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Litter dynamics in a mixed oak forest on the New Jersey Piedmont[1]

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LANG, GERALD E. (Dept. Bot., Rutgers Univ., New Brunswick, New Jersey 08901). Litter dynamics in a mixed oak forest on the New Jersey Piedmont. Bull. Torrey Bot. Club 101: 277–286. 1974.—Litter deposition and the standing crop of the L and F layers of the forest floor in the William L. Hutcheson Memorial Forest were measured over a two-year period from September 1971 to September 1973. The mean annual total litter fall was 648.1 g m^{-2}; 72% was leaf tissue, 17% branches, and 11% fruits. 87% of the leaf fall occurred during the autumn months while both fruit and branch deposition were continuous but variable throughout the year. The three-year mean minimum standing crop of leaf litter in the L and F layers was 483.7 g m^{-2}; branches ≤ 2.5 cm in diameter and fruit parts accounted for an additional 371.2 and 18.2 g m^{-2}, respectively. Turnover time for leaf litter was calculated to be 1.5 years, and for branches approximately 4 years. Leaf litter decomposition rates were estimated to be 3.75 g m^{-2} day^{-1} during the autumn months and 0.8 g m^{-2} day^{-1} during the remainder of the year. Using litter fall data, net above-ground production was calculated to be 15.5 mt ha^{-1} yr^{-1}. Predictions based on actual evapotranspiration gave net production estimates of 10.7 and 14.0 mt ha^{-1} yr^{-1}. These three estimates are compared with the range of values cited in the literature.

The importance of the detritus pathway in terrestrial and especially forest ecosystems is well documented. From the literature cited by Rodin and Bazilevich (1967), I have calculated a 30–94% range (65% average) for annual detritus input as a percentage of net above-ground production for 12 deciduous forests, over a range of ages and types. For 12 coniferous forests, the range is 39–80% (67% average). Detrital input increases as a percentage of net production with age. The remaining net production is divided disproportionately between the grazing pathway (*ca.* 5–10%) and tree biomass accumulation. Eventually, of course, much of this accumulated biomass is added to detritus if not harvested, often in a catastrophic event. With maturity, and before such an event, as much as 90% of net above-ground production in mature forests will eventually enter forest floors through leaf, branch, and bole deposition. This dead organic matter plays a major role in determining ecosystem structure and function. For example, detritus represents an energy source for heterotrophic organisms, a nutrient reservoir for intrasystem cycling, and a regulatory factor influencing forest hydrology.

If, through ecosystem development, forests evolve to steady-state conditions, forest floors must also attain such status. In the steady-state condition, energy storage would be relatively constant since input to the forest floor through litter fall should theoretically equal output due to decomposition (Olson 1963). However, old age status of forest floors is difficult to establish. Deviations from steady-state conditions are caused by seasonal and annual variations in leaf litter input, large pulse inputs of falling trees and branches, and environmental constraints on decomposer activity. Thus, one must realistically expect a certain margin of variation around a steady-state average.

This paper explores the likelihood of steady-state conditions within a mature forest by measuring forest floor dynamics. It is hypothesized that if the forest floor

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is in steady-state and remains undisturbed, the pool size of the litter (L) and fermentation (F) layers, *sensu* Lutz and Chandler (1946), should remain relatively constant from year to year since input and output would be equal. Specifically, the objectives were to: 1) quantify litter deposition, 2) measure the standing crop of the L and F layers of the forest floor, and 3) estimate turnover rates for these layers.

Study site. This study was conducted at the William L. Hutcheson Memorial Forest, a 26.3 ha mixed oak forest located on the New Jersey Piedmont (40°30′ N, 74°34′ W) 14 km west of New Brunswick. Hutcheson Forest is a remnant of a once much broader forest type characteristic of the New Jersey Piedmont. It receives approximately 112 cm of rainfall each year (Biel 1958) and has an average annual actual evapotranspiration of 64.8 cm (Robertson 1973). Three species of oak including white oak (*Quercus alba* L.), red oak (*Q. borealis* Michx.), and black oak (*Q. velutina* Lam.) dominate the overstory with some red hickory (*Carya ovalis* (Wang.) Sarg.) and white ash (*Fraxinus americana* L.) present. The understory is dominated by flowering dogwood (*Cornus florida* L.) and the shrub layer by maple-leaved viburnum (*Viburnum acerifolium* L.). Monk (1957, 1961) has described the vegetation in detail.

