A Preliminary Study of Organic Detritus in a Tropical Forest Ecosystem*

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(Received for publication October 8, 1964)

Studies made on various ecosystems, such as marshes (TEAL, 11, ODUM and DE LA CRUZ, 8), old fields (ODUM, CONNELL and DAVENPORT 9; MEN-HINICK, 5; WEIGERT and EVANS, 12), and forest (BRAY, 1, 2; ODUM, 6), have indicated that a very small percentage of plant material is consumed while in the living state. Most of the organic matter in the form of dead plant parts is channelled to the ground where it decays, and as detritus, becomes food for a host of heterotrophic organisms. In the forest where the greater portion of treeleaves falls to the forest floor, the major energy pathway, therefore, is via the detritus food chain, i. e., the consumption of dead plant tissue rather than the green living parts as in the grazing food chain.

Five aspects of detritus were studied in a tropical Lower Montane Wet Forest in Costa Rica, namely; 1) the utilization of living tree-leaves; 2) the rate of leaf fall; 3) the decomposition of litter; 4) the standing stock of organic detritus; 5) the litter-soil organisms.

^{*} This work was undertaken as a part of the Fundamentals of Tropical Biology Course held at the Universidad de Costa Rica during the summer of 1964. The program was under the auspices of the Organization for Tropical Studies and financially supported by a grant from the United States National Science Foundation (GE-4705).

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THE STUDY AREA

The major portion of this work was carried out 30 Km NW of San Jose, Costa Rica. The study area was located on a mountain slope about 1980 m in elevation, with a thick secondary growth, and classified according to HOLD-RIDGE's system of world plant formations and life zones (3) as a Lower Montane Wet Forest: 12-24°C (Av. Mean Monthly Temperature $>O^\circ$) and 2000-4000 mm annual precipitation).

MATERIALS AND METHODS

Freshly fallen intact leaves (indicated by green or yellow coloration and superficial position on the lap of the forest litter) were collected at random while pacing the forest floor and picking up leaves (which were immediately dried in a plant press) at specified pace intervals. Per cent of leaf area removed by insects as indicated by "holes" eaten in the leaves was determined after the methods of BRAY (1) and ODUM (6). The total leaf area and the damaged-eaten areas were measured by means of the "dot" grid. Each leaf was overlain with the transparent dot grid (160 dots/sq. in.) plastic sheet and the number of dots over the total leaf and over the holes within the leaf area were counted. In cases, where portions of a leaf edge were removed, an outline estimate of the original leaf perimeter was drawn. Per cent utilization was estimated on area basis as computed from the number of dots counted. Ten-gram samples of dead leaves collected in like manner were enclosed in series of nylon net bags (15 \times 25 cm with 2.5 mm mesh-openings), returned to the forest floor and analyzed for the following: 1) Decomposition as measured by weight loss after the manner of OLSON and CROSSLEY (10) and ODUM and DE LA CRUZ (8). A series of litter bags were grouped in sets of 3 bags. Two bags out of the set of 3 were processed for the decomposition study (the remaining 1 bag was saved for arthropod extraction) by collecting one set every 2 weeks, washing gently of soil material and weighing. With sets of assumed identical bagged samples, periodic measurements were made without disturbing or interrupting decomposition; 2) Arthropod composition by means of funnel extraction. A Berlesé apparatus was improvised consisting of a 6-inch diameter laboratory glass funnel ringed on an iron stand and heated by a desk lamp with a 40-watt bulb. Extraction of the bagged litter samples was carried out for 8 hours; 3) the role of litter arthropods in decomposition by application of insecticide. Four litter bags were separated into sets of 2; 1 set was sprayed in excess with commercial Dieldrin-DDT compound 1 (treatment was repeated every 2 weeks) and the other set left untreated for 6 weeks.

By means of 0.5 m^2 baskets fashioned of chicken wire (2 cm mesh), rate of leaf fall was measured by periodic collection of the leaves falling into the baskets. Four baskets were positioned and pegged on the forest floor and "harvested" every 2 weeks.

¹ Registered commercial trademark - Black Flag Insecticide.

