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Reviewed work(s):

Source: *Ecological Monographs*, Vol. 42, No. 1 (Winter, 1972), pp. 71-94

Published by: [Ecological Society of America](#)

Stable URL: <http://www.jstor.org/stable/1942231>

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STRUCTURE AND ENERGETICS OF THREE MINNESOTA FORESTS¹

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ABSTRACT

Three contiguous ecosystems, an upland oak forest, marginal fen, and cedar swamp, were analyzed along a gentle topographic gradient on the Anoka Sand Plain in east-central Minnesota. The organic structure and aboveground primary productivities of these forests were compared with similar data for other natural ecosystems of the sand plain. Living, aboveground biomass totals of the oak, fen, and swamp forests were 124.6, 98.8, and 159.6 mt/ha, respectively. Aboveground, net annual productivities were 8.9, 7.1, and 10.3 mt/ha, respectively, which compared well with other forest data for the region and with a predicted value based on actual evapotranspiration.

Several measures of structure were compared in the analysis. Species richness and equitability were greatest in the marginal fen where biomass and productivity were the least. Richness and equitability were lowest in the oak forest. The highest biomass-to-production ratio was found for the *Thuja* swamp, although it had the highest annual production. Apparently the high production in the swamp was achieved with a large mass of relatively inefficient foliage concentrated in *Thuja occidentalis*.

The percentages of primary production entering detritus pathways were 52, 62, and 48 for oak, fen, and swamp, respectively. Total detritus, including dead boles, branches, and forest floors, was large in relation to living biomass in all three forests, but was especially important in the fen and swamp systems where deep forest floors had accumulated. Total detritus was 61%, 331%, and 577% of aboveground biomass in the oak, fen, and swamp, respectively.

All data were produced in caloric as well as weight units.

INTRODUCTION

The primary objective of this study was to compare certain structural characteristics of three forests with some fundamental measures of energy flow.

¹ Received January 11, 1971; accepted June 28, 1971.

Structural characteristics of special concern were basal area, density, biomass, foliage biomass, and complexity in terms of the distribution of primary productivity among species. The aspects of energy flow measured were primary production, flow through

detritus pathways, and the accumulation of energy in detritus. A second objective was to compare these results with data published for other ecosystems of the study area in order to analyze patterns of primary production between landscape units.

The study area

This work was carried out on the Anoka Sand Plain of east-central Minnesota, a sandy outwash plain of approximately 2,202 km² (850 square miles) lying just north of Minneapolis-St. Paul, Minnesota (Fig. 1). The geological character and origin of the plain have been described by Cooper (1935). Although generally level, local relief is contributed by kettle lakes, drainage courses, and dunes. The steep moisture gradient caused by a high water table and droughty sand, together with slope aspects of dunes and a long fire history, have created a richly varied vegetational complex. Natural vegetation units include prairie; oak savanna; oak, pine, and swamp forests; shrub carrs; marshes; littoral communities; and lakes and bogs (Rand 1953, Pierce 1954). Agriculture has never been more than moderately successful on the sand plain, so that much of the area is in natural, albeit disturbed, vegetation.

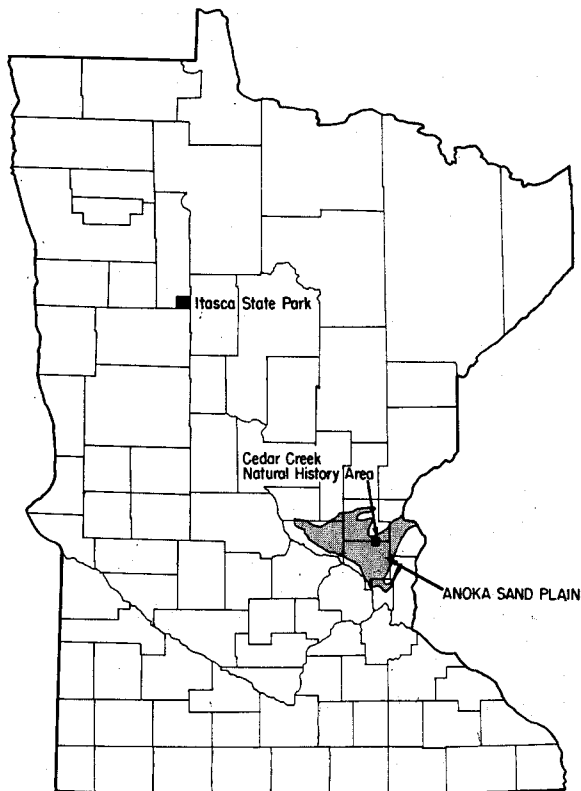


FIG. 1. Cedar Creek Natural History Area, the site of this study, is shown within the Anoka Sand Plain of east-central Minnesota. Itasca State Park is indicated in the northwestern part of the state (see section on phytosociological relationships).

This study was conducted at Cedar Creek Natural History Area, located 48 km (30 miles) north of Minneapolis on the sand plain (Fig. 1). The three forest types investigated are typically found in close proximity along topographic gradients extending from the sand upland to peat-filled basins of old lakes or water courses. Water, and probably nutrients, limit vegetation growth on upland sites, but both become increasingly available downslope towards the intersection of sand and organic substrata. Here the water table approaches the surface, and nutrients leached from the upland become available for the growth of vascular plants and the nutrition of heterotrophic microorganisms. At increasing distances in the basin away from this point of intersection, nutrients become less available and peat less humified.

Vegetational physiognomy varies markedly along these topographic gradients. In the site studied (SW 1/4, Sec 27, T 34 N, R 23 W) the swamp forest of the basin is dominated by an evergreen conifer, *Thuja occidentalis* (white cedar), which produces a dense canopy and strong microclimatic effect throughout the year. Here the soil freezes late in the fall and may not thaw until late May, and understory strata are sparse. The upland forest is dominated by *Quercus ellipsoidalis* (northern pin oak). A moderate amount of light penetration through the canopy contributes to the growth of shrub and herbaceous strata. This more open canopy, the well-drained sandy soil, and a slight southern exposure permit significant temporal variation in air temperature, soil temperature and moisture (Reiners 1968), soil frost conditions, and snow depth.

The zone of intersection between the upland oak forest and cedar swamp has been termed a "marginal trench" (Cooper 1913), a "moat" (Curtis 1959: 233), and in this and other wetland areas of Minnesota, a "marginal fen" by Conway (1949). Conway described a marginal fen as that part of a bog under the influence of relatively base-rich waters draining down the slopes of higher ground, and having a sedge-alder-willow vegetation on neutral or near-neutral peat. The term is the exact homologue of the Scandinavian term "lagg" (cf. Godwin and Conway 1939). In the interest of preserving terminology, marginal fen has been retained as the name of this ecosystem.

Marginal fen physiognomy and species structure reflect the high water table and nutrient-rich conditions of this zone. Tree growth and survival are restricted, possibly due to fluctuations in depth of the narrow rooting zone, or chronic loss to windfall. Although occasional *Thuja occidentalis* grows in this zone, most of the canopy species are deciduous, including *Fraxinus nigra* (black ash), *Acer rubrum* (red maple), and *Ulmus americana* (American elm). The canopy is thin and incomplete, contributing to

patchy patterns of stratification, microclimate, and species distribution. Below the canopy layer, *Alnus rugosa* (alder) and *Corylus cornuta* (beaked hazel) thickets are intermixed with luxuriant fern beds and sedgy swards. In all three forests, heights of dominant trees are approximately 17 m.