The forest is located on well drained, silt-loam, Brown Earth soil developed under a podzolic soil-forming environment from underlying Triassic red shales at a depth of $\geqq 0.7$ m (Ugolini 1964). The litter (L) layer averages 2–3 cm thick before autumn leaf fall and up to 6 cm immediately afterwards (Lang unpublished data). A 1–2.5 cm F layer is present above an amorphous, highly organic A_1 horizon (Ugolini 1964). According to Bridges (1970), the surface organic matter would be classified as a moder or acid mull humus.

The history of the forest is well known back to 1701 and has been described by Buell et al. (1954) and Buell (1957). Two specific historical aspects are important. First, no fires, either natural or unnatural, have occurred since 1711, and second, the forest has not been cut. The biggest disturbance to the forest resulted from a series of hurricanes and the consequent natural harvest of trees (Reiners and Reiners 1965). Some windthrown trees were removed after a major storm in 1950, but these trees were located in an area excluded from this study (Monk 1957). Thus the forest floor has probably not been unnaturally disturbed for at least two centuries. Hutcheson Forest has been described as approximating climax (Bard 1952), near-virgin (Monk 1957), and mature (Monk 1961). The many large trees, some exceeding 63.5 cm dbh and 225 years of age (Monk 1957), suggest that at least the adjective mature is valid, although there is some evidence suggesting further change in species structure (Monk 1961, Sulser 1971). In terms of community structure and energetics (Odum 1969), the present forest probably approaches steady-state conditions.

Methods. LITTER DEPOSITION. Sixteen litter traps were placed at random on the forest floor to measure tree and shrub litter inputs from September 1971 to September 1972; only ten traps were used between September 1972 and September 1973. Each trap was 0.67 m^2 and constructed of wooden sides 15 cm high with a fiberglass mesh bottom. The interval between collection dates varied according to the rate of litter deposition and the rate of litter decomposition. When either was high, collections were made more frequently; collections were made weekly during the fall, monthly during the winter, and biweekly during the spring and summer. I assumed that no decomposition of the captured litter occurred during the interval between collections. *In situ* litter decomposition studies verified that such decomposition was insignificant. Litter was separated into leaf, flower and fruit, and branch components. Leaf material was dried at 105 C for 24 hr and weighed to the nearest 0.1 g. Branches and fruits were dried for 48 hr before weighing.

FOREST FLOOR STANDING CROP. The standing crops of the L and F layers of the forest floor were sampled in September 1971, August and December 1972, and March and August 1973. The August and September samples represented a minimum mass and were assumed to be more readily comparable from year to year. Eight 0.5×1.0 m plots were established at random within a 50×100 m study area. The L and F layers were collected separately; bark and branches $\leqq 2.5$ cm diameter and fruit structures were pooled from both layers. All material was dried and weighed as

Table 1. Annual litter deposition (oven dry weight) for the periods September 16, 1971 to September 18, 1972 and September 18, 1972 to September 16, 1973 in Hutcheson Forest.[1]

Component	1971–1972			1972–1973			Average	
	g m^{-2}	SE	% of total	g m^{-2}	SE	% of total	g m^{-2}	% of total
Leaf	493.4a	9.8	68.9	439.1a	27.4	75.6	466.3	71.9
Branch and bark	127.4a	6.5	17.8	94.0a	12.9	16.2	110.7	17.1
Flower and fruit	94.9	15.0	13.3	47.4	1.6	8.2	71.2	11.0
Total	715.7	21.9	100.0	580.5	16.3	100.0	648.1	100.0

[1] Statistically similar means for yearly deposition for each component were determined by the Least Significant Interval Method with $P \leq .05$ (Sokal and Rohlf 1969) and are indicated by similar lower case letters. The standard error of the mean (SE) is given as a measure of variation for each mean.

reported for the litter deposition measurements.