Samples of detritus at various stages of decay (arbitrarily designated as litter, duff and humus, according to position in the forest floor strata) were collected and bacterial suspension of each fraction was prepared by crushing each of the 3 samples into a homogeneous mass and suspending 2 gm aliquots in 10 ml BHI medium. Bacterial composition was examined by ordinary plating technique on nutrient agar and on other selective types of media.

The standing stock of organic detritus was determined by random sampling of the forest floor with m² quadrats. Samples collected included only the loose material (i. e., litter and duff) easily raked from the ground surface. Standing stock of detritus in other forest types such as Montane Rain, Tropical Moist and Tropical Dry forest were obtained and compared with the study (Lower Montane Wet) forest.

RESULTS AND DISCUSSION

UTILIZATION OF LEAVES BY HERBIVORES

The per cent utilization of tree-leaves for a small sample of 3 species and a mixed sample of 16 species was estimated as shown on Table 1. The per cent "grazed" by insects is lower than the 6-12% utilization stimated for northern broad-leaved forests (BRAY, 2), but within the 1-7% utilization observed for a Puerto Rican Forest (ODUM, 6). It appears that herbivore consumption of treeleaves is greater in higher latitudes than in the tropics. The differential amount of utilization in different species is probably due to: 1) ecological position of the species, (ODUM estimated 1-5% utilization for overstory species and 8% for understory species as compared to 0.3% and 2-5% respectively in the present work) and 2 leaf palatability, as demonstrated by BRAY when leaf utilization was correlated with nutrient content. It may be noted that grazing by mammals, birds and others is not considered here. Furthermore, utilization by organisms which leave no holes (e. g., sucking insects) is not measured by the present method.

Table 2 shows the rate of leaf fall. Anolysis of variance showed no statistically significant difference (0.975 > p > 0.950 with 2 df) among the 12 individual samples collected (Table 2), thus indicating a constancy in the rate of leaf fall during the short period the study was made. Leaf fall was estimated to be 21 gms/m²/mo or approximately 3 tons/ha/yr. KIMURA (4) calculated for two types of Japanese forests 4-5 ton/ha/yr of organic matter deposition and observed seasonal variation in the rate of leaf fall (a phenomenon especially true in deciduous forests). Estimates of organic matter accumulation in the present effort were conservative and partial since stems, branches, bark, etc. were not included.

STANDING STOCK OF DETRITUS

The mean standing stock of detritus in the study forest was 613 gms/m² (500-766 gms/m²) or approximately 6.5 tons/ha. Table 3 compares the standing stock of detritus in the study forest with other types of tropical forests examined

TABLE 1

Utilization of tree-leaves in a Tropical Lower Montane Wet Forest, in Costa Rica

Species	Ecological niche	No. lvs. sampled	Mean leaf area con- sumed cm²	Mean orig- inal leaf area cm ²	% Utilization		
					Mean	S. D.	Range
Oreopanax	Overstory	10	0.07	36.1	0.28	0.57	0.0-1.9
Miconia	Understory	10	0.48	26.8	1.85	0.49	().()-4.()
Drimys	Understory	10	1.16	29.9	4.78	5.11	().3-14.8
Mixed sample (16 species)		23			5.59	6.94	0.7-20.3

TABLE 2

Collection Date	Gm/m² dry wt.	Calculated Gm/m²/y
July 25	10.45	250.80
Aug. 23	10.90	261.60
Aug. 9	9.80	235.20
Mean (S.D.)	10.38 (3.8)	272.80

Rate of leaf fall measured as gm dry weight of litter accumulated per 2 weeks in a Tropical Lawer Montane Wet Forest in Costa Rica. (Each number represents the mean of 4 individual basket-samples)

in Costa Rica. It can be seen in Table 3 that the Tropical Moist Forest had the lowest standing stock of detritus indicating that the optimum rate of decomposition takes place in the warm-moist environment. The amount of detritus present on the forest floor is dependent on the rate of leaf fall and on the decomposition

TABLE 3

Standing stock of organic detritus in 4 different types of forest ecosystems in Costa Rica. (Forest types classified according to the Holdridge Lize Zone System)

	Number	Calc. D	Dry Weight	(Gm/m²)
Forest Ecosystems	of Samples	Mean	S. D.	Range
Montane Rain (Poás)	8	1046	313	666-1500
Lower Montane Wet (Vara Blanca)	10	613	95	500- 766
Tropical Moist (V. del General)	10	455	155	266- 733
Tropical Dry (Guanacaste)	6	800	202	500-1000

rate. Leaf fall is influenced by both the physiological properties of the plant and physical factors, primarily wind. Decomposition, on the other hand, is influenced by local conditions of moisture and temperature. Data on both leaf fall and decomposition rate in the 4 forest types examined are necessary to further evaluate the existing differences in the standing stock of litter detritus.

DECOMPOSITION OF LITTER

Organic matter accumulation is a function of both the rate of deposition and the rate of decomposition. Figure 1 shows the decomposition rate of litter in the study area. After 35 days in the field, approximately 50 % of the original weight of the sample was lost (i. e., decomposed). This rate was faster than that reported by WITKAMP and OLSON (14) for pine, oak, and maple forests where the half-time (T $\frac{1}{2}$), i. e., the time required for half of a given amount of litter to decompose was 393 days. KIMURA (4) found decomposition rate of 25% in one year in a Japanese forest where the mean temperature was 70° C. Decomposition, in the present study, measured only the relative rate material was removed from the 2.5 mm mesh nylon net bags.

LITTER-SOIL ORGANISMS

The microfauna and microflora of forest detritus are important ecological components that require intensive studies to understand the metabolism of forest ecosystems. An attempt was made to examine the organisms in the litter to determine whether: 1) the litter arthropods play a significant role in the initial breakdown of detritus, a condition that may be necessary for optimum microbial activity; 2) a heterotrophic succession occurs during the process of decomposition.

By means of a Berlesé funnel, litter arthropods were extracted and examined from 10 gm litter samples contained in nylon mesh bags and exposed in the field for 7, 12 and 21 days. Table 4 shows that collembola increased in

TABLE 4

Two dominant arthropod components of 10-gm litter samples enclosed in mesh bags and exposed in the field for different lengths of time. (Each figure is the result of analysis of 1 litter bag sample. Number in parenthesis indicates number of kinds or species recognized)

Dominant Forms	Number of days in the field			
	7	14	21	
Collembola		20 (2)	30 (2)	
Mites	10 (4)	70 (9)	60 (11)	

number while the mites showed increasing kinds as the bagged litter sample was exposed for longer periods of time. Two species of collembola and 11 species of mites were recognized. Other groups of organisms such as millipedes, dipterans spiders, snails, insect larvae, etc. were also noted.

To assess the role of arthropods as "preliminary decomposers", samples of litter were sprayed with commercial Dieldrin-DDT compound. Comparing treated and untreated samples, the treated sample exhibited very little decomposition and a decided absence of arthropods. Bacterial suspensions of treated and untreated samples were plated on nutrient agar at the end of the experiment. Superficial examinations made on both plated samples showed bacterial growth, suggesting that the bacterial population presumably was not affected or only initially affected by the insecticide treatment. Only one test, based on superficial appearance of the plates, was made. Neither qualitative nor quantitative determination was carried out so that the above suggestion is subject to further study and analysis. Consideration of the general effect of insecticides on forest litter (with all the implications thereof), although it may lead one into "controversial grounds", is an intriguing subject for research and is extremely important.

Examinations made on the litter, duff and humus (as representative components of detritus in varying states of decay) indicated that microbial population varies in the 3 fractions. Nutrient agar, as well as other types of media: Levine EMB, MC and SS (Difco Manual, 9th edition) plates of humus samples in general had fewer kinds of bacterial colonies than the litter and duff fractions. The following observations were noted: 1) presence of orange colonies in all 3 fractions suspected to be *Flavobacterium*, a genus of Achromobacteriacea; 2) absence of yellow colonies presumably of the protein digesting *Pseudomonas* group in the humus fraction; 3) presence of higher fungal growth in the humus fractions. It has been reported that seasonal as well as successional changes occur in the microbial populations of leaf litter (WITKAMP, 13).

CONCLUSION

In the tropical forest types examined in this study, the major energy flow is undoubtedly via the detritus food chain. Detritus is a very important component of the forest floor and in itself may be considered as a dependent ecosystem exhibiting heterotrophic succession and diversity (ODUM and DE LA CRUZ, 7). The composition (i. e., structure) of the detritus ecosystem in the forest floor is dependent on the types of forest vegetation, and its metabolism (i. e. function) is controlled for the most parts by activities of the microfauna and microflora that inhabit it. There are presumably as many "detritus formations" as there are "plant formations" supporting as many "litter-animal associations" and influencing formation of as many "soil types". The detritus ecosystem is a stratified ecosystem and its component parts exhibit size gradient, from the leaf-size of the upper litter-layer to the microscopic partides in the humus stratum. The stratification is a physical manifestation of the sequence of fragmentation and decomposition, and the food value of the detritus particle increases as microbial activity transforms the original organic base to bacterial protoplasm. The detritus system further offers a wide gradient of food size to the detritus consumers, a condition that not only allows for diversity but also favors stability of the ecosystem (ODUM and DE LA CRUZ, 7).

ACKNOWLEDGEMENTS

I am grateful to Miss Ivana M. Gardner of the University of California (Santa Barbara) for valuable assistance in the initial stages of the field work; to Dr. James L. Vial of the OTS for the use of his laboratory facilities and to Dr. McDonald Fulton of the L.S.U. - I.C.M.R.T. for his help in the bacterio-logical aspects of this study and for the tentative identification of the bacteria. Thanks are also due to Lic. Maryssia Nassar C. and Lic. Norma Rivero O. of the Universidad de Costa Rica for the use of their laboratory equipment. I am also grateful to my OTS co-participants and collegues who shared the expenses for the rental of field vehicle, especially to Sr. Ronaldo Zuccho of the Universidade de Río Claro, Soo Paulo, Brasil. To Dr. Richard G. Wiegert of the University of Georgia Radiation Ecology Laboratory who reviewed and criticized the manuscript, my utmost appreciation.

SUMMARY

A study of organic detritus in a Lower Montane Wet Forest site in Costa Rica was carried out, showing that herbivores consumed about 5% of leaf material, while 95% or less became forest floor detritus; litter fall averaged 21 gm/m²/mo or approximately 3 ton/ha/yr.

The standing stock of organic detritus and average rate of detritus weight los were measured, and estimates of species and number of arthropods present in the litter were attempted. Insecticide treatment of litter slowed in the litter were attempted. Insecticide treatment of litter slowed. down the rate of decay indicating the role litter-soil arthropods may play in fragmentation of detritus. Differences observed in the microbial population of litter, duff and humus components suggest that a heterotrophic succession accompanies the process of decomposition.

RESUMEN

En el ecosistema de bosque, el flujo mayor de energía se lleva a cabo vía cadena alimenticia detritus, es decir, el consumo de tejidos vegetales muertos en lugar de partes verdes vivientes como ocurre en la cadena alimenticia herbívora.

En un bosque húmedo montano bajo en Costa Rica, el porcentaje de utilización de hojas vivas por herbívoros fue de 5% o más, mientras que un 95%o menos de hojas caían al suelo del bosque y, como detritus, servían de alimento a numerosos heterótrofos. La caída de detritus tuvo un promedio de 21 gms/m²/mes o aproximadamente 3 toneladas/hectárea/año. La existencia de detritus orgánico era de 613 gms/m² o cerca de 6.5 toneladas/ha. Aproximadamente 50 % del peso original de muestras de detritus puestas en redes de nylon se perdió (por descomposición) después de 5 semanas de exposición en el campo. Se intentó estimar el número de especies de artrópodos presentes en el detritus. Muestras de detritus tratadas con insecticida, cuando se compararon con muestras no tratadas mostraron una descomposición más lenta, indicando el importante papel que juegan los artrópodos en la fragmentación preliminar y descomposición del detritus. Exámenes bacteriológicos del detritus en diferentes estados de descomposición mostraron una diferencia en la población microbiana del detritus, polvo y componentes húmicos, lo que sugirió que una sucesión heterotrófica acompaña el proceso de descomposición.

El detritus orgánico del bosque tropical es a la vez una reserva y una fuente de energía. La gran abundancia de detritus orgánico en el piso del bosque es un índice incuestionable de su importancia, y demanda, por lo tanto, estudios detallados posteriores para determinar el papel que juega en la ecología de los bosques tropicales.

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Fig. 1. Decomposition rate as per cent loss of initial dry weight at start of experiment of litter in a Tropical Lower Montane Wet Forest. (Each point represents average of 2 litter bags).

