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ECOLOGICAL STUDIES ON *POLYDESMA UMBRICOLA* BOISD. IN HAWAII (LEPIDOPTERA: NOCTUIDAE)

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INTRODUCTION

The noctuid moth, Polydesma umbricola Boisd., commonly known as the monkey pod caterpillar, was first discovered in the Hawaiian Islands by Van Zwaluwenburg (1945) on Oahu (Figure 1). In quick succession it was reported from the other islands: Molokai (Williams, 1945), Maui (Pemberton, 1945), Kauai (Fullaway, 1945), Hawaii (Williams, 1946), and Niihau (Fullaway, 1946).

In the Hawaiian Islands P. umbricola is a well-known serious defoliator of the monkey pod tree, Samanea saman (Jacq.) Merrill (Figure 2). In recent years, this tree has considerably gained in economic importance due to its tough and light- and dark-colored wood which has become very popular for hand-carving platters and bowls (Neal, 1948). The large influx of tourists to Hawaii has helped to identify these carvings as exclusively Hawaiian products. The demand for the wood exceeds the supply to such an extent that monkey pod wood is now imported from Fiji.

The tree and its products have been brought to other uses in remarkably different ways in the various places where it is grown. In Central America, its place of origin, the pods are fed to cattle and the wood, especially cross sections of the trunk, is used for cart wheels (Neal, 1948). In India and Ceylon the leaves and pods have been reported to be quite nutritious food for horses and cattle (Tempany and Girst, 1958). The wood, originally thought to be useful as railway fuel (Cowen, 1952), is now considered to be of no value (Blatter and Millard, 1954), except as household fuel (Randhawa, 1957). Gill (no date given), in the Carribean, reports the wood to be useful for construction of

FIGURE 1. THE NOCTUID MOTH, POLYDESMA UMBRICOLA BOISD., A WELL KNOWN SERIOUS DEFOLIATOR OF MONKEY POD TREES.

FIGURE 2. THE MONKEY POD TREE, <u>SAMANEA SAMAN</u> (JACQ.) MERRILL. THIS PARTICULARLY SYMMETRICAL TREE IS GROWING ON THE GROUNDS OF THE MOANALUA GARDENS, HONOLULU.

posts, etc. From Bermuda (Britton, 1918) to China (Sauer, 1947) it is prized as an ornamental and roadside-shade tree.

In India the monkey pod's shade has been utilized to protect delicate plants in their early stages of development (Cameron, 1894). In New Caledonia (Sarlin, 1954), and the Carribean it has been employed as a shade tree in plantations of coffee and cacao, though its use is very much less at present than formerly (Little and Wadsworth, 1964). Williams (1949) in East Africa and Worthington (1959) in Ceylon report the wood to be excellent for furniture construction.

A review of the literature indicates that little work has been done on _P_. _umbricola_. The reason for this is that this insect is not a pest in the areas outside of Hawaii. Very little is known about its life-history and behavior, much less about the influence of various environmental conditions upon its abundance. The objective of this investigation is to make a study on some of these aspects of this insect, and, in addition, to probe into the interrelationships between seasonal abundance and the various environmental factors. It is envisioned that a study of this sort would contribute towards (1) an understanding of the population ecology of the noctuids, and (2) the development of control procedures based on the ecology of the moth.

MATERIALS AND METHODS

Studies on the biology of the monkey pod caterpillar were conducted in the laboratory and field during portions of 1962, 1963, and 1964. Most of the life-history and behavior studies were conducted in the laboratory. The ecological work, however, was carried out in the field.

Laboratory Methods

Laboratory work was conducted at room temperature (between 69° F and 92° F) in the laboratories of the Entomology Department, Hawaii Agricultural Experiment Station. The adults of P. umbricola were obtained from pupae collected in the field and kept in small 3½ x 2 inch bottles. These bottles had caps fitted with 80 mesh brass screen (Figure 3). A small piece of cotton wool was placed on the bottom of the bottles to provide the pupae with a soft surface. Thick cloth was arranged circularly inside the bottles to provide the emerging moths with a vertical surface on which they could crawl up for the expansion of their wings. These bottles were used for the emergence of both field-collected and laboratory-reared pupae. Only one pupa of known sex was placed in each bottle so that upon emergence the moths had a known history of age, sex, and mating.

Three types of cages were utilized in keeping the moths in captivity. The cage used for behavior studies was 28 x 17 x 21 inches with a wooden frame and bottom (Figure 4). The top, sides, and back were covered with nylon cloth. The upper section of the front was constructed to accommodate a horizontally sliding 28 x 12 inch glass panel through which the moths could be observed. The lower section of the front was

FIGURE 3. SMALL BOTTLE WITH A BRASS SCREEN CAP AND THICK CLOTH ARRANGED CIRCULARLY INSIDE. THIS TYPE OF BOTTLE WAS USED FOR THE EMERGENCE OF THE MOTHS.

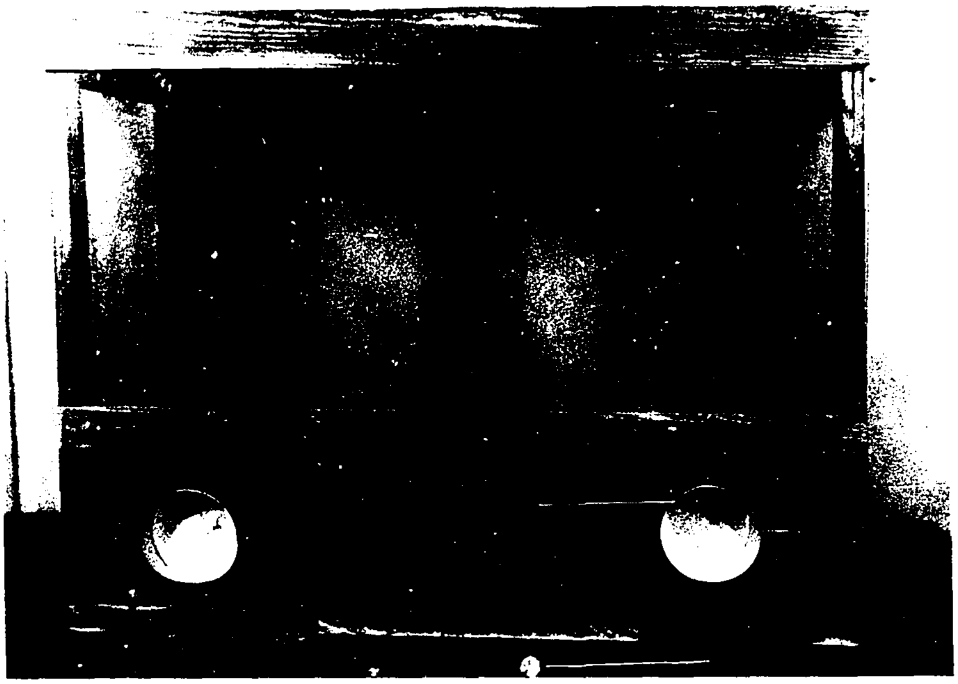

FIGURE 4. WOODEN CAGE FITTED WITH A SLIDING GLASS PANEL. THIS TYPE OF CAGE WAS USED IN BEHAVIOR STUDIES.

made of wood through which two holes, five inches in diameter, were cut out and covered with a sheet of black rubber. At the center of these rubber sheets, smaller holes of approximately 3½ inches in diameter were made through which all manipulations dealing with food, leaves, and insects were made. Circular paper cartons with diameters slightly larger than the openings in the rubber were plugged into the holes to close them. Hereafter, this cage will be referred to as the observation cage.

For oviposition studies, two types of cages were used. The first type was made of a metal framework 27 x 15 x 15 inches in dimension (Figure 5). All four sides were covered with thin nylon cloth. There were two circular openings, four inches in diameter, to the cage. The opening on one side was seven inches from the bottom and the one on the opposite side fifteen inches from the bottom of the cage. These openings were utilized for introducing or taking out various materials, and, when not in use, were covered by nylon cloth held in place by rubber bands.

On the inside of the cage the top seven inches were covered with corrugated cardboard to supply resting places for the moths. About fifteen inches from the bottom, there were horizontally placed planks of wood on two sides of the cage, each supporting two Petri dishes containing some cotton wool soaked in a ten percent solution of honey. This served as food for the moths. The top was made of cardboard and supplied with a few hooks on the inside. These hooks were used to hang fresh monkey pod leaves for the moths to oviposit upon. The cages of this type were used mainly in the fecundity studies and will hereafter be referred to as the oviposition cages.

FIGURE 5. THE METAL CAGE HAVING FOUR SIDES COVERED WITH NYLON CLOTH. THIS TYPE OF CAGE WAS USED IN OVIPOSITION STUDIES.

The second type of cage used for fecundity studies consisted of glass gallon jars. They were always put in racks in an almost horizontal position and had lids fitted with brass screen, eighty meshes per inch. A syracuse dish with cotton wool soaked in a ten percent solution of honey was put in each jar (Figure 6). Fresh monkey pod leaves were placed horizontally inside the jar where they served as resting and oviposition sites for the moths.

The gallon jars were also used for rearing larvae in life history studies. For this purpose, their bottoms were cut off and the cut ends covered with thin nylon cloth held in place with white glue. The jars were always sterilized to avoid any diseases spreading in the culture. Approximately two feet of crumpled paper toweling were introduced in each jar to provide a more extensive surface and hiding places for the caterpillars, as well as to absorb excess moisture in the jar. Every other day larval frass was removed and fresh paper introduced.

Field Studies

Field work was carried out on the University of Hawaii Manoa Campus. Figure 7 shows a sketch of the University campus with exact location of eighty-seven monkey pod trees which were studied. The trees were divided into four series and all the trees in each series were used in gathering information. The trees in Series 2, however, were used only in a few minor phenological studies.

The year-round abundance of new moths was primarily estimated by making monthly counts of caterpillars. Use was made of permanent burlap bands around the tree trunks to "trap" the larvae, which where then counted each month. Figure 8 shows the manner of construction of these

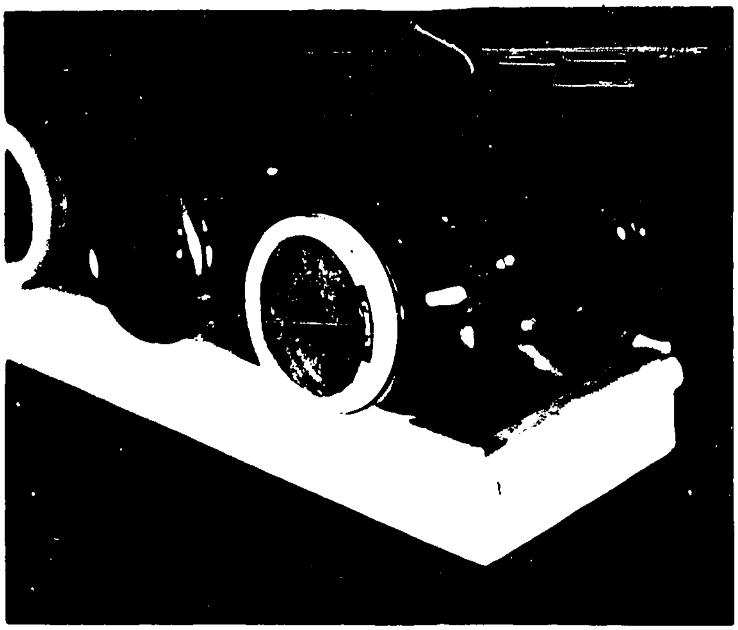

FIGURE 6. GLASS GALLON JARS ARRANGED IN RACKS IN OVIPOSITION STUDIES.

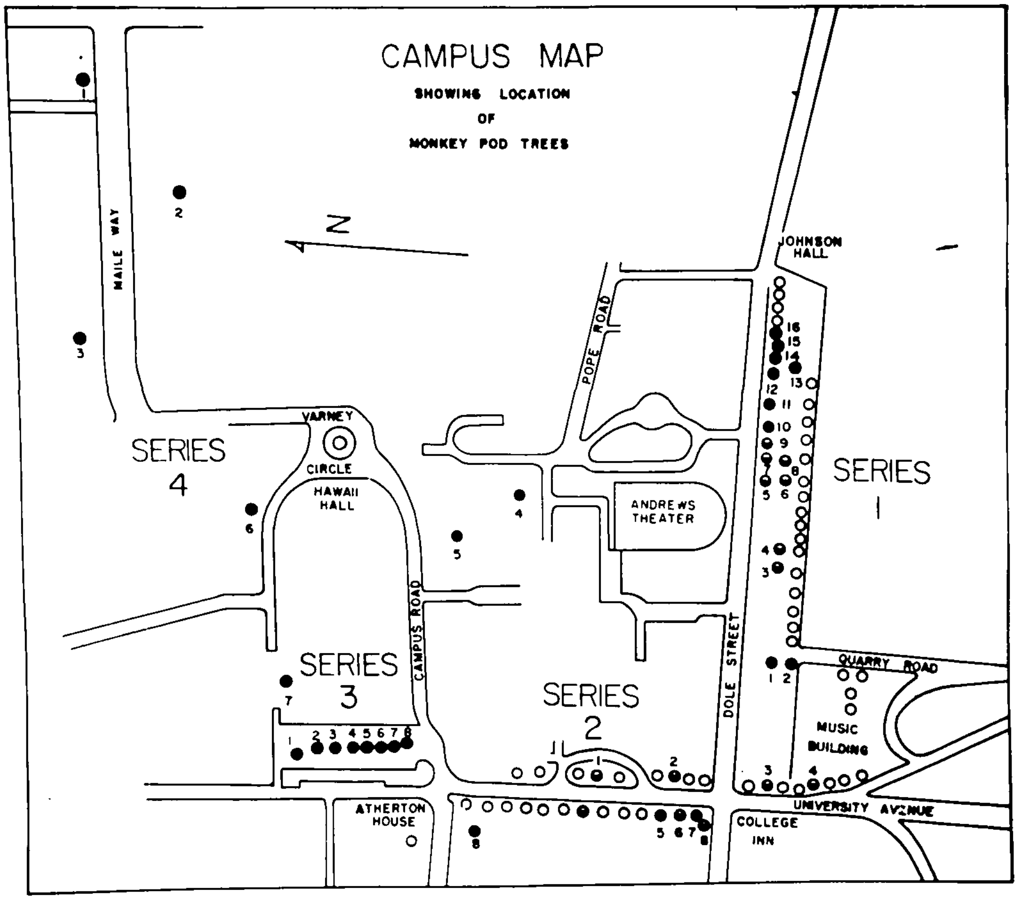

FIGURE 7. MAP OF THE UNIVERSITY OF HAWAII CAMPUS, SHOWING LOCATION OF MONKEY POD TREES UNDER STUDY. DARK CIRCLES DENOTE TREES WITH BURLAP BANDS AROUND THEIR TRUNKS; HALF SHADED CIRCLES, TREES WHICH WERE SAMPLED FOR PHENOLOGICAL DATA; AND OPEN CIRCLES, TREES WHICH WERE NOT STUDIED.

FIGURE 8. PERMANENT TRAPS USED IN MAKING MONTHLY COUNTS OF *P. UMBRICOLA* LARVAE. THE TOP PHOTOGRAPH SHOWS THE "INTERNAL WOODEN SKELETON"; THE BOTTOM ONE, THE COMPLETED TRAP WITH BURLAP BAND.

bands. Wooden sticks (10 x ½ x 1 inches) were stapled on two 1-inch cloth bands that were placed two inches from each end of the sticks. This resulted in a ladder-like structure which was then wrapped around the tree trunk two feet from the ground in order to provide the "internal skeleton". All the sticks were nailed onto the trunk; however, the nails near the tops of the sticks were not driven in (Figure 8, top) so that when a burlap cloth, one foot in width, was wrapped around and tied with strings it produced a structure which was a little open at the top, but closed at the bottom (Figure 8, bottom). Larvae coming down the tree trunk at dawn crawled under the bands and, not being able to go down any farther, they remained there. Dark circles on the map denote such trees with bands around their trunks (Figure 7).

The monthly abundance of the pest was also estimated by sampling twigs of monkey pod trees for their eggs. Each month ten twigs, each six inches in length, were cut at random from each series and all the eggs of P. umbricola found on them were counted.

Some of the trees were utilized for monthly phenological observations. The amounts of new growth, defoliation by the pest, and the shade afforded by the green canopy of the trees were recorded.

HOST PLANTS

The caterpillars of P. umbricola have been reported defoliating various trees in different parts of the world. Table I gives a list of these trees together with the regions from which they have been reported.

The monkey pod tree, also known as the rain tree, is by far the most preferred host of P. umbricola. It is a native of tropical America, but is now widely distributed under cultivation (Kanehiro, 1935). It is recorded in the literature under various different common names. On the Indo-Pakistan subcontinent it is usually called "Velaiti siris" (Worthington, 1959). In Saipan it is known as "Ameriki-nemu" (Kanehiro, 1935). Cubans call it "El algarroba del pais" (Maza, 1914), and in New Caledonia it is known as "Boir noir de Haiti" (Sarlin, 1954).

Trees infested with this moth are conspicuous by their amount of defoliation. In extreme cases the leaves are eaten as soon as they unfold and the trees are often devoid of foliage (Figure 9). Prolonged and continued attack results in the formation of gall-like structures and often in the death of terminal twigs and branches (Holdaway and Nishida, 1946) (Figure 10). Since the monkey pod, with its dark-green canopy and pink flowers, is one of the most valued ornamental trees in Hawaii, this damage detracts considerably from its beauty and value.

TABLE I. THE HOST PLANTS OF _P_. _UMBRICOLA_ AS REPORTED FROM VARIOUS PARTS OF THE WORLD

Species	Family	Region	Reference
Samanea saman (Jacq.) Merrill.	Leguminoseae	Hawaiian Islands	Van Zwaluwenburg (1945)
Pithecolobium dulce (Roxb.) Bentham.	"	Hawaiian Islands	Rosa and Van Zwaluwenburg (1945)
		Guam	Swezey (1945)
Cassia grandis Linn.	"	Hawaiian Islands	Van Zwaluwenburg (1946)
Albizzia lebbek (Linn.) Bentham.	"	Hawaiian Islands	Rosa and Van Zwaluwenburg (1945)
		India[1]	Gardner (1948)
		Mauritius Island	Mamet (1948)
Albizzia saponaria	"	Hawaiian Islands	Pemberton (1946)
Albizzia sp.	"	New Caledonia	Williams (1945)
Acacia-like tree[2]	"	Tahiti	Collenette (1928)
Rose buds	Rosaseae	Hawaiian Islands	Fullaway (1946)

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[1] Gardner erroneously reported the caterpillars feeding on the bark of this tree.

[2] This is probably the monkey pod tree.

FIGURE 9. A TOPPED MONKEY POD TREE SHOWING DAMAGE BY P. UMBRICOLA. ALL THE BRANCHES ARE SECONDARY GROWTHS FROM THE ORIGINAL TRUNK.

FIGURE 10. GALL-LIKE STRUCTURES PRODUCED BY TWIGS WHOSE LEAVES WERE CONTINUOUSLY ATTACKED BY P. UMBRICOLA LARVAE.

DISTRIBUTION

P. umbricola was first described by Boisduval in 1833 from Madagascar (Hampson, 1894). Since then it has been reported from West and South Africa, throughout the Indo-Pakistan subcontinent, Ceylon, Burma, Andaman Islands, and Taiwan (Hampson, 1894). Collenette (1928) recorded it from Tahiti; Swezey (1945) found it in Guam; and Williams (1945) reported it from New Caledonia.

The original home of the monkey pod tree is reported to be Brazil (Randhawa, 1957) or Venezuela and Colombia (Worthington, 1959). From these places it has spread under cultivation all over the tropical and subtropical regions of the world (Kanehiro, 1935). It has been reported from Bermuda (Britton, 1918) and all the Carribean Islands (Williams, 1949). It was introduced into Ceylon in 1850 (Worthington, 1959) and from there to Banglore, India, in 1878 (Cameron, 1894) and now has been planted all over the Indo-Pakistan subcontinent.

The tree was introduced into the Philippine Islands in about 1869 (Merrill, 1925). Kanehiro (1935) records it from the Micronesian Islands. Sarlin (1954) reported it from New Caledonia. It has been reported in central Africa growing under cultivation (Pellegrin, 1948).

The date of arrival of the monkey pod tree in the Hawaiian Islands is not known, but the fact that it is presently found in abundance on all the major islands indicates that it arrived at an early date. The plant seems to thrive on the climate of these islands. With its dense, green canopy and pink flowers, it is a prominent feature of the Hawaiian landscape.

Figure 11 illustrates the distribution of _P_. _umbricola_ and the probable distribution limits, both north and south, of the various leguminous trees on which it feeds. The latitudes of 30° N and 30° S seem to be, approximately, the limits of their distribution. _P_. _umbricola_ may be said to have a distribution covering the whole of the Ethiopian and Oriental regions from west Africa to Hawaiian Islands and from south-east Africa to Tahiti. It appears to be absent from the Americas. A few related species of _Polydesma_ have been reported from the Lesser Antilles by Hampson (1898), but there is no record of the occurrence of _P_. _umbricola_ in the new world.

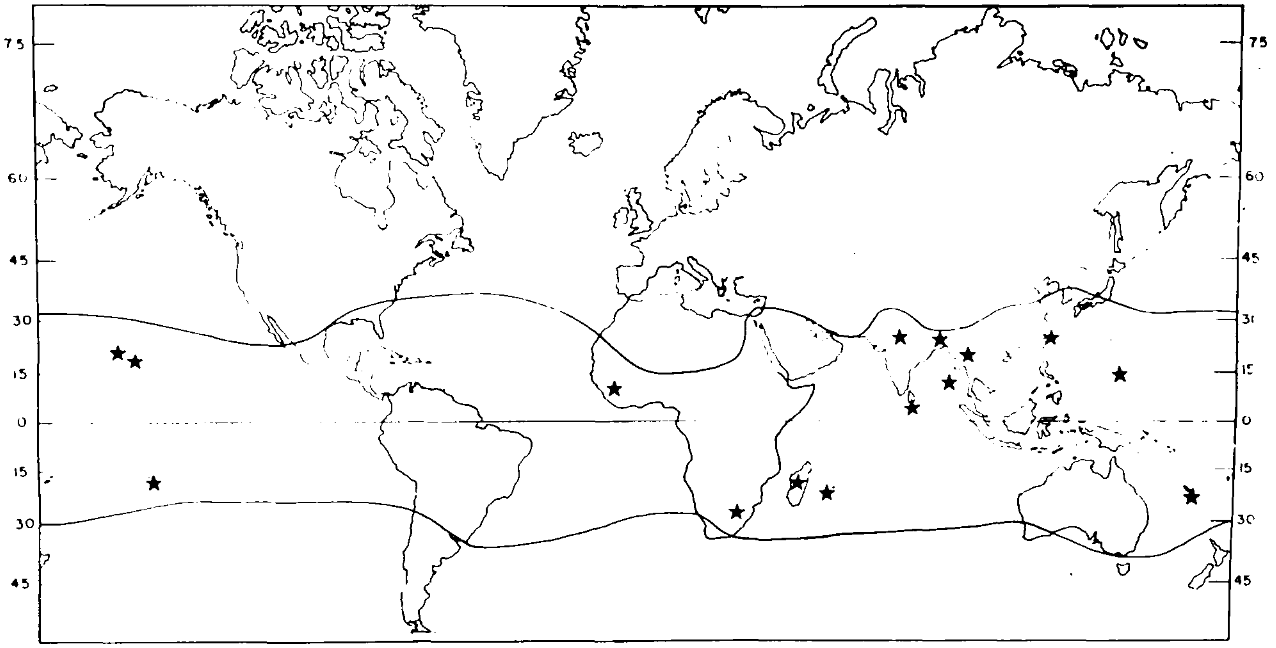


FIGURE 11. MAP SHOWING THE WORLD-WIDE DISTRIBUTION OF *P. UMBRICOLA* (STARS) AND ITS HOST TREES. DARK LINES INDICATE THE NORTHERN AND SOUTHERN DISTRIBUTION LIMITS OF ITS HOST TREES.

LIFE HISTORY STUDIES

The life cycle of P. umbricola is similar to other noctuid moths. The eggs are laid on monkey pod twigs and leaves. The larvae feed on the tender foliage of the terminal shoots. When fully grown, the larvae pupate in crevices in the bark.

Studies on life cycle were conducted in the laboratory during the summers of 1962 and 1963. The average temperature during the first summer was 79.6° F and ranged between 73° F and 88° F; while in the second summer, the average temperature was 79.5° F and ranged between 72° F and 89° F. Since the results and the average room temperature were quite similar, the data for the two periods were combined.

The studies were initiated by starting a laboratory culture of the insect. For this purpose, pupae of P. umbricola were collected in the field and the imagoes allowed to emerge in oviposition cages where they were supplied with monkey pod leaves on which they laid eggs (Figure 5). These eggs were placed in small 2 3/4 x 3/4 inch vials where their further development was observed. Since it was desirable to keep records of individual larvae, only one egg was placed in each vial. Cotton wool was used to plug the open end of the vials. In order to help keep diseases at a minimum all equipment was sterilized. The emerging larvae were fed on fresh and tender monkey pod leaves which were changed every day.

Description of Stages

The newly laid eggs are rather flattened spheres with a mean diameter of 0.62 ± 0.03 mm. (Table II). They are a whitish-green color which later changes to a dull brown. They have radial ridges extending towards

TABLE II. THE DIMENSIONS OF EGGS AND PUPAE AND THE HEAD WIDTHS AND BODY LENGTHS OF THE LARVAE OF P. UMBRICOLA

Measurements of the Various Stages		No. Examined	Mean (mm.)	Stand. Dev. (mm.)	Range (mm.)
EGGS	Diameter	30	0.62	0.03	0.56 - 0.67
LARVAE					
First Instar					
	Head width	30	0.25	0.04	0.22 - 0.33
	Body length	30	1.95	0.11	1.78 - 2.17
Second Instar					
	Head width	30	0.51	0.04	0.39 - 0.61
	Body length	30	6.11	0.39	5.50 - 6.83
Third Instar					
	Head width	30	0.84	0.07	0.67 - 1.06
	Body length	30	8.15	0.32	6.66 - 8.66
Fourth Instar					
	Head width	30	1.35	0.10	1.11 - 1.62
	Body length	30	9.06	1.33	7.50 -11.16
Fifth Instar					
	Head width	30	1.95	0.12	1.67 - 2.23
	Body length	30	13.89	2.10	9.16 -16.99
Sixth Instar					
	Head width	30	2.68	0.20	2.28 - 3.12
	Body length	30	33.51	5.20	18.99 -39.65
PUPAE					
Max. width		30	0.45	0.05	4.00 - 5.00
Max. length		30	17.50	0.98	15.00 -20.00

the periphery, which call to mind the spokes of a wheel. Because of these ridges the eggs have a hairy appearance to the naked eye. Halfway across the radial lines there is a dark brown band running circularly around the upper surface of the egg. This band becomes progressively darker with age.

The first instar larvae are very light greenish brown. The mean body length and head width are 1.95 ± 0.11 mm. and 0.25 ± 0.04 mm., respectively (Table II). The first two pairs of abdominal prolegs are rudimentary.

The second instar larvae are green and the small, dark, sclerotized bases of the setae stand out prominently. The mean length of these larvae is 6.11 ± 0.39 mm. and the head width 0.51 ± 0.04 mm.

The third, fourth, and fifth instars resemble each other very much. The measurements of their body lengths overlap and it is difficult to distinguish these instars. Instead of being greenish in color these instars are brown with dark lines running along the length of the body.

The sixth instar larvae stand out from the earlier instars because of their body size. Their mean body length is 33.51 ± 5.20 mm. and mean width of the head capsules, 2.68 ± 0.20 mm. (Figure 12).

The sixth instar larvae of _P. umbricola_ resemble very closely the young larvae of the black witch moth, _Erebus odora_ Linn., which occupy the same habitat. In the early part of this investigation this was a source of confusion. Upon examining the two types of larvae under the microscope, it was found that there were some significant differences in the chaetotaxy of the two insects. Among these, the only relatively simple method of distinguishing between the two types of larvae was the

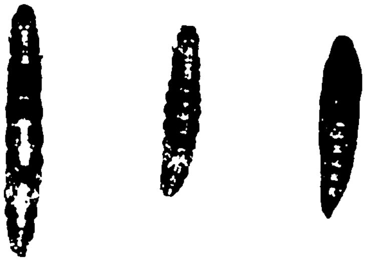


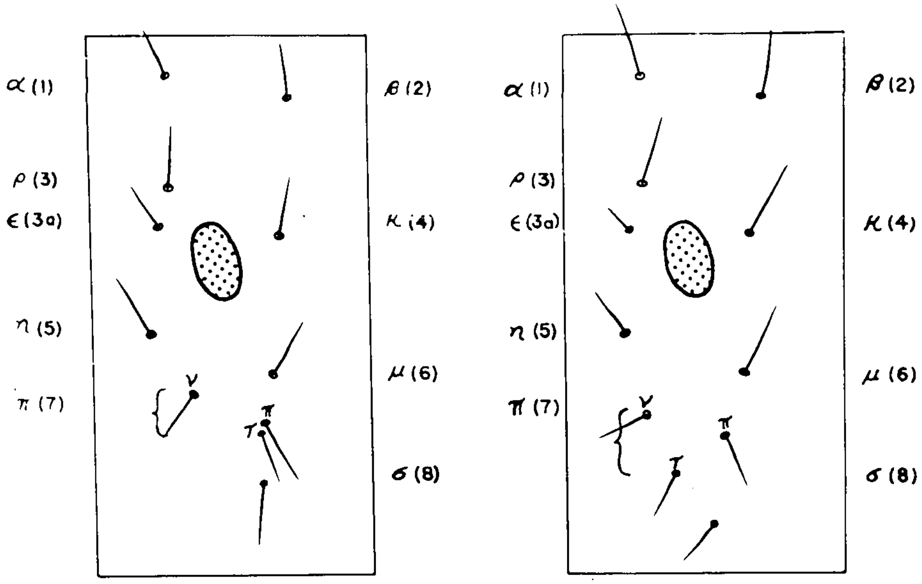
FIGURE 12. LATE DEVELOPMENTAL STAGES OF P. UMBRICOLA. LEFT TO RIGHT: SIXTH INSTAR LARVA, PREPUPA, AND PUPA.

position of the seta τ in the π (7) group (Peterson, 1962). In *P. umbricola* seta τ is much nearer to seta π and quite far removed from seta σ (8) (Figure 13). In *E. odora* seta τ is situated at an equal distance from setae π and σ. The older instars of *E. odora* take on a pinkish hue of color and increase greatly in size, measuring up to 90 mm. in length. At this stage they become very different from *P. umbricola* larvae.

The sixth instar larvae spin cocoons before pupating. The site of pupation can be any crevice or crack on the bark or in the coarse soil around the tree trunk. In the laboratory the larvae have spun cocoons on every possible surface excepting an absolutely smooth glass surface. Crumpled paper, cloth, leaves, end of a glass vial, all seem to do very well. The cocoons are of a thin, tough, silken meshwork, the larvae spending from about thirty minutes to three hours weaving it. If a larva is disturbed while starting to spin its web and placed in a new location, it immediately starts a new one. This second web is, however, not as well woven and as extensive as the first one. If disturbed a few more times the larva does not build any web and pupates "naked". During pupation the larva shrinks considerably in size (Figure 12). About six hours after the start of weaving the web the insect becomes quite immobile. The pupae measure 17.50 ± 0.98 mm. in length and 0.45 ± 0.05 mm. at their greatest width (Figure 12).

Number of Instars

Dyar (1890) showed from observations on various species of lepidopterous larvae that the width of the head capsule increases in a regular



1 Polydesma umbricola Boisd

2 Erebus odora Linn.

FIGURE 13. SETAL MAPS OF THE FIRST ABDOMINAL SEGMENTS OF LARVAE OF P. UMBRICOLA AND E. ODORA. THE THREE SETAE IN THE π (7) GROUP ARE ARRANGED DIFFERENTLY IN THE TWO SPECIES.

geometrical progression in successive instars. This observation, now known as Dyar's Law (Richards and Davies, 1960), purports that measurements of heavily sclerotized portions of insects do not change during a larval stadium but increase only at the time of molting.

Examinations of the larvae of P. umbricola were made each evening between three and six o'clock. Each vial was examined carefully to locate the molted head capsule. The head capsules were measured under a dissecting binocular microscope fitted with an ocular micrometer. This procedure was followed for each instar except the last one in which the larva, when pupating, splits the head capsule. In this instar the head capsules excised from the larvae were placed on a microscopic slide and measured.

The frequency distribution of the observed head measurements is given in Figure 14. The distribution falls into six groups which, in spite of some overlapping, are fairly distinct from each other. Each of these six groups was assumed to represent a different instar. Figure 15 shows the straight-line relationship between existing logarithm values of head width and the six assumed instars.

Duration of Instars

The duration of the larval instars was determined along with the studies on the larval instars. The data, presented in Table III, show that the mean incubation period of the eggs was 3.5 ± 1.3 days. The mean durations of the first to sixth larval instars were: 1.7 ± 0.8, 2.3 ± 0.6, 2.7 ± 0.8, 2.5 ± 0.7, 2.7 ± 0.6, and 5.3 ± 1.8 days, respectively. The prepupal and pupal stages had a mean duration of 2.7 ± 0.6, and 13.4 ± 1.2 days, respectively. The duration of all the immature

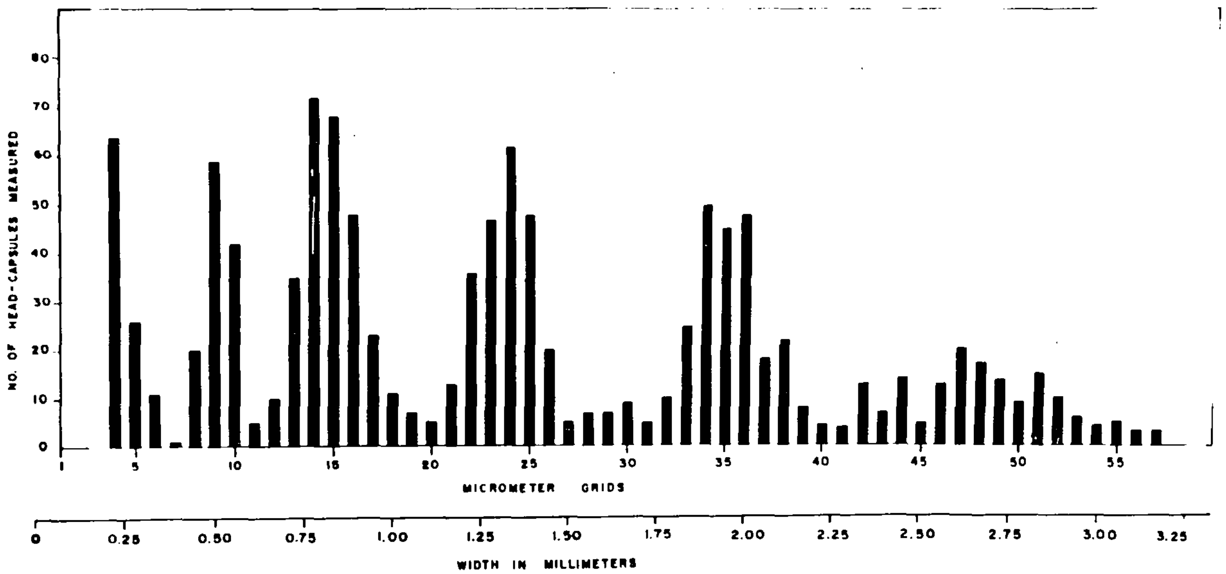


FIGURE 14. THE FREQUENCY DISTRIBUTION OF THE WIDTHS OF HEAD CAPSULES OF LARVAL INSTARS OF <u>P</u>. <u>UMBRICOLA</u>. EACH OF THE SIX PEAKS REPRESENTS A SEPARATE LARVAL INSTAR.

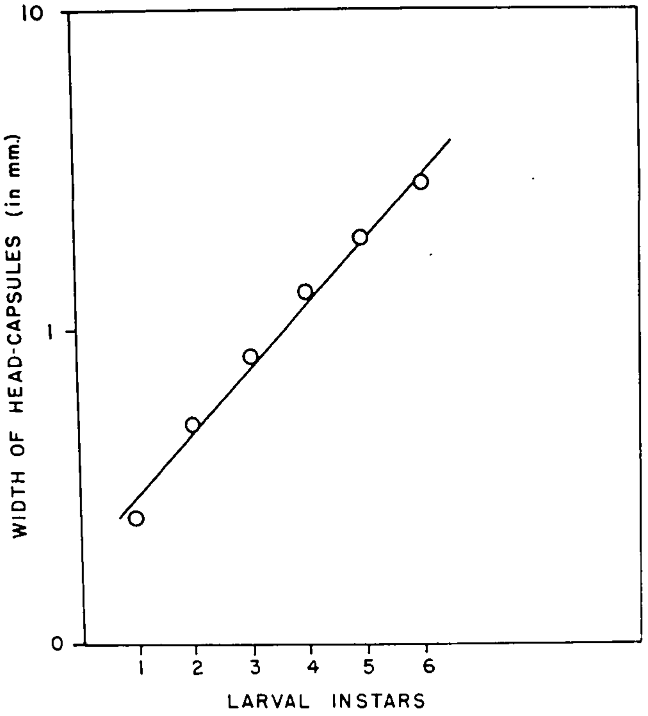


FIGURE 15. THE STRAIGHT-LINE RELATIONSHIP BETWEEN THE WIDTHS OF LARVAL HEAD-CAPSULES AND THE NUMBER OF LARVAL INSTARS IN P. UMBRICOLA.

TABLE III. DURATION OF THE IMMATURE STAGES OF *P. umbricola*

Stage	No. Examined	Mean (Days)	Stand. Dev. (Days)	Range (Days)
EGGS	30	3.5	1.3	2 - 6
LARVAE				
First Instar	30	1.7	0.8	1 - 4
Second "	30	2.3	0.6	2 - 4
Third "	30	2.7	0.8	2 - 4
Fourth "	30	2.5	0.7	1 - 4
Fifth "	30	2.7	0.6	1 - 5
Sixth "	30	5.3	1.8	2 - 8
PREPUPAE	30	2.2	0.6	1 - 4
PUPAE	30	13.4	1.2	11 -15

stages was found to average 36.2 ± 8.3 days and ranged between 23 and 54 days.

PHYSICAL CHARACTERISTICS OF THE HOST TREE

Bark Conditions

The amount of bark on a monkey pod tree seems to be an important factor in the distribution and abundance of *P. umbricola* larvae on it. Observations on the monkey pod trees have indicated that the larvae are normally found in cracks and crevices in the bark. It seems that the more bark a tree has the more hiding places it can provide for the larvae. It has been noticed in the field that rough-barked trees always seem to support larger numbers of larvae of *P. umbricola* than smooth-barked trees (Figure 16). In this way the amount of rough bark directly influences the abundance of the pest. The distribution pattern of the larvae is also greatly influenced by the amount of rough bark. Since a rough-barked tree has ample hiding places, the larvae never need to go down near the base of the trunk. A smooth-barked tree affords very few hiding places so that the larvae tend to aggregate in the debris at the foot of the tree. It might be mentioned here that of all the leguminous trees attacked by this pest, only the monkey pod tree, *Albizzia lebbek*, and *Pithecolobium dulce* normally display a lot of rough bark.

Age of Tree

The number of hiding places provided by the tree depends upon the age of the tree. Rough bark with cracks and deep crevices is characteristic of old trees. The rough bark is present on the lower portions of the trees; however, high up in the trees the bark is smooth. As the tree gets older the rough bark extends higher up the tree. On young trees the bark is smooth throughout the entire tree.

FIGURE 16. THE BARK OF AN OLD (TOP), AND A YOUNG (BOTTOM) TREE. THE ROUGH BARK ON OLD TREES PROVIDES HIDING PLACES OF THE LARVAE OF *P. UMBRICOLA*.

Height and Size of Tree

The height and size of a monkey pod tree *per se* do not seem to have any effect on the distribution and abundance of *P. umbricola* larvae. They effect the abundance of the pest only insofar as the amount of rough bark increases with the increase in height and size of the tree. This in itself is a result of the increase in age of the tree.

DISTRIBUTION OF THE IMMATURE STAGES ON THE HOST TREE

Distribution of Eggs

In order to investigate the sites of oviposition of P. umbricola, a search was made on various parts of the monkey pod tree. It soon became apparent that the terminal twigs of the trees were the principal, if not the only, site of oviposition. An experiment was conducted to determine the relative abundance of eggs on the various parts of the twigs. Thirty samples of leafy terminal twigs, each about 1½ feet long, were cut from monkey pod trees. Each twig was divided into three parts, upper, middle, and lower, each part being six inches in length. Counts were made of all the eggs present on the leaves and the stem in each of these three parts.

The results show that the upper six inches contain 55.0 percent of the total eggs counted, the middle six inches 36.9 percent, and the lower six inches 10.0 percent (Figure 17). It seems clear that most eggs are laid near the tips of the twigs, the number of eggs decreasing sharply with the distance from them. Oviposition probably never takes place on older parts of branches more than two or three feet away from the tip of the young shoots.

Another experiment was conducted to pinpoint the exact site of oviposition on the upper six inches of the twigs. Thirty samples consisting of the terminal six inches of twigs were collected and the eggs on them counted in two categories: firstly, those on the stem and the petioles and, secondly, those on the pinnules of the leaflets.

Results show that the stem and petioles contain more than double the number of eggs on the pinnules of the leaflets (Figure 18). This

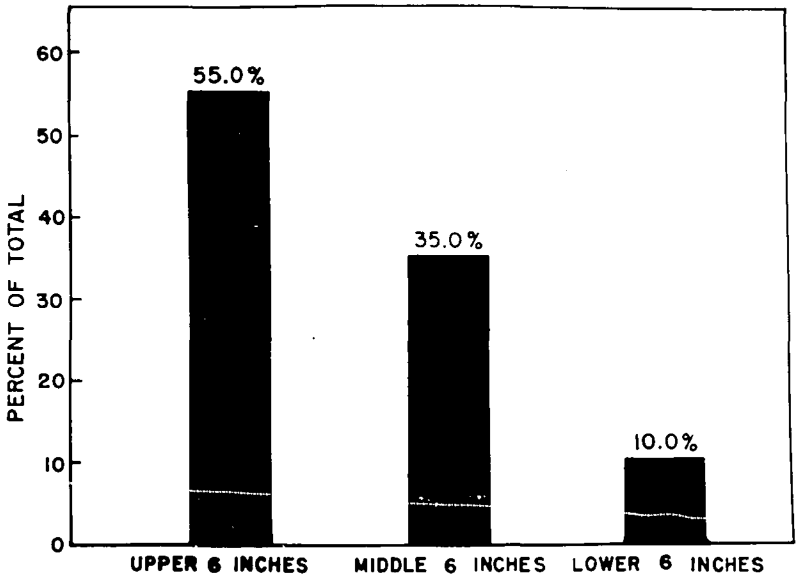


FIGURE 17. DISTRIBUTION OF EGGS OF *P. UMBRICOLA* ON THE TERMINAL TWIGS OF THE MONKEY POD TREE.

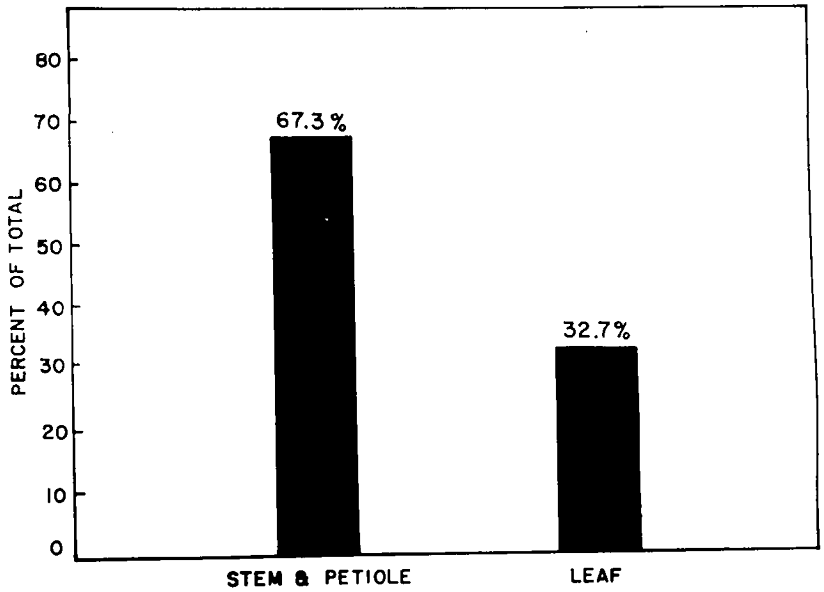


FIGURE 18. DISTRIBUTION OF EGGS OF _P_. _UMBRICOLA_ ON THE STEM AND PETIOLES, AND ON PINNULES OF THE LEAFLETS OF THE MONKEY POD TREE.

indicates that of all the possible oviposition sites available to the imagoes the best are the stems and leaf petioles of the upper six inches of the twigs.

In the months of February and March some trees were seen to be supporting large _P_. _umbricola_ populations. This was at a time when spring growth was just beginning, and the trees were still completely leafless. An experiment was carried out to determine the most favorable sites of oviposition on these leafless trees. Twenty samples of 1½ feet long terminal leafless twigs were taken and the eggs counted in the same manner as in the previous experiment.

The results show that the egg distribution on leafless twigs closely follows that on leafy shoots (Figure 19). The terminal six inches seem to be the preferred site of oviposition.

Distribution of Larval Stages

The first instar larvae of _P_. _umbricola_ remain on the young foliage near the tips of the terminal twigs. The second instar larvae occupy very much the same microhabitat. Beginning with the third instar the larvae are found, during daylight hours, under the bark of trees and in debris collected under the bark and between the forks of trunks. On young trees with smooth bark most of the older instar larvae accumulate in the debris at the base of the tree. On old rough-barked trees, however, there are numerous hiding places for the larvae on the tree trunks and the older branches so that most of the larvae are found in the cracks and crevices in the bark. Figure 20 illustrates diagrammatically the differences that exist in the distribution of the larval stages on a young and on an old tree.

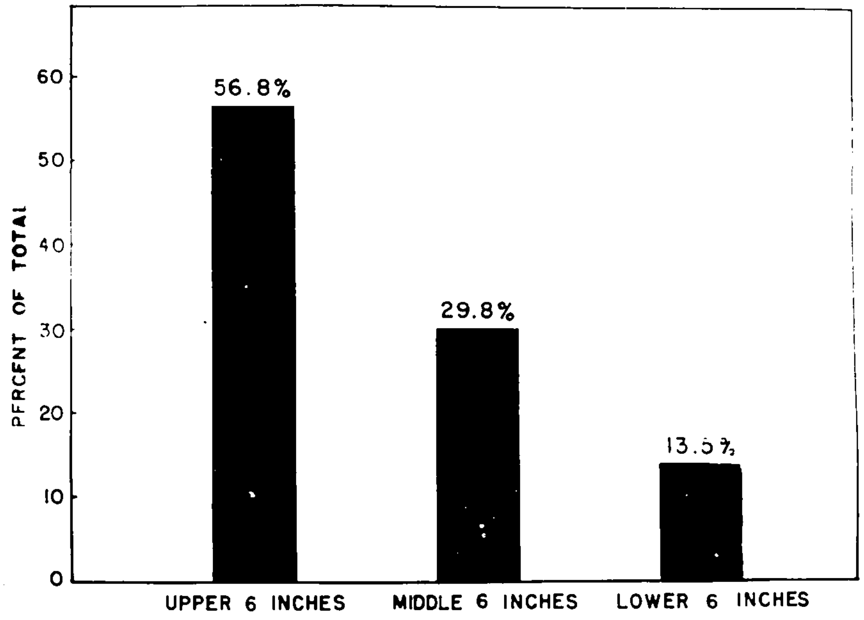


FIGURE 19. DISTRIBUTION OF EGGS OF P. UMBRICOLA ON THE TERMINAL LEAFLESS TWIGS OF THE MONKEY POD TREE.

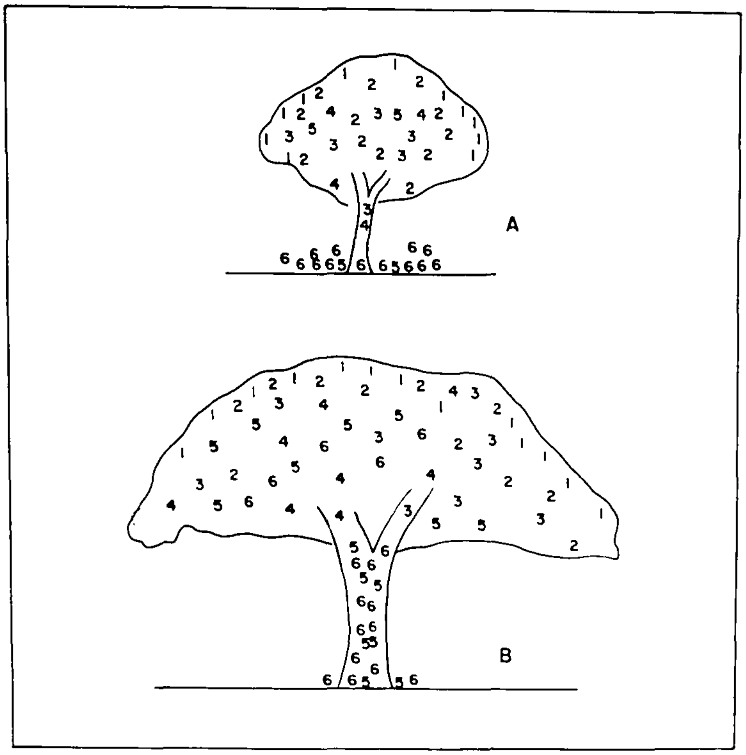


FIGURE 20. A DIAGRAMMATIC REPRESENTATION OF THE DISTRIBUTION OF LARVAL STAGES OF P. UMBRICOLA ON A YOUNG AND OLD MONKEY POD TREE. A, YOUNG AND SMOOTH-BARKED TREE, AND B, OLD ROUGH-BARKED TREE. THE NUMBERS REPRESENT THE LOCATION OF THE RESPECTIVE INSTARS.

Distribution of Pupae

The pupae of P. umbricola are usually found in the crevices in the bark of the monkey pod trees. During the summer months any old rough-barked tree can be approached, its bark peeled off, and the pupae obtained. No pupa was ever encountered on the trunks of young smooth-barked trees. In such cases they are found in the debris at the base of the trees.

BEHAVIOR STUDIES

Behavior in General

Soon after emergence the first instar larvae of P. umbricola move about very actively. In general, their tendency is to move upwards onto the terminal twigs of the trees. If a larva happens to reach the top of a twig without encountering any tender foliage, it promptly secretes a silk thread from its spinneret and suspends itself from it. On heavily infested trees many of these minute larvae can be seen suspended by their silk threads and being blown by the wind.

Secretion of a silk thread seems to be an essential part of the behavior of the first five larval instars. Whenever a monkey pod twig is shaken many of these larvae, if present, secrete their silk threads and hang from them. This appears to be a very useful adaptation for dispersal and, furthermore, it ensures them a quick way of getting into the vicinity of their food.

Observations in the field indicate that these silk threads usually vary in length from a few inches to about two feet; however, those as long as four feet have been observed. In the laboratory, though, longer threads were obtained by artificially teasing the larvae. Once suspended by a thread, it is possible for the larvae to "climb" back on it. This is accomplished by winding the thread around the mouthparts and the forelegs. Each winding movement is accompanied by a strong twisting of the whole body. The mass of rolled thread is then discarded. Instances were observed where the mouthparts and the forelegs of the larva were entangled in its own thread so that the larva was unable to get rid of it. In such cases death by starvation follows.

The ability to take advantage of the silk thread decreases with the increase in the body size of the larva. Whereas the first three larval instars take to hanging by the thread at the first opportunity, the fifth instar larvae resort to it only when disturbed. However, often the delicate threads are not strong enough to support the larvae. Sixth instar larvae, though possessing the ability to secrete the silk thread, probably never use it in this manner. Whenever a twig bearing sixth instar larvae is shaken these larvae simply drop to the ground.

When disturbed, the larvae of _P. umbricola_ "double up" in a manner in which the three pairs of thoracic legs seem to grasp the abdominal prolegs. The larvae then discharge a fluid which appears to be defensive in function. It is the product of a ventral sac-like eversible gland opening on to the prothoracic sternum. Not all the instars seem to resort to this type of defense mechanism. The first and second instars do not appear to discharge any fluid at all. It would appear that their readiness to suspend themselves by the silk threads makes up for the lack of this defense mechanism.

Among the later instars the color and quantity of the secretion varies with the age of the larva. The third instar larvae produce only a little of it, and at this stage it is usually green. In the older larvae the quantity increases, reaching its maximum in the sixth instar. The color becomes darker, the sixth instar larvae secreting a reddish brown fluid. When freshly emitted, the discharge is very watery, but later becomes thicker in consistency.

While conducting experiments on the life-history of this insect, it was discovered that the larvae could harm themselves by their own defensive secretion. This was found to be especially true of larvae confined in glass vials. Some larvae were found to have discharged the defensive fluid in the vial, got themselves stuck in it, and died.

Observations in the field indicated that the larvae under the tree bands usually appeared to favor one side of the tree trunk and were always more numerous there. This was especially found to be so in the case of trees in Series 3 (Figure 7). An experiment was conducted to inquire into any differences that might exist in the concentration of larvae on the various sides. The tree bands on all eight trees were divided into four sectors corresponding to the four sides. Each tree trunk was examined daily at 5:00 PM for three days and the numbers of larvae found on each side recorded.

The results show very clearly that south and east sides of the tree trunks are favored by the larvae. Figure 21 gives a diagrammatic representation of the abundance of larvae on each side.

An experiment was carried out to check whether the larvae might be returning to the same particular hiding places day after day. Four wooden sticks on each side of the burlap bands were marked with red fingernail polish. All the larvae found between or clinging to these sticks were given a dab with the nail polish approximately on the dorsal side of the second thoracic segment. On the next day the bands were opened and the numbers of marked larvae on each side counted. A record was kept of the distance at which each marked larva was found from the marked sticks. Seven replications of this experiment were obtained, three on tree No. 4 in Series 3 and four on tree No. 7 in Series 3 (Figure 7). It was found that 82.4 percent of the marked larvae returned to a place

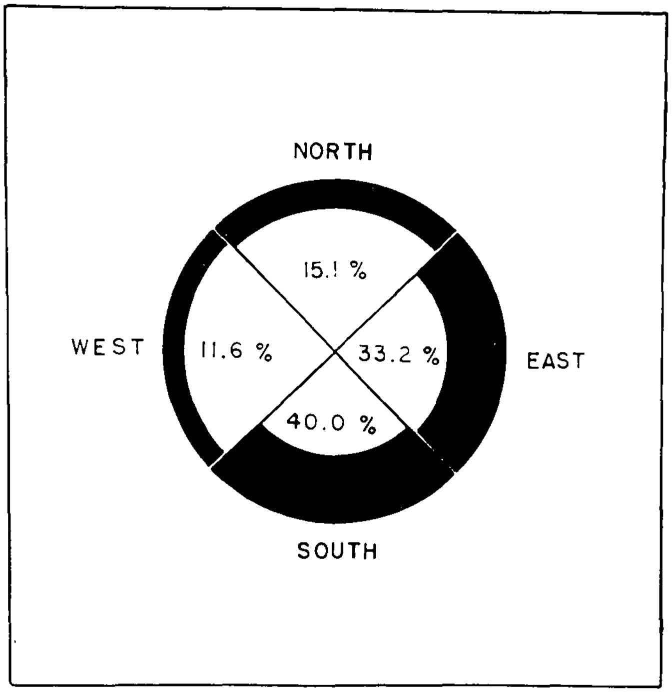


FIGURE 21. DIAGRAMMATIC REPRESENTATION OF THE RELATIVE ABUNDANCE OF P. UMBRICOLA LARVAE ON THE FOUR SIDES OF THE TRUNKS OF MONKEY POD TREES.

never more than six inches away from their original location. Of these, however, only 39.3 percent returned to exactly the same spot from which they started. Figure 22 shows a graphic representation of the percentage of the larvae found at various distances.

The imagoes begin their activities in the evening and oviposition takes place at night. The rate of egg laying is very sporadic, the females laying only a few eggs at a time for prolonged periods. The eggs are always laid singly and scattered over the petioles, leaves, and stems. If at any time the eggs are piled on each other they probably were laid, not by the same individual at one sitting but, by several different imagoes or the same imago at different times. Cracks and crevices on the terminal twigs seem to be the places where the eggs are usually laid on top of each other.

In a previous experiment the preferred sites of oviposition in the field were found to be the top six inches of terminal twigs of the monkey pod tree (Figure 17). An experiment was conducted to find out whether the moths laid eggs on other materials in the laboratory. The following materials were tested in three replications: monkey pod leaves, leaves of Pithecolobium dulce, canex, cloth, crumpled paper towels, wax paper, and wood. The material being tested was introduced into the large stock culture cage and left there overnight. The next day all the eggs laid on it were counted and recorded. The results, illustrated in Figure 23, indicate that monkey pod leaves were the most favored material for oviposition.

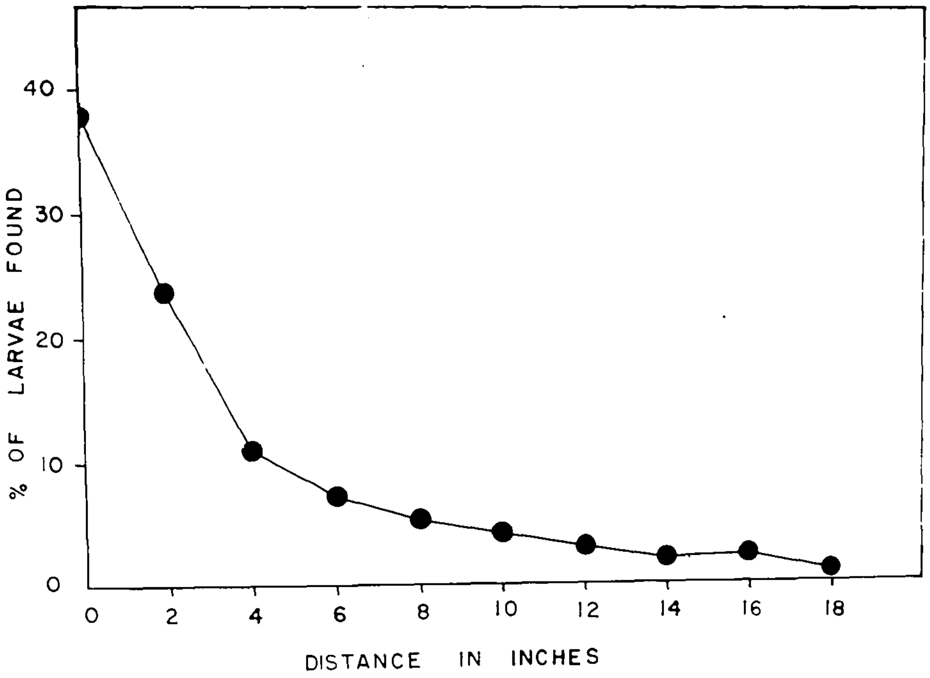


FIGURE 22. PERCENTAGE OF P. UMBRICOLA LARVAE FOUND AT VARIOUS DISTANCES AROUND THE TREE TRUNKS AWAY FROM THEIR ORIGINAL RESTING PLACE.

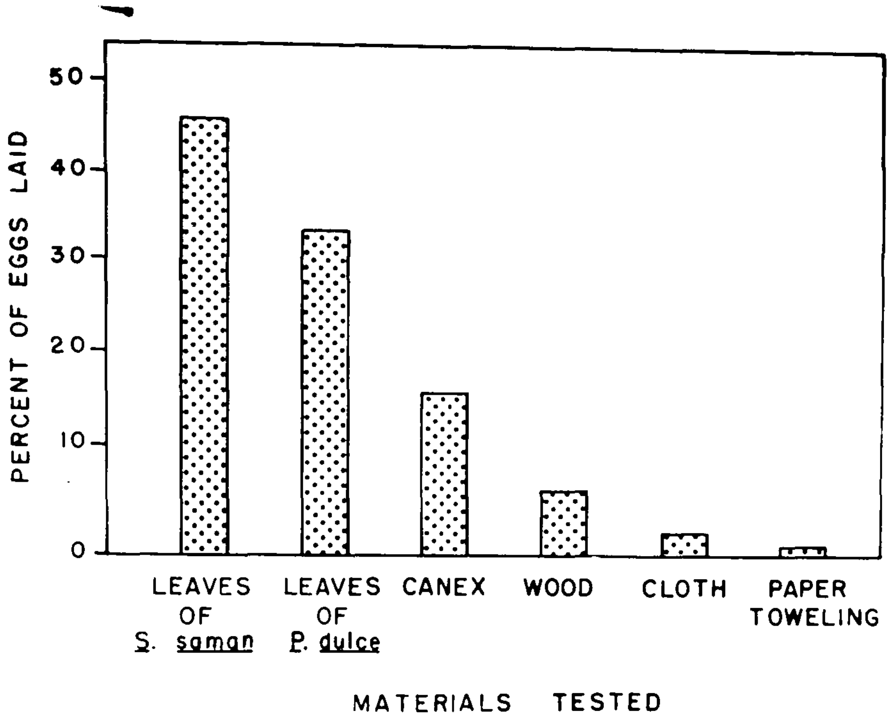


FIGURE 23. THE PERCENTAGE OF EGGS LAID BY <u>P</u>. <u>UMBRICOLA</u> ON VARIOUS MATERIALS.

Feeding Behavior of Larvae

The larvae of *P. umbricola* feed only on the meristematic tissue of the shoot tips and the young tender foliage near them. The first instar larvae are very active and if they do not come into contact with tender foliage they continue to wander around. Upon encountering young foliage, the larvae start feeding at once. The mode of feeding at this stage differs remarkably from the usual one exhibited by later instars. Whereas in the latter instars the leaf is eaten from the edge, the first instar larvae feed only on the under-surface of the tender leaves leaving a thin membrane of the upper cell layers of the leaf.

The first and second instar larvae differ from older larvae in another aspect. While older larvae are, as a rule, nocturnal feeders, the young ones feed continuously around the clock. This conclusion is a result of numerous observations in the field in which first and second instar larvae were seen actively feeding all hours of the day. As a result of this feeding behavior, the first and second instar larvae do not descend to the base of the tree as older instars do, but remain near the terminal twigs where food is plentiful.

The older larvae have a characteristic manner of feeding. They grasp a leaflet on its edge with their forelegs and place the edge of the leaflet in the notch on the labrum. Then they move the head in an antero-posterior direction, going first downwards and then upwards. Meanwhile, the mandibles are busy chewing; this results in a semicircular cut in the edge of the leaf. With each successive movement a larger semicircle is cut out until the whole leaf is consumed.

Daily Rhythm of Activity

It is a common observation that many species of animals are not equally active throughout the twenty-four hours of the day. Usually they display intermittent bursts of activity, spaced between periods of rest. *P. umbricola* imagoes, as well as larvae, are active at night. During the day hours they remain immobile in their hiding places. It is only at sunset that any activity can be observed. Two experiments were conducted in order to investigate the nature of this activity and its probable causes.

Observations on the rhythmic activity of the larvae were carried out on two trees, No. 1 in Series 3 and No. 8 in Series 4 (Figure 7). All the larvae found moving at any one time were recorded in two categories: firstly, those moving upwards and secondly, those moving downwards. Observations were made at one-half hour intervals during the evening and morning and at hourly intervals from 9:00 PM to 5:00 AM. Only the third to sixth instar larvae on the main trunk of the trees were involved in this study. Observations at night were made by use of a flashlight.

The results, illustrated in Figure 24, show very clearly that there are two peaks of activity. The peak of upward movement occurred at 7:00 PM and declined rapidly; however, the peak of downward movement was observed at about 6:00 AM. It may be noted from the data provided that both the upward and downward movements were lowest during 1:00 - 2:00 AM which shows that these movements are definitely crepuscular. In the evening the decreasing light seems to bring the larvae into activity and they move upwards. The increasing light early in the morning seems to induce them to start their downward movement, so that when the first rays of sunlight strike the trees the larvae have all hidden themselves.

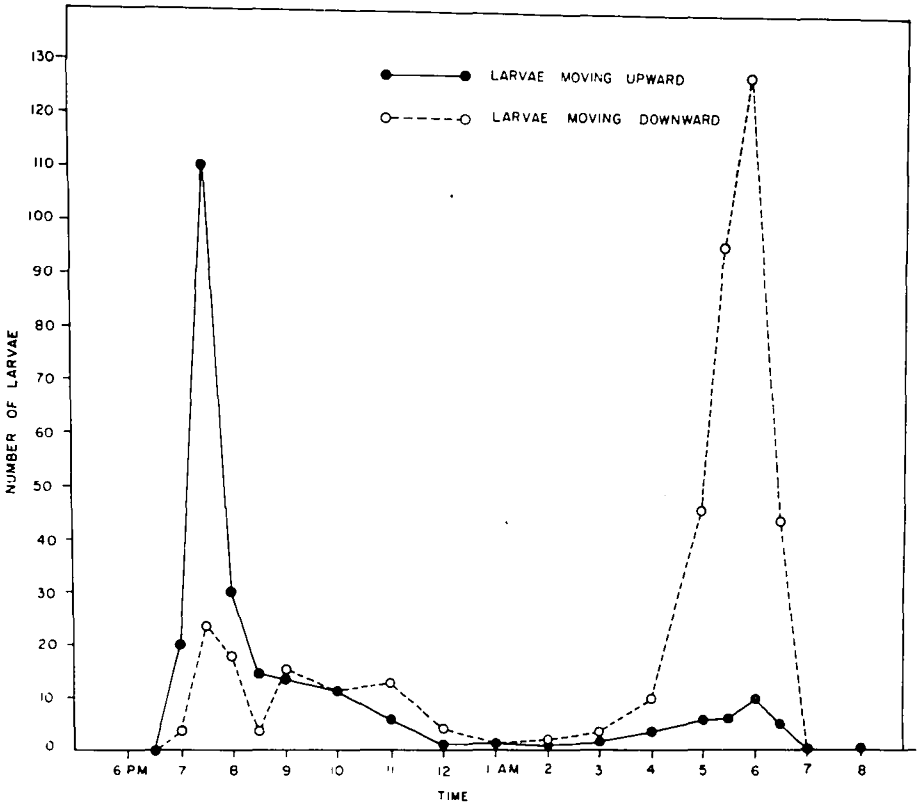


FIGURE 24. THE DAILY RHYTHM OF ACTIVITY OF P. UMBRICOLA LARVAE ON MONKEY POD TREES.

The following experiment was carried out in the laboratory in order to determine the periods of activity of the imagoes under controlled conditions. The observation cage was used to confine the imagoes in this experiment (Figure 4). A 10-watt bulb was used at a distance of ten feet as a constant source of light. The light source was so arranged as to avoid any direct light falling on the cage. In this manner all activity took place at one intensity and not at varying intensities as would occur in the field.

The activity of the moths in the cage was determined in the form first adopted by Callahan (1958) in his work with the corn earworm. Each time ten movements were noted, a tally was made. This would indicate one imago moving ten times or ten imagoes moving once each. The records obtained were totaled for each hour from 7:00 PM until 5:00 AM on two different nights. Sometimes an imago would start vibrating its wings and continue for as long as ten minutes; however, such movements were still counted as only one movement. An imago had to come to complete inactivity before it was counted again. Only ten imagoes were used, as the activity of numerous moths could not be observed accurately.

Figure 25 graphically illustrates the results. The moths start to move at about 7:00 PM and reach a peak of movement at approximately 9:00 PM. This activity is maintained until about 2:00 AM, although at a lower level. After 2:00 AM there was a decline with the activity ceasing between 5:00 AM and 6:00 AM.

These data indicate that in its overall activity the moth is nocturnal rather than crepuscular. This experiment, however, did not

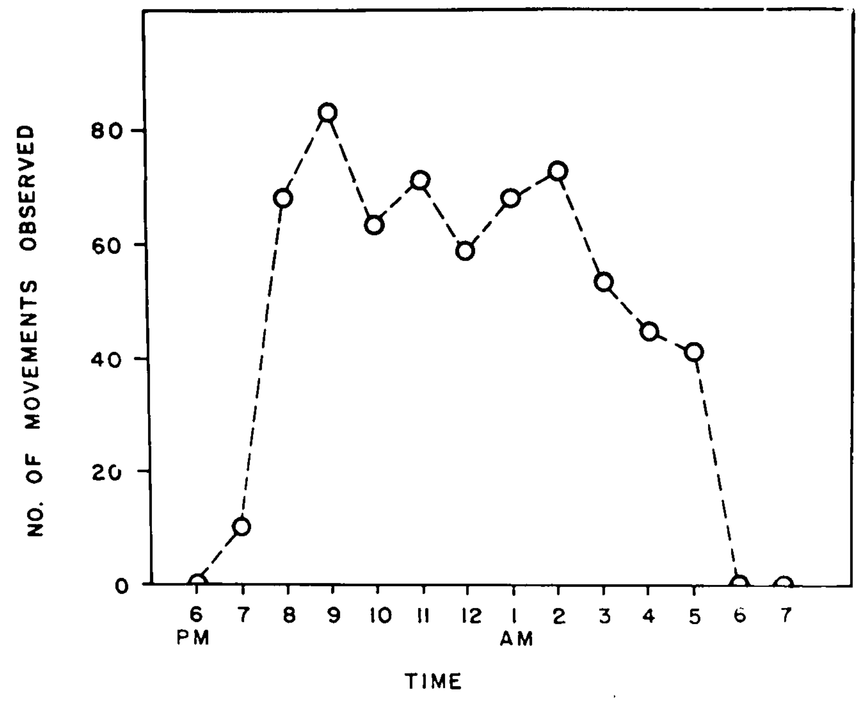


FIGURE 25. THE PERIOD OF NOCTURNAL ACTIVITY OF THE IMAGOES OF P. UMBRICOLA.

show what the period of activity of the moths would be in the field with light conditions varying from crepuscular intensities to darkness.

Response to Light

In the laboratory culture it was observed that at sunset the larvae always became active in the rearing jars. However, when light was turned on they would all "seek" hiding places and, having found them, cease to move. Switching the light off seemed to bring them back to activity. Since light seemed to play such an important role it was decided to carry on investigations dealing with the role of light on the behavior of *P. umbricola*. These studies were carried out in the laboratory using artificial light.

Studies on the response to light of the various larval instars were made by the use of an ordinary desk, five by three feet, covered with thick white paper. A laboratory lamp fitted with a 60-watt bulb was arranged so that it just peeked over the edge in the middle of one of the larger sides. A line, AB, parallel to the side of the desk was drawn nine inches from the edge. The experimental larvae were released, one at a time, on the line opposite the lamp. The direction of movement was determined by measuring the angle between the line of movement and the line AB. The angles were recognized at twenty degree intervals only. All the angles encountered in between were recorded with the next higher unit (Figure 26).

The results showed that the various instars differed in their reactions to light. The first instar larvae always seemed to move at random and showed no definite response to light. It was noticed that

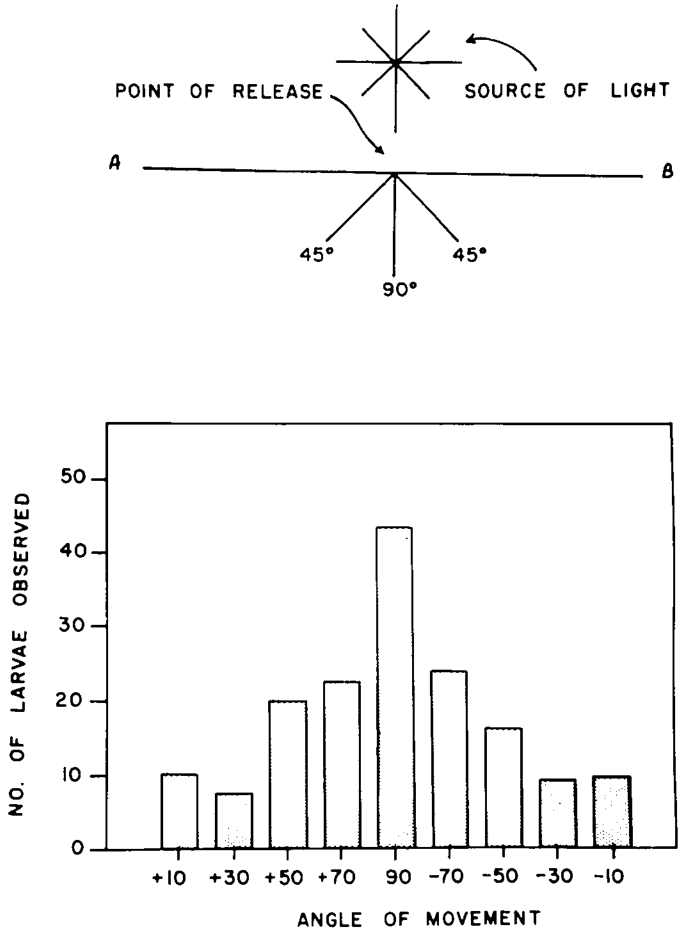


FIGURE 26. THE REACTION OF THE SIXTH INSTAR LARVAE OF P. UMBRICOLA TO A POINT SOURCE OF LIGHT.

in spite of the heat generated by the bulb the larvae would sometimes draw very close to it, even attempt to crawl onto it. This apparent insensitiveness to light and especially heat seems all the more remarkable considering the fragile body of the young larvae.

The reactions of the second to sixth instar larvae differed from those of the first instar. The second instar larvae yielded quite varied results. Some individuals moved toward the light source while others seemed to move consistently away from it. The third, fourth, fifth, and sixth instars always moved away from the source of light. Figure 26 illustrates the results obtained from the sixth instar larvae which can be said to be typical of the instars three to six. This figure indicates clearly that the larvae definitely move away from the source of light.

Another experiment was carried out on the effect of light on larval behavior. A wooden rod 1 x ½ x 72 inches was placed in a vertical position. A 200-watt bulb was hung from the ceiling in such a manner that it was about six inches from the top end of the wooden rod. The experiment was started at 7:00 PM since this is the time when the larvae exhibit their upward movement on the monkey pod trees under natural conditions. Sixth instar larvae were placed on the rod, one at a time, near its lower end and their progress observed.

The results showed that if the overhead light was off, the larvae moved upwards. If the light was turned on they headed downwards. If a larva was allowed to crawl upwards three-fourths of the way in darkness and then the light was turned on, it still headed downwards. This experiment showed that the larvae of P. umbricola moved away from the light. Fraenkel and Gunn (1961) referred to such directed movements as phototactic movements. Since the larvae moved away from the light this movement may be called negatively phototactic.

Another experiment was conducted to determine the effect of diffused light on the movements of larvae. A large 4 x 3 foot glass window pane was covered with tracing paper and placed horizontally under two 8-foot fluorescent light tubes so that when a 4 x 3 foot board was placed three feet under it, the light rays incident on it were quite diffused. The larvae were released individually in the center of this board and their movements observed.

It was found that all stages of larvae exhibited random and apparently aimless movements. However, if they came across any hiding places they crawled into them and ceased to move. It seems that any sort of light condition, whether a point source or a field of strong diffused light, is sufficient to make the larvae "search" for cover.

OVIPOSITION STUDIES

Effect of Space on Oviposition

Preliminary experiments showed that the moths readily laid eggs when confined in large metal oviposition cages (Figure 5), but laid few or no eggs when kept in small glass gallon jars (Figure 6). It seemed that the amount of space was an important factor on the number of eggs laid.

An experiment was conducted to detect any influence that space and crowding might have on the number of eggs laid. It was also anticipated that this experiment would disclose the optimum combination of males and females to use in further oviposition studies. The following three combinations of sexes were used: 1) one female and one male, 2) three females and three males, and 3) five females and five males. The two types of cages mentioned above were used with all three of these combinations. Eggs in the respective cages were counted daily at 3:00 PM. In cages belonging to the first combination (1:1) the daily counts of eggs per cage represented those laid by individual females and were recorded as such. In cages belonging to the second (3:3) and third (5:5) combinations the daily counts of eggs per cage represented those laid by three and five females, respectively. In these cases the calculated average per female was recorded. The observations for each combination were replicated ten times.

The results are presented in an abbreviated form in Table IV. An analysis of variance was carried out to detect any differences among the mean numbers of eggs laid. The mean square for the three combinations was not significant indicating thereby that the number of pairs confined in a cage does not have any effect on the number of eggs laid. The mean

TABLE IV. EFFECT OF TYPE OF CAGE AND MALE : FEMALE COMBINATION ON THE NUMBER OF EGGS LAID BY *P. UMBRICOLA*

Male : Female Combination[1]	Type of Cage[2]	No. of Replications	Eggs Laid		
			Mean Number of Eggs Laid per Female	Standard Deviation	Range
1 : 1	Gallon Jar	10	303.4	41.5	257-373
	Metal Cage	10	256.2	31.5	226-321
3 : 3	Gallon Jar	10	244.1	37.3	192-305
	Metal Cage	10	406.5	89.1	231-506
5 : 5	Gallon Jar	10	155.8	61.6	93-313
	Metal Cage	10	368.6	49.3	311-461

[1] Male : Female Combinations: F = 0.69 (d.f. 2, 3) $P > 0.25$. Difference not significant.

[2] Cage Type: F = 76.85 (d.f. 3, 54) $P < 0.005$. Difference highly significant.

square for the two types of cages turned out to be highly significant. This clearly indicates that the size of the cage has a marked effect on egg laying. The number of eggs laid in the metal oviposition cages was significantly higher than that in gallon jars. The combination of three females and three males in these cages yielded slightly higher, though not statistically significant, average number of eggs than the other combinations. This combination of imagoes confined in metal cages was selected for all subsequent studies on oviposition.

The lack of sufficient space in the gallon jars affected the imagoes in that their wings were injured rapidly. Instances were observed where the imagoes were almost wingless after their first week of confinement. Imagoes confined in large metal cages, however, never suffered such wing injury.

Rate of Oviposition

The effect of age of the imagoes on the daily rate of oviposition was investigated. Since the previous experiment indicated that the combination of three females and three males in metal cages was optimum for oviposition, this procedure was used. Eggs were counted in the manner described earlier. Fifteen replications of this experiment were obtained, ten in July - August 1963 and five in July 1964.

The data on the daily rate of egg laying for a period of twenty-two days are given in Figure 27. Each dot represents the mean number of eggs laid by three imagoes. The solid line passes through points which represent the mean for each day. The figures show clearly that oviposition was at its maximum between the fourth and the twelfth days after emergence. No imago laid eggs on the first day after emergence.

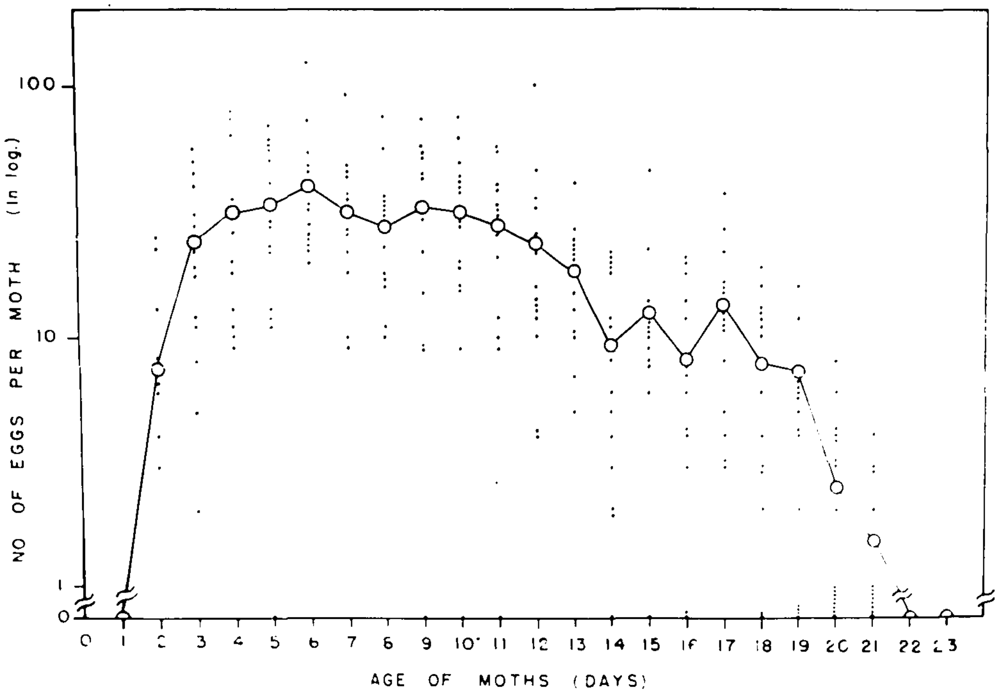


FIGURE 27. EFFECT OF AGE ON THE NUMBER OF EGGS LAID BY IMAGOES OF *P. UMBRICOLA*. EACH DOT REPRESENTS THE MEAN NUMBER OF EGGS LAID PER DAY BY THREE FEMALES; THE CIRCLES THE MEAN NUMBER OF EGGS FOR EACH DAY.

Egg laying ceased after the moths were twenty-one days old. The data on preoviposition, oviposition, and postoviposition periods, presented in Table V, indicate that the mean durations of these periods are: 1.2 ± 0.6, 19.1 ± 3.7, 2.3 ± 1.4 days, respectively. The mean number of eggs laid per female was 390.8 ± 89.0 eggs.

Age of Imagoes and Egg Viability

In the previous experiment on the daily rate of oviposition, records were taken on egg viability at various intervals to determine the effect of age of imagoes on the percentage hatching of eggs laid. Every second day a sample consisting of forty eggs was taken at random from five cages. The eggs were kept in small 3½ x 2 inch bottles and their hatching observed.

The results shown in Table VI show that the viability of eggs increases rapidly from the second to the fourth day. The percent viability remains high until the sixteenth day and then declines. The data also show that the percent viability of eggs is highest during the period when egg laying is the highest.

Oviposition and Longevity of Mated and Unmated Females

To investigate any differences in egg laying and longevity between mated and unmated females, the following experiment was carried out. Five oviposition cages were used in this experiment (Figure 5). Three newly emerged females were introduced in each cage and their egg laying observed daily at 3:00 PM for twenty-five days. When any imago was found dead, it was immediately dissected, the eggs in the ovarioles counted, and the number added to the total eggs already laid. This

TABLE V. PREOVIPOSITION, OVIPOSITION, AND POSTOVIPOSITION PERIODS AND FECUNDITY OF P. UMBRICOLA

	Preoviposition Period (Days)	Oviposition Period (Days)	Postoviposition Period (Days)	Eggs Laid per Female
Maximum	3.0	21.0	4.0	506.0
Minimum	1.0	7.0	0.0	231.0
Average	1.2 ± 0.6	19.1 ± 3.7	2.3 ± 1.4	390.8 ± 89.0

TABLE VI. THE EFFECT OF AGE ON THE PERCENTAGE OF VIABLE EGGS LAID BY P. UMBRICOLA

Age of Imagoes (Days)	2	4	6	8	10	12	14	16	18	20	22	24
Mean No. of Eggs Laid per Female	6.5	55.1	74.1	62.6	64.9	52.0	27.9	20.2	19.4	7.7	0.5	0.0
Percent Viability	10.2	67.5	92.5	90.8	97.5	87.5	77.5	85.0	52.5	52.5	42.5	-

experiment was repeated three times, once in July and twice in July - August 1964. Since the results were almost identical, the data were pooled and compared with those obtained from mated females in a previous experiment (Table V). Eggs laid by unmated females were non-viable.

Results show that the mean numbers of eggs laid by mated and unmated females were: 390.8 ± 89.0 and 379.3 ± 82.0, respectively (Table VII). An analysis of variance showed that there was no significant difference between the means of the two groups indicating that egg laying in P. umbricola is not influenced by mating. The eggs laid by unmated females were, however, all non-viable. The mean longevity of the mated and unmated females turned out to be 20.1 ± 4.9 and 18.3 ± 5.7 days, respectively. An analysis of variance showed no significant difference between the means signifying that the two groups have the same span of life. Figure 28 illustrates graphically the longevity of both the mated and unmated females.

The laying of infertile eggs is often discussed in the literature. Quaintance and Brues (1905), working with the cotton bollworm, reported that infertile eggs were laid very rarely in nature. Callahan (1958) found that the corn earworm, Heliothis zea (Boddie), never laid infertile eggs in the sense that oviposition was a natural process. He thought that unfertilized imagoes absorbed most of their eggs before they matured. Since P. umbricola freely lays unfertilized eggs, it can be concluded that, in this insect, oösorption probably never takes place.

TABLE VII. MEAN NUMBER OF EGGS LAID AND LONGEVITY OF MATED AND UNMATED IMAGOES OF *P. umbricola*

	Sets of Imagoes with Three Pairs Each	Number of Eggs Laid			Longevity (Days)		
		Mean[1]	Standard Deviation	Range	Mean[2]	Standard Deviation	Range
Mated	15	390.8	89.0	231-506	20.1	4.9	10-25
Unmated	15	379.3	82.0	257-525	18.3	5.7	5-24

[1] Mean Eggs: F = 0.14 (d.f. 28, 1) $P > 0.25$. Difference not significant.

[2] Mean Longevity: F = 0.86 (d.f. 28, 1) $P > 0.25$. Difference not significant.

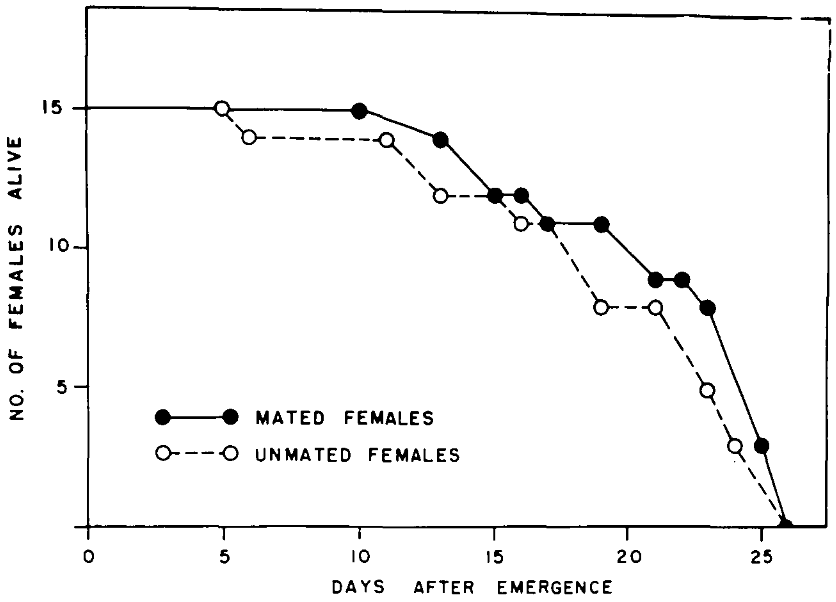


FIGURE 28. LONGEVITY OF MATED AND UNMATED FEMALES OF P. UMBRICOLA.

PHENOLOGY OF THE MONKEY POD TREE

Growth of Trees

The leaves of the monkey pod trees remain green throughout most seasons of the year. At first glance this gives the impression that food of the larvae of P. umbricola is available at all times of the year. However, this impression is not correct because the amount of young terminal foliage varies considerably from season to season. The lack of young foliage on a tree at certain times may cause a shortage of food for the larvae. Since the amount of young foliage on trees is a direct result of their growth, an investigation was carried out to determine the rate and time of growth of the trees.

The growth of the trees can be measured by recording the activity of their growing tissues. There are three such tissues in trees: apical meristems in stem and root tips, primary cambiums, and secondary or cork cambiums. Growth occurring at apical meristems is usually classified as "primary growth" and, in the case of shoots, results, among other things, in the production of new foliage. Growth from lateral meristems results in increase in diameter. It is called "secondary growth". The measurement of both of these types of growth can be carried out. In this investigation measurements of the growth of trees were made by observing the primary growth of the shoots.

The amount of new foliage on the young shoots of the trees as a result of their meristematic activity was estimated in a subjective manner. The terminal shoots on all four sides of the trees were examined and given a value out of a maximum of ten depending upon the number of actively growing twigs. If all the twigs on a particular side were found to be sprouting that side would rate ten out of ten, whereas a side on which no growth was taking place would get zero. Another side on which approximately fifty percent of the twigs were sprouting would score five out of ten, and so on. The figures obtained from all four sides were combined for each tree so that the pooled figure for the growth activities of a particular tree varied from zero to forty. In all, thirty-two trees were sampled, sixteen in Series 1, eight in Series 3, and eight in Series 4 (Figure 7). No observations were made on the trees in Series 2 as these were mostly very young trees and did not support much foliage. Growth of all the trees in the Series 1, 3, and 4 was recorded in the same uniform manner. The figures obtained for a particular month from all the trees were pooled and plotted as shown in Figure 29.

In January 1963 when sampling was started, the monkey pod trees were beginning their new growth. From February to November 1963 the trees in all the three series were growing vigorously and the amount of new growth was high. The months of November and December 1963 and January 1964 saw the least amount of new growth. The trees in Series 3 underwent the longest period without new growth; the records show no new growth for the three months of December 1963 and January and February 1964. The growth renewed in February 1964 and shot up to a high value by March 1964. It remained at that high value until June when sampling was stopped. A comparison of the three series shows that the growth of the trees displayed very much the same form.

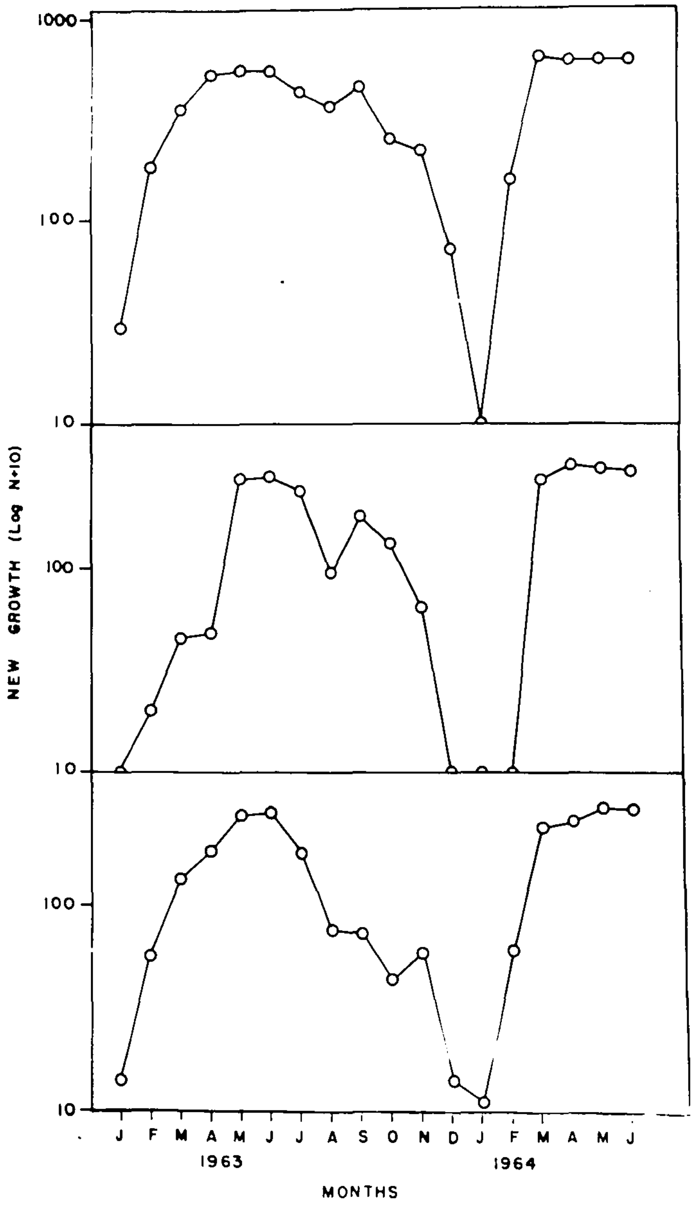


FIGURE 29. THE AMOUNT OF NEW GROWTH ON MONKEY POD TREES IN SERIES 1 (TOP), SERIES 3 (MIDDLE), AND SERIES 4 (BOTTOM).

Relationship between Growth of Trees and Climate

The relationship between the seasonal growth of the monkey pod trees and the various factors of the environment was investigated. Monthly values for mean temperature, total precipitation, mean daily duration of sunlight, and mean daily incident solar radiation were obtained and compared to the corresponding figures for the growth of the trees. It was found that the monthly values of the mean daily incident solar radiation measured in gram calories and total monthly precipitation were closely related to fluctuations in the growth of trees. Figure 30 shows the pooled value for growth of trees in the three series plotted with these two components of the environment.

This figure shows that an increase in the amount of solar radiation and heavy rains in the period from January to April 1963 coincided with a rapid increase in the growth of the monkey pod trees. By the month of August 1963 the amount of solar radiation had maintained a high value, but the rainfall had decreased considerably. Following this period, along with decreasing solar radiation and little rain, a slackening of tree growth took place. In November 1963 it declined very rapidly, ceasing altogether in January 1964.

It can be noticed that the growth picture of the period from January to March 1964 was quite different from that of the corresponding period in 1963. The early part of 1963 was unusually wet. This might have had a direct influence on tree growth or an indirect one through controlling the amount of solar radiation reaching the trees. On the whole, it may be said that increasing solar radiation and abundant rainfall in the spring season brought about a rapid increase in the growth of monkey pod

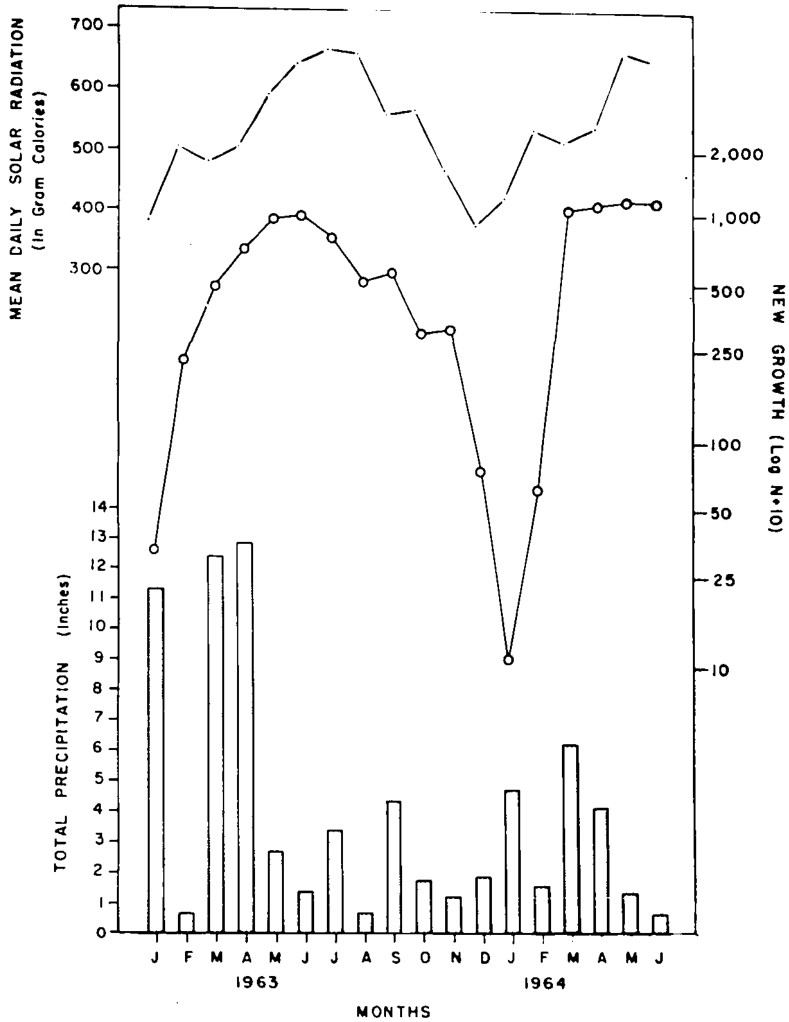


FIGURE 30. THE RELATIONSHIP BETWEEN THE GROWTH OF MONKEY POD TREES, AND THE TOTAL MONTHLY PRECIPITATION AND THE AMOUNT OF INCIDENT SOLAR RADIATION. THE PRECIPITATION AND SOLAR RADIATION DATA ARE TAKEN FROM METEOROLOGICAL RECORDS OF P.R.I., AND H.S.P.A., RESPECTIVELY.

trees. Decreasing solar radiation and scarcity of rain in autumn appear to have led to its diminution.

Damage to Trees

The larvae of P. umbricola feed only on the meristematic tissue of the shoot tips and the young tender foliage. In the literature such shoot tip and leaf feeding insects have rarely been credited with bringing about the death of trees (Kramer and Kozlowski, 1960). They are, nevertheless, very important in reducing the amount of photosynthetic tissue and thereby decreasing the amount of carbohydrates available for growth. Reduction in growth of partially defoliated trees is often discussed in the literature, and is usually believed to be proportional to the amount of foliage removed (Church, 1949). In old trees with low growth rates this can lead to irreparable damage.

The amount of defoliation caused by P. umbricola larvae on monkey pod trees varies markedly from season to season. To obtain an idea of the extent of damage to the trees, a monthly record was kept of each tree. These data were collected in the same manner as those for growth. The terminal twigs on all four sides of the trees were examined and given a value out of a maximum of ten depending upon the number of twigs showing damage. If all the twigs on one particular side showed damage that side would rate ten out of ten, whereas another side, on which approximately fifty percent of the twigs showed damage, would score five out of ten. The figures obtained from all four sides were combined for each tree so that the pooled figure for the damage of a particular tree varied from zero to forty. All of the thirty-two marked trees in Series 1, 3, and 4 were sampled (Figure 7). A subjective reading of the four sides of each tree was made each month. The figures from each side were pooled for each tree and the combined totals of all the thirty-two trees for each month plotted. The results are shown in Figure 31.

The figure shows that a considerable amount of damage was observable in the period from January to April 1963. During the months of May and June it declined, but underwent a prolonged increase from July to November 1963. At approximately this time another decline set in which lasted until March 1964. The amount of damage increased in the months of April and May 1964 and had reached a high value in June when sampling was discontinued.

It is quite apparent that the damage to monkey pod trees shows strong fluctuations in its intensity. The months of February, March, and April 1963 and also September through December of the same year saw the most damage. The extent of damage was probably very closely associated with the numbers of the pest present and the stage of growth of the trees. These relationships are investigated in the next section.

Shedding of Leaves

The monkey pod trees shed their leaves once every year. The shedding, however, is very irregular and seldom complete. At no time can all trees in one locality be seen without leaves. On the whole it can be said that the shedding of leaves is intensified in the months of February and March.

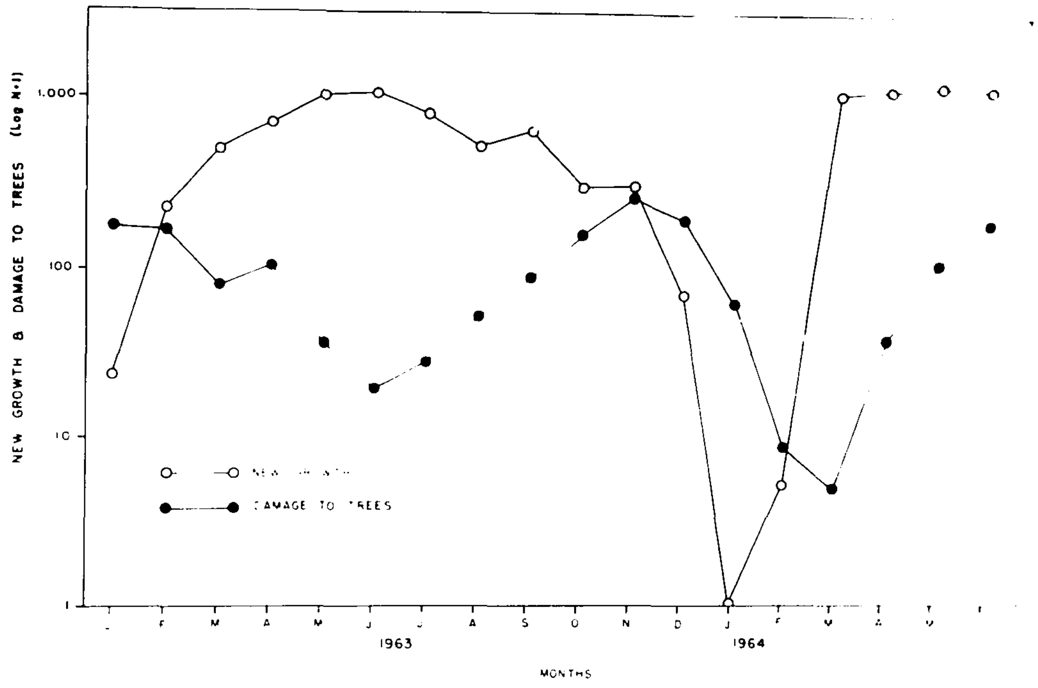


FIGURE 31. THE AMOUNT OF NEW GROWTH AND THE DAMAGE DONE BY P. UMBRICOLA LARVAE ON MONKEY POD TREES.

SEASONAL ABUNDANCE OF P. UMBRICOLA

In order to study the seasonal fluctuations in populations of P. umbricola, attempt was made to take samples of eggs, larvae, and imagoes. It was found that sampling of eggs and larvae was satisfactory, but the imagoes did not lend themselves to any adequate method for counting. Their response to light traps was very poor. Night observations on monkey pod trees revealed that the population density of imagoes was probably very low. It was decided to abandon sampling for imagoes.

Egg Population

Favorable results for estimating the population fluctuations were obtained by taking monthly samples of terminal twigs of monkey pod trees and counting and recording the number of eggs found on them. Since the eggs are laid primarily on the terminal twigs, the samples consisted of the terminal six inches of young twigs (Figure 17). Only the trees in Series 1 and 3 were sampled (Figure 7). Ten samples were collected at random from each of these two series.

The results are illustrated in Figure 32. It shows clearly that, in Series 1, the egg counts started from a maximum in January 1963 and, after passing through two minor fluctuations, reached their minimum in February 1964. After this period the eggs became more abundant. In Series 3, the counts remained high from October 1963, after which they declined rapidly. They reached their minimum value in January 1964, maintaining this until March 1964. Their numbers rose again in April and May 1964; this increase, however, was very slight.

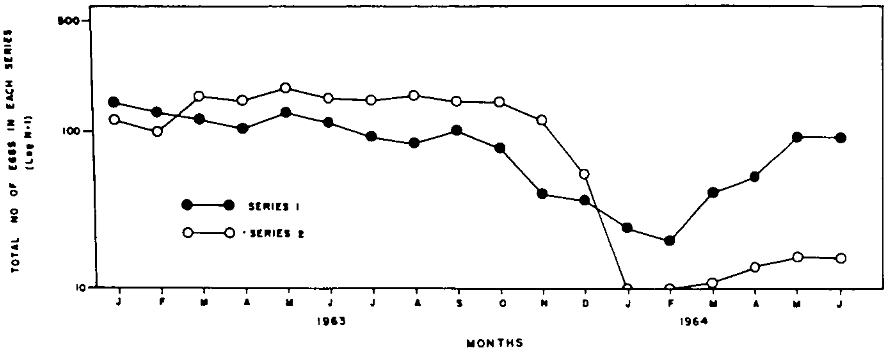


FIGURE 32. THE ABUNDANCE OF THE EGGS OF _P. UMBRICOLA_.

A comparison of the two sets of data indicates that, although the fluctuations are more severe in Series 3, the nature and time of these fluctuations are very similar in the two cases.

Larval Population

In order to estimate the pest population in the field by counting the larval stages of *P. umbricola*, the burlap band traps were utilized (Figure 8). The traps were opened once a month and all the larvae hiding in them were counted and recorded. In all, twenty-five trees were sampled in this manner, nine from Series 1, eight from Series 3, and eight from Series 4 (Figure 7).

The results are illustrated in Figure 33. It is quite evident that in January 1963, when sampling was started, the pest population was on the increase in all three series, reaching its peak around February and March 1963. It underwent a decline during the ensuing months (April and May), but increased to another peak in September 1963. Another and much more severe decline followed in which the larval counts were at their minimum. A study of the three series shows that the pest was most scarce in January 1964. In February 1964 the population started to increase, reaching another peak by May 1964. By June 1964 two of the Series, 1 and 4, showed a decline in their populations. This may be compared to a similar decline in March and April of the previous year.

When the abundance of the eggs and the larval stages is compared, it is found that they both show almost identical trends. This close similarity between the two methods of sampling probably substantiates the general faithfulness of the population picture obtained by sampling to the one existing in nature.

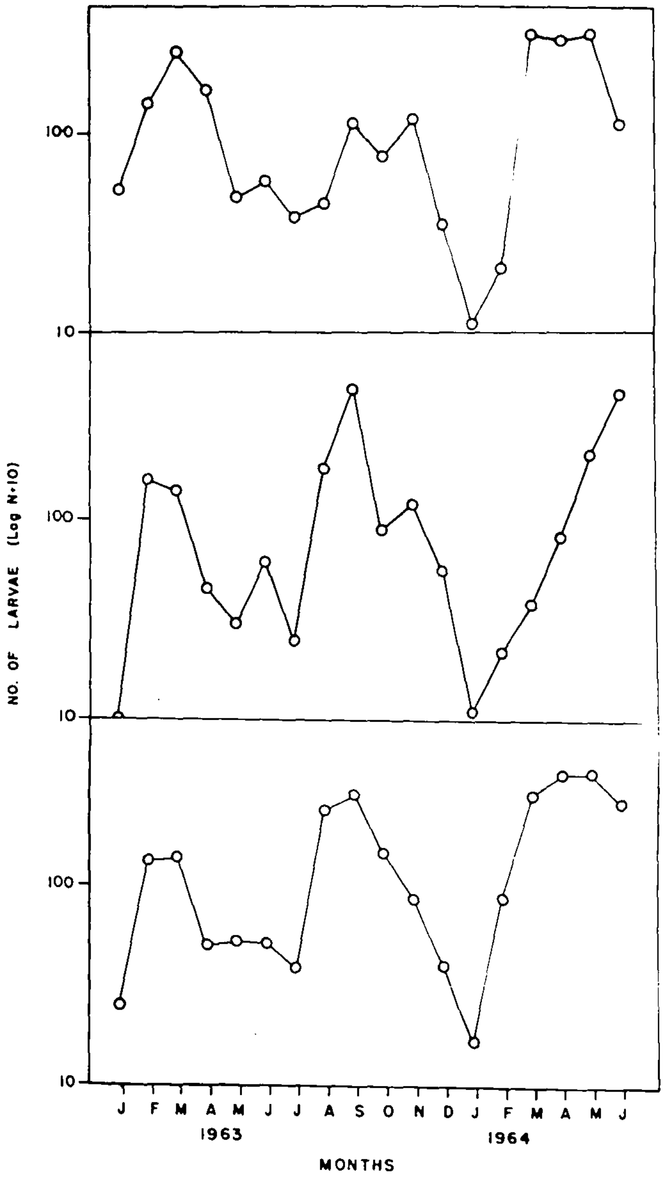


FIGURE 33. THE MONTHLY ABUNDANCE OF P. UMBRICOLA IN THE THREE SERIES.

Relationship between Abundance of P. umbricola and Growth of Trees

A comparison between the abundance of *P. umbricola* and the growth of monkey pod trees shows that the two are probably very closely related. An examination of Figure 34 shows that renewed growth of trees in the period January to March 1963 was accompanied by a sharp increase in the pest population. The growth continued at a rapid rate throughout summer until November. During this period the pest population maintained itself at a fairly high level. The months April through July, however, saw a slight decrease in the pest population in spite of the fact that there was no diminution in the growth of the trees. It seems that some other factor, or factors, was responsible for this. Natural enemies of *P. umbricola* probably enter the picture. This will be discussed in the next section.

The decline in tree growth in the month of December resulted in a sharp decline in the pest population. It is significant to note that the lowest values for both tree growth and pest population were recorded at the same time, this being in January 1964. In the month of February 1964 growth was resumed and by March 1964 it had shot up to a high value. The pest population during the same period seems to have followed the same course. The period from March to June 1964 was a time of high tree growth and also high pest abundance.

Relationship between P. umbricola and E. odora

The black witch moth, *Erebus odora* Linn., and its immature stages occupy very much the same habitat as *P. umbricola*. The biologies of the two species are also similar. The eggs of *E. odora* are usually found on

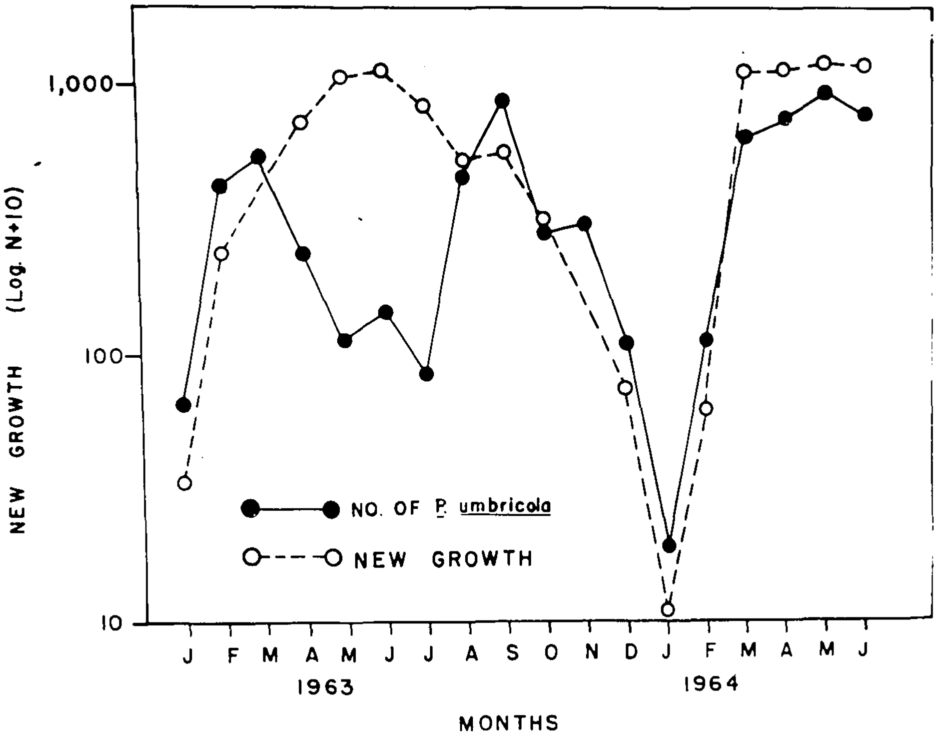


FIGURE 34. RELATIONSHIP BETWEEN THE NUMBERS OF P. UMBRICOLA AND GROWTH OF MONKEY POD TREES.

the leaves. The larvae are nocturnal feeders, hiding during the daylight hours in cracks and crevices in the bark or in debris at the foot of the trees. Their food consists of tender leaves on the terminal twigs of the monkey pod trees.

An investigation was carried out to find out whether there was any difference in the seasonal abundance of these two species and, whether the two species, while occupying the same habitat, also occurred together in terms of time. The population of E. odora was sampled monthly. The sampling was done on the same trees as for P. umbricola since the burlap bands on the monkey pod trees used to trap P. umbricola larvae were found to be equally efficient in trapping larvae of E. odora. Figure 35 illustrates the results which are plotted with corresponding figures for P. umbricola.

A comparative study of the population curves of the two species shows that the increase in numbers of P. umbricola in January - February 1963 was followed immediately by an increase in E. odora population. A slight decrease in numbers of P. umbricola in April and May was followed by a decrease in E. odora. In July 1963, however, the numbers of E. odora started to increase and kept on increasing until August. By this time the numbers of P. umbricola had multiplied considerably. This seems to have had some effect on the E. odora population which decreased sharply. The population of P. umbricola underwent a decline from October 1963 to January 1964, while the population of E. odora was increasing. Both species increased in February and March 1964, but again it can be seen that, in the face of a high population of P. umbricola, the numbers of E. odora diminished drastically. During the month of June 1964 the

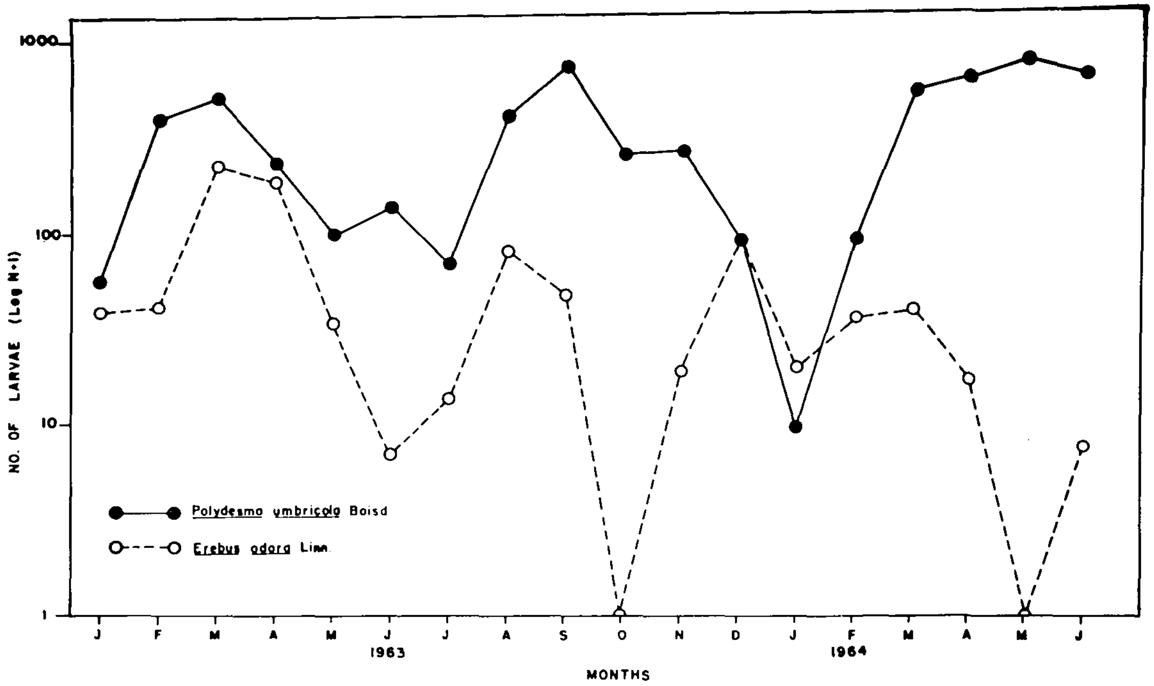


FIGURE 35. THE SEASONAL ABUNDANCE OF P. UMBRICOLA AND E. ODORA LARVAE UNDER THE BURLAP BAND TRAPS.

data show a decline setting in in the _P_. _umbricola_ population. The _E_. _odora_ population increased again in this month.

It seems that high numbers of _P_. _umbricola_ are followed by decreases in _E_. _odora_ populations. This is especially evident in the months of September - October 1963 and April - May 1964. The picture is a little less clear for the early part of 1963, but the general trends can still be made out.

In order to bring out this difference in the time of the relative abundance of these two species. The data obtained during sampling for seasonal abundance of the two species was rearranged and the number of _P_. _umbricola_ larvae found on a tree was plotted against the number of _E_. _odora_ larvae found on the same tree in the form of a frequency of co-occurrence graph (Figure 36). The size of the circles in the figure represents the relative concentration of the plotted dots in that particular area.

The distribution of the circles in Figure 36 shows clearly that the two species of insects occur together only when the numbers of both are small. When one species is present in large numbers the other one seems to decrease in numbers or to disappear altogether. The results indicate that the two species possessing common requisites may be involved in some sort of interspecific competition.

Relationship between P. umbricola and Damage to Trees

Since _P_. _umbricola_ is a defoliator of the monkey pod tree, it was anticipated that its abundance would be closely related to the amount of damage observed on the trees. Figure 37 gives the plotted values for

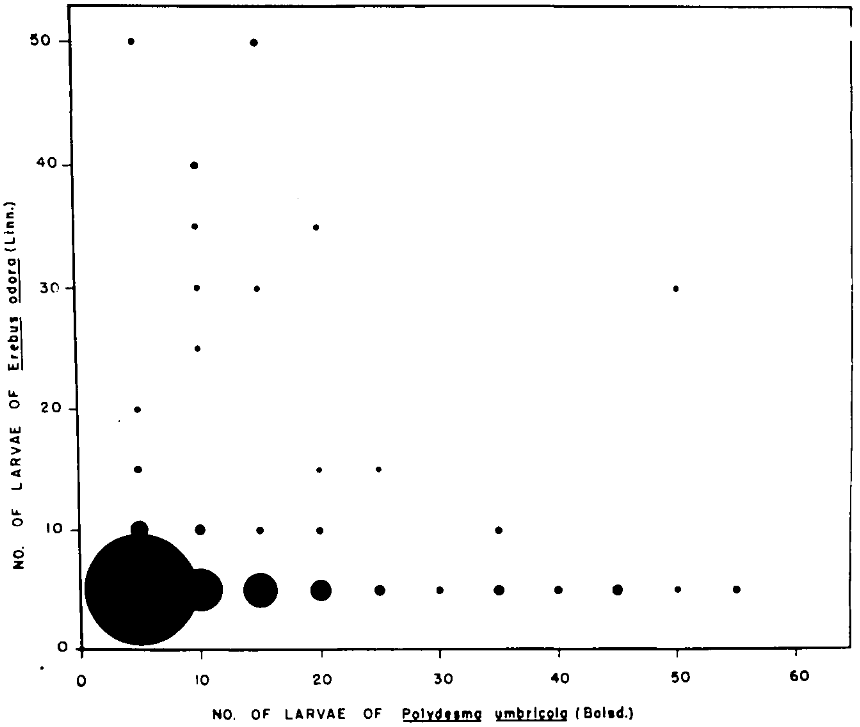


FIGURE 36. GRAPH SHOWING THE FREQUENCY OF CO-OCCURRENCE OF LARVAE OF P. UMBRICOLA AND E. ODORA UNDER THE BURLAP BAND TRAPS.

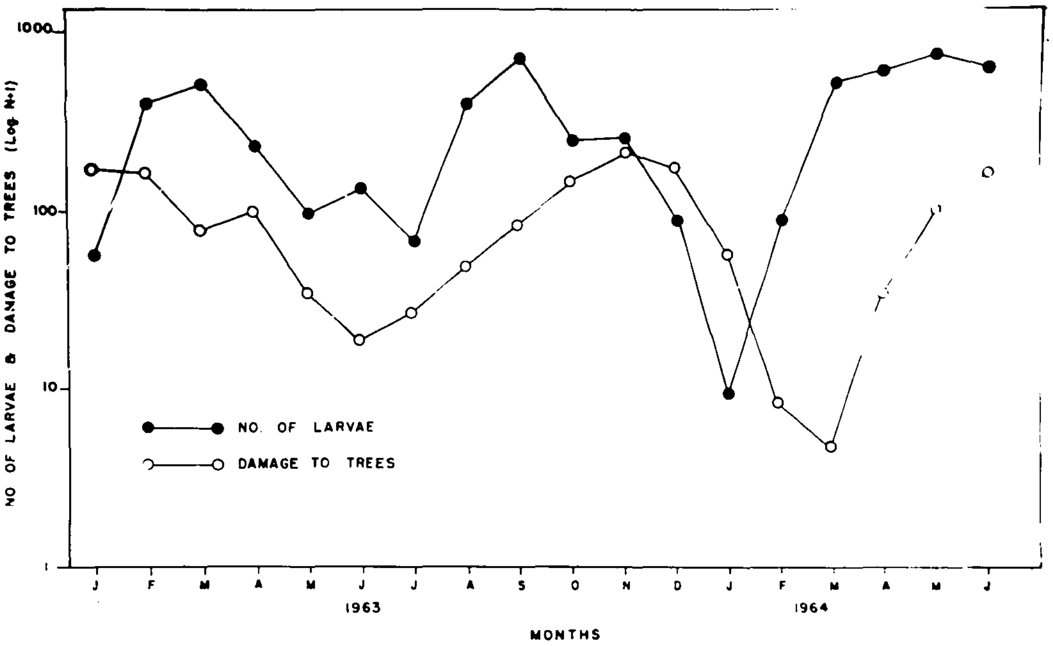


FIGURE 37. RELATIONSHIP BETWEEN NUMBERS OF P. UMBRICOLA AND THE VISIBLE DAMAGE TO MONKEY POD TREES.

the abundance of *P. umbricola* and the amount of damage observed. It shows that the trees suffered appreciable damage in the early part of 1963. At that time the population of *P. umbricola* was quite high. With a decrease in numbers of *P. umbricola* in the period from April to July 1963, the damage also decreased appreciably. When, in the months of August and September 1963, the pest population increased, the amount of damage followed suit. The decrease in pest population in the months of December 1963 and January 1964 was closely followed by a corresponding decrease in the amount of damage. The increase in pest population in February and March 1964 was closely followed by an increase in damage to trees. This close relationship between the two curves confirms that the damage is, at least for the most part, caused by *P. umbricola*.

NATURAL ENEMIES AND THEIR IMPORTANCE

Parasites

The first observation on parasitism in P. umbricola was made by Van Zwaluwenburg (1945). He noted that the parasite was a tachinid fly, though he did not identify it. Williams (1945) reared a tachinid fly from larvae of P. umbricola collected from the island of Molokai. He identified it as Eucellatoria armigera (Coquill.). Rosa (1945) reported another tachinid parasite, Chaetogaedia monticola (Bigot) which was reared from the pupae of the moth. During the course of this investigation, a third tachinid was found to be parasitizing the larvae of P. umbricola. This was identified by Dr. D. Elmo Hardy as Achaetoneura archippivora (Will.).

E. armigera and A. archippivora are very much alike in the manner in which they parasitize P. umbricola. They are both larval parasites. Full-grown parasite larvae bore out of the last instar host larvae just before the onset of the prepupal stage. Instances have been observed where the parasitic larvae do not bore their way out until after the host larvae have started to spin pupal cocoons. In such cases the adults of the parasites frequently get trapped in the cocoon and death occurs.

C. monticola is a larval-pupal parasite. The full grown larvae of this parasite do not bore their way out but pupate inside the host pupae, breaking their way out at the time of emergence. Adults of this parasite were also often encountered in the field trapped in the pupal cocoons of the host. This was probably due to the fact that P. umbricola larvae have a habit of pupating in deep crevices out of which it is sometimes difficult even for their own imagoes to escape.

A parasitic ichneumonid wasp, Hyposter exiguae (Viereck) was reported by Williams (1945) who reared it from young larvae of P. umbricola. During the course of this investigation it was observed that the larvae of this parasite always bored their way out of the host larvae when the latter were in the third or fourth instar. The parasites then spin their cocoons. The shriveled remains of the host larvae can be seen still attached to the cocoons of the parasites.

Williams (1945) reported rearing two parasites from the pupae of P. umbricola: an ichneumonid, Ephialtes hawaiiensis (Cameron), and a chalcid, Brachymeria obscurata (Walker). These parasites, however, were not encountered during the course of this investigation.

In order to gain an accurate idea of the incidence of parasitism, P. umbricola larvae were collected each month and reared in the laboratory. Each month's sample consisted of forty larvae of all ages collected at random from the various traps in Series 1, 3, and 4. In the months of January and February 1964 the samples consisted of only twenty caterpillars each. This was because the pest was rather scarce at that time of the year. In the laboratory the larvae were fed on fresh, tender monkey pod leaves until such time when they pupated or the parasites emerged. The results, shown in Figure 38, illustrate diagrammatically the incidence of parasitism during the period March 1963 to June 1964.

It is evident that C. monticola was most abundant from May to July 1963, after which it underwent a decline. It increased in numbers in November 1963 but by March 1964 its activity had diminished. It seemed

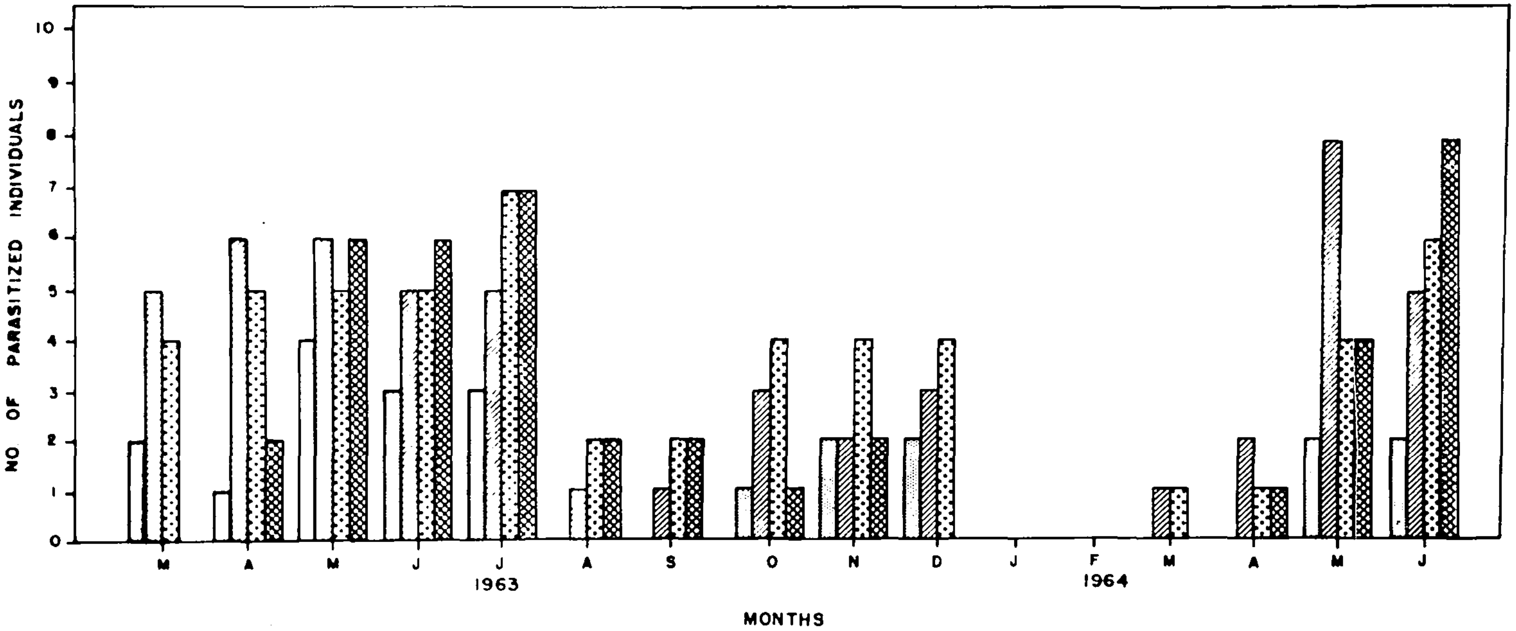


FIGURE 38. MONTHLY ABUNDANCE OF VARIOUS PARASITES OF *P. UMBRICOLA*. COLUMNS WITH FINE STIPPLING REPRESENT THE INCIDENCE OF *C. MONTICOLA*; SLANTING LINES *E. ARMIGERA*; HEAVY STIPPLING *A. ARCHIPPIVORA*; AND CROSSLINES *H. EXIGUAE*.

to be picking up again in May and June 1964 when sampling was discontinued. _E_. _armigera_ was most abundant from April to July 1963 and again in May and June 1964, with a minor peak from October to December 1963. _A_. _archippivora_ shows almost the same abundance pattern as _E_. _armigera_ except for the fact that it attained a higher peak in the October - December 1963 period.

The ichneumonid, _H_. _exiguae_ was very abundant from May to July 1963, after which it underwent a sharp decline. It was not until May 1964 that it increased again. It reached a new peak in June 1964 when the sampling was stopped.

Relationship between Abundance of P. umbricola and its Parasites

The relationship between the abundance of _P_. _umbricola_ and its parasites was investigated. To this effect the monthly abundance of _P_. _umbricola_ and its percent parasitism were plotted for each month. As the amount of new tree growth is very important for a complete understanding of the abundance of _P_. _umbricola_, its monthly values were also plotted (Figure 39).

It can be seen that the increase in host population in February and March 1963 was followed by an increase in the incidence of parasitism. The latter increased from March to May 1963 at which time the host population had started to decrease. Parasitism reached its peak in July 1963 just when the host population reached its lowest point for that year. It is interesting to note that this happened in spite of the presence of abundant food for the host larvae. After this there was a considerable decline in the incidence of parasitism. In the months of October and November 1963 the host population started to decrease and

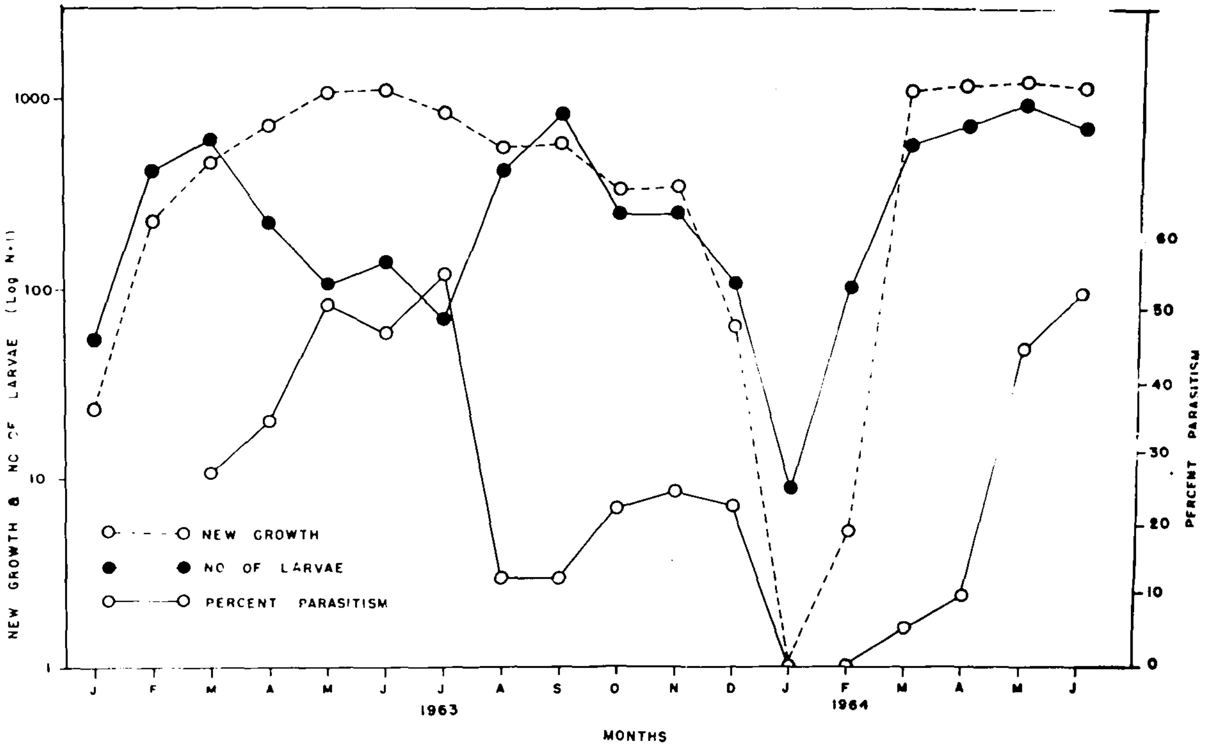


FIGURE 39. GRAPH SHOWING THE SEASONAL GROWTH OF THE MONKEY POD TREE AND THE FLUCTUATIONS IN THE PEST POPULATION AND ITS PARASITES.

at the same time an increase in parasitism could be observed. Both the populations underwent a more or less simultaneous decline in December 1963 and January 1964. Due to almost complete absence of young foliage the numbers of host were very low. The samples did not yield any parasitized individuals.

Renewed growth of trees in February 1964 was followed by a rapid increase in the host numbers. Percentage parasitism also increased and had passed the fifty percent mark in June 1964 when sampling was discontinued.

It is interesting to note that the decrease in the population of _P_. _umbricola_ during the period from March to July 1963 corresponded with a period when the incidence of parasitism was very high. From March to August 1963 the growth of the trees was proceeding at a high rate, so that the amount of food available had very little to do with this decrease in the numbers of _P_. _umbricola_. During the months of December 1963 and January 1964, due to the lack of food, the host population declined greatly. The incidence of parasitism also decreased. The parasitism increased during April, May, and June 1964. This probably was the cause of the decline which seemed to be setting in in the host population in June 1964 when sampling was discontinued.

Table VIII gives a list of all parasites recorded from _P_. _umbricola_.

Predators

Williams (1945) observed Polistes wasps flying around the tree trunks of monkey pod trees. He suggested that they might be predators on the larvae of _P_. _umbricola_. During the course of this investigation, numerous cases were observed where these wasps would "skin" the larvae in their characteristic fashion and fly away with the skinned carcass.

TABLE VIII. PARASITES OF P. UMBRICOLA

Name of Parasite	Family	Stage of Host Attacked	Reference
Eucellatoria armigera (Coquill.)	Tachinidae	Larval	Williams (1945)
Chaetogaedia monticola (Bigot)	"	Larval-pupal	Rosa (1945)
Achaetoneura archippivora (Will.)	"	Larval	Author
Hyposter exiguae (Viereck)	Ichneumonidae	"	Williams (1945)
Ephilates hawaiiensis (Cameron)	"	Larval-pupal	"
Brachymeria obscurata (Walker)	Chalcidae	"	"

Lizards and centipedes were also found to be associated with *P. umbricola* larvae. Their activity was especially noticeable under the burlap bands around tree trunks and at the base of trees where they were almost constantly present. That they fed on *P. umbricola* larvae was very easy to observe under these bands. During this investigation an attempt was made to exclude these two species of predators from the burlap bands. Advantage was taken of the fact that the two predators, especially the centipedes, normally are found near the base of the trees. A long, three inch broad strip of rubber was stretched around the tree trunks a little below the burlap bands and daubbed liberally with tangle foot. This seemed to be quite effective, as observations a week later showed many dead lizards entangled in the tangle foot. The tangle foot, however, was soon found to be covered with dead leaves and other debris blown by the wind and, within a week, lizards and centipedes were again found under the burlap bands. The effort to keep these predators out of the bands was then discontinued.

The common giant toad was also observed on many occasions to feed on the larvae of *P. umbricola*. When toads collected near monkey pod trees were dissected, their stomachs were always found to contain *P. umbricola* larvae in them. The larvae of *E. odora* were also frequently encountered in the stomach contents.

Zimmerman (1946) reported observing mynah birds and English sparrows feeding on the larvae of *P. umbricola*. During this investigation the Brazilian cardinal was also found to feed on these larvae.

Chrysopid larvae were often encountered among the terminal twigs of the monkey pod trees where they sucked *P. umbricola* eggs.

Table IX gives a list of all predators recorded from _P_. _umbricola_.

TABLE IX. PREDATORS OF *P. UMBRICOLA*

Name of Predator	Class	Stage of Host Attacked	Reference
Polistes fuscatus var. *aurifer* (Sauss.)	Insecta	Larval	Williams (1945)
Lizards	Reptilia	Larval-adult	Author
Centipedes	Myriapoda	Larval	"
Giant toad *Bufo marinus* (Linn.)	Amphibia	"	"
Mynah bird *Acridotheres tristis* (linn.)	Aves	"	Zimmerman (1946)
English sparrow *Passer domesticus*	"	"	"
Brazilian Cardinal	"	"	Author
Chrysopid Larvae	Insecta	Eggs	"

DISCUSSION

Studies on the geographical distribution of P. umbricola showed that the insect enjoys a distribution covering all the tropical and subtropical areas of the world except the new world. The monkey pod tree, however, originates from tropical America. This shows that the association between P. umbricola and the monkey pod tree is a secondary one. The date of introduction of the monkey pod tree into the Hawaiian Islands is not known; records show that it was not introduced into India until 1878, indicating that there, P. umbricola and the monkey pod tree have been associated for less than one hundred years. Indeed, the only plant on which P. umbricola has been reported in the Oriental and Ethiopian regions is Albizzia lebbek. It can be concluded that the association between P. umbricola and A. lebbek is longer than that between P. umbricola and the monkey pod tree, and that A. lebbek is probably the original host of P. umbricola.

Studies on the daily rhythmic activities demonstrated that the larvae of P. umbricola move up the monkey pod trees at sunset and at sunrise come down towards the base of the trees. The main components of the environment which might be responsible for such rhythmic activity are temperature, moisture, and light, all of which undergo daily fluctuations. Of these, it seems, light plays the most important part. The fading light in the evening seems to activate the larvae and they exhibit their upward movement. In the early hours of the morning the increasing-light condition seems to induce them to start moving down. The response to light is a valuable adaptation; firstly, because of the components of the environment mentioned above light may be the most consistent and reliable; secondly, because it enables the caterpillars to gain access to a place where there is likely to be plenty of food and, thirdly, because the predatory birds are diurnal. This has been reported to be quite characteristic of adaptations associated with light (Andrewartha and Birch, 1954). Fraenkel and Gunn (1961), referring to this sort of role played by light, termed it a "token" stimulus, the "token" being a sign which represents something else. In the case of P. umbricola, light indicated a situation which, for another reason (i.e., abundance of food, and possibly avoidance of predators), is favorable, and the larvae possessing the appropriate adaptation respond accordingly.

The nocturnal movements of the imagoes of noctuids, in general, may be associated with feeding, mating, and oviposition. Observations in the field indicated that P. umbricola is probably crepuscular in its feeding habits and nocturnal in its mating and oviposition habits. Relative scarcity of the moths and darkness make it extremely difficult to record individual observations of the above three different types of behavior. Even in the laboratory under controlled conditions, it seemed that the only practical way to study their nocturnal activity was to record their overall movements. The experiment conducted in the laboratory showed that, on the basis of their overall activity under constant illumination of very low intensity, the imagoes of P. umbricola could be called nocturnal rather than crepuscular. In the field, however, where the light conditions vary from crepuscular intensities to complete darkness, the periods of activity of the imagoes might vary.

Studies showed that the physical condition of the monkey pod tree is of great significance in understanding the abundance of pest larvae on it. The amount of bark determines the number of hiding places which to a large extent influences the number of pest larvae which can survive on the tree. It is interesting to note that generally, old trees with an abundance of rough bark did not have much young foliage on them, whereas young trees possessing abundant foliage lacked hiding places for the larvae. Both of these situations are not suitable for the survival of the larvae. The topped trees, however, provided suitable hiding places as well as an abundance of food. Such artificially created situations were, consequently, especially suitable for supporting high pest populations. Errington (1934, 1946), working with populations of vertebrates, especially birds and rodents, expressed somewhat the same idea in the term "carrying capacity". He believed that the carrying capacity of an area was largely determined by the presence of sufficient food, and amount and suitability of places for hiding and sheltering during winter. The topped monkey pod tree has a high carrying capacity in terms of easy availability of both "cover" and food, which results in severe defoliation of the tree year after year.

It is interesting to note the relationship between the climatological phenomena, such as precipitation and solar radiation, and the seasonal periodicity in the growth of monkey pod trees. A rapid increase in the amount of solar radiation and precipitation in the first three months of 1963 explains the high initial value for new growth recorded at that time. The corresponding period in 1964 saw much less rain, resulting in a delay in the growth of trees. In conclusion it may said that the time and intensity of these two components of the environment seem to be the key to the growth of the monkey pod trees.

The availability of fresh foliage on the monkey pod trees is of utmost importance for the multiplication in numbers of *P. umbricola*. It seems clear that the low pest population in the month of January 1964 was due only to the lack of sufficient food.

The phenomenon of the reduction of a population of insects due to lack of food has been discussed extensively in the literature (Elton, 1938; Andrewartha and Birch, 1954). Andrewartha and Birch (1954) maintain that: "It is common experience that the prevailing low numbers of animals in nature is not often due to shortage of food; ...". Elton (1938) has stated that "... animal numbers seldom grow to the ultimate limit set by food-supply, ... although it does occasionally happen, as with certain moth caterpillars that abound on oak trees in some years and may cause complete defoliation." The amount of available food is, therefore, in some cases, of major importance in determining the low numbers of natural populations. Usually, however, the relationship is more subtle than the simple one represented by an absolute shortage of food over an extensive area (Andrewartha and Birch, 1954). In the case of the monkey pod trees, larval abundance seems to depend upon the interaction of two main factors: food and shelter for the larvae. An old rough-barked tree, for instance, may suffer almost complete defoliation by P. umbricola whereas a young smooth-barked tree growing nearby may escape damage. The larvae on the old tree thus can experience an acute shortage of food in spite of the fact that there is an abundance of food nearby, but which is inaccessible.

In conclusion it may be said that the decline of P. umbricola population in January 1964 was directly a result of the lack of food. The decline of the pest population in the period from April to July 1963 was, as far as this present investigation reveals, not related to the availability of food.

The amount of larval damage recorded on monkey pod trees showed considerable seasonal variation. It is quite clear that peaks in larval populations were followed closely by peaks in the amount of damage. The damage could also be attributed to the activity of the larvae of E. odora, but the population peaks of the latter do not give any indication of such a trend. It seems fairly obvious that the damage on monkey pod trees is wrought, for the most part, by the larvae of P. umbricola. The larvae of E. odora, despite the fact that they are bigger and eat correspondingly more, do not seem to figure prominently in the picture.

The larvae of P. umbricola and Erebus odora living together on the monkey pod trees are what has been termed by Andrewartha and Birch (1954) as "nonpredators which require to share the same resources." The data indicate conclusively that the two species do not have their population peaks during the same periods. The result, however, is still as if they were together, jostling for an opportunity to eat the same leaf, the presence of one resulting in less food for the other. Indeed the data are fairly clear in pointing out that an increase in the numbers of P. umbricola is followed by a decrease in the E. odora population. Since each species forms part of the environment of the other, this sort of relationship may be analyzed in terms of "interspecific competition".

In the literature two types of competition have been mentioned concerning a requisite in short supply (Nicholson, 1954). In the "contest" type the requisite is composed of indivisible entities. Successful individuals can claim an entity which enables them to survive. Other individuals have no access to the requisite. In the "scramble" type, the requisite can be divided into many small parts and all competitors have access to at least one or more of these parts. The competition between _P_. _umbricola_ and _E_. _odora_, if it exists, can only be of the scramble type.

The influence of the activity of the parasites on the population fluctuations of _P_. _umbricola_ is quite interesting. The decrease in the numbers of _P_. _umbricola_ during the months from April to July 1963 seems to be due to the activity of the parasites. The fact that the incidence of the parasitism increased during those months indicates a close relationship between the two factors. The picture during December 1963 and January 1964 was quite different, but it appears that the decrease in the numbers of _P_. _umbricola_ at this time of the year was the direct result of cessation of tree growth. The parasites may be said to have played no part in this decrease in _P_. _umbricola_ population.

In conclusion, it may be said that the distribution and abundance of _P_. _umbricola_ is a result of the following interacting factors: 1) Old monkey pod trees with a large quantity of bark provide enough hiding places for large numbers of _P_. _umbricola_. In case an old tree is topped, the conditions become more favorable for the pest. 2) Precipitation and solar radiation affect the amount of new growth and time of onset of the growing period of the monkey pod trees. 3) The growth of monkey pod trees results in the production of abundant young foliage providing the pest with food. The population of the pest fluctuates, for the most part, with the amount of food available. 4) There seems to be a strong interaction between populations of _P_. _umbricola_ and _E_. _odora_. Lack of sufficient food for the two species may result in competition between them.

5) Fluctuations in the incidence of parasitism indicate that the seasonal abundance of *P. umbricola* is, to some extent, determined by the activities of its parasites.

SUMMARY

Studies on the biology and ecology of the noctuid moth, P. umbricola Boisd., were conducted in the laboratory and field during portions of 1962-64. This pest is a well-known serious defoliator of the monkey pod tree, Samanea saman (Jacq.) Merrill.

Laboratory studies on the life-history showed that the moth has six larval instars. The average durations of the stages of development were as follows: eggs, 3.5 ± 1.3 days and the first to sixth larval instars, 1.7 ± 0.8, 2.3 ± 0.6, 2.7 ± 0.8, 2.5 ± 0.7, 2.7 ± 0.6, and 5.3 ± 1.8 days, respectively. The duration of the egg to pupal stages was found to average 36.2 ± 8.3 days.

The various larval instars seem to differ markedly in their feeding behavior. The first instar larvae appear to feed only on the undersurface of the tender leaves leaving a thin membrane of the upper cell layers of the leaf. The older larvae consume leaves by making progressively larger semi-circular cuts on the edges of the leaves.

Both the larvae and the imagoes of P. umbricola are nocturnal in their activity. The decreasing light intensity in the evening appears to bring them into action. The larvae come out of their hiding places and crawl upward to the terminal twigs of the trees. The increasing light intensity early in the morning seems to induce the larvae to move down the trees and seek hiding places. The imagoes also exhibit nocturnal activity. They become active in the evening and inactive in the morning.

Experiments carried out to investigate their response to light showed that with the exception of first and second instar larvae all the larval stages and imagoes of *P. umbricola* are negatively phototactic.

Studies on oviposition showed that, on the average, 390 eggs were laid over a period of about 22 days. Oviposition started on the second day after emergence and was at a peak from the fourth to the twelfth day. Imagoes confined in glass gallon jars, on the whole, laid fewer eggs than those confined in larger metal cages.

Studies in the field indicated that there is a direct relationship between precipitation and temperature, and the growth of monkey pod trees.

There was found to be a close relationship between fresh growth on trees and the abundance of the pest. Fresh growth of the monkey pod trees started in early spring of 1963 and continued into the fall of the same year. The pest was most abundant during this period. In the month of January 1964 the trees were in a dormant state and the pest population declined significantly.

The association of the larvae of *P. umbricola* and the black witch moth, *Erebus odora*, is very interesting. Both occupy the same habitat and share the same resources. Increases in the populations of *P. umbricola* seemed to result in decreases in numbers of *E. odora*.

Field data indicated that in 1963 the parasites and predators of *P. umbricola* were most active during the months of April to June, and in 1964 they were active during March to June. It was noted that with an increase in percentage parasitism there was an immediate decrease in the pest population.

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