Results. LITTER DEPOSITION. Table 1 compares the total annual litter deposition for the two years and presents the two year average. Deposition was greater in 1971–1972 for every component of the litter, and the total for 1971–1972 was 135 g m^{-2} higher than for 1972–1973. Leaf deposition was 54.3 g m^{-2} lower in 1972–1973; this represents a 10% decrease from the 1971–1972 value. Fruit deposition in 1971–1972 was twice that for 1972–1973. Most of this difference is accounted for by a peak mast year for acorns in 1971. Yearly differences in fruit and branch deposition were 50 and 26% lower, respectively, in 1972–1973 than in 1971–1972. The fraction of the total litter that each component makes up is quite similar for both years.

The seasonal rates of leaf litter deposition are given in Table 2. Seasons are based on the phenology of the forest and correspond to autumn leaf fall, winter dormancy, and summer growth. Although the time intervals are slightly different for each season from year to year, the percentage of the total annual deposition is similar (Table 2): 87% of leaf fall and 72% of the total litter input occur during the mid-September to mid-December interval. Peak leaf deposition occurred during a 7–10 day interval in the last part of October and the first part of November in each year. By mid-December, all leaves had fallen except for a few isolated oak leaves. The early summer inputs are associated with the production of leaf fragments as a result of insect larval activity. Branch and fruit input on the other hand were continuous but variable throughout the year with no pronounced peaks.

Analysis of the variation in litter fall revealed that only ten litter traps were required to produce a 5% standard error of the mean for total leaf input, so that 16 traps were adequate for making deter-

Table 2. Seasonal input of litter (oven dry weight) for the period September 16, 1971 to September 16, 1973 in Hutcheson Forest.

Season	Number of days	Litter dry weight (g m^{-2})	g m^{-2} day^{-1}	% of annual total
LEAF LITTER				
September 16–December 17	92	422.5	4.59	85.6
December 17–May 17	152	3.0	.02	.6
May 17–September 18	124	67.9	.55	13.8
Annual total	368	493.4	1.34	100.0
September 18–December 12	85	386.8	4.55	88.0
December 12–May 27	166	8.9	.05	2.1
May 27–September 16	112	43.4	.39	9.9
Annual total	363	439.1	1.21	100.0
TOTAL LITTER				
September 16–December 17	92	513.3	5.58	71.7
December 17–May 17	152	54.8	.36	7.7
May 17–September 18	124	147.6	1.19	20.6
Annual total	368	715.7	1.94	100.0
September 18–December 12	85	417.7	4.91	72.0
December 12–May 27	166	71.2	.43	12.2
May 27–September 16	112	91.6	.82	15.8
Annual total	363	580.5	1.60	100.0

minations of statistical size differences between years. The amount of leaf litter deposited per unit area was quite comparable on an annual basis. Litter traps were designed specifically to measure leaf input and thus their small sample areas were not as effective in measuring branch fall. A 20% standard error was obtained for branch deposition with ten traps.

FOREST FLOOR STANDING CROP. The mean forest floor standing crop for all sample dates is presented in Table 3. The mean values for the five sampling periods for each component were compared using the Least Significant Interval Method, $P \leq .05$ (Sokal and Rohlf 1969).

Three important points arise from these data. First, no significant difference occurs between the L and F layers when the pool size is at a minimum. This year-to-year constancy is suggestive of an unvarying net interaction between decomposition and deposition. Factors which affect net aboveground production and subsequently the amount of litter deposition most often affect decomposition too, and in the same direction. For example, a growing season with greater than average precipitation may increase net production and litter deposition, but it will also increase decomposition. A hot, dry growing season may have the opposite effect. Second, seasonal variations in the L and F layers obviously reflect increases due to inputs from leaf fall, as in December, and reductions following input as decomposition progresses. This seasonal oscillation is especially evident in the L layer standing crop but is still apparent for changes in the F layer. December and March F layer values are statistically different using $P \leq .10$ level of significance. Third, the large variation in the branch component prevents any discernment of seasonal trends in that compartment. This occurs as a result of large spatial variation in branch deposition on the forest floor. This response is probably true for fruit parts as well.