Since primary productivity varies with successional age of stands (Møller, Muller, and Nielsen 1954, Ovington 1962, Rodin and Bazilevich 1967), it was important to estimate the maturity of the three forests in the study area. Increment borings and other evidence (Reiners and Reiners 1970) indicate that both the present-day oak and fen forest trees are 45–50 years old. The cedar swamp contains dominant trees of two age classes: one 90–100 years and another about 70 years old. Present interpretation is that the swamp was clear-cut or leveled by windfall about 100 years ago, and then partially cut or blown down about 70 years ago. In general terms, trees of the oak and fen forests are of equal age, 45–50 years, about half the age of trees in the cedar swamp.

Botanical nomenclature throughout this paper follows Fernald (1950).

The forest floors, representing detritus pools of these ecosystems, have been described by Reiners and Reiners (1970). The oak forest floor is relatively thin, approximately 7–8 cm deep, varying locally between a mor and mull. The fen forest floor consists of a muck about 25 cm deep below thin L and F layers. The cedar swamp forest floor is massive by definition since it is a woody peat deposit ranging from 1 to 2 m deep. It consists of L and F layers and some portion of the peat layer (H). The portion of peat to be included as forest floor is defined by an estimate of the zone of active mineral exchange in this deposit. Although roots rarely penetrate below 35 cm, vertical transfer of nutrients is likely at greater depths through downward leaching during dry seasons and upward transport in the fall and spring when water tables rise. As a solution to this problem of definition, the upper 70 cm of peat (H) was arbitrarily delimited as the "active" zone and also the "forest floor."

METHODS

The study area was composed of the three forest types occurring in sequence along a gradual slope. Contour lines and borders between forest types were approximately linear and parallel in the study area permitting the definition of sample areas for the three forests into contiguous rectangular units, 20 m down the slope and 80 m along the contours. Each of these units was subdivided into sixteen 10- by 10-m contiguous quadrats. The following data were obtained: solar radiation input; forest biomass; aboveground, net, primary production; energy flow through detritus pathways; and energy accumulation in detritus

of forest floors. All organic values were estimated in terms of mass and energy.

Solar radiation

Radiation data were collected by Prof. Donald G. Baker, University of Minnesota, at a station in St. Paul, Minnesota, located 48 km (30 miles) south of the study area. Radiation was sensed with a 50-junction Eppley pyranometer (180° pyrliometer) and recorded on a model 15 Honeywell recorder with an integrator. Wavelengths transmitted through the glass dome of this sensor ranged from 0.29 to 5.0 μ with greater than 70% transmissivity between 0.32 and 4.2 μ , and with greater than 90% transmissivity from about 0.35 to 2.5 μ . (Baker and Haines 1969).

Visible light data were collected between 1100 and 1300 hr CST on a clear day in mid-June with a Weston illumination meter. Readings were recorded at 1 m and ground level at 60 points in each forest. The points were established at 2-m distances along long axes of the forests.

Vegetation

Trees.—All stems, dead and living, and taller than 1.4 m (4.5 ft), were tallied in the study plots excepting those of American hazel (*Corylus americana*) and beaked hazel (*Corylus cornuta*), which were defined as shrubs. Information collected on each tree included species, location by quadrat, diameter at breast height to 0.1 inch (0.225 cm), whether living or dead, and whether it was an individual stem or member of a sprout ring. Every stem was given an identification number, and data were recorded on punch cards. Each species population was divided into dead and living classes, and these, in turn, were organized into 0.5-inch (1.125-cm) interval dbh size classes.

Sample trees were chosen from each species population by first tabulating the size-class distribution pattern for the species, then determining the size classes to be represented in sampling. The criteria for these decisions were: (1) at least 10% of the total stems in a population were sampled; (2) sampling was weighted around the peaks of the size-class distribution curves; and (3) the entire range of size classes was represented. Individual stems were then randomly selected from within size classes to be sampled.

Restrictions within Cedar Creek Natural History Area prohibited cutting living trees for assessment of mass and growth rates. Alternatively, trees were climbed to gather necessary data. Each tree was climbed with the aid of a sectional ladder as high as flexibility of the main stem permitted. This height was determined primarily by the taper and stiffness of the main stem. Thus, within species, trees were sampled at approximately the same stem diameter.

The following data were collected on each living tree: (1) diameter above basal swell; (2) diameter of the stem at the highest point climbed; (3) thickness of basal bark; (4) thickness of bark at the highest point climbed; (5) length of bole from the ground to the highest point; (6) average annual wood increment over the last 10 years at breast height; (7) weight of dead wood attached directly to the bole up to the highest point; and (8) number of branches within basal diameter size classes (0.5-cm increments up to 5 cm diameter and 1-cm increments above 5 cm). Seventy-six living trees were sampled in this way—the number within species varying with size-class range and population size. Several minor species were not sampled. The following substitutions were made for these species: regressions for *Betula papyrifera* were used for *Populus grandidentata*, *Prunus serotina*, and *Larix laricina*; regressions for *Ostrya virginiana* were used for *Carpinus caroliniana*; and regressions for *Ulmus americana* were used for *Cornus alternifolia*.

Branch data from sample trees were tabulated by size classes within each species. Representative branches of these classes were randomly selected as described for sample trees and cut in late August and early September for separation into dead wood, leaves, current shoots, old wood and bark, and fruits. This season was the approximate peak of biomass (Ovington, Heitkamp, and Lawrence 1963) and preceded the translocation of nutrients from leaves back into woody tissues. The portions of the sample trees above the point reached in climbing were treated as branches, so within a species several trees were topped and added to branch samples for dissection. Samples of branch material were oven-dried for 48 hr at 55° C in forced-draft ovens. Dry weight corrections were then applied to fresh weights.

Thuja occidentalis presented a special problem in separating current foliar growth from total foliar mass. A search of the literature and several inquiries among plant morphologists and ecologists established that apparently no-one has yet analyzed the complex pattern of terminal appressed leaf growth, scale thickening, and branchlet abscission in *Thuja* and related conifers to determine the proportion of foliage representing a current year's production. The assumption that turnover of cedar foliage is about 35% was made in this study on the basis of foliage turnover in other conifers. Similar percentages are 45% for *Pinus rigida* (Whittaker and Woodwell 1969), ca. 50% for *Pinus echinata* (Whittaker, Cohen, and Olson 1963), 26% for *Abies balsamea* (Baskerville 1965), and 35% for *Picea g'auca* (Clark 1961). Discussion of the range of error associated with this assumption is given in the following section.

Log-log, and in a few cases, arithmetic linear regression equations were calculated for dry weight of

branch components by branch basal diameter. Annual lateral growth of combined wood and bark of old branch material was estimated by dividing total weight by age estimates derived by age/diameter regressions. Estimates of total weight of branch components on sample trees were then calculated on the basis of these regressions together with branch inventories taken while climbing trees. From these estimates new regressions of weight of branch fractions by bole diameter at breast height were calculated. These regressions were applied, in turn, to the inventory of stems on the forest plots to estimate total weight of branch material by species within forests.

Tree boles were treated as frustra of right cones in this study since they were truncated at the upper limit of bole measurement. The total volumes of the truncated boles were estimated by the equation

$$V = \pi \frac{h}{3} (r_1^2 + r_1 r_2 + r_2^2),$$

in which h is the bole height, r_1 is the radius at the base, and r_2 is the radius of the truncated top. The volume of the woody portion of the bole was calculated by subtracting bark thicknesses from bole radii and recalculating volume. The difference between total bole volume and wood volume was bark volume.

