collenette and Talbot (1928) and Arms et al. (1974) used dead and paper butterflies to concentrate adults at puddling locations. Decoys may be reasonable targets for research on concentration of adults.

Possibility of undesirable side effects

The concentration of adults could (1) attract the butterflies away from their optimum breeding areas, (2) cause severe defoliation of host plants near the attraction site, (3) shorten longevity of adults if adult food sources and shelter are not available, (4) result in overcollecting by unscrupulous collectors and/or (5) increase likelihood of disease, parasitism, and predation. Parasites and predators often respond to host plant characteristics and pheromones attractive to their prey (Birch, 1974). The damage to the aesthetic value of the site by heavy defoliation could be avoided by interplanting with species not acceptable for larval feeding. This might require studies with starving larvae of various ages as many larvae greatly expand their host range under starvation stress and/or as they mature [e.g. the Baltimore, *Euphydryas phaeton* (Drury) covered in the following section].

MANAGEMENT IN RELATION TO LARVAL FOOD PLANTS

Increasing density of food plants

Except for disturbed habitats and certain temperate forest types where extensive defoliation is an important factor in the maintenance of the climax type, defoliating Lepidoptera usually do not increase to the limits of their food plants. Parasites, predators, disease, changes in population quality, larval behavior, oviposition habits, and climatic factors that adversely affect survival usually reduce population levels so that starvation rarely occurs (Dethier, 1959; Wellington, 1964; Gilbert and Singer, 1975). The relatively low utilization of Minnesota's vast stands of nettles by its butterfly fauna seems to support this view.

Dethier and MacArthur (1964) extended the carrying capacity concept to butterflies by demonstrating that artificial additions or subtractions of larvae of Harris' Checkerspot, *Chlosyne harrisii* (Scudder), did not influence the populations of the next generation in spite of an apparent excess of larval food. Although food was not limiting to carrying capacity in this study, Gilbert and Singer (1975) review studies on western *Euphydryas* spp. showing that larval food supply was limiting in several populations. Owen (1971) observed complete defoliation by butterfly larvae in disturbed habitats in Africa. He also found that many larvae prefer leaves or other plant parts in certain stages of development or in particular microhabitats. Therefore, suitable food may be in short supply in the midst of an abundance of the host plant (also see Urquhart, 1960; Newman, 1967). Owen also reported that larvae feeding on specialized plant parts (e.g., flowers and seeds) are more likely to be food-limited than species feeding on foliage. Gilbert and Singer (1975) cite several papers demonstrating so much variation between and within species that researchers should not be intimidated by the fatalistic overtones of a generalized carrying capacity concept.

Increasing the range of host plants

Probably a more promising approach to butterfly management than increasing host plant density is increasing the range of the host plant on a local and regional basis. One of the best examples of a butterfly responding to the distribution of primary host plants is the pestiferous Alfalfa Butterfly. It was first abundant in California in 1850 and spread as an economic pest of its major host plant, alfalfa, *Medicago sativa* L., as alfalfa culture developed eastward across the country. In western areas it also became more widespread and abundant in response to the extended range and growing season for alfalfa afforded by irrigation (Smith and Allen, 1954).

The Monarch Butterfly, *Danaus plexippus* (L.), a new world species, has greatly expanded its range because its larval host plant, milkweed (*Asclepias* spp.), was introduced into areas where natural forces (sometimes augmented by ships) have dispersed the butterfly. They are now established in Australia, New Zealand, Hawaii, Canary Islands, and other areas. Urquhart (1960) feels that there are many additional locations where the Monarch Butterfly could become established if suitable host plants were provided.

The Giant Swallowtail, *Papilio cresphontes* Cramer, a butterfly native to the central and southern states, has been found recently in the Imperial Valley of California. It feeds on *Citrus* spp. and appears to be extending its range in the state via citrus orchards (Tyler, 1975).

The Pipevine Swallowtail, *Battus philenor* (L.), has spread more than 1000 miles out of its range, following the planting of its primary host plant, pipevine, *Aristolochia dureor* Hill. Brown (1957) reports that the swallowtail occurs in Colorado only where pipevine is planted, because the vine is not native to the state. The eastern form of the butterfly spread across the Midwest because of the widespread use of pipevine as a porch vine. The decline in the number of homesteads and vine-covered porches is probably having a detrimental effect on the distribution of this butterfly. Clark (1932) has reported on the abundance of the butterfly on planted pipevine in Washington, D.C. In this case, the extension was within the native range of the plant.

With this data it seems reasonable to start research on the response of *P. philenor* to plantings of pipevine. Although the vine is hardy to 45° latitude (Rosendahl, 1955), the butterfly is generally rare north of 40° latitude (interpretation from Clark, 1932; Macy and Shepard, 1941; and the general literature). No data exist to help separate the effects of host plant scarcity from the effect of cold temperatures on the rarity of this insect in the North. However, it is interesting that Brown (1957) attributed the disappearance of the swallowtail from a Colorado Springs location to the winterkilling of the vine. Emmel and Emmel (1973) suggest the planting of *Aristolochia* in southern California to extend the southward range of the Pipevine Swallowtail.

The Baltimore, *Euphydryas phaeton*, is another butterfly that shows promise for management by the extension of its host plant range. In Minnesota, the Baltimore is restricted to wet peaty meadows where it oviposits on turtlehead, *Chelone glabra* L. In nature turtlehead is restricted to this type of habitat, but I have grown it on upland sites. Tietz (1972), in a review of literature, reports: "It is said that the newly hatched larvae must start with this plant, but the older larvae can mature on the other plants . . ." His list contains 17 plants representing several families. The ability of late instar larvae of Lepidoptera to feed on plants, not acceptable to younger larvae, is well known. If colonies of the Baltimore can be kept going on upland sites, the larvae probably could defoliate other desirable plants in the immediate area. The population could be managed by collecting the adults and the conspicuous larval nests or by introducing its parasites (see Clark, 1932 for parasite data). Feeding trials on desirable plants likely to occur in upland areas should be conducted to guide the selection of natural areas for management and to determine what plants can be safely planted near turtlehead in gardens. Transplanted wetland Baltimores should not be confused with the rare natural occurrence of upland colonies that live on a honeysuckle, *Lonicera canadensis* Bartr., and possibly represent a sibling species (Howe, 1975).

In my studies, the Baltimore oviposited and developed normally on *C. glabra* and an exotic turtlehead, *C. lyoni* L., in an upland caged garden.

In most of these examples, the limited distribution of food plants is probably the major factor affecting the distribution of their butterfly herbivors. I suspect that we could greatly expand the breeding range of some of these butterflies by (1) establishing the host plants in new habitats (e.g., turtlehead on upland sites), (2) increasing local distribution by providing adequate seed bed conditions (e.g., milkweed seed requires bare soil), or (3) increasing the broad geographical range of host plants (e.g., alfalfa, thistle, and milkweed were spread by agriculture and commerce).

Use of exotic plants

Exotic plants in the same genus as native host plants should be checked for their acceptability for oviposition and larval development. If they have desirable aesthetic qualities and wider habitat tolerances or other advantages for culture, they could be useful in extending the host plant range of butterflies. In the case of the Baltimore, my studies suggest that we can utilize an exotic plant, *Chelone lyoni*, not previously reported as a host.

Food quality and secondary compounds

Food quality has already been covered as it relates to host plant preferences, shading, sprouting, and stage of plant development. The latter two are especially important for Lepidoptera since they usually feed on the succulent new foliage which is higher in nutrients than older foliage. There seems to be little agreement on the main purpose of secondary compounds in plants. Many of the compounds are detrimental to behavior and survival of larvae and digestibility of food. However, many insects, especially butterflies, have developed ways to coexist with the materials, often using them to their advantage for feeding stimulants and host-finding signals or as deterrents and poisons for protection from predators.

White (1974) in an extensive review of Lepidoptera defoliators, hypothesizes " . . . that most herbivorous insects usually remain at a low level of abundance relative to the apparent abundance of their food because most of them die when very young from a relative shortage of nitrogen in their food. Only occasionally do their food plants become a sufficient source of nitrogen to allow a high proportion of the young insects to survive, and the population to increase to outbreak levels. The plants become a richer source of nitrogen when they are stressed by random fluctuations in the summer and winter rainfall, although other factors such as soil type and topography may contribute to this stress." Because secondary compounds are often reduced in stressed plants, it seems reasonable to assume that their reduction also might contribute to better larval survival.

Increases in foliage nitrogen by adding fertilizers often benefits larval survival too, especially in agricultural corps (Nickel, 1973). However, the relationship is less consistent. Possible larval survival is enhanced by greater foliage succulence and nutrients or larval survival is reduced (or balanced) by excessive nutrients and/or an increase in secondary compounds resulting from fertilization (Slansky and Feeny, 1977).

Some cases of shading, sprout induction, and use of special host plants may be ready for butterfly production trials, but most nutrition related possibilities for manipulating larval survival needs more basic research information.

Reestablishment of devastated floras

The severe freeze of 1899 eliminated many tropical plants from central and northern Florida and thus the butterflies dependent upon them (Kimball, 1965). Reestablishment of these plants probably would extend the range of several butterflies to their former northern limits. In the lower Rio Grande Valley, extensive agricultural and housing development has reduced the range of a unique Mexican subtropical flora in the United States and their butterfly predators (Kendall, 1974). In both areas, many of the plants would be suitable for parks and private yards as well as unmanaged habitats.

Agriculture and forestry in relation to butterfly host plants

Alteration or destruction of virgin habitats has been beneficial as well as detrimental to butterfly populations. In mountainous forest areas, habitat diversity is increased by clearings for agricultural fields and modern forestry management practices, thus increasing the supply and extending the range of food plants for butterflies using crop plants, prairie flora, annuals, and pioneer species. In prairies, however, large continuous areas are managed intensively as monocultures leaving few refuges for the native flora. The remaining areas of undisturbed prairie are of limited value because they are small and widely separated and the fire and grazing influences are different from the undisturbed state. As mentioned earlier, agricultural development in North America has extended the geographical range of many butterflies (e.g., Alfalfa Butterfly, Pipevine and Giant Swallowtails). Native and introduced weeds also have flourished in agricultural areas benefiting many butterflies [e.g., Monarch, Painted Lady, *Vanessa cardui* (L.)].

In any disturbance of habitats, butterflies dependent on host plants in restricted habitats (e.g., bogs) are most likely to be affected adversely. Ford (1945) reviews the effects of British agriculture, especially drainage of wetlands, on the butterfly fauna. In Africa, Owen (1971) feels that forest butterflies adapt less well to agriculture than do savanna species, many of which can feed on agricultural weeds. The influence of insecticides, herbicides, grazing, mowing, and fire are covered later.

MANAGEMENT OF MIGRATORY BUTTERFLIES

In Canada and northern United States, many butterflies do not survive the winter. They recolonize each spring from insects that have specific northernly migration habits, from insects that expand their summer range in response to the expansion of acceptable weather and food, and by being carried by wind. Since the relative importance of fixed migration habits, expansion, and wind in insect recolonization of northern habitats is not known for many species, all of these colonizers will be called migrants. Williams (1958) considers only butterflies with fixed directional flight as migrants.

Management practices that enhance population density or range of migrant butterflies in the North would probably be less rewarding than management practices for resident butterflies since residents overwinter in or near their summer habitats. Except for a very few species, migrants do not return to southern locations where they could survive the winter. Therefore, summer populations of migrants in the North cannot influence the starting populations the following season. However, species that breed every summer and, at least in some seasons, become abundant in the North could be good candidates for butterfly production management, if their host plants can be managed or if the butterflies can be introduced early in the season.

The Little Sulphur, *Eurema lisa* (Boisduval and Le Conte), and the Dainty Sulphur, *Nathalis iole*, are migrants that might be good candidates for management. They satisfy many of the aesthetic and accessibility requirements, have several generations per season, and are not economic pests. The Dainty Sulphur usually arrives in August and the Little Sulphur in mid-July, but neither becomes abundant until late summer (Macy and Shepard, 1941; Ebner, 1970; and unpublished Minnesota records). Probably all populations of the Little and Dainty Sulphurs are dependent on migrants coming north each season and reproducing here. Although the favorite host plants, *Cassia* spp., of the Little Sulphur are somewhat limited in distribution, the populations of both pierids in Minnesota is probably limited by the scarcity of breeding stock until mid-summer.

Another migrant that might be considered for early season introduction is the Giant Swallowtail. The larvae are common in the South on citrus, but they feed on prickly ash, *Xanthoxylum americanum* Mill., in the North. Although the Giant Swallowtail has fewer generations per season than the aforementioned pierids, it is such a spectacular butterfly that only a few sightings may justify a management effort. The larvae also feed on gas plant, *Dictamnus albus* L., an attractive hardy perennial garden flower.

The Monarch, one of the few butterflies that migrates south in fall, might be considered for management because the oviposition preference for smaller plants and new sprouts (Urquhart, 1960) could be utilized for management by shading or cutting large plants in midsummer. Because the Monarch has two to three generations in the North, studies to test the effectiveness of these treatments on population response seem appropriate. Although the treatments may help local populations for the season, it is unlikely that they will have a discernable effect on the number of butterflies returning to that location the following year because the treatments could be applied to only a miniscule fraction of the utilized breeding area.

INTRODUCTION OF EXOTIC BUTTERFLIES

In this paper, butterflies are considered exotic if the particular species, subspecies, etc., is absent from at least one intervening life zone. The Pipevine Swallowtail would not be exotic in Minnesota even though there is only one record of its occurrence here. It occurs in Iowa and Wisconsin (Ebner, 1970) in habitats that are generally continuous into Minnesota. (See Howe, 1975 for life zones.)

The accidental introduction of the pestiferous Cabbage Butterfly and its displacement of other pierids in disturbed habitats (Clark, 1932; Klots, 1951) illustrates the need for great care in butterfly introduction on ecological as well as economic bases. Therefore, we can consider only introductions of species that would not cause significant harm to other desirable life forms. The disagreement on whether or not it is "proper" to introduce "safe" butterflies will not be considered here. Ford (1945), Newman (1967), S.P.N.R. (1970), and Pyle (1976) discuss some of the controversy on this subject and propose guidelines. Informing other local biologists of plans and recording the event in the literature are minimum requirements.

Exotic butterflies that feed on weeds are probably the best candidates for introduction at this time because only the weed control programs have the methodology and facilities to screen out potential pests (Huffaker, 1964). Their criteria should be applied to all introoduction considerations. Holloway (1964) reported that two Lycaenidae, *Strymon echion* (L.) and *S. bazochii* (Godart), were introduced into Hawaii for the *Lantana* control program. Whether or not "safe" butterflies could be introduced for weed control programs if their potential for weed control was only low to moderate would depend on the program strategies and the appreciation of butterflies by the decisionmakers.

Introduced exotic butterflies that cannot overwinter in their new location could be managed with the methods proposed for migrants in the previous section. There is the same degree of safety here because the program comes to a natural cutoff point each winter. Introduction of butterflies that are not able to feed on native or established exotic plants, but whose host plants are inconsequential or desirable and could be cultured in the new locations, could also be considered.

There is an interesting possibility for the introduction of a winterhardy form of a butterfly that normally occurs in

Minnesota only as a seasonal migrant. Shapiro (1974) mentions an apparent winterhardy population of the Giant Swallowtail in western New York State feeding on prickly ash. Because the winters in southern Minnesota are similar and the growing season is longer, a form of the Giant Swallowtail that could overwinter in New York State might be a candidate for introductions in Minnesota. Prickly ash is a common, somewhat undesirable, shrub in the southern half of the state. The New York insects should be reared in captivity until a population can be released that is large enough to withstand genetic dilution from nonwinterhardy migrants that invade Minnesota from the South in the summer.

It might also be possible to introduce butterflies from populations with more generations per year into an area where vegetation management or agricultural practices now provide a suitable food supply for an additional generation that was not previously available. The resident population would have evolved an obligatory diapause or migration at a day length or temperature normally coincident with the shortage of suitable food even if temperatures were suitable for insect development. Temperate zone insects have largely relinquished sensitivity to food quality to day length and/or temperature to initiate diapause or migration, but in some cases diapause or migration can be hastened by senescent foliage or crowding. Diapause in Lepidoptera has been recently reviewed by Tilden (1976). Dingle (1975) mentions that in the tropics where day length and temperature are relatively constant, diapause and migration apparently are controlled by the proximate cause, food quality, which is governed mostly by alternating wet and dry seasons.

The success of introductions depends on proper matching of the needs of the butterfly in the old and new locations and on the impact of native competitors, parasites, predators, etc. Because exact matching is never possible, the adaptability of the introduced insect is also important.

BUTTERFLY GENETICS

Although there is a rather large literature on genetics of Lepidoptera (Ford, 1945; Remington, 1968; Robinson, 1971), developing butterflies with desired aesthetic or biological characteristics seems impractical at this time. However, with early introductions of migrants or use of exotic species, we can select races with desirable characteristics. Remington (1968) suggests that there could be advantages to selecting insects from either the population margin or center depending on the qualities needed. Margin populations are more likely to have been under selective pressure for adaptability to severe conditions. Center populations are more likely to have been under selective pressure for reproductive capacity and stability, but large samples probably would include the whole range of genetic material that has been magnified in the margin populations.

It is generally considered desirable to have management areas sufficiently close to each other or continuous with at least marginal habitats to insure enough population exchange to reduce the likelihood of undesirable genetic drift or extinction (Sullivan and Schaffer, 1975). With exotic species, occasional booster introductions might be needed.

In England, Dempster (1976) suggests that the smaller size of *Papilio machaon* L., in an isolated colony as compared to cosmopolitan colonies, was indicative of a decreased tendency for dispersal. Wellington's (1964) studies show that nutritional and/or genetic factors affect the dispersal and other biological factors of certain moths. If similar dispersal-related tendencies occur in butterflies selected for management, they could be useful in reducing movement of butterflies out of the management area.

MISCELLANEOUS MANAGEMENT CONSIDERATIONS

Impact of collecting

"All available evidence indicates that it is exceedingly difficult to damage a population of mobile invertebrates, such as most insects, through collecting. Given the facts of insect population biology, including their rapid replacement and vast overproduction, overcollecting of insects is a hollow threat. Only in cases of extremely weak, depleted, local and environmentally stressed populations can intensive collecting be a long-term depreciative factor." This statement in the proposed policy on insect collecting by the Xerces Society (1975) seems justified in light of current information. Some biologists feel that the impact of collecting, even on the so-called "endangered species," has been grossly overstated (Miller, 1975). However, several British entomologists suspect that collecting affected the decline and/or extinction of some butterflies (e.g., Duffey, 1968; Spooner, 1963), but they always emphasize the primary cause as habitat destruction or unusual weather conditions (also see Gilbert and Singer, 1975). Spooner (1963) feels that collecting in small isolated areas will lower population levels so that surpluses will not be available for poor seasons or to boost neighboring weak colonies during good seasons with additional breeding stock and genetic material. In general, collection of rare species and species in isolated habitats where local races might have developed should be done with moderation (e.g., Ehrlich et al., 1975; Gilbert and Singer, 1975; Owen, 1971). In like manner, highly accessible congregations of butterflies need protection. Urquhart (1960) reported that Pacific Grove, California, has a city law protecting the Monarch Butterflies that overwinter there in such great numbers that they provide a tourist attraction.

Except for parks, managed areas (e.g., Heal, 1973; Jackson, 1976; Pyle, 1974), and rare species, conflicts between viewers and reasonable collectors seem unlikely.

The impact of commercial collecting is difficult to assess because of the paucity of quantitative data. Owen (1971) reviews the subject quoting prices for species and giving examples of some of the practices in tropical Africa and southeastern Asia. He refers to reports of $30 million a year from the sale of Taiwanese butterflies. In Brazil, Carvalho and Mielke (1972) studied the procedures and preferred species of butterflies collected in forests and surmised that the commercial harvesting had little effect on populations. However, they anticipate population declines from the conversion of forests to agriculture. Owen (1971) feels that in addition to habitat protection, regulations are needed for rare and endangered species and species easily trapped in large numbers (e.g., *Charaxes* spp.).

Insecticides

Although alteration and/or destruction of native habitats, as well as insecticides, are associated with intensive agriculture and forestry, it is convenient to blame insecticides for the alleged decline in nonpestiferous butterflies because they are made specifically to kill insects. Because quantitative data are scarce, I have selected a few references that represent prevailing attitudes. Insecticide spraying to kill adult mosquitos for malaria control in the tropics could be important because wooded areas near villages and home gardens are important havens for butterflies (Owen, 1971). Evans (1968) refers to butterfly population reduction from malaria control operations in butterfly-rich Sikkim that caused serious losses for commercial butterfly collectors. Kendall (1974) feels that most butterflies escape the impact of pesticides in Texas because few depend solely on larval host plants in agricultural fields. On the basis of research studies, Moriarty (1969) concluded that insecticides probably had little effect on the apparent decline in British butterflies. Substituting biological control for insecticides does not assure safety for butterflies because many predators and diseases and some parasites (especially in complex habitats, Kulman, 1970) have wide host ranges that often include butterflies. Unlike modern insecticides, these agents spread and often become established outside of target areas.

If butterfly production management programs are undertaken near sprayed areas, managers might consider (1) avoiding locations on the leeward side of prevailing winds, (2) providing flowers for adult feeding in areas free from insecticide drift, (3) encouraging butterflies with life cycles not in synchrony with pest insects, and (4) in long term programs, planting rows of shrubs or trees to help intercept insecticide drift.

Because competition for larval food plants is rarely limiting for butterflies, insecticides probably would not be used in butterfly management except for the elimination of accidently introduced butterflies that are pestiferous or threaten to displace native or more desirable species.

Herbicides, fire, grazing, and mowing

In heavily forested or intensively cultivated areas, roadside vegetation is probably important for butterflies because rights-of-way can provide several levels of grass, herbs, brush, and in some localities aquatic vegetation in ditches. If roadsides are mowed, larvae can feed on the remaining lower parts of plants and on subsequent shoot growth. However, early mowing might be detrimental to population growth of some species. Herbicides that affect broadleaved plants (e.g., 2,4-D) probably will be more damaging than grass controlling materials (e.g., Maleic Hydrazide) because grass is less likely to be in short supply and does not have flowers for adult butterfly food.

Many ecology texts refer to the importance of fire and grazing to prairie maintenance. Dethier and MacArthur (1964) observed that occasional mowing maintained old fields in a successional stage beneficial to Harris' Checkerspot. Urquhart (1960) reports that the Monarch prefers the new small leaves for oviposition. New sprouts can be made available throughout the season by cutting older plants in mid- and late summer. The regrowth of nettles is also reported to be attractive to its butterflies (Newman, 1967 and 1969). Howarth (1973) reports that grazing and fire are important for the maintenance of plant and ant food for *Maculinea arion* L. in Great Britain.

Mowing, grazing, fire, and herbicides may be useful in maintaining preferred successional stages for management of certain butterflies. The disruptive effects could be moderated by strip treatments in alternate years. Selective herbicides might be useful in providing a special advantage to desired plants, especially if they have been newly established in an area.

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On the Population Dynamics of Neodiprion Sawflies

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ABSTRACT

The life cycles, biology, and behavior of *Neodiprion* sawflies are examined with reference to causes of variation in abundance, and an outline is given of the population dynamics of two important pine defoliators, *N. swainei* Midd. and *N. sertifer* (Geoff.).

In southern Ontario, most outbreaks of *N. sertifer* are unsynchronized, independent events initiated by the discovery of young, previously uninfested pine forests containing few natural control agents. In such stands, sawfly density increases rapidly for 4 to 6 years and then declines continuously to a low level. Key-factor analysis of life table data from a typical outbreak shows that the continuous increase in generation mortality that reversed the rising density trend was accompanied by increases in mortality in three life cycle periods: late feeding larvae (due to starvation), prespinning larvae (due to parasitism by *Exenterus* spp.), and late cocooned larvae (due to insect predators and ichneumonid parasites).

Outbreaks of *N. sertifer* in stands of large pines are more persistent and irregular as well as more destructive than those in small trees and are characterized by a variable incidence of prolonged eonymphal diapause. In one case, prolonged diapause in effect sequestered many sawflies in a year of high density and transferred them to a later, smaller generation in which their contribution to reproduction was predominant.

INTRODUCTION

In this paper I consider the way populations of some familiar conifer sawflies are regulated naturally. I deal first with some aspects of the biology of *Neodiprion* spp. that are or may be relevant to population change and then examine the results of studies undertaken specifically to determine the reasons for variation in abundance of several species. I will not deal more than circumferentially with such questions as the definition of population, the best strategy for studying population dynamics, methods of estimating density, and the impact of mortality agents. Some of these topics already have received a good deal of attention (McLeod, 1961; Lyons, 1964a, 1969).

BIOLOGY

It is scarcely possible, or appropriate, to treat this subject fully here, but several reviews are available (Atwood, 1961; Lyons, 1964b; Coppel and Benjamin, 1965; Pschorn-Walcher, 1965; Kolomiets *et al.*, 1972; Knerer and Atwood, 1973). I shall therefore limit discussion to those aspects of sawfly biology that seem most important in sawfly population dynamics, with the understanding that all of an insect's responses, behaviors, activities, abilities, etc., are relevant to its abundance.

Neodiprion sawflies have two distinct types of life cycle. In the cycle shared with other diprionids, eggs are laid in spring or summer, winter is spent as an eonymphal larva in a cocoon, and adults eclose in spring or early summer of the following year. Some species in this category are multivoltine (e.g., *N. lecontei* [Fitch], depending on latitude), some are univoltine (e.g., *N. swainei* Midd.), and some may have a partial second generation (e.g., *N. rugifrons* Midd. and *N. nigroscutum* Midd.). In the latter case, a portion of the cocooned larvae metamorphose in the same season and give rise to progeny that finish feeding and form cocoons before winter.

In the other type of life cycle, adults eclose in the autumn, eggs overwinter, and larvae feed in the spring. Examples include *N. sertifer* (Geoff.), *N. pratti banksianae* Roh., *N. p. pratti* (Dyar), *N. nanulus nanulus* Schedl, *N. abietis* complex, *N. hetricki* Ross, and others in eastern North America, as well as probably all of the western species. Species in this category are ordinarily univoltine, but some populations, such as those of *N. sertifer* at high altitude, are hemivoltine spending the first winter as eggs and the second as cocooned eonymphal larvae before completing development (Pschorn-Walcher, 1970).

Voltinism and life cycle type seem to bear little relation to abundance. Although the most abundant species, *N. lecontei*, is also the most multivoltine, there have been serious outbreaks of both egg- and cocoon-overwintering univoltine species, e.g., *N. swainei*, *N. p. pratti*, *N. taedae linearis* Ross, and *N. tsugae* Midd.

Eggs are laid in individual slits carved by females on the edge of new or old needles, depending on species, and are commonly arranged in rows. Some species tend to oviposit in the needles of a single shoot but others deposit fewer eggs in a number of shoots. Eggs are highly dependent on host needles for moisture, and if the needles die so do the eggs. Eggs may be killed by low winter temperatures. Sullivan (1965) showed that in *N. sertifer* in southern Ontario the undercooling temperature, below which freezing and death occur, averaged about -32°C and varied between -24°C and -37°C in different individuals. At the same latitude the mean undercooling temperature of *N. p. banksianae* eggs was about -34.5°C, but in northern Ontario it was about -39°C and that of *N. n. nanulus* about -41.5°C.

Almost all clusters of eggs include both males and females, usually more of the latter. The sexes are indistinguishable by causal examination at this stage, but in *N. sertifer* males are more susceptible to winter mortality than females (Lyons and Sullivan, 1974). Mortality due to egg parasites is sometimes very great especially in species that overwinter as cocooned larvae. For example, Benjamin (1955) recorded almost complete mortality of *N. lecontei* on roadside pitch pines (*Pinus rigida* Mill.) in Illinois by *Closterocerus cinctipennis* Ashm. Egg-overwintering sawflies usually are attacked only lightly, if at all, but there are conspicuous exceptions (Lyons, 1974). Aggregation or clustering of eggs is deleterious to survival in the face of parasitism (Lyons, 1962), but is advantageous to larvae, if not also to the parental females, although the latter has not been demonstrated.

Larvae of most species feed colonially, usually on older needles but sometimes on current ones. In *N. swainei*, colony size and larval survival are directly correlated (Lyons, 1962). There is also evidence that egg and larval survival are directly correlated (Lyons, 1967), which suggests that the impact of events in the egg stage may be partially deferred to the larval period. Possibly the mortality of eggs affects the mortality of larvae by restricting colony size.

In many species females moult more often, continue feeding longer, and become much larger than males. Thus, they are more exposed to hazards and frequently experience greater mortality due to starvation, disease, and parasitization. Their size and the amount of material they reserve for later production of eggs are greatly affected by a number of factors, including quantity and quality of food, temperature, disturbance by parasites, etc. (Lyons, 1970). Hard (1974) has interpreted the lower fecundity and sex ratio of *N. tsugae* in heavily defoliated stands of western hemlock (*Tsuga heterophylla* [Raf.] Sarg.) as a feedback mechanism preventing the sawfly from reaching damaging levels. However, it is unlikely that these impairments alone regulate sawfly density.

Larvae that have finished feeding moult to a final nonfeeding instar (termed the prespinner), which spins a cocoon, usually in the soil. Adults of *Exenterus* spp. (Ichneumonidae) parasitize late feeding larvae and prespinners and often attack more females than males.

Cocooned insects may metamorphose immediately and reach the adult stage in a few weeks, or they may undergo diapause. Sawflies that overwinter as eggs normally have an eonymphal diapause during the summer. As a rule, both within and between species, the earlier they complete the feeding period the longer the diapause (Lyons and Griffiths, 1962). According to Sullivan and Wallace (1967), eonymphal diapause in *N. sertifer* is induced by long photoperiods during larval feeding. Short larval photoperiods induce "nondiapause," and cocooned insects kept at 21°C develop forthwith. However, if cocoons are kept at 10°C, most insects enter a prolonged diapause. Geographically distinct populations of this species differ appreciably in their response to factors inducing prolonged diapause (Popo, 1967; Sullivan and Wallace, 1968; Austara, 1969). That is, with identical photoperiods and temperatures, the incidence if not also the intensity of prolonged diapause varies from one population to another. Clearly, population models will be in error unless this variation is accommodated.

Prolonged diapause probably occurs in all species, but seems to be most prevalent at high latitudes and altitudes. In effect it removes individuals from one generation, as does mortality, and adds them to subsequent ones, as does immigration. There may be low survival during diapause and reduced fecundity in individuals that do complete development (Sullivan and Wallace, 1967; Lyons, 1970), but the course of outbreaks can be significantly altered, as will be seen.

Cocooned sawflies are exposed to attack by fungi, nematodes, insect parasitoids, insect predators, and vertebrate predators, and mortality may be differential as to sex.

Neodiprion adults are characteristically ready to reproduce when they eclose from cocoons, and their active life is brief. The mating ability of *N. sertifer* males is variable (i.e., some individuals are able to mate more often than others) and is inversely associated with the proportion of females in the progeny (Lyons, 1975). This suggests that males have a role in determining the sex ratio. Almost all females of this species are able to mate and oviposit, but Bobb (1972) reported massive oviposition failure in *N. p. pratti* and suggested that it was reponsible for terminating an outbreak in Virginia. It is not known if experiences during morphogenesis affect the ability of adults to mate and oviposit, but the size and fecundity of females are greatly affected by the quantity and quality of larval food, the presence of encapsulated parasites, the incidence and intensity of prolonged diapause, and temperatures (Lyons, 1970). In *N. swainei*, egg size and fecundity are inversely related in insects of the same size, and interfamily differences in egg production are partly due to differences in egg size (Lyons, 1970). In some species, e.g., *N. n. nanulus* and *N. swainei*, there is interfemale variation in egg color, but its significance for survival and reproductive performance is not known. Probably all species are outbreeders. Only haploid males and diploid females have been identified in natural populations, but Smith and Wallace (1971) obtained diploid males, which were reproductively incompetent, in an inbred laboratory stock of *N. nigroscutum* and showed that sex determination is allelic, as in higher Hymenoptera.

OUTBREAKS

Not all *Neodiprion* sawflies undergo outbreaks, and among those that do only a few have outbreaks that are severe enough to damage tree growth. Studies to explain outbreaks have been confined to a few species, e.g., *N. swainei* and *N. sertifer,* although single-year life tables have been prepared for populations in the *N. fulviceps* complex by Dahlsten (1967). A number of species are ordinarily uncommon but occasionally become very abundant for 1 to 3 years. Population studies on such species are difficult because the outbreaks are so brief, but they may provide useful clues to regulation of the more abundant species.

As with many other forest insects, climatic factors are commonly thought to initiate outbreaks, although the evidence is tenuous since it is not based on direct measurement of mortality and its year-to-year variation. Often there is some conspicuous mortality, such as parasitism or disease, to which the termination of outbreaks can be ascribed. Casual, nonquantitative observations are unquestionably useful and informative but they can also be misleading and are a poor device for comprehending the system that regulates population size. The correct interpretation of population events, and the devising of effective strategies for population control, must rely on the analysis of the numerical and qualitative changes of the insect in response to all of the control agents, natural and otherwise, impinging on it.

Neodiprion swainei in Quebec

In northwestern Quebec and northeastern Ontario there have been repeated outbreaks of *N. swainei*, a cocoon-overwintering species, in maturing and mature stands of jack pine (*Pinus banksiana* Lamb.) especially on poor sites in the vicinity of bodies of water. Tripp (1965) found that in this area the weather in September is often too cold for cocoon spinning and suggested that outbreaks require several consecutive years in which above-average temperatures promote early adult eclosion and rapid larval development. Studies by McLeod (1970, 1972) have revealed a great deal about the outbreak behavior of this economically important species. The salient features are:

(1) Population trends tend to be continuous with density increasing or decreasing for a number of years before changing direction, i.e., sawfly numbers oscillate slowly and regularly.

(2) Outbreaks tend to be synchronized over large areas, but are patchy and localized rather than continuous.

(3) Outbreaks tend to be cyclic, recurring on the average every 8 years. The amplitude of the cycles is about 68X, i.e., maximum sawfly density is 68 times as great, on the average, as minimum density. However, even at the low point of the cycles there is noticeable defoliation of trees. McLeod considers *N. swainei* unusual compared with other forest defoliators such as the spruce budworm (*Choristoneura fumiferana* Clem.) and the larch budmoth (*Zeiraphera griseana* Hbn.) in that its population fluctuations have a high mean density and a narrow amplitude.

These characteristics suggest that *N. swainei* density may oscillate in response to the action of density-dependent agents. Supporting evidence came serendipitously during the suppression of the pest with insecticide. In 1965 when *N. swainei* was approaching the top of its cycle and endangering tree survival, some jack pine stands were treated with a single aerial application of phosphamidon. When this was done, a small amount of insecticide drifted into an adjacent nontarget stand in which population events had been monitored for a number of years. McLeod observed population trends for the next 5 years in these stands and in unsprayed ones.

The accidentally treated or "drift" stand received enough insecticide to raise larval mortality from about 3 percent to about 65 percent, and there was higher than usual mortality in most of the later life cycle stages. Density declined markedly the next generation but then recovered and resumed fluctuating in synchrony with untreated populations. The return to "normal" density was accompanied by increases in fecundity and the proportion of females and in reduced mortality in all stages. McLeod (1972) does not identify the regulating agents that resumed control so quickly, but his graphs suggest that the key intervals of the life cycle were the prespinner period and the late cocoon period, when parasite and predator impact is great.

Population events in the normally sprayed stand were very different. Here the insecticide killed more than 99 percent of the larvae. Density plunged dramatically in the next two generations and for at least 5 years after the spraying remained at a level averaging less than 0.4 percent of that in untreated stands, far below the usual minimum density. Clearly, the system controlling the high-level oscillations of *N. swainei* was profoundly disrupted by the single application of phosphamidon. Although the factors responsible for maintaining the very low density have not been identified, McLeod (1972) considers his results suggest "that although population regulation can be maintained in the face of considerable stress, as evidenced by the quick return to normal in the spray-drift area, there is a limit beyond which either disregulation of the system may occur or it may begin to oscillate around a different mean level of density . . . ."

Neodiprion sertifer in Ontario

This sawfly, which overwinters in the egg stage, has had periodic outbreaks in Europe for many years. Outbreaks have occurred as far south as Yugoslavia and Spain and as far north as northern Finland, well inside the Arctic Circle. For the most part, however, they have been concentrated in central Europe. They tend to occur synchronously over large areas at intervals of 6 to 13 years and to last 2 to 4 years, but the pattern varies geographically (Lyons, 1964b). Pine stands on sites with low water tables are most often affected.

In Europe, outbreaks are generally thought to be initiated by climatic change and connections have been noted between their occurrence and (1) "wine years" (i.e., those with warm, dry weather in late summer), (2) forest fire frequency, and (3) warm, dry weather in May and June. The implication is that the greater survival afforded directly or indirectly by good weather permits the sawfly to escape its usual restraints. Most outbreaks are considered to be terminated by a polyhedral virus disease, but other explanations have been advanced including predation by birds and mammals and the unsuitability of needles for oviposition.

N. sertifer was accidentally introduced to North America at least 50 years ago and now occurs as far west as South Dakota and north to Sault Ste. Marie in Ontario. Most infestations in Ontario have been in Christmas tree plantings and on recently reforested land, but there has also been heavy defoliation in stands of large trees. Population behavior has evidently differed from that in Europe in that outbreaks have not occurred synchronously.

Figure 1 shows population density curves for eight southern Ontario pine stands. They resemble the population curves of *N. swainei* in Quebec in that there tend to be runs of increasing and decreasing density, but absolute densities are very much lower. In number 1 to number 7 these population changes ensued only a few years after the trees were planted, but in number 8 the trees were about 25 years old when the sawfly reached them. Peak density occurred in different years in plantations only a few miles apart, e.g., number 1 and 2. The critical factor appears to be the time when the plantation first became infested. The age, size, species, and spacing of the trees seem unimportant. In numbers 1, 2, 4, 5 and 6 there was a steep rise in sawfly numbers for several years followed immediately by a comparable decline and no appreciable resurgence. All of these populations, regardless of how long *N. sertifer* had been in that region of Ontario, were isolated from established populations of this and native sawflies by at least several miles. In contrast, numbers 3 and 7, which did not experience outbreaks, were adjacent to or surrounded by stands of larger trees in which *N. sertifer* and its natural control agents were established. The pattern is consistent with the idea that the sawfly was able to colonize some newly planted areas, i.e., isolated ones, sooner than its natural control agents and to increase rapidly for a time until they caught up. Where the natural control agents were already close at hand, i.e., numbers 3 and 7, no appreciable rise in sawfly numbers occurred, and the implication is that these agents kept the sawfly under control (Lyons *et al.*, 1972). Similar patterns seem to be developing in southern Wisconsin (Lyons *et al.*, 1974).

Stand number 8 represents a different and rather more complex story. The jack pines there were about 25 years old when *N. sertifer* reached that part of Ontario, probably no later than 1958 (Lyons, 1964b). The outbreak did not reach a peak until 1965, and there was probably a very rapid rise in numbers in the preceding several years rather than a slow

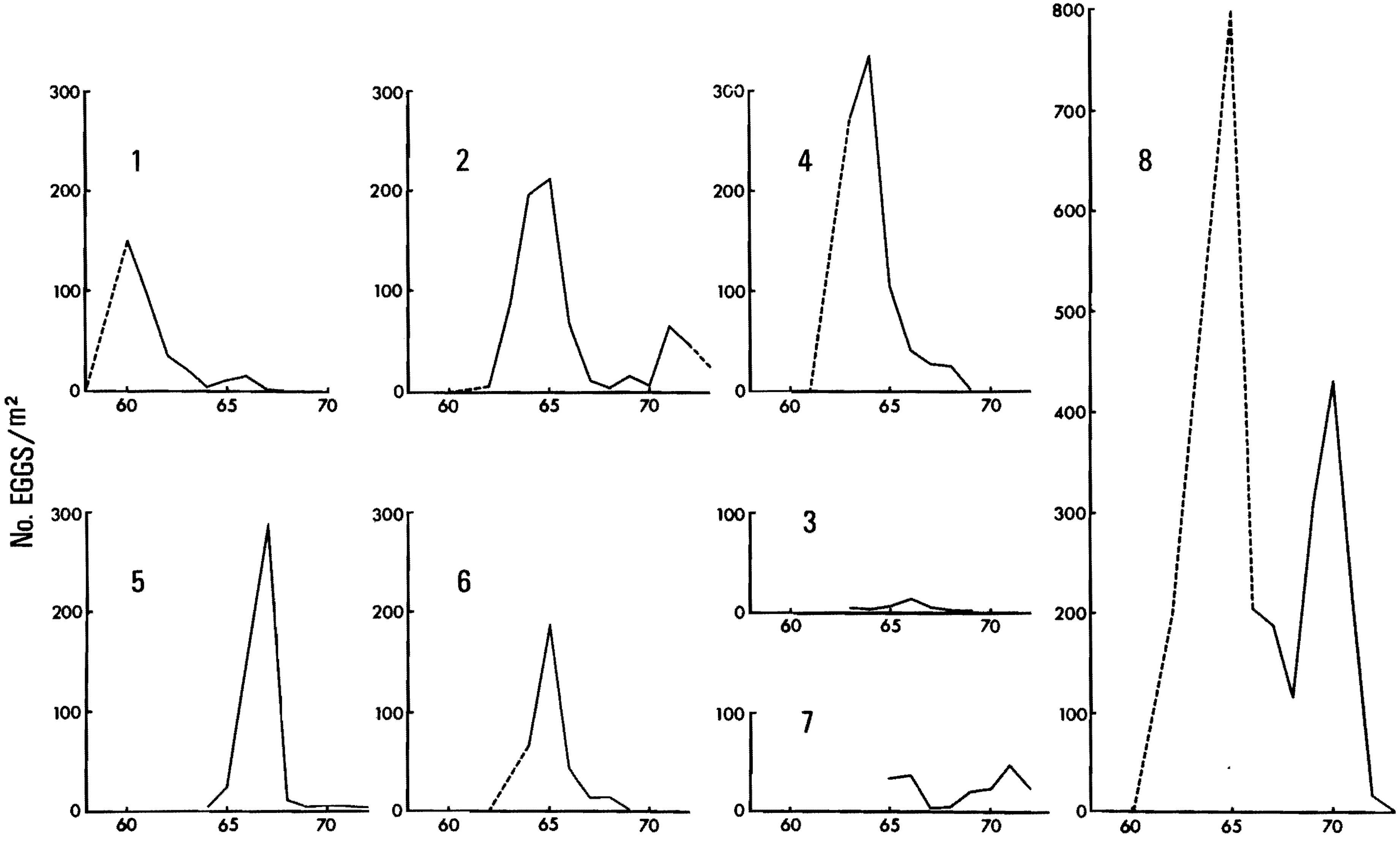

Figure 1. Population trends of *Neodiprion sertifer* in pine stands in southern Ontario.

increase for a longer period. Instead of declining continuously, as did populations in small trees following peak density, this one declined for a few years but returned to a subsidiary peak in 1971 and then declined again, this time to a very low level. Prolonged diapause made the difference. In 1965 about 75 percent of the cocooned eonymphs remained in diapause instead of metamorphosing, and their removal from reproduction that year constituted a significant part of the generation loss. A large number of these insects completed development in 1968 and initiated the second phase of the outbreak. In this stand the highest incidence of prolonged diapause coincided with the year of highest sawfly density, but it is not known if the connection was causal.

Figure 1 summarizes the gross changes in population density from year to year and does not reveal what was responsible for the changes. For that information, life tables are needed for the time in which the observed changes occurred. Life tables themselves do not provide answers, although they sometimes are spoken of as if they did. Their value, if they are prepared carefully and with an awareness of how mortalities should be measured and assigned, is that they oblige a complete accounting of population losses within the generation. This accounting permits rational and informed conclusions about the cause of population change.

The key-factor method described by Varley *et al.* (1974) is an appropriate device for examining *N. sertifer* life table data to determine the relative importance of various mortalities. It is certainly more useful and informative in a preliminary analysis than searching for density dependence. In this method the mortality in each interval of the life cycle or the mortality caused by a particular natural control agent is expressed as the difference between the common logarithms of successive densities, i.e., densities before and after the mortality. Individual mortality values (k) expressed this way may be added to determine total or generation mortality (K), such that:

$$k_{\text{eggs}} + k_{\text{larvae}} + k_{\text{pupae}} + k_{\text{adults}} = K.$$

Figure 2 shows egg density generation mortality (K), and seven age-interval mortalities (k) for *N. sertifer* in stand number 2 (figure 1) for the period 1962 to 1972, inclusive. Two refinements have been introduced: (a) the loss of *females* only is considered, in order to remove the effect of the pronounced differential mortality that occurred in some generations and (b) female densities are adjusted downward in proportion to the reduction of reproductive potential in larvae that survived the feeding period. Thus the k-values no longer express the loss or mortality of individual insects; instead, they express the population's loss of egg production and assign it to the age interval in which it originated.

Sawfly density was very low in 1962, the insects having arrived only a few years earlier, but climbed steeply (as much as 15x per year) until 1965 and declined from then until 1968. In 1971 there was another modest and brief rise in numbers. Generation mortality increased steadily from 1962 to 1967, and sawfly density declined when K exceeded about 2.0 in 1965. The k-values for age intervals show that late larval mortality, prespinner mortality, and late cocoon mortality all followed the same trend as generation mortality, which suggests that they determined the observed changes in sawfly numbers during that period.

Egg mortality, which was almost entirely due to low winter temperatures, was clearly of no importance in population trends because it was low and varied only slightly. That is, winters from 1962 to 1967 were not cold enough to affect the eggs significantly. In some localities, however, low temperatures in that period sometimes caused very high egg mortality. There was no parasitism of eggs. The same lack of importance can be attached to the mortality of young larvae, i.e., first, second, and early third instars, because it was low and did not vary in accordance with generation mortality. The mortalities were not density dependent.

Late larval mortality was estimated as the difference between the reproductive potential of third-instar larvae and that of larvae that spun cocoons and includes the mortality of prespinners that did not spin cocoons. The trend coincided well with the trend in generation mortality from 1962 to 1965, increasing from 7 percent to 88 percent. Starvation was clearly responsible; in both 1964 and 1965 the trees were completely defoliated well before the end of the larval period. It is uncertain why the loss of late larvae returned to such a high level (about 84 percent) in 1967. Sawfly density was low by then, so the larvae had ample food. There was no mortality due to nuclear polyhedrosis, and parasitization by the recently introduced ichneumonid *Lophyroplectus luteator* (Thunb.) was very light. Perhaps predation, a change in food quality, or disturbance of the feeding larvae by *Exenterus* adults, was responsible.

Mortality estimates for late larvae and subsequent life cycle stages are lacking for 1968, 1969, and 1970. They represent the populationist's dilemma: density was low and adequate samples of cocoons were thought to be prohibitively expensive. Sampling became practical again in 1971 because of higher densities. The increase in late larval loss of 1972 coincided with the rise in generation mortality but did not involve sex differentiality or lowered reproductive potential in the survivors. Late larval loss operated density dependently early in the outbreak but not subsequently. The lack of dependence in the full sequence of generations is explained partly by the natural increase in the foliage complement of the growing trees.

Mortality of prespinners was due to parasitization by *Exenterus* spp. (Hymenoptera: Ichneumonidae) and was determined only for larvae that spun cocoons. Most attack by *Exenterus* is on prespinners but they also oviposit on feeding larvae (Griffiths, 1969); their searching and attack activity disturb the larvae and sometimes make them fall off the tree. Hence, the impact of *Exenterus* is not fully expressed by the proportion of larvae that have been parasitized. In any case, parasitization increased irregularly from 20 percent in 1962 to 85 percent in 1967, in accordance with the trend in generation mortality, but was evidently of little importance in 1971 and 1972. Mortality from 1962 to 1967 was almost exclusively by one species, *E. nigrifrons* Roh. By 1971 and 1972, however, *E. amictorius* Panz. had become the dominant species. No density dependence is evident in the data.

Early cocoon mortality refers to eonymphs that died in the first few weeks of the cocoon period. Fungi of the genus *Beauveria* were involved, as well as parasitic nematodes, but very often the cause of death was not diagnosed. The extent of loss varied from year to year, but not in accordance with generation mortality, and did not act density dependently in these data.

Late cocoon mortality, estimated in samples of cocoons shortly before adults eclosed, included the effect of parasites and predators as well as a small proportion of insects dying for other reasons. The incidence of prolonged diapause, which acts as a mortality factor in the generation in which it originates, was never more than negligible. Losses due to both predators (mostly insects) and parasites (mostly ichneumonids)

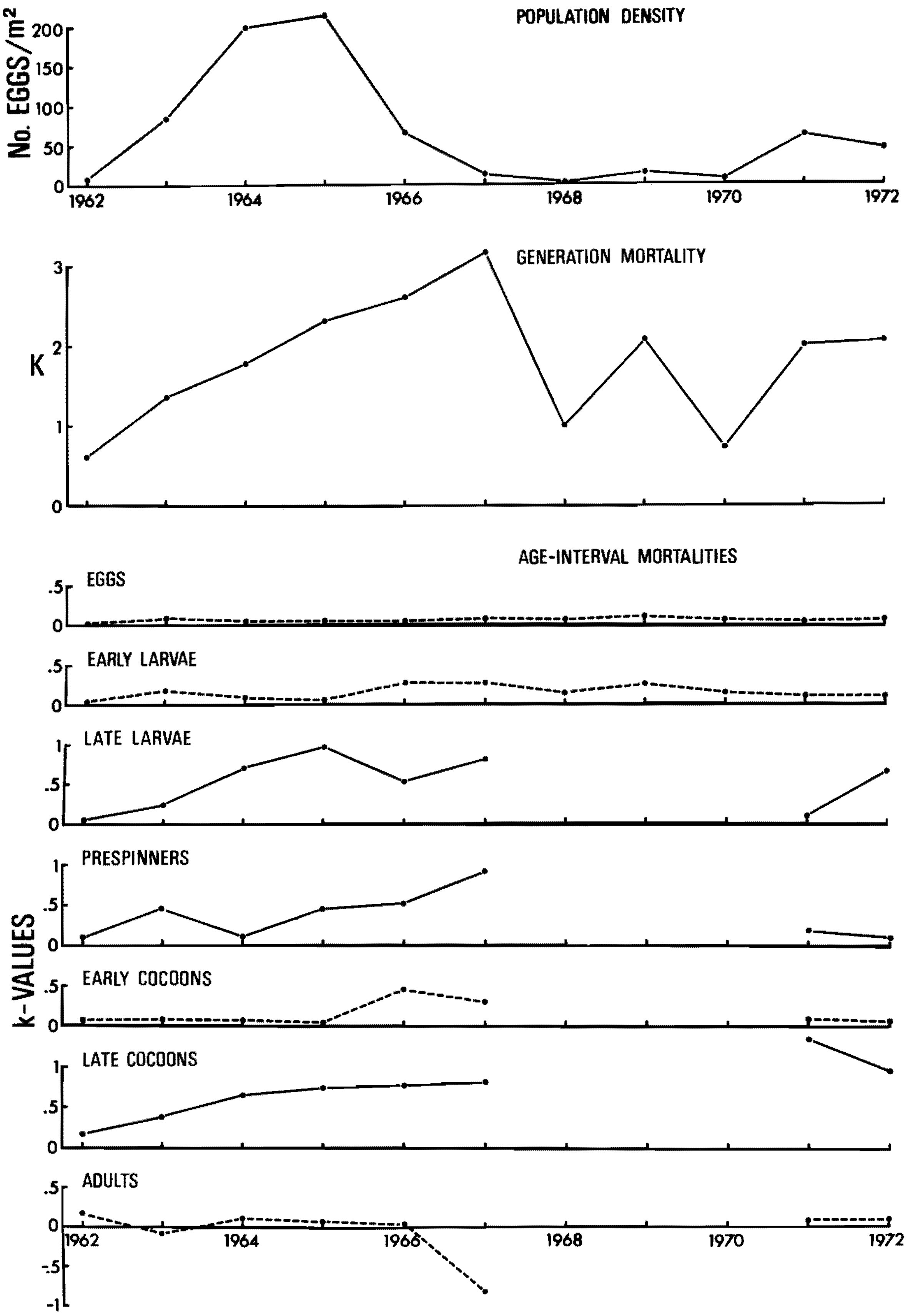

Figure 2. Population density, generation mortality, and seven age-interval mortalities of *Neodiprion sertifer* in area number 2, Chatsworth, Ontario, 1962-1972.

increased to a combined total of about 85 percent in 1967. These agents were evidently responsible for suppressing the minor population surge in 1971. *Pleolophus basizonus* (Grav.) (Ichneumonidae) was particularly evident then, but apparently did not occur in the stand in 1962. Late cocoon mortality did not act density dependently for the entire 1962-1972 period, but this was a time of increase in the size of the parasite complex and in the diversity of the predaceous fauna.

The adult losses shown in figure 2 were estimated as the difference between the density of eggs contained by eclosing females and the density of eggs on the trees in the next generation. They include the loss of adults, or eggs, due to emigration, predation, inability to oviposit, and incomplete oviposition, but are in fact the difference between those losses and the gain in eggs deposited by immigrating females. In most years there was a net loss of adults, or of eggs contained by adults, but it was modest and unrelated to generation mortality. However, in 1963 and 1967 there was a net *gain* of eggs; this is shown in figure 2 as "negative mortality," i.e., below the abscissa. Immigration in 1967 greatly augmented the resident adult population, which was very small following high generation mortality. In retrospect it seems particularly unfortunate that mortality estimates were not obtained for the period 1968 to 1970, inasmuch as the minor increase of 1971 may have been inaugurated by an injection of immigrant females.

In this outbreak the main factors determining density were obviously late larval mortality, parasitism by *Exenterus* spp., and late cocoon mortality, especially by parasites. Judging by the slope of the regression of k-values on total K, a test for key factors suggested by Podoler and Rogers (1975), late cocoon mortality contributed more than other factors to changes in generation mortality. It probably did so also in the other outbreaks illustrated in figure 1.

CONCLUSION

The foregoing outline of *Neodiprion* population dynamics is far from complete but some generalizations may be ventured. In *N. sertifer,* most of the outbreaks that have been studied intensively evidently occurred when the sawfly invaded previously unoccupied pine stands and was able to multiply for a few years before its natural enemies overtook it. Probably this pattern will persist as *N. sertifer* expands its range in North America and as reforestation continues to supply it with exploitable habitats. The more familiar pattern, shown by this species in Eurasia and by many native species, including *N. swainei*, in North America, i.e., that of outbreaks in forests in which both the sawfly and its parasites have been long-time residents, has so far been infrequent here. The origin of such outbreaks by *N. sertifer* remains obscure. Possibly climatic amelioration acting directly or indirectly somehow "releases" the sawfly from its normal restraints, or the situation could be like that in *N. swainei*, where there are grounds for thinking that population fluctuations are regulated or "driven" by natural enemies. It is hoped that the question will be answered by further life table studies on these and on other species.

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The Biology of Invasions

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ABSTRACT

Man as a historically active invader can readily appreciate the problems of invasion and the subsequent spectrum of colonization and reproductive patterns exhibited after arrival in a new area, as presented in this review of invasion. Dispersal strategies and patterns including migration are related to the influence of density on production of pioneers. The sources of pioneers from the original population distribution and the several varieties of fringes characteristic of population distributions are described with specific examples. Colonization, with the concurrent problems of founder's effect and inbreeding depression are shown to influence rates of success, dependent on the composition of the preexisting fauna.

The resistance of an ecosystem to invasion by exotics is seen as a problem in ecological stability and species packing, with limits according to faunal composition and climatological patterns.

The results of invasions and intentional introductions are summarized, and reasons for these introductions reviewed. Patterns of invasion success are described with specific examples. The continuing lack of predictability in the long-term organismal implications and environmental upsets of introduced species is reviewed and analyzed.

Conclusions as to the evolutionary advantages of colonization strategy are presented. Man's activities in manipulating introductions are reviewed with emphasis on the need for expanded research and modifications in land use policy.

A study of man's history yields not only a record of his continual progress in the arts, literature, science, and philosophy, but his frequent role as warrior and wanderer. Much of our literature is concerned with the exploits and genealogies of conquerors and the fates of those peoples conquered. Another of the great historical patterns has been the discovery and colonization of new areas, notably the "New World," Australia, and Africa.

These two interacting aspects of man's history, as warrior and wanderer, are founded in his characteristic population biology. As with other animals, our species moves when living conditions are not good. When man migrates, he begins to invade new territory or at least the territory is new to those making the move. He has found frequently that other men live in the area and, if so, these other men may fight to keep the area for themselves. In this situation the invading men must either conquer, die, be assimilated, or move on. Their history is one of war with the indigenous inhabitants and the eventual victory and subjugation of the conquered lands or the invader's extinction. An interesting recent account of this type concerning the displacement of American Indians by Europeans is available (Brown, 1971).

If man moves into territory that is uninhabited by *Homo sapiens* he still faces the problem of survival within the environmental limits of the new area. He has attempted to enhance his chances for survival in new areas by bringing some of the useful (and accidentally the harmful) parts of the old environment with him. Rather than relying on the unknown plant and animal species that may be present in a new land, man has brought his previously domesticated plants and animals along. So he not only has the problem of whether he can survive in a new environment, but whether the new environment will or can be made to adapt to support the other species he brings with him. Thus, we each have an abiding, though frequently subconscious, interest in man's wanderings and their outcomes.

Man is certainly the most influential single species that has ever invaded most ecosystems. Through a variety of land uses, he modifies the existing ecosystem and its trophic structure to produce desired agricultural and other natural products, thereby establishing, through time, a dynamic balance between the manipulated environments maintained by man the invader and those species of the pre-existing ecosystems that can tolerate the manipulated environment. Man is also greatly involved in the accidental introduction of alien species though frequently unconcerned as to the potential hazards and benefits of introducing exotic species into a new ecosystem. The following discussion is designed to bring out the various aspects of significance in the biology of invading animals in the hope that such an effort will stimulate others to investigate this subject area.

Let us begin by considering what an invasion is and what it implies. The definition of invasion by previous authors has contained two specific elements: arrival of the species in a new area and survival of the species through continued successful reproduction by each generation. The problem with compartmentalizing the definition of this biological process is that a spectrum of responses exists for animals entering a new environment, dependent on the degree of fitness exhibited by the animal to that new environment.

Animal species have entered areas they previously did not inhabit and have managed to become integral units within the new ecosystems (invaders within the classical definition). However, this definition does not account for the cases where the entering species eventually dies out, even after a number of generations have been produced, or for those that manage to survive for some time in the new environment, but fail to reproduce. These are all invaders with various degrees of success measured in terms of reproduction and length of survival (figure 1). A broader definition of the term that includes the spectrum of success would be one that defines *invasion* as *arrival of individuals of a species in an ecosystem that does not already have that species existing in it.* Of course, multiple invasions by a species may also occur as when different races of a previously established species invade and themselves become established.

The term invasion is interrelated and frequently confused with dispersal, migration, and colonization, several related terms used in animal biology. *Dispersal, the tendency for movement,* results in a scattering of individuals from their point of origin as they seek food, shelter, mates, etc. *Migration* is an *adaptive dispersal,* often linked with the need of a population to relinquish a habitat that is only transiently suitable for survival or breeding. Migration is characterized as being a persistent intensification of locomotion with a high degree of undistractedness, that is, it is nonappetitive. Reproductive stimuli fail to elicit a response by migrants and feeding stimuli are generally ignored except when fuel reserves become exhausted. Migrants orient themselves so as to leave their old habitats either by passive or active transport, with direction determined by air and water currents, or by controlling their own track. The population, or that portion of it leaving the habitat, may ultimately seek a new site for reproduction after a migration, or it may return to its original breeding grounds as conditions for breeding again become more favorable.

The migrant may not leave the populational area but simply move through some part of the contiguous population distribution, or it may emigrate, leaving the population's area of distribution. If it successfully locates another suitable habitat that is already occupied by members of its own species, it is an immigrant to that habitat. However, if the habitat is not already occupied by its own species, then it is an invader.

Not all invaders are active migrants; they may be invaders as the result of passive movements. Invaders may be transitory, disappearing either before reproduction (vagrants) or after a few generations (unsuccessful colonizers). If they find the new area suitable for reproduction, they may be the pioneering (first) generation in the establishment of a colony. *Colonization is the ability of a species to utilize environmental resources of areas previously uninhabited by the species for production of young and continued existence in the new area.* Successful colonization eventually results in the integration of the colonizing species within the ecosystem with adjustments by both the colonizing species and the other elements of the ecosystem (figure 1). The adjustments involved in integration are the final aspects of the establishment of the species in its new ecosystem.

The immediate implications of an invasion resulting in successful establishment are that the species must have some way of getting from its source ecosystem to the invaded ecosystem. Although most of the literature is focused on the method and frequency of movement from one ecosystem to another, a large array of factors within the source ecosystem and invaded ecosystems bear on successful colonization as much as the responses of the invading species to its new ecosystem (figure 2).

DISPERSAL

Dispersal resulting in a scattering of individuals is an important consideration in a discussion of invasions. The dispersal stage of an organism, due to its tendency to move, is precisely the one likely to invade new areas. This dispersal stage may not always be determined easily, except when it is the only stage with obvious locomotory appendages like the wings of adult insects, but it does tend to be resistant to environmental extremes. Because these extreme conditions are most apt to injure tissues undergoing rapid change, the dispersal stage also tends to be other than the embryonic

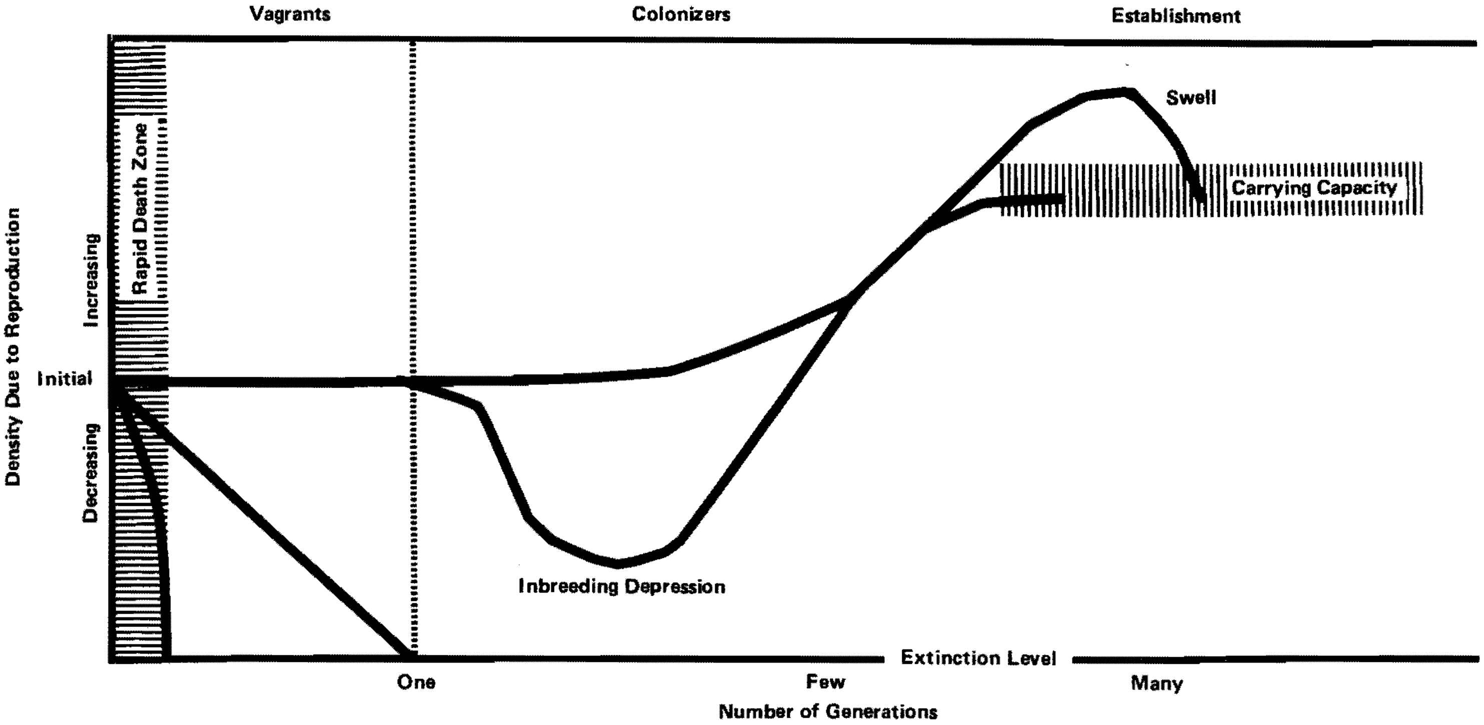

Figure 1. A spectrum of invasions is presented by the common reproductive responses of invaders in a new environment. Specific examples of animal invasions that illustrate these generalized responses are presented in the text.

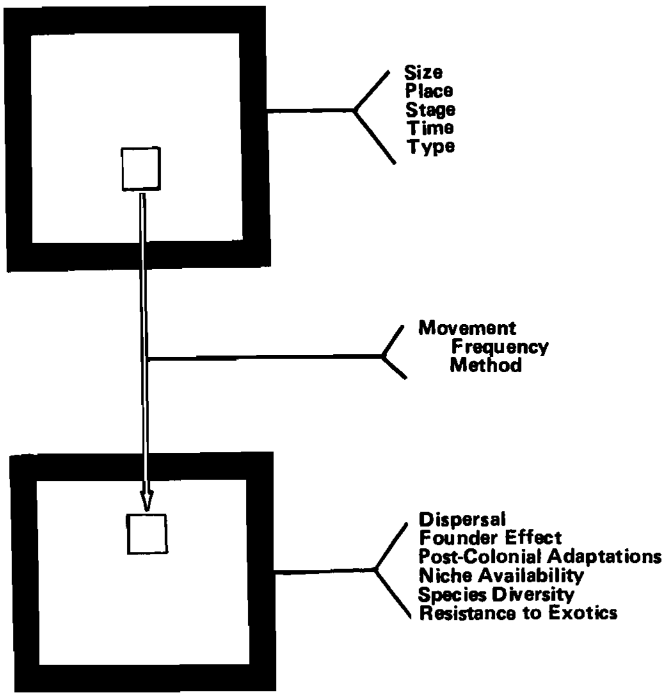

Figure 2. Descriptive model of the factors involved in invasions.

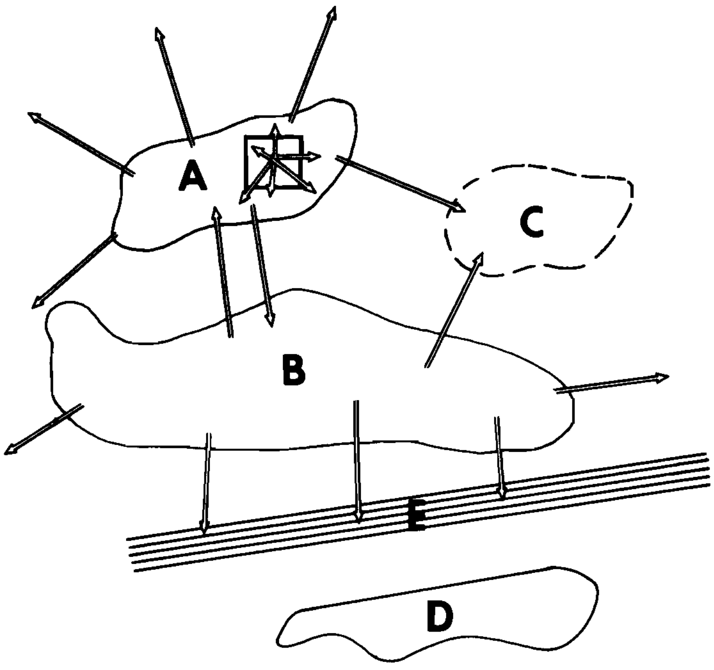

Figure 3. The total distribution of a single hypothetical species consisting of three isolated populations (A, B, and C). Dispersal of individuals from area A and/or B quickly repopulate area C, where the population has recently been eliminated, as by a late frost. Movement between local populations tends to swamp locally selected genotypes and mixes the total gene pool. Area D is potentially suitable for the species, but invasion cannot proceed unless barrier E is overcome in some way (unusual storm, mechanical movement by man, etc.). The inset of area A indicates that movement away from a single source (young mice deserting a nest, aphids dispersing from a plant, etc.) is multidirectional.

one, or if the egg acts as the dispersal stage it does so when embryogenesis is not active.

Dispersal in animals functions to repopulate areas in which the species may have been eliminated through deleterious conditions such as when a local population of insects is killed by frost. Dispersal also acts to mix the gene pool by transmitting genetic material from one part of the species' distribution to others and tends to overwhelm locally selected genotypes, depending on the numbers involved and the differences in selective forces between the habitats. Of course dispersal frequently sets the stage for successful invasion into areas previously lacking the species by production of dispersal forms into an environment with conditions right for transfer across previously effective barriers (figure 3).

Plants, insects, and other terrestrial invertebrates have similar distribution patterns that differ rather drastically from those of mammals and birds. These differences in distributions are partially a result of the relative powers of dispersal in the various groups. Plants have greater dispersal powers than higher vertebrates and tend to bridge water barriers with much less difficulty. However, once the mammal or bird does cross, it tends to become established more easily. Therefore, while plants and land invertebrates are better at dispersal, the higher vertebrates are better at colonization (Mayr, 1965).

Passively dispersed organisms are at the mercy of the dispersing force (air currents, water currents, or a moving substrate for phoretic organisms) for the direction and extent of movement before ultimate deposition. Actively dispersing forms normally must undergo a minimum period of dispersal activity before the stimuli that cause settling have any effect. Aphids probably receive the proper stimuli for settling, such as a yellow substrate, soon after they have begun their dispersal flight. The primary stimulus is visual. However, the settling threshold is very high so that flight continues until the settling threshold is lowered and the locomotory threshold rises above it. Also, a direct positive correlation has been shown between the distance an aphid flies and the number of progeny it can produce. Therefore, long distance flights or at least long flight periods are selected for in the Aphidae.

Passive methods of dispersal involve the use of flotation, sail, and clinging devices. Active methods involve the locomotory structures available to the organism. They may be special structures used only for dispersal, such as the wings of termites that are broken off after the dispersal flight. They might also be locomotory structures that are used in day-to-day living.

In the higher plants the seed or other propagule usually serves as the dispersal stage, e.g., winged seeds of maple or clinging burs. In most insects and many other animal groups, i.e. land vertebrates, the immature adult is responsible for dispersal. For instance, the wings of insects are functional only in the adult stage. Many of the higher vertebrates have relatively helpless young that require maternal care to some degree so that the adult is the only stage that could disperse. The lower vertebrates vary with respect to use of the young as dispersal forms. Certainly many fish follow the typical mollusc-echinoderm pattern where the young are planktonic and act as the dispersal stage. The very specialized zooparasites with their highly evolved parasitic nature depend to a large extent on the dispersal characteristics of their hosts. Parasitoids, the insect parasites of other insects, are not as dependent on their host's ability to disperse, because the adult stage usually has very good dispersal characteristics of its own.

Various modes of dispersal exist. They may be generally categorized by a modified Udvardy (1969) scheme.

1. Accidental long-distance transport by physical or biological carriers.
2. Slow penetration through an ecologically acceptable habitat, without an adaptive dispersal mechanism.
3. Migration (adaptive dispersal) which probably does not lend itself to invasion but does lend itself to the chance for invasion.
4. "Wandering" or "irruptions" (Welty, 1962) because of major habitat disruptions.

Migration, an adaptive dispersal in insects, is not an unpredictable act by adults of various ages that have perceived currently adverse factors or some appropriate signal. For most insects at least, migration is ontogenetic not opportunistic and is an adaptive departure not merely a casual change of place. No doubt migration does occur when there are qualitative or quantitative changes in the food or environment as a result of crowded populations. Increased population density or deficiency of food may tend to increase locomotor activity, but these are probably not causes for immediate behavioral responses to adversity.

In insects a biochemical maturation of the flight ability occurs after the adult emerges. The brain enzymes (cholinesterase) associated with increased motor efficiency increase. The tissue enzymes associated with efficient flight-muscle contraction (ATP-ase and acid-glycerophosphatase for quick release of energy from ATP and for metabolism of glycogen) mature. Also the various factors associated with the ability to fly mature (i.e. hardness of the cuticle develops, acquisition of fuel in the fat body). All of these factors mature together, although at different rates for different insect species (Johnson, 1969).

In such insects as the sapsucking plant bugs, *Dysdercus*, there is a period of flight after the adult emerges and undergoes biochemical maturation. However, if no food is encountered, no breakdown of wing muscles supplying nutrients for the developing eggs occurs, and the eggs do not develop. Thus, *Dysdercus* continues its flight until food is found (Dingle, 1972).

Many species that occur in unstable environments, e.g., temporary pools, carrion, and decaying wood, make a considerable "investment" in dispersal. These populations with a high risk of extinction have a sufficient chance of founding a new population only if they make such a high "investment" in dispersal. An interesting example of this phenomenon occurs in some Carabid ground beetles living in shore habitats. The beetles are dimorphic, some being brachypterous (short-winged) and others macropterous (fully developed wings). Long established populations of these beetles tend to be brachypterous, because the fully winged morphs (dispersal forms) tend to disperse away from the original site. Consequently, newly established populations are primarily macropterous. The species breeds itself out of existence by positive feedback of the brachypterous into a diminishing habitat and removal of macropterous forms as they disperse from the site (den Boer, 1970).

Long range dispersal in birds is the exception rather than the rule, because of their characteristic *philopatry (return to their birthplace for breeding)*. During the nonbreeding season, however, the birds may be widely scattered. Migratory birds might be thought to be likely to invade new areas. However, although they can cover vast distances in their migrations, the problem of invasion into a new habitat is compounded because not only must the breeding area be suitable for reproduction, but the area to which they will later migrate when not breeding must also be suitable. An example of the extremes of such a problem may be seen in the case of the Pectoral Sandpiper, which has recently extended its breeding area from North America to north central Siberia. Those individuals now breeding in Siberia still make the long migration to their winter quarters in South America. The kinds of birds that are likely to be involved in invasions are those that occur in temporary aquatic habitats. As has been stated by Darlington (1971), those animals most likely to make long dispersals and to occupy new areas are the ecologically unspecialized ones that are not closely bound in stable communities. These forms, upon reaching a new environment, such as a new island, frequently become members of new communities.

Endoparasites, usually characterized by a reduction of locomotory organs, depend on the dispersal abilities of their hosts to provide for their dispersal. Dispersal and migration of the host lead to wide dispersal of parasites, but also frequently bring the parasites back in close contact when the hosts, i.e. migratory birds, return to their breeding grounds. Dispersal and transmission of parasites frequently are triggered by physiological changes of the host, such as reproduction, that stimulate parasite reproduction. Parasite dispersal is insured when aerobic conditions are required for the eggs. Such conditions are met by release from the host's body. This mechanism also prevents excessive multiple infestation of any given host and increases the potential success of the offspring by introducing them into an environment with a high host density. For most parasites the transmission stage is also the dispersal stage, if one must be designated (Croll, 1966). However, parasitoids, the insect parasites of insects, usually are winged as adults and provide their own dispersal. The parasitoid also tends to kill its insect host before the host can reproduce partly because of the relatively small difference between the body size of the parasitoid and its host.

It is now thought that *Trypanosoma vivax* and *Necator americanus*, both human parasites, were introduced into North America with slaves brought from Africa. The hookworm (*N. americanus*) has become established, in part because of its direct life cycle. However, the tsetse fly, the intermediate host of *Trypanosoma vivax*, is absent in the New World. Without a suitable insect intermediate host, *Trypanosoma vivax* never became established.

At least two parasites, a cestode and a trematode, were introduced into Great Britain with the muskrat. Such parasites may become established in other hosts that occur in the area of introduction. Thus, a Siberian cestode was introduced into Bering Island with the Red-Backed Vole and has become established in the island's fox population (de Vos et al., 1956).

The Influence of Density on Production of Pioneers

Whether the population is newly introduced or endemic, an important aspect of population biology is the influence of population density and composition on the rate of reproduction and the kind of offspring produced. Given environmental conditions within the range of tolerance, the reproductive rate is maximal within some range of optimum population densities. Population densities above and below this optimum range yield both decreased reproduction and decreased survival. Because a newly introduced population would seldom be introduced into an area in such large numbers that overcrowding phenomena would act on the initial population, density characteristics that would actively influence reproduction and survival of pioneers must be those of the undercrowding phenomena.

A continuum seems to exist with respect to the influence of population density on the tendency to disperse or produce specialized dispersal forms. The aphids are an example of a type of animal tending toward an adaptive dispersal when triggered by population increase; the other extreme is exemplified by *Drosophila* which tends toward dispersal regardless of the size of the population. The degree of influence of population density on dispersal would have a direct bearing on the potential success of an invading species if the invasion were on a continental level, particularly with respect to the accidental or intentional mechanical introduction of an exotic species. The more dispersal is controlled by population density, the better chance the species has to establish itself in an area. The potential weakness of dispersal forms produced in response to high population densities usually does not occur because the organisms, through evolution, can detect environmental signals of impending events early enough to escape before the environmental quality deteriorates too far.

The Influence of Population Distribution on the Source of Pioneers

One of the ultimate controls of population density is the effect of short-term physical factors (weather fluctuations) operating within the distribution range of an animal. Because of the inherent limitations of a species built into its gene pool it tolerates a given range of conditions, both physical and biotic, within which it may exist through specialization within its own sets of limits to successfully utilize the environment. If we consider that a population generally is restricted to its role in an ecosystem's structure by the greater survival of those that remain in the area where the environmental requisites are relatively common, then a delicate biological balance may exist between those factors that cause organisms to remain where they are and those factors that cause organisms to move out of the habitat even under conditions that are seemingly satisfactory for survival. Significant differences may exist between species that live in temporary habitats and those in more stable ones. The part that fluctuating physical factors play is important in determining where and how a species distribution, even for extremes, is discontinued. However, the effects of these and the other determining factors require that we consider the distribution characteristics of populations.

Two general areas can be designated within a population distribution. The first is where the population does relatively well over a long period of time based on survival and population density. The population in this area should be termed the main population. The second area, surrounding the first and extremely variable in size, is the fringe area which is characterized by extreme variation of survival, size, and density of the population over the long term. Area one is not necessarily the area of optimal conditions for the population. Certainly there are many examples of animals living outside the optimal conditions because of factors, such as interrelated physical factors or intraspecific and interspecific competition. However, the main area is closer to optimal conditions than the fringe area.

A consideration of the relative importance of each of these areas as contributors to invading populations yields at least two circumstances. One is when the population within core regions contributes to the production of pioneers with no input from the fringe population. This would probably be the situation with animals that were dispersed primarily due to overcrowded conditions, such as some aphids. Another facet of this category would be that species fitting this situation would necessarily be capable of moving over very great distances, thereby passing over the region containing the fringe populations. This means that the invading nucleus would not have the advantage of genetic composition present in the fringe and would, therefore, probably be less fit to face the immediate problems of a colonizing population.

In the second case the fringe population would contribute more toward the invading population if dispersal were independent of population density because they are closer to potential areas of invasion. The problem these groups have is that their numbers would be small over the long period because of the low population density of fringe areas (Andrewartha and Birch, 1954).

Townsend (1952) and Carson (1955) both report differences between populations on the fringe and those located more centrally in the distribution. These characteristics are genetic in nature and concern chromosomal polymorphism. Da Cunha and Dobzhansky (1954) state that the amount of chromosomal polymorphism in a species *(Drosophila)* is a function of the number of ecological niches occupied or exploited by that species. Thus, where a given species is apparently the most successful and has relatively the highest population densities, its environmental mastery appears to be reflected in a high degree of chromosomal polymorphism. Of course, this also implies that in areas where the same species is less dense and less well adapted to its environment there will be a correspondingly lower degree of chromosomal polymorphism. Homozygosity of gene arrangement at the periphery may be due to genetic drift operating in small populations. This, however, does not seem to be the case because there are examples of clines of inversion frequencies that are very regular and gradual, and as the margin is approached homozygosity appears in a consistent and orderly fashion.

Inversions (as chromosomal polymorphs) appear to function primarily as restrictors of recombination through their limiting effects on crossing over. A new rigid group of linked genes is produced that effectively isolates it from recombination. Therefore, when a fit genotype is produced in this form the fitness is maintained and sexual recombination is reduced. This method of maintaining populational homeostasis approximates metagenesis. Because of this, peripheral populations with their reduced polymorphism and reduced heterozygous balance are far more capable of responding to new selection pressures and new evolutionary opportunities because they are less tightly knit genetically (Lewontin, 1957).

Remington (1968) evaluated the interaction between colonizing size and source of the colonizers. He emphasized the greater potential for success by invaders from fringe populations over those from the population center. In contrast, Lucas (1969) argues that the best chance of establishing a population would be when the founders were from an ecologically central population, because of their high heterozygosity and, therefore, increased variation. The best chance for *evolution* of a new type in the new environment would also occur when the founders were from the ecologically central population. He further states that sample size of the founder population is most critical when a central population is the source because the variation in the founder population is increased with sample size. For a founder population established from the fringe populations, size of the founder population is not very important because there is such a high degree of homozygosity.

Fringe Area Populations

Early discussion of fringe populations concerned a study of the elm, *Ulmus americana*, and its distribution (Carson, 1955). Two types of fringe were indicated. One "stable" geographic or topographic fringe exists in the eastern U.S. where the tree is limited only by the marine environment. This provides a firm, practically invariable boundary to the distribution based on the genetic material. The other fringe may vary tremendously and is categorized as "dynamic." In this fringe varying conditions cause perennial fluctuations in the extent of range. This dynamic border would seem the one most likely to provide material appropriate for invasion. Given a rather strict reasonable distance any propagule could move, the dynamic fringe could provide propagules a better chance to cross barriers than could the stable fringe.

In Chiang's (1961) work with fringe populations, he concluded that because the range of the distribution usually is delimited by barriers and because the fringe population is exposed more directly to these forces than is the main population, there must be as many types of fringe populations as there are types of barriers. He describes climatic, topographic, biotic, artificial, and actively moving fringe populations.

Climatic fringe populations are limited by unsuitable climatic conditions. Work with the European corn borer indicates that the northern boundary of corn borer distribution in the midwestern U.S. has been reached and constitutes a fringe area about 200 miles wide. This is the distance between the furthest recorded spread north and subsequent recessions. The fringe seems to be maintained by harsh climatic conditions including heavy rains and winds, low summer temperatures, and early frosts. Population levels remain low and fluctuate widely (Chiang and Hodson, 1959).

Topographic fringe populations are limited by topographic characteristics such as mountain ranges, rivers, and oceans. One characteristic of the topographic fringe population must be that it is the same as or very similar to the main population. Unless there is an ecotone present that is large enough to support a population and at least as wide as the normal range of dispersal of an individual, the fringe could not maintain itself as a distinct entity.

Biotic fringe populations of animals are those in which the population reaches its furthest limits as determined by the organisms used as food and their distribution limits. This type of fringe is particularly well demonstrated in insects because many have very specialized food habits. More general feeders are less likely to be as restricted. This is also more common in phytophagous animals than in carnivorous ones. Chiang reports several modifications of the type. In one the population becomes adapted to feed on a new and more widely distributed food species. This causes an advancing fringe until other limits are again met. An example of this is the Colorado potato beetle, originally limited to the distribution of the Buffalo Burr, its original host. After the introduction of potatoes into North America the beetle underwent an additional extension of its distribution. It is still expanding since its introduction into Europe. A different modification of this type is the intentional expansion of the distribution of species, mostly plants, by man. This presents an opportunity for the organisms to undergo an expansion if they can modify to fit the new environments into which they are introduced. Plant species often are bred to fit a new environment; for instance, corn is bred to complete its cycle in the abbreviated growing seasons of the north. Some animal species also have been able to foreshorten their own life cycles to utilize the new areas; others have not.

Artificial fringe populations are best exemplified by populations that are contained by man's efforts at the quarantine. If the quarantine is effective, the population range of the species may be stabilized. This would fit only in those species with a natural barrier and would then only be a special modification of the climatic type. Domestic quarantines usually are not effective over the long term unless they are used to maintain the effect of a natural barrier, such as a desert or mountain range. These quarantines are maintained to restrict movements to the natural spread of the animal concerned and to stop man's mechanical transfer of propagules.

The actively moving fringe population is the most interesting one in the ecology of invasions. This fringe population may be either moving forward or retreating. Every species must at some time have gone through a period of active movement when climatic changes were drastic.

A characteristic of the actively advancing population is the "swell" phenomenon that has been noticed with many newly introduced species. The population density just behind the advancing front is usually far greater than in areas where the species has been present longer (Chiang, 1961). This seems contradictory to the negative logarithmic relationship between population density and the distance of dispersal from the population source as reviewed by Wolfenbarger (1946) and, therefore, deserves further consideration.

Chiang (1961) summarized a variety of hypotheses that would explain the "swell." One explanation is differential intrinsic vitality where animals in new areas of infestation seem to be more active than those in areas of older infestation (Wellington, 1957). Another explanation is differential reproduction due to exercise. As reported by Johnson (1958), some insects have a positive correlation between exercise (flight) and productivity. Those insects flying the furthest would probably produce the most young. Experiments by Dobshansky and Wright (1943) also show that a small percentage of the population flies much further than the majority in any given dispersal flight. This achieves some degree of isolation if only at the fringe, and because of the distance flown and resultant exercise, the fringe population, though low in numbers, probably produces more young per female. As in certain European eels, females may constitute a greater percentage of the fringe population than of the main population, thus increasing the population density in the swell due to greater reproduction.

Another possible explanation of the swell phenomenon might be the differential speeds of spread of the animal concerned and its natural enemies. If the mobility of the animal is greater than that of its natural enemies, the population in the advancing fringe region will have outdistanced its natural enemies and could maintain a higher population in that area until the natural enemies caught up. This type of phenomenon holds true primarily with the host specific type of natural enemy (Chiang, 1961).

Chiang (1972) analyzes one of the best documented cases of the swell phenomenon, that occurring in the invasion and subsequent establishment of the European corn borner in Minnesota and South Dakota. In his analysis of this moth, population peaks behind the front, that were originally described (Chiang, 1961) as "a pattern of change after the population spread had reached its limit," take on the pattern of population swells subsequent to the original invasion. Such swells are projected as being sequential invasions of different European corn borer biotypes that have evolved at other sites.

The Japanese beetle demonstrates the swell phenomenon quite well. It seems to have invaded the U.S. in about 1911. In 1919 it was reported that a single person could gather 20,000 beetles in a day. In one orchard containing 156 not very old peach trees, 208 gallons volume of the beetles was taken in 2 hours, and the next day the numbers on the trees appeared unchanged (Elton, 1958). Another possible explanation for the swell phenomenon is covered later in this paper in the section dealing with resistance of the ecosystem to invasion by exotic species.

Competitive Ability

A major contributing factor toward a species' success as an invader is its competitive ability. DeBach (1965) indicates this in his analysis of successfully colonized entomophagous species. He states that many introduced species fail to become established in spite of host specificity and the presence of many hosts. It frequently has been assumed that physical factors are too harsh for the introduced species, but DeBach says perhaps competition with other species already present may be the primary reason why many species have not become established.

In their book on island biogeography, MacArthur and Wilson (1967) state that a species can't colonize unless it is a good competitor. They also bring out the idea that the more competition that is present, the fewer propagules will be able to reach a safe population level, that is, one not in immediate danger of extinction. The number of potential competitors present depends upon the size of the island. Therefore, they conclude that size of the invaded territory, whether the whole island or some ecologically distinct part of it, will determine the rate of colonizing success.

In the early stages of colonization the population can expand without any difficulties presented by its own population pressures. It can grow at an exponential rate limited only by external physical forces and competition from other species that it may face for its requisites. Later in colonization, competition with other individuals of the same species will become significant (Lewontin, 1965).

Successful competitive capacities can dramatically affect the invaded area because most consumer levels already have been filled by animals indigenous to the area or invaders from the distant past. The process of adaptation to the environment occurs in trophic level "n" (that containing the invader), level "n-1" (the one supporting the invader's trophic level, that is, its food), and level "n+1" (the level supported by the invader's level, that is, its natural enemies). These adaptations, normally covering millions of years, are drastically upset by the introduction, accidentally or naturally, of other organisms into any trophic level.

The virtual elimination of any dominant organism in an ecosystem must have drastic effects on the entire community through the dramatic modification of the food web and environment. The invasion of a single species must have caused these changes in some cases; e.g., introduction of the chestnut blight organisms not only eliminated the American chestnut from the North American forests, but must have entirely changed the character of this community by also eliminating all animals relying on the chestnut, directly or indirectly, as a shelter or energy source.

COLONIZATION

Once pioneers have been produced and have actively or passively made the invasion movement, they face contact with the new environment. A number of events, both intrinsic and extrinsic, affect the success of their invasion in this new environment. The extrinsic factors are discussed in the next section. Among the important intrinsic aspects affecting the success of an invading species are the size of the initial population, the founder effect and inbreeding depression, dispersal and reproduction characteristics, and post-colonial adaptations.

Size of the Initial Population

Although an invading species may reach a new and suitable habitat in any number, a minimum population is required to give the invading species an appreciable probability of becoming established. The minimum level depends on a variety of biological characteristics of the species involved, but most important are the replacement rate of the species per generation and method of reproduction, including whether the species is sexual and, if so, its mechanisms of mate location.

MacArthur and Wilson (1963) calculated some of the pertinent information concerning the required size of the initial population, assuming several biological characteristics of that population (the frequency distribution of the descendents, several arbitrary replacement rates), and compared them with the probability of extinction of various-sized initial populations due to chance. From these data they calculated the size (number of pairs) of the initial population required to give the invaders a 50:50 chance of survival.

A propagule of infinite size is required for species with a replacement rate of 1, but the required propagule size drops off rapidly as replacement rate is increased. With a sexual species, a replacement rate value approaching 1 is probably realistic because of the problems of mate location (MacArthur and Wilson, 1963). However, the improbable happens occasionally in nature according to the studies of Carson (1971). In his work on the evolution of *Drosophila* species in Hawaii, the genetic evidence supports his statement that some island populations must have originated from the invasion of a single gravid female. Such a situation gives the opportunity for extreme *genetic drift (variations in gene frequencies that arise because of sampling errors in finite populations)*, because such a small sample of the original gene pool reached the island. This must have been followed by a population flush with the opportunity for mutation and excessive recombination. Because of the temporary relief from natural selection (at least some of the factors), a number of odd recombinants survived. When the population crash finally occurs in such a situation, a number of isolated and semi-independent demes (local populations) are formed. Then, when interdeme selections occur, new species may result. Carson terms this nonadaptive evolution. Following species formation, the new independent gene pools undergo adaptation. This is intrapopulational adaptation by mutation, recombination, and selection.

The Founder Effect and Inbreeding Depression

The initial population of an invading species will be small compared to the total population from which it is derived and will have only a small sample of the genetic material present in that parental stock. Because of this, the founder population will tend to have a gene pool rather different from and more restricted than that of its parental population both in the variety and proportion of genetic material available. The smaller the initial population, the less predictable is its gene frequency. This is the "founder effect" (see Halkka et al., 1970).

Not only does the initial population have the genetic indeterminacy of small populations with which it must cope to survive, but it also may have depressed reproduction. The depressed reproduction is due to the population's small size but not necessarily to "undercrowding" as discussed earlier. This inbreeding depression is an overall reduction of genetic fitness and may involve greater susceptibility to disease, loss of fertility, lower fecundity, lower activity and other general weakening. Severe inbreeding depression and the concommitant trend toward homozygosity gives the opposite genetic reaction of what occurs in heterotic situations (Mayr, 1963).

A subsidiary effect that would greatly influence the potential success of the invaders is whether they originated from the main population with its trends toward chromosomal polymorphism or a fringe population with homozygous trends. Source of the invaders would then have a great influence on the required numbers of individuals bearing that quantity of genetic diversity necessary for survival. A difficulty lies in the fact that the fringe populations, while more homozygous, are also typically closer to unoccupied environments and may be able to adapt to situations more easily than do main populations (MacArthur and Wilson, 1967; Remington, 1968; and Lucas, 1969).

Dispersal and Reproduction of Colonists

If the initial population is large enough and has sufficient genetic variety to survive the bottleneck effects of severe inbreeding depression of those first few generations, it is also exposed to and must solve the problem of dispersal in the new colony. Species in which production of dispersal forms is triggered by high densities are favored in the new environment, even though these same characteristics may not be beneficial in production of the original founders.

The advantage of maintaining the integrity of any new colony through reduced dispersal of colonists is obvious. Density dependent dispersal allows for population buildup in discrete locations and gives some initial advantage in mate encounters for reproductively mature bisexual forms. Those that undergo dispersal without control by density tend to fail more frequently because of the hazards of sparse population effects acting upon them. Individuals from the core population would survive best if their dispersal were triggered by density. Fringe individuals with density independent dispersal habits would also do well. However, the other two combinations might well produce good invaders that were poor at colonizing after reaching the new environment and vice versa.

Habitat selection and mating are so specific in some animals, i.e. some ant and termite species, that their colonizing abilities are greatly restricted. However, that very restriction would be advantageous in keeping the first generations of a founding population together if they have already entered the new area. By keeping the population in a restricted area, a compact nucleus of colonizers capable of slow penetration throughout the new area is formed. Small dispersal power resulting in slow dispersal through the environment is an advantage to the species that has recently invaded an environment. In effect, it approaches the density dependent dispersal response of other species by restricting individuals within an area and thereby optimizing contact between the sexes.

In an analysis of selection for colonizing ability, Lewontin (1965) examined the effect and relative significance that small changes in fecundity, longevity, and length of developmental period have on the rate of increase. He concluded that the reduction in the number of time units for development that would be required to be equal to an equivalent increase in overall fertility is least with animals of high fertility and rapid development. With animals of low fertility and lengthy development, greater time changes would be necessary to give equal increase in overall fecundity. Regardless of this detail of relationship, the general rule of a small change in developmental rate equalling the effect of a much greater increase in fertility holds true. A 10 percent change in rate of development equals almost a 100 percent change in fertility. Therefore, colonizing species should have little genetic variance in development time but may have a large variance in fecundity because selection will have acted more efficiently to shorten development time than to increase fecundity. In a founder population the theoretical trend will be for selection toward a shorter developmental time, a longer reproductive life, and greater fecundity.

Post-Colonial Adaptations

Complete pre-colonization adaptation to the new environment seems to be the rule for successful colonization of biological control agents (DeBach, 1965). In most cases, whenever a series of insect natural enemies are introduced to control a pest species no matter how many in the series, only one, if any, successfully becomes important in control. DeBach could determine no common characteristics in those outstanding biocontrol agents when compared to other and unsuccessful species. All species seemed well adapted to the host and were quite host specific.

DeBach's reports of post-colonization trends in distribution and abundance for six species of scale parasite in California demonstrate the lack of accurate predictability as to the changes that occur and the results. He also shows that, at least for biological control agents, very few have ever shown evidence of post-colonization increase in genetic fitness.

Not only does the previously discussed work of Lewontin (1965) theorize post-colonization adaptations, but MacArthur and Wilson (1967) also indicate changes in invading species. The latter authors point out that the invading species reacts to its new environment in one of two ways. A shift in diet or habitat preference and either a contraction or expansion of diet or habitat is possible. Although either diet or habitat may be modified, habitat would seem to be changed most easily. The more species present in the new habitat, the greater is the restriction from competitors on a probability that larger numbers of species indicate a relatively rich energy source. Sparsely inhabited environments allow for wider habitat use and dietary variety within the limitations imposed by the lower trophic levels.

Keast (1971) provides an example of habitat expansion by island birds. Robins (genus *Petroica*) are usually characterized as staid and somewhat dumpy birds that sit motionless at a lookout until suddenly pouncing on their prey. However, in Tasmania, which lacks flycatchers in open country and dry forest areas, robins have expanded their niche to partially usurp the flycatcher niche with its characteristic restlessness, hovering, and insect-flushing forms of behavior.

Although a variety of postcolonial adaptations have been theorized, few have been recorded. One such case is the European corn borer that has evolved at least three biotypes in North America that differ in aspects of their ecology and morphology. The three biotypes studied were from Missouri, Iowa, and Minnesota. Among the characteristics in which the biotypes differed were percent survival, percent of larvae entering diapause, rate of development, sensitivity to host-resistance factors, and the dimensions of certain morphological structures (Chiang, Keaster, and Reed, 1968; Kim et al., 1967; and Chiang et al., 1970).

INFLUENCE OF THE INVADED ECOSYSTEM

Although the species' characteristics discussed in the preceding sections are of primary importance in determining production of pioneers and their ultimate colonizing ability, the characteristics of the species are not the only determinants of success in establishment. A number of characteristics of the invaded ecosystem and its interactions with the invaders must also be discussed. These aspects are availability of niches, timing of life processes, utilization of the environment, species diversity within the invaded area, and resistance of the ecosystem to invasion by exotic species. Although these aspects are interdependent, they will be introduced as units. There is a vast array of interactions possible between them.

Availability of Niches

To make a successful invasion, the immigrating propagule must arrive at a location that has the niche available for which the genetic constitution of the propagule has been preadapted. If the *niche (a species' role in the structure of an ecosystem, including its environmental requisites)* to which it is preadapted is not available in the new location, the propagule does not survive. If it is available, the individuals making up the propagule will make an active choice of habitat through a series of behavioral patterns it has evolved that facilitate suitable habitat location. The propagule must be able to outcompete any indigenous species present for requisites.

A species may be lacking when its niche apparently is present and available. A number of factors, other than the species' ability to get to the area, may account for its absence. The habitat may be suitable, but only temporarily. A species occupying a broad niche that encompasses the niche of the "missing" species may replace the species. The area of the habitat may be so restricted that it cannot support the species. The habitat also may be superficially suitable but lack some of the ecological requirements of the species. This last explanation is probably the most common cause for the lack of a species in a "suitable" habitat. However, Howard (1965) states that empty niches probably exist in all biotas. He specifically points out that most biotopes have many unoccupied vertebrate niches. However, even with the number of empty niches in the ecosystem, an invader cannot survive unless its specific niche is unoccupied or it is a better competitor than the indigenous species or it can change its niche (MacArthur and Wilson, 1967) by expanding or contracting within the limits of its "fundamental niche."

An organism's *fundamental niche* is *the totality of the ecologically significant variables in the environment and the organism's responses to these variables, including only the environmental states* (the particular combinations of variables) *in which the organism* (population) *can maintain itself indefinitely.* An environmental state can be included within the fundamental niche only if each variable of the environmental state is within the tolerance range for the species. Even though the species can maintain itself indefinitely at this particular state, it may not be functioning optimally because one or more of the variables may be outside the optimal range. Individual animals have the power to respond to suboptimal conditions by undergoing adaptation. At the population level, conditions that are suboptimal for the first generation invader may be overcome in future generations through evolution.

The expression of fundamental niche by birds under competitive pressure has been identified in part. Cohabiting bird species may be restricted in a number of ways, e.g., to a specific vegetation type. They also have specialized behaviors in which feeding is restricted to a particular vertical level in the vegetation. In some cases as many as ten different levels have been identified. Feeding may be further specialized in that the cohabiting species feed on different foods or on similar foods but in different proportions. Finally, seasonal or diurnal patterns of feeding may differ (Keast, 1971).

Timing of Life Processes

How and with what ease an organism enters a resting stage greatly influences its colonizing abilities. Because the progress of seasons is likely to be at a different stage in the invaded ecosystem, the environmental signals (photophase, moisture levels, etc.) could induce *diapause, the condition of arrested growth and development,* or other behavior to allow the invader to escape temporarily adverse conditions. Organisms with obligate diapause and/or migration are likely to be out of synchrony with the invaded area and die as a result.

Utilization of the Environment

How the potential invader utilizes its environment will partially determine its success in a new area. This is accomplished through different selective pressures dependent on the species' diversity and population densities of the area. Productivity of a species is favored in uncrowded environments. The species that can harvest the most food is favored. Even if its use of requisites is wasteful, it (the r-strategist) will rear the largest number of offspring and be the most fit. However, extractive efficiency is favored under conditions of overcrowding. The favored species (the K-strategist) is that in which individuals can replace themselves with the least waste in converting food into offspring (MacArthur and Wilson, 1967). Obviously then the outcome of the potential invasion may be determined by how the intruding species utilizes the environment it enters and the population levels already present in that environment.

Mobility and movement of the species after it enters initially are certainly affected by the carrying capacity of the environment. This has been shown with the invasion of Australia by the aborigines. Australia has a much greater *carrying capacity (ability to support biomass per unit area)* for man along its coastal areas than in its interior. This is primarily a function of precipitation. Aboriginal man probably entered Australia across the Sunda and Sahul Shelves and then penetrated the entire continent. The rate of penetration was determined by the carrying capacity of the environment, even though extractive efficiencies of the migrants may have changed in different regions. Along the coastal regions penetration was slow because colonizing groups didn't have to move far from their parent colonies to enter an environment that could support them. Once in a virgin area the colony could grow to considerable size in the relatively mild environment before the carrying capacity was reached and a new colony budded off from it to move south into new territory.

In the harsher continental interior of Australia with its low carrying capacity for humans, those establishing a new colony had to move a great distance to leave the extensive home territory of the parent group. The new colony could not increase in numbers appreciably without reaching the low carrying capacity, when new colonists were forced out of it (Birdsell, 1957).

Species Diversity Within the Invaded Area

The size of an area limits the number of species in that area and, if restricted enough, it also limits the size of the populations present. The relationship between size of an area and the number of species can be expressed in the formula:

$$N = PA^z$$

where N is the number of species within a given taxon. A taxon is a group of real animals recognized as a formal unit at any level of a hierarchic classification; examples are Insecta (a class) Culicidae (the family of mosquitoes) and *Homo sapiens* (the species of man). In the formula, A is the area, z is a parameter with very slight fluctuations when calculated among taxa or within a taxon on the worldwide basis, and P is a complex parameter based on the taxon involved, the population density, and the minimum number required for survival of the taxon.

The parameter z falls between 0.20 and 0.35 for most island biotas; at the continental level it falls between 0.12 and 0.17 (MacArthur and Wilson, 1967). Further discussion and extensive examples of the species-area relationship are presented in Preston (1962a and b) and MacArthur and Wilson (1967).

The important question to be considered in the effect of area on species diversity is how a species can enter and successfully become established. With a rather rigid species-area relationship, it seems nearly impossible to add species into the existing fauna. However, species may be added by displacing indigenous species with better competitors or by changing the overall density/minimum number required for survival. Of course, species could also be added if a fauna really were depauperate as some oceanic islands have been assumed to be. Preston (1962b) has attacked this last idea as false. He has shown that remote islands act as universes whereas equally sized areas (biological islands) on continents act as samples and tend to have many more species. A characteristic of samples versus universes is that samples tend to have a much higher ratio of species to individuals than universes and many more species represented by very few individuals. (See Preston 1962b for details.) Biotas of large islands pick up species because of the typical increase in environmental variation with flooding from neighboring biotas.

Limitation of species diversity probably exists in all biomes, although it is certainly easier to see in island faunas. This limitation may be accomplished by disallowing an organism to find enough requisites to survive in small areas. At least on islands, the density of individual species may reach a level of total rarity whereby all could become extinct (MacArthur and Wilson, 1967). In smaller areas competition may be more direct and less complex than in large ones (Darlington, 1957). The relative density of competitors, influenced by the size of the area invaded, also influences the size of the propagule necessary to reach a "safe" population level. Therefore, an organism may not be able to maintain large enough populations for survival.

Extinction rates may also be influenced by area. Fluctuations in the carrying capacity of the "home environment" caused by the vagaries of weather may force emigration. For species established continentally this aids in spreading and maintaining the population. For species limited to small specialized biotopes this could easily lead to extinction. Island species tend to lose their powers of dispersal and therefore to eliminate this problem. However, drastic loss of dispersal ability also leads toward even further isolation of *demes, local populations*, and tends toward situations where additional speciation is likely.

Both the distance and size of the invaded area from the various sources of invaders are determining factors in the rates of invasion and extinction of species. As the environment fills up with species that have invaded, the rate of invasion (numbers of species/unit time) drops because the numbers of species that can invade are approached by the numbers of those that have invaded. Conversely, the numbers of species that go to extinction in any biological or geographic island rise as the biotic environment becomes more diversified. The numbers of species that can invade are increasingly restricted with greater distance between the source and target because of their different powers of dispersal. Size of the invaded territory determines the numbers that can be contained because of the area-diversity relationship.

The number of species an area can hold is determined also by environmental production and its fluctuation. Theoretically, there is no limit to the number of species that can be packed into a constant environment if they improve the fit of utilization to production. However, the closer the species are packed in a fluctuating environment, the more susceptible they are to the fluctuations of the environment (MacArthur, 1970).

Resistance of the Ecosystem to Invasion by Exotic Species

Given the area-diversity relationship, the evolved fitness of indigenous species toward utilization of a fluctuating environmental productivity, and the expansion of fundamental niche toward such utilization, a real ecosystem resistance exists toward invasion by exotics.

If a species enters a new biotic community, it probably will enter an occupied trophic level and become a competitor with indigenous species that have evolved into that niche; i.e. it is another species joining one of the trophic levels made up of the species that derive their energy from vegetation. More species eating the same array of plants intensifies the competition between the plant feeders and results in a lower mean density of each species. Not only is mean density changed, but stability within the complex of competitors is increased (case I, figure 4). This increased stability frees the producer trophic level (the vegetation) to fluctuate more violently. This is why simple communities with one or a few species in the producer trophic level and in the primary consumer (herbivore) and secondary consumer (carnivore) trophic levels oscillate more and are more easily upset than biotically rich communities with many species at each level.

A characteristic of most accidental or intentional introductions of exotics is that their natural enemies are not introduced with them, in many cases because of the small sample size of the founder population. This lack of natural enemies is one of the prime reasons why species sometimes do reach outbreak proportions when they have been introduced into a new biotic community. The high density tends to be stable and is unacceptable if it assumes pest proportions. Introducing natural enemies will decrease both the mean density and stability of the large pest population and bring about some degree of suppression (case II, figure 4). This theoretical aspect is receiving much attention in applied biological control. Past attempts at introducing the natural enemies of exotics from their source areas frequently involved releasing as many species of natural enemies as could be transported, if they passed primitive screening procedures concerning their own pest potential. Now it is urged that releases of a

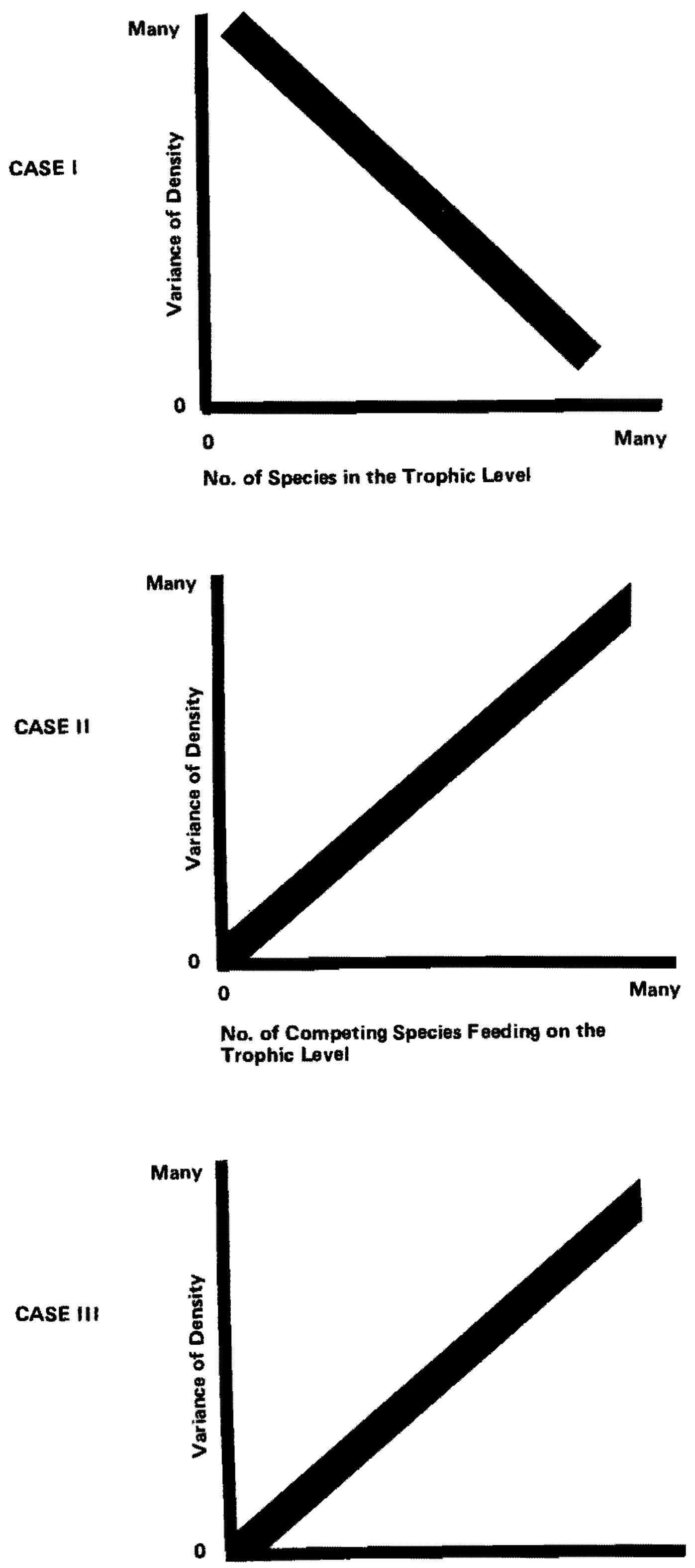

Figure 4. The effect of competition, natural enemies, and food quantities on stability of a trophic level. (See text for details.)

biological control agent be restricted to a fully screened species that would become a part of the complex of natural enemies only if:

1. it fills a functional niche not already occupied; i.e. it attacks some stage of the pest not attacked by other natural enemies, or
2. it more effectively fills its niche than some other species that already occupies it.

Such events with introduced wasp parasites of scale insects are recorded in the entomological literature (Watt, 1965).

Stability of an introduced species is also affected by the availability of food, i.e. the percentage of the trophic level on which it depends that can be used as food (case III, figure 4). This explains why such different organisms as the pine moth, a Lepidopteran, and the grasshoppers have such great instability (Varley, 1949). The pine moth is *stenophagous, feeding on only a few species*, but these few form the vast majority of plants in its habitat. The grasshopper is *euryphagous, capable of feeding on a wide variety of foods*, the majority of the many plant species in its habitat. The mechanism that accounts for this instability is isolation. When isolation losses are minimal (where the probability of the animal becoming lost over useless terrain is minimal), the abundance and instability of the species is maximal (Watt, 1965).

Thus, the overall effect on stability in an invaded area because of colonization by an exotic would be to:

1. increase stability of the native species in the same trophic level as the exotic,
2. change the exotic's own stability dependent on the number of competitors in the new environment compared to the original one,
3. lower the mean abundance of the native competitor species,
4. change the mean abundance of the invading species dependent on its abundance and competition in the area of origin,
5. tend to free the trophic level on which the exotic depends so that this trophic level becomes less stable, because of the increased stability within the introduced organism's own trophic level,
6. increase the stability of the exotic's population because of the host-specific natural enemies left behind when it invaded, and
7. increase the exotic's population stability, but around a smaller mean abundance in an environment with a small percentage of useful food (Watt, 1965).

Pimentel (1961, 1968) describes a mechanism he termed "genetic feedback" as the method where organisms evolve to better fit their environments. This mechanism is not limited to the interaction that occurs when a species invades a new biotic community, but may adequately account for events that typically occur after a successful invasion.

When a species invades a vast population buildup occurs, often followed by a decline to lower numbers, the "swell" phenomenon. The buildup can occur only if a high percentage of the organisms acting as food for the invader are susceptible to its attack. The buildup acts as a selection pressure on the food organisms, previously well suited to the former environmental stresses, thus modifying the gene pool through removal of the susceptible genotypes. A high percentage of remaining individuals offers some type of resistance to the attack of the exotics, but they were not as suited as the susceptible genetic combinations that previously dominated the populations. With the greater percentage of the food species somewhat resistant to the exotics, the invader population drops, easing the selection toward resistance and resulting in a resurgence of the susceptible but otherwise suited genotypes of the food species. The result of such a series of interactions may be recurring uniform cycles of abundance or more generally dampened fluctuations.

The interactions result in regulation toward survival of both interacting species. They evolve toward a balanced economy of supply and demand between the eating and eaten species and increase homeostasis within the ecosystem. Such regulation has occurred in the European rabbits introduced into Australia and the myxomytosis virus introduced to control them. The rabbit had increased to outbreak population levels before myxomytosis was introduced. When the virus was introduced (from South American rabbits), infection caused almost 98 percent mortality, but dropped to about 25 percent mortality by the sixth virus epidemic. The virus had evolved a less virulent strain and the rabbit had evolved some resistance to the virus. Less virulent forms of the virus became predominant in the rabbits simply because the rabbits didn't die as rapidly and were more often a source of virus to the vector (a mosquito) than the rabbits infected with the quick-killing virulent form of myxomytosis. The virus form with demands balanced by supply had greater survival value than the virus with the greatest rate of increase and highest density in its host.

THE RESULTS OF INVASIONS

Most records of animal invasions can be traced directly to man's activities. Most introductions are accidental and usually occur as man transports commercial goods that are infested with animals, but undetected by man. The worldwide flow of commerce, travel, and movement of agricultural products provides invasion opportunities for thousands of animal species. Although vertebrates, mollusks, mites, plant diseases, and nematodes are frequently introduced, the vast majority of potential or known pest species that are moved in world commerce are the insects. Table 1 shows the scope of interceptions made by a single national quarantine and inspection service. Such an operation probably detects less than 50 percent of the organisms that are moved across its national borders. Laws governing the restrictions on the movement of potentially dangerous animals have existed for less than 100 years. These restrictions have been seriously enforced only in the last few decades by most countries.

Table 1. Interceptions of known or potential agricultural pest insects by the plant quarantine division, U.S. Department of Agriculture. These figures constitute only about 18 percent of the actual interceptions of all insects made during any single year. Comparisons of interceptions between continents in part reflect the quantities of importations from each continent.

	Year			
Source	1966	1967	1969	1970
Africa	252	276	249	175
Asia	1516	1943	3184	3300
Australia	1158	1184	343	311
Europe	1723	1425	1119	903
North America*	1062	1827	2277	2742
South America	283	321	191	193
Unknown†	270	173	467	434
Total	6264	7149	7794	8058

*including Central America, Hawaii, and the Caribbean Islands
†including sources outside the listed land masses

Intentional Introductions

Man has intentionally introduced animals into many new areas throughout the world. Some of the earliest intentional introductions were by the European explorers who released domestic animals into island and continental faunas to act as a food source for subsequent explorers. Populations of feral goats and pigs are still found on many islands because of such releases. The early colonists in such areas as North America, Australia, and New Zealand released animals for food and also contributed a number of species through the escape of domesticated livestock and subsequent establishment of feral populations. Burros, horses, camels, cattle, dogs, cats, pigs, goats, and other species now exist in the faunas of several areas because of escape from domestication.

Naturalization and acclimatization societies were organized in several countries with the primary goal of introducing exotic animals into their areas. Many of the introductions began as an attempt to increase the faunal diversity, especially to increase the variety of game animals and thus to increase both the pleasure and productivity of hunting. Deer species, rabbits, pheasants, and partridge were favored, but many species were tried (de Vos *et al*, 1956; Wodzicki, 1950; and Phillips, 1928). These societies and other organizations were also responsible for introducing many additional avian species. Birds were brought in to act as natural enemies of pest insects, if the bird seemed to have contributed to the control of such insect groups in its land of origin. However, the introduction of many bird species seems to have been based on sentiment alone. Familiar birds were brought in from the human population's country of origin to add a touch of color or song reminiscent of the "old country." In effect, this type of introduction was an attempt to increase the faunal diversity.

Animals were introduced to supply natural products otherwise not attainable. Fur bearers were introduced into many areas usually with little success. The yield of rabbit pelts in Australia has provided considerable national income, although it has not compensated for the decrease in an already low carrying capacity for domesticated animals by the enormous rabbit populations that followed their introduction. The gypsy moth (*Lymantria dispar*) was introduced from Europe into North America to establish a silk industry. The gypsy moth escaped and causes extensive defoliation in the Northeastern United States in certain years, injuring and sometimes killing forest trees.

Many of the animal introductions have been based on the assumption that empty ecological niches existed and that the introduced animal would fill one of these empty niches as it apparently did in the country of origin. Certainly empty niches (in the narrow sense) were created by successful introductions when epidemic populations resulted partially because of the lack of predation pressure (an unoccupied niche) on the introduced pest. Recognition of this basic ecological imbalance has led to further introductions, but of parasitic and predatory animals potentially capable of suppressing the epidemic populations. Such natural enemies came from the country where the introduced pest originally evolved. The search for natural enemies is concentrated in such a source area because it is where the natural enemies will have evolved efficient mechanisms of detection and capture for the specific pest involved.

This last basis for introduction of exotics has developed into a separate field of scientific study. Built on the principle that an ecological balance can be restored at least partially between pests and their natural enemies and that a large majority of the crops and livestock species grown in any area have themselves been introduced, interested scientists now study applied biological control, or biocontrol. Such studies have not been limited to the parasites and predators of animals, but have been expanded successfully to include the natural enemies of poisonous plants, weeds, and aquatic organisms. A further extension of these studies is introducing efficient, but generalized, parasites and predators capable of attacking a number of species, sometimes all the members of a pestiferous genus, family, or order.

A summary of reasons for intentionally introducing animals into a new area would include:

1. to increase the faunal diversity,
2. to provide a source of food,
3. to provide greater pleasure, productivity, and diversity for hunters,
4. to fill empty niches,
5. to provide income through sale of natural products from the introduced species, e.g., furs, silk, honey
6. to provide color or song reminiscent of the settler's country of origin,
7. to provide a natural balance between an introduced pest species and the natural enemies that have evolved to attack it but are missing in the new area,
8. to replace one species in the environment with another one that is a better competitor (such competitive displacement can be used to eliminate a pest species or to supply a more useful species).
9. to increase the complex of generalized parasites and predators capable of attacking groups of pest organisms.

Various results have been obtained from the intentional release of exotic animals. However, the types of response to a new environment fall into four general categories:

1. The animals cannot be found in the environment into which they were released, that is, they disappear. Many parasitic and predatory insects fit this pattern. However, the introduced species may be observed in a localized area for a time, but their numbers continually decline, e.g., the *Coturnix* quail in the many releases within the United States.
2. The new arrivals undergo an initial period of success at least locally. They may gain a local foothold and produce young, but they fail to spread to adjacent habitat. After a period of time, the numbers decline. The moose, *Alces americanus*, has been released twice in New Zealand. An initial population increase from the 10 released to about 70 occurred over a number of years, but the population has declined to less than 40 evidently because of their slow rate of reproduction and high calf mortality. This may be an example of inbreeding depression operating over a few generations in a small population after introduction. In his original description of this kind of result from an introduction, Phillips (1928) states that some "initial stimulation" dies out in such a population.
3. The released animals become permanently established in the new ecosystem, but population levels, even after many generations, remain low. Because of such low population densities, the introduction of animals with this result never causes the changes in the ecosystem for which the introduction was intended. Dowden (1962) lists 45 species of predatory or parasitic insects that have become established after introduction into the United States to combat various forest insect pests. However, 8 of the 45 species have never reached population levels that contribute significantly to the control of the pests. Among the established but ineffective natural enemies are species of tachinid flies, coccinellid beetles, and eulophid, braconid, and ichneumonid wasps.
4. The introduced species, even from a founder population of only a few pairs, increases tremendously and spreads over large areas. Such species may be far more prolific than in their native habitats and build to epidemic proportions before reaching a balance within the new ecosystem. Numerous examples of such results are cited for mammals (de Vos et al., 1956), birds (Phillips, 1928) and illustrated for insects (Commonwealth Institute of Entomology, Distribution Maps of Insect Pests). Classic cases have been described for the giant African snail by Mead (1961) and the English sparrow in the United States (Barrows, 1889). The results of many different introductions into a single area have been described for vertebrates in Australia (Rolls, 1969) and mammals in New Zealand (Wodzicki, 1950). The general result for wildlife introductions throughout the world is discussed by Laycock (1966). Elton (1958) has discussed the analysis of introductions and the evolutionary implications of such introductions and has presented several classic continental invasions by animals.

Problems with Programs of Introductions

Many problems have developed when man has undertaken intentional introductions of exotic animals. In fact, introductions have caused more problems than they have solved. However, such programs have mixed results depending on the program goals. The results of programs designed to introduce game animals, thereby increasing the biomass and diversity of game available, have been relatively unsuccessful, not only because such species seldom become established but also because those that do become established often reach population levels that cause economic harm. Programs designed to counteract pest insect populations with insect natural enemies have been much more successful in achieving positive results with few, if any, harmful results. An examination of the problems encountered should, however, make one appreciate the complexity and thoroughness of the studies required before introduction. This does not mean that one should be categorically opposed to the theory behind introductions and to such introductions if the answers to a thorough and complete screening program indicate a high potential for success and low potential for disaster.

The primary difficulty with introductions is the low rate of success. Exotic species that seem to have the desired qualities for the new ecosystem either have undesirable qualities that are discovered in the screening program or fail to become established when released in the new ecosystem after passing the screening program. Even when ecological conditions have been acceptable, exotic species have failed to become established because the numbers released have not been sufficient to overcome the initial problems of introduction. Such was the case in the first few attempts to introduce starlings into the United States. On a worldwide basis, 90 percent of the organisms introduced for biological control fail to become established (Turnbull, 1967).

The introduced species that do become established usually fail to accomplish the goals for which the introduction was intended. Because of the overlapping niche requisites of most game species and the limits to the carrying capacity of the environment, the introduction of a game species seldom adds to the total standing crop of game. Native species suffer reduction in population densities as a reaction to the new competitors, sometimes with a resulting extinction of native species. The established exotics may displace their ecological equivalents, often because the exotics have a higher reproductive potential.

Exotics frequently seem to change their habits after introduction so that their actions are not those originally sought. Such changes may be caused by the founder principle and genetic drift, but more often are a result of a more complete expression of the species' fundamental niche. For example, highly efficient predators have been introduced into many areas to suppress pest populations. However, predators are characteristically nonspecific in prey selection. Because they are general feeders, the introduced predators may fail to suppress the populations of pests that were intended and tested as acceptable prey species. For the same reason the introduced predator may aid the pest population in its displacement of native competitors by preying on the native species that have not evolved defense mechanisms against the efficient predators. This does not necessarily mean a genetic change in the predator population, but may express their generalized predatory behavior as they take the prey of convenience (de Vos et al., 1956).

As mentioned earlier, many introduced species that become established fail to have the effect man desires simply because their populations never reach significant levels. Not only may they fail to produce the effect because of insufficient densities, but the effect produced may be counter to that sought because increase in number of pathways through a trophic level increases its stability.

The possibility of introducing unwanted parasites and diseases is a hidden danger in introduction programs. Serious livestock diseases have been introduced into continents with livestock importations. The diseases may spread through the populations of domestic animals and may be transmitted to the native animals. The diseases may be more severe in the native animals because they have not evolved resistance to the disease-producing organisms. Biocontrol scientists work toward preventing the accidental introduction of natural enemies with a biological control agent in their screening programs. Few such mistakes have been made because of careful screening. However, the early programs did lead to erroneous introductions, e.g., *Eupteromalus nidulans*, a Pteromalid wasp. This insect was introduced into the United States to act as a parasite of the brown-tail moth, an introduced pest. The wasp has been proven, subsequently, to be a *hyperparasite (parasite of a parasite)* on *Apanteles* and other parasitic wasps that are valuable biocontrol agents (Dowden, 1962).

The introduced species that have been eminently successful are those that generally have proven most troublesome. A high degree of success typically results in populations that are so abundant that they are considered pests. Such species are usually herbivores whose high populations directly affect the entire ecological community. The effect may be a change in the vegetation as dominants are removed and replaced by less palatable species, e.g., the effect created by feral goats on many islands. In such invasions the species spreads over great geographic areas entering various ecosystems and becoming so widely distributed that control programs become nearly unfeasible.

The general result of introduction programs on a worldwide basis has been economically and ecologically disastrous. Most introduced animals either fail or, if successful, become so abundant that the species causes economic damage. However, the programs designed to introduce the natural enemies of insect pests have generally been successful and economically rewarding because of the high specificity so common among the parasitic insects emphasized by most of the programs.

Programs designed to increase the abundance of wildlife are economically more rewarding when the focus is to improve the carrying capacity of the environment for those species already present. Such programs and those that release large numbers regularly (stocking programs) have been receiving more attention both in wildlife organizations and entomological programs. Leaders in some of the entomological groups anticipate increasing parasite stocking because such programs provide the pest suppressions necessary without the problems that are caused by pesticide use.

In summary, the introduction results are generally too unpredictable, both as to the establishment of the introduced species and its effect on the new community if it succeeds. The reasons for our failures are that we do not know the fundamental niche of the introduced animal (its genetics, biotic associations, and physical requisites) and know too little about the ecosystem into which it is released. Some introductions have been successful, most notably those of the specialized insect natural enemies that cause the least disturbance to the ecosystem.

CONCLUSIONS

Given the potential for success of the invasion strategy with the "empty niches" (Howard, 1965), power for dispersal (Wolfenbarger, 1946), and post colonial adaptability (MacArthur and Wilson, 1967), why then are there so many failures in establishment, both from vagrants arriving through natural movements (Glick, 1939; Johnson, 1969) and from man's efforts at intentional introduction (DeBach, 1965; DeVos et al 1956; Phillips, 1928; Wodzicki, 1950)? One obvious problem lies in the species-area relationship and the biological necessity to overcome extant species with overlapping niches for a place in the biota. The evolutionary pressure for genetic flexibility in maintaining a fit population in the presence of a wide assortment of competitors makes for a biota with powerful conservative forces. Harper (1965) has shown that establishment of an introduced species was most difficult (statistically) into communities with a low diversity index. The resistance of communities to invasion may be described as an "ecological homeostasis." Furthermore, the weather and phenological progression, even in an invaded area with appropriate requisites, must work against successful invasion on the basis of probabilities. Given that a species sometimes does invade an acceptable habitat, it still has intrinsic problems to overcome based upon the size of the invading nucleus, its characteristic replacement rate, and the bottleneck of founder effect and inbreeding depression.

A probable reward to invading species is a better chance at survival not only through exposure to new environments but to the competitors currently utilizing the limited resources in that environment. Survival by escape of expeditions from one impermanent site to another is an obviously beneficial strategy. The typical impermanence of the fresh-water environment, with its demand for great mobility by those that use it, has led to very widespread distribution of waterfowl. Mayr (1965) reports that most truly widespread avians are waterfowl species. Most insect species and other shortlived animal groups living in temporary environments may produce varying proportions of migrant offspring that are genetically distinct from those destined to stay in the habitat. Such differences are obvious in aphids where adaptive dispersal is feasible only in the winged portion of the adult population. Techniques for distinguishing such differences in other insects have not been developed. Indeed, genetic control for varying degrees of dispersive drive probably exists in all species that actively disperse.

The more environments colonized by a species, the higher its probability of surviving in at least one as the environments evolve. Even if the environments differ only slightly, there is some advantage. Therefore, colonization may be an effective strategy for survival (Wilson, 1965). The colonizing strategy not only increases the chances for survival of a species, it also provides for a situation where species packing through infrequent but repeated invasions and subsequent specialization, either by convergence or divergence (MacArthur and Wilson, 1967), yield maximum speciation. Although a successful invasion may benefit the invading species through testing of its competitive abilities and expanding its opportunities for speciation, invasion has some other significant biological results. Not only is there dislocation of species and increased ecosystem complexity but also widespread adaptations in each trophic level including changes in ecological stability. The consequences of such changes are frequently unexpected and may cause man new difficulties. Flexibility in niche acceptance by invading species in combination with man's vast disruption of the environment and his increasingly rapid transport of large quantities of biological-agricultural materials has set the stage for even greater invasion rates. The ultimate result will be biomes with much greater similarities because of large numbers of species in common and many fewer species unique to individual biomes. Many of these changes that are certain to be exceedingly drastic will be brought about by species that have been introduced by man or have invaded through other means.

Future Control of Invasions

Invasions will continue to occur through man's inadvertent movement of animals with materials he transports. The potential for such invasions is increased as new commerce lanes are established between countries and as new commodities are marketed intercontinentally; for example, a visit to the local grocery store reveals fresh fruits such as Kiwi berries from New Zealand, apples from Africa, oranges from Spain, grapes from Argentina, bananas from Ecuador, Hawaiian pineapple, etc. Each circumstance provides the potential for invasion.

Potential invasions by pests are increased as the introduction of exotic agricultural crops continues to expand. Soybeans are being produced in large areas now compared to in the past. Safflower plantings have jumped from 17,000 acres (1949) to more than 300,000 (1968) in the U.S. As such exotic plants are introduced and become significant in a new region, the stage is set for pests specific to these crops, if they arrive at the new location by some means and the other ecological conditions are within their tolerance range.

The pattern of agricultural efficiency, at least in the United States, is extending the monoculture technique to its extreme. As agriculturists strive for maximum productivity by using all land available, the field margins and fence rows are reduced significantly. These edges are the last bastion of species diversity in heavily managed agricultural regions. By drastic reduction of plant diversity, the alternate food supplies, nesting sites, and refuges of many species are effectively eliminated further simplifying the ecosystem and increasing ecological instability.

To increase our capabilities for suppression and prevention of invasions we must modify land use policy, increase our governments' flexibility in responding to invasions, and redirect some of the biological research toward solving invasion problems. Governments have provided legislation to establish quarantines, but such efforts at detection and survey should be increased substantially. Seldom is there a governmental mechanism to rapidly and adequately focus its scientific manpower toward eradication procedures against pests in the early stages of colonization. Governmental policies toward land use would be more effective agriculturally if the ecological stability of agricultural regions (as well as reinforcement of the ecosystem's resistance to invasion, which already exists) were considered.

More support for biological research in the applied aspects of genetics and ecology would provide the impetus to initiate or extend studies leading toward control. Such studies could yield new techniques for genetic manipulation of introduced pests and their destruction before they have achieved a wide distribution. Other aspects might lead toward competitive displacement of introduced pests or the breeding of genetically tailored natural enemies that have greater specificity for destruction of pests.

As has been demonstrated, manipulations of pest species or elements in the environment are available or can be developed to prevent invasions or to minimize the effects that invasions have on the newly colonized ecosystem.

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Some Aspects of the Ecology of Grasshopper Populations Inhabiting the Shortgrass Plains[1]

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ABSTRACT

Sampling of grasshopper populations, eight treated and two check, in the shortgrass prairie of southeastern Wyoming over a period of 6 years indicated that outbreaks on rangeland develop through a gradual increase in numbers over several years followed by a year of marked increase of 3 to 5 X's. A big rate increase occurred in the outbreak year of all sites, but only in two sites where numbers were sufficiently high the preceding year did grasshoppers reach outbreak densities. Of approximately 20 species comprising a range grasshopper complex, the majority showed increases in the outbreak year with only a few showing decreases. Populations of individual species increased as much as 6 X's in the outbreak year over the preceding year. Although a species' rank in a range grasshopper complex may change as a result of natural factors or of insecticidal treatment, the dominant species tended to remain dominant over a period of years in individual rangeland sites. Increase in density of all 10 populations and of the majority of species indicate a favorable environmental factor acting over the entire study area. The unusual increase of populations in the outbreak year appears to have resulted from the greater longevity of adults in the preceding year.

Violent fluctuations of grasshopper populations inhabiting the shortgrass plains of western North America have been recorded from the early 19th century to present times (Munro, 1949; Pfadt, 1949; and Smith, 1954). Yet little is known of the details of just how and why populations increase. Scharff (1960) has provided evidence that on Montana ranges the critical time for increase in populations of the migratory grasshopper, *Melanoplus sanguinipes* (F.), is in August and September when the grasshoppers are adult. At this time the favorable host plants, chiefly forbs, are often mature, dry, and unpalatable, furnishing suboptimum nourishment for egg development; however, when rainfall is adequate and vegetation green, fecundity of females and survival of eggs are correspondingly high. Newton and Gurney (1956) cite that more than 100 species of grasshoppers feed on range vegetation. Because most of these feed on grasses of which at least parts remain green through the insects' adult as well as nymphal stage, food does not appear to be a limiting factor. Little published information exists on how populations of these range species, which number around 20 in a complex, increase to injurious levels. Even less information is available on how numbers of the individual species within the complex fluctuate.

The rate at which populations increase annually on rangeland has economic importance because it determines the length of protection beyond the year of insecticidal treatment. In their review of this subject, Blickenstaff et al. (1974) could find only nine studies in USDA files that provided untreated check areas along with the treated areas for valid comparisons. Two showed protection from grasshoppers lasting beyond the year of application. The other seven failed because of reinvasion of treated areas or natural changes in the population of untreated check areas.

Based on his long years of experience with grasshopper outbreaks in the West, Parker (1939) proposed a model with the hypothesis that prior to an outbreak a gradual increase in a population occurs for several years. He gave the following example for a cropland population that doubles each year until the 5th and outbreak year when it triples or quadruples itself.

Year	1	2	3	4	5
Number grasshoppers/yd^2	1	2	4	8	24 or 32
Rate of increase		2	2	2	3 or 4

Parker (1939) pointed out that 24 grasshoppers per square yard are enough to injure crops severely and to be considered an outbreak. This number of grasshoppers severely damages shortgrass prairie and may likewise be considered an outbreak.

Hastings and Pepper (1964) contend that populations of the bigheaded grasshopper, *Aulocara elliotti* (Thomas), on Montana rangeland do not fluctuate in any particular pattern. They report that during a 3-year period, four of nine populations underwent a drastic reduction, two increased markedly, and three showed no appreciable change despite a reasonably uniform weather pattern over their entire study area.

Although the original purpose of the present study was to determine the duration of control beyond the year of insecticidal treatment of rangeland infestations, information about the fluctuations of grasshopper populations and of the individual species within each population was obtained. These data, which provide an opportunity to test the validity of Parker's model for populations or range grasshoppers, constitute the primary concern of this report.

METHODS

Each year in recent decades a government-organized control program has been carried out somewhere on the shortgrass

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prairie of Wyoming. Infestations in parcels of several thousand acres are currently treated by air with 8 fl. oz/acre of ULV malathion. In the 1969 program, eight areas of 100 acres each were selected for study. Six areas were located within larger control areas, and two were check (no treatment) areas. In 1970 two other treated areas were added to the study. The territory of the sites, all in southeast Wyoming, extended approximately 45 x 70 miles. For reasons still unknown, the 10 study areas are grasshopper "hot spots" or outbreak areas that become infested recurrently.

In the year of control sampling of grasshoppers was done before treatment and two times after treatment. In subsequent years sampling was done twice, once when the majority of grasshoppers was in the late nymphal stage and once when the majority was in the early adult stage.

Species of grasshoppers that overwinter in the nymphal stage and become adult early in spring have been excluded from this report because they usually are not present in economic numbers and their populations are affected little by treatments of insecticide made in late June or early July. These species included *Psoloessa delicatula* (Scudder), *Eritettix simplex tricarinatus* (Thomas), *Xanthippus corallipes* (Haldeman), and *Arphia conspersa* Scudder.

The procedure in sampling the grasshoppers was to select a line transect of approximately 1500 ft in a 100-acre study area. Every 10 to 15 ft the grasshoppers were counted on a square foot of ground. The number of each species, the instar, and the sex of adults were recorded. A square foot was visually estimated about 10 ft ahead of the observer. The selected area was then approached carefully, and when close enough the observer (always the author) recorded the grasshoppers resting in it. If a grasshopper jumped or flew out, it was identified on landing. The final operation was to run one's hands over the sampling area to flush any still unseen grasshoppers, resting in or hidden by the vegetation. At each study site 100 one-sq ft areas were inspected on each sampling date.

The reliability of the sq ft count method was examined by making four replications of 50 one-sq ft samples along the same transect in a shortgrass site (table 1). If a species was represented by an average of two or more per 50 sq ft, the densities in all replicates were not significantly different. In all of the samplings on treated and check sites, double this number of samples, or 100 per site, were taken.

The accuracy of using an estimated square foot was checked by comparing results from a series of estimated square feet with a series of measured preset square feet. Fifty 1-sq ft areas replicated twice were sampled in early fall on shortgrass prairie by the two methods. No significant differences in numbers of grasshoppers counted appeared between the two methods (table 2). In practice the open span of eight fingers was used to define a square foot when doubt arose whether a grasshopper was in or outside a sample area.

RESULTS AND DISCUSSION

The density and annual rate of change of grasshopper populations varied in the 10 outbreak areas of southeastern Wyoming (table 3). Because of inadvertent late timing of treatments, poor population control was obtained at four sites, Lingle-2, Guernsey-1, Hartville-1, and Kaspiere. Populations decreased only 58 to 76 percent between the year of treatment (year 1) and the following year. Although these populations were reduced from 93 to 99 percent in the year of treatment, the early maturing species, particularly *Cordillacris occipitalis* (Thomas), had time to deposit substantial numbers of eggs before the application of insecticide. Three of these populations decreased in year 3 (the 2nd year after teatment) and one increased. The reason for the decline in the three sites is uncertain but may have been due to emigration or increased pressure of predators on a smaller host population. The data indicate that the adults of year 2 comprised the responsive or affected population. Survival from the late nymphal to the early adult stage was 0 percent at Kaspiere, 4 percent at Lingle-2, and 20 percent at Hartville-1, but it was 68 percent at Guernsey-1 where a small increase of 1.39 X's in the population occurred in year 3. All four of these populations increased in years 4 and 6, and three increased in year 5.

Four populations, Ft Laramie-1, Douglas, Lingle-3, and Lingle-1, were treated at opportune times, and good population controls (96 to 98 percent) between year of treatment and the following year were achieved. At two sites, Ft Laramie-1 and Douglas, populations increased at high rates the 3rd year, at moderate rates the 4th year, and at high rates in 1974, the 5th year. The population at the Lingle-1 site was small in the year of treatment and was treated only because of its close proximity to more heavily infested areas. Rates of increase at this site were high in years 2 and 3 and moderate in years 4 and 5. Moderate rates of increase occurred in the population at the Lingle-3 site in years 3, 4, and 5 followed by a high rate of increase in 1974 (year 6). When densities of grasshoppers were very low, one to six per 100 sq ft, the data show a big rate of increase the following year in four cases out of six. The results may have been caused by immigration, relaxation of biotic pressure, or merely sampling error.

Populations in the two check areas appeared to increase and decrease in the same manner. The populations decreased in 1970, increased in 1971, then decreased in 1972. In 1972 one of the check populations (Hartville-2) lay within a larger control area and was treated with insecticide. Both populations increased at high rates in 1974.

Of the eight treated populations, five increased in 1974 at the high rates of 3.18 to 4.69 and three at lesser rates of 1.77 to 2.55. The rise of all 10 populations in 1974 indicates a favorable factor operating over the entire region. High rates of increase in 1974 did not lead to outbreaks in all areas as only two populations reached such high densities, those at the Guernsey-1 and Lingle-2 sites. For outbreaks to occur both high rates of increase and ample numbers of grasshoppers the previous year are necessary.

Based on the APHIS figure of eight grasshoppers per sq yd as justifying treatment, duration of control in the study sites was 3 years at Guernsey-1, 4 years at Douglas and Ft Laramie-1, 5 years at Lingle-2, 6 years at Harville-1 and Lingle-3, and more than 6 years at Kaspiere. The results at Lingle-1 were not included in the above because the population was treated when density was less than eight per sq yd; however, the population increased to 7.1 per sq yd by 1974, near the economic threshold.

In two sites, Lingle-2 and Guernsey-1, grasshoppers reached outbreak densities in 1974 and allowed a test of Parker's model. In the Guernsey-1 site grasshoppers increased 1.4, 1.7, and 1.8 X's in the years preceding the outbreak and then 3.2 X's in the year of the outbreak. Multiplication of the population was not as high in the years preceding the outbreak as in Parker's example, and it started at a higher density, 3.7 per sq yd. In the Lingle-2 site grasshoppers were at a low density, 1.5 per sq yd, in 1971; they then increased 2.7 and 1.3 X's preceding the outbreak and 4.7 X's in the year of the outbreak. Both sites show a gradual increase of grasshoppers before the outbreak as Parker hypothesized and then a big increase in the year of the outbreak.

Although all 10 populations showed rate increases in 1974 ranging from 1.8 to 4.7, rates of increase of individual species within the populations ranged more widely, from 0.2 to 6.3 (table 4). While most species increased in the year of the outbreak, a few decreased. In his discussion of outbreaks Parker (1939) hinted at an increase of 10 X's in some years by the migratory grasshopper, *Melanoplus sanguinipes* (F.). None of the range species in this study approached such a high rate when a minimum density limitation of four per 100 sq ft in the previous year was imposed. The four dominant range grasshoppers showed the following maximum rates: *Cordillacris occiptalis* (Thomas), 5.1; *Aulocara elliotti* (Thomas), 6.0; *Ageneotettix deorum* (Scudder), 6.3; and *Amphitornus coloradus* (Thomas), 6.3. Because of apparent environmental resistance, the increase of 10 X's in nature is much less than the capacity for increase of the migratory grasshopper when it is reared under favorable cage conditions. Based on the rearing results of several investigators Pfadt and Smith (1972) calculated that this grasshopper has the capacity to multiply itself 82.6 times per generation.

Upon lifting of the limitation of four grasshoppers per 100 sq ft, higher rates of increase are observed. For example, in the Ft Laramie-1 site *A. elliotti* increased 9 X's in 1972 and *Metator pardalinus* (Saussure) 16 X's in 1974 (table 7). In the Glendo site both *A. elliotti* and *A. coloradus* increased 7 X's in 1971, and *Trachyrhachys kiowa* (Thomas) increased 7.5 X's in 1974 (table 9). These high rates of increase appear possible and may be real.

The rate of increase of an individual species in 1974 varied from site to site (table 4). For example, *A. elliotti* increased by factors of 2.1 to 6.0 among five sites and *A. deorum* by factors of 2.6 to 6.3 among three sites. Also the rank of dominant species was often different from site to site (tables 5-9). At the start of each study of a site, in 1969 or 1970, *Phlibostroma quadrimaculatum* (Thomas) was first in density at one site, *A. elliotti* at four sites, and *A. deorum* at five sites. Treating the populations with malathion with varying success appeared to be responsible for the shifted rank of species in 1974. Yet, with few exceptions, the dominant species at the start of the study were also dominant in 1974, as indicated by percentage representation of species in populations (tables 5-9). The data show that even though all sites were within an area considered shortgrass prairie, the sites were sufficiently different in topography, soil, or species composition of vegetation to foster a different ranking of species of grasshoppers. Guernsey-1, Lingle-2, and Kaspiere favored *A. deorum* and *C. occipitalis*; Hartville-1, Hartville-2, Ft Laramie-1, and Douglas favored *A. elliotti*; Glendo favored *A. deorum*; and Lingle-3 favored *P. quadrimaculatum.*

In Montana Anderson (1973) found species rank of grasshoppers varied among different "community types" of grassland. Two types that he examined occurred in four sites of the present study. The *Bouteloua-Carex-Stipa* type occupied the Kaspiere site, and the *Bouteloua-Stipa* type occupied the sites of Lingle-1, -2, and -3. Six Wyoming sites supported types not included in Anderson's study. The sites of Glendo, Guernsey-1, and Hartville-1 and -2 supported a *Bouteloua-Stipa-Carex* type, the Douglas site supported a *Carex-Stipa* type, and the Ft Laramie-1 site supported an *Agropyron-Sporobolus* type.

The rank of dominant species may vary as a result of the differential operation of natural factors, such as weather and disease. For example, from 1955 to 1958 the grasshoppers in the Glendo site were present in outbreak numbers with *C. occipitalis* first in abundance, *A. elliotti* second, and *A. deorum* third. In the summer of 1958 an epizootic of *Nosema locustae* struck the population and ended the outbreak. On return of the population to moderate numbers (9.5 per sq yd) in 1968 the most abundant species was *A. deorum,* while both *A. elliotti* and *C. occipitalis* remained relatively sparse. Although the host range of *N. locustae* among grasshoppers is extensive as Henry (1969) has shown, present circumstantial evidence indicates that susceptibility varies. The disease greatly reduced populations of *C. occipitalis* and *A. elliotti* but not of *A. deorum.*

The increase of all populations in 1974 suggests a causal environmental factor, such as weather, operating over the entire study area. Weather has been suggested by MacCarthy (1956) as important in the population fluctuations of the migratory grasshopper, *M. sanguinipes* (F.), in Saskatchewan. He found that temperature, especially daily minima during the previous June and August and daily maxima during the previous August and the current June, seemed to influence populations more than other factors. Correlations of grasshopper numbers with weather, however, are not very enlightening because they do not disclose the actual responses of grasshoppers; they tell us neither the exact stage of the grasshopper being affected nor how a stage is reacting.

Results of this study indicate that in 1973 the adults lived longer and, therefore, had opportunity to produce more eggs (table 10). Comparing survival rates of adult *A. elliotti* shows that in the Ft Laramie-1 site 11 percent survived to August 4, 1972, while 70 percent survived to August 16, 1973, and that in the Lingle-2 site 17 percent survived to August 10, 1972, while 44 percent survived to August 9, 1973. Comparing survival rates of adult *C. occipitalis* shows that in the Lingle-2 site 32 percent survived to August 10, 1972, while 69 percent survived to August 9, 1973. That these differences in survival were not due to differences in developmental rate between the 2 years is indicated by the similar percent having become adult by late June. The rate increases, as shown in table 10, were much higher in 1974 than in 1973. Unfortunately the present data are insufficient to suggest the reason for the longer adult survival in 1973.

CONCLUSIONS

1. The data appear to support Parker's model of a grasshopper outbreak. Several years of gradual increase of a population at rates of around 2 X's are followed by a year of explosive increase of 3 to 5 X's, enough to initiate an outbreak.
2. Individual species of grasshoppers may increase at rates as high as 6 X's or even higher in the initial outbreak year.
3. In an outbreak year most species in a population of grasshoppers show an increase in numbers; a few species may show a decrease.
4. In a grasshopper complex ranks of species based on abundance may change as a result of natural factors or insecticidal treatment.
5. Dominant species of grasshoppers tend to remain dominant over a period of years in individual sites on the shortgrass prairie.
6. The increase in density of all populations and almost all species in 1974 indicates a favorable environmental factor acting over the entire study area.

7. The unusual increase of populations in 1974 appears to have resulted from greater longevity of adults in the summer of 1973.

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Table 1. Results of replicated sampling of grasshoppers in a shortgrass prairie site by the visual square foot method

	Number grasshoppers per 50 one-sq ft samples				
Species	Rep 1	Rep 2	Rep 3	Rep 4	Mean
Opeia obscura	13	11	12	12	12.00
Cordillacris crenulata	7	10	10	11	9.50
Trachyrhachys kiowa	6	6	9	8	7.25
Melanoplus infantilis	1	2	1	3	1.75
Others (8 spp)*	3	2	4	5	3.50

*Each species averaged less than one per 50 sq. ft.

Note: Analysis of variance yields a nonsignificant F value of 2.93 (5 percent level) for the replicates and a significant F value of 57.90 (1 percent level) for the species. Duncan's new multiple range test indicates densities of all listed species significantly different from each other at the 5 percent level.

Table 2. Comparative results of sampling grasshoppers in two replicate plots of the shortgrass prairie using visually estimated square feet and measured preset square feet

Replicate 1	Est sq ft	Preset sq ft
Present*	9	7
Absent	41	43
Total sq ft	50	50

Chi Square statistic with 1 degree of freedom = .2976 (nonsignificant at the P >0.05 level)

Replicate 2	Est sq ft	Preset sq ft
Present*	4	5
Absent	46	45
Total sq ft	50	50

Chi Square statistic with 1 degree of freedom = .1222 (nonsignificant at the P >0.50 level)

*None of the square feet samples in which grasshoppers were present contained more than one individual.

Table 3. Density and rate of change of grasshopper populations in outbreak sites of southeastern Wyoming.*

	No/100 sq ft					
Site	1969	1970	1971	1972	1973	1974
Lingle-2	165†	69	17	46	58	272
Guernsey-1	154†	41	57	97	170	540
Hartville-1	187†	45	18	33	29	74
Kaspiere	191†	45	4	6	13	23
Ft Laramie-1		127†	3	22	34	127
Douglas		246†	5	29	48	172
Lingle-3	152†	6	9	13	22	76
Lingle-1	23†	1	4	22	37	79
Glendo	68	32	62	44	37	116
Hartville-2	152	115	275	169†	17	45
		Rate of change				
Lingle-2		0.42	0.25	2.71	1.26	4.69
Guernsey-1		0.27	1.39	1.70	1.75	3.18
Hartville-1		0.24	0.40	1.83	0.88	2.55
Kaspiere		0.24	0.09	1.50	2.17	1.77
Ft Laramie-1			0.02	7.33	1.55	3.74
Douglas			0.02	5.80	1.66	3.58
Lingle-3		0.04	1.50	1.40	1.70	3.50
Lingle-1		0.04	4.00	5.50	1.68	2.14
Glendo		0.46	1.94	0.71	0.86	3.05
Hartville-2		0.76	2.39	0.61	0.10	2.65

*Grasshoppers sampled in late June or early July when the majority were in the late nymphal stage.

†Indicates treatment of area with ULV malathion in the year of column.

Table 4. Rate of increase of individual species* of grasshoppers in the outbreak year

Species	Site	No/100 sq ft 1973	No/100 sq ft 1974	Rate of increase
Ageneotettix deorum	Guernsey-1	16	100	6.3
	Lingle-1	6	16	2.7
	Glendo	14	37	2.6
Amphitornus coloradus	Lingle-2	4	25	6.3
	Guernsey-1	27	74	2.7
	Lingle-3	6	14	2.3
	Glendo	4	6	1.5
	Lingle-1	5	2	0.4
Aulocara elliotti	Douglas	8	48	6.0
	Lingle-2	9	43	4.8
	Ft Laramie-1	10	46	4.6
	Hartville-2	4	9	2.3
	Guernsey-1	39	83	2.1
Cordillacris occipitalis	Lingle-2	36	183	5.1
	Guernsey-1	62	218	3.5
	Kaspiere	4	7	1.8
Cordillacris crenulata	Guernsey-1	6	20	3.3
	Glendo	5	5	1.0

Species	Site	No/100 sq ft 1973	No/100 sq ft 1974	Rate of increase
Phlibostroma quadrimaculatum	Lingle-3	7	25	3.6
Spharagemon equale	Guernsey-1	6	11	1.8
	Douglas	11	15	1.4
	Lingle-1	5	1	0.2
Trachyrhachys kiowa	Lingle-1	8	31	3.9
	Ft Laramie-1	4	7	1.8
Melanoplus foedus	Douglas	4	12	3.0
Melanoplus infantilis	Ft Laramie-1	4	13	3.3
	Douglas	5	16	3.2
	Hartville-1	10	27	2.7
	Glendo	5	12	2.4
	Hartville-2	4	6	1.5
	Guernsey	7	5	0.7
Melanoplus occidentalis	Douglas	15	49	3.3
	Guernsey	7	17	2.4
Melanoplus sanguinipes	Ft Laramie-1	4	6	1.5
	Lingle-1	4	1	0.3

*Limited to species with minimum density of 4/100 sq ft in 1973.

Table 5. Density of individual species of grasshoppers inhabiting the Guernsey-1 site, rate of increase in 1974, and species representation in the populations of 1969 and 1974

Species	No/100 sq ft 1969*	1970	1971	1972	1973	1974	Rate of increase 1974/1973	% of population 1969	1974
Cordillacris occipitalis	15	16	16	27	62	218	3.5	10	40
Ageneotettix deorum	64	2	4	6	16	100	6.3	42	19
Aulocara elliotti	33	14	17	27	39	83	2.1	21	15
Amphitornus coloradus	24	5	9	14	27	74	2.7	16	14
Cordillacris crenulata	2	1	4	4	6	20	3.3	1	4
Melanoplus occidentalis	6	2	5	6	7	17	2.4	4	3
Spharagemon equale		1	1	6	6	11	1.8		2
Melanoplus infantilis	2			2	7	5	0.7	1	1
Melanoplus foedus				1		4			0.7
Melanoplus sanguinipes				1		3			0.6
Trachyrhachys kiowa	3			1		2		2	0.4
Melanoplus gladstoni				1		2			0.4
Opeia obscura	3					1		2	0.2
Phlibostroma quadrimaculatum	2							1	
Melanoplus confusus			1						
Trimerotropis campestris				1					
Total	154	41	57	97	170	540	3.2	100	100

*Population treated with 8 fl oz/acre of ULV malathion

Table 6. Density of individual species of grasshoppers inhabiting the Lingle-2 site, rate of increase in 1974, and species representation in the populations of 1969 and 1974

Species	No/100 sq ft 1969*	1970	1971	1972	1973	1974	Rate of increase 1974/1973	% of population 1969	1974
Cordillacris occipitalis	34	45	6	19	36	183	5.1	21	67
Aulocara elliotti	34	6	11	18	9	43	4.8	21	16
Amphitornus coloradus	14	6		2	4	25	6.3	8	9
Trachyrhachys kiowa	7				3	9	3.0	4	3
Ageneotettix deorum	47					5		28	2
Melanoplus sanguinipes	5	2				3		3	1
Melanoplus confusus	2	1				2		1	1
Melanoplus foedus	13	2				1		8	0.4
Melanoplus occidentalis	3	4		1	1	1	1.0	2	0.4

(Continued on next page)

Table 6. **Density of individual species of grasshoppers inhabiting the Lingle-2 site, rate of increase in 1974, and species representation in the populations of 1969 and 1974 (Continued)**

	No/100 sq ft						Rate of increase	% of population	
Species	1969*	1970	1971	1972	1973	1974	1974/1973	1969	1974
Phlibostroma quadrimaculatum	3							2	
Melanoplus infantilis				4	3				
Opeia obscura	1			1	1			0.6	
Brachystola magna		2			1				
Hadrottettix trifasciatus	1							0.6	
Acrolophitus hirtipes		1							
Spharagemon collare	1							0.6	
Spharagemon equale				1					
Total	165	69	17	46	58	272	4.7	100	100

*Population treated with 8 fl oz/acre of ULV malathion

Table 7. **Density of individual species of grasshoppers inhabiting the Ft Laramie-1 site, rate of increase in 1974, and species representation in the populations of 1970 and 1974**

	No/100 sq ft					Rate of increase	% of population	
Species	1970*	1971	1972	1973	1974	1974/1973	1970	1974
Aulocara elliotti	74	1	9	10	46	4.6	58	36
Metator pardalinus	2		1	1	16	16.0	2	13
Cordillacris occipitalis	35		2	3	13	4.3	28	10
Melanoplus occidentalis	9		1	3	13	4.3	7	10
Melanoplus infantilis			3	4	13	3.3		10
Trachyrhachys kiowa	1		1	4	7	1.8	1	6
Melanoplus sanguinipes		1		4	6	1.5		5
Amphitornus coloradus	2				3		2	2
Melanoplus confusus			1		3			2
Hadrotettix trifasciatus	1		2	3	2	0.7	1	2
Acrolophitus hirtipes					2			2
Spharagemon equale					2			2
Aeropedellus clavatus	1	1	1		1		1	1
Ageneotettix deorum	1						1	
Spharagemon collare				2				
Derotmema haydenii			1					
Melanoplus sp.	1						1	
Total	127	3	22	34	127	3.7	100	100

*Population treated with 8 fl oz/acre of ULV malathion

Table 8. **Density of individual species of grasshoppers inhabiting the Douglas site, rate of increase in 1974, and species representation in the populations of 1970 and 1974**

	No/100 sq ft					Rate of increase	% of population	
Species	1970*	1971	1972	1973	1974	1974/1973	1970	1974
Aulocara elliotti	134	2	6	8	48	6.0	54	28
Melanoplus occidentalis	6		1	15	49	3.3	2	28
Melanoplus infantilis	3		1	5	16	3.2	1	9
Spharagemon equale	1	1	10	11	15	1.4	0.4	9
Melanoplus foedus	1		2	4	12	4.0	0.4	7
Amphitornus coloradus	5		1	2	9	4.5	2	5
Aeropedellus clavatus		1	5	2	5	2.5		3
Melanoplus sanguinipes					5			3
Ageneotettix deorum	7				3		3	2
Melanoplus gladstoni					3			2
Hadrotettix trifasciatus			2	1	2	2.0		1
Phlibostroma quadrimaculatum	76				2		31	1
Trachyrhachys kiowa					2			1
Hesperotettix viridis	10				1		4	0.6
Metator pardalinus	3						1	
Melanoplus confusus			1					
Acrolophitus hirtipes		1						
Total	246	5	29	48	172	3.6	100	100

*Population treated with 8 fl oz/acre of ULV malathion

Table 9. Density of individual species of grasshoppers inhabiting the Glendo check site, rate of increase in 1974, and species representation in the populations of 1969 and 1974

Species	No/100 sq ft 1969	1970	1971	1972	1973	1974	Rate of increase 1974/1973	% of population 1969	1974
Ageneotettix deorum	24	9	13	9	14	37	2.6	35	32
Trachyrhachys kiowa	5	2	2	2	2	15	7.5	7	13
Melanoplus infantilis			1	3	5	12	2.4		10
Opeia obscura	7	1		1	2	10	5.0	10	9
Amphitornus coloradus	9	3	21	9	4	6	1.5	13	5
Aulocara elliotti	3	1	7		1	6	6.0	4	5
Cordillacris crenulata	1	5	4	3	5	5	1.0	1.5	4
Cordillacris occipitalis		2	2	4	2	5	2.5		4
Phlibostroma quadrimaculatum	11	5	7	7		5		16	4
Melanoplus occidentalis			2	1	2	4	2.0		3
Melanoplus sanguinipes	2		2	1		3		3	3
Spharagemon equale	1	1		1		3		1.5	3
Melanoplus foedus	1	1	1	2		2		1.5	2
Hadrotettix trifasciatus						2			2
Melanoplus gladstoni	3			1		1		4	1
Acrolophitus hirtipes		1							
Hesperotettix viridis		1							
Melanoplus confusus	1								
Total	68	32	62	44	37	116		100	100

Table 10. Relationship of adult survival of grasshoppers to rate of increase the next year

	1972		1973		1974
	A. elliotti Ft Laramie-1				
Date	6/29	8/4	6/28	8/16	6/18
No/100 sq ft	9	1	10	7	46
% in adult stage	44		40		
% survival adults		11		70	
Rate increase			1.1		4.6
	A. elliotti Lingle-2				
Date	6/30	8/10	6/27	8/9	6/27
No/100 sq ft	18	3	9	4	43
% in adult stage	17		22		
% survival adults		17		44	
Rate increase			0.5		4.8
	C. occipitalis Lingle-2				
Date	6/30	8/10	6/27	8/9	6/27
No/100 sq ft	19	6	36	25	183
% in adult stage	53		56		
% survival adults		32		69	
Rate of increase			1.9		5.1

A Classification of Western Canadian Defoliating Forest Insects by Outbreak Spread Characteristics and Habitat Restriction

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ABSTRACT

A classification of outbreak patterns of forest defoliators is proposed. Successive years of defoliation mapping were used to indicate the changes in pattern of outbreaks, and a comparison with ecological maps indicated the degree of restriction of outbreaks to forest communities or zones. The outbreak characteristics of 12 pest species are described and classified. The implications of such a classification upon control strategies are discussed.

INTRODUCTION

During the past 30 years, population studies of forest insects have concentrated on changes over time. Some important factors leading to the rise and fall of populations, particularly those that pinpoint weaknesses in an insect's ecology, have been identified which are vital to the development of better control systems. Less emphasis has been given to changes in populations over space, but an understanding of spacial relationships could be useful in designing control strategies suitable for minimizing losses caused by the various defoliators (Morris, 1971).

One starting point for such a study is to look at historical descriptions, damage characteristics, and patterns of outbreaks of many different species of defoliators as depicted by maps, photographs, and written and verbal accounts. The Canadian Forestry Service has records covering more than 30 years in Western Canada, where there is a complex of problem insects in diverse habitats.

Forest communities occur in discrete patches with narrow ecotones when the topography is rugged, such as in British Columbia. Outbreak patterns are relatively easy to interpret under these conditions, because patterns are dependent upon the nature of the environment as well as on the behavior of the insect. In flat or gently rolling country, restrictive experimental factors are likely to occur in gradients with no obvious boundaries. This effect, compounded by regional climatic differences among outbreaks, makes the pattern of outbreaks more difficult to interpret.

Special edge effects, possibly related to moth behavior, are sometimes apparent and must be considered when interpreting patterns. For example, in a homogenous forest, insects such as the western spruce budworm (*Choristoneura occidentalis* Free.) can occur in even density gradients from the center outward. Dispersal may occur in all directions, tending to smooth population differences. Along a forest edge, however, dispersal may be only outward with no counterbalancing return flight, resulting in a reduction in population density with a corresponding green border along the edge (plate 1, figure 1). The opposite effect has also been noticed, *i.e.*, a red border where edges of stands attacked by the western blackheaded budworm, *Acleris gloverana* (Wlshm.), are often the most heavily defoliated portion, presumably because the moths prefer the edge habitat or because they are inhibited from dispersing away from a stand edge, tending to collect and oviposit there. Similarly, moths may converge on large dominant trees or on trees along mountain ridges (Drooz, 1970).

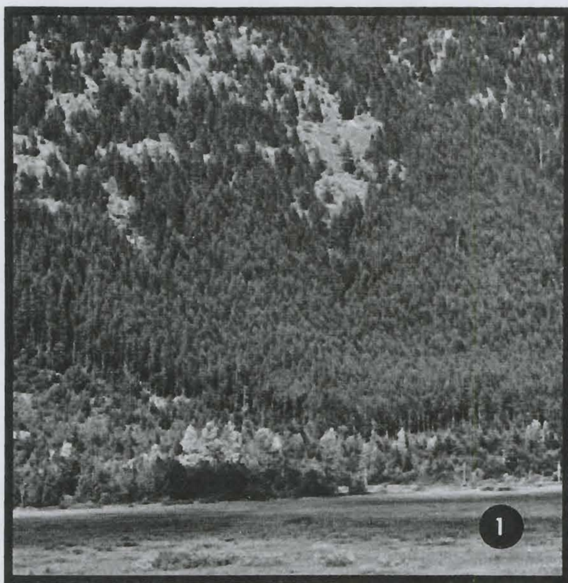
I propose to classify the outbreak types, describe the outbreak characteristics of defoliating insects typical for each class, and point out the implications that such a classification can have in designing survey and control strategies. Much of this work is developed from observations; therefore, the proposed ideas are speculative and untested.

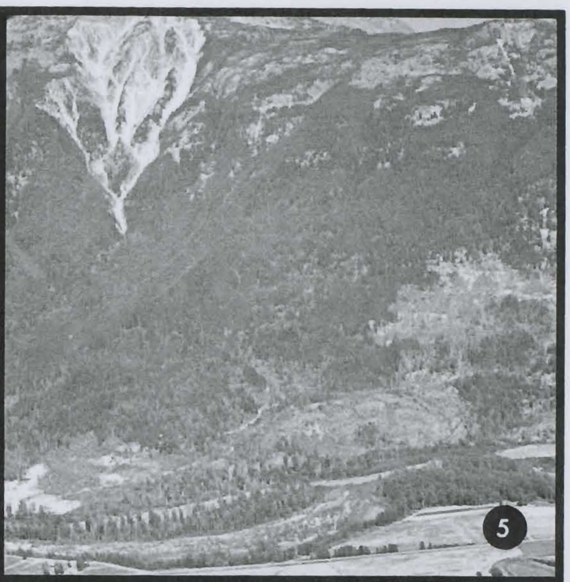
CLASSIFICATION OF OUTBREAK TYPES

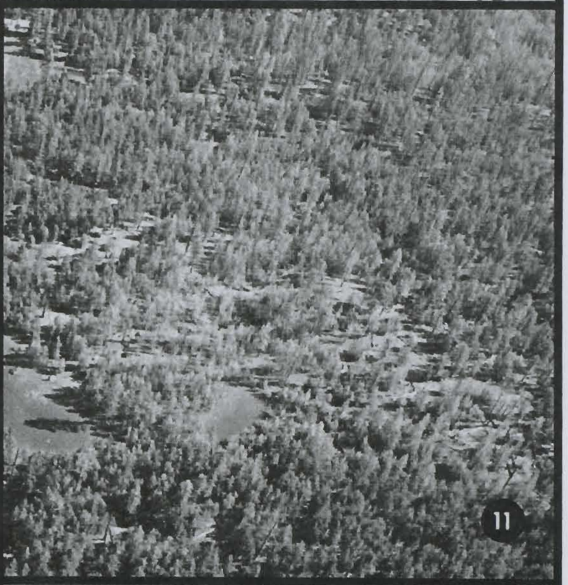
A classification is proposed based on the spreading or nonspreading nature of the outbreak and the degree of restriction of outbreaks to specific sites, zones, or host distributions. The term outbreak is defined as an insect density sufficient to cause defoliation noticeable from the ground or air. The classification of spreading or nonspreading is based upon spacial changes in outbreak patterns between annual defoliation maps.

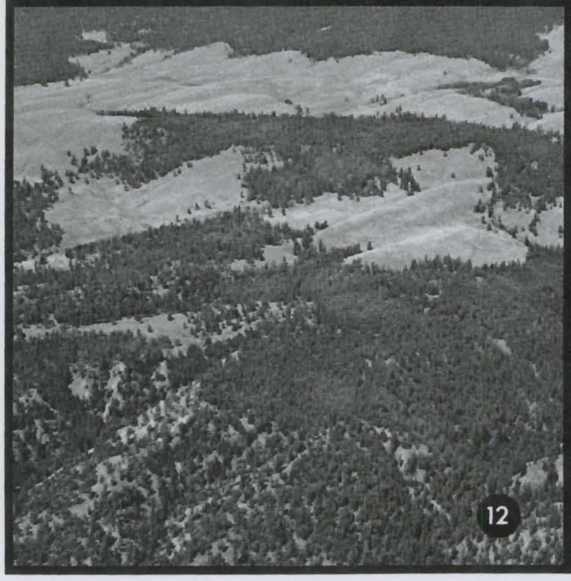
Nonspreading outbreaks occur through a rise in density of the local (autochthonous) population. Dispersal is generally limited and insect density is not dependent upon immigration to reach outbreak levels (figure 2). Insects that have been classified as spreading not only have separate local outbreaks, but also spread from these initial centers into adjacent areas (figure 3).

Not enough is known about dispersal to determine if spread is through insect movement or successive population increases of adjacent stands. When populations are low, even small numbers of insects dispersing into an area can easily double or triple the population and thus shorten the time required for the population to build up to an outbreak level. When populations are relatively high, a large number of dispersing insects will be required to double or triple a local population. Thus, the effective dispersion may be of low density during the years before the outbreak. For instance, in an area of convergent wind patterns, there may be, over a number of generations, a continual settling of moths originating from a large forest into a restricted area eventually resulting in an outbreak when concentrations reach sufficient density.









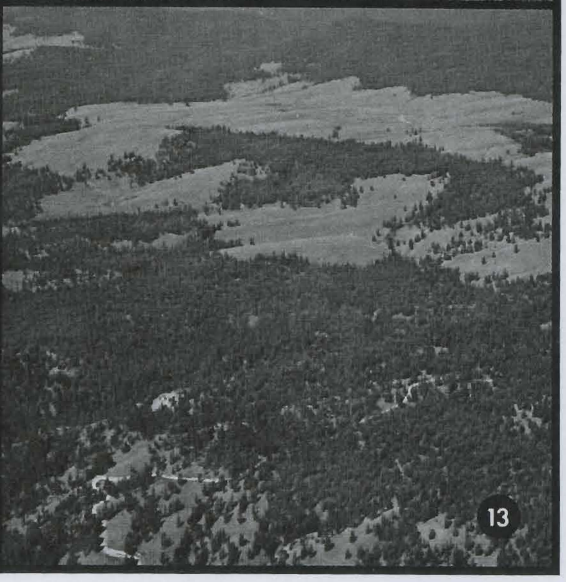


Figure 1. Defoliation by western spruce budworm illustrating green edge effect. **Figure 5.** Defoliation by western spruce budworm illustrating a mid-slope band (A. Dawson). **Figure 9.** Defoliation by black-headed budworm in both mature and immature forest with the latter being more obvious (J. Harris). **Figure 11.** Defoliation by Douglas-fir tussock moth illustrating the spread in a 'halo' effect around a defoliated spot of the previous year (A. Dawson). **Figure 12.** Spotty defoliation by Douglas-fir tussock moth the 1st year of an outbreak (A. Dawson). **Figure 13.** The spread and coalescence of defoliation of the area in figure 12 during the 2nd year of the outbreak (A. Dawson).

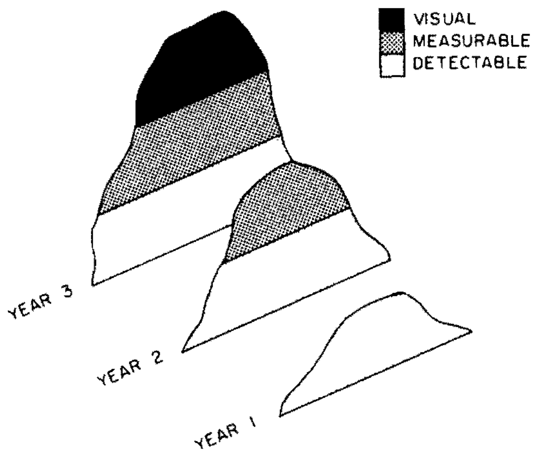


Figure 2. Diagram of a rise in density of a nonspreading defoliator. Visual means defoliation is detectable from a distance; measurable means a population density high enough to be estimated through usual branch sampling techniques, but defoliation is not obvious; detectable means the insect can be found but density can not be estimated within acceptable confidence limits with usual sample techniques.

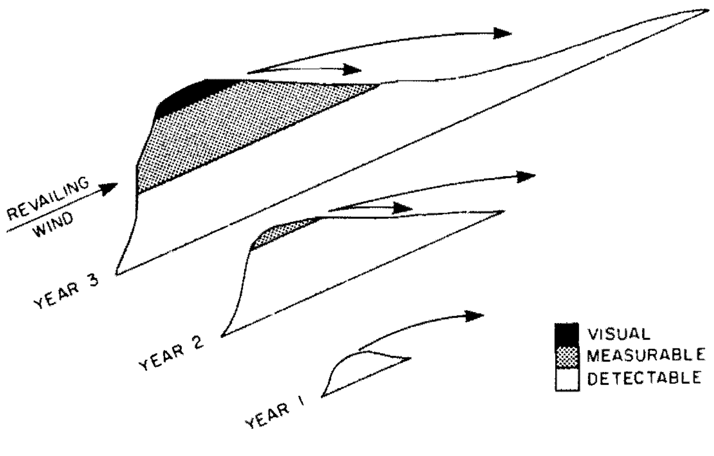


Figure 3. Diagram of a rise in density of a spreading defoliator.

Table 1. A 2x3 classification of defoliator outbreaks by spread characteristics and habitat restriction with representative species indicated for each class

Restricted to	Spreading	Nonspreading
Specific sites	1. Lodgepole needle miner, Western tent caterpillar*	4. Two-year cycle spruce budworm (within Rocky Mts.), Black army cutworm*†
Biogeoclimatic zones	2. Western spruce budworm, two-year cycle spruce budworm	5. Hemlock looper,*† Western black-headed budworm,* Western false hemlock looper,*† Douglas-fir tussock moth*†
Host distributions	3. Forest tent caterpillar*	6. Larch sawfly, Aspen leaf miner

*Short-term outbreaks of 1-3 years are usual in any specific stand.
†Capable of causing significant tree mortality the 1st year of outbreak.

In addition to these spreading characteristics, outbreaks can be grouped into three classes of spacial limitations by their degree of restriction to certain sites or forest communities. Into the first and most severely restricted class fall some insect outbreaks that occur only in specific sites; presumably there are severe environmental restrictions upon these populations. Environmental differences, such as forest composition, local soil or climatic factors, or parasite, predator, or disease incidence, may be important. Descriptions of plant associations, forest type, land use, topographic sites, cloud patterns, etc., may be useful in identifying stands or sites of rapid population increases (Miller, 1975; Shepherd, 1959; Wellington, 1965).

In the second category of spacial limitations, outbreaks may be restricted to certain biogeoclimatic zones which encompass conditions enabling a species to maintain itself and occasionally provide an environment that allows this population to increase to the outbreak level. These zones depict the second level in a hierarchical series of land demarcations or forest communities based upon geomorphology, soils, climate, and vegetation (Krajina, 1965; Packee, 1972). Each zone encompasses a group of forest communities with the same dominant forest species. They reflect similarities in the long-term climate and/or soil conditions within the zones, with distinct differences among zones. These zones may be widespread geographically, and outbreaks may occur in different parts of a zone at various times, depending upon short-term weather patterns during that period.

The third category occurs where there appear to be few spacial restrictions upon the insect populations and outbreaks are limited mainly by the distribution of the host. Thus, there are two methods of classification that result in six classes: spreading and nonspreading, and within each of these, site-restricted, zone-restricted, and host-restricted (table 1).

EXAMPLES OF OUTBREAK CLASSES

Class 1: Spreading-site Restricted

The lodgepole needle miner (*Coleotechnites starki* Free.) in the Canadian Rocky Mountains is a good example of a species that usually has been restricted to a certain topographic location but has spread to adjacent stands when conditions permitted (Stark, 1959; Shepherd, 1964). The species was restricted to a few mountain valleys, a central elevation band on the mountain slope being the most favorable site (figure 4). Above this band, the summer evening weather was usually just warm enough to allow sufficient oviposition to maintain the population at a low density. Increases occurred only during exceptionally warm years. The oviposition

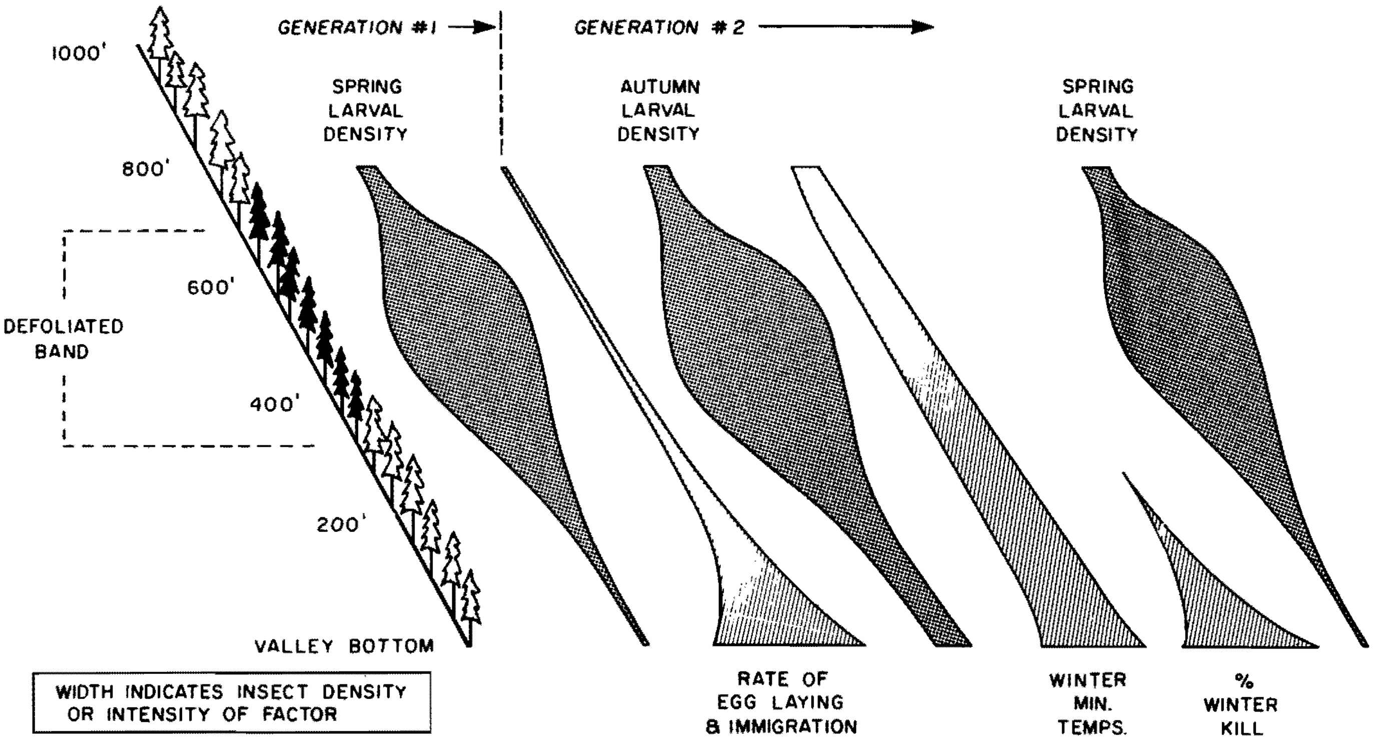


Figure 4. Diagram of increases and decreases of lodgepole needle miner populations over a mountain slope.

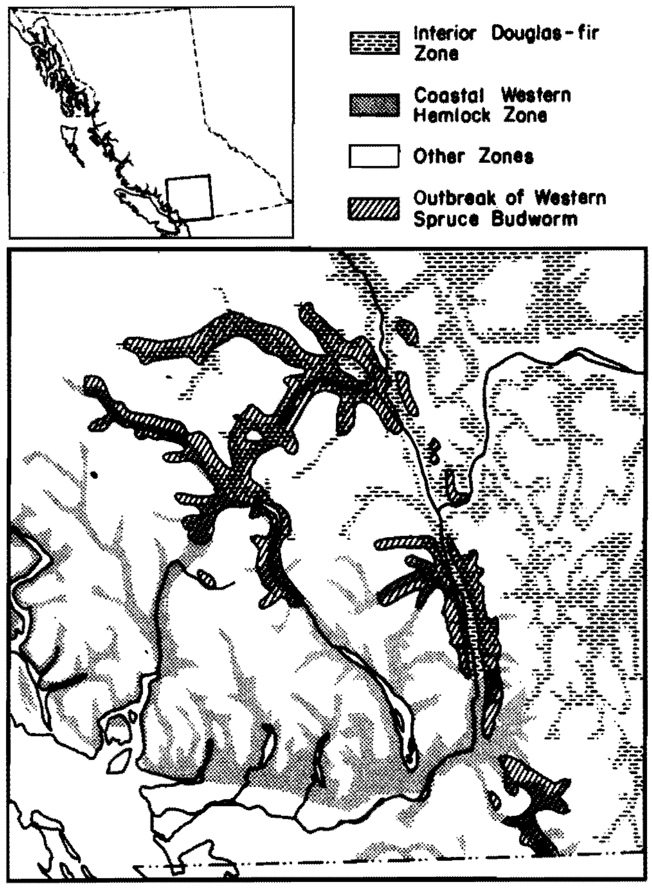
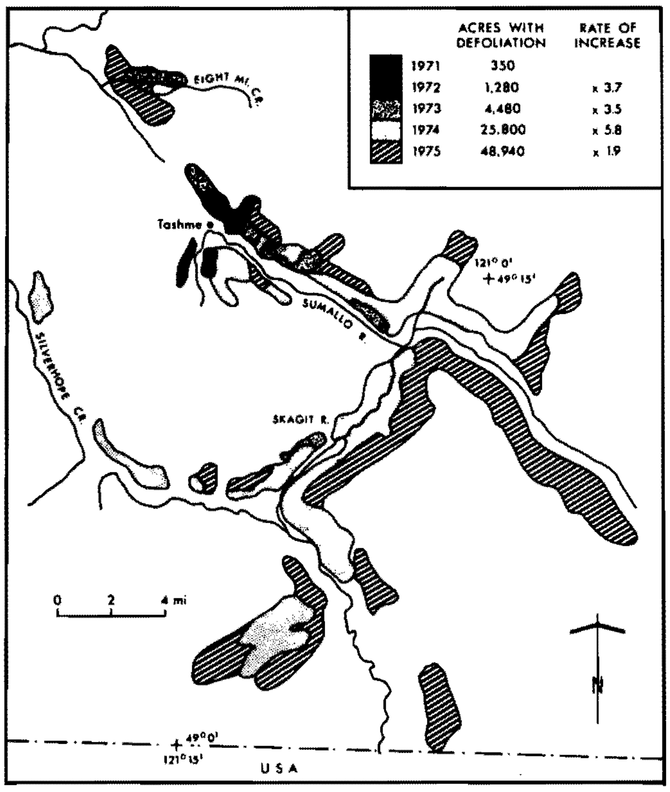


Figure 6. Map of biogeoclimatic zones of S.W. British Columbia with the distribution of all recorded western spruce budworm outbreaks superimposed.



		ACRES WITH DEFOLIATION	RATE OF INCREASE
■	1971	350	
■	1972	1,280	x 3.7
▒	1973	4,480	x 3.5
□	1974	25,800	x 5.8
▨	1975	48,940	x 1.9

Figure 7. Map of spread in an outbreak of western spruce budworm in a typical area between 1971 and 1975.

rate increased progressively down the slope, resulting in large population increases at valley bottom. However, low winter night temperatures under inversion conditions were lethal at the lower elevations so that populations could only maintain themselves and increase in the mid-slope area. During every generation, the moths drifted downward with the katabatic evening air flow, reinfesting the lower slopes. Thus, the balance between immigration, emigration, mortality, and fecundity varied over the mountain slope and resulted in the mid-slope areas being the epicentres of the population. The mid-slope outbreak pattern was similar to the current outbreak of western spruce budworm (plate 1, figure 5). Over the years, populations of the needle miner fluctuated in numbers but did not follow any consistent density cycle. Damage was usually restricted to defoliation and growth loss (Cook, 1961), but in California a closely related species caused dieback and mortality (Struble, 1972).

Wellington (1965) described a similar relationship for the western tent caterpillar (*Malacosoma californicum pluviale* Dyar), a species that feeds on deciduous trees and shrubs adjoining farms and roadsides. Locations of persistent populations coincided with the warmest, sunniest sites. The less favored sites were cooler, as they were associated with heavier cloud patterns. During warm dry years, populations spread out from the epicenter and occupied transitory sites. During cool, wet years, the insects could survive only in the warmest sites. Outbreaks lasted 2-4 years in any given area, as the insects passed through a more-or-less regular cycle of abundance. This is similar to the theories proposed by Andrewartha and Birch (1954).

Class 2: Spreading-zone Restricted

Outbreaks of the western spruce budworm in British Columbia fall within the second class, occurring in a certain zone and capable of spreading to adjacent stands. This budworm's prime host is Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, and outbreaks generally occurred north in the Cascade Mountains from the USA boundary up the Fraser Canyon to Lillooet and west through the deep valleys of Carpenter Lake and the Upper Lillooet River. Both young and old stands were defoliated within the western reaches of the Interior Douglas-fir Biogeoclimatic Zone (Wetter Subzone) and in the ecotone of this zone with the Coastal Western Hemlock Zone in the southwest parts of the outbreak and with the Subalpine Engelmann Spruce-Subalpine Fir Zone in the northwest part of the outbreak (figure 6). In these ecotones with the cooler and wetter zones, the outbreaks often occurred on the hotter south-facing slopes. The outbreak of the 1950's was heaviest in the valley bottoms, while the current outbreak is 1,000 – 3,000 ft. above valley bottoms (plate 1, figure 5). However, in one stand, ring analysis indicated four separate outbreaks have occurred during the last 60 years.

A budworm outbreak pattern of spread is described using, as an example, an area in the south Cascade Mountains of British Columbia where the first defoliation appeared in 1971 (figure 7). The pattern of outbreak from 1971 to 1973 indicated a spread from Tashme to the Skagit River, with an independent outbreak arising on Eight Mile Creek. In 1974, the spread continued southeast, but at the same time, other spots of defoliation appeared in the Silverhope Creek and Skagit River valleys greatly increasing the acreage defoliated. The defoliation did not disappear in the older areas, so the total outbreak continued to increase. Thus, it appears that increases occurred in the local populations resulting in defoliated stands in many locations. At the same time, dispersal may have been occurring, augmenting the local population and reducing the time necessary to reach densities sufficient to cause noticeable defoliation. The relative contribution of local individuals versus immigrants to the defoliating population would be expected to vary from stand to stand and year to year, depending upon the effects of weather, topography, etc., upon reproduction, survival, and dispersion. A similar pattern was obvious in the outbreak of the eastern spruce budworm, *Choristoneura fumiferana* (Clem.), in Quebec during the 1940's and 1950's (Brown, 1970; Pilon and Blais, 1961). Outbreaks lasted for many years fluctuating irregularly through the period with no regular density cycles. Tree mortality occurred, but only after a number of years of heavy defoliation; crown and growth loss, terminal dieback, and branch mortality were more common.

The two-year cycle spruce budworm (*Choristoneura biennis* Free.) is a unique species within the spruce budworm complex having a second over-wintering diapause, allowing the insect to utilize 2 years to complete its life cycle in cooler climates where 1 year is not sufficient. Most of the insects are synchronized to mature in the same year. The heaviest feeding occurs the same year as moth flight, producing an alternation in defoliation intensity.

Outbreaks have occurred in two zones: the Sub-Boreal Spruce and the Subalpine Engelmann Spruce-Subalpine Fir; the latter will be described under class 4. Within the Sub-Boreal Spruce Zone, outbreaks have been large and spreading, but mortality has been restricted largely to understory trees.

Class 3: Spreading-host Restricted

The forest tent caterpillar, *Malacosoma disstria* (Hbn.), is a wide-ranging species over North America attacking many hosts; in Western Canada, outbreaks have been closely associated with stands of trembling aspen (*Populus tremuloides* Michx.). Where aspen stands were common, outbreaks of forest tent caterpillar have usually occurred. In the initial stages of an outbreak in any one area, small patches of defoliated trees first appeared. Female moths, being strong fliers, dispersed widely (Brown, 1965), rapidly filling in the areas between patches so that the whole area became completely defoliated the following year. During the 3rd year, parasitism and disease were common and the outbreak collapsed. At the same time, the outbreak often spread across the country, new ones occurring in some areas and old ones collapsing in others. When maps of defoliated stands were studied, outbreaks appeared amoebic, spreading and disappearing in an irregular manner (Condrashoff, 1957; Duncan et al., 1956; Hildahl and Reeks, 1960; Sippell, 1962). Defoliation was nearly always apparent somewhere. Outbreaks were often so immense that they must have depended upon the local population for most of the numbers. Dispersal was also important and the pattern often indicated a spread, suggesting that a "nomadic" theory of survival was operating. Biological control agents rapidly overtook and eliminated the populations, and only by continuous dispersal could the population keep ahead of the control agents and survive. Outbreaks in any one location were usually short-lived, limiting damage to crown and growth loss.

Class 4: Nonspreading-site Restricted

Outbreaks of the two-year-cycle spruce budworm within the Canadian Rocky Mountains were confined to a specific plant community, the *Picea engelmanni – Abies/Peltigera* *aphthosa* association, within the Subalpine Engelmann Spruce – Subalpine Fir Zone. Even though the moths dispersed, populations did not appear to reach outbreak levels in other communities, as contrasted with outbreaks in the Sub-Boreal Spruce Zone. Damage was usually of the crown- and growth-loss type because the trees had a chance to recover every 2nd year. Populations fluctuated irregularly over time, showing no regular pattern. Similar site-restricted outbreaks appeared to occur in the same zone of other mountainous areas of S.E. British Columbia, but observations did not include the forest association involved.

Also in class 4 is a little known insect that has recently risen to a major outbreak level for the first time in 23 years, the black army cutworm (*Actebia fennica* Tausch.). Outbreaks of this insect on nonagricultural land have been restricted to burned areas such as wild forest fires or cut and slash-burned areas. Outbreaks were short-lived, usually lasting only 1 year on a given site, with extremely dense populations of larvae feeding on all vegetation a year or two after the burn. Seedlings planted in the areas often were defoliated and killed. No spread from existing outbreaks was found, as outbreaks were too short-lived. In fact, evidence indicates there may be a strong concentrating effect of the moths from the surrounding forests.

Class 5: Nonspreading-zone Restricted

Outbreaks of insects within this class are common in British Columbia. The hemlock looper, *Lambdina fiscellaria fiscellaria* (Guenee); western false hemlock looper, *Nepytia freemani* Monroe; and blackheaded budworm and Douglas-fir tussock moth, *Orgyia pseudotsugata* (McDunn.), all seem to fall within this class. Outbreaks of the green-striped forest looper, *Melanolophia imitata* Wlk., and saddleback looper, *Ectropis crepuscularia* (Schiff.), have not been common or well studied, but the few observations available indicate a similarity to this class. It is interesting that all these species,

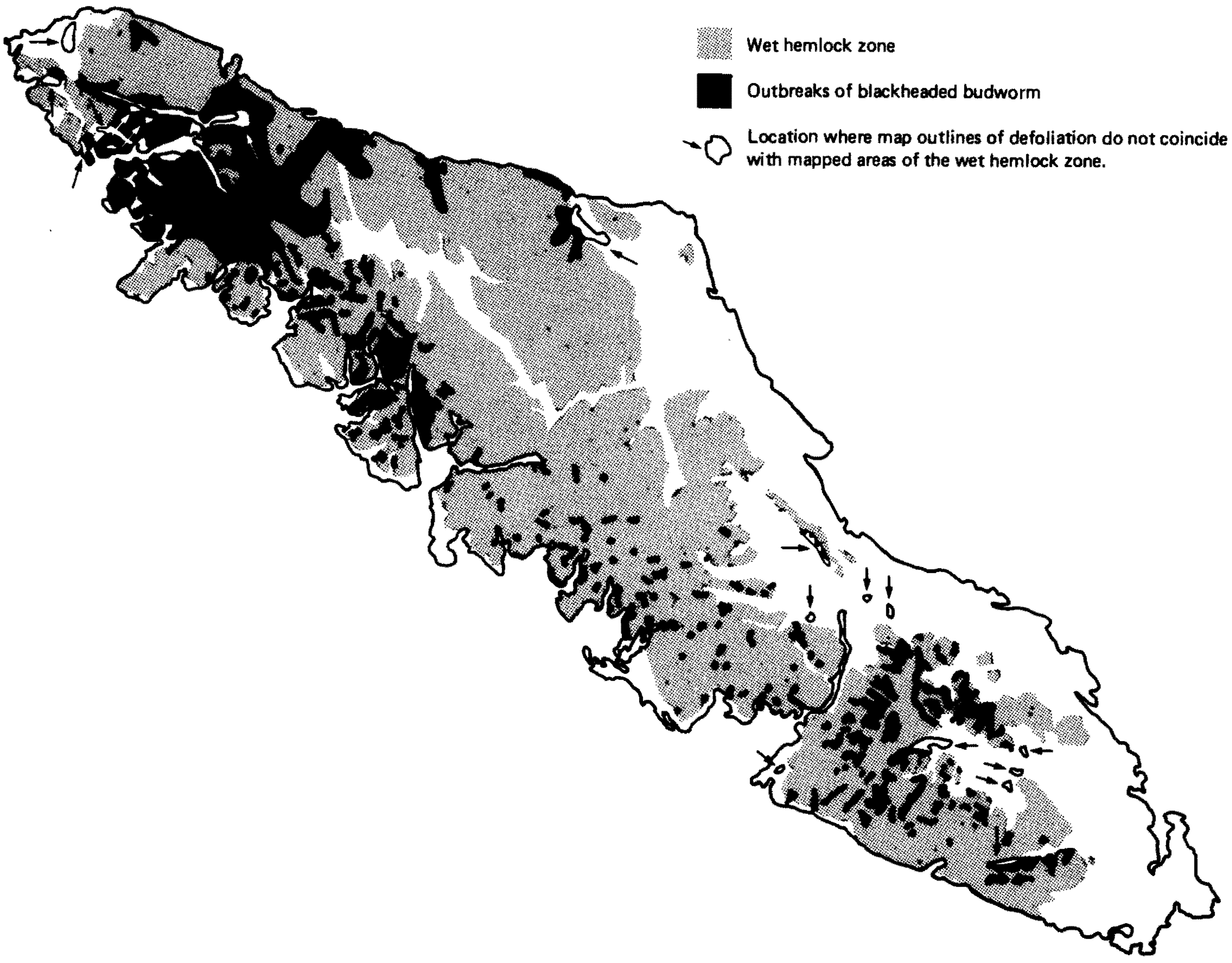


Figure 8. Map of biogeoclimatic subzones of Vancouver Island with the distribution of all recorded blackheaded budworm outbreaks superimposed.

like the western and forest tent caterpillars previously described, have followed short cyclic outbreak patterns. Also, all the species in this class, except the blackheaded budworm, have caused significant tree mortality.

The hemlock looper outbreaks occurred in valley bottoms of the Coastal and Interior Western Hemlock Zones. Outbreaks were quite discrete, showing little indication of spread (Kinghorn, 1954). Defoliation was rapid, with subsequent tree mortality; outbreaks on a specific site were short-lived, lasting only 2 or 3 years before population collapse.

The western false hemlock looper outbreaks were extremely transitory, lasting only 1 year on any specific site. Characteristically, a stand may suffer severe defoliation for 1 year only; either viable eggs were not laid or the larvae disappeared the following spring. The female moths are good fliers, but outbreaks did not last long enough to allow spread to become evident. Tree mortality often resulted from 1 year's defoliation. Outbreaks have occurred only in the Interior Douglas-fir Zone (Drier Subzone).

Blackheaded budworm usually followed a 3-year pattern at any one location, with scattered spots the 1st year, an intensification and coalescence the 2nd year, followed by population collapse the 3rd year. Tree mortality was usually scarce, being confined to a few intense spots. This may be because the blackheaded budworm, along with the spruce budworm, lays eggs on the needles and, as trees become defoliated, there is a compensating loss of laying sites.

Outbreaks appeared in the western hemlock, *Tsuga heterophylla* (Raf.) Sarg., forest in a regular progression up and down the Pacific Coast, the whole series lasting 5 or 6 years (Prebble and Graham, 1945). Moths were secretive, usually making short, nocturnal tree-to-tree flights, although occasional mass flights have been reported. Females were difficult to find, and dispersal appeared to be quite local. A composite overlay of all three recorded outbreaks was compared with the Vancouver Island Map of Biogeoclimatic Zones (Packee, 1972), and all defoliated stands, except a few pinpointed, fell within the Wet Coastal Hemlock Subzone (figure 8). The exceptions could well be mapping errors. Stand maturity seemed to have little effect on the distribution of the defoliation (plate 1, figure 9), but the regional pattern varied between outbreaks due presumably to regional weather differences, i.e., defoliation was restricted to that Subzone, but different parts of the Subzone were defoliated in different outbreaks. In 1951-60, for instance, the outbreak was confined to that part of the Subzone that occurred on the northern end of Vancouver Island; but in 1938-44 and 1970-73, the outbreaks occurred within the Subzone over most of the Island (Anonymous, 1972). Outbreaks also occurred in the Interior Western Hemlock Zone, but were more sporadic and less damaging.

The Douglas-fir tussock moth often followed a similar 3-year outbreak cycle on a given area, with collapse occurring during the 3rd year (Wickman et al., 1973). Defoliation was severe and tree mortality common. Again these outbreaks were confined to certain zones, usually centering on the ecotone between the Interior Douglas-fir (Drier Subzone) and Ponderosa Pine-Bunchgrass Zones (figure 10). Outbreaks reappeared somewhere in this Zone; five have been recorded at more or less regular intervals in British Columbia. This was the northern limit of tussock moth outbreaks that occurred in the hottest, driest part of the Douglas-fir range. Farther south, in parts of Oregon and Washington, outbreaks occurred in more moist sites where *Abies grandis* (Dougl.) Lindl. was commonly mixed with Douglas-fir and was a prime host (Wickman et al., 1973). In British Columbia, *Abies grandis* was not usually attacked. Here it appeared that cool climate was limiting the outbreaks to the warmest part of the Douglas-fir forest; where, farther south, other factors may have been more important. Tussock moth females are flightless, and dispersal is by first-instar larvae floating on silk threads. Spread of large numbers was limited to a few hundred meters, and the effect appeared as a "halo" or ring of new defoliation surrounding a spot defoliated the previous year (plate 1, figure 11). The 1st year of an outbreak was characterized by discrete spots of defoliation (plate 1, figure 12) and often in valleys of small water courses. The next year the forest surrounding these spots became defoliated, often coalescing to form a large single outbreak (plate 1, figure 13).

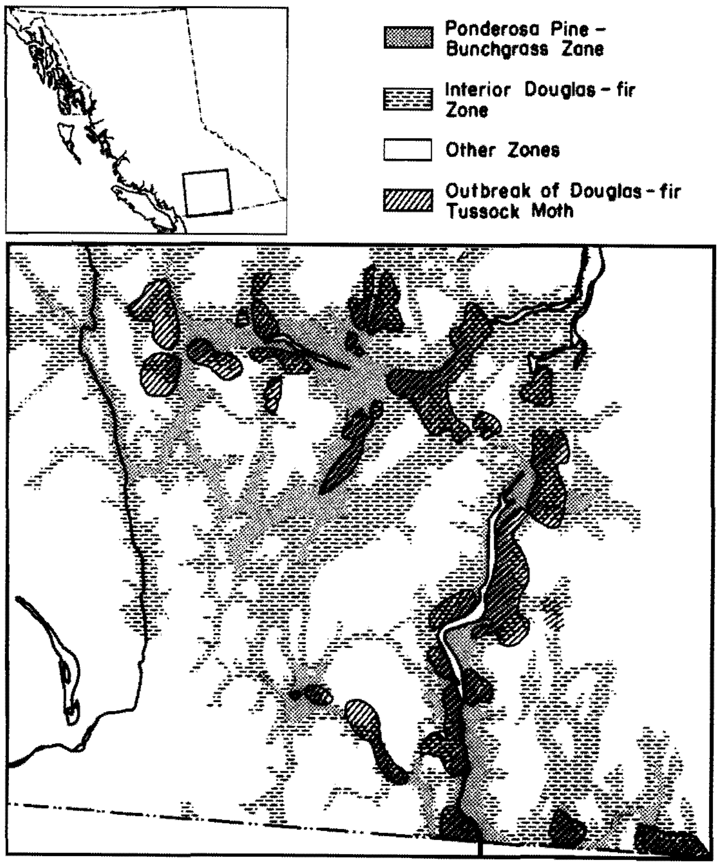


Figure 10. Map of biogeoclimatic zones of south-central British Columbia with the distribution of all recorded Douglas-fir tussock moth outbreaks superimposed.

Class 6: Nonspreading-host Restricted

Although not thoroughly studied in British Columbia, the larch sawfly, *Prestiphora erichsonii* (Htg.), apparently does not disperse rapidly (Turnock, 1972; Ives et al. 1968, yet it was present in almost all stands of western larch (*Larix occidentalis* Nutt.) from 1933 to 1949 when high populations were present (Ruppel, 1958), and from 1965 to 1967. Outbreaks were scattered throughout the host range (McLeod, 1952); damage was limited to defoliation and growth loss.

The aspen leaf miner (*Phyllocnistis populiella* Cham.) is also a wide-ranging insect occurring on aspen stands in the interior of British Columbia. Little is known of outbreak characteristics, but there appears to be relative independence among broad geographic areas in population trends, suggesting that numbers of the aspen leaf miner are influenced largely by regional climatic factors rather than by outbreak spread (Condrashoff, 1964).

IMPLICATIONS FOR CONTROL STRATEGIES

When enough information is available to confidently classify outbreaks by their ability to spread and their degree of restriction to sites or zones, some of the considerations in making control decisions are clarified. If the pest insect is the spreading type and a significant area of noninfested susceptible habitat is available, it should be considered for early treatment with an objective of controlling the insect. With nonspreading insects that experience short outbreak cycles, foliage protection would be a more logical control objective, instigated only when projected damage levels exceed acceptable thresholds.

The rate of population increase and degree of defoliation the 1st year is also an important consideration. Insects, such as the Douglas-fir tussock moth, black army cutworm, and hemlock looper, can cause significant mortality the 1st year of an outbreak. This places additional emphasis upon an early warning system involving pheromone traps or branch-beating samples and timely planning of control projects so they can be implemented quickly. The chance of placing an early warning system in the right location is greater with site-restricted species than with zone or host-restricted species; similarly, boundary demarcation of designated control areas is easier with the site-restricted species.

The ability of populations to rebound in numbers sufficient to require respraying is an important consideration. Populations that normally go through short-cycle outbreaks (table 1) may often be controlled by a single application. Insects, such as the spruce budworm, which fluctuate over time with no regular cycle would have a greater probability of rebounding and requiring retreatment.

Control of forest defoliators through stand management usually is concerned with the conversion of pure stands to stands of mixed species either on a group or individual tree basis. If the pest insects occur in a restricted site, the feasibility of conversion would generally appear greater than with pests that are either zone or host restricted. Species, such as black army cutworm, that have quite specific site requirements, would be expected to be more amenable to control through forestry practices.

Applied biological control through the release of parasites or predators is more difficult to appraise, because it depends upon the interaction with another biological system. It could be carried out with either of two objectives. The first would be to breed massive numbers of parasites or predators for release to inundate and destroy the pest insects. The second would be to release a breeding population that could increase and overtake the pest population (Miller and Varty, 1975). The first seems more feasible with a species of restricted-habitat or perhaps a nonspreading species that is zone restricted. With a spreading species or a nonspreading species that is only host-restricted, the chance of finding a successful parasite to swamp a pest appears to be poor. Within the second objective, success depends upon the relative rates of dispersal and increase of the pest and parasite populations. If the pest has site-restricted outbreaks and the parasite is a poor disperser, it obviously would be wise to make many small introductions rather than one large one. Long-term control with an introduced parasite may depend on the presence of alternate insect hosts on other specific plants which, in turn, may be site or zone restricted.

A knowledge of the changes in the spacial patterns of insect outbreaks and of the types of habitats that can support outbreaks of specific insects would be extremely useful from many points of view. Insect surveys could be deployed more efficiently, and forest entomologists could design more effective control strategies. These factors would also be extremely useful to the forest manager in making control decisions and should be added to the usual factors prepared for his or her consideration:

1. The type of damage expected and when it will occur.
2. The value of the stand from economic and other social points of view.
3. The control options available and impact of these upon other resources.
4. The population cycles, rebound abilities, and rates of spread of the pest insects.
5. The degree of restriction of outbreaks to sites, zones, or hosts.

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Most of the background information on the outbreak characteristics of defoliators, as well as some photographs, came from records and observations of the staff of the Forest Insect and Disease Survey, Canadian Forestry Service.

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Adaptability and Stability of Insect Pest Populations in Prairie Agricultural Ecosystems

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ABSTRACT

The major factors influencing phytophagous insects on the Canadian prairies from presettlement to the 1970's are examined. The settlers attempted to develop a stable agriculture and thus a stable human society in a highly variable environment. Grazing, cultivation, introduced plant species (crops and weeds), agricultural chemicals, and the reduced frequency of fire have affected native phytophagous insects. Examination of the life system and population patterns of 13 native phytophagous species suggests that the adaptability of native insects to agricultural crops is related to the host-plant specificity of the insect, the relationship of the crop to native vegetation, and the specificity of other environmental requirements of the insects (e.g. special egg-laying sites). The adaptability of native parasites and predators is affected by similar factors. The population patterns of these species fall into three groups: opportunistic species with two equilibrium states, one stable at low densities and the other instable but highly resilient at high densities; species with a single, unstable equilibrium state, which apparently lack effective natural enemies; and species with a single stable equilibrium state, which have effective natural enemies. Shifts in equilibrium states are associated with weather, except in the case of the wheat stem sawfly, *Cephus cinctus*, where the introduction of resistant wheat varieties was largely responsible for the shift to a lower equilibrium state. The available data do not indicate any continuing effect of insecticide use on the population patterns.

INTRODUCTION

Agriculture in most of the prairies and parkland areas of western Canada is less than a century old. This century has been marked by a series of perturbations of the native and agricultural ecosystems that have affected the distribution and abundance of the biotic components of those ecosystems. Bird (1961) has summarized the responses of many native species, noting cases of extinction, decreased and increased populations, and adaptations to new habitats. This paper will examine the population behavior and life systems of a number of native phytophagous insects in relation to the introduction and development of the agricultural system.

The major emphasis will be qualitative, including an attempt to relate available information to ecological principles, particularly the relationship between stability and resiliency of species and ecosystems in the face of perturbations (Holling, 1973). Agricultural ecosystems have largely been ignored in the current discussions of the characteristics of ecosystems, their stability, and the proper approach to their management. This is unfortunate, because both ecologists and agriculturalists could gain from such analyses: the ecologist because agricultural systems are the oldest and most intensively managed "semi-natural" ecosystems on the earth; the agriculturalist, particularly the pest manager, because a better understanding of population behavior within the system could improve prediction and suggest new approaches to pest control.

PRESETTLEMENT CONDITIONS

The Prairie Ecosystems

The agricultural areas of western Canada were originally occupied by three major vegetation types: short-grass prairie, mixed prairie, and parkland (interspersed mixed prairie and aspen grove forest) (figure 1). In recent years, agriculture has expanded northward into some adjacent areas of the boreal forest. The long-term distribution of these vegetation types coincides roughly with the major soil zones but the boundaries between the vegetative types have shifted dynamically over time in response to climatic factors. (figures 2 and 3). Thus, present parkland vegetation occurs throughout the black soil zone and extends southward into the dark brown soils and northward into the black-grey soils. Historically, however, mixed prairie vegetation occurred much further east and north

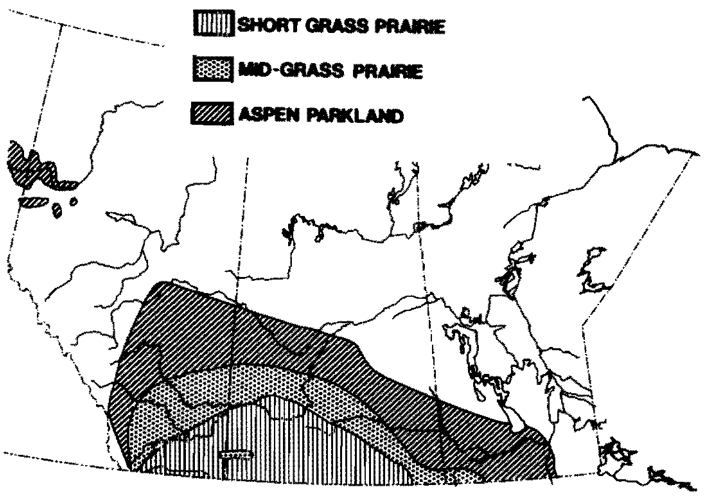

Figure 1. Major vegetation types of the Canadian prairies (from: Atlas of Canada, Canada Dept. of Mines and Tech. Surveys, Geographical Br., 1957).

than it does now. Bird (1961) concluded that the boundary between mixed prairie and parkland was at about its present location early in the 1800's, after which it moved eastward and northward. Early in the 20th century, prairie covered southeastern Saskatchewan and a large part of southwestern and southcentral Manitoba, but by 1955 the prairie had again retreated southwestward.

Natural Perturbations

The major factors affecting the distribution and composition of the natural ecosystems were weather, fire, the dominant herbivores, and man (Bird, 1961). Precipitation dominated these systems, through its effects on plant growth, reproduction, and survival, on the frequency and extent of fires, and on movements of herbivores. Low precipitation tended to expand the area of short-grass prairie and to extend the mixed prairie into the parkland by killing drought-susceptible species and allowing fires to spread and consume the aspen forests. A series of wet years would reverse the process (Moss, 1932).

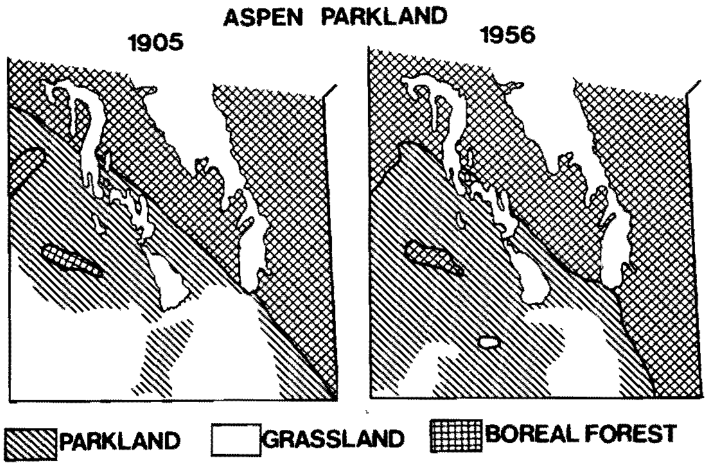

Figure 2. Major soil types of the Canadian prairies (from: Atlas of Canada, Canada Dept. of Mines and Tech. Surveys. Geographical Br., 1957).

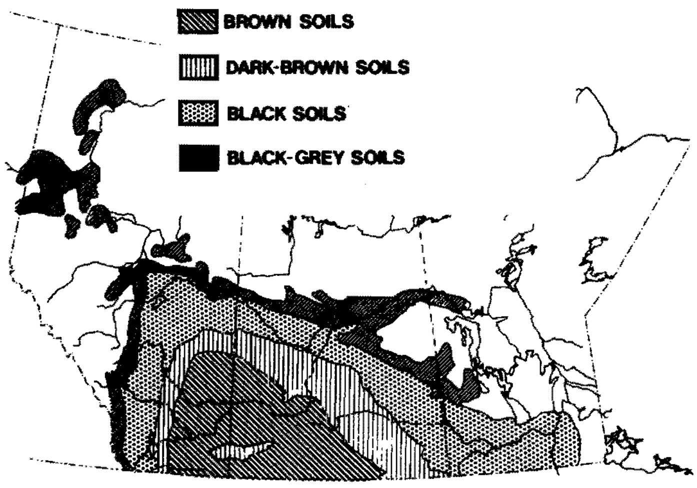

Figure 3. Changes in the extent and boundaries of grassland and parkland vegetation in Manitoba 1905-1955 (adapted from Bird, 1961).

The dominant herbivore, the bison, also affected the vegetation. It often overgrazed sections of prairie and created patches of bare ground by trampling and wallowing. The passage of a herd of bison could also destroy groves of trees by rubbing and trampling.

Fires were frequently set by the native tribes. These and naturally occurring fires favored short-grass vegetation and maintained a prairie subclimax in the parkland. The impact of these fires was exacerbated or minimized by the amount of precipitation.

The original ecosystem of the area therefore had a highly variable environment. Changes in weather patterns, the frequency and extent of fires, and the unpredictability of the bison movements created an ecosystem in which the quantity and quality of food varied greatly within and between years. The writings of explorers, fur traders, and early settlers give evidence of the wide fluctuations in the numbers of phytophagous insects, including plagues of migratory grasshoppers and outbreaks of the wheat stem sawfly on native grasses (Bird, 1961). These and other phytophagous insects developed mechanisms to survive in an environment subject to extreme perturbations, and presumably their populations were characterized by wide amplitude fluctuations and frequent local extinctions followed by recolonization.

Perturbations Associated with Settlement and Agricultural Development

The transformation of the native ecosystems, which began with the fur traders and has continued through settlement and agricultural development, was achieved through a complex of actions. The persistent theme of these actions has been to develop a stable agriculture and thus a stable human society despite the inherent instability of the prairie climate. A part of this goal has been to stabilize farm income by reducing the variability in yields. Heavy inputs of energy, through machinery for cultivation, new crop varieties, drainage and flood control programs, and applications of fertilizers and pesticides, have all contributed to the reduction of the general instability of the system. The following factors have directly or indirectly affected the native ecosystems and tested the resiliency of native phytophagous insects:

1. **Grazing:** The native grasslands were subject to severe but sporadic overgrazing by the bison. Between 1870, when the bison had been virtually exterminated, and 1910, when settlement began to have a significant impact, the native grasslands were released from grazing pressure. From 1900 to 1920, the pressure on native grasslands from grazing and haying increased as the cultivated acreage and the number of livestock increased (figures 4 and 5). Since 1920, few native grasslands have been free from grazing or haying, but the impact of this agricultural usage is more consistent and less severe in the short term than the periodic devastation of the bison herds.
2. **Fire:** The native hunting economy apparently was a major factor in the incidence of fires. When the native societies collapsed in the late 19th century because of the loss of the bison and the devastation caused by disease and whiskey, the frequency of fires presumably also dropped. A series of wet years in the 1880's and

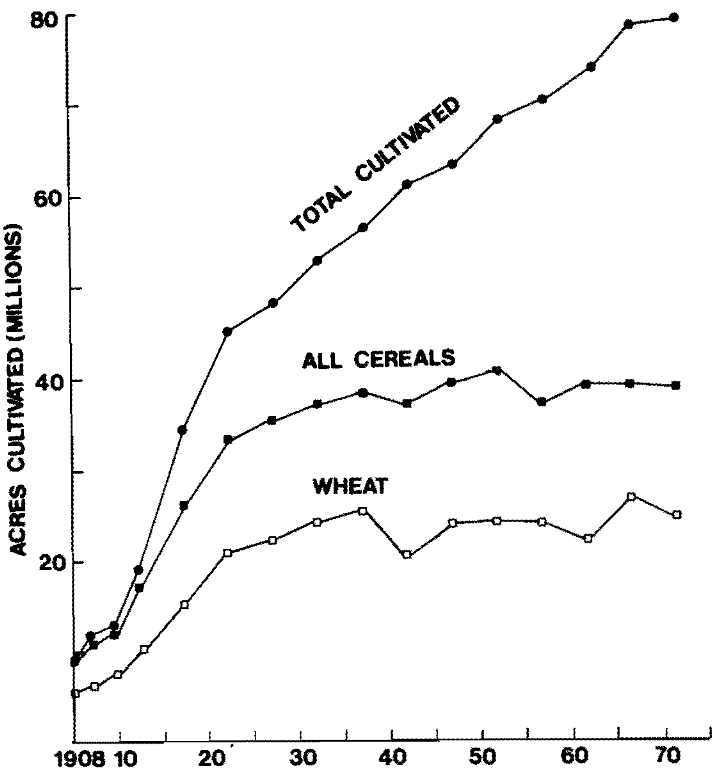

Figure 4. Total acreage under cultivation (crops, tame hay, and fallow) in the Canadian prairies from 1908-1972 (from: Handbook of Agricultural Statistics, Part I, Field Crops, 1908-63; Dom. Bureau of Statistics. Agric. Div. 1964; and Canada Year Books, 1965-1973).

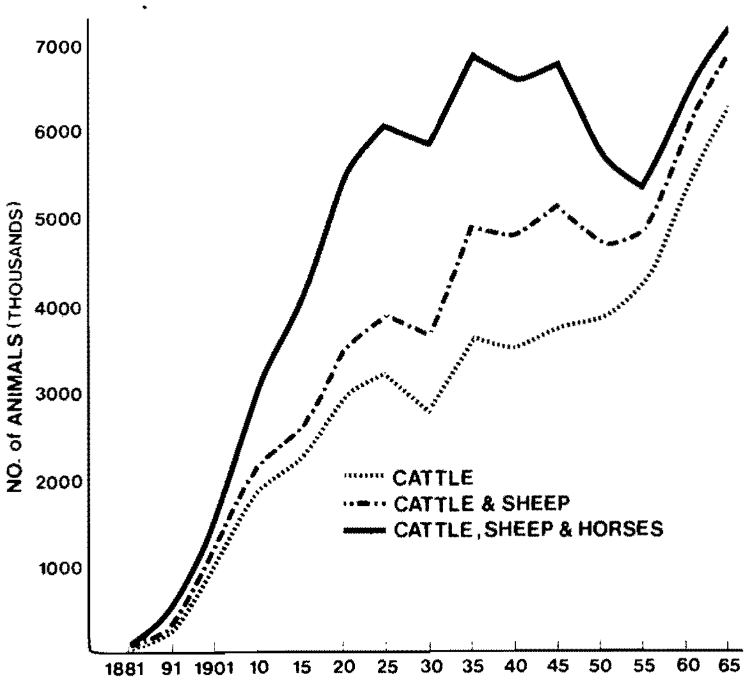

Figure 5. Numbers of livestock in the Canadian prairies, 1871-1965 (from: Handbook of Agricultural Statistics, Part VI, Livestock and Animal Products 1871-1965. Dom. Bureau of Statistics Agricultural Div. Nov. 1966).

1890's coincided with the change in the human factor. Immediately following settlement, the incidence of fires in grasslands appears to have increased because of the spread of fires set to clear woodlands and those started by trains. In well settled areas, fires occur less frequently; fires set to burn excess straw on the fields or to clear roadsides and railroad right-of-ways may spread into woods and grasslands.

3. **Cultivation:** The area of native ecosystem destroyed by conversion to fields increased steadily from the first settlement until 1965 and has remained fairly stable since then (figure 4). At first, the short-grass and mixed prairies were subjected to most of the destruction as settlement followed the railways westward and northwestward. The drought of the 1930's changed the pattern of cultivation; fields in drier areas were abandoned and settlement moved northward into the parkland belt and the better soils on the fringes of the boreal forest zone. Since 1950, although the agricultural frontier has moved further northward, better equipment, crops, and management have also expanded cultivation on land that had previously been considered too wet, too dry, or too heavily treed. Cultivation is the most severe perturbation faced by native grassland insects. The destruction of their natural habitat forces them into refugia that are often very small or regularly subjected to grazing and haying. Many species have had their numbers reduced by cultivation (Bird, 1961) and those that could not adapt to cultivated croplands or the altered grassland ecosystem have become rare or extinct.
4. **Introduced Plants:** The crop plants and weeds that were introduced with settlement represent a major perturbation to insects. In addition to creating new agricultural ecosystems, some of the plants have invaded the uncultivated lands and replaced native species. For example, awnless brome grass, *Bromus inermis* Leyss, has largely replaced native grasses that were hosts of the wheat stem sawfly, *Cephus cinctus* Norton (Bird, 1961). Cereal crops dominate the cultivated area (figure 4) but since 1940 flax, sunflowers, sugar beets, rape, and a number of experimental crops have become important.
5. **Agricultural chemicals:** Since 1950 use of agricultural chemicals has increased. DDT and other persistent insecticides were used widely against grasshoppers, the sugar beet maggot, *Tetanops myopaeformis* (Röder), and other pests and undoubtedly affected nontarget insects. Although these insecticides have been replaced by less persistent ones, insect populations are still stressed by insecticide application. The use of herbicides has changed cultivation practices and undoubtedly affects the abundance of many insect species.

Native Pests of Field Crops

The beginning of agriculture on the Canadian prairies is associated with the arrival of the Selkirk settlers at the Forks of the Red River (now Winnipeg) in 1812. They introduced wheat, barley, oats, rye, corn, and potatoes (Morton, 1957), but most of their varieties were ill-adapted to the climate. In addition, isolation and political problems affecting this small settlement delayed the time when introduced crops became abundant enough to threaten native habitats and to offer a significantly large area of alternate host plants to native insects. By 1876, varieties had improved and the reputation of Manitoba-grown hard red spring wheat had become known. Following this, a rush of immigration to western Canada opened large areas of cropland for utilization by insects.

The introduced crops were, with the exception of sunflowers, of Eurasian origin and generally had few or no closely related species on the Canadian prairies (table 1). Remarkably few specific insect feeders have been able to adapt to these major crops. Although cereals have been the dominant field crop for more than a century (figure 4), only one species, the wheat stem sawfly, has become adapted. Flax, with five native cogeneric species on the Canadian prairies, has been attacked by two native insect species: the Bertha armyworm, *Mamestra configurata* (Wlk.), which is a fairly general feeder apparently preferring rape; and the flax bollworm, *Heliothis ononis* (D. & S.), which is a little-known species and a pest during the 1940's but not subsequently. Sugar beets, grown for about 65 years in Alberta and 35 years in Manitoba, have two native insect species adapted to them. In the 30 years since rape and sunflowers have been grown, two native species have become adapted to the former and five species to the latter. In addition, three species, at present rare, may be in the process of adapting to sunflowers. The following sections will examine the life systems of some native insect species that have been affected by the establishment of agriculture.

General Feeders

The development of agriculture on the prairies has provided an environment to which a number of polyphagous insects have successfully adapted. Such species have been less affected by cultivation than insects requiring specific food plants (Bird, 1961). General feeders that are now regarded as major crop pests include the grasshoppers (4 spp.), cutworms (3 spp.), and wireworms (6 spp.). Of these, the infestation history of the grasshoppers has been best documented and will be examined in detail.

Grasshoppers are prominent inhabitants of the prairies and graphic accounts of their migrations and abundance appear in the journals of early travellers. Reviews of reports of grasshoppers before the initiation of regular surveys in 1931 (Riegert, 1968; Bird, 1961; Mitchener, 1954) indicate that outbreaks occurred during the years 1799-1802, 1818-1821, 1857-1874, 1899-1903, 1918-1924, 1929-1930. *Melanoplus spretus* (Walsh) was apparently the major pest species up to the early years of settlement. In those years, it was generally accepted that native prairie and uncultivated lands were the chief menace in the continuation of grasshopper outbreaks (Buckell, 1937). However, the outbreaks of 1918-1924 and 1929-1930 demonstrated that a second group of grasshoppers, including *Melanoplus sanguinipes* F., *Camnula pellucida* (Scudder), and *M. bivattatus* Say, had adapted to agricultural conditions. Settlement and agricultural development have presented somewhat different opportunities for each of these four species as indicated by the following consideration of their interactions with the natural and agricultural ecosystem.

1. *Melanoplus spretus*, the Rocky Mountain grasshopper, was apparently the dominant species in the outbreaks until 1874. Outbreaks originated in the short-grass prairie where overgrazing, trampling, and making of dust wallows by bison created favorable egg-laying sites. During periods of drought, great swarms of grasshoppers left their breeding sites and invaded the mixed prairie and parkland regions, usually in late July and early August. Eggs were laid in these areas, giving rise to outbreaks that persisted for 1 or 2 years before unfavorable weather conditions eliminated local populations.

M. spretus was unable to adapt to the changes associated with settlement. The major wet period of the 1880's and 1890's can be regarded as a normal perturbation that forced this species back into refugia in the most suitable (dry) parts of the short-grass prairie. Simultaneously, however, the bison were exterminated, presumably placing an additional stress on *M. spretus* by drastically reducing the number of suitable egg-laying sites. Its numbers increased during the dry period of 1899-1902, but it has not been collected since then and is regarded as extinct. Thus, a species with a high degree of instability and resiliency, which was adapted to an environment characterized by unpredictable extremes in weather, fire and grazing, was unable to adapt to the removal of the dominant herbivore in the system.

2. *Melanoplus sanguinipes*, the migratory grasshopper, is closely related to the Rocky Mountain grasshopper and has replaced it as the dominant grasshopper in the drier parts of the prairies. *M. sanguinipes* oviposits in stubble fields in light and medium soil types and to a lesser extent in abandoned weedy fields and drifted soil. It feeds primarily in grain fields and moves considerable distances in late July and August if local food is used or dried up (Paul and Putnam, 1960).

In Saskatchewan, *M. sanguinipes* was the dominant species in 22 of the 32 years of grasshopper outbreaks since 1929: 1929-46, 1951, 1964, 1965, and 1971 to date (Riegert, 1968; Peters, 1972; Peters & Pickford, 1971, 1973, 1974) (figure 6). The abundance of *M. sanguinipes* appears to be strongly controlled by weather (Edwards, 1960; MacCarthy, 1956). Egg parasites are not of critical importance (Putnam, 1953), and this species is less susceptible to infection by *Entomophthora* spp. (Pickford and Riegert, 1964).

M. sanguinipes may have occupied similar habitats and utilized similar egg-laying sites to *M. spretus* in the native prairie, but has now become almost entirely an inhabitant of cultivated fields, even to the point of not infesting undisturbed grasslands (Paul and Putnam, 1960). In addition to its ability to adapt to the agricultural ecosystem, the present

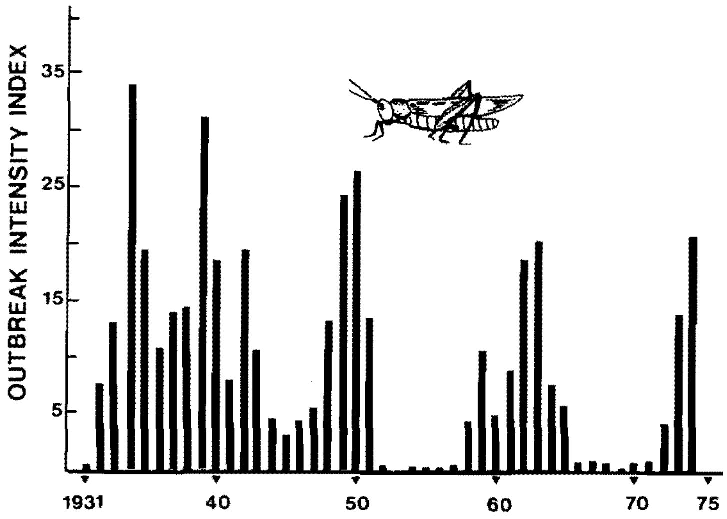

Figure 6. Population patterns of grasshoppers in Saskatchewan 1931-74. Data on outbreak intensity (grasshopper abundance x area affected) courtesy of R. Pickford, Agriculture Canada Research Station, Saskatoon.

dominance of *M. sanguinipes*, with its highly unstable population pattern and great resiliency, may be related to the extinction of *M. spretus.* In native grasslands *M. sanguinipes* may have been an inferior competitor, restricted in habitats and numbers by the dominant *M. spretus.*

3. *Camnula pellucida*, the clear-winged grasshopper, has been the second most important species in Saskatchewan, being dominant in 8 of the 32 outbreak years (1949, 1950, 1958-1963) and second to *M. sanguinipes* in many of the other years. It characteristically oviposits in warm, dry, sparsely vegetated areas of grassland (Riegert et al., 1965) where the survival of the nymphs depends on the proximity of areas with succulent vegetation. Such areas are too small in relation to the total area of grassland and contain too high a proportion of poor food plants to sustain large populations. On cereal crops, particularly wheat, nymphal survival is higher, adults are larger, and up to 20 times more eggs are produced than on native grasses (Pickford, 1963).

C. pellucida is well adapted to the agricultural system. It oviposits in prairie associated with croplands, pastures, undisturbed road allowances, and slough margins. Soon after hatching the nymphs move to seedling cereal crops, where they feed and develop to the adult stage. The adults move back and forth between fields and grassland to feed and oviposit.

Like the other prairie grasshoppers, the abundance of *C. pellucida* is determined basically by weather. Egg parasitism is rare, probably because the eggs are laid later in the season than those of *M. sanguinipes* (Pickford, 1964). It is very susceptible to epizootics of *Entomophthora grylli* Fres., which caused heavy mortality in 10 years since 1931 in Saskatchewan (Riegert, 1968). This susceptibility probably prevents this grasshopper from being an even more devastating pest.

4. *Melanoplus bivattatus*, the two-striped grasshopper, is the most omnivorous of these grasshoppers, feeding on a number of forbs as well as on grasses. It prefers to oviposit in disturbed ground, where weedy forbs as well as grasses are present. This species is favored in areas with heavy soils and poor drainage because ditches are frequently redredged, maintaining the pioneer forbs and grasses. Oviposition may also occur in lighter soils (blow-outs, drift soil), but *M. sanguinipes* appears to be better adapted to such situations.

During outbreak years in Saskatchewan, *M. bivattatus* has only once been the dominant species, but is often second in abundance, particularly on the heavier soil areas. It is a common and preferred host of egg parasites, *Scelio* spp. (Pickford, 1964), but parasitism is not a critical factor except locally (Putnam, 1953). It is susceptible to an *Entomophthora* spp., which reduced its abundance in 1950, 1951, 1954, and 1966 (Riegert, 1968) but appears less susceptible to these epizootics than *C. pellucida.*

5. *Summary:* These three pest grasshoppers have all responded to the agricultural ecosystem by increasing the levels and magnitude of fluctuation of their populations. Although weather remains the overriding mechanism for controlling their abundance, agricultural practices are important (Smith, 1969). *M. sanguinipes* has almost entirely abandoned the native grasslands to oviposit and feed in grain fields of the prairies. In outbreak years, it migrates to the north and east to establish populations in the parklands. *C. pellucida* still oviposits in grasslands but depends to a large extent on grain fields for nymphal and adult food. Because the coincidence of prairie and cropland is necessary, its foci of abundance are in the more heavily cropped areas of the prairies rather than the drier areas favored by *M. sanguinipes.* The distribution of *C. pellucida* suggests that its requirements for warm, dry weather are not as strict as those of *M. sanguinipes.* Its susceptibility to epizootics during moist summers periodically reduces its populations even in dry areas and usually prevents it from becoming a problem in the humid prairie climate of the Red River Valley. For *M. bivittatus,* the aspect of the agricultural ecosystem which is important in determining its abundance is the redredging of ditches. These periodic disturbances create a mixture of weedy forbs and grasses that are ideal for oviposition and nymphal development. In areas where the ditches are undisturbed, *M. bivattatus* populations are much lower.

Cereal Feeders

Cereals were the first field crops grown by the settlers and continue to occupy a large portion of the cultivated acreage in the prairie provinces. Despite their large acreage and relatively long history in the area, only one native insect species, excluding general feeders, has adapted to cereals. The wheat stem sawfly has become a pest of wheat, and no native species are pests of oats, barley, or rye.

Cephus cinctus Norton, the wheat stem sawfly, occurs from Manitoba to the interior of British Columbia and south to Nebraska, Nevada, and California. It is an important pest of spring wheat in those areas of the Great Plains where annual precipitation is about 37 cm (Holmes, 1956). In Canada, this coincides approximately with the area of the brown soil zone (figure 2).

Adults of *C. cinctus* emerge, mate, and oviposit from mid-June to mid-July. The eggs are laid in grass stems. The larvae spend the summer mining up and down these stems, feeding on both parenchyma and vascular tissue. When the plants begin to mature, the larvae move to the lower end of the stems, girdle them from the inside just above the ground surface, and over-winter in a silken cocoon beneath the surface. Larval feeding may affect the vascular system of the stem to such an extent that seed fails to mature but the greatest loss in grain crops is caused by cutting the stems, which causes the plants to fall to the ground where they are lost to harvesting equipment.

The abundance and suitability of host stems are major factors determining the survival and abundance of the wheat stem sawfly. The adults show little discrimination and will oviposit on wheat, oats, rye, barley, and flax as well as native and introduced grasses. However, larval survival is virtually zero in oats, rye, and flax, and low in western rye grass, *Agropyron Trachycaulum* (Link) *Malte*; awnless brome grass, *Bromus inermis Leyss.*; and most varieties of barley (Holmes and Peterson, 1964; Farstad and Platt, 1946; Farstad, 1944; Criddle, 1923). Survival in spring wheat is generally high except in the resistant varieties that have been grown since 1946. Resistance to wheat stem sawfly is determined by the amount and distribution of the pith in the stem (Holmes and Peterson, 1964). The stems of all resistant wheats are at least partially filled with pith, which increases egg and larval mortality (Holmes and Peterson, 1961, 1962). Resistance is not complete and can be largely lost under weather conditions that cause rapid and lush growth of the stems and reduce stem solidness. The relationships between weather and the survival and abundance of *C. cinctus* in grasses have not been studied but are presumably similar to those described in wheat by Seamans (1945). In wheat, extreme weather conditions can prevent oviposition and cause direct mortality to the larvae and pupae. However, the indirect effects of weather through the host plants are much more important. In general, high survival is associated with above-normal precipitation and temperatures from August to October and normal rainfall and warm temperatures from May to July; decreases in population are associated with cold, dry weather from August to October and cool, moist weather from May to July. Parasitism can also be effective in reducing populations, and when high egg densities occur, cannabalism can be a major source of larval mortality (Holmes and Peterson, 1962).

Before settlement, the major factors controlling its abundance appear to have been parasitism and the availability of suitable stems of its host plants, principally *Agropyron* and *Elymus* spp. (Criddle, 1915, 1922). Other factors probably affecting abundance were fire and grazing by bison. Although evidence is lacking, it seems likely that presettlement populations of *C. cinctus* were more abundant in the moister mixed prairie than the short-grass prairies. Since settlement, the following periods with differing population patterns of the wheat stem sawfly have occurred:

1. Early settlement, 1875-1907: During this period, particularly from 1875-1900, populations of the wheat stem sawfly were released from mortality associated with bison grazing and simultaneously benefitted from a period of above average rainfall. There was little land clearing before 1885 and few livestock were present (figures 4 and 5). Under these conditions, populations of the wheat stem sawfly increased and were limited by the abundance of suitable stems, parasitism, and periodically by the unfavorable effects of too much summer rainfall. The first reports of damage to wheat were from 1895 to 1897 (Bird, 1961). An enormous outbreak on native grasses occurred in 1906, and in 1907 the sawflies moved in large numbers into wheat fields (Criddle, 1915). This apparently marked the beginning of a change in the habits of the sawfly from preferring native grasses and occasionally attacking grain to being adapted to the agricultural ecosystem.
2. Adaptation, 1907-1925: During this period, a number of factors reduced the suitability of grasslands and stimulated the adaptation of *C. cinctus* to the agricultural system. In Manitoba and southeastern Saskatchewan, there were serious infestations on wheat, but there was evidence that the grasses still supported the population. Couchgrass, *Agropyron repens L. Beauv.,* was introduced from Eurasia and spread into the fields, where it was an excellent host for *C. cinctus* and provided foci of infection for wheat (Bird, 1961; Criddle, 1915). By 1925, southwestern Manitoba ceased to be a favorable area for the wheat stem sawfly. The grasslands were invaded by unsuitable grass species such as awnless brome grass and were grazed or hayed. The control of couchgrass in the fields by better agricultural machinery and the introduction of other crops into rotation with wheat further reduced the abundance of suitable hosts. Sawfly populations have remained low in this area since 1925, except from 1938 to 1942 and possibly in 1948, when light to moderate infestations occurred. In contrast, the sawfly population increased in southern Alberta and Saskatchewan and it became a major pest after 1925.
3. Outbreak, 1926-1949: During this period, there was an almost permanent outbreak of the wheat stem sawfly in southern Alberta and Saskatchewan. Losses were so heavy that the yield of wheat for the whole province of Saskatchewan was reduced by an average of 4.6 percent per year from 1926 to 1945 and by a maximum of 10.3 percent in 1941 (Saskatchewan Department of Agriculture Annual Reports, 1926-1945). Yield loss in southeastern Saskatchewan was consistently lower than in the remainder of the outbreak area, apparently because of lower populations of wheat stem sawfly and denser stands of wheat that held up the cut stems until harvest. Weather, notably drought, reduced sawfly numbers in some areas but parasitism was generally insignificant. High egg and larval mortality undoubtably occurred when oviposition was on crops unsuitable for larval survival, but such crops occupied a low percentage of the seeded acreage. Barley and flax were sown in some fields that were heavily infested with sawfly the previous year (Farstad and Platt, 1946; Farstad, 1944) but the practice apparently was not sufficiently popular to affect sawfly numbers except in local areas. In the outbreak area, the development of an agricultural system that attempted to minimize the effects of climatic perturbations allowed the wheat stem sawfly to exist at a higher level and with greater stability than had been possible in native grasslands. In adapting to this system, the sawfly became almost entirely dependent on wheat for its survival. The remaining grasslands became capable of supporting only small populations, because haying and grazing reduced the numbers of suitable host stems and unsuitable introduced grasses replaced suitable species (Bird, 1961).
4. Recent, 1949-present; The severity and persistance of losses due to wheat stem sawfly led to a search for resistant varieties. The resistant spring wheat, Rescue, was first grown in 1946, and the acreage seeded to this variety increased until between 1951 and 1954 it became the second most common variety of spring wheat in Canada (Holmes, 1956). Other resistant varieties, including Chinook (spring wheat), Golden Ball, and Stewart (durum wheats) were released later. Populations of the wheat stem sawfly declined from 1949 to 1954 and since then have fluctuated about a much lower mean than during the previous 23 years. Since 1954, yield loss within the infestated areas of southern Alberta and Saskatchewan has varied between 5 and 20 percent, and populations have been increasing since 1972 (N.D. Holmes, personal communication, March 1975). The growing of resistant varieties cannot be given the whole credit for this population behavior, because the acreage of these varieties has not continued at the high level noted for 1951 to 1954. Since 1957, when Rescue and Chinook occupied 20 percent of the seeded acreage in the heavily infested areas of southern Alberta and Saskatchewan, the acreage of resistant varieties has dropped steadily. Resistant varieties of spring, durum, and winter wheats occupied 9.6, 7.0 and 5.9 percent of the seeded acreage in 1972, 1973, and 1974. (Data from: Seed Time and Harvest, Federal Grain Co., Winnipeg). Perhaps more significant, in relation to reports of increasing wheat stem sawfly infestations, is the increase in the acreage seeded to susceptible wheat varieties, from 53 percent in 1972 to 63 percent in 1973 and 1974. The causes of the relatively stable population behavior of the wheat stem sawfly since 1954 have not been fully explained. The continued use of resistant varieties, the sowing of unsuitable crops and awnless brome grass, and unfavorable weather have contributed to this stability. In addition, a parasite, *Bracon cephi* (Gahan) has become more abundant in wheat fields and effectively

reduces sawfly numbers under suitable weather conditions (N.D. Holmes, personal communication, Feb. 1975; Holmes *et al,* 1963). This is the only parasite species that has become adapted to the agricultural system. An attempt was made to introduce two parasite species from England but large scale releases from 1930 to 1938 were not successful (McLeod, 1962).

The efforts to increase the stability of yields and income in the agricultural system have also succeeded in stabilizing the population levels of the wheat stem sawfly. Its population fluctuations appear to be much less extreme than in the presettlement grasslands, because it is no longer subject to the perturbations associated with unpredictable grazing or the variability in the abundance of suitable stems for oviposition and larval development.

Rape Feeders

Rape is a relatively recent crop in the prairie provinces. Its acreage has increased rapidly since its introduction in 1943 (figure 7), and it now occupies 5 to 10 percent of the seeded acreage and more than 15 percent in the cooler and moister portions of the agricultural zone (figure 8). Despite its relatively recent introduction, this crop has been attacked by a number of species. Two of the three most destructive species are Nearctic and are discussed below.

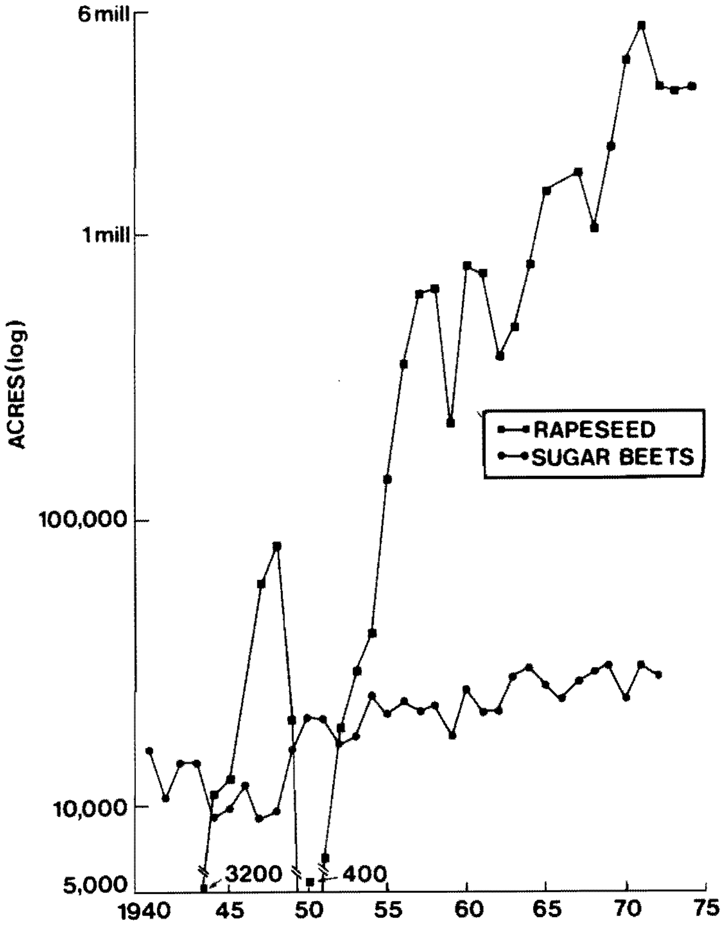

Figure 7. Total acreage seeded to rape (1943-1974) and sugar beets (1940-1972) in the prairie provinces (from: Handbook of Agricultural Statistics Part I. Field crops 1908-63, Dom. Bureau of Statistics, Agric. Div. 1964, and Canada Year Books, 1964-73).

1. *Mamestra configurata* (Wlk.), the bertha armyworm, appears to be native to grasslands across the Canadian prairies to the interior of British Columbia and south along the cordillera to Mexico City. Before agricultural development, bertha armyworm probably was a relatively rare species. Correspondence with entomologists from Wyoming south indicates that its status has not changed in those areas. In Washington, Oregon, and the Canadian prairies, it attacks a wide variety of cultivated field and garden crops as well as garden flowers and introduced weeds (King, 1928). Only a few nonintroduced hosts have been reported. The bertha armyworm overwinters in the pupal stage. The adults emerge during June and early July and lay clusters of up to 150 eggs. The younger larvae feed nocturnally on leaves of rape, flax, sweet clover, alfalfa, peas, and beans, but older larvae may feed on the green pods of these plants. The larvae usually complete their feeding around mid-August and enter the soil to pupate.

The bertha armyworm first became an agricultural pest on flax, sweet clover, and alfalfa. King (1928) notes that it had been observed as a crop pest "only within the past 12 to 15 years" (1912 to 1915). Local infestations of short duration occurred from 1921 to 1930, primarily on flax and garden vegetables. The causes of these population collapses are unknown, although King (1928) notes instances of almost complete pupal mortality, heavy larval mortality caused by disease, and larval parasitism up to 25 percent.

As the acreage of rape increased (figure 7), its importance as a host of the bertha armyworm similarly increased. The light infestations of 1940 to 1944 and 1947 to 1948 occurred on flax and rape, and the heavy infestations of 1953 to 1956 was mainly on rape. During the light infestations of 1962 to 1963 and 1966 to 1968 and the major outbreak of 1970 to 1974, the bertha armyworm has been primarily a pest of rape. The small number of reports of damage to flax and the

Figure 8. Distribution of rape production in the prairie province 1972 (from: Rapeseed, Canada's Cinderella Crop. Rapeseed Assoc. of Canada, Pub. No. 33, April 1974).

absence of reports of damage to garden crops, alfalfa, and sweet clover suggest that these are not preferred foods of the bertha armyworm.

The most recent outbreak began in 1970, when widespread but generally light infestations occurred. In 1971, an unusually heavy flight of moths occurred, and conditions for oviposition and larval survival must have been optimal, because heavy larval populations (up to 200-400 larvae/yd^2 were found throughout the main rape growing areas in a belt about 50 miles wide extending from Dauphin and Swan River in Manitoba to Edmonton, Alberta. An estimated 968,000 acres (17.7 percent of the seeded acreage) were sprayed with insecticide. Other fields were destroyed because of the unexpected severity and extent of the outbreak and the attendant difficulties in obtaining insecticide and spray aircraft. In 1972, populations were somewhat reduced, but large areas still required insecticidal treatment. The decline continued through 1973, and in 1974 only a few fields required treatment.

Precise data on the cause of the termination of the outbreak are lacking, but observations suggest the following contributing factors:

1. Heavy parasitism, particulary by the ichneumon, *Banchus flavescens* Cress, and a tachinid, *Athrycia cinera* (Coq.);
2. Reduced adult emergence and oviposition because of inclement weather;
3. Reduced early larval survival because of cool, wet weather and invertebrate predation;
4. Reduced survival in the third and fourth instars attributed in different areas to disease, bird predation, and early harvesting of the crop.

The bertha armyworm has shown itself to be very adaptable to the changing agricultural system. Soon after settlement, it attacked a wide variety of introduced plants, exhibiting an unstable population pattern characterized by high variation about a rather low mean (1921 to 1952). Since rape became a major crop, the bertha armyworm seems to be developing a population pattern characterized by a short period of very high populations over a wide area followed by a decline phase with generally low populations and local outbreaks. It has not been found on native hosts, and it appears that it and its major parasites and predators are now almost entirely adapted to the rape crop. Weather still plays a large role in determining abundance, with parasitism, disease, and predation contributing to population declines. The interaction between effective natural enemies, and the rapid population increases possible with high fecundity and favorable weather will determine the future population pattern of this species.

2. *Entomoscelis americana* Brown, the red turnip beetle originally fed on native cruciferous plants throughout areas of North America with cool, fairly moist continental climates (Stewart, 1973). This species overwinters in the egg stage near the soil surface. Hatching occurs in early May and the larvae feed on the leaves of cruciferous plants. Following completion of the pupal stage, adult beetles emerge in early June and feed on leaves and flowers of host plants. At the end of June these adults enter the soil to aestivate. In late July and early August they emerge from aestivation, feed on the flowers and pods of suitable hosts, mate, and oviposit until they are killed by cold weather (Gerber, 1974). No parasites or predators have been reported.

The movement from native hosts to cruciferous garden plants occurred very soon after settlement. Sporadic reports of such attacks between 1887 and 1927 appear in the Canadian Insect Pest Review. From 1931 to 1952, such reports became annual. Populations varied from light and local to severe and widespread. In 1943, the year of the first commercial planting of rape, the red turnip beetle was reported feeding on this new food. Since then, rape is the host mentioned in most of the survey reports, although attacks on garden crucifers still occur. Another outbreak, from 1956 to 1963 was followed, after 1 year of very low populations, by a series of years with light to moderate populations that seem to have built up to the current major outbreak in the Peace River district of Alberta.

The red turnip beetle has adapted to the abundant food resource and become an ubiquitous pest of rape and other crucifers in the cooler parts of the prairies. The range of population fluctuations seems to be wide. The factors controlling population changes have not been studied but probably include the effects of weather. Fall and spring cultivation affect egg survival and the abundance of larval food plants. Chemical insecticides are used when spring adults enter rape fields, but there is no evidence that the practice affects population trends.

Sugar-beet Feeders

Sugar beets have been grown on the prairies since the early days of settlement but the acreages were small until about 1940. Fields are concentrated in two areas in Alberta and Manitoba. Two native species have become pests of sugar beets in Canada. The sugar-beet root aphid, *Pemphigus betae* Doane, occurs in Alberta (Harper, 1963) and the sugar-beet maggot in both areas. Discussion will be limited to the latter.

Tetanops myopaeformis (Röder), the sugar-beet maggot, has readily adapted to the introduction of new food plants. Its wild hosts include lambsquarters, *Chenopodium alba* L., and red-root pigweed, *Amaranthus retroflexus* L. (Harper, 1962). It was first reported as a pest of sugar beets in Utah in 1920 (Hawley, 1922) and has since become a problem in other sugar-beet producing areas of the U.S.A. and in Alberta and Manitoba. In Canada, a period of years appears to have elapsed between the planting of significant acreages of sugar beets and the appearance of sugar-beet maggot as a serious pest: 9 years in Alberta and 14 years in Manitoba. Because sugar beet growing areas tend to be isolated, this delay may mark either the time needed for population increase in the newly abundant host stands or for immigration and adaptation of local populations to the sugar beet fields.

The sugar-beet maggot completes its feeding in the fall and overwinters in the larval stage in the soil. Pupation and adult emergence occur in late spring. Eggs are laid in the soil around host plants. The larvae feed on the roots and scar the root surface. No parasites, diseases, or significant predators are known. Populations of the sugar beet maggot are usually confined to light and medium soils. Larvae are found occasionally in heavier soils but seem to be incapable of overwintering in such soil types.

In Manitoba, sugar beets are grown primarily south of Winnipeg on the west side of the Red River Valley. Major cultivation of this crop began in 1940 and has since increased to about 30,000 acres (figure 7). Following the identification of a serious sugar beet maggot problem in 1954, the area of infestation increased from 300 to 1,500 acres between 1955 and 1959 to between 8,000 and 10,000 acres by 1965 and has remained at this level since that time (W.L. Askew, unpublished data). This part of the sugar-beet acreage is consistently susceptible to infestation.

Within the infested area, surveys of untreated fields and untreated plots in experimental fields showed that populations varied from 2 to 85 maggots per beet from 1957 to 1974 (table 2). This 42.5-fold variation is rather low for pest insects particularly in the temperate continental climates. The sugar beet ecosystem, however, is more stable than most of the western Canadian crop ecosystems; the acreage of sugar beets has not varied greatly, and the climate is less extreme and less subject to drought than elsewhere on the Canadian prairies. The rates of insecticide application, designed to avoid phytotoxicity, residue problems, and high cost (Allen and Askew, 1966; Askew et al., 1973), normally reduce larval populations by between 68 and 81 percent (table 2). Although higher mortality (86-93 percent) tended to occur in years with low populations and lower mortality (38-63 percent) with higher populations, mortality caused by insecticides does not seem to have influenced the annual population trends (figure 9). From 1957 to 1968, during and immediately following the period of heptachlor usage, the populations fluctuated about a mean of about 20 maggots per beet and the amplitude of the fluctuations increased over the decade (figure 9). The increasing amplitude of the fluctuations initially corresponded with an increasing incidence of resistance to heptachlor (Allen et al., 1971), but the change to new insecticides in 1965 did not reduce or stabilize populations. Populations reached a peak in 1969 and then fluctuated about a mean of about 55 maggots per beet for a few years. In 1973, inclement weather during oviposition and maggot establishment caused high mortality and reduced population to 24 maggots per beet (Askew et al., 1973).

Sunflower Feeders

Sunflowers, which are native to America, were introduced to Europe in the 16th century and reintroduced to America in the late 19th century. Commercial sunflower production began in southern Manitoba in 1943 and has been restricted to a relatively small area (Westdal, 1975). Sunflower acreage fluctuated irregularly from 3,000 to 48,000 acres from 1943 to 1969 and then increased rapidly to 270,000 acres by 1973.

In Manitoba, a rather large number of native insects are found in commercial sunflower fields (Westdal, 1973). Several of these species are rare and poorly known, but five species are at least partially adapted to the agricultural system:

Rhynchites aenus (Boh.), a sunflower curculio, is a stem feeder that also attacks wild rose. Attacks on sunflowers have not been severe and have been limited to field margins. This suggests that the curculio is either not well adapted to the sunflower as a host or cannot survive the winter in open fields. In either case, it has not fully adapted to the agricultural system, and its abundance and presence in sunflower fields may be dependent on the occurrence of native hosts along field margins.

Zygogramma exclamationis (F.), the sunflower beetle, feeds on sunflower leaves in both the adult and larval stages. The adults overwinter and are most destructive in the spring when they emerge from hibernation and feed on sunflower seedlings. Natural control, primarily by insect predators, usually is effective but outbreaks were recorded in 1952, 1957 to 1959, and 1971 to 1974. The sunflower beetle and its predators appear to have adapted quite well to the sunflower fields. Population fluctuations of the sunflower beetle seem to reflect a periodic, climate-related escape from normally effective natural control.

Strauzia longipennis (Wild.), the sunflower maggot, spends the larval stage tunnelling in the pith of the stalk. This feeding does not directly or significantly affect crop yield and therefore control measures are not warranted. Infestations in sunflower fields are consistently high (Westdal and Barrett, 1962), suggesting that these fields now provide the major population foci for the species. Parasitism is normally low and fluctuations may be related to food abundance, intra-specific competition, and weather.

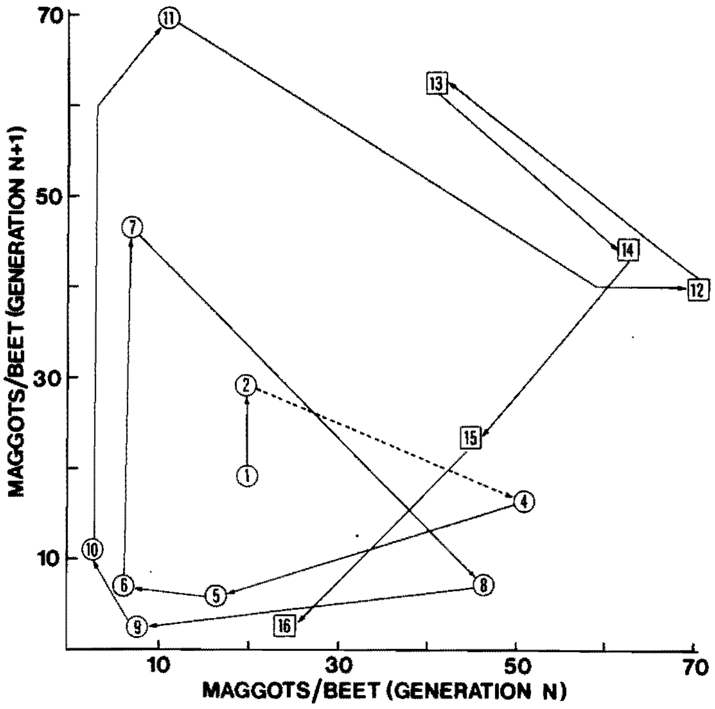

Figure 9. Population changes of the sugar-beet maggot in Manitoba, 1957-74. [1=generation n (1957) vs generation n + 1 (1958)... 16=generation n (1973) vs generation n + 1 (1974)] – data from W.L. Askew, Agriculture Canada, Research Station, Winnipeg.

Homeosoma electrellum (Hulst), the sunflower moth, and *Phalonia hospes* (Wlshm.), the banded sunflower moth, have similar life histories and population patterns. Their larvae feed on sunflower florets and seeds and pupate in the ground. Both species occurred at outbreak levels for a few years after the introduction of commercial sunflower growing to Manitoba but have since fluctuated at low levels. Efficient natural control by parasites is credited with keeping them at low levels, and chemical control generally is not used against them. These species seem to have transferred to sunflower fields with their natural control complex intact, although information on wild populations is lacking. The outbreaks at the outset of sunflower cultivation probably were caused by an escape of the two phytophages from their parasites and were controlled by the parasites invading and adapting to the agricultural habitat and system.

DISCUSSION

Presettlement populations of phytophagous insects in the prairie ecosystem were adapted to survive major short- and long-term perturbations. The short-term perturbations included fire, the devastating effects of bison grazing and trampling, and the extremes of weather such as floods, droughts, frosts, and thaws. The long-term perturbations included changes in the distribution of vegetation and amount of precipitation. Under these conditions populations of insect phytophages must have been both highly unstable and highly resilient.

Settlement and the development of agriculture have tended to reduce the effect of natural perturbations on phytophagous insects by providing a much less variable vegetative cover. At the same time, however, the native grassland vegetation was either destroyed or subjected to much more constant pressure from grazing and haying. The crops that replaced the native grasses were, with the exception of sunflowers, derived from plant genera that were poorly or not at all represented in the native flora.

The ability of the native phytophagous species to adapt to the more stable agricultural system has not matched their resiliency following natural perturbations. The species of plants cultivated, rather than monocultural agriculture, seems to have imposed the greatest barrier to adaptation by phytophagous species. General feeders, such as grasshoppers, cutworms, and wireworms, and specific feeders on a native crop, sunflowers, have adapted quickly and well to the agricultural system. In contrast, adaptation to exotic crop species has been slow, and only a few native species have been successful. For both general and specific feeders, current population patterns depend on weather and the degree of adaptation of the phytophages and their biotic control factors to the crop system.

Adaptability

The 13 species considered in this paper include one species that has failed to adapt to agricultural conditions, three that appear to be in the process of adapting, and nine that have adapted to the point where a pattern of population behavior can be discerned. Although Bird (1961) notes that grassland insects with general feeding habits have been more successful in adapting to agriculture than those with more specific feeding habits, the only known species that has become extinct is the Rocky Mountain grasshopper, *Melanoplus spretus*. This species, although a general feeder, appears to have been unable to adapt to potential oviposition sites after its original sites were destroyed following settlement. Undoubtedly, other insect species whose activities were less conspicuous than the swarms of grasshoppers have also become extinct, and many more now exist in refugia at very low population densities.

Species apparently in the process of adapting include *Mamestra configurata, Entomoscelis americana,* and *Rhynchites aeneus*. Both *M. configurata* and *E. americana* became sporadic pests of various garden and field crops early in this century but have been adapting to rape since it was introduced in 1943. Two major parasites of *M. configurata* have also adapted to field conditions, but no parasites or predators of *E. americana* have been identified. *R. aeneus* is poorly adapted to sunflower fields and infestations have been limited to plants near field margins, a pattern similar to that reported for *Cephus cinctus* when it first attacked wheat. Parasites or predators have not been reported on *R. aeneus*.

The species that have adapted to agricultural conditions include three general feeders and six species with more limited feeding habits. The grasshoppers, with general feeding habits, adapted very quickly to the agricultural system becoming pests whenever weather conditions become favorable. Their parasites have similarly adapted but are no more effective in the agricultural ecosystem than they apparently were in native grasslands.

Tetanops myopaeformis required some 15 years to adapt to cultivated sugar beets. Once adapted, however, its numbers increased rapidly. None of its parasites or effective predators have become adapted to sugar-beet fields.

Cephus cinctus began to attack cereal crops soon after they were cultivated in the mixed prairie. Adaptation to wheat apparently required decades (1907-1925) following which populations increased to and remained at very high levels (1926-49). Since then, the planting of resistant wheat varieties and the adaptation of a parasite to cultivated land have reduced its abundance. *C. cinctus* is still imperfectly adapted to cereal cultivation, because it continues to oviposit in resistant wheat varieties and other crops, such as oats, barley, and flax, in which the eggs and larvae do not survive.

Four species attacking sunflowers (*Zygogramma exclamationis, Strauzia longipennis, Homeosoma electellum,* and *Phalonia hospes*) adapted to the agricultural system as soon as sunflower cultivation began. The predators and parasites of *Z. exclamationis* apparently adapted as quickly as their host, because there was no initial outbreak and a high level of natural control normally occurs. *H. electellum* and *P. hospes* apparently escaped their natural enemies for a few years, but these enemies adapted soon after and have been effective ever since. A parasite of *S. longipennis* became established soon after it adapted to cultivation, but the parasite is not very effective.

Stability

The term "stability" is regularly used in ecology in a number of different ways (Orians, 1975). In this paper, it is defined as "the ability of a system to return to an equilibrium state after a perturbation; the more rapidly it returns and the less it fluctuates, the more stable it would be" (Holling, 1973). Perturbations which move a population outside the domain of one equilibrium state may move it into the domain of another equilibrium state. Species may have more than one equilibrium state; in pest species "endemic" and "outbreak" states are commonly recognized. This simple categorization is inadequate to describe the different equilibrium states that may exist, over time and space, in a species with population patterns that are affected by adaptation to new crops, resistance to insecticides, changes in the types or effectiveness of biotic agents, new cultural practices, etc. Quantitative data on population fluctuations over a considerable time period are needed to describe these equilibrium states with precision. Such data are lacking for the species discussed in this paper. Nevertheless, major equilibrium states and shifts in their mean abundance can be identified.

The grasshoppers lack effective natural enemies and have a very wide range of population fluctuations. Two equilibrium states can be recognized, a stable endemic state where fluctuations are minor and a less stable outbreak state. The endemic state, although stable, is relatively easily perturbed by weather factors to the extent that populations rise to the outbreak state. The latter state has persisted for as long as 20 years, despite its instability, and only the most severe perturbations, such as extreme weather conditions or weather-related epizootics, have driven the populations back into the endemic domain. The agricultural system, by providing abundant food in all but the most severe drought years, has increased the resiliency of outbreak populations.

Mamestra configurata, before the appearance of rape as its preferred host, had a population pattern characterized by brief and local outbreaks. More recently, the duration and extent of outbreaks have increased and two equilibrium states may be developing. The situation apparently is in flux: although two parasites are well-adapted to agricultural conditions and have caused high mortality in the declining phase of the last outbreak, their effectiveness in maintaining an endemic equilibrium state is unknown. Under favorable weather conditions, the high natural fecundity of the bertha armyworm may counteract the biotic agents. In this case, the population pattern could fit that of a single, highly unstable equilibrium state.

Zygogramma exclamationis, like the grasshoppers, has two well-defined equilibrium states. An effective parasite and predator complex has maintained a stable endemic state during most of the 35 years that sunflowers have been grown in Manitoba. The range of population fluctuations during the outbreak state has not been recorded.

Tetanops myopaeformis appears to have two equilibrium states, but the data sequence is too short to show if the higher density state will recur. The lower state, which appears to fluctuate about a mean of 20 maggots per beet, is quite unstable and the range of fluctuations includes populations above and below the damage threshold. The upper equilibrium state, about a mean of 55 maggots per beet, was associated with unusually favorable weather and terminated by unfavorable weather. Parasites and effective predators are unknown, and the food supply is stable. Thus, the factors responsible for the observed population fluctuations of this species within the lower equilibrium state also appear to be weather related.

Entomoscelis americana populations appear to have fluctuated within the domain of a single highly instable equilibrium state since 1931. This state includes population levels above and below the economic threshold. Reports of damage have been more widespread since 1956 than previously, probably reflecting the increased abundance of rape.

Cephus cinctus has had two equilibrium states since it became adapted to wheat about 1925. The outbreak state, apparently characterized by moderately large population fluctuations, persisted until about 1954 when resistant wheat varieties became dominant. Since then, populations have remained in an endemic equilibrium state; favorable weather has increased populations but never beyond the domain of the endemic state. Parasitism also has apparently contributed to this stability. This is the only example among the species examined in this paper where a perturbation resulting from deliberate human actions has shifted the population from one equilibrium state to another. The endemic state has proven highly resilient persisting in the face of a decreasing proportion of resistant wheat. In the future any prolonged and significant increase in the area of susceptible wheats probably will enable favorable weather to shift the population into the domain of the outbreak state, a change that might only be reversed by a large increase in the acreage planted to resistant varieties.

Homeosoma electellum and *Phalonia hospes* briefly escaped their natural enemies immediately after commercial sunflower growing began in Manitoba. After a brief period in the outbreak state, the populations have remained at an uneconomic level. The range of population fluctuations has not been recorded but the species seem to be persisting in a stable, endemic equilibrium state.

Strauzia longipennis, which lacks effective parasites and predators, also appears to persist in a stable equilibrium state. It feeds on the sunflower pith and appears well protected from such natural enemies. Its stability may be related to its protected feeding site and the stability of food supply provided by the agricultural system.

Rhychytes aeneus is apparently only poorly adapted to the agricultural system and the information on its population levels is very sparse.

CONCLUSIONS

The change from a highly unstable system in presettlement grassland to the more stable agricultural system of the present has led to the destruction and reconstitution of the relationships between hosts and phytophagous insects. The following generalizations appear valid:

1. The ability of native insects to adapt to the agricultural system and the speed with which this adaptation occurs is related to:
    a) the feeding habits of the insect -- many species with general feeding habits adapted quickly to the agricultural system, while very few species with specific feeding habits have been able to adapt;
    b) the type of crop — crops derived from native plants (e.g., sunflowers) are quickly attacked by a variety of specialized native insects, whereas crops only distantly related to native vegetation are attacked by a small number of specific feeders;
    c) other environmental requirements — one general feeder, *Melanoplus spretus*, became extinct apparently because it could not adapt to the destruction of its oviposition sites;
2. Native parasites and predators can adapt with their hosts to crop conditions and their speed of adaptation is apparently related to the similarity of the crop plant to the native food plants of their hosts.
3. The native insect pests fall into the following categories of population stability:
    a) Opportunistic species. These have a "wide-amplitude type of population behavior" (Watt, 1968) and periodically reach very high densities in response to favorable environmental conditions. They have two clearly defined equilibrium states, a stable endemic state and an instable but highly resilient outbreak state. Species that lack effective natural enemies, such as the three species of grasshoppers, persist in the outbreak state longer and have a less resilient endemic state than those with reasonably effective natural enemies such a *Zygogramma exclamationis* and probably *Mamestra configurata.*
    b) Specific feeders without effective natural enemies. These usually tend toward a single unstable equilibrium state that may include both endemic and outbreak population levels (e.g., *Strauzia longipennis* on sunflowers and *Cephus cinctus* on wheat from 1925 to 1949). *Entomoscelis americana* on rape seems to be showing this type of equilibrium state. *Tetanops myopaeformis* may have both an unstable equilibrium state encompassing both damaging and noneconomic population densities and a higher equilibrium state of briefer duration occurring when environmental conditions are exceptionally favorable.
    c) Specific feeders with effective biotic control. These have a single stable equilibrium state at noneconomic levels. *Cephus cinctus* on wheat, from 1954 to date, *Homeosoma electellum*, and *Phalonia hospes* show this type of population behavior.
4. Insecticides have had no noticeable effects on population fluctuations. Insecticides have proven effective in protecting crops against grasshoppers, *Entomoscelis americana, Mamestra configurata, Zygogramms exclamationis,* and *Tetanops myopaeformis* but do not appear to

have affected their population patterns either by terminating outbreaks or by prolonging them by destroying natural enemies. Low grasshopper populations from 1952 to 1957 coincide with the use of persistant insecticides, but their subsequent population behavior is not consistent with any hypothesis that insecticidal residues in the soil have a continuing effect on the numbers of these insects.

5. Shifts in the equilibrium level of native agricultural pests in the Canadian prairies commonly have been associated with changes in weather or the adaptation of parasites and predators to the agricultural system. A planned control program has caused such a shift in only one case, the introduction of wheat varieties resistant to wheat stem sawfly, *Cephus cinctus.*
6. There is too little known of the population ecology of species to prescribe approaches to shifting their equilibria to lower and less damaging levels. The available evidence suggests that the breeding of resistant varieties, the use of biotic agents, and special cultivation practices should be investigated.

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Table 1. Summary of major field crops and their native insect pests in the Canadian prairies

Crop				
Species	Mean annual seeded acreage 1961-71 (thousands)	First widespread planting	Number of native cogeneric species*	Specific insect pests †
Wheat *Triticum aestivum L.*	25298	ca. 1870	0	*Cephus cinctus* Nort.
Barley *Hordeum vulgare L.*	7673	ca. 1870	2	
Oats *Avena sativa L.*	5656	ca. 1870	0	
Rye *Secale cereale L.*	708	ca. 1870	0	
Flax *Linum utilatissimus L.*	1902	ca. 1870	5	*Mamestra configurata* (Wlk.)‡ *Heliothis ononis* (D. & S.) ‡
Sugar beet *Beta vulgaris L.*	66	ca. 1910	0	*Tetanops myopaeformis* (Roder) *Pemphigus betae* Doane
Rape *Brassica napus L.* *B. campestris L.*	1860	1943	0	*Mamestra configurata* (Wlk.) *Entomoscelis americana* Brown
Sunflower *Helianthus annuus L.*	70	1943	7	*Rhynchites aeneus* (Boh.) *Zygogramma exclamationis* (F.) *Strauzia longipennis* (Wild) *Hemeosoma electellum* (Hulst) *Phalonia hospes* (Wlshm.)

* Species of plants in the same genus native to the Canadian prairies, from Budd (1957).
† Excluding general feeders and minor pests.
‡ Not major pests in recent years.

Table 2. Populations (maggots per beet) of the sugar beet maggot in Manitoba, 1957-68 (from data provided by W.L. Askew, Agriculture Canada Research Station, Winnipeg)

		Experimental fields		
Year	Untreated fields*	Untreated plots	Insecticidal plots	Reduction (%)
1957	-	20	4	80
58	19 (4)	20	4	77
59	29 (4)	30	6	79
60	85 (1)	-	-	-
61	49 (4)	51	12	75
62	16 (4)	16	5	68
63	6 (4)	6	0.4	93
64	7 (6)	7	1	90
65	13 (15)	46	9	81
66	3 (26)	8	2	75
67	7 (36)	2	0.3	86
68	11 (23)	12	3	76
69	17 (42)	70	34	52
70	7 (27)	40	20	51
71	14 (23)	62	23	63
72	-	45	28	38
73	-	24	8	68
74	-	2	7	-

*Number of fields sampled given in parentheses, 25 samples/field in 1958-64, 100 samples/field in 1965-74.

Some Reforestation Practices that Increase Insect Pest Buildup

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ABSTRACT

Planting practices in the Great Lake States have sometimes encouraged rather than discouraged insect outbreaks. Major factors have been closeness of plantings to infested stands and mixtures of closely related tree species. The latter encourages insects to heavily attack tree species normally low in susceptibility. Attacks can be curtailed by manipulating stand diversity, planting resistant trees, modifying sites before and after planting, and planting in areas distant from insect inoculum.

INTRODUCTION

Some reforested stands in the Great Lake States have increased rather than discouraged insect buildup. These undesirable plantings are discussed briefly and some preventive measures are proposed for future plantings.

Most early plantings, and some recent ones, were planted as monocultures with little regard for the potential source of insect inoculum in the vicinity. Consequently, such plantings were often quickly invaded by insects, and in numerous cases outbreaks ensued.

Some early attempts were made to diversify stands by planting mixtures of tree species to reduce insect attacks. Mixed stands in general appear resistant to insect attack compared to pure stands, but most mixtures planted over the years have been no better than monocultures as far as the insects were concerned. In fact, some of the planted mixtures have encouraged insect outbreaks.

REFORESTATION PRACTICES CONDUCIVE TO INCREASED INSECT ATTACK

Closeness of Plantings

Plantings that are established disregarding the insect inoculum at or near the site often become major problems. In one step the nearby donor host harboring the insect infects the recipient hosts, the planting. This occurs when susceptible recipients are: (1) planted in an area already occupied by at least one (but often more than one) large donor or brood tree; (2) planted as an understory beneath donor trees; or (3) planted near donor trees. How near before infestation occurs depends on access, dispersal, and searching capability of the insect. Sometimes the recipient host is also an alternate host. That is, both donor and recipient are used to complete development of the insect. The donor host may be a tree or shrub in this case.

These three situations arise for almost all forest insect pests. For instance, one commonly sees a young red pine planting with a few older brood trees in its midst that harbor and donate one or more forest pest species when the planted trees grow to susceptible size.

Some jack pine stands infested with jack pine budworm are underplanted to red and eastern white pine. Although budworm moths seldom oviposit on red and white pine, underplanted trees usually become heavily or completely defoliated from the less discriminating larvae that drop down and feed on them. Rudolph (1950) also found that white pine suffers the heaviest budworm damage when it occurs under jack pine.

One Scotch pine planting that I recall was planted next to a long Scotch pine windbreak infested with European pine sawfly. Most of the planting became infested 2 years later, and though controlled for 2 consecutive years thereafter, the infestation became greater each year from the insect inoculum on the windbreak trees.

Also, red and jack pine stands are often planted in fields abounding in sweetfern, thus providing the perfect situation for an infestation of Saratoga spittlebug which needs sweetfern as an alternate host. If the sweetfern covers more than 40 percent of the ground, probability of a severe outbreak is high (Wilson, 1971).

White grubs (*Phyllophaga* spp.), the larvae of June beetles, become serious pests in some plantings. Seedlings planted in old grassy fields near hardwoods are attacked by white grubs. The grubs normally feed on the grasses but attack seedlings when grasses are removed. Hardwoods are the alternate host for the adults.

Mixed Plantings

The concept of mixed plantings arose early — sometimes for limiting pest damage and sometimes for other reasons (Kittredge, 1929). The 1933 Lake States Annual Planting and Nursery Report states, "Looking toward a greater protection from the Blister rust disease . . . an experiment with mixed plantations in which (eastern) white pine, Norway spruce, and Norway (red) pine were planted in different combinations to break the susceptible canopy . . . On the Argonne (Nicolet National Forest) white pine and yellow birch were mixed in equal amounts in alternate rows on 18 acres with the thought that this might lessen the damage in pure stands."

Thereafter, mixed plantations were established in several localities using predominantly the native species such as red, jack, and eastern white pine, spruces, larch, and a few less abundant exotics such as Scotch and ponderosa pine. Most common mixtures were red-white or red-jack pine combinations, but others such as white pine-white spruce or red-white-jack pine occurred.

Mixed plantings can be mixed in age as well as species. Some possibilities are: (1) alternating rows of species or alternating species within rows, (2) one or more species scattered among another, (3) side-by-side plantings or alternating blocks of trees of different species, (4) trees of one or more species planted at different times in any combination to provide an uneven age structure, and (5) scattered replanted trees following poor survival.

Plantings today are still vulnerable to heavy insect attack if the tree species are closely related or if the age differences are not large. Infestations in these mixed plantings proceed in two steps. A donor host containing the insect inoculum infects one or more susceptible recipient hosts in the mixed planting. Then, as the insect pest builds up, these trees infect the less suceptible trees or younger trees.

Some case histories show the range of the problems for different forest pests.

Case No. 1. In northwestern Michigan there are numerous mixed plantings consisting usually of 10-row blocks of jack pine alternated with 10 to 20 row blocks of red pine at 6 x 6 foot spacing. The jack pine was planted first; the red pine usually 5 years later. Spaces occurring from poor survival of red pine were usually replanted 2 to 5 years later. Thus, these stands have a two-species and three-age structure. Some red pine of both ages have died in all plantings with mortality sometimes exceeding 20 percent. Examination of several infestations revealed the jack pine in each case had originally become infested by the pine root collar weevil (*Hylobius radicis* Buch.) from some outside preferred host, such as natural jack pine or planted Scotch pine. In turn, it infected the red pine. Both the red and jack pine then provided brood material for the young replant red pines. In contrast, comparable pure stands of even-aged red pine in the same area of the state have never been more than moderately infested – only an occasional dead tree.

Case No. 2. In the same or similar stands, red and jack pine are commonly infested with the jack pine tip beetle (*Conophthorus banksianae* McP.) which attacks and kills shoots. The red pines were always infested in a pattern suggesting that the attacks were from "overflow" insects from the donor jack pines. Measurements in one stand (McPherson et al., 1970) showed that on the jack pine no distinct relationship existed between the number of attacked shoots and their proximity to red pine, but there was a distinct relationship between the numbers of attacked shoots on red pine and the proximity to jack pine. Pure young jack pine stands often have this beetle, but pure red pine stands never have more than an occasional sporadic or random attack indicating that it is not normally a host of this insect.

Case No. 3. A private 4-acre block of Scotch pine in Michigan, adjacent to the same size block of white pine, had about 15 percent Scotch pine mortality from the pine root collar weevil when first examined. Some of the eastern white pine in the rows adjacent to the Scotch pine had weevil attacks at that time. When examined 5 years later, over 95 percent of the Scotch pine (the preferred host) had died and many of the eastern white pine (the most resistant host) in border rows were heavily weeviled or dead. Although mortality in the eastern white pine was about 1 percent, if the white pine had been alternated with the Scotch pine, it certainly would have been even greater. White pine is almost never attacked in pure stands; heavy resin flow after an injury is thought to be the reason for its resistance. Repeated attacks, as occurred here because of their proximity to Scotch pine, probably weakened the trees and made them more susceptible.

Case No. 4. Another private planting in Michigan, consisting of alternating rows of 5 to 6 foot tall Scotch pine and Austrian pine, when last observed showed all the Scotch pine to be attacked and 20 percent dead from the weevil. The normally more resistant Austrian pine was about 50 percent infested and 2 percent dead. Austrian pine is rarely planted in this manner; the degree of attack is more severe when there is an adjacent donor host than when it is planted as a windbreak or ornamental.

Case No. 5. A state planting in Michigan contains a 5-acre block of red pine adjacent to a 3-acre block of jack pine. The jack pine was a few years older than the red pine and heavily infested with white pine weevil (*Pissodes strobi* Peck). The red pine was moderately infested (about 25 percent) in the rows adjacent to the jack pine but progressively less infested away from the jack pine. This suggests the red pine became the recipient host because of the proximity to the jack pine, especially since red pine is rarely attacked by this weevil.

Case No. 6. A similar instance occurs in Newaygo County, Michigan between adjacent blocks of white spruce and eastern white pine. The pine is moderately infested by the white pine weevil. Several of the white spruce closest to the white pine are also infested. White spruce is not normally attacked by this weevil.

Many other case histories could be cited from experience and the literature. There are even instances where a polyphagous insect will change from hardwoods to conifers to feed. Red pine planted under hardwoods is sometimes attacked by the leaf roller, *Archips argyrospilus* (Walker), which normally feeds on the hardwoods. A similar situation sometimes occurs with the oblique banded leaf roller, *Choristoneura rosaceana* (Harris), (Simeone and Engelken, 1959). Most mixtures like this, however, are beneficial if a less polyphagous insect is involved. For example, white pine planted under hardwoods discourages white pine weevil attack on the pine.

PREVENTING PLANTATION INSECT PROBLEMS

If the best cure of an ill is prevention, many insect problems of mixed forest plantations can be curtailed in future plantings by manipulating or treating the plantation components before, during, or after establishment in ways that are unfavorable to destructive insects. Prevention involves taking advantage of all factors and relationships between the tree and the site to maximize their effects against one or more insect species so that damage to the host is kept below a certain economic or aesthetic level.

Forest plantations are more amenable to prevention than are natural stands because we have some control over the stand from the beginning. We can select the trees and planting site, decide on the spacing and species mixture, and modify or manipulate the environment to some extent with regard to any one or more insect pests in an area. Appropriate preventive practices, of course, should conform with multiple use concepts and should not conflict with sound forestry economics and sound management practices.

Some actions we can take are: (1) reduce the proportion of the area containing the insect's useful food, that is, create diversity or some kind of mixture, (2) reduce energy flow through the pest population, that is, provide maximum plant resistance both genetically and by site enrichment, and (3) favor other biological interactions that provide conditions that deter pest buildup.

Stand Diversity

To mix or not to mix, that is the question. Evidence today concerning the degree of diversity in a forest stand relative to insect outbreaks or injury is conflicting. Some diverse natural stands such as the mixed hardwood-hemlock forests or the pine-hardwood-spruce forests almost never appear severely injured by insects. And some uniform natural forests that are predominantly pine, balsam fir, aspen, or birch are frequently subjected to insect outbreaks and sometimes are severely damaged (Dowden, 1957; Graham, 1951). Nevertheless, many typically diverse forests are injured considerably (Varley and Gradwell, 1962) and many "pure" stands develop to maturity with no appreciable injury.

Diversification of forest plantings, could adversely affect some destructive insects by disrupting their behavior and habit patterns. Way (1966) points out that quality of diversity rather than quantity is more important, because pest outbreaks still can occur in a relatively diverse environment. The kind of diversity cannot be generalized because it differs for each species of insect because of feeding habits and habitat requirements. The monophagous insect, for instance, will attack only one species of tree regardless of the number of species present, but some diversity in the stand may very well curtail attacks by retarding the insects' mobility and searching behavior. In contrast the number of tree species attacked by the polyphagous insect depends largely on the number of species present, so that stand diversity alone would not be sufficient to curtail an insect outbreak. For the typical plantation pest, which has feeding requirements intermediate between the above extremes, some stand diversity might provide certain plantings a modicum of protection.

We have learned that for most forest plantation pests, mixtures must consist of neither two or three tree species of the same or closely allied genera nor the simple two or three age group structure because a strong donor-recipient relationship develops. To deter the average plantation insect, most stands should consist of at least two diverse taxa that the insect perceives to be vastly different. Insects perceive at different levels than we do and diversity to them may be due to small physiological or biochemical differences that are not apparent to our senses. Also various factors may influence an insect's perception. The adult female may be strongly influenced by the food on which she fed when immature (V. Dethier, personal communication). Adult insects seek primary hosts but may attack hosts that usually are secondary with equal or greater frequency if these hosts are in their field of attack, which might occur when certain barriers to sense perception are cloaked. Immature insects first feed on the hosts on which they hatched, but as they develop they may become less discerning than their parents in perception and then feed on other hosts with equal or greater voracity.

As yet we do not know the degree of diversity needed to control insect pests, but first we might try to emulate the natural pine-hardwood or pine-spruce-hardwood forest or something similar until we better understand the parameters of diversity. In red pine, for instance, a mixed planting might consist of red pine and compatible hardwood trees or shrubs. Random spacings, as in nature, would be logical but alternating rows, strips, or blocks of trees are more practical depending on the purpose of the planting. Block patterns might prove more effective than alternate rows against sawflies and other insects that respond strongly to edge rows. Alternate rows of different sized trees could appear as "edges" to them and attacks might become more intense throughout the stand. On the other hand, alternate row plantings might provide barriers that limit less mobile insects such as the pine root collar weevil. Only ideas and theories can be proposed at this time until more data are forthcoming. In many instances stand mixtures alone may not suffice; resistant trees and site modification may also be needed.

Host Resistance

Choose insect-resistant planting stock if available and make sure the site is suitable to help achieve success for a plantation.

There has been much interest in genetic resistance of hosts to the white pine weevil (Connola, 1966; Gabriel, 1957; Hiemburger, 1963; Kriebel, 1954; Kulman and Harman, 1967; Plank and Gerhold, 1965; Santamour, 1964; Stroh, 1964; Stroh and Gerhold, 1965; Wright, 1959). Resistance in eastern white pine appears to be connected with the mechanisms of nonpreference and antibiosis. Also some information has been gathered on resistance of jack pine to the white pine weevil (Arend et al., 1961; Batzer, 1961, 1962).

Red pine has shown low genetic variability in several characteristics including resistance to insect attack. With this species it is best just to have good healthy stock and provide it with the best site conditions that are practical.

Scotch pine, which is attacked by numerous insects, is highly variable and has varieties that are resistant to attack. Southern European varieties that generally grow faster than central or northern varieties, show significantly more resistance to pine root collar weevil and Zimmerman pine moth (Wright and Wilson, 1972; Wright et al., 1975). The northern variety *uralensis* from Russia is more resistant than all others to the European pine sawfly (Wright et al., 1967).

Site evaluation and modification should become a part of plantation management along with mixed planting and genetic selection to prevent insect attacks. We know that forest trees planted on the "proper" sites generally are much more resistant to attacks by insects and especially defoliators (Bennett, 1965; Bess et al., 1947; Craighead, 1925; Grimal'skii, 1961; Schwenke, 1966; and Vité, 1961). A vigorous tree on the proper site is minimally attractive to forest pests, has a high degree of passive resistance, and maintains maximum recuperative powers if injured (Graham, 1963; Keen and Salman, 1942; Prebble, 1951). The term "site" encompasses a broad assemblage of factors that collectively govern the quality of a parcel of land. Factors include soil type, aspect, depth and texture of surface soils and subsoil, drainage, ground cover, depth to water table, hard pan, previous forest cover, and others. The key to the combination of factors that should keep the tree in the best physiological state has not been found for each tree species.

One problem we must face is that many of the remaining plantable areas left today are not considered good sites because the best ones were planted first. Unfortunately, poor sites are being planted yearly regardless of the consequences (Wilde et al., 1964). If we are to provide sites favorable to the tree and unfavorable for pest buildup, we must learn the various site factors that need modification and then modify them.

Sites can be modified logically in several ways to help the trees resist the insect. For instance, a plantable area can be plowed, disked, drained, irrigated, tilled, fertilized, weeded, etc. as for any crop. Some such modifications raise the site index for certain species of trees by as much as 15 units (Morris, 1965; Wittenkamp and Wilde, 1964; Worst, 1964), which alone might offset the site preparation costs. Wollum and Youngberg (1964) found that the site quality could be increased by planting snowbush and alder, plants that made nitrogen more available to pines. The pines grew well from the start and apparently were able to compete and continue to grow well along with these plants. More mychorrizal associations with the tree's roots also will increase the tree's growth and vigor.

Water relationships help determine site quality. White (1958) stresses that either too much or too little water decreases the tree's resistance to insect attacks. Unless the planting is proposed for intensive culture, irrigation is likely impractical for most plantings on dry sites, but there are a few ways to reduce water losses. Early removal of ground vegetation by plowing, using herbicides, or both, cuts water and nutrient losses. Van Haverbeke (1965) showed that in areas of limited precipitation the soil should be plowed 2 years before planting to build up soil moisture. Others have noted that many of the dry, deep, sandier soils support mats of *Cladonia* spp. which prevent water from entering the soil to the extent that 212 times more water is available in open areas than in soil covered by *Cladonia.* On certain other sites *Cladonia* may be useful in preventing invasion and competition by other plants (Gysel, 1966; Porter and Woollett, 1929).

The growth of pines may be adversely affected by grasses and other plants (Vasil'ev, 1961) not only from competition, but from insect pests they harbor. Grasses not only compete on a planting site, but may also harbor white grubs. Sweetfern competes with pines, thereby causing stress during an insect outbreak; it also serves as alternate host to the spittlebug. If sweetfern is abundant, the spittlebug population may become high (Kennedy and Wilson, 1971a). Bracken fern also causes stress by competing with pines and making them vulnerable to the redheaded pine sawfly.

All factors considered, a grass like *Agropyron,* which does not serve as a host to spittlebug (Ewan, 1961) and which has less influence on height, survival, diameter, and root spread of pines, could be established after tree planting on poor sites to displace plants like sweetfern and bracken fern. Fortunately, on good sites sweetfern gives way to plants less favorable to the spittlebug. Plowing should probably not be used to control sweetfern as recent evidence suggests that sweetfern is actually stimulated to sprout more profusely.

Standard fertilizers sometimes increase a tree's vigor and growth. Saplings and young pines in plantations respond favorably to fertilizer applications to the soil but enhance sucking insect damage (Nickel, 1973). Mulching of conifers may increase survival by 20 percent (Champagne, 1954) and decrease fire danger (LaMois, 1958).

Biological Interactions

Minimizing one-step infestations is an obvious and logical step in preventing or curtailing insect attack. It is senseless to plant trees among or in the vicinity of infested brood trees, overstory trees, or a stand or windbreak nearby unless these donor hosts are treated or removed ahead of time. How far away must the donor host be from the recipients? This depends on the insect, its access to the planting, and its ability to disperse and search out the recipient hosts. Damage from the pine root collar weevil, a poor flier, is directly related to the distance a plantation is from the donor (Kennedy and Wilson, 1971b). Only light weevil damage occurred when the distance was more than 1/2 mile; most heavy infestations occurred when the distance was under 1/8 mile. The Saratoga spittlebug, also a poor flier, might show similar distance relationships. Clearly, distance may not eliminate an infestation, but it could curtail one long enough to allow the trees to grow out of susceptible size.

One might also encourage certain plants that harbor parasites. Syme (1966) noted that the abundance of wild carrot (*Daucus carota* L.) was related to the incidence and parasitization of the European pine shoot moth. Survival of the adult parasitoids were high because they fed on the wild carrot.

DISCUSSION

Hopefully, serious insect outbreaks can be prevented in many plantings by diversifying the stand, using insect-resistant planting stock, modifying sites, and planting in areas distant from insect inoculum. Research has just crossed the threshold in this area and has yet to provide enough useful information for suitable preventive measures. Even when measures are available, the purpose or value of the planting will further dictate the measures we can apply.

If a planting's value remains low, as occurs with some of our stands currently managed for pulpwood and sawtimber, our input will be low. We may be able to diversify stands considerably in future plantings, but the modifications needed to fully prevent insect attack may be impractical if a profit is to be made. On the other hand, if much diversification is impractical for certain stands, it is then better to plant a truly *pure* stand rather than attempting mixtures of closely related species as has occurred. If stand value is high, however, as occurs under intensive culture where maximum fiber production is the goal, we may be able to afford research into insect resistance and then enrich the site using fertilization, irrigation, and intensive site preparation. In this case, it may be undesirable to diversify because these stands are best managed as monocultures. Because this system also tends to be ecologically unstable, some pesticides may have to be applied, but hopefully only for a few pests and only to a limited degree.

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