Discussion. LITTER DEPOSITION. Yearly fluctuations in the amount of litter deposited have been demonstrated by Bray and Gorham (1964), Sykes and Bunce (1970), Gosz et al. (1972), and this study. The two-year average for litter deposition is, I believe, a good estimate for the relative quantity of the different components and in particular leaf input. The 28% non-leaf litter value falls within the 27–31% range given by Bray and Gorham (1964). Temporal variations both within and between years are closely correlated to environmental and biological agents. In general, storms may cause premature litter deposition within years and clearly influence annual variation in branch and bole inputs. Insect consumption, disease, and reduced net production may act as important biological agents affecting litter fall. These variations should be considered as part of the normal pattern of ecosystem dynamics and clearly demonstrate the need for studying deposition for longer than one year if accurate characterization and description are the primary objectives. For a detailed assessment of the temporal dynamics of leaf fall and subsequent impact on nutrient input and release, see Gosz et al. (1972).

Litter deposited in the litter traps is primarily from understory and canopy

Table 3. Standing crop of the litter (L) and fermentation (F) layers of Hutcheson Forest.[1]

Component	Sept. 1971		Aug. 1972		Dec. 1972		Mar. 1973		Aug. 1973		Mean minimum pool size[2]	
	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE
L layer	244.8a	28.3	220.4a	17.6	341.9b	22.4	310.4b	21.8	235.1a	14.2	233.4	11.8
F layer	233.4a	16.8	258.9ac	16.8	328.5b	30.0	291.8bc	21.8	267.6ac	17.4	250.0	10.2
L + F	468.2a	33.6	479.3a	25.8	670.4b	38.4	602.2b	18.2	502.7a	26.6	483.4	11.0
Woody tissue[3]	387.1a	58.4	414.4a	84.0	369.8a	92.0	not measured		312.1	28.2	371.2	35.0
Fruit parts[4]	16.3a	5.5	14.6a	2.5	not measured		not measured		23.8	4.6	18.2	4.6
Total	871.6a	67.0	908.3a	82.6					838.7a	49.4	872.8	37.8

[1] Values represent the mean of eight samples expressed in g dry wt m^{-2} with one standard error of the mean (SE). Statistically similar means ($P \leq .05$) for each component are indicated by similar lower case letters.

[2] Mean of September 1971, August 1972 and August 1973 samples.

[3] Includes branches ≤ 2.5 cm diameter and bark.

[4] Mostly acorns.

trees. The contribution of the understory shrubs was minimal since their density was low. However, two additional sources of error potentially exist in estimating litter deposition. First is the unaccounted for herbaceous flora. In the spring of the year, mayapple (*Podophyllum peltatum* L.) virtually covers the entire forest floor. An independent estimate of the little input due to *Podophyllum* was made as shoots of the population died in 1972 and suggests that approximately 20 g m^{-2} were added to the forest floor. Some of this material was collected in litter traps, but certainly underestimated. The 20 g are less than 4.5% of the average leaf input and only 3% of the total litter deposited. Both values are low when compared to the 9% average for herbaceous flora reported by Bray and Gorham. Because estimates were not made in 1973, these data were excluded from Tables 2 and 3 so comparisons could be made. A 20 g m^{-2} correction factor could be made to account for this added source of input.

Second, foliar inputs of organic matter via throughfall and stemflow were not assessed. From the data of Eaton et al. (1973) these inputs are probably minor and account for only slight underestimations. Subterranean inputs from dead roots were not assessed, since they do not directly affect litter layer dynamics in Hutcheson Forest.