Lateral wood increment was calculated with the formula for a curved surface of the frustrum of a right cone:

$$A = \pi (r_1 + r_2) \sqrt{h^2 + (r_1 - r_2)^2}.$$

Area data calculated by this formula were multiplied by the mean wood increment derived from increment borings corrected for variation with height by a factor of 1.2 (Whittaker 1966), which gave volume estimates of lateral wood production.

Lateral bark increment on boles was estimated as a proportion of wood increment (Whittaker 1966):

$$\Delta \text{ bark} = \text{total bark} \times \frac{\Delta \text{ wood}}{\text{total wood}}.$$

Conversions of wood- and bark-volume estimates to dry weight were obtained by multiplying volumetric estimates by wood and bark density values. Densities in dry g/fresh cm³ were determined by both immersion and direct volume measurements of increment cores, cross sections of large branches, and bark samples removed from living trees.

By these procedures estimates of total bole wood, lateral wood increment, total bark, and bark increment were calculated for each sample tree. Dead wood in the form of dead branches attached directly to the bole had been directly measured by weight in the sampling process. Log-log regressions for all of these parameters were calculated on tree diameter at breast height. From these regressions and tree inven-

tories, bole parameters were calculated for all trees in the three forests.

Standing dead trees were tabulated in diameter classes and samples selected as described for living trees. These were felled, sectioned, weighed, and corrected to dry weight.

Shrubs.—*Corylus americana* and *C. cornuta* were the only species treated as tall shrubs. In each forest these were sampled in two, randomly placed 1- by 1-m quadrats in every 10- by 10-m quadrat. Shrub sample area represented 2% of the area in each forest. All stems within these quadrats were clipped at the base and divided into dead wood, old wood and bark, current wood and bark, and leaves.

Herbs and low shrubs.—Two 1- by 0.5-m quadrats were randomly placed in each 10- by 10-m quadrat. Thus each forest study plot had 32 herb quadrats representing 16 m², or 1% of the area for herb sampling. These quadrats were visited fortnightly through the summer of 1967, and density data were recorded until senescence in individual species began to appear. At that time plants of the species in question were collected in the vicinity of quadrats in which they had been recorded. Plants were collected regardless of condition along lines extending from a specified corner of the herb quadrat to the center of the 10- by 10-m quadrat. The number of individuals collected near a quadrat was determined for each species by plant size, density, and number of quadrats in which it occurred. This material was separated into aerial and subterranean organs, cleaned, dried as described for trees, and weighed. Density data were multiplied by dry weight per plant to give subterranean and aerial weights for herbs and low shrubs by species.

In the cases of low shrubs, further separation into old wood and bark, current wood and bark, and leaves was required.

Litter fall

Tree and tall shrub litter fall was collected from June 1965 through May 1967 in square, 0.5-m² litter traps with 15.2-cm side walls and bottoms of copper window screen. The screen bottoms were held in light contact with the forest floor. Six of these traps were randomly placed in each forest.

Tree and tall shrub litter was collected weekly from these traps during autumn, fortnightly during spring and summer, and whenever snow and ice permitted during the winter. The bulk of the litter consisted of leaves, but also included twigs, bark, flower parts, fruits, dead insects, and insect frass.

Litter contribution by herbs and low shrubs was also collected in the small herb quadrats described above. The shoots of herbs and leaves of low shrubs were collected in weekly visitations as they died through late summer and fall of 1966 and during

early spring 1967. All litter material was dried for 5 days at 55° C.

Forest floors

Forest floors were sampled during August 1966, the month when detritus was minimal. L, F, and H layers were collected from sixteen 0.5- by 0.2-m quadrats placed stratified-random fashion in each forest. In the fen and swamp, deeper samples were collected from two soil pits in each forest. Details of sampling are given in Reiners and Reiners (1970). Forest-floor material was air-dried for 2 weeks or less, then oven-dried at 55° C for 48 hr.

Calorimetry

Subsamples of all the tissues were burned in a Parr adiabatic, oxygen bomb calorimeter to obtain caloric equivalents. Subsamples from three sample trees or branches, depending on the material, were selected within each species. Each of these was tested twice or until caloric values were obtained within 100 cal/g dry weight; mean values of these replicates were used in calculating caloric content of forest mass of a particular tissue. Appropriate corrections were made for acid formation and fuse wire ignition (Parr Instrument Company 1960). Special procedures required for some of the forest-floor samples are described in Reiners and Reiners (1970).

RESULTS AND DISCUSSION

Plant-community structure

Density, basal area, frequency (percentage occurrence in sixteen 10- by 10-m quadrats), and importance values of tree populations are given in Table 1. Biomass and production data are given for tall shrubs in Table 6 and for herbs in Table 7.

Community integrity.—Species-distribution data in Tables 1 and 7 suggest a community continuum along the topographic gradient rather than three distinct forest types. This impression is supported by field observation of certain variables. Many herbaceous species were common to both the marginal fen and swamp forests, and minor vegetation and soils of the fen were definitely transitional with those of the oak forest. On the other hand, *Quercus ellipsoidalis* and *Fraxinus nigra*, the dominants of the oak and fen forests respectively, overlapped only slightly so that from the ground and air the boundary between canopies was evident. Also, the occurrence of the swamp forest dominant, *Thuja occidentalis*, in fen tabulations was based partly on fallen but still living stems extending over the fen area.

Thus, in some respects these three communities were discrete, and in other respects, continuously distributed. For purposes of interpreting data of this study, it may be most practical to view the three

TABLE 1. Structure of tree populations in the oak, fen, and cedar swamp forests—Cedar Creek Natural History Area, Minnesota

Species ^a	Oak forest				Marginal fen				Cedar swamp			
	Density (stems/ ha)	Basal area (m ² /ha)	Frequency (%)	Importance value ^b	Density (stems/ ha)	Basal area (m ² /ha)	Frequency (%)	Importance value	Density (stems/ ha)	Basal area (m ² /ha)	Frequency (%)	Importance value
<i>Populus grandidentata</i>	6	0.10	6.2	2.2								
<i>Ostrya virginiana</i>	88	0.16	31.2	12.8	6	0.02	6.2	1.4				
<i>Prunus serotina</i>	31	0.30	31.2	10.1	12	0.25	12.5	3.6				
<i>Amelanchier</i> species	200	0.23	56.2	25.3	56	0.11	18.8	6.2				
<i>Quercus alba</i>	275	1.80	75.0	39.8	12	0.05	12.5	2.8				
<i>Quercus ellipsoidalis</i>	688	19.84	93.8	135.5	112	3.70	37.5	24.7				
<i>Betula papyrifera</i>	81	1.89	37.5	20.5	44	0.40	25.0	7.3	212	6.65	81.2	42.0
<i>Acer rubrum</i>	394	2.08	81.2	49.0	312	2.46	81.2	33.4	119	0.12	43.8	14.6
<i>Alnus rugosa</i>	19	0.03	6.2	2.7	1,319	0.79	68.8	54.6	300	0.15	50.0	22.6
<i>Fraxinus nigra</i>	6	0.04	6.2	2.0	762	7.91	100.0	71.9	631	3.11	8.2	32.1
<i>Thuja occidentalis</i>					356	7.42	62.5	51.2	1,100	27.36	100.0	127.2
<i>Ulmus americana</i>					238	1.24	93.8	28.6	281	2.26	56.2	28.4
<i>Betula lutea</i>					31	0.67	18.8	6.9	50	1.67	50.0	17.1
<i>Carpinus caroliniana</i>					19	0.01	6.2	1.7	31	0.01	18.8	5.4
<i>Cornus alternifolia</i>					69	0.02	25.0	6.5	31	0.89	31.2	10.3
<i>Larix laricina</i>												
Total	1,788	26.49		299.9	3,348	25.07		300.8	2,755	42.22		299.7

^aSpecies are arranged in an approximate continuum from upland species to swamp species based on importance values.
^bImportance values represent the sums of relative density, dominance, and frequency.

forests as dominance types along a community continuum.

