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Foliage Production and Consumption in an Oak Forest

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FOLIAGE PRODUCTION AND CONSUMPTION IN AN OAK FOREST

by

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INTRODUCTION

Processes concerning primary production and energy transfer between trophic levels have long been recognized as being important in the consideration of forest ecosystems. There have, nevertheless, been only a few studies involving primary production in woodland environments (Ovington, 1965), and most of these studies relate to non-leaf portions of the plant materials. Since leaf materials represent the main food source available to primary consumers (Bray, 1961) an understanding of the use of energy present in primary forest production must necessarily include a consideration of foliar as well as woody materials (Bray and Gorham, 1964). Information relating to litter production is directly applicable to research concerning soil formation, populations of fungal decomposers and insectivorous herbivores and is indirectly related to the maintenance of consumers in subsequent trophic levels.

Although estimates of leaf production can be derived from measurements of stem wood production, direct measurement of foliage is probably more reliable (Whittaker, 1966). Perhaps the most systematic technique for gathering leaf materials for biomass determination involves collecting falling leaves in, or on, receptacles distributed throughout a study area (Traczyk, 1967). Techniques for determining leaf areas and areas consumed range from visual observations to the use of graph paper planimeters (Bray, 1961). Data concerning amounts of energy equivalent to

given weights of plant material have been determined by bomb calorimetry (Ovington and Heitkamp, 1960; Crossley, 1966).

This study involves the determination of leaf production and primary consumption in an oak forest community in southern Michigan during the 1966 and 1968 seasons and is similar to work done by Bray (1961, 1964) on three forest stands in southern Ontario.

DESCRIPTION OF THE STUDY AREA

The 18.4-acre study area is located in the W ½ of the NW ¼ of Sect. 30, R 14 W, T 2 N, of Valley Township, Allegan County, Michigan, and is rectangular in shape (800 x 1000 ft.) with division lines and stakes at 200 foot intervals. Much of this portion of what is now the Allegan State Game Area is a former lake plain and was once occupied by oak-pine forest. In the 1880's logging resulted in the removal of most of the white pine (*Pinus strobus*) thus making the well-drained, sandy soil available for the present community of second-growth white and black oaks (Kenoyer, 1934).

Vegetational analysis of the area by the point-centered quarter method (Cottam and Curtis, 1956) indicated values of 122 and 283 trees per acre for individuals of at least five inches dbh and 1.5-4.99 inches dbh respectively (Boyce, 1969). The canopy is composed mainly of black oaks (*Quercus velutina*) which number 88 trees per acre and have a basal area of 77.3 square feet per acre (Table 1). White oaks (*Quercus alba*) predominate among the smaller trees with 212 individuals per acre, or approximately 8.8 square feet per acre basal area. Small black oaks and flowering dogwoods (*Cornus florida*) are nearly equal in abundance with 21 and 24 trees per acre respectively. Minor tree and shrub species not necessarily encountered during point-centered quarter analysis include sassafras (*Sassafras albidum*), witch hazel (*Hamamelis virginiana*), hawthorn (*Crataegus* spp.), sour gum (*Nyssa sylvatica*), red maple (*Acer rubrum*),

Table 1. Tree composition of the study plot based on point-centered quarter analysis (Boyce, 1969). In instances where trees of one species were encountered in each size class, Sm. indicates trees 1.5-4.99 inches dbh whereas Lg. denotes trees at least 5.0 inches dbh. Misc. species include Pinus strobus, Sassafras albidum, and Prunus serotina. Data are based on 30 sampling points.

	Quercus velutina		Quercus alba		Cornus florida	Acer rubrum	Misc. spp.
	Sm.	Lg.	Sm.	Lg.			
Trees per acre	21	88	212	34	24	13	14
Average diameter (in.)	2.9	11.9	2.6	9.5	2.5	2.9	2.4
Basal area per acre (sq. ft.)	1.1	77.3	8.8	20.7	.88	.60	.53
Frequency	.1	.9	.96	.7	.3	.07	.16
Relative Frequency (%)	6.3	56.2	60.4	43.8	18.9	4.4	10.1
Relative Density (%)	7.5	72.5	75.0	27.5	10.0	1.7	5.8
Relative Dominance (%)	9.2	79.2	72.9	20.8	8.6	4.6	4.8
Importance Value	23.0	208	208	92	38	11	21

black cherry (*Prunus serotina*), and shad-bush (*Amelanchier* sp.). Important members of the ground flora on the plot include species of *Carex*, *Vaccinium*, *Smilacina*, *Gaultheria*, *Rubus*, *Solidago*, *Desmodium*, and *Ceanothus* which together totaled 104,000 stems per acre (Hodgson, 1969). *Desmodium* sp., tick-trefoil, *Ceanothus americanus*, New Jersey tea, and *Smilax rotundifolia*, greenbrier, were the ground flora species encountered in leaf samples.

METHODS

Random samples of litter material provide one method of determining leaf production and consumption. From such samples total leaf area and area consumed per leaf can be estimated. Based on the number of leaves per species collected, the number of leaves per acre can be projected. These projected values, along with total leaf areas, make possible estimations of total energy per acre in the form of leaf material available to primary consumers. Similarly, from total areas consumed per leaf, energy consumed per acre can also be determined.

Assuming that import and export of leaves balance, which should be the case except near the edge of a forest, then the number of leaves per unit area on the forest floor should, on the average, equal the number of leaves in a column of the same cross-sectional area projected through the canopy in the growing season. A sample of relatively small total area can be used to project values for the entire plot because of the integrating effect produced in leaf fall. The resultant pattern is an expanding cone shape with a ground area considerably larger than the mean area per tree. This mixing of leaves is increased by the presence of wind.

Leaf samples were obtained from litter which had fallen on squares of hardware cloth placed throughout the plot. Mesh squares were used so as to provide conditions as similar to the forest floor as possible. Collecting devices with sides were not utilized

because the sides tend to trap leaves thus preventing a true integrating effect and in addition artificially reject leaves partially on the squares. Squares were placed in close proximity to 25 stakes (randomly chosen from the total of 30) which divided the area into 200 foot sections (see Figure 3). Orientation with reference to the stakes was determined randomly and was uniform for all squares except where such orientation would place the square outside the plot boundaries. In 1968 the majority of squares were placed six paces northeast of the stakes; however, squares at points B-6, C-6, and D-6 were six paces southeast, E-6 six paces southwest, and E-1 six paces northwest to keep them within the boundaries. Generally similar procedures were employed in 1966 and 1967.

Squares were put out in the early fall prior to leaf abscission (August 25, 1966, September 2, 1967, and early September 1968) and were collected after most leaves had fallen (November 11, 1966, November 22, 1967, and December 6, 1968). Gathering squares required the work of several persons and was facilitated by bright paint markings placed on nearby twigs or saplings at the time the squares were distributed. Determining the exact boundaries of the mesh was accomplished by pressing lightly on the litter surface. In most instances the differential resistance between litter subtended by mesh and that standing alone was sufficient for these determinations. Once boundaries had been ascertained the collector placed a ten-inch-square piece of plywood, equipped with a handle,

over the litter and mesh while sliding a hand under the mesh. This technique allowed the collector to lift the litter sample intact. At this point a second individual removed all leaves which were less than half on the mesh. Each unit of litter was inserted into a newspaper packet and placed in a plant press. Samples were dried over a plant drier and then stored at a constant temperature of 70° F. and approximately 40 per cent humidity. Twenty packets from the 1966 and 21 from the 1968 season were recovered in usable condition.

Each packet of litter was weighed in order to gain an estimate of total litter weight per unit area. Prior to weighing, non-leaf litter was removed from the packets. Five packets from each season were oven-dried at approximately 95° C. to determine the dry litter weight. Oven-dried weights were then projected for the entire collection of each season.

The number of leaves per species in each packet was determined and in conjunction with this task the point of collection was marked on each leaf. At times it was necessary to steam leaves apart so as to count and classify each one. Using a random numbers table and a large piece of cardboard sectioned into twenty-four numbered squares, virtually all the leaves of a given species were considered in randomly selecting one hundred for measurement. All the leaves of species for which the total leaf count numbered less than one hundred were measured. In instances where selected leaves were folded a steaming process was utilized to flatten the leaf prior to

measurement. Leaves possessing amounts of petiole and midrib which seemed insufficient to indicate approximate leaf size were rejected for measuring purposes.

Measurement of leaf area was accomplished with a plane polarizing planimeter. Where actual leaf margins were absent theoretical margins were drawn on a heavy gauge plastic sheet covering the leaf. Areas which appeared to have been eaten were also outlined on the plastic coverture. Most of the consumption was the result of feeding by various species of lepidopteran larvae. Areas consumed by mining insects were measured if the degree of consumption was such that one could see through the leaf. When the measured leaf was removed from beneath the plastic cover the area consumed could be ascertained by counting squares on graph paper (100 squares per square inch). Only those squares one half or more within the tracing of the consumed area were counted. Tracings of each leaf were easily removed from the sheet of plastic before other leaves were considered.

After measurement petioles were removed so as to eliminate as much inedible material as possible and the leaves of each species weighed. Weights for the total litter fall of each species were then estimated in kilograms per acre and were converted to energy units. Areas consumed, weights of these areas, and probable energy consumed per acre were also determined. Weight per acre values were determined by multiplying leaf blade weights times the number of leaves per acre.

In statistical tests, probability values of five per cent or less were considered to indicate significant differences.

RESULTS AND DISCUSSION

Packet Weights and Leaf Numbers

The total litter weight of the twenty packets selected in 1966 was 462.56 gm. (oven-dried weight) or an average weight per packet of 23.13 gm. Packet weights ranged from 11.69 to 34.30 gm. Dominant species, as represented by numbers of leaves, were black and white oaks with totals of 1,072 and 553 leaves respectively (Table 2). The 1967 sample had an average weight of 17.5 gm. per packet with a range from 5.4 to 25.7 gm. for the 28 points (Wenger, 1969). Total litter weight was 490.8 gm. Twenty-one packets from the 1968 season exhibited a somewhat lower oven-dried weight of 351.53 gm. The average packet weight was 16.74 with a range from 8.53 to 24.14 gm. (Table 3). Black and white oaks retained their dominance in both 1967 and 1968 with 1,238 and 489, and 668 and 340 leaves respectively. A comparison of mean leaf weight per packet using Student's *t*-test indicated no significant differences among the years; however, a paired *t*-test, which is probably more appropriate, indicated that there was a significant decrease between 1966 and 1968 for the points (14) sampled in both years.