According to Bray and Gorham's broad geographic criteria, Hutcheson Forest lies on the latitudinal boundary between cool and warm temperate forests. A 1.4 ratio for total litter to leaf litter deposition is less than the 1.6 average for warm temperate forests but identical to the value for cool forests. In terms of absolute deposition, Hutcheson Forest is higher than the 3.5 and 5.5 mt ha^{-1} yr^{-1} averages reported for cool and warm temperate forests and 4.8 mt ha^{-1} yr^{-1} average for oak forests alone. Duvigneaud and Denaeyer-De Smet (1970) report values of 3.2, 1.6 and 0.5 mt ha^{-1} yr^{-1} for leaf, branch, and fruit input, respectively for a mature oak-ash forest in Belgium, while the total for Russian high oak forests averages only 3 mt ha^{-1} yr^{-1} (Rodin and Bazilevich 1967). Hole and Nielson (cited in Bray and Gorham 1964) studied a 125-year-old forest dominated by white and black oak in northern Wisconsin (43° N). Leaf and non-leaf deposition averaged 4.6 and 1.5 mt ha^{-1} yr^{-1}, respectively. These values agree quite well with the 4.7 and 1.8 mt ha^{-1} yr^{-1} values reported here. Bray and Gorham note that once the forest canopy is closed, there is no trend for more or less leaf litter deposition, thus supporting the suitability of comparison between these two sites of different ages.

ESTIMATION OF NET PRODUCTION. None of the numerous accounts in the literature concerning Hutcheson Forest reports measured or estimated net production. Jordan (1971) developed a relationship between energy available during the growing season and the ratio of wood production to (leaf) litter production. Estimating 120 kcal cm^{-2} available solar energy during the growing season at Hutcheson Forest (Kondratyev 1969), a 2.2 ratio for the expected wood to (leaf) litter production was obtained. Multiplying this ratio by the 4.66 mt ha^{-1} of leaf litter input results in an estimate of 10.2 mt ha^{-1} annual wood production. Added to the leaf and fruit data, annual net above-ground production is estimated to be 15.5 mt ha^{-1}. For comparison, two additional estimates were made from empirical models which use actual evapotranspiration. From Rosenzweig's (1968) and the Box-Lieth (Lieth and Box 1972) models, values of 10.7 and 14.0 mt ha^{-1} were obtained as estimates of annual net production. These values are well within the range reported by Whittaker (1970) for temperate deciduous forests and near the 13.0 average. For specific comparisons, Whittaker (1966) reports values of 12.0 and 14.7 mt ha^{-1} yr^{-1} for a 30 m tall oak-hickory and chestnut oak forest in the Smoky Mountains. Duvigneaud and Denaeyer-De Smet (1970) give the net productivity for a mature *Quercus robur L.–Fraxinus excelsior* L. forest, 115–160 years old and 24 m tall, as 14.3 mt ha^{-1} yr^{-1}. The estimates for Hutcheson Forest are only a first approximation and need verification and revision.

TURNOVER TIMES. Turnover times (average pool size divided by input) are often used as expressions for estimating the residence times for material in a particular ecological compartment. That fraction of the pool annually transferred is the inverse of the turnover time ratio expressed as a percent (Reiners and Reiners 1970) and is an estimate of decomposition when considering forest floors. This parameter, which is equivalent to k′ for steady-state forest floors (Olson 1963), integrates the biological and environmental factors affecting decomposition as measured by weight loss. Under steady-state conditions, such estimates are reasonable and provide a valuable means for comparing various pools and their fluxes.

In this study, the forest floor standing crop represents the pool, and the inputs through litter deposition are assumed equal to the outputs through decomposition. The mean standing crop was determined by averaging the mean minimum value (Table 3) and the theoretical maximum value (the minimum plus the average annual litter deposition from Table 1). The high pulse input of litter during the autumn months, which accounts for 87% of leaf fall (Table 2) and 72% of the total annual input, makes this a realistic maximum standing crop estimate. Table 4 contains the calculated turnover times.

The 100% turnover of the L layer in Hutcheson Forest results from the definition used to separate the forest floor organic matter. Shortly after leaf fall most of the previous year's litter comminutes and would be classified as F layer material, i.e. fragmented and partially decomposed dead organic matter. Thus this material has a one-year residence in the L layer, and a pulse input of a fraction of the old L material into the F layer occurs at the end of the growing season.