Distribution of numbers.—The fen had the highest density of tree stems (3,348/ha), the swamp an intermediate density (2,755), and the oak forest the lowest density (1,788/ha) (Table 1). Thirteen per cent of the stems counted as trees in the fen were alders, which might, in fact, be considered tall shrubs. If alder stems were subtracted from the totals, density in the fen would still be somewhat higher than in the oak forest, but less than in the swamp.

Basal areas in the oak and fen forests were very similar, 26.5 and 25.1 m²/ha, and much less than the basal area of the swamp, 42.2 m²/ha. *Quercus ellipsoidalis* contributed 75% of total basal area, denoting marked dominance by this species in terms of basal area. Although basal area of *Thuja occidentalis* in the swamp was higher than that of *Quercus ellipsoidalis* in the oak forest (24.4 compared with 19.8 m²/ha), *Thuja* contributed a smaller percentage of total basal area of the swamp (65%). Basal area was evenly distributed in the fen between the principal contributors, *Fraxinus nigra* and *Thuja occidentalis*.

Comparison of frequency data with density data for oak forest trees suggests clumping, or contagious distribution, for *Ostrya virginiana*. Similar comparisons with fen data indicate contagious distribution for *Thuja occidentalis*, and especially *Alnus rugosa*. Contagious distributions are also indicated for *Ulmus americana*, *Alnus rugosa*, and *Fraxinus nigra* in the swamp. All three of these species were most prominent in the fen, and their restricted distribution in the swamp resulted from their local high densities in a lobe of fen which crossed the linear fen-swamp boundary.

Importance values are synthetic measures of importance based on density, basal area, and frequency as described by Curtis (1959:74). In general, they paralleled density and basal area values, but differences occurred where species differed significantly in size from other species or were contagiously distributed (Table 1).

Densities of tall shrubs were not recorded. Biomass and production estimates for this stratum are presented in Table 6.

Density data on herbs and low shrubs are of little value for describing structure of these forests because of the great range of individual size among the numerous species. Comparisons between forests with regard to this stratum are better discussed in terms of biomass and production to follow later (Table 7).

Phytosociological relationships.—Modern phytosociological analyses have not been carried out for the Anoka Sand Plain, but studies for nearby areas provide some opportunity to relate these forests to a broader synecological context. The oak forest of this

study appears to have no clear relationship with any of Janssen's (1967) relevés for vegetation in the vicinity of Lake Itasca, Minnesota (Fig. 1). *Quercus ellipsoidalis*, the dominant upland species in the Cedar Creek oak forest, is unlisted for the Itasca stands, and the flora encompasses a wide range of upland hardwood and coniferous relevés. In comparison with Wisconsin work (Curtis 1959), the oak forest most closely resembles northern-xeric forests, but lacks the generally associated pines.

The marginal fen is closely related to Janssen's (1967) *Alno-Fraxinion nigrae* alliance, both in floristic details and ecological site characteristics. It also appears to be a special case of Curtis's (1959) northern wet-mesic forest. Curtis makes no mention of the occurrence of marginal forests of this type although he does mention a "moat" between conifer swamps and the upland (1959:233).

The cedar swamp has the closest affinities with Janssen's *Dryopterideto cristatae-Piceetum* association, a eutrophic subdivision of the *Copti-Piceion* alliance (1967). It is related to Heinselman's "rich swamp forest" which occupies minerotrophic sites of the Lake Agassiz peatlands of northern Minnesota (Heinselman 1970) and also to Curtis's *Thuja*-dominated northern wet-mesic forest (1959).

Community richness.—Since woody species were inventoried in each study area, their listing in Table 1 is complete. The listing in Table 7 for herbaceous and low shrub species only includes those recorded in the sample quadrats, however, so it is less than a full floristic list.

The upland oak forest was composed of 39 species: 10 tree species, 1 tall shrub species, and 28 herbaceous and low shrub species (Tables 1 and 7). The marginal fen forest was composed of 59 species: 14 tree species, 1 tall shrub species, and 44 herbaceous and low shrub species. The cedar swamp was composed of 43 species: 9 tree species and 34 herbaceous species. The comparative richness of the fen is, in large part, predictable because of its intermediate position between oak and swamp forests and the incursion of species into this boundary zone. The equitability component of diversity will be discussed in terms of primary production in a later section.

Energetics and structure

Tree strata.—Tree biomass and production data are given in terms of weight (Table 2) and caloric content (Table 3). Caloric coefficients can be calculated from these tables, and more specific data are available on request. Energy content of forest components basically parallel weights of components, so distribution of biomass and production are discussed in terms of weight only. Variations from this parallel relationship are described in a later section.

Aboveground biomass varied 1.6 times between

TABLE 2. Aboveground dead wood, biomass, and net annual production of the tree strata in the oak, marginal fen, and cedar swamp forests, Cedar Creek Natural History Area, Minnesota—expressed in kilograms per hectare