Foliage production, in general, was related to the importance (density, dominance, and frequency) of the species in the forest. Differences in litter weights from point to point might be expected to indicate variations in density and dominance throughout the plot;

Table 2. Weight of leaves in each packet and the number of leaves per species per packet for the 1966 season. Leaf weights are estimated oven dry weights and represent 91.3 per cent of the air dry weights. Misc. species include 31 *Smilax rotundifolia*, 31 *Sassafras albidum*, 23 *Hamamelis virginiana*, 5 *Ceanothus americanus*, 5 *Desmodium* sp., 5 *Prunus serotina*, 3 *Crataegus* spp., 2 *Nyssa sylvatica*, and 1 *Amelanchier* sp. leaf.

Sample point	Leaf weight (gm.)	Leaves per species					
		Q. velutina	*Q. alba*	*Cornus Florida*	*Acer rubrum*	Misc. spp.	Total
A-1	26.39	79	18	1	-	6	104
A-3	16.72	41	17	1	-	4	63
A-4	23.98	53	19	31	1	7	111
A-5	11.69	34	8	-	-	21	63
A-6	18.35*	41	28	-	3	2	74
B-1	31.86	81	14	-	-	6	101
B-4	22.88	45	21	-	-	22	88
B-5	34.30*	77	55	3	-	1	136
C-1	33.78	67	22	52	-	-	141
C-3	15.85	46	7	-	1	9	63
C-4	27.90*	64	46	1	-	11	122
C-6	27.48	60	56	10	-	3	129
D-2	17.10*	48	3	-	2	-	53
D-4	29.78	85	7	8	8	3	111
D-5	30.87	56	54	12	-	1	123
E-2	10.70*	22	30	-	-	1	53
E-3	30.96	57	51	1	4	2	115
E-4	17.31	44	29	1	-	-	74
E-5	16.62	22	45	1	-	5	73
E-6	17.54	50	23	7	-	3	83
Total	462.56	1072	553	129	19	107	1880
Average	23.13	53.6	27.6	6.4	.95	5.4	94.0

*Represent actual, rather than estimated, oven-dry weights

Table 3. Weight of leaves in each packet and the number of leaves per species per packet for the 1968 season. Leaf weights are estimated oven dry weights and represent 95.8 per cent of the air dry weights. Misc. species include 22 *Smilax rotundifolia*, 17 *Hamamelis virginiana*, 16 *Sassafras albidum*, 14 *Prunus serotina*, 4 *Crataegus* spp., and 1 *Nyssa sylvatica* leaf.

Sample point	Leaf weight (gm.)	Leaves per species					
		Q. velutina	*Q. alba*	*Cornus Florida*	*Acer rubrum*	Misc. spp.	Total
A-4	24.05*	47	12	-	-	2	61
B-1	18.20	39	10	-	-	1	50
B-2	22.25*	38	2	11	4	-	55
B-3	11.98	27	8	27	-		62
B-4	19.54	36	14	-	-	18	68
B-6	9.68	24	8	5	-	3	40
C-1	9.39	23	9	18	-	-	50
C-2	20.41	44	4	1	6	1	56
C-3	19.90*	36	8	8	3	1	56
C-4	8.53	27	11	-	-	-	38
C-5	24.14	42	17	17	-	-	76
C-6	16.33	25	24	-	-	34	83
D-2	23.55*	51	27	2	25	-	105
D-3	20.07	40	15	-	-	5	60
D-4	9.58	28	2	6	-	1	37
D-5	14.27	13	40	7	-	-	60
D-6	16.76	32	19	-	3	3	57
E-2	8.53	16	11	13	-	-	40
E-3	12.02	21	32	1	-	-	54
E-4	19.45	34	23	-	-	4	61
E-6	22.90*	25	44	3	-	1	73
Total	351.53	668	340	119	41	74	1242
Average	16.74	31.8	16.2	5.7	1.9	3.7	59.6

*Represent actual, rather than estimated, oven-dry weights

however, a comparison of litter weights and total basal area of the eight trees sampled for point-centered quarter analysis at each point showed great variability. This probably results from the fact that leaves move away from their points of origin and hence away from the collecting points, and because flowering dogwoods produce many leaves while having only small dbh's. Although it has been indicated that there is a logarithmic relationship between tree diameters and leaf weight (Rothacher, Blow, and Potts, 1954), Bray and Gorham (1964) believe that leaf productivity estimates based on factors of growth over long periods of time, such as basal area, are probably less useful than factors relating to current growth. Challinor (1968), in working with red oak and three other tree species, also found that there was little if any correlation between basal area per plot and litter production.

The average number of leaves per packet showed a general decrease from 1966 to 1968, with values of 94, 79, and 60 leaves for the respective years (Tables 2,3,4). Corresponding standard deviation values were 26.2, 28.7, and 14.8. Using Student's t-test, a comparison of the mean number of leaves per packet in 1968 indicated significant differences between the values for both 1966 and 1967. Black oak leaves ranged from 53.6 in 1966 to 44.2 and 31.8 leaves per packet in 1967 and 1968 respectively. The range for white oak leaves was less pronounced but still showed the same decreasing trend with averages of 27.6, 17.5, and 16.2 leaves per packet for 1966 through 1968. Flowering dogwood, however, showed

Table 4. Number of leaves per species per acre. Values are projections of actual numbers of leaves collected, except where the estimates are related to tree dbh. Misc, species include _Sassafras albidum_, _Prunus serotina_, _Hamamelis virginiana_, _Crataegus_ sp., _Nyssa sylvatica_, and _Amelanchier_ sp. when present.

	Q. velutina	_Q. alba_	_Cornus florida_	_Acer rubrum_	Misc. species
Number of leaves estimated from tree dbh	2,878,500	3,115,120			
Number of leaves as projected from litter					
1966	3,364,258	1,735,480	404,841	59,628	335,788
1967	2,773,987	1,095,702	793,208	145,646	109,794
1968	1,992,329	1,015,580	355,457	122,468	155,326
Average	2,710,191	1,282,254	517,835	109,247	200,306

a fluctuating average with values of 6.4, 12.6, and 5.7 for the respective years.

Bray and Gorham (1964) have pointed out that annual fluctuations in total litter fall are not unusual. Black and white oak species have been found to exhibit a ratio of maximum to minimum leaf fall between seasons of 1.4, as opposed to the highest value recorded of 2.7 for a forest in New Zealand. In determining corresponding ratios for the current study it was found that the ratio for white oak leaves between 1966 and 1968 was 1.6, and that for black oak 1.7.

Rothacher et al. (1954) reported a logarithmic relationship between leaf numbers and branch diameter which can also be converted for use with tree diameters. For white and black oak respectively they found that:

$$\text{Log } N = 2.91178 + 1.82547 \, (\text{Log } X)$$

$$\text{Log } N = 2.43913 + 1.86381 \, (\text{Log } X)$$

where Log N equals the number of leaves and Log X the tree dbh. In spite of the trend away from the utilization of such estimates, it is of interest to compare values with those obtained in this study. Average diameters of trees in four size classes measured for point-centered quarter analysis were used to determine the number of leaves per tree and this value was then multiplied by the number of trees per acre per size class to determine total leaves per acre. Values based on actual leaves collected were lower than projected values in all instances except for black oak

in 1966 (Table 4).

Several points come to mind as possible explanations of the differences obtained. First of all, values projected from dbh may be inaccurate and of little meaning. A second factor concerns the percentage of leaf fall each year. Oak trees tend to retain some of their leaves in autumn which would reduce the number of leaves collected in litter samples and thus decrease the estimated number per acre. In November 1966 an attempt was made to estimate the number of leaves remaining on the trees in a column of 100 sq. in. above each sampling grid (R. Brewer, personal communication). This was done by using a vertically directed zoom telescope, with the field of view regulated to the appropriate diameter at heights of 25, 45, and 65 feet. The sample size (23) was considered small and lacked precision because of the uncertainty of the boundaries of the column at intermediate heights. The results, nevertheless, left no doubt that the number of leaves remaining on the trees was very small relative to those which had fallen. The mean number of leaves per 100 sq. in. column was 2.1, or just over two per cent of the average number collected on the screens (about 2.7 per cent of the oak leaves). Among the leaves remaining on the trees, there was a preponderance of white oak leaves (about 70 per cent) and leaves at lower heights. In view of the small number of leaves remaining as opposed to those collected this source of error in leaf numbers is probably negligible.

Leaf Area, Weight, and Available Energy

The average area prior to consumption for the measured black oak leaves was 6.9 sq. in. for both 1966 and 1967, and 7.8 sq. in. during the 1968 season (Table 5). The black oak leaves were the largest leaves collected with a mean average area of 7.2 sq. in. for the three year period. Dogwood leaves were the smallest of the four major species measured, ranging from an average of 3.0 sq. in. in 1968 to 3.5 sq. in. in 1966. The mean average was 3.3 sq. in. White oak and red maple had leaf areas between those of black oak and flowering dogwood. White oak areas ranged from 4.6 in 1966 to 5.6 sq. in. in 1968, with a mean average being 5.0 sq. in.

The leaf areas indicated in this study are lower than those reported by Bray (1961, 1964). The mean areas over a three-year period for Bray's leaves were 8.25 and 10.98 sq. in. for white and black oak species respectively. One of his samples indicated white oak leaves to be larger on the average than their black oak counterparts. This could be due in part to his small sample size for the white oak leaves, 10 as opposed to 94 for black oak. In addition the unsystematic methods of collecting reported by Bray (1961) do not inspire confidence that the areas obtained are representative. Other studies in second-growth oak forests have shown white oak leaves to be 6.0 sq. in. at Oak Ridge, Tennessee (Whittaker, Cohen, and Olson, 1963) and 5.9 sq. in. in another part of the Allegan State Game Area (Gottshall, 1967).

Table 5. Average values for leaf area and weight prior to consumption, area consumed, per cent consumed, and leaf weight after consumption during the 1966, 1967, and 1968 seasons. Misc. species include *Hamamelis virginiana*, *Sassafras albidum*, *Prunus serotina*, *Crataegus* spp., *Amelanchier* sp., and *Nyssa sylvatica* when present.

	Species of leaves				
	Q. velutina	*Q. alba*	*Cornus florida*	*Acer rubrum*	Misc. spp.
Ave. area/leaf (sq. in.)					
1966	6.9	4.6	3.5	3.5	4.5
1967	6.9	4.9	3.3	3.6	4.8
1968	7.8	5.6	3.0	3.0	3.7
Ave. area consumed/leaf (sq. in.)					
1966	1.1	0.6	.12	.15	.15
1967	1.2	0.6	.16	.10	.61
1968	1.8	0.8	.30	.25	.67
Ave. per cent consumed/leaf					
1966	15.9	13.0	3.4	4.3	3.3
1967	17.4	13.1	4.7	2.8	12.7
1968	23.1	14.2	10.0	8.3	18.1
Ave. wt./leaf with and without petiole					
1966	.341	.160	.091	.124	.10
	.315	.153	.088	.111	.09
1967	.350	.190	.070	-	-
	.320	.180	.070	-	-
1968	.403	.213	.086	.092	.091
	.370	.200	.084	.085	.086
Ave. wt./leaf blade prior to consumption					
1966	.375	.176	.091	.116	.093
1967	.387	.205	.074	-	-
1968	.481	.233	.093	.093	.105

The importance of leaf area is evident when one realizes that surface area available to receive sunlight is perhaps the most important factor regulating total primary production in the forest ecosystem. The annual efficiency for conversion of solar energy to net productivity available to consumers is only about 1 per cent (Ovington and Heitkamp, 1960; Woodwell and Whittaker, 1968), thus necessitating large numbers of leaves with substantial surface areas in order to fix significant amounts of energy. In most broadleaf forests the leaf area on one surface of the blade exceeds the ground area of the plot by three to six times (Woodwell and Whittaker, 1968). Based on the average area per leaf per species and on the number of leaves per species per acre, leaf area per acre of the important species has been calculated (Table 6). Results indicate ratios of total leaf area 3.7 to 5.1 times that of the ground surface. Oak stands in Tennessee exhibited similar results with foliage area ranging from 4.3 to 5.2 times the ground area (Rothacher et al., 1954).

The total leaf weight for all species ranged from 1,251.51 to 1,642.02 kg. per acre with an average value of 1,416.79 kg. The trend is for a decreasing leaf weight from 1966 to 1968 (Table 6), as would be expected from the trend in leaf numbers (Table 4). The values of 849 to 1,538 kg. per acre for oak litter reported by Ovington (1965) and the 1,288 kg. per acre from an oak forest reported by Gottshall (1967) are similar to those indicated in this study.

Table 6. Leaf areas, weights, and energy values per acre per species prior to consumption. Misc. species include *Sassafras albidum*, *Prunus serotina*, *Hamamelis virginiana*, *Crataegus* sp., *Nyssa sylvatica*, and *Amelanchier* sp. when present.

	Q. velutina	*Q. alba*	*C. florida*	*Acer rubrum*	Misc. spp.	Total
Total leaf area/acre (sq. ft.)						
1966	161,204	55,439	9,840	1,449	10,494	238,428
1967	132,920	37,284	9,011	3,641	3,660	186,516
1968	107,918	39,495	7,405	2,551	3,991	161,360
Average	134,014	44,073	8,752	2,547	6,048	195,435
Total leaf wt./acre (kg.)						
1966	1,261.60	305.44	36.84	6.91	31.23	1,642.02
1967	1,073.53	224.62	58.70	-	-	1,356.85
1968	985.31	236.63	33.06	11.39	16.30	1,251.51
Average	1,197.81	225.56	42.87	9.15	23.76	1,416.79
Energy/acre (kcal.)						
1966	6,031,710	1,460,309	176,132	33,036	149,311	7,850,498
1967	5,132,547	1,073,908	280,645	-	-	6,487,100
1968	4,581,680	1,131,328	158,060	54,456	77,930	5,983,470
Average	5,248,646	1,231,848	214,946	43,746	113,621	6,740.356

There are several factors which could affect these litter weights. Bray and Gorham (1964) report that weight loss by respiration after leaf fall but prior to desiccation may be quite high. Such a loss could range from 3 to 43 per cent of the leaf weight depending on the soil substrate, moisture, and leaf type. If the value of three per cent weight loss seven weeks after leaf fall for white oak leaves given by Bray and Gorham (1964) is indicative for the leaves in this study, it would not seem an important factor. Consumption by earthworms and fungi is another possible source of error. Methods for the prevention of earthworm consumption, such as sides on the collecting squares, are unacceptable due to their interference with natural leaf fall.

The average energy available to insect herbivores, in the form of leaf blade material, during the study period was 6,740,356 kcal. per acre per year (Table 6). The highest total value was 7,850,498 kcal. in 1966 and the lowest 5,983,470 kcal. in 1968. Again it is evident that these values parallel the decreases in leaf number and weight. Black oak leaves with their large areas resulted in an average of 5,248,646 kcal. per acre as opposed to 1,231,848, 214,946, and 43,746 kcal. for white oak, flowering dogwood, and red maple respectively. All energy values were based on the average values for four oak species (4.781 kcal. per gm. dry weight) as reported by Ovington and Heitkamp (1960). A minimum estimate of energy available from the leaf material prior to consumption would be about 97.2 per cent of those values present on Table 6, or an

average of 6,551,626 kcal. per acre. This minimum is based on a conservative factor of 4.6 kcal. per gm. dry weight of plant material (Golley, 1961).

Total energy available per square yard each season ranged from 1,622 kcal. in 1966 to 1,340 and 1,237 kcal. in 1967 and 1968. The 1966 value compares favorably with the 1,577 kcal. per sq. yard reported by Gottshall (1967) for another oak forest in the Allegan State Game Area. Values for a maple and beech forest in Ontario were several hundred kcal. per sq. yard greater than those reported here (Bray, 1964).

Leaf Consumption

Consumption of black oak leaves ranged from an average of 1.1 to 1.8 sq. in. per leaf from 1966 to 1968, while the average consumption for white oak leaves was from .6 to .8 sq. in. per leaf (Table 5). Bray (1964) reported similar values of .92 to 1.02 and from .62 to .96 sq. in. consumed per leaf for black and white oak respectively. Flowering dogwood and red maple followed in order of decreasing consumption per leaf with ranges of .12 to .30 and .10 to .25 sq. in. per leaf respectively (Table 5). Leaf area for leaf area the utilization decreased in the order of black oak, white oak, flowering dogwood, and red maple. A comparison of actual areas consumed per species between 1966 and 1968 indicated that there were significant increases for black oaks and flowering dogwoods but not for white oak leaves.

There are several possible explanations for the greater con-

sumption per unit area in black versus white oak leaves. The species of insects present, a possible relationship between nutrient content and leaf palatability, and the earlier leafing of black versus white oaks could all influence ultimate utilization. Another possibility might be that consumption by leaf mining insects is more on white than black oak leaves. This seems particularly plausible for 1967, when the white oak leaves appear to have been mined more extensively than in other years. Because not all consumption by leaf mining was measured, values for consumption per unit area of white oak leaves are probably underestimated somewhat.

The marked increases in the consumption of flowering dogwood and red maple leaves in the 1968 samples are of considerable interest, for these values may provide some clue as to the changes in populations of herbivorous insects. Because the amount of material consumed increases from 1967 to 1968, one might guess that the populations of the invertebrate consumers are increasing. If weight consumed is a good criterion for insect numbers, then the 1968 population was greater than that of 1967 (Table 7). In addition to increased weight of material consumed the leaf numbers show a decrease. Such a situation might necessitate the utilization of leaves not normally eaten; that is, flowering dogwood and red maple leaves.

Total consumption for all species averaged 244.3 kg. per acre, with a range of 216.4 to 261.8 kg. per acre (Table 7). Considered as a percentage of total leaf weight prior to consumption the above

Table 7. Leaf weight per acre after consumption, leaf weight consumed per acre and energy utilized per acre per species. Misc, species include *Sassafras albidum*, *Hamamelis virginiana*, *Crataegus* sp., *Nyssa sylvatica*, and *Amelanchier* sp. when present.

	Q. velutina	*Q. alba*	*C. florida*	*Acer rubrum*	Misc. spp.	Total
Total leaf wt./acre (kg.)						
1966	1,059.74	265.53	35.63	6.62	30.22	1,397.74
1967	887.38	197.23	55.52	-	-	1,140.43
1968	737.16	203.12	29.86	10.41	13.36	993.91
Average	894.49	221.96	40.34	8.52	21.79	1,187.10
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	888,549	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

values show an increase in consumption from 15 per cent in 1966 to 16 and 20.9 per cent in 1967 and 1968. Values for mean yearly per cent consumption reported by Bray (1964) of 7.4 to 12.4 and the 5.4 per cent consumption indicated by Gottshall (1967) are considerably lower. Values ranging from 3.7 to 6.7 per cent consumption in a single season for a Tennessee oak stand (Rothacher et al., 1954) are also lower than the current data indicate.

There are several potential difficulties in the determinations of material consumed. The methods used do not take into account those leaves almost or completely eaten, which would lead to an underestimation of both consumption and production. In addition, as leaves are lost throughout the season they may be replaced by the tree. This would result in lower production values than indicated. In the case of cherry trees new leaves can be produced after complete defoliation so that, if defoliation occurred by consumption, consumption would be underestimated. Another problem concerns leaves partially eaten early in the season. These leaves may continue to grow and in doing so give the appearance of greater consumption than actually occurred. Where insects cut an entire lobe off the leaf blade apparent consumption would be greater than that material actually utilized. The determination of consumption on such a leaf would be an overestimation. Consumption by mining and sap sucking insects represents another possible underestimation of primary consumption.

Leaf weights consumed when converted to energy units result

in values of 1,167,903, 1,034,705, and 1,251,569 kcal. per acre for all species for the 1966 through 1968 seasons. This is an average of 1,175,552 kcal. per acre, or 242.9 kcal. per sq. yard. Yearly averages for energy consumed per sq. yard far exceed the 60.2 kcal. reported by Gottshall (1967) and the 87 kcal. indicated by Bray (1964).

Reducing energy values to kcal. per sq. yard per day, for a 120-day season, indicates that primary consumers utilize 1.91, 1.78, and 2.15 kcal. per day for each sq. yard.

Consumption as Related to Leaf Area

In an attempt to understand how consumption was related to leaf area a linear regression line was computed by the least squares method for black and white oak species from each year (Table 8). All slopes were found to be significantly different from zero (that is, a horizontal line). The leaf samples of black and white oak from both the 1966 and 1968 seasons are of interest in that they result in intercept values which are negative. This would mean that for small leaf areas there would be no leaf consumption (Figures 1 and 2). On the whole, linear regression lines seemed to represent the data adequately. In most instances, the central portions of the regression lines were nearly the same as those curves constructed by grouping leaves into size classes, averaging areas and portions consumed, and graphing the results. The central parts of the regression lines (*i.e.* those leaves

Table 8. Slope and intercept values relating to regression lines for black and white oak from 1966 through 1968. Slope is designated as M and the intercept as B in the formula Y=MX + B, where X is the leaf area and Y the area consumed. Confidence intervals given are for the 95 per cent level.

	Slope	Confidence intervals	Intercept	Confidence intervals
Black oak				
1966	.1822	.0710-.2935	-.1920	-.5962- .2122
1967	.0686	.0076-.1295	.7010	.4827- .9193
1968	.2312	.0980-.3644	-.0629	-.5138- .3879
White oak				
1966	.2386	.1783-.2988	-.5396	-.7109--.3683
1967	.0999	.0612-.1387	.1325	.0179- .2471
1968	.1557	.0980-.2199	-.1275	-.3678- .1127

Figure 1. Regression lines for the relationship of leaf area to area consumed for black oak leaves from 1966 through 1968.

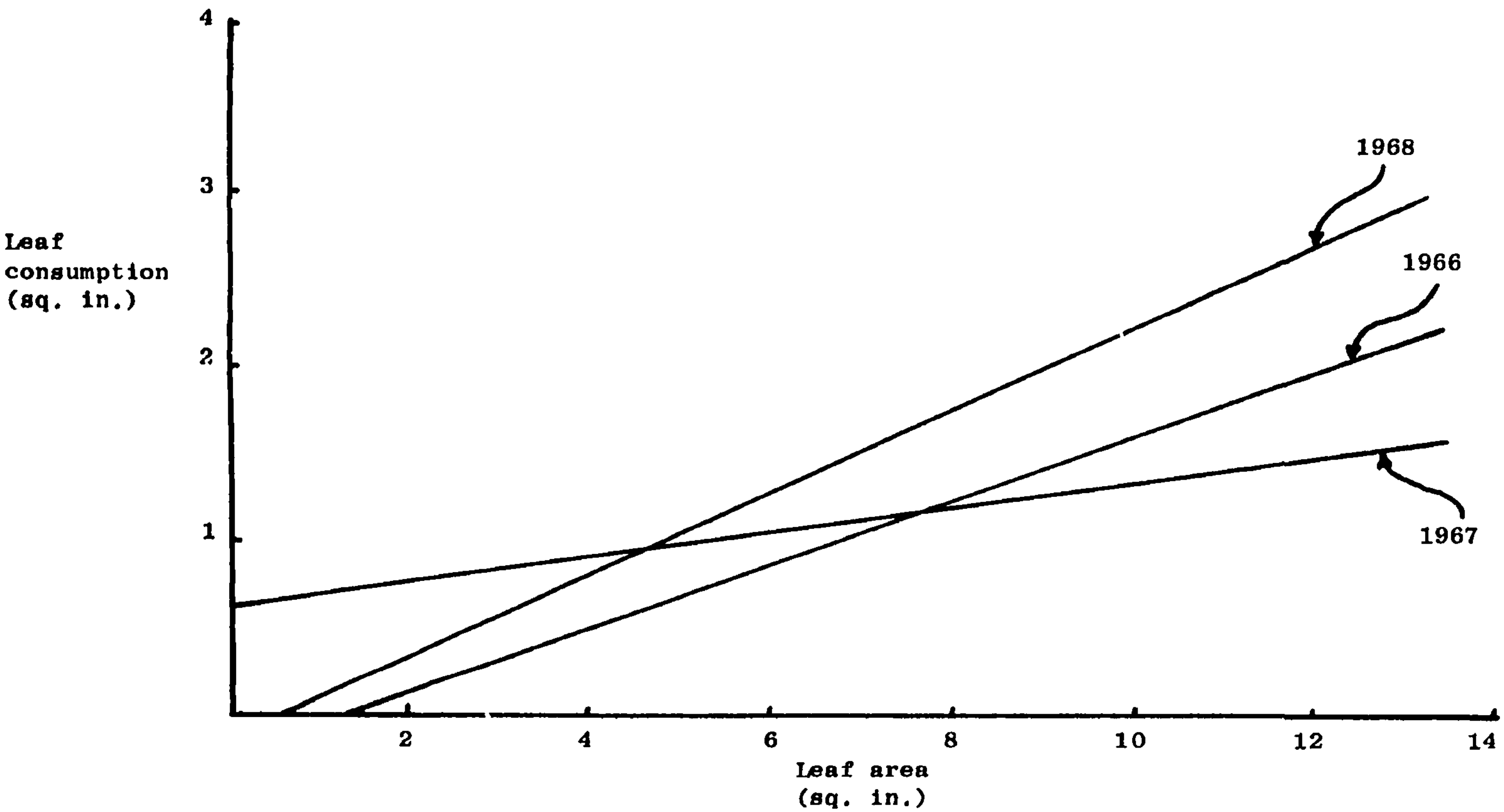
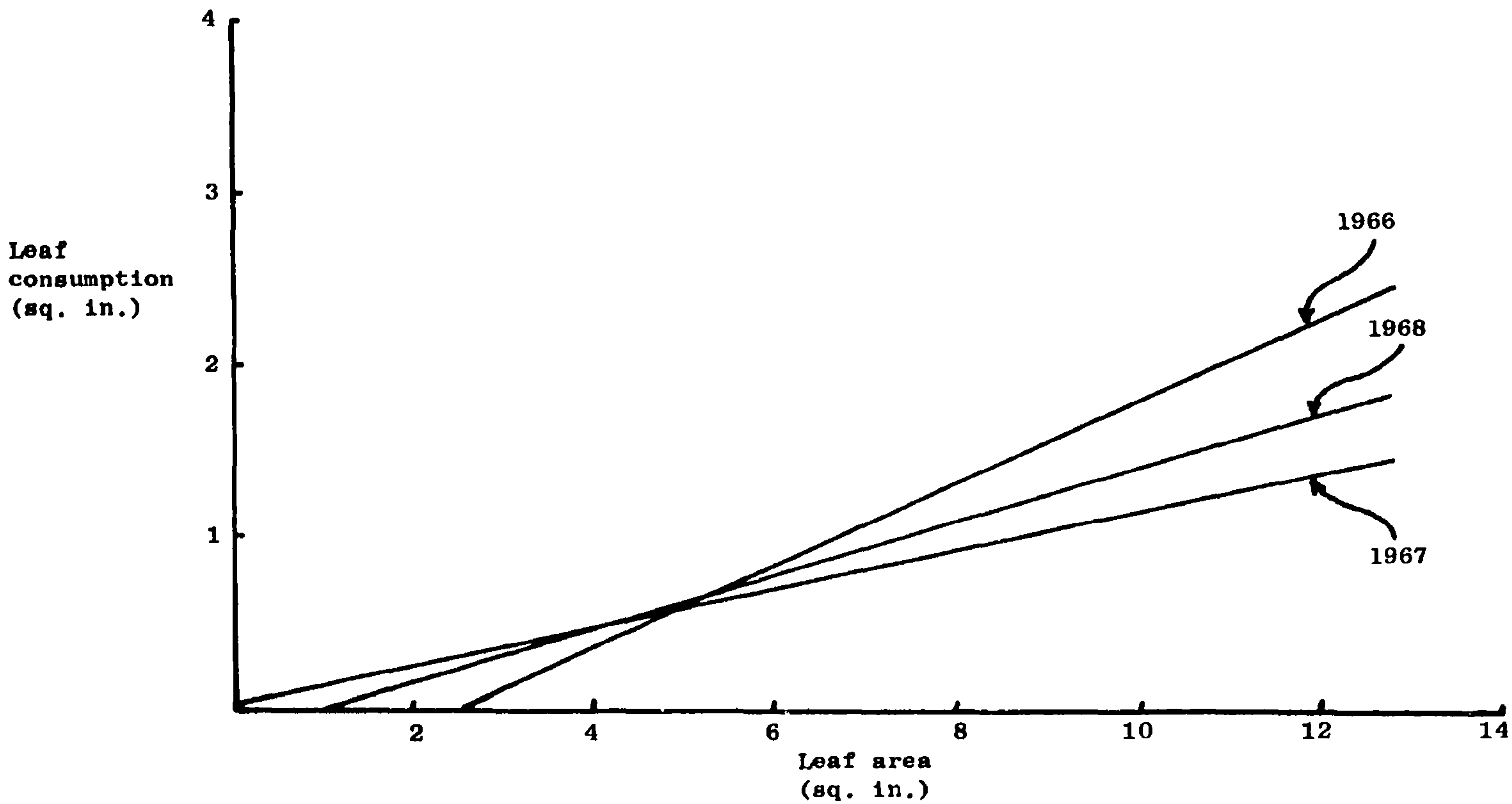


Figure 2. Regression lines for the relationship of leaf area to area consumed for white oak leaves from 1966 through 1968.



2 to 10 sq. in.) comprise from 69 to 75 per cent of the black oak and 57 to 64 per cent of the white oak leaves. Variations from the calculated regression lines were evident primarily for the large leaves, which represented only a small portion of the total sample.

The explanation for the increase in area consumed with increase in leaf area is uncertain. This may involve the evaluation of leaf area by an insect before, or as, it undertakes the task of consumption. This phenomenon is contrary to an insect eating to satiety or until the leaf is devoured, as might be expected. The problem is further complicated if there are several individuals eating a single leaf. It is difficult to imagine any interaction between individual insects which would account for the consumption of only a given portion of the leaf. Because there is no indication of how many leaves are eaten entirely there may be some inherent error involved with these results.

Further study of the data by way of Student's t-test (Table 9) has shown that there is no significant difference between the rate at which consumption increases with respect to increased leaf area for black versus white oak leaves of any given year. This is true despite the fact that the actual amount of consumption for a leaf of a given size is greater for the black oak than white oak. There are, however, such differences within a given species between seasons. The slope for black oak leaves in 1967 was significantly lower (at the two per cent level) than the slopes for 1966 and 1968. (Figure 1, Table 9).

Table 9. t-test results for comparing slopes between black and white oak leaves of a given year, black oaks of different years, and white oak leaves of different years. Significant differences are indicated by the 5 per cent level.

Comparison	t value	df	Acceptance level (%)
Black v. white 1966	1.04879	196	20.0
Black v. white 1967	0.79700	206	60.0
Black v. white 1968	1.44005	196	20.0
Black'66 v. black'67	2.33639	199	2.0
Black'67 v. black'68	3.10955	199	1.0
Black'66 v. black'68	0.82807	196	50.0
White'66 v. white'67	3.39301	203	0.1
White'67 v. white'68	1.39779	203	90.0
White'66 v. white'68	1.84578	196	10.0

For white oak leaves a similar situation appears to exist, with higher values for slope in 1966 and 1968 than 1967. The difference between 1968 and 1967 does not, however, reach significance at the 5 per cent level (Figure 2, Table 9).

The decreasing rate of consumption as compared to leaf area for the 1966-67 period could indicate a reduction in feeding pressure. Reductions in population size would be a plausible explanation, and would be in line with the decreased weight of plant material consumed over this period. With the feeding pressure decreasing the insects would not be required to eat as much of a given leaf as was necessary in the previous year. Leaf numbers also decrease over the same period and must be considered in this discussion. If populations remained the same over the two-year period while the number of leaves decreased, one would expect the rate of consumption versus area increase to be greater in 1967 than in 1966. Since this did not occur, and because the total leaf weight utilized was less in 1967, it seems that the populations must have been reduced to some extent.

In the following year, 1967 to 1968, the consumption of black oak leaves increased at a rate greater than the rate of increased area. This situation could be the result of population levels remaining at the 1967 level while leaf numbers continued to decrease.

Consumption in Relation to Plot Position

The average amount of consumption per leaf at each sampling point for black and white oak leaves from 1966 was .95 sq. in.

(Table 10). From the seventeen points considered there were five points at which the average consumption was greater than the average consumption for all black and white oak leaves. Such points have been sectioned off, and combined when possible, so as to illustrate possible areas of high insect density (Figure 3). The results indicate three independent and two related points of high consumption. Six of the seven points have leaves on the average larger than all the black and white oak leaves combined, and in addition, four points have total basal areas, for the eight closest trees in two size classes, which are below the average basal area per point for the plot. From the above information one might assume that the insects are utilizing the larger shade leaves on the plot. These leaves would be located, in large part, in the understory trees and in lower portions of the canopy trees. This might account for the lower basal area around these points.

The increased consumption in 1968 is exemplified by twelve points which show average areas consumed per point that are greater than the overall average area consumed per leaf of 1.18 sq. in. (Table 11). These twelve points can be grouped together, as indicated on Figure 4, to show four regions where insect densities may be greater than in other parts of the plot. As with the 1966 results, most of the points in question have average leaf areas per point that are larger than the average for all the black and white oak leaves. In this case nine of the twelve points have average areas above 6.4 sq. in. The correlation with basal area is still somewhat evident, but only five of the twelve points are below the

Table 10. The number of leaves, total area, average area, total area consumed, average area consumed, and per cent consumed per sampling point for black and white oak leaves from 1966. Area values are in square inches.

Point	Number	Total area	Ave. area	Total consumed	Ave. consumed	Percent consumed
A-1	10	89.6	8.9	13.26	1.33	14.8
A-3	14	82.9	5.9	10.64	0.76	12.8
A-4	14	78.2	5.6	7.83	0.56	10.0
A-5	4	14.1	3.5	2.74	0.68	19.4
A-6	15	70.4	4.7	4.49	0.30	6.4
B-4	7	51.7	7.4	5.46	0.78	10.6
B-5	15	94.4	6.3	13.88	0.93	14.7
C-3	6	38.2	6.4	8.36	1.93	21.9
C-4	14	64.6	4.6	8.73	0.62	13.5
D-2	6	47.6	7.9	11.04	1.84	23.2
D-4	12	86.9	7.2	10.52	0.88	12.1
D-5	19	87.7	4.6	8.55	0.45	9.7
E-2	9	37.2	4.1	8.75	0.97	23.5
E-3	19	106.6	5.6	14.12	0.74	13.2
E-4	18	94.6	5.2	13.62	0.76	14.4
E-5	8	44.8	5.6	4.40	0.55	9.8
E-6	10	61.0	6.1	16.30	1.63	26.7
Total		1150.5		162.69		
Average			5.8		0.81	

average basal area of 3.53 sq. ft. Further study involving insect frass at each sampling point might yield information on population densities which would aid in substantiating these speculations.

Figure 3. Plot arrangement with division stakes at each intersection. Points at which the average consumption per leaf per point surpassed the average for all black and white oak leaves of 1966 are sectioned into possible areas of high insect density. 1 in.= 200 ft.

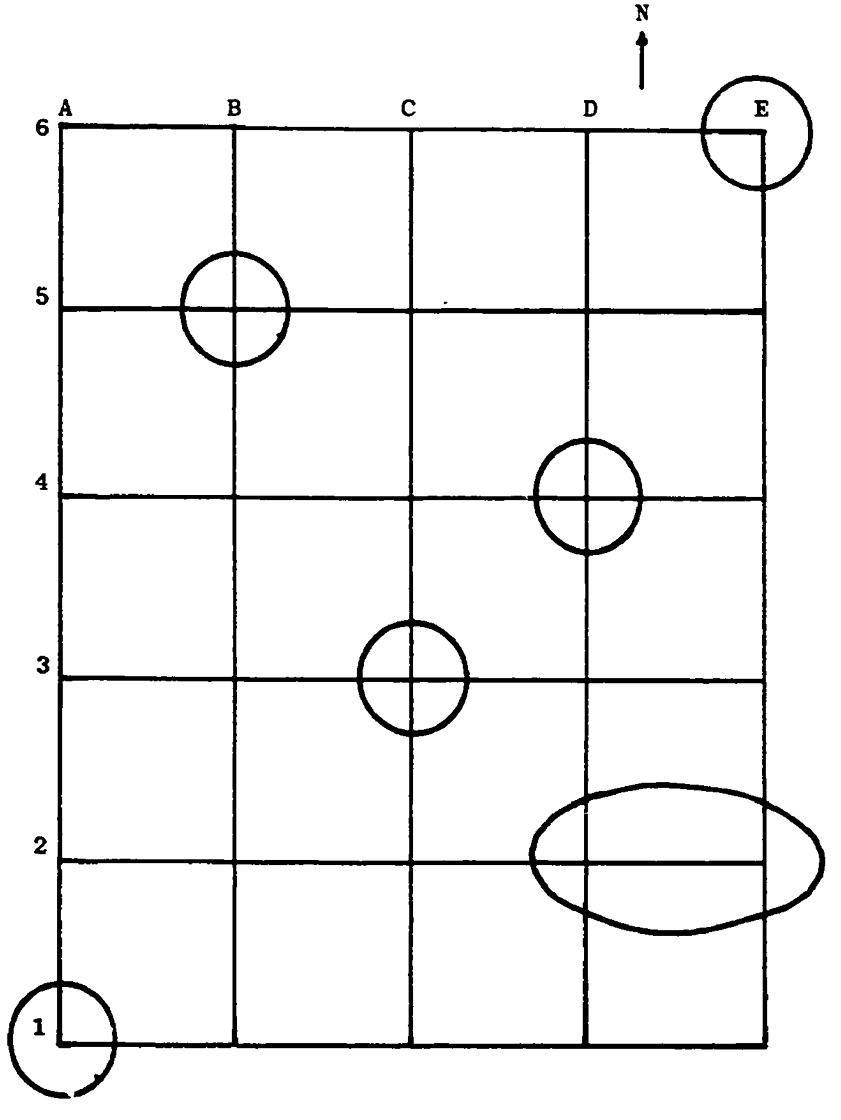
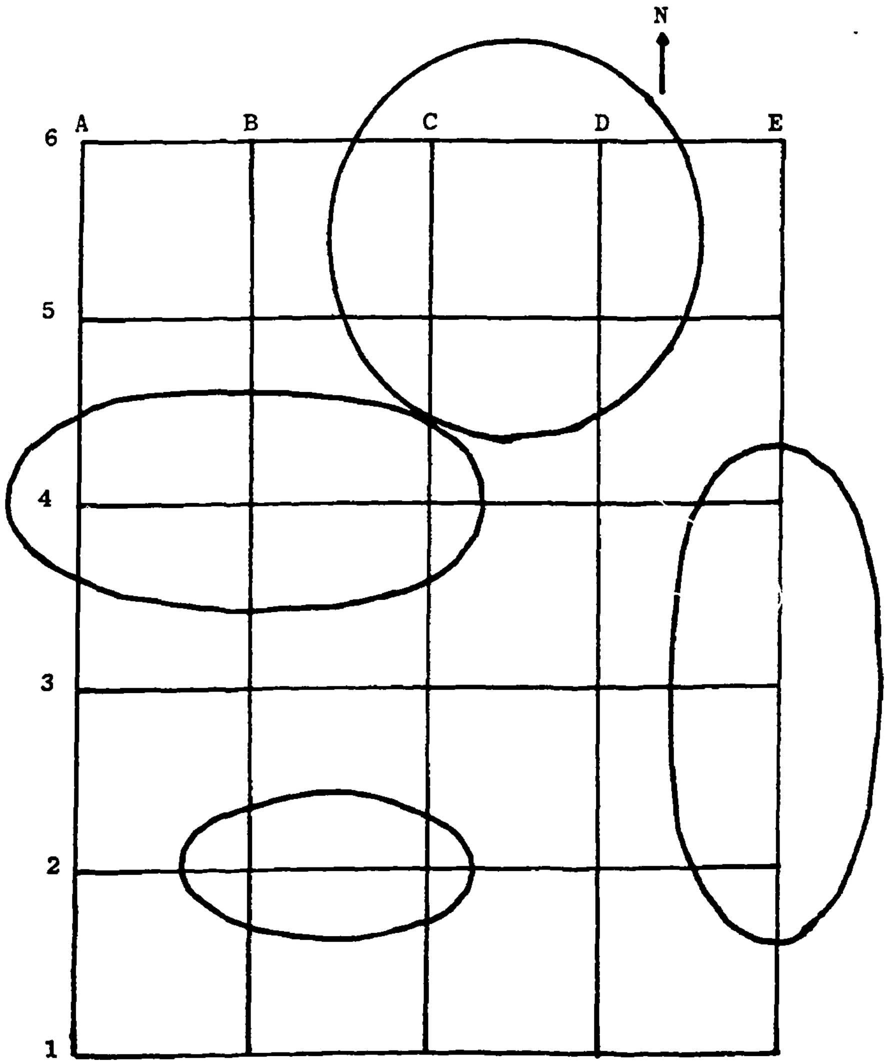


Table 11. The number of leaves, total area, average area, total area consumed, average area consumed, and per cent consumed per sampling point for black and white oak leaves from 1968. Area values are in square inches.

Point	Number	Total area	Ave. area	Total consumed	Ave. consumed	Percent consumed
A-4	9	74.9	8.3	17.70	1.96	23.6
B-1	12	86.2	7.2	11.38	0.95	13.2
B-2	3	21.0	7.0	6.28	2.09	29.9
B-3	2	10.4	5.2	0.30	0.15	2.9
B-4	8	59.5	7.4	11.12	1.39	18.7
B-6	7	44.8	6.4	6.52	0.93	14.6
C-1	4	17.3	4.3	1.63	0.41	9.4
C-2	10	87.2	8.7	15.36	1.50	17.6
C-3	4	37.4	9.4	4.35	1.09	11.6
C-4	11	62.4	5.7	15.00	1.36	24.0
C-5	10	57.3	5.7	14.42	1.44	25.2
C-6	13	94.1	7.2	17.74	1.36	18.8
D-2	20	117.2	5.9	16.78	0.84	14.3
D-3	13	69.0	5.3	9.47	0.73	13.7
D-4	3	23.1	7.7	1.73	0.58	7.5
D-5	16	112.3	7.0	29.46	1.84	26.2
D-6	10	60.8	6.0	15.24	1.52	25.1
E-2	3	21.7	7.2	7.01	2.34	32.3
E-3	8	53.5	6.7	10.58	1.32	19.8
E-4	17	143.8	8.5	24.94	1.47	17.3
E-6	15	84.5	5.6	10.40	0.69	12.3
Total		1338.4		247.41		
Average			6.4		1.18	

Figure 4. Plot arrangement with division stakes at each intersection. Points at which the average consumption per leaf per point surpassed the average of all black and white oak leaves of 1968 are sectioned into possible areas of high insect density. 1 in.= 200 ft.



SUMMARY

Foliage production and consumption were studied in a southwestern Michigan oak forest during the period 1966-1968. These data are pertinent to the interception and utilization of solar energy, the interception and runoff of moisture, to soil formation and nutrient cycling, and, in particular, to the energy availability and consumption by primary consumers.

Litter collected on hardware cloth squares (100 sq. in.) weighed an average of 23.13 gm. in 1966, 17.5 in 1967 (Wenger, 1969), and 16.74 gm. in 1968. This represents a significant decrease in the average litter weight per square between 1966 and 1968. The average numbers of leaves per square were 94, 79, and 60 in 1966 through 1968, with significant differences indicated for 1968 as compared with 1966 and 1967. Black oak leaves were the most plentiful with a mean average of 43.2 leaves per square, whereas white oak leaves averaged 20.4 and flowering dogwood 8.2 per square.

The forest produced an average of 4,819,833 leaves per acre per year for all species. This number was composed of 56.2 per cent black oak, 26.6 white oak, 10.0 flowering dogwood, 2.3 red maple, and 4.2 per cent miscellaneous species. Of the three major species black oak had the largest mean average area per leaf with 7.2 sq. in. followed by white oak with 5.0 and flowering dogwood with 3.3. The total areas of all leaves averaged 195,435 sq. ft. per acre per year, whereas the total weight per acre per year

amounted to 1,416.79 kg. Weights per leaf for black and white oak and flowering dogwood were .414, .204, and .104 gm. respectively. Leaf weight per acre decreased 390.5 kg. over the study period. For the three years, there was an average of 6,740,356 kcal. of leaf material per acre per year available to primary consumers. Of this energy available 77.9 per cent was in the form of black oak and 18.3 per cent white oak leaves.

The mean average consumption per leaf for black oak was 1.37 sq. in. and decreased to .66 and .19 sq. in. for white oak and flowering dogwood. Leaf area for leaf area, consumption decreased from black oak to white oak to flowering dogwood. Consumption, which showed an increase from 15 per cent in 1966 to 20.9 per cent in 1968, averaged 241.69 kg. per acre per year. This is equivalent to an average of 1,175,552 kcal. per acre per year, or 242.9 kcal. per sq. yard per year, which herbivorous insects consume. Consumption seems to be related to leaf size with larger leaves suffering greater consumption than smaller ones. This phenomenon lacks a good explanation and is deserving of further study.

Areas of high insect density throughout the plot were estimated by considering the average consumption per point for the black and white oak leaves. Further study concerning amounts of frass per point may provide additional information on insect densities.

APPENDIX

Table 1. Quercus alba leaf area data from 1968.

Sample point	Leaf area (in^2)	Area consumed (in^2)	Sample point	Leaf area (in^2)	Area consumed (in^2)
A-4	2.8	.09	D-2	4.7	.40
A-4	5.4	.24	D-2	7.0	.84
B-1	11.4	1.50	D-2	7.1	3.62
B-1	7.9	.05	D-2	3.2	.02
B-1	3.4	.14	D-2	2.6	.84
B-1	2.4	.02	D-2	0.4	.02
B-3	1.6	.00	D-2	2.8	.14
B-3	8.8	.30	D-2	3.2	.51
B-4	7.0	.15	D-3	1.9	.19
B-4	6.5	.32	D-3	4.3	1.40
B-4	8.1	.13	D-3	6.3	.18
B-6	3.1	.76	D-3	6.6	1.70
B-6	4.0	.40	D-3	2.4	.25
B-6	10.8	.51	D-3	2.2	.00
C-1	4.7	.03	D-3	5.2	.28
C-1	3.4	.04	D-3	5.8	.19
C-2	6.6	.21	D-5	5.1	2.50
C-3	13.9	.26	D-5	0.8	.00
C-4	5.0	.66	D-5	2.5	.83
C-4	11.2	.06	D-5	11.5	6.11
C-4	7.8	4.10	D-5	4.6	.35
C-4	1.5	.01	D-5	3.6	.01
C-4	3.4	.40	D-5	6.4	2.88
C-4	4.9	.79	D-5	8.5	.60
C-5	9.3	.07	D-5	5.4	.11
C-5	3.1	.18	D-5	10.3	.20
C-5	2.1	.41	D-5	4.0	.13
C-5	1.3	.57	D-5	23.1	5.79
C-6	2.6	1.35	D-5	1.0	.02
C-6	4.5	.35	D-6	2.0	.17
C-6	5.8	.08	D-6	5.0	.67
C-6	8.3	.88	D-6	7.9	.37
C-6	1.3	.00	D-6	2.8	.95
D-2	4.9	.14	D-6	4.3	.02
D-2	2.8	.12	E-2	7.3	.24
D-2	10.9	.13	E-2	10.4	5.68
D-2	11.9	2.19	E-3	14.1	.11

Table 1. (continued)

Sample	Leaf area (in^2)	Area consumed (in^2)
E-3	6.4	.52
E-3	6.7	.15
E-3	1.8	.09
E-3	8.2	2.93
E-3	1.7	.01
E-4	1.4	.25
E-4	2.2	.19
E-4	6.3	.09
E-4	14.3	.24
E-4	5.0	.84
E-4	11.2	4.21
E-4	7.6	.21
E-4	12.4	.59
E-4	8.3	.00
E-6	3.8	.04
E-6	4.6	.92
E-6	8.1	.79
E-6	7.6	1.16
E-6	6.5	.46
E-6	1.6	.18
E-6	6.1	2.35
E-6	2.5	.72
E-6	2.9	1.05
E-6	1.7	.51
E-6	1.6	.33
?	5.7	.71
Total	564.9	75.50
Average	5.6	.76

Table 2. Quercus velutina leaf area data from 1968.

Sample point	Leaf area (in^2)	Area consumed (in^2)	Sample point	Leaf area (in^2)	Area consumed (in^2)
A-4	6.0	.13	C-4	4.3	.01
A-4	6.2	1.80	C-4	7.1	1.07
A-4	15.6	6.21	C-4	5.3	2.16
A-4	11.5	2.14	C-4	3.9	1.34
A-4	11.9	1.48	C-5	6.6	3.67
A-4	6.7	.84	C-5	5.2	2.55
B-1	2.9	1.05	C-5	4.6	.99
B-1	11.5	4.22	C-5	5.7	1.46
B-1	10.9	.06	C-5	7.7	1.73
B-1	7.9	.63	C-5	11.7	2.79
B-1	9.4	.15	C-6	10.5	2.36
B-1	7.4	.15	C-6	8.5	.90
B-1	6.0	2.17	C-6	7.2	.08
B-1	5.1	1.24	C-6	7.6	.35
B-2	4.9	2.33	C-6	17.5	4.02
B-2	5.0	.89	C-6	11.0	1.25
B-2	11.1	3.06	C-6	7.0	4.87
B-4	7.2	.83	C-6	2.3	1.25
B-4	6.6	2.64	D-2	14.6	.26
B-4	7.4	2.78	D-2	10.4	3.37
B-4	10.3	2.76	D-2	5.6	.22
B-4	6.4	1.51	D-2	5.0	.02
B-6	9.5	2.32	D-2	9.3	.11
B-6	8.7	1.70	D-2	4.0	1.78
B-6	1.5	.00	D-2	5.0	1.89
B-6	7.2	.83	D-2	1.8	.16
C-1	1.8	.02	D-3	9.3	2.20
C-1	7.4	1.54	D-3	4.5	.48
C-2	13.2	3.62	D-3	6.2	.71
C-2	8.9	.33	D-3	10.6	1.36
C-2	10.3	1.02	D-3	3.7	.53
C-2	9.6	.08	D-4	8.2	1.09
C-2	7.4	2.73	D-4	7.4	.44
C-2	6.2	.50	D-4	7.5	.20
C-2	14.6	5.68	D-5	7.1	2.77
C-2	6.4	.01	D-5	6.8	.87
C-2	4.0	1.18	D-5	11.6	6.29
C-3	11.6	.50	D-6	14.0	4.19
C-3	6.4	3.55	D-6	5.4	.71
C-3	5.5	.04	D-6	5.8	.01
C-4	8.0	4.40	D-6	9.6	6.15
A-4	8.8	4.77			

Table 2. (continued)

Sample point	Leaf area (in^2)	Area consumed (in^2)
D-6	4.0	2.00
E-2	4.0	1.09
E-3	4.8	2.46
E-3	9.8	4.31
E-4	3.5	.87
E-4	8.3	.25
E-4	6.1	.58
E-4	7.8	1.50
E-4	16.2	8.37
E-4	14.4	1.66
E-4	10.3	1.14
E-4	8.5	3.95
E-6	13.5	.26
E-6	14.6	.40
E-6	6.8	.80
E-6	2.6	.43
?	6.8	2.42
Total	784.0	175.04
Average	7.8	1.75

Table 3. <u>Cornus florida</u> leaf area data from 1968.

Sample point	Leaf area (in^2)	Area consumed (in^2)	Sample point	Leaf area (in^2)	Area consumed (in^2)
B-2	3.1	.11	C-1	3.1	.57
B-2	1.2	.00	C-1	2.4	.00
B-2	4.9	.97	C-1	3.6	.00
B-2	3.8	.02	C-1	2.3	.00
B-2	2.9	.47	C-1	3.1	.00
B-2	3.5	1.04	C-1	2.2	.04
B-2	3.0	.56	C-1	1.4	.00
B-2	3.8	.00	C-1	2.1	.11
B-2	6.2	1.87	C-1	3.1	.30
B-2	4.0	.10	C-1	2.7	.00
B-3	5.2	.01	C-1	2.0	.00
B-3	2.8	.00	C-1	2.7	.09
B-3	3.6	.00	C-1	1.7	.03
B-3	4.4	.00	C-2	0.7	.00
B-3	3.5	.02	C-3	3.9	.00
B-3	3.0	.03	C-3	3.8	.07
B-3	3.7	.07	C-3	4.0	.12
B-3	3.1	.02	C-3	2.0	.00
B-3	5.0	.34	C-3	4.1	.43
B-3	2.9	.13	C-3	2.5	.07
B-3	3.3	.00	C-3	2.6	.09
B-3	3.1	.10	C-3	3.6	.17
B-3	0.5	.02	C-5	4.1	1.25
B-3	2.9	.12	C-5	3.0	1.12
B-3	4.4	.46	C-5	3.1	1.68
B-3	2.5	.52	C-5	2.1	.19
B-3	4.5	.10	C-5	2.7	.24
B-3	3.1	.00	C-5	3.3	.26
B-3	3.4	.52	C-5	3.6	.02
B-3	1.1	.02	C-5	2.8	.10
B-3	4.2	.22	C-5	0.7	.08
B-3	2.4	.70	C-5	1.2	.05
B-3	1.2	.07	C-5	2.1	.73
B-3	1.0	.08	C-5	1.5	.90
B-3	2.8	.80	D-2	2.5	.67
B-6	1.8	1.07	D-2	5.0	1.35
B-6	0.7	.03	D-4	4.3	.07
C-1	3.0	.18	D-4	4.0	2.06
C-1	6.7	.70	D-4	3.7	.00
B-3	4.8	.27	D-4	4.2	.03

Table 3. (continued)

Sample point	Leaf area (in^2)	Area consumed (in^2)
D-4	3.1	1.34
D-5	3.3	.06
D-5	3.6	.01
D-5	3.1	.13
D-5	1.2	.03
D-5	2.0	.22
D-5	2.0	.61
D-5	0.9	.01
E-2	0.7	.00
E-2	4.2	.07
E-2	5.1	.05
E-2	2.9	.01
E-2	1.7	.17
E-2	5.8	.21
E-2	6.2	1.18
E-2	1.9	.89
E-2	0.8	.13
E-6	2.9	.20
E-6	1.9	.07
E-6	1.1	.00
Total	298.9	30.02
Average	3.0	.30

Table 4. *Sassafras albidum*, *Hamamelis virginiana*, *Smilax rotundifolia*, *Acer rubrum*, *Prunus serotina*, *Nyssa sylvatica*, and *Crataegus* spp. leaf area data from 1968.

Sample point	Leaf area (in^2)	Area consumed (in^2)	Sample point	Leaf area (in^2)	Area consumed (in^2)
Sassafras albidum			*Smilax rotundifolia*		
A-4	5.8	.13	C-6	6.1	.05
A-4	10.9	.00	C-6	1.8	.06
B-1	1.1	.00	C-6	1.1	.01
B-4	5.3	.12	C-6	1.6	.50
B-6	13.4	1.99	C-6	1.3	.13
B-6	5.7	.27	C-6	0.7	.00
B-6	4.3	.01	C-6	1.2	.01
C-2	2.4	.06	C-6	2.5	.61
C-3	7.6	6.14	C-6	2.3	.36
D-3	5.2	.25	C-6	1.0	.33
D-3	7.1	6.24	C-6	1.2	.17
D-4	1.7	.03	C-6	1.6	.09
E-4	3.8	.05	C-6	1.7	.04
E-4	1.0	.10	C-6	1.5	.26
E-4	5.6	2.51	C-6	1.5	.02
E-6	1.9	.06	C-6	5.5	.24
			C-6	1.4	.01
Hamamelis virginiana			C-6	2.5	.18
B-4	4.5	.80	C-6	2.4	.04
B-4	5.0	.44	C-6	6.5	.02
B-4	4.1	1.18	D-6	3.2	.00
B-4	2.8	1.17	D-6	1.8	.00
B-4	4.5	1.06			
B-4	7.7	.70	*Acer rubrum*		
B-4	5.4	.07	B-2	6.2	1.11
B-4	8.8	.25	B-2	2.9	1.01
B-4	2.7	1.02	B-2	2.1	.04
B-4	4.8	2.47	B-2	5.3	.01
B-4	2.4	.56	C-2	2.1	.00
B-4	2.9	1.64	C-2	1.6	.05
B-4	2.0	.93	C-2	1.6	.06
B-4	4.0	2.80	C-2	0.9	.00
B-4	2.8	.14	C-2	2.5	.10
B-4	1.0	.14	C-2	4.4	.89
B-4	1.3	.00	C-3	4.4	.09
			C-3	3.1	.11
			C-3	0.3	.00

Table 4. (continued)

Sample point	Leaf area (in²)	Area consumed (in²)
	Acer rubrum	
D-2	5.7	.16
D-2	5.7	.14
D-2	4.7	.00
D-2	4.4	.08
D-2	5.4	.00
D-2	3.7	.77
D-2	4.1	.02
D-2	1.5	.00
D-2	1.1	.00
D-2	1.5	.02
D-2	2.4	.19
D-2	4.0	.05
D-2	4.0	.40
D-2	4.0	.35
D-2	3.2	.70
D-2	2.3	.64
D-2	1.0	.07
D-2	2.2	.03
D-2	0.8	.07
D-2	2.0	.08
D-2	1.7	.01
D-2	1.8	.01
D-2	4.4	2.10
D-2	1.4	.12
D-6	6.4	.24
D-6	2.3	.33
D-6	1.8	.02
	Prunus serotina	
C-6	2.5	.00
C-6	2.9	.00
C-6	2.1	.00
C-6	3.0	.00
C-6	0.8	.00
C-6	2.6	.10
C-6	1.0	.00
C-6	1.8	.00
C-6	2.0	.19
C-6	2.8	.21
	Prunus serotina	
C-6	1.8	.00
C-6	2.1	.21
C-6	1.7	.18
C-6	2.1	.74
	Nyssa sylvatica	
D-6	8.7	.00
	Crataegus spp.	
D-3	1.5	.06
D-3	0.9	.03
D-3	2.2	.01
E-4	2.0	.01
Total	365.3	48.27
Average	3.2	.42

Table 5. Quercus alba leaf area data from 1966.

Sample point	Leaf area (in².)	Area consumed (in².)	Sample point	Leaf area (in².)	Area consumed (in².)
A-1	3.8	.03	C-4	1.9	.23
A-1	14.0	.79	C-4	2.8	.00
A-3	5.1	.00	C-4	6.4	.29
A-3	7.0	.14	C-4	7.7	.06
A-3	5.8	.89	C-4	1.4	.07
A-3	1.5	.06	D-5	2.9	.25
A-3	3.2	1.58	D-5	2.2	.51
A-3	2.6	.11	D-5	2.0	.00
A-3	7.4	1.21	D-5	8.4	.07
A-4	4.7	.11	D-5	7.2	.06
A-4	2.2	.67	D-5	2.4	.27
A-4	2.2	.29	D-5	2.2	.03
A-4	5.6	.21	D-5	1.0	.02
A-4	2.8	.01	D-5	2.9	.00
A-5	2.1	.08	D-5	8.1	.01
A-5	3.4	.45	D-5	0.5	.08
A-5	2.1	.06	D-5	5.0	.65
A-6	8.2	.39	D-5	6.9	2.56
A-6	8.4	2.48	E-2	7.4	.48
A-6	5.2	.00	E-2	2.2	.94
A-6	5.2	.03	E-2	6.0	2.17
A-6	2.6	.00	E-2	3.3	.06
A-6	2.9	.10	E-2	3.8	1.34
A-6	2.4	.05	E-3	6.7	.01
A-6	1.2	.00	E-3	5.1	.00
A-6	3.9	.10	E-3	3.6	.00
A-6	2.7	.11	E-3	4.4	.46
B-4	3.8	.15	E-3	6.6	.18
B-4	5.5	.04	E-3	4.6	.08
B-4	4.3	.71	E-3	3.4	.02
B-5	5.8	.17	E-3	6.0	1.12
B-5	0.8	.13	E-3	4.2	.08
B-5	7.9	1.07	E-3	12.7	5.49
B-5	3.2	1.52	E-3	3.5	.80
B-5	3.6	.01	E-3	1.1	.39
B-5	4.6	.01	E-3	1.1	.00
B-5	14.4	4.35	E-3	7.0	.83
C-3	4.7	.00	E-4	5.8	.76
C-3	3.2	.02	E-4	4.8	.30
C-4	5.7	.00	E-4	5.3	.53

Table 5. (continued)

Sample point	Leaf area (in^2)	Area consumed (in^2)
E-4	2.5	.95
E-4	4.0	.37
E-4	2.2	.32
E-4	1.0	.03
E-4	6.7	.07
E-4	4.7	.02
E-4	8.3	.45
E-4	6.2	1.27
E-4	2.1	.67
E-5	5.1	.02
E-5	6.2	.60
E-5	4.0	1.14
E-5	4.4	.13
E-5	4.7	.36
E-5	3.7	.55
E-6	13.6	8.38
E-6	11.9	1.31
E-6	1.2	.13
E-6	2.1	.36
E-6	2.4	.10
Total	463.2	56.56
Average	4.6	.57

Table 6. Quercus velutina leaf area data from 1966.

Sample point	Leaf area (in^2)	Area consumed (in^2)	Sample point	Leaf area (in^2)	Area consumed (in^2)
A-1	12.8	.46	B-5	5.2	3.65
A-1	6.4	.04	C-3	6.6	.19
A-1	9.4	.35	C-3	7.0	3.18
A-1	13.5	9.17	C-3	9.4	4.45
A-1	13.6	.29	C-3	7.3	.52
A-1	6.8	.08	C-4	8.8	.09
A-1	4.3	.75	C-4	4.8	1.07
A-1	5.0	1.30	C-4	6.2	.53
A-3	6.6	.90	C-4	5.2	1.90
A-3	5.6	.02	C-4	3.0	.03
A-3	8.0	.07	C-4	3.4	.75
A-3	7.7	.23	C-4	4.9	2.99
A-3	7.4	1.29	C-4	2.4	.72
A-3	3.4	.82	D-2	7.5	.00
A-3	11.6	3.32	D-2	6.0	1.11
A-4	12.0	.07	D-2	17.5	9.26
A-4	5.4	.62	D-2	7.4	.00
A-4	5.0	.30	D-2	6.5	.57
A-4	8.8	.85	D-2	2.7	.10
A-4	8.7	1.88	D-4	9.3	.12
A-4	4.9	.03	D-4	11.0	1.05
A-4	6.6	.04	D-4	16.5	2.45
A-4	5.2	1.79	D-4	7.5	.19
A-4	4.1	.96	D-4	2.9	1.20
A-5	6.5	2.15	D-4	5.4	.35
A-6	9.0	.19	D-4	11.2	.01
A-6	4.1	.01	D-4	8.8	3.87
A-6	5.5	.01	D-4	6.9	.00
A-6	4.5	.10	D-4	3.1	.50
A-6	4.6	.92	D-4	1.4	.29
B-4	17.5	1.21	D-4	2.9	.49
B-4	11.4	1.63	D-5	16.8	1.02
B-4	3.5	.85	D-5	2.4	.00
B-4	5.7	.87	D-5	3.8	.03
B-5	5.2	.26	D-5	7.4	.46
B-5	11.8	.60	D-5	5.5	2.49
B-5	7.6	.16	D-5	0.1	.04
B-5	7.0	.90	E-2	4.7	2.37
B-5	3.8	.59	E-2	2.8	1.37
B-5	1.7	.00	B-5	11.8	.46

Table 6. (continued)

Sample point	Leaf area (in^2)	Area consumed (in^2)
E-2	3.4	.01
E-2	3.6	.01
E-3	7.0	.95
E-3	9.6	1.45
E-3	11.4	2.02
E-3	4.9	.00
E-3	3.7	.24
E-4	6.6	.00
E-4	7.1	3.25
E-4	7.1	.93
E-4	12.2	1.61
E-4	2.6	.96
E-4	5.4	1.13
E-5	10.0	.51
E-5	6.7	1.09
E-6	13.4	4.72
E-6	6.7	.10
E-6	5.0	.54
E-6	3.2	.43
E-6	1.5	.23
Total	687.3	106.13
Average	6.9	1.06

Table 7. Cornus florida, Sassafras albidum, Smilax rotundifolia, Hamamelis virginiana, Acer rubrum, Prunus serotina, Nyssa sylvatica, Amelanchier sp., Crataegus spp., Desmodium sp., Ceanothus americanus, and unidentified leaf data from 1966.

Sample point	Leaf area (in^2)	Area consumed (in^2)	Sample point	Leaf area (in^2)	Area consumed (in^2)
	Cornus florida				
A-1	2.9	.00	D-4	7.1	.66
A-3	3.7	.00	D-4	4.8	.00
A-4	3.5	.00	D-4	2.5	.00
A-4	6.4	.04	D-4	3.7	.01
A-4	7.2	.23	D-4	6.8	.00
A-4	3.2	.06	D-4	4.6	.00
A-4	4.1	.13	D-4	3.4	.03
A-4	5.3	.01	D-4	6.2	.02
A-4	5.7	.00	D-5	2.7	.01
A-4	1.8	.02	D-5	3.3	.02
A-4	5.1	.37	D-5	3.6	.01
A-4	2.3	.17	D-5	6.2	.02
A-4	3.3	.01	D-5	5.3	.00
A-4	2.3	.40	D-5	4.7	.11
A-4	2.2	.04	D-5	2.5	.00
A-4	3.2	.19	D-5	5.4	.04
A-4	3.2	.13	D-5	1.7	.00
A-4	4.0	.55	D-5	2.8	.18
A-4	5.3	1.40	D-5	3.4	.07
A-4	4.1	.54	D-5	1.2	.00
A-4	4.8	.63	C-4	3.5	.50
A-4	3.8	.97	E-3	2.9	.00
A-4	1.7	.05	E-4	6.6	.00
A-4	4.2	.07	E-5	3.3	.00
A-4	2.9	.40	E-6	4.5	.00
A-4	1.1	.00	E-6	6.5	.00
A-4	0.6	.00	E-6	1.6	.02
A-4	0.6	.00	E-6	1.5	.00
A-4	0.5	.03	E-6	4.4	.00
A-4	0.4	.00	E-6	3.9	.00
A-4	0.4	.00	E-6	1.8	.02
A-4	0.3	.00			
A-4	1.7	.01		Sassafras albidum	
B-5	6.9	.03	A-1	9.5	.01
B-5	3.6	.03	A-1	0.5	.00
B-5	2.5	.00	A-1	7.1	2.27

Table 7. (continued)

Sample point	Leaf area (in²)	Area consumed (in²)
	Sassafras albidum	
A-3	4.6	.02
A-3	9.9	.00
A-3	4.3	.00
A-3	1.6	.00
A-4	5.2	.00
A-4	4.4	.00
A-4	7.2	.00
A-4	5.3	.29
B-5	0.8	.00
C-3	1.4	.00
C-3	16.8	.01
C-3	6.3	.27
D-4	2.6	.00
D-4	2.0	.00
D-4	0.7	.01
D-5	6.7	.10
E-3	2.8	.00
E-3	8.7	.09
E-6	0.5	.00
E-6	2.5	.03
	Hamamelis virginiana	
B-4	2.3	.00
B-4	1.6	.01
B-4	4.3	.37
B-4	1.2	.00
B-4	1.9	.11
B-4	8.3	.86
B-4	5.2	.04
B-4	6.7	.05
B-4	10.3	.10
B-4	5.4	.35
B-4	6.5	.22
B-4	4.6	.05
B-4	6.2	.33
B-4	6.2	.19
B-4	7.8	.63
B-4	6.2	.08
B-4	4.9	.68
B-4	4.8	.60
B-4	2.0	.05
B-4	3.0	.00
B-4	2.2	.03
B-4	1.6	.10
B-4	10.6	.23
A-5	1.8	.00
	Smilax rotundifolia	
A-5	1.0	.00
A-5	0.7	.00
A-5	0.8	.00
A-5	1.4	.00
A-5	3.3	.00
A-5	0.7	.00
A-5	2.9	.00
A-5	2.2	.00
A-5	2.2	.00
A-5	1.1	.00
A-5	1.3	.00
A-5	0.9	.01
A-5	2.0	.00
A-5	2.0	.04
A-5	2.5	.00
A-5	0.5	.00
A-5	1.4	.28
A-5	0.5	.00
A-5	1.0	.00
A-5	2.2	.00
C-4	1.1	.00
C-4	1.0	.00
C-4	1.4	.00
C-4	1.3	.00
C-4	1.7	.13
C-4	1.3	.00
C-4	1.2	.03
C-4	1.0	.02
C-4	2.7	.00
C-4	1.1	.00
C-4	2.2	.01

Table 7. (continued)

Sample point	Leaf area (in^2)	Area consumed (in^2)	Sample point	Leaf area (in^2)	Area consumed (in^2)
	Acer rubrum			Desmodium sp.	
A-4	0.4	.00	C-3	0.6	.00
A-6	3.8	.03	C-3	0.6	.02
A-6	5.0	.08	C-3	0.3	.02
A-6	2.1	.00	C-3	0.3	.02
C-3	1.5	.00	C-3	0.2	.00
D-2	3.5	.84			
D-2	1.1	.00		Ceanothus americanus	
D-4	6.7	.69	E-5	0.6	.00
D-4	3.5	.01	E-5	0.1	.00
D-4	4.3	.18	E-5	0.7	.00
D-4	5.5	.00	E-5	1.1	.03
D-4	4.4	.07	E-5	1.2	.30
D-4	4.8	.79			
D-4	0.9	.05		Unidentified	
D-4	1.0	.06	E-6	0.3	.00
E-3	3.8	.12			
E-3	4.5	.00	Total	606.2	20.42
E-3	4.2	.02			
E-3	5.6	.00	Average	3.3	.11
	Prunus serotina				
A-6	3.1	.01			
A-4	1.6	.25			
E-2	1.7	.03			
	Nyssa sylvatica				
A-4	7.4	.02			
	Amelarchier sp.				
A-6	2.7	.00			
	Crataegus spp.				
A-1	0.6	.00			
A-1	2.1	.00			
A-1	0.9	.00			

LITERATURE CITED

Boyce, D. A. 1969. Vegetational Analysis of Several Oak Forest Stands Located in the Allegan State Game Area. Unpublished manuscript. Pp. 1-23.

Bray, J. R. 1961. Measurement of Leaf Utilization as an Index of Minimum Level of Primary Consumption. Oikos 12:70-74.

_______________. 1964. Primary Consumption in Three Forest Canopies. Ecology 45:165-67.

Bray, J. R. and E. Gorham. 1964. Litter Production in Forests of the World, p. 101-157, in Cragg, J.B., (Ed.), Advances in Ecological Research, Vol. 2. Academic Press, New York.

Challinor, D. 1968. Alteration of Surface Soil Characteristics by Four Tree Species. Ecology 49:286-90.

Cottam, G. and J. T. Curtis. 1956. The Use of Distance Measure in Phytosociological Sampling. Ecology 37:451-60.

Crossley, D. A. 1966. Radioisotope Measurement of Food Consumption by a Leaf Beetle Sp. *Chrysomela Knabi* Brown. Ecology 47:1-8.

Golley, F. B. 1961. Energy Values of Ecological Materials. Ecology 42:581-84.

Gottshall, T. B. 1967. An Analysis of the Leaf Litter of an Oak Forest Area, to Determine Estimates of Leaf Production and Consumption. Unpublished manuscript. Pp. 1-27.

Hodgson, J. R. 1969. Populations of Some Mammals of Oak Forests in Southwestern Michigan. Unpublished Master's thesis, Western Michigan University. Pp. ii + 85.

Kenoyer, L. A. 1934. Forest Distribution in Southwestern Michigan as Interpreted from the Original Land Survey (1826-32). Papers of the Michigan Academy of Science, Arts, and Letters 19:107-11.

Ovington, J. D. 1965. Organic Production, Turnover, and Mineral Cycling in Woodlands. Biological Reviews 40:295-336.

Ovington, J. D. and D. Heitkamp. 1960. The Accumulation of Energy in Forest Plantations in Britain. J. Ecology 48:639-646.

Rothacher, J. S., F. E. Blow, and S. M. Potts. 1954. Estimating the Quantity of Tree Foliage in Oak Stands in the Tennessee Valley. J. Forestry 52:169-73.

Traczyk, T. 1967. Studies on Herb Layer Production Estimate and the Size of Plant Fall. Ekologia Polska Seria A, 15(47):837-67.

Wenger, J. D. 1969. Primary and Secondary Energy Availability in an Oak Forest. Unpublished manuscript. Pp. 1-17.

Whittaker, R. H. 1966. Forest Dimensions and Production in the Great Smoky Mountains. Ecology 47:103-21.

Whittaker, R. H., N. Cohen, and J. S. Olson. 1963. Net Production Relations of Three Tree Species at Oak Ridge, Tennessee. Ecology 44:806-10.

Woodwell, G. M. and R. H. Whittaker. 1968. Primary Production in Terrestrial Ecosystems. Am. Zoologist 8:19-30.