Total input to the F layer was determined to be 308 g m^{-2} yr^{-1}, 223 g from the old litter added to the F layer shortly after autumn leaf fall and 75 g from comminution of leaves in the L layer throughout the year (Lang 1973). If one-half of the F layer is added to the humus or A_1 soil horizon as an estimate of the actual transfer, and no net accumulation occurs, this further implies that *ca.* 100 g m^{-2} yr^{-1} are turned over in these horizons.

Table 4. Turnover times and fractional annual turnover for various floor components in Hutcheson Forest. See text for description of the calculations.

Component	Turnover time (years)	Fraction of annual turnover %
L layer	1.00	100.0
F layer	1.31	76.2
L and F layers	1.53	65.1
Woody tissue[1]	3.85	25.9
Total weighted average	2.36	42.4

[1] Includes branches ≤ 2.5 cm diameter and bark.

The kinetics of the combined L and F layers give a 65.1% fractional turnover value (Table 4). This estimate is very similar to direct independent estimates of decay rates (k′) which give a 69% weight loss in one year to tethered white oak leaves lying on the forest floor (Lang 1973). Woodwell and Marples (1968) found a 66% weight loss after one year for similarly tethered white oak leaves in an oak-pine forest on Long Island. My data suggest that the average turnover time for leaf material on the forest floor at Hutcheson Forest is 1.5 years.

As a check on branch turnover, I determined the decay rates for tethered small branches, 1.0–2.5 cm in diameter, of red maple (*Acer rubrum* L.) and black oak (unpublished data). After one year, the red maple branches had lost between 16–24% of their initial weight compared to only a 10–15% loss for black oak. Considering that the decay of wood is slow initially due to high C:N ratios and reduced surface to volume ratios, these values underestimate the overall process, and suggest that a four-year turnover is reasonable.

A weighted turnover time for the total leaf, branch, and fruit material lying on the forest floor is 2.4 years (Table 4). It is difficult to make comparisons to many other forests because of the lack of uniformity in sampling and reporting of data. However, I was able to calculate a 3.2- (2 years for the L) and 5.2-year turnover time for similar L and F material from the data of Reiners and Reiners (1970) for a northern pin oak forest and from Woodwell and Marples (1968), respectively. A 2.3 year turnover was also obtained for the "litter" of a *Q. robur* forest from the data of Rodin and Bazilevich (1967). As a final comparison, Hopkins (1966) reported a six month turnover for fresh leaf material in the moist semi-evergreen deciduous forest at Olokemeji, Nigeria. If the refractory humus (H layer) were included in the above calculations, the turnover times would, of course, be much longer. In general, turnover times are fastest in warm humid environments with active soil flora and fauna populations, for example, tropical forests, and slowest in cool, nutrient-limited conditions

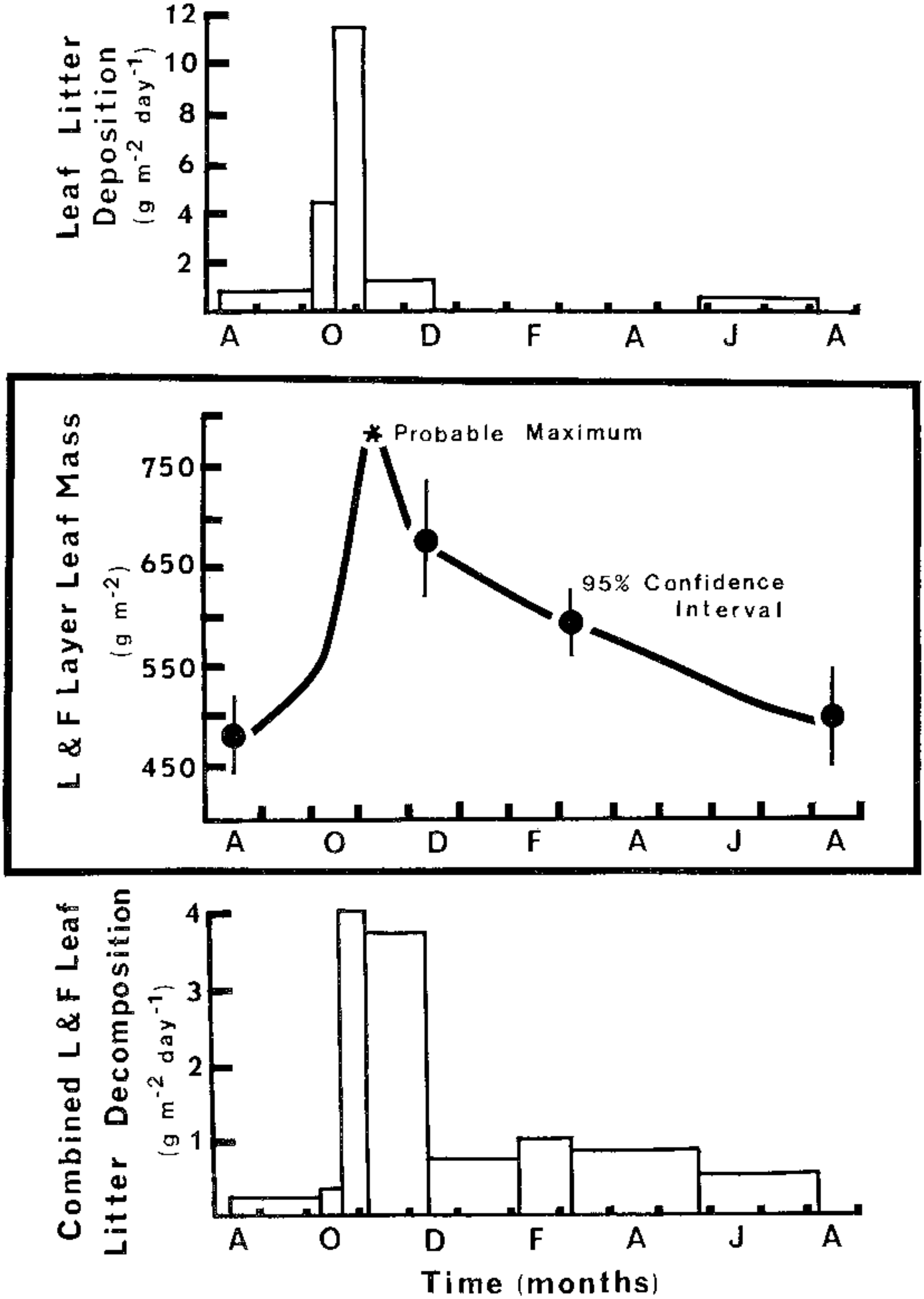

Fig. 1. Annual patterns for dynamics of leaf litter on the forest floor and regulatory processes in Hutcheson Forest. See text for explanation of data.

with reduced soil fauna activity, e.g. northern boreal forests.

FOREST FLOOR DYNAMICS. According to Olson (1963), a theoretical maximum limit for forest floor storage at steady-state conditions would be the minimum storage pool plus litter input. For Hutcheson Forest, a rough estimate of this value for leaf material within the L and F layer would be 880 g m^{-2} (480 g minimum mass plus a 400 g input in the fall of the year). This value is probably an overestimate, since decay is continuous and initially rapid for leaf material and since decomposition is spread over a two month period. A more realistic value for maximum storage might center around 780 g m^{-2}. This value is based on the pulse input of *ca.* 300 g m^{-2} in late October. By December, L and F mass was only 670 g m^{-2}. The mean steady-state standing crop, taken as half the value between the probable maximum and observed minimum, would be 630 g m^{-2}. With the addition of the mean branch and fruit pool sizes from Table 3, which are assumed to estimate steady-state conditions for these components, since their input is continuous throughout the year, a 1020 g m^{-2} steady-state storage value is obtained for the combined L and F layers.