Species	Dead wood		Biomass							Production			
	Bole	Branches	Bole wood	Bole bark	Branch wood and bark	Current twigs	Foliage	Fruits	Total	Bole wood	Bole bark	Branch wood and bark	Total ^a
A. Oak forest													
<i>Acer rubrum</i>	90	12	4,449	430	2,500	32	468	—	7,880	317	47	130	995
<i>Alnus rugosa</i>	—	2	—	—	41	0.5	1	—	42	—	—	2	4
<i>Amelanchier</i> sp.	15	16	492	77	111	1	33	—	715	57	9	8	109
<i>Betula papyrifera</i>	59	8	5,875	970	2,592	32	249	48	9,764	235	38	154	755
<i>Fraxinus nigra</i>	2	0.1	98	16	25	0.6	6	—	145	4	0.6	1	12
<i>Ostrya virginiana</i>	7	0.4	408	46	118	5	30	0.8	608	32	4	9	80
<i>Populus grandidentata</i>	2	0.6	313	46	102	2	13	—	475	15	2	8	39
<i>Prunus serotina</i>	3	0.9	478	73	173	2	20	—	745	22	3	12	60
<i>Quercus alba</i>	109	89	6,266	782	1,157	42	303	—	8,551	297	38	54	734
<i>Quercus ellipsoidalis</i>	8,700	1,535	74,060	9,740	9,045	188	2,315	—	95,348	2,582	340	489	5,913
Total ^b	8,988	1,663	92,439	12,181	15,862	305	3,437	48	124,273	3,561	482	867	8,700
B. Fen forest													
<i>Acer rubrum</i>	118	16	5,619	457	3,307	31	534	—	9,949	317	44	142	1,069
<i>Alnus rugosa</i>	—	20	—	—	1,028	9	52	—	1,089	—	—	75	136
<i>Amelanchier</i> sp.	13	17	243	34	43	0.6	11	—	332	22	3	3	40
<i>Betula lutea</i>	17	0.1	2,127	320	1,103	2	77	37	3,666	65	10	39	230
<i>Betula papyrifera</i>	2	2	1,221	216	510	12	52	7	2,018	43	8	36	158
<i>Carpinus caroliniana</i>	0.2	0.03	26	3	10	0.7	3	0.1	43	3	0.3	0.9	8
<i>Cornus alternifolia</i>	0.3	1	45	9	17	1	7	—	79	3	0.7	1	13
<i>Fraxinus nigra</i>	676	37	20,410	3,064	7,595	98	912	—	32,079	552	86	281	1,928
<i>Ostrya virginiana</i>	1	0.05	58	6	16	0.5	4	0.1	85	4	0.5	1	10
<i>Prunus serotina</i>	8	1	762	129	350	4	33	—	1,278	29	5	20	91
<i>Quercus alba</i>	3	1	138	20	29	1	9	—	198	8	1	1	20
<i>Quercus ellipsoidalis</i>	1,664	317	14,345	1,836	1,789	35	440	—	18,444	499	64	93	1,131
<i>Thuja occidentalis</i>	832	4	17,207	1,361	3,853	—	1,523 ^c	44	23,989	529	43	148	1,297
<i>Ulmus americana</i>	110	155	2,650	424	1,533	18	204	—	4,828	94	15	51	381
Total ^b	3,446	571	64,851	7,880	21,182	212	3,860	89	98,075	2,168	280	892	6,512
C. Swamp forest													
<i>Acer rubrum</i>	3	0.4	193	32	93	3	28	—	349	29	5	9	74
<i>Alnus rugosa</i>	—	4	—	—	193	2	11	—	206	—	—	14	27
<i>Betula lutea</i>	49	0.2	5,442	808	2,828	4	185	120	9,387	154	23	94	579
<i>Betula papyrifera</i>	34	21	21,666	3,785	10,937	238	964	184	37,773	553	97	700	2,736
<i>Cornus alternifolia</i>	0.06	0.3	15	3	5	0.5	2	—	27	1	0.3	0.5	5
<i>Fraxinus nigra</i>	191	8	7,307	1,168	2,201	41	443	—	11,159	263	44	100	890
<i>Larix laricina</i>	5	3	2,823	496	1,250	29	122	18	4,738	81	14	86	350
<i>Thuja occidentalis</i>	3,111	13	62,295	5,029	13,977	—	5,634 ^c	160	87,094	1,945	160	548	4,785
<i>Ulmus americana</i>	172	267	4,788	771	2,711	30	372	—	8,673	171	28	92	693
Total ^b	3,566	317	104,528	12,093	34,195	348	7,761	482	159,406	3,196	372	1,643	10,139

^aProduction total is the sum of current twigs, foliage, and fruits, plus lateral bole wood, bole bark, and branch wood and bark.

^bDifferences between sums of columns and printed totals are due to rounding errors.

^cOnly 35% of *Thuja occidentalis* foliage was added as production.

the lowest total, 98 mt/ha in the fen, and the highest, 159 mt/ha in the swamp. The oak forest was intermediate with 124 mt/ha. Percentage distributions of biomass among tree fractions (Table 9) indicate a decrease in relative bole weights and an increase in branch components in the order oak, fen, swamp.

Production of the tree strata paralleled biomass. The highest production was 10.1 mt/ha in the swamp, 1.6 times greater than production in the fen at 6.5 mt/ha. The oak forest was again intermediate with 8.7 mt/ha (Table 2).

Within tree strata the contribution of bole wood and bark to production was especially high in the oak forest, on both a weight and percentage basis (46% compared with 38% and 35% in the fen and swamp forests) (Table 9). Whittaker (1966) generalized that stem-wood production was in the range

of 35% for climax forests of more favorable environments. The exceptionally high percentage in the oak forest was the result of high wood density and a low proportion of branches to total weight in both *Quercus alba* and *Q. ellipsoidalis* (Table 2).

The percentages of total production contributed by lateral wood and bark on branches were 10.0, 13.7, and 16.2 for oak, fen, and swamp, respectively. The low contribution of branches in the oak forest in particular reflects the small biomass of branches in both oak species in that stand. A comparable percentage for the more open Long Island oak-pine forest, also a northern sand plain forest, is 24.3% (Whittaker and Woodwell 1969). Whittaker (1966) stated that the relative contribution of branches to total production increased from denser to more open stands, and Satoo (1967) showed that branch bio-

TABLE 3. Aboveground dead wood, biomass, and net annual production of the tree strata in the oak, marginal fen, and cedar swamp forests, Cedar Creek Natural History Area, Minnesota—expressed in kilocalories per hectare $\times 10^{-4}$, or kilocalories per square meter

Species	Dead wood		Biomass							Production			
	Bole	Branches	Bole wood	Bole bark	Branch wood and bark	Current twigs	Foliage	Fruits	Total	Bole wood	Bole bark	Branch wood and bark	Total ^a
A. Oak forest													
<i>Acer rubrum</i>	40	20	1,979	184	1,083	14	207	—	3,466	141	20	56	438
<i>Alnus rugosa</i>	—	1	—	—	19	0.2	0.5	—	20	—	—	1	2
<i>Amelanchier</i> sp.	7	7	226	34	50	0.6	15	—	325	26	4	4	50
<i>Betula papyrifera</i>	28	4	2,795	529	1,247	16	136	23	4,745	112	21	74	381
<i>Fraxinus nigra</i>	0.9	0.03	44	6	11	0.2	2	—	64	2	0.2	0.6	5
<i>Ostrya virginiana</i>	3	0.2	181	19	52	2	13	0.4	268	14	2	4	36
<i>Populus grandidentata</i>	0.8	0.3	149	25	49	0.8	7	—	231	7	1	4	20
<i>Prunus serotina</i>	2	0.4	227	40	83	1	11	—	362	10	2	6	30
<i>Quercus alba</i>	49	40	2,836	290	511	18	137	—	3,793	134	14	24	328
<i>Quercus ellipsoidalis</i>	3,986	703	33,934	4,356	4,056	85	1,093	—	43,513	1,183	152	219	2,732
Total ^b	4,117	762	42,371	5,482	7,161	139	1,622	23	56,932	1,630	216	392	4,022
B. Fen forest													
<i>Acer rubrum</i>	53	7	2,516	199	1,447	13	233	—	4,409	142	19	62	470
<i>Alnus rugosa</i>	—	9	—	—	481	4	22	—	507	—	—	35	61
<i>Amelanchier</i> sp.	6	8	111	15	19	0.3	5	—	151	10	1	1	18
<i>Betula lutea</i>	8	0.03	979	154	504	0.9	33	17	1,688	30	5	18	1,026
<i>Betula papyrifera</i>	0.9	0.7	570	111	230	6	23	4	944	20	4	16	73
<i>Carpinus caroliniana</i>	0.07	0.01	12	1	4	0.3	1	—	19	1	0.1	0.4	3
<i>Cornus alternifolia</i>	0.1	0.5	20	4	8	0.6	3	—	34	1	0.3	0.7	6
<i>Fraxinus nigra</i>	301	16	9,099	1,231	3,352	43	372	—	14,096	246	34	124	819
<i>Ostrya virginiana</i>	0.6	0.02	26	3	7	0.2	2	0.04	37	2	0.2	0.5	4
<i>Prunus serotina</i>	4	0.5	363	70	169	2	18	—	621	14	3	10	46
<i>Quercus alba</i>	2	0.7	62	7	13	0.6	4	—	88	3	0.4	0.7	9
<i>Quercus ellipsoidalis</i>	763	145	6,573	821	802	16	210	—	8,422	229	29	42	523
<i>Thuja occidentalis</i>	392	2	8,111	600	1,782	—	742 ^c	22	11,258	249	19	69	619
<i>Ulmus americana</i>	48	68	1,162	169	678	8	80	—	2,097	41	6	22	157
Total ^b	1,578	258	29,603	3,386	9,496	95	1,747	43	44,370	989	121	401	2,914
C. Swamp forest													
<i>Acer rubrum</i>	2	0.2	86	14	41	1	12	—	155	13	2	4	33
<i>Alnus rugosa</i>	—	2	—	—	90	0.8	5	—	96	—	—	7	12
<i>Betula lutea</i>	23	.07	2,504	390	1,294	2	78	54	4,322	71	11	43	259
<i>Betula papyrifera</i>	16	10	10,109	1,940	4,940	121	428	95	17,634	258	50	316	1,268
<i>Cornus alternifolia</i>	0.03	0.1	7	1	2	0.2	1	—	12	0.5	0.1	0.2	2
<i>Fraxinus nigra</i>	85	4	3,257	470	971	18	181	—	4,896	117	18	44	377
<i>Larix laricina</i>	2	1	1,317	254	564	15	54	—	2,205	38	7	39	153
<i>Thuja occidentalis</i>	1,467	6	29,366	2,217	6,464	—	2,746 ^c	81	40,874	917	71	253	2,283
<i>Ulmus americana</i>	76	117	2,099	308	1,199	13	146	—	3,766	75	11	41	286
Total ^b	1,670	140	48,746	5,594	15,567	171	3,651	230	73,959	1,489	170	747	4,673

^aProduction total is the sum of current twigs, foliage, and fruits, plus lateral bole wood, bole bark, and branch wood and bark.

^bDifferences between sums of columns and printed totals are due to rounding errors.

^cOnly 35% of *Thuja occidentalis* foliage was added as production.

mass, and presumably production, declined with increasing density. The oak and swamp forests were relatively dense and the oak stand in particular was undergoing significant thinning through natural selective processes. Evidence for this thinning lies in the high weight of dead trees and branches (Tables 2 and 8).

Percentages of tree production contributed by current twigs and "fruits" were 4.1, 4.6, and 8.2 for the oak, fen, and swamp, respectively. No current twigs were registered for *Thuja occidentalis* because of its growth habit. Nevertheless, production contributed by current twigs and fruits of the swamp was more than double that of the oak and fen forests, due, in large part, to the heavy ament and cone production of *Betula lutea*, *B. papyrifera*, and *Thuja*. Fruits were also recorded on *Ostrya virginiana* in the oak forest.

Fruits of trees bearing in early summer, such as *Acer rubrum*, *Ulmus americana*, *Populus grandidentata*, and *Amelanchier*, were not assessed. Acorns were not found on the oaks.

Foliage production of trees was roughly equal in all three forests on a percentage basis (39.5%, 44.1%, and 40.4% in oak, fen, and swamp, respectively), while the absolute differences varied by ratios of 0.84/0.70/1.00 in the same order. A comparable percentage from the Long Island oak-pine forest is 44.1% (Whittaker and Woodwell 1969), and percentages for some Japanese forests range from 25 to 41 (Satoo 1970).

The sum of percentages of production for all branch components (lateral branch growth, current shoots, foliage, and fruits) were 53.6%, 64.4%, and 64.8% for oak, fen, and swamp, respectively. A com-

parable figure from the Long Island oak-pine forest is 78% (Whittaker and Woodwell 1969). The range from six Japanese forests is 35–66% (Sato 1970). Whittaker (1966) gave a range of branch-to-stem production ratios from 25% to 108%, indicating that variation is high and comparisons between forests are likely to be broad.

Summarizing comparisons among components of the tree stratum, the first outstanding difference among the three forests is the unusually large proportion of productivity contributed by bole growth in the oak forest. This was conversely reflected in the low contribution by branch components in comparison to fen and swamp forests. The difference among branch components of the three forests was greatest for lateral growth and less for current twig and foliage growth. Trees of the oak forest appear to invest nearly the same proportion of energy into new leaves as trees of the fen and swamp, without a concomitant investment in branch growth.

Reliability of tree-strata estimates.—Tree-strata estimates are subject to several kinds of assumptions and errors. Bole volumes and therefore biomasses are probably slightly low because the truncated conic volumes underestimate parabolic volumes which better represent tree geometry. Parabolic volumes were difficult to estimate because of the bole-truncation technique required in this work.

The accuracy of estimating bole radial growth was limited by the inability to determine radial growth up the length of tree boles to develop adjusting coefficients for each species. Whittaker (1966) cited a range of coefficients from 1.0 to 1.6 in arborescent shrubs and 1.2, 1.4, and 1.5 in three tree species. Application of a coefficient of 1.2 to all species represented a small improvement over no adjustment, but may have been inaccurate for specific species such as *Thuja occidentalis* which has a strong taper to the bole. For the forests in general, the coefficient of 1.2 probably slightly underestimated bole radial growth.

The method used for estimating lateral growth of branches very likely underestimated production. Division of branch weight by age gives an average value for the lifetime of the branch rather than current growth. Since surface area increases with size, the proportion of total weight added actually increases each year as long as radial increments remain the same. To this systematic underestimate was added the random error of dividing branch weight by an estimated age derived from regressions, instead of the actual age of each particular branch. Another method, which takes into account growth rate with age (Whittaker 1965a, Whittaker and Woodwell 1968), was applied to these data, but results were unrealistically high and were not used. Based on other published ratios of branch production to branch

biomass (Whittaker 1966), the estimates for branch lateral growth could be as low as half of true values, which might lead to an underestimate of total forest production by slightly less than 10%.

Regressions for branch fractions on branch diameter are listed with correlation coefficients and estimates of the deviation of y around x (Table 4) in forms developed by Whittaker and Woodwell (1968). Estimates of deviation (E values) for linear regressions (denoted by asterisks) are the standard errors of estimate divided by mean y 's. These estimates are analogous to a coefficient of variation. Standard errors of estimate for regressions transformed to a log-log form are logarithms; therefore the antilog is a factor by which y is multiplied or divided. The measure of deviation represented by E in these cases is the antilog of the standard error of estimate.

The high correlation coefficients in Table 4 lend misleading confidence in these regressions. Much of the high correlation is contributed by the very great range of values involved in the computations. The more useful statistics are the estimates of deviation (E). In general, high values of E (> 2.0) are associated with extremely variable and relatively unimportant dead wood and fruit fractions. Ovington, Forrest, and Armstrong (1967) experienced similar difficulties with these fractions. Dead wood was not included in estimates of biomass, and fruits were not only of minor importance in terms of weight, but were present on a minority of species as well. Although estimates for these two fractions are sometimes poor, they represent a reasonable work effort with respect to their importance, a criterion which must be considered in view of the expense in collecting field data for dimensional analyses of mixed forests.

Excluding dead wood and fruit regressions, 10 of 47 regressions in Table 4 have E values greater than 2.0. Of these 10, seven involve regressions for current twigs. Current twig growth was extremely variable and often quite reduced in comparison with the weight of leaves produced. *Betula lutea* presented an extreme case in which many large branches had only short-shoot twig growth at apices, but each short-shoot had generous clusters of leaves.

These measures of deviation seem, in general, large, and it is not known if they are atypical. Few forest-production studies provide measures of deviation with regressions (Attiwill 1966, Loomis, Phares, and Crosby 1966, Whittaker and Woodwell 1968, Madgwick 1970). Unfortunately, none of these include estimates of deviation for comparable regressions of branch fractions on branch basal diameter.

Whole-tree regressions (Table 5) provide estimates of tree fractions based on bole measurements of sample trees, plus the application of branch regressions

TABLE 4. Regressions for branch fractions and age on branch diameter for trees (Asterisked statistics are for linear regressions of the form $y = A + Bx$ in which y is weight in grams (or age in years) and x is branch diameter in centimeters. The remaining regressions are log-log transformations of the form $\log_{10}y = A + B \log_{10}x$. Correlation coefficients are given as r . See text for explanation of E statistic.)

Species	Statistic	Dead wood	Wood and bark	Age	Current twigs	Foliage	Fruits
<i>Acer rubrum</i> (oak)	A	0.8416	1.5294	0.8016	0.2934	1.0420	—
	B	1.9857	2.8099	0.6364	1.2658	2.1448	—
	r	0.938	0.922	0.912	0.927	0.968	—
	E	1.626	1.539	1.285	1.860	1.964	—
<i>Acer rubrum</i> (fen)	A	-6.9714	1.5099	0.9562	0.3505	1.2548	—
	B	3.0795	2.9661	0.7567	1.6286	2.2451	—
	r	0.962	0.998	0.875	0.898	0.994	—
	E	0.990*	1.228	1.397	2.284	1.301	—
<i>Amelanchier</i> sp.	A	-1.1030	1.5479	0.9655	0.2138	1.1360	—
	B	6.9510	2.2945	0.7394	0.4510	1.8333	—
	r	0.927	0.932	0.864	0.413	0.895	—
	E	6.733	1.836	1.173	1.969	1.861	—
<i>Betula lutea</i>	A	-1.9004	1.4722	0.7600	0.2038	1.0339	-1.8893
	B	2.0251	3.0322	0.8234	1.1222	2.1779	5.1386
	r	0.354	0.984	0.971	0.615	0.979	0.846
	E	269.907	1.777	1.259	4.504	1.613	29.568
<i>Betula papyrifera</i> (oak)	A	-.5813	1.6044	0.6955	0.1294	1.0658	-117.0200
	B	2.6742	2.6622	0.6132	2.1601	2.1114	42.3074
	r	0.992	0.995	0.925	0.873	0.913	0.999
	E	1.079*	1.269	1.260	2.813	2.250	1.275*
<i>Betula papyrifera</i> (swamp)	A	-.5813	1.3706	0.7453	0.2324	1.0178	-117.0200
	B	2.6742	3.3421	0.5375	2.7111	2.4878	42.3074
	r	0.992	0.995	0.919	0.881	0.926	0.999
	E	1.079*	1.345	1.272	3.476	2.380	1.275*
<i>Fraxinus nigra</i>	A	-2.2940	0.8983	0.8043	0.0445	1.3422	—
	B	5.2188	4.0370	0.9208	2.4561	1.8574	—
	r	0.754	0.927	0.953	0.836	0.810	—
	E	62.989	4.398	1.311	4.357	3.409	—
<i>Ostrya virginiana</i>	A	-1.0254	1.5200	0.9655	0.3364	1.0864	0.4606
	B	3.4358	3.3447	0.7394	1.0300	2.6068	0.3498
	r	0.580	0.975	0.864	0.787	0.976	0.795
	E	28.104	1.694	1.173	1.749	1.500	0.979*
<i>Quercus alba</i>	A	-.8455	1.2678	1.1750	0.3841	1.1176	—
	B	4.8454	3.2485	0.3204	2.0283	2.3652	—
	r	0.886	0.977	0.638	0.934	0.980	—
	E	11.624	1.993	1.275	2.111	1.595	—
<i>Quercus ellipsoidalis</i>	A	-.1113	1.4061	0.7387	0.5002	1.3508	—
	B	3.7810	2.8558	0.7010	1.7974	2.1429	—
	r	0.955	0.985	0.932	0.924	0.985	—
	E	3.745	1.773	1.331	2.310	1.520	—
<i>Thuja occidentalis</i>	A	-2.3063	1.2916	1.0166	—	1.3251	-0.4284
	B	3.8521	2.8913	0.7558	—	2.0576	2.5503
	r	0.766	0.986	0.888	—	0.946	0.321
	E	21.364	1.588	1.490	—	1.955	42.419
<i>Ulmus americana</i>	A	-128.2310	1.3441	0.9885	0.3237	1.0177	—
	B	87.0059	3.0698	0.6648	1.6662	2.3200	—
	r	0.997	0.994	0.945	0.935	0.982	—
	E	0.556*	1.429	1.316	1.898	1.566	—

to branch diameters of sample trees. The errors resulting from biases and variances in branch regressions are not visible in whole-tree regressions. Variations in these regressions result from tree-to-tree differences in bole form, lateral increment, and populations of branches as enumerated by branch di-

ameters. All whole-tree regressions are log-log transformations, and standard errors are expressed as antilogs of the standard errors of estimate (E) as described for branch regressions.

Of the 108 regressions in Table 5, 16 have E values greater than 2, the remainder range between

TABLE 5. Regressions for tree fractions on bole diameter at breast height (All regressions are in the form $\log_{10} y = A + B \log_{10} x$ in which y is weight in grams and x is diameter at breast height in inches. Correlation coefficients are given as r . E statistics are antilogs of the standard error of means.)

Species	Statistic	Bole dead wood	Bole wood	Bole bark	Bole wood production	Bole bark production	Branch dead wood	Branch wood and bark	Branch wood and bark production	Branch current twig	Branch foliage	Branch fruits
<i>Acer rubrum</i>	<i>A</i>	1.0996	2.8824	2.2475	2.2436	1.5469	0.0948	2.5221	1.6582	1.3391	2.1328	—
	<i>B</i>	2.3693	2.2344	1.6287	1.4067	1.1683	2.5403	2.3994	1.7425	1.2404	1.8782	—
	<i>r</i>	0.820	0.994	0.915	0.927	0.917	0.836	0.963	0.967	0.854	0.915	—
	<i>E</i>	4.089	1.235	1.846	1.626	1.547	4.139	1.772	1.476	1.904	1.999	—
<i>Alnus rugosa</i>	<i>A</i>	—	—	—	—	—	0.5907	2.8462	1.7704	0.6911	1.6394	—
	<i>B</i>	—	—	—	—	—	4.0329	1.8770	1.3885	0.2393	0.5384	—
	<i>r</i>	—	—	—	—	—	0.758	0.940	0.917	0.157	0.459	—
	<i>E</i>	—	—	—	—	—	8.818	1.533	1.457	2.579	1.922	—
<i>Amelanchier</i> sp.	<i>A</i>	0.8182	2.9898	2.2788	2.2455	1.5345	0.6174	2.5368	1.5091	1.0953	2.0865	—
	<i>B</i>	4.2728	2.1314	1.7674	1.3327	0.9687	4.9723	1.3197	0.7234	0.1665	0.9449	—
	<i>r</i>	0.976	0.999	0.957	0.965	0.928	0.995	0.999	0.958	0.308	0.986	—
	<i>E</i>	2.609	1.058	1.717	1.439	1.479	1.626	1.054	1.245	1.662	1.172	—
<i>Betula lutea</i>	<i>A</i>	0.1444	2.9679	2.2524	2.0958	1.3804	— .8989	2.6624	1.7444	1.0800	2.0610	—0.2107
	<i>B</i>	2.9629	2.2362	2.1296	1.5898	1.4832	1.6028	2.2561	1.7212	1.0299	1.7012	3.6442
	<i>r</i>	0.994	0.999	0.998	0.993	0.996	0.988	0.991	0.989	0.985	0.989	0.994
	<i>E</i>	1.811	1.002	1.287	1.430	1.284	1.600	1.781	1.636	1.403	1.630	2.098
<i>Betula papyrifera</i> (oak forest)	<i>A</i>	—0.0954	3.2397	2.1467	2.3663	1.2733	1.3931	2.1373	1.5874	0.7757	1.7264	0.4968
	<i>B</i>	3.4082	1.9508	2.2984	1.3462	1.6939	0.7706	2.7759	2.0314	2.1699	2.1089	2.6772
	<i>r</i>	0.977	0.992	0.977	0.943	0.970	0.957	0.961	0.966	0.968	0.968	0.985
	<i>E</i>	1.637	1.180	1.396	1.368	1.316	1.166	1.689	1.408	1.446	1.431	1.369
<i>Betula papyrifera</i> (cedar swamp)	<i>A</i>	0.4007	3.0002	2.2842	2.3573	1.6413	0.7904	1.8625	1.0892	0.6914	1.400	—0.8546
	<i>B</i>	2.0122	2.2266	2.1831	1.2174	1.1739	1.3798	3.0873	2.6599	2.5866	2.4116	4.0292
	<i>r</i>	0.315	0.994	0.996	0.708	0.650	0.812	0.959	0.952	0.951	0.945	0.902
	<i>E</i>	47.782	1.160	1.133	2.167	2.395	1.879	1.847	1.719	1.711	1.700	3.409
<i>Fraxinus nigra</i>	<i>A</i>	0.6581	2.8649	2.2131	1.9903	1.3385	—1.3763	1.7899	0.9805	0.9366	2.2488	—
	<i>B</i>	3.2772	2.3390	2.1085	1.3811	1.1506	4.2154	3.1751	2.3696	1.8067	1.3222	—
	<i>r</i>	0.792	0.996	0.995	0.957	0.948	0.993	0.994	0.994	0.987	0.961	—
	<i>E</i>	10.047	1.210	1.218	1.464	1.420	1.603	1.362	1.268	1.307	1.418	—
<i>Ostrya virginiana</i>	<i>A</i>	0.6446	3.0870	2.2127	2.1384	1.2641	0.1480	2.6856	1.6690	1.5823	2.2130	0.8074
	<i>B</i>	3.8622	2.0463	1.8428	1.6149	1.4114	1.7032	1.6558	1.3059	0.7451	1.2845	0.6493
	<i>r</i>	0.978	0.991	0.996	0.962	0.973	0.992	0.993	0.999	0.983	0.999	0.808
	<i>E</i>	3.144	1.458	1.223	1.901	1.595	1.353	1.309	1.045	1.211	1.026	1.935
<i>Quercus alba</i>	<i>A</i>	1.7738	2.7018	2.1535	1.7043	1.1560	0.2556	2.3148	1.1778	1.3995	2.1426	—
	<i>B</i>	1.5497	2.8083	2.2886	2.3318	1.8121	3.6403	2.3018	2.0099	1.4752	1.6684	—
	<i>r</i>	0.932	0.985	0.975	0.957	0.900	0.892	0.927	0.936	0.975	0.961	—
	<i>E</i>	1.493	1.394	1.420	1.608	1.798	3.437	1.869	1.655	1.254	1.378	—
<i>Quercus ellipsoidalis</i>	<i>A</i>	2.0066	2.7644	2.2556	1.3256	0.8168	0.1296	1.5552	0.8466	0.7386	0.8922	—
	<i>B</i>	2.3728	2.5602	2.1542	2.5396	2.1336	3.5792	2.8800	2.2741	1.9377	2.2630	—
	<i>r</i>	0.723	0.970	0.976	0.899	0.787	0.951	0.929	0.885	0.838	0.883	—
	<i>E</i>	1.778	1.177	1.130	1.368	1.530	1.445	1.436	1.460	1.490	1.461	—
<i>Thuja occidentalis</i>	<i>A</i>	2.2087	2.7147	2.0166	1.5168	0.8187	—1.4147	2.1000	1.0502	—	2.0977	0.0708
	<i>B</i>	1.5124	2.3665	1.9492	2.0425	1.6252	2.8330	2.3307	1.9528	—	1.9151	2.4226
	<i>r</i>	0.944	0.995	0.993	0.994	0.982	0.980	0.987	0.987	—	0.987	0.976
	<i>E</i>	1.582	1.223	1.228	1.222	1.308	1.637	1.394	1.317	—	1.314	1.592
<i>Ulmus americana</i>	<i>A</i>	0.6398	2.9529	2.2640	1.8308	1.1420	1.3223	2.5173	1.4802	1.4179	2.1373	—
	<i>B</i>	3.2090	2.1032	1.9642	1.6609	1.5220	2.5928	2.3507	1.7763	1.1723	1.7043	—
	<i>r</i>	0.978	0.996	0.999	0.887	0.879	0.977	0.980	0.977	0.953	0.976	—
	<i>E</i>	2.290	1.236	1.071	2.812	2.688	1.973	1.777	1.593	1.564	1.579	—

1 and 2. Among the 16 *E* values greater than 2, 11 involve dead wood or fruits, which are exceptionally variable tree fractions and relatively insignificant in biomass and production estimates of most forests. *E* values for bole dead wood in particular are sometimes very high.

E values in Table 5 are comparable with those published for the Long Island oak-pine forest regressions (Whittaker and Woodwell 1968). Regressions of dead wood, cones, or fruits on basal diameter were not published in that paper. Although comparable regression statistics may indicate comparable precision, they do not necessarily signify equal accuracy of estimation for all fractions. The method used for bole biomass and production estimates in the Long Island study probably provided greater accuracy in terms of true values than did the non-destructive method used in this study.

The reliability of fen and swamp production estimates are considerably affected by the assumption of 35% turnover in *Thuja* foliage, since *Thuja* foliar biomass is very high in these forests. Alternative percentages of 20% and 50% might be regarded as extreme ranges of turnover, giving estimates of 9.47 and 11.16 mt/ha respectively, for swamp forest tree-stratum production. These outside estimates represent differences of 7% and 10% of the tabulated estimate of 10.14 mt/ha.

Shrub strata.—The contributions of tall shrubs, *Corylus americana* and *C. cornuta*, to forest biomass and production were small (Table 6). Biomass was only 212 and 281 kg/ha and production 58 and 65 kg/ha in oak and fen forests, respectively. Neither species occurred in the swamp. Distribution of tall shrubs was spotty, causing high variation around means. Standard errors for biomass were 84 kg/ha in the oak forest and 86 kg/ha in the fen.

Production in the shrub strata was estimated by only two components: foliage (86% and 89%) and current twig growth (14% and 11%) in oak and fen forests, respectively. According to Ovington et al. (1963), another 30% of total shrub production is contributed by lateral growth in old stems. This missing 30% is trivial in relation to the contribution of shrubs to forest production: 0.6% and 0.9% in the oak and fen forests, respectively.

Herