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Frass Production in Oak Forests in Southern Michigan

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FRASS PRODUCTION IN OAK FORESTS IN SOUTHERN MICHIGAN

by

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Production of frass (insect fecal material) was determined for five slightly different oak forest habitats in Allegan State Game Area, Allegan County, Michigan, for the 1968 growing season. Frass samples were collected on 30 or more 9 X 9 inch collecting surfaces in each of the study areas. It was found that 1.66 grams or 87.36 square inches of white oak leaf consumed was the equivalent of one gram of frass produced. This was determined from five muslin bags enclosing white oak branches and containing fifteen assorted insect larvae from four species believed to be responsible for most of the frass production on the study areas. Core samples were taken from white oak and black oak leaves to determine any differences in leaf weight at the time of consumption and after natural leaf fall. Frass production on an acre basis by weight and the maximum available energy to be transferred to the next trophic level ranged from 17,909 gms and 26,612 Kcal for the small oak area to 3,948 gms and 5,867 Kcal for the large pine area.

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INTRODUCTION

Frass-drop (the number of frass pellets falling to the ground) was first used as an index of both population numbers and insect damage by German forest entomologists Rhumbler (1929) and Gösswald (1935). Most studies using frass production as a measure of insect numbers or populations have relied simply on counting the number of frass pellets falling on a collecting surface. The size of the frass pellet varies between larval species, but for each larva the pellet size is proportional to the instar in which it was produced. The pellet size increases with each instar and the larva generally has six instars prior to pupation. In order for frass samples to be of maximum value for population estimation the following facts must be known: identity of the species, the developmental stage, information of the quantity of frass produced per individual per unit of time, and the proportion of the frass produced that falls to the ground and is collected in the sample (Southwood, 1966). Waldbauer (1964) has indicated that weight of frass is much more closely correlated than number of pellets with the amount of food consumed; consequently, weight is the primary measure of frass production used in this study.

Although frass is not a new term in the literature, very little research has utilized frass production to

project energy flow for various ecosystems. There have been only a few studies involving primary production in woodland environments (Ovington, 1965) and most of these studies relate to biomass and not energy flow at the herbivore level. The study presented is believed to be the first attempt to determine energy flow in forest ecosystems utilizing frass production.

In forest ecosystems there are many variables that cannot be controlled or even totally accounted for. This fact may have discouraged extensive research in this area. Lacking refined techniques, the estimates of energy flow presented here serve only to give an insight of their order of magnitude at the herbivore level.

The underlying purpose of this study is to provide a comparison between five slightly different oak forest habitats in terms of energy flow at the herbivore level.

DESCRIPTION OF THE STUDY AREAS

The five study areas are located in the Allegan State Game Area, Allegan County, Michigan, and are rectangular in shape with division lines and stakes at 200 (occasionally 100) foot intervals. The soil of this region has been derived from a former lake plain and glacial till. Oak-pine forest predominated until logging operations in the nineteenth centure removed most of the white pine (Pinus strobus). At present a community of second-growth white and black oaks (Quercus alba and Q. velutina) occupies the study areas.

The small pine area is located in the SW ¼ of Sect. 16, R 14 W, T 2 N, of Valley Township, Allegan County, Michigan, with an acreage of 14.7 acres. This area differs from the other study areas in possessing an understory layer composed of white pine planted in 1938.

The large pine area is located in the NE ¼ of Sect. 16, T 2 N, R 14 W, of Valley Township, Allegan County, Michigan, with an acreage of 9.6 acres. This area is unique in that there are a number of mature white pine trees in the canopy.

The large oak area is located in the NW ¼ of Sect. 30, T 2 N , R 14 W, of Valley Township, Allegan County, Michigan, with an acreage of 18.4 acres. This area is an oak forest that is rapidly approaching maturity and is

the most ecologically advanced of all the study areas.

The small oak area is located in the NW ¼ of Sect. 24, R 14 W, T 2 N, of Valley Township, Allegan County, Michigan, with an acreage of 16.5 acres. The forest of this area is denser and of generally smaller trees than that of the large oak area.

The greenbrier area is located in the NW ¼ of Sect. 25, R 15 W, T 2 N, of Valley Township, Allegan County, Michigan, with an acreage of 18.4 acres. It is a rather heterogeneous area, with some areas resembling the large oak area, some the small oak area, and also open areas. A ground layer of greenbrier (*Smilax hispida*) is present on most of the tract.

The canopy of all areas is composed mainly of white oak and black oak; white oak predominates among the smaller trees. Vegetational analysis of the area (Boyce, Brewer, Hodgson, Wenger and Mills, 1960, Unpublished Manuscript) revealed that minor tree and shrub species includes sassafras (*Sassafras albidum*), witch hazel (*Hamamelis virginiana*), hawthorn (*Crataegus* spp.), sour gum (*Nyssa sylvatica*), red maple (*Acer rubrum*), black cherry (*Prunus serotina*), large toothed aspen (*Populus grandidentata*), and shad-bush (*Amelanchier* sp.).

METHODS

Standard 9 X 9 inch floor tiles were chosen as a collecting surface for several reasons. They are available at a moderate cost in precise sizes. They are thin and have a flat surface without sides which would tend to trap a sample. Thick collecting surfaces would not have allowed as much of the sample to bounce or be blown on to the tiles as would have been lost by these processes. Their texture is a reasonable approximation of that of the forest floor. It is assumed that a free interchange took place between the tiles and the forest floor and that a given area of tile accurately measured frass accumulation on the same area of the forest floor.

Thirty standard 9 X 9 inch floor tiles were systematically placed five paces to the northwest of each stake in all the study areas with the exception of the small and large pine areas. Tiles in the small pine area were placed at 63 stakes at 100 foot intervals on this area and a 200 foot strip that forms the western boundary was not used. Frass samples collected from 63 tiles in the small pine area and 27 tiles in the large pine area were standardized to frass production for 30 tiles by appropriate conversion factors. Frass-drop samples were collected from the tiles by means of a 1" paint brush and swept into plastic bags. The collection period extends from May 25, 1968, through

June 24, 1968. Observation indicated that frass production outside these dates was negligible for all practical purposes. Samples were usually collected on Monday, Wednesday, and Friday from each of the study areas. When rain fell either on a collecting day or the day before, samples were collected after the tiles were dry from as many of the study areas as time permitted. A sample consisted of frass contaminated with twigs, sand, and plant down.

The samples were brought back to the laboratory and sorted with forceps until only frass remained. Volumetric measurements were taken using a 10 ml graduated centrifuge tube. Each sample was given the same treatment of 25 finger taps on the side of the tube before taking measurements. Before weighing, the samples were oven-dried for 24 hours at 95°C and then placed in a desiccator for 2 hours and allowed to cool to room temperature.

The cumulative weight of frass produced from each of the study areas provided a basis for comparison and were projected to give values in terms of acreage for each of the study areas. In addition, the projected values were utilized to give an index of energy flow at the herbivore level.

Included and handled in the same manner were samples taken from four muslin enclosures placed under field conditions for four days in May of 1969 and one enclosure for nine days in 1968. These were placed on areas adjacent

to the small oak area. A muslin enclosure was a bag 3 feet long supported by wire hoops roughly 20" in diameter. The muslin bag, open at both ends, was slid over a living white oak tree limb about five feet above the ground and 15 caterpillars and leaf miner larvae were placed inside the enclosure. The open ends of the bag were then tied securely to the tree limb. Leaves with consumed areas on them were first removed so that only whole intact leaves remained. White oaks were utilized because of the accessibility of intact leaves. Small black oaks in the understory were scarce and, on those present, too few leaves were left after removing those with consumed areas to support the 15 caterpillars and leaf miners. Malacosoma americanum was not included among those species placed inside the enclosure because this species had already undergone pupation.

After the prescribed period of time the tree limb was removed just above the muslin bag and brought to the laboratory where the leaves were removed and the frass and litter collected. By measuring the area consumed a correlation between leaf area consumed and weight of frass produced was established. The petioles were removed prior to taking measurements because they are not considered to be a palatable portion of the leaf (Bray, 1961). Measurements of total leaf area and area consumed in square inches were taken by placing each leaf under a piece of heavy gauge plastic and using a Bruning

areagraph (transparent plastic with randomly placed dots in known numbers). An areagraph of 97 per cent precision for areas over ten square inches was randomly placed over each leaf. Those dots more than half enclosed inside the leaf were counted. The total number of dots was then divided by one hundred to give leaf area in square inches. Leaves that had an area of five square inches or less were counted twice and an average taken. Measurements were made of consumed areas by placing each leaf over a piece of graph paper and counting the number of squares (100 squares per square inch) one half or more consumed. The results for each of the enclosed samples appears in appendices A through E.

Twenty-five leaf samples of white and black oak leaves were collected during the peak of caterpillar feeding in 1969, during the time that the muslin enclosures were in the field. These leaves were pressed and placed in a constant temperature room at 70°F and relative humidity 40 per cent. After four days, core samples were taken with a cork borer from each of the white oak leaves and the black oak leaves and weighed on a Mettler balance. In the same manner one hundred core samples totaling 26 sq. in. were taken from leaves of the same species collected in the fall of 1968 after dropping from the tree. This was done to determine any difference in weight between leaves taken during the

growing season and fallen leaves. Care was taken to take each core from the same area of the leaf which lacked coarse leaf veins so as not to bias the results.

Caterpillars and leaf miner larvae were collected in the field for placing in the enclosures and for identification. The larvae were reared to adults in order to make positive identification.

RESULTS AND DISCUSSION

INSECT SPECIES INVOLVED

Collections indicated that the larvae responsible for most of the foliage consumption were members of five species, four lepidopterans and one coleopteran. The specific insects involved are described in the following sections.

Bucculatrix *ainsliella* Murtfeldt

The larvae are ¼ inch long when full grown. The body is stout and there are five pairs of prolegs. *Bucculatrix* belongs to the family Lyonetiidae and is often referred to as the ribbed cocoon maker because the cocoon has silk threads in a regular pattern between longitudinal ridges and is attached longitudinally to a twig or the trunk (Forbes, 1920).

The adult beetle has a wing spread of 5/16 inch. The wings are narrow; hindwings have a broad fringe of hair. The forewings are brown or black with light markings. The hindwings are gray (Anderson, 1960).

The larva normally feeds on black oak; in an epidemic it will attack a variety of tree species. The eggs are deposited upon the leaves. The larvae bore directly into the leaf tissue at the point of attachment of the egg. The larvae then move to the upper layer of the parenchyma

and there tunnel out narrow serpentine tunnels. The tunnels are almost always filled with frass.

While the larvae continue to mine they are smooth, but when they emerge as external feeders they are rough and possess wart-like tubercles bearing hairs. Once emerged they eat away one cuticle and most of the soft interior tissue, leaving the cuticle on the under side of the leaf and the fibrovascular system intact. Before each molt, a special molting cocoon is spun. The cocoon has the form of more or less circular, flat webs spun upon the leaves, somewhat smaller in diameter than the length of the larva. In about a day the larvae emerge and feed in the following instar in the already described way. There is only one generation produced per growing season.

Bucculatrix is not considered to be a serious forest pest because defoliation of the tree occurs late in the summer when growth has already been produced.

Paleacrita vernata Peck

The caterpillars are about 3/4 to 1 inch long when full grown. The color varies from olive green to dark green or gray in advanced instars. *P. vernata* belongs to the family Geometridae and is commonly referred to as spring cankerworm and has only two pairs of prolegs.

The adult female moth is wingless, gray to black and approximately ½ inch long. The male is a slender brownish-gray moth with a wing spread of 5/8 to 1 1/5 inches. There are three irregular dark lines crossing the male's forewings (Anderson, 1960).

The spring cankerworm prefers the foliage of elm and basswood but will utilize the foliage of many other species of deciduous trees. The eggs are irregular masses of 50 deposited on the twigs, limbs, and trunks of the host tree. The larvae appear in late April or early May. At first the larvae eat small holes through the leaves; in advanced stages of maturity, they devour the whole leaf with the exception of the mid rib and some of the coarser veins.

The caterpillars have a long slender form and the habits of a measuring worm or looper. When it is not eating, the larva adheres only by its hindmost forelegs, extending the body from this point of support at an angle of about 45 degrees. It also has the habit of spinning down the tree at the end of a thread (Forbes, 1911).

About a month from hatching the larvae are full grown and leave the tree to pupate in the earth. Pupation takes place in the ground at a depth of two to five inches. The pupa remain in the ground and emerges as an adult sometime in April (one generation per year).

P. vernata frequently defoliates extensive areas of

a forest, but because epidemics usually last only a few years and because deciduous host trees seldom die as the result of the defoliations, spring cankerworms are not considered to be a major forest pest (Anderson, 1960).

Malacosoma americanum Fabricius

M. americanum belongs to the family Lasiocampidae and is referred to as the eastern tent caterpillar. The caterpillars are dark colored with a white stripe along the mid-back line bordered on both sides with orange. A small oval, blue spot lies within a larger black spot on the sides of each segment.

Pupation takes place inside cocoons placed in protected crevices or in rolled leaves.

The adult moths are moderately robust with a wing spread of 1 to 1 3/4 inches. They are tan to reddish tan in color with two thin parallel cross lines on the forewings. The hindwings are a uniform tan (Anderson, 1960).

The eggs are laid in masses of 100 to 300 and usually encircle a twig. Soon after hatching the larvae make a communal, silken tent in the crown of the host tree. The tent consists of numerous layers of dense sheets of silk webbing and contains excrement and numerous molted skins.

The caterpillars feed by consuming most of the leaf surface except the larger veins and petioles. If any host tree other than Prunus is utilized the larvae seldom

live to maturity. Host trees seldom die even after several annual defoliations. The major tree injury consist of retarded growth and sometimes the death of branches.

There is but one generation per year with the adult moths on the wing soon after mid-summer.

Archips argyrospilus Walker

A. argyrospilus belongs to the family Tortricidae and is commonly known as the apple leaf roller. The caterpillars are 3/4 to 1 inch long when full grown. The body is naked and pale green in color. The larvae have five pairs of prolegs.

Pupation takes place inside rolled leaves, usually with only one larva living in each rolled leaf.

The adult is small and is a bell-shaped moth with a wing spread of 1 to 1¼ inches. The forewings are irregularly mottled with a mixture of straw yellow, red-brown and often black-brown scales, having the appearance of a series of cream colored quadrate patches. The hindwing is mouse gray.

The eggs are laid in large masses on the upper leaf surfaces. After hatching the larvae feed by skeletonizing the leaves. The larva forms a tube or fold by rolling the leaf margin back or by fastening two or more adjacent leaves together. Skeletonizing takes place while the larvae live within the enclosed leaf spaces. One generation occurs per year.

Sparaganothis pettitiana

Cenopis pettitiana appears in the literature as a synonym. Common names are linden leaf roller and maple leaf roller. Both S. pettitianna and A. argyrospilus are members of the family Tortricidae and share similar life cycles and taxonomic characteristics.

Caterpillars are 3/4 to 1 inch long when fully grown The body is naked and dark green to almost brown or black with five pairs of prolegs.

The adult moth is small with a wing spread of 1 to 1¼ inches. The forewings are uniformly gray and bell-shaped when folded.

Field observation on this species indicate that S. pettitiana under epidemic conditions often feeds on the exposed leaf margins, leaving only the more coarse veins. This characteristic differs from that of A. argyrospilus which seldom leaves the shelter of the leaf roll to feed. Neither species is considered to be a major forest pest.

FRASS PRODUCTION

The average daily weight of frass produced was obtained by dividing the weight of each frass sample collected by the amount of time between collecting days (Table 1). The average daily weight of frass produced for the small pine area from May 31 to June 5 is cited as an example. By taking .3 gms collected on June 5 and dividing that weight

Table 1. The average weight of frass in grams per day from 30 9 X 9 inch collecting surfaces in each of the study areas during May and June 1968. Each entry is an average for the period from the day of entry to the preceeding entry.

	Small pine	Large pine	Large oak	Small oak	Green-brier
May 25					
26					
27	.00				
28					
29		.01	.01		.01
30					
31	.01	.03		.01	.06
June 1					
2					
3		.09	.07	.10	.12
4					
5	.06	.10	.36	.25	.21
6					
7	.39	.30	1.00	.66	.61
8					
9					
10					
11				.67	
12					
13	.30		.38	.65	.37
14		.02		.37	
15					
16					
17					
18					
19	.05	.04	.12	.06	.05
20					
21					
22					
23					
24	.01	.00	.00	.01	.01

by five (the number of days between collecting dates) the value of .06 gms is obtained. Production peaks occurred in each of the study areas in the vicinity of June 7, with the possible exception of the small oak area. The pattern shown by the small oak area may appear different because of more frequent sampling in that area. This area was the first to dry after a heavy dew or after a rain. Because intact samples could only be collected when the tiles were dry, some days did not allow enough time for samples to be collected from all study areas.

The peaks for frass production in the five study areas are further supported by peaks for the average volume of frass in milliliters per day (Table 2). Southwood (1966) reports that the relationship between weight and volume of frass collected is not necessarily parallel. As much as 30 per cent of the weight of the frass sample can be leached out by rain and weathering without any corresponding loss in volume. On this basis perhaps volume of frass collected from each of the study areas is a more valid standard for comparison than weight of frass from each study area.

Although some differences appear in correlating weight and volume, the peak in productivity by volume occurred on the same date as the peak by weight. Differences between weight and volume correlations become more apparent when accumulated weight and volume are compared

Table 2. The average volume of frass in milliliters per day from 30 9 X 9 inch collecting surfaces in each of the study areas during May and June 1968.

	Small pine	Large pine	Large oak	Small oak	Green-brier
May 25					
26					
27	.01				
28					
29		.08	.05		.05
30					
31	.03	.13		.06	.23
June 1					
2					
3		.19	.20	.33	.37
4					
5	.19	.67	.99	.70	.62
6					
7	1.05	.89	2.50	1.05	1.65
8					
9					
10					
11				1.43	
12					
13	.30		.95	1.35	.97
14		.33		.89	
15					
16					
17					
18					
19	.05	.10	.35	.14	.15
20					
21					
22					
23					
24	.01	.01	.06	.06	.04

Table 3. The cumulative weight of frass in grams collected from 30 9 X 9 inch collecting surfaces in each of the study areas during May and June 1968.

	Small pine	Large pine	Large oak	Small oak	Green-brier
May 25					
26					
27	.00				
28					
29		.07	.06		.05
30					
31	.03	.12		.10	.17
June 1					
2					
3		.38	.42	.40	.53
4					
5	.33	.59	1.14	.89	.94
6					
7	1.10	1.19	3.13	2.21	2.15
8					
9					
10					
11				4.90	
12					
13	2.92	1.33	5.32	6.20	4.34
14				6.57	
15					
16					
17					
18					
19	3.22	1.52	5.99	6.88	4.63
20					
21					
22					
23					
24	3.26	1.53	6.05	6.94	4.67
Total	3.26	1.53	6.05	6.94	4.67

Table 4. The cumulative volume of frass in milliliters collected from 30 9 X 9 inch collecting surfaces in each of the study areas during May and June 1968.

	Small pine	Large pine	Large oak	Small oak	Green-brier
May 25					
26					
27	.02				
28					
29		.33	.20		.20
30					
31	.12	.58		.40	.66
June 1					
2					
3		1.14	1.20	1.40	1.76
4					
5	1.07	2.47	3.17	2.80	3.00
6					
7	3.17	4.25	8.17	5.90	6.30
8					
9					
10					
11				11.59	
12					
13	6.99	6.25	13.87	14.29	12.10
14				15.18	
15					
16					
17					
18					
19	8.29	6.83	15.94	15.88	13.00
20					
21					
22					
23					
24	8.34	6.90	16.24	18.88	13.20
Total	8.34	6.90	16.24	18.88	13.20

for each study areas (Tables 3 and 4).

Although leaching has a potential weight loss of up to 30 per cent for frass samples, this rarely happens provided that the samples are collected from the field before extreme exposure occurs. However, minor differences did occur. Several factors may contribute to differences between weight and volume. When samples could not be collected from all study areas on the same day, some samples were left in the field and were exposed to weathering for a longer period of time than those samples that were collected. Smaller pellet size of the frass at the beginning of the study may have allowed earlier samples to pack down in the graduated centrifuge tube and give a smaller volume than larger pellets collected later in the study but having the same weight. This possibility is partially confirmed by the data. Frass collected during the last 10 days (June 13-24) had a volume of about 4.2 ml (3.2-6.2) per gm of frass whereas frass collected during the first 10 days (to June 5) had a volume of about 3.3 ml (2.8-4.2) per gm of frass. During the middle of the collecting period, when frass production was greatest the volume to weight ratio was, however, still lower, about 3.0 ml (2.2-5.1) per gm of frass. For the whole collecting period, the volume to weight ratio is 2.6-2.8 for all areas, except for the large pine area (Tables 3 and 4). The ratio for the large

pine area is 4.5. Further investigation would be necessary to explain why weight of frass in the large pine area has a disproportionately high volume as compared to the other study areas, but the difference is marked enough that some fairly important factor (such as a major difference in the composition of the caterpillar fauna) may be involved.

Ranking the data from Tables 3 and 4, the study areas in terms of frass production by weight and volume are as follows: small oak 6.94 gms, 18.88 ml; large oak 6.05 gms, 16.24 ml; greenbrier 4.67 gms, 13.20 ml; small pine 3.26 gms, 8.34 ml; and large pine 1.53 gms, 6.90 ml. Several obvious vegetational traits for each of the study areas, such as tree density, density in various size classes, and numbers of white oak and black oak did not reveal a simple relationship between frass production and vegetation present on each study area. Perhaps closer scrutiny of the study areas on the basis of palatable tree and shrub species present would give an insight to the difference in frass production. Palatable species as judged by per cent consumption was determined by Wenger (1969, unpublished manuscript) for the large oak area. His findings were: black oak 16.99 per cent consumed, white oak 13.13 per cent, flowering dogwood 4.72 per cent, and miscellaneous species 8.58 per cent.

The immediate cause for differences in frass production among the five areas must be a difference in insect numbers or populations present on each area unless factors that affect the rate of frass production affected one area differently than another. Local climatic factors cannot be ruled out, but have not been studied in detail. The only other factor that would seem to have this characteristic is that of the presence of parasites or carnivorous groups utilizing the caterpillars. The study was conducted during the peak of nesting activity for many species of birds. Caterpillars make up the bulk of food items fed to the nestlings of most birds nesting in these forests (R. Brewer, personal communication). Adult birds were seen foraging on caterpillars.

Another variable that must be accounted for is the proportion of the frass produced that actually reaches the ground and is collected. A greater proportion of the frass produced will be retained on the foliage on a calm day than more windy conditions. Such things as the topography of the area and the presence of a dense understory vs. a sparse understory would influence the amount of actual frass produced reaching the collecting surfaces. The only area for which an obvious bias might be produced in this way is the small pine area with its dense white pine understory.

From the data obtained from 30 9 X 9 inch floor tiles, values were projected for frass production in terms of weight and volume per acre (Table 5). The conversion factor used to put frass production on an acre basis is (X gms of frass produced) (43,560 sq. ft.)/16.88 sq. ft.

RELATED DATA

Gere (1956) related frass weight to weight of food consumed for various stages of the larval development of the lepidopteran larvae Hyphantria cunea Drury. Gere divides larval development into three time periods or growth phases. The first period began at the 2nd day after hatching and terminated with the second molt which corresponds to the 14th day. The second period began on the 15th day and terminated on the 24th day or fourth molt. The final or third period began on the 25th day and terminated on the 32th day at which time all of the larvae had begun pupation and were no longer feeding.

The first period begins with the second day because this is the time when the newly hatched larvae first begin to feed on the host plant, box-elder, Acer negundo. The study was conducted over a three-year time period with experiments consisting of a group of ten caterpillars for each experiment.

Table 5. Projected values from the data obtained from 30 9 X 9 inch collecting surfaces in each of the study areas during May and June 1968.

	Small pine	Large pine	Large oak	Small oak	Green-brier
Total frass ml/acre	21,522	17,806	41,908	48,721	34,064
Total frass gms/acre	8,413	3,948	15,612	17,909	12,051

Frass production during the first period accounts for 51.4 per cent of the food ingested by weight. Another 33.4 per cent was expended in maintenance of body processes. The remainder or 15.2 per cent was exhibited in the form of gained body weight. The assimilation of a relatively large portion of the food ingested for body weight was at the expense of high energy loss.

In the second period frass production accounts for 70 per cent of the food ingested by weight. Another 8.3 per cent is lost in maintenance of body processes. Gain in body weight constitutes 27.7 per cent of the food ingested. During this period the most rapid weight gain occurs so that the caterpillar weighs 22 times as much at the end of the second period as at the end of the first period. Fifteen times as much food was consumed in the second period as compared to the first period, but a larger amount of the food consumed contributes to gain in body weight. The weight of frass in the second period was 20.5 times the weight of frass produced in the first period.

In the third and final period 64.1 per cent of the food ingested by weight constitutes frass production; 26.5 per cent for maintenance of body processes; and 9.4 per cent to gain in body weight. At the end of the third period gain in body weight is 2.6 times greater

than at the end of the second period. Frass production during the third period is 3.8 times more than in the second period and food consumption is 4 times greater in the third period.

Waldbauer (1964) using the tobacco hornworm, Protoparce sexta Johan, found similar values for the correlation between the mean dry weight of food consumed and the mean dry weight of frass produced. Tobacco hornworms in their fourth instar of development and fed on a variety of foods were used. His finding for frass weight ranged from 44.2 per cent to 68.1 per cent of food weight.

In Gere's discussion frass production peaks only at pupation and production increases with each period of growth until the larvae are no longer foraging. Table 1 may appear as a direct contradiction to the trends that Gere establishes with H. cunea. However, one must keep in mind that Gere is working with a single species under controlled labratory conditions. It is my belief that any one insect species in this study follows the trend established with H. cunea. But by dealing with five species of larvae under field conditions a false peak results by combining frass production from all five species. It is more likely that all five species did not begin to produce frass on May 27 and terminate production on June 24, but rather that all five species

were producing frass only during part of this time interval. If two or three species began frass production nearly at the same time and were later joined by the remaining species, a peak would develop when one or more species began to terminate production and undergo pupation. A decline in total frass production would result, but production would not halt for the remaining species. Individual variation in hatching time within a single species may also be involved.

Perhaps Malacosoma americanum should not have been included as a frass-producing species in this study, because at the time the study was conducted the larvae had stopped feeding and were actively searching for sites to undergo pupation. Also the larvae rarely if ever fed on Quercus species. M. americanum is mentioned because the larvae may have contributed to frass production during the first few days of this study.

LEAF CONSUMPTION

From the data of the four muslin enclosures the relationship between leaf area consumed and the weight and volume of frass produced was established (Table 6). The data from enclosure B deviates from the other samples to the extent that it biases the results. For this reason 165.54 square inches of leaf area consumed for every one gram of frass produced is not used to project values of total leaf area consumed for the total amount of frass collected in each of the study areas. By omitting the data of enclosure B, a mean of 87.93 square inches per one gram of frass produced is obtained. This value is in agreement with 87.36 square inches per one gram of frass produced obtained by dividing mean frass weight into mean area consumed. Also the median of the five samples falls in this general range. All calculations for projected values of leaf area consumed for total frass produced by the acre for each of the study areas is based on 87.36 square inches (Table 7). By the same criteria 31.36 square inches per one milliliter of frass produced is used for projected volumetric values.

Table 6. Data from four, four-day muslin enclosures from May 1969 and one nine-day enclosure from May 1968; enclosing portions of white oak limbs and containing fifteen assorted larvae from four insect species.

	Total leaf area (square inches)	Total area consumed (square inches)	Frass (gms)	Frass (ml)	No. of square inches consumed per gm of frass	No. of square inches consumed per ml of frass
Enclosure A	77.34	8.92	.18	.60	49.56	14.87
Enclosure B	182.33	4.76	.01	.05	476.00	95.20
Enclosure C	187.30	22.19	.23	.50	96.48	44.38
Enclosure D	326.64	17.20	.19	.50	90.53	34.40
Enclosure E *	366.93	8.06	.07	.30	115.14	26.87
Average	228.11	12.23	.14	.39	165.54	43.14

* Nine-day sample

Table 7. Projected values of leaf consumption for the total amount of frass produced by weight and volume in square inches per acre of leaf area consumed for each of the study areas in May and June 1968.

	Square inches consumed projected from gms/acre	Square inches consumed projected from ml/acre
Small pine	734,926	674,928
Large pine	344,921	558,394
Large oak	1,363,903	1,314,249
Small oak	1,564,543	1,527,895
Green-brier	1,052,798	1,068,232

LEAF WEIGHT

Core samples were taken from twenty-five white and black oak leaves collected during the peak of caterpillar feeding activity and from the same species collected after natural fall to correlate frass weight with leaf weight. Core samples were also used to determine if significant weight differences existed between leaf weight at the time of consumption and leaf weight after natural fall.

The following results were obtained from the core samples (each 26 square inches) and serve as the basis for projecting values of leaf weight for leaf area consumed per acre for each of the study areas: white oak at the time of consumption .50 gms; white oak after natural fall 1.05 gms; black oak at the time of consumption .82 gms; and black oak after natural fall 1.35 gms.

It is apparent that differences exist between leaf weight at the time of consumption and leaf weight after natural fall. Presumably the oak leaves lignify and gain weight by the end of the growing season. Projected caloric values based on leaf weight will vary extremely depending on the leaf weight used in calculating projected values.

From the data of the enclosure samples, 87.36 square

inches is the equivalent of one gram of frass based on white oak samples. Using 87.36 square inches the percentage of one gram of leaf that was expended as frass can be calculated. White oak leaves at the time of consumption weighed .019 gms per square inch (.05 gms for 26 square inches). Consequently, 1.66 gms of leaf (87.36 x .019) were consumed for each gram of frass produced. Frass weight as a percentage of leaf weight consumed, accordingly, was 60.2 per cent. In the same manner the percentage of leaf by weight to be expended as frass was calculated for white oak after natural fall as 28.7 per cent, black oak at consumption, 35.7 per cent; and black oak after natural fall, 22.0 per cent.

The weight of white oak leaves per gram at the time of consumption was used to project energy flow in kilo-calories per acre. The weight of white oak leaves per gram tends to be an average for black oak, flowering dogwood, red maple, witch hazel, and other miscellaneous species both by the percentage of utilization (Wenger, 1967 unpublished manuscript) and leaf weight per gram of each of the species. The value of 60.2 per cent of white oak leaf weight to be expended as frass is in agreement with Gere's figures of 51.43 per cent in the first period, 69.98 per cent in the second period, and 64.11 per cent in the third period.

From Gere's research the values for the percentage

food intake by weight to be subdivided into frass, respiration, and the production of new protoplasm may be used to establish limits in terms of energy flow for this study.

ENERGY FLOW

Gere's work with Hyphantria cunea indicated that the first period 51.43 per cent of the gross intake by weight becomes frass and 15.14 per cent becomes new protoplasm. In the second period 69.98 per cent of the gross intake becomes frass and 21.75 per cent becomes new protoplasm. In the third and final period 64.11 per cent of the gross intake becomes frass and 9.44 per cent becomes new protoplasm. Using Gere's extreme values, a range of energy intake and of production of new protoplasm can be established for the five study areas.

Calculations for the upper limit for the small pine area are shown as an illustration:

$$\frac{8{,}413 \text{ gms of frass per acre}}{X \text{ total gms consumed}} \qquad \frac{69.98\% \text{ frass by weight in the second period}}{100\% \text{ gross intake}}$$

The total gms of leaf consumed to give 8,413 gms of frass is 12,022. This value is multiplied by 4.781 kilocalories per gm to give kilocalories per acre or 57,475 kilocalories. The conversion factor of 4.781 kilocalories per gm of oven dried material for Quercus

species, was established by Ovington and Heitkamp (1960). The figure 57,475 kilocalories per acre is the total energy consumed and is multiplied by 21.75 per cent to give the value in terms of new protoplasm produced or energy potentially available to be transferred to the next trophic level. That value is 12,501 kilocalories per acre. This value is an estimate of net production for the frass-producing consumer of foliage. The upper limits for energy in Kcal/acre available for the next trophic level range from 26,612 to 5,867 in the five study areas, while the lower limits range from 15,716 to 3,465 (Table 8).

Boyce (1969) arrived at caloric values for the large oak study area by sampling leaf consumption in the following manner. Twenty-five hardware cloth squares were randomly placed at twenty-five stakes(out of thirty) which divide the area into 200 square foot sections. After autumn leaf drop, the leaves covering the squares were collected. Leaves more than half off were rejected and the samples were dried over a plant drier and stored at a constant temperature of 70° F and approximately 40 per cent relative humidity. The number of leaves per species and the weight was determined. From this data a total leaf weight per acre of 1,251.81 kg was projected with an average of 1,416.79 kg per acre over a three-year period (1966-1968). Using Ovington's and Heitkamp's value of 4.781 kilocalories for each gram

of <u>Quercus</u> species, 1,251.81 kg becomes 5,983,470 kilocalories per acre. The three-year average is 6,740,356 kilocalories per acre.

A smaller sample of one hundred leaves was then randomly chosen to measure for leaf consumption. Measurement of leaf area was done with a plane polarizing planimeter. Where actual leaf margins were absent theoretical margins were drawn on a heavy guage plastic sheet covering the leaf. Consumed areas were measured by using graph paper (100 squares per square inch) under the plastic sheet, and counting all squares one half or more within the traced outline of the consumed area. The projected value for total leaf consumption per acre from this sample for all species of leaves was 261.78 kg per acre for 1968 and an average of 241.67 kg per acre for 1967 and 1968 (Table 8). When kilograms consumed per acre was converted to caloric values 1,251,568 kilocalories for 1968 and an average of 1,175,552 kilocalories consumed per acre was obtained.

The value of 145,131 kilocalories per acre consumed was computed for the large oak area from the weight of frass collected and Gere's percentages for food utilization by weight (Table 8). Boyce's estimate of energy flow for the white oak per acre would have been 72,480.41 kilocalories per acre instead of 160,211 kilocalories (Table 9), had he used a leaf weight of

Table 8. The upper and lower limits of energy flow in kilocalories per acre that is available to be passed on to the next trophic level and the projected leaf consumption in kilocalories per acre for each of the study areas during May and June 1968.

	Small pine	Large pine	Large oak	Small oak	Green-brier
Upper limits (Kcal/acre)	12,501	5,867	23,199	26,612	17,908
Total leaf consumption for upper limits (Kcal/acre)	78,208	36,701	145,131	166,484	112,028
Lower limits (Kcal/acre)	7,383	3,465	13,700	15,716	10,575
Total leaf consumption for lower limits (Kcal/acre)	57,477	26,973	106,660	122,353	82,332

Table 9. Leaf weight consumed per acre and energy utilized per acre per species include Sassafras albidum, Hamamelis virginiana, Crataegus sp., Nyssa sylvatica, and Amelanchier sp. when present from Boyce (1969).

	Q. velutina	Q. alba	C. florida	Acer rubrum	Misc. spp.	Total
Leaf wt. consumed per acre (kg)						
1966	201.86	39.91	1.21	0.30	1.00	244.28
1967	185.85	27.39	3.18	-	-	216.42
1968	221.15	33.51	3.20	0.98	2.94	261.78
Average	202.95	33.60	2.53	0.64	1.97	241.69
Energy consumed per acre (kcal)						
1966	965,093	190,810	5,785	1,434	4,781	1,167,903
1967	88.549	130,952	15,204	-	-	1,034,705
1968	1,057,318	160.211	15,299	4,685	14,056	1,251,569
Average	980,320	170,658	12,096	3,060	9,418	1,175,552

.019 grams per square inch (that is, the weight of the leaves for white oak at the time of consumption rather than a higher value after leaf fall). In the same manner, if .031 grams per square inch was used for black oak leaf weight, 544,986.19 kilocalories per acre would have been obtained instead of 1,057,318 kilocalories. When Boyce's values for energy flow in kilocalories for red maple, flowering dogwood, and miscellaneous species are summed with 72,480 and 544,986, his projection for the large oak area becomes 907,912 kilocalories per acre as compared with the 145,131 kilocalories estimated in this study based on the amount of frass collected, and Gere's results. Caloric values for red maple, flowering dogwood, and miscellaneous species are not corrected values, because leaf weight per gram at the time of consumption for these species was not determined.

Being based on leaf weight after natural fall, Boyce's values for energy flow in the large oak area are overestimated. However, as can be seen, using leaf weight from naturally fallen leaves does not account for the total difference between the two estimates. Some possibilities come to mind that may help to account for part of the difference. A sample size of one hundred leaves may not have been adequate to make projections when there were several species present and the percentage

of utilization of each tree or shrub species by the caterpillars and leaf miner larvae was different for each leaf species. The question arises as to whether a hole eaten in the leaf by the larva in the early spring remains the same size or does the hole continue to grow larger as the leaf grows larger, consequently giving larger values for leaf consumption when energy flow is based on the area consumed after the autumn leaf fall. Also it was not determined if additional leaf consumption took place after June 24 by other insect larvae. If this occurred energy flow would be underestimated in the present study.

While Boyce tends to overestimate energy flow, any factors preventing frass from reaching or remaining on the tiles, and weight loss due to exposure before the samples were collected would tend to make estimates of energy flow based on frass production lower than it actually was. Since an average leaf weight per gram for palatable leaf species at the time of consumption was not determined, the weight of white oak leaves per gram used in projecting energy flow may not have been an average leaf weight for palatable leaf species but rather below average.

THE SIGNIFICANCE OF ENERGY FLOW AS RELATED TO THIS STUDY

The insight of energy flow at the herbivore level gained through this study projects the possible limits

for potential protoplasm in caloric terms that is available in each oak forest habitat to be transferred to higher trophic levels, in this case primarily birds. Energy flow may then be reflected by the density of the birds population and also the average size of the territory per species. Studies on these problems are being carried out by other personnel.

BIOENERGETICS

In a related study by Varley (1967) energy flow was determined for the winter moth Operophtera brumata. This species feeds on Quercus robur and has a single generation per year with five larval stages. Varley reports a gross caloric intake of 56,480 calories per square meter (228,575 Kcal/acre) with 7,480 calories per square meter available to be passed on to the next trophic level (30,272 Kcal/acre).

Wiegert and Evans (1964) report caloric values for a population of grasshoppers in a 30-year-old grassland in southern Michigan. Secondary production available to the next trophic level was .51 Kcal/M^2 (2,064 Kcal/acre) and a total caloric intake of 3.71 Kcal/M^2 (15,014 Kcal/acre). Spittlebugs in the same grassland had a total caloric intake of 1.51 Kcal/M^2 (6,111 Kcal/acre) and a net production of .08 Kcal/M^2 (324 Kcal/acre).

Wiegert and Evans also report caloric values for

the grasshopper *Orchelimum fidicinium* and a leafhopper *Prokelesia marginata* in a coastal Georgia salt marsh. For *P. marginata* there was a total intake of 413 Kcal/M^2 (1,671,411 Kcal/acre) and 70 Kcal/M^2 was available to be passed on to the next trophic level (283,290 Kcal/acre). For *O. fidicinium* the total caloric intake was 107 Kcal/M^2 (433,029 Kcal/acre) and 11 Kcal/M^2 was available to be passed on to the next trophic level (44,517 Kcal/acre).

The estimates of energy flow for the five study areas are generally higher than for most other ecosystems at the invertebrate herbivore level. This is perhaps to be expected considering the biomass per unit area available to support herbivore populations. Agreement with the study by Varley (1967) on English oak woods is fairly close. The only invertebrates that would tend to be exceptions are those species that have more than one generation per year and/or those species that feed both as larva and adults.

SUMMARY

Frass production was studied in five slightly different oak forest habitats in southwestern Michigan during May and June 1968. The data obtained from frass production were used to project values of energy flow at the herbivore level. Five species of insect larvae were believed to be responsible for most of the frass production. Those species were Bucculatrix ainsliella, Paleacrita vernata, Malacosoma americanum, Archips argyrospilus, and Sparaganothis pettitana.

Frass was collected from 9 X 9 inch collecting surfaces in each of the five study areas. The weight and volume of frass collected was projected on an acre basis for the small pine area as 21,522 ml and 8,413 gms, for the large pine area 17,806 ml and 3,948 gms, for the large oak area 41,908 ml and 15,612 gms, for the small oak area 48,721 ml and 17,909 gms, and for the greenbrier area 34,064 ml and 12,051 gms.

One hundred core samples were taken from white oak and black oak leaves to determine leaf weight in relation to leaf area at the time of consumption and after natural fall. Leaf weight per square inch was as follows: white oak at the time of consumption .019 gms, white oak after natural fall .040 gms, black oak at the time of consumption .32 gms, and black oak after natural fall .052 gms.

Four muslin bag enclosures containing fifteen larvae were placed on white oak limbs in the field. From the leaf area consumed and frass produced it was determined that 87.36 square inches of leaf area was the equivalent of one gram of frass produced. Based on the weight of white oak leaves at the time of consumption, 1.66 grams of leaf were consumed for every gram of frass produced. The percentage of leaf weight per gram to be expended as frass was 60.24 per cent.

Probable upper and lower limits for secondary production or energy available to be transferred to the next trophic level was projected in kilocalories per acre for the small pine area as 12,501 and 7,383, for the large pine area 5,867 and 3,465, for the large oak area 23,199 and 13,700, for the small oak area 26,612 and 15,716, and for the greenbrier area 17,908 and 10,575.

Appendix A Leaf consumption data from a four-day muslin bag enclosure containing 15 caterpillars and leaf miner larvae. The tree species is _Quercus_ _alba_.

	Leaf area (in.^{2})	Area consumed (in.^{2})
	.82	.00
	2.62	.08
	5.11	.16
	4.85	.00
	2.93	.00
	5.36	.00
	2.27	.00
	4.72	1.79
	2.76	.37
	3.72	.00
	6.66	.91
	7.70	2.79
	5.58	.16
	3.96	.56
	3.40	.43
	5.72	.00
	3.20	.93
	2.98	.47
	2.98	.27
Total	77.34	8.92
Average	4.07	.47

Appendix B Leaf consumption data from a four-day muslin bag enclosure containing 15 caterpillars and leaf miner larvae. The tree species is *Quercus alba*.

	Leaf area (in.^{2})	Area consumed (in.^{2})	Leaf area (in.^{2})	Area consumed (in.^{2})
	5.08	.33	2.15	.00
	6.00	.00	6.58	.00
	6.85	.00	7.69	.06
	5.66	.00	10.85	.02
	6.83	.01	4.09	.00
	2.80	.00	3.74	3.25
	2.87	.18		
	.57	.00		
	2.93	.10		
	1.16	.00		
	.74	.00		
	2.86	.00		
	7.09	.05		
	6.27	.12		
	2.62	.00		
	3.33	.00		
	3.16	.00		
	3.74	.00		
	6.96	.00		
	7.74	.10		
	3.12	.00		
	7.48	.00		
	10.43	.00		
	4.52	.12		
	8.21	.00		
	9.36	.00		
	5.31	.00		
	2.38	.00		
	5.04	.00		
	.93	.02		
	2.96	.00		
	2.23	.32		
Total			182.33	4.76
Average			4.80	.13

Appendix C Leaf consumption data from a four-day muslin bag enclosure containing 15 caterpillars and leaf miner larvae. The tree species is <u>Quercus alba</u>.

	Leaf area (in.^{2})	Area consumed (in.^{2})	Leaf area (in.^{2})	Area consumed (in.^{2})
	6.02	.00	5.12	1.04
	3.30	.00	2.85	.41
	8.21	1.04	1.37	.38
	5.24	.00	1.97	1.46
	1.90	.00	1.41	.22
	3.71	.70	3.75	3.63
	5.76	.00	3.37	3.16
	12.55	.75		
	10.73	3.22		
	11.89	.00		
	10.98	.72		
	7.18	.00		
	1.23	.00		
	.97	.01		
	8.72	.00		
	6.97	.08		
	1.69	.58		
	2.82	.00		
	4.91	.36		
	3.69	1.42		
	5.44	.00		
	5.25	.00		
	3.61	.00		
	1.82	.00		
	5.57	.02		
	3.20	.23		
	5.66	.55		
	5.92	1.02		
	2.60	.02		
	3.33	.02		
	3.55	1.09		
	3.04	.06		
Total			187.30	22.19
Average			4.80	.57

Appendix D Leaf consumption data from a four-day muslin bag enclosure containing 15 caterpillars and leaf miner larvae. The tree species is <u>Quercus alba</u>.

	Leaf area (in.^{2})	Area consumed (in.^{2})	Leaf area (in.^{2})	Area consumed (in.^{2})
	8.50	.12	6.12	.78
	3.52	.19	3.18	1.02
	10.76	.01	1.98	1.60
	2.06	.00	6.62	.00
	1.47	.01	7.33	.35
	.27	.00	3.13	.00
	6.34	.00	2.21	.05
	6.91	.31	4.67	.00
	7.13	.00	6.03	.97
	2.07	.00	4.37	.00
	8.26	.00	8.85	.03
	3.95	.00	4.59	.00
	3.98	.04	7.30	.78
	4.20	.00	4.33	.10
	9.91	.00	6.97	.41
	10.39	.21	7.15	.00
	12.50	3.62	5.70	.00
	10.12	.61	5.32	.02
	8.06	.00	3.57	.13
	11.35	.43	4.29	.27
	4.46	.89	4.93	.00
	2.79	.16	4.59	.05
	1.38	.03	3.74	.12
	2.98	.00	2.40	.00
	.26	.00	3.26	.00
	1.38	1.34	5.84	.15
	1.92	.15	5.92	.02
	9.51	.00	5.47	.00
	6.61	.00	3.53	.61
	13.01	.60		
	5.05	.40		
	2.15	.62		
Total			326.64	17.20
Average			5.35	.28

Appendix E Leaf consumption data from a nine-day muslin bag enclosure containing 15 caterpillars and leaf miner larvae. The tree species is <u>Quercus alba</u>.

	Leaf area (in.^{2})	Area consumed (in.^{2})	Leaf area (in.^{2})	Area consumed (in.^{2})
	4.54	.05	12.69	1.19
	5.62	.04	4.31	.04
	6.24	.34	1.90	.00
	1.94	.00	2.13	.00
	8.34	.28	3.70	.00
	7.57	.09	3.53	.02
	2.68	.54	9.37	.01
	5.94	.05	1.73	.00
	8.39	.00	7.29	.00
	3.20	.34	4.13	.39
	2.05	.00	6.85	.10
	5.15	.05	7.23	.01
	6.77	.57	1.60	.00
	1.36	.00	8.99	.02
	6.34	.00	9.81	.90
	4.49	.18	6.07	.02
	4.80	.02	4.63	.18
	3.94	.00	7.97	.16
	7.30	.01	8.68	.09
	5.05	.05	4.31	.00
	4.18	.00	3.94	.00
	5.71	.95	5.83	.00
	11.62	.04	6.18	.02
	3.02	.00	5.41	.22
	3.50	.01	10.82	.11
	1.59	.05	6.02	.00
	6.08	.00	11.47	.19
	7.83	.00	2.79	.19
	6.31	.01	10.39	.10
	3.28	.06	6.86	.32
	2.61	.00	4.93	.04
	2.42	.00	2.08	.00
	8.11	.01	5.32	.00
Total			366.93	8.06
Average			5.56	.12

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