Again, it is difficult to make meaningful comparisons to other forests. At best, the minimum total L and F layer mass (872 g m^{-2}, Table 3) for Hutcheson Forest is less than the 1260 g m^{-2} L and F layer total mass in a Minnesota oak forest reported by Reiners and Reiners (1970), the 1595 g m^{-2} litter, excluding humus, given by Woodwell and Marples (1968) for the oak-pine forest of Long Island, and the 1184 g m^{-2} "litter" reported by Monk et al. (1970) for an oak-hickory forest in Georgia. The reduced mass at Hutcheson Forest probably reflects the relatively fast turnover previously discussed.

Fig. 1 is a graph of the seasonal dynamics for the forest floor standing state and the dominant regulatory processes for the period August 1972 to August 1973. The histogram for leaf litter input was plotted from the data. The pattern for the total L and F leaf litter standing crop is based on the rates of litter deposition and observed storage values, the asterick (*) value represents the probable maximum of 780 g m^{-2}. This curve would not be as smooth as shown, but in fact, would be irregular with many minor peaks associated with additional input and deep troughs correlated with high decomposer activity. However, the general trend is correct. The histogram for decomposition rates, which represent reductions in the combined L and F leaf litter mass, was computed by means of the following equation:

$$(P_t + I) - P_{t+1} = D$$

P_t *and* P_{t+1} are, respectively, pool size at the beginning and end of some time interval; I is the input from leaf litter deposition and D is the amount lost through microbial respiration or transfer to the underlying A_1 or humus layer as determined by subtraction.

Based on these calculations, decomposition of the total leaf litter mass in both the L and F layers of the forest floor was highest in the late autumn months, averaging 3.75 g m^{-2} day^{-1} between mid-October and mid-December. This is attributable to the high amount of material present, part of which is also of high nutritional quality (Gosz et al. 1972), and to the rather warm and moist environment at this time of year, which favors microbial activity and the leaching of soluble organic and inorganic material. During the remainder of the year, the rate of decomposition was about 0.8 g m^{-2} day^{-1}, dropping to a low of 0.2 g m^{-2} day^{-1} during August and September. Low temperature limits microbial activity in the winter months, and litter desiccation and low quality material limit microbial activity during the summer. On a much finer scale, however, there would be many isolated short-term periods throughout the year when the rate of decay would be greater or less than the seasonal averages.

FOREST FLOOR STEADY-STATE. The small differences in minimum values for forest floor mass support the probability that conditions are as close to a steady-state as may be found for an ecosystem like Hutcheson Forest. Based on my data, this steady-state pool has a high degree of constancy, i.e. similar year to year storage conditions that include fluctuations due to seasonal and annual temporal dynamics. There is no evidence to suggest that the forest floor has any internal control on its steady-state but rather it is dependent on both the quality and quantity of inputs and environmental conditions as they affect plant productivity, input periodicity, and microbial activity. Pool size will show little variability to the extent that these factors remain constant. If, for example, a surface fire burned off the L and F layers but did little other damage to the forest, it would take three years for leaf litter storage (11.5 years for small branches) to reach 95% of its previous mass based on previous rates of litter deposition and decomposition according to Olson's models for forest floor dynamics (substitute turnover time values from Table 4 herein for *k* in Tables 1 and 2 in Olson (1963) for branch and leaf litter, respectively).

There are many variables which can cause changes in standing pool size. For example, if, as suggested by Monk (1961) and Sulser (1971), there are ongoing changes in species composition which will change the species structure of the forest, there may be a slow compensatory readjustment of the steady-state mass over a long time period. Also, if forests go through periods of catastrophic destruction followed by regrowth (Reiners and Reiners 1965), the associated changes in the quality of litter plus modification of microclimatic features may alter standing states of forest floors. Additionally, any change in the present forest environment to longer periods of moist, warm weather, or an increase in an essential nutrient limiting to microbial populations (e.g. aerosol deposition) would act to increase decomposition and reduce the standing crop. Acid rain, on the other hand (Likens et al. 1972), may cause essential nutrients to be leached from the litter and soil horizons, thus decreasing nutrient availability for mircoorganisms and thereby reducing decomposition rates and increasing forest floor standing states. If nutrient availability is decreased over a period of years, plant productivity may also be reduced, thereby causing less litter deposition and a smaller pool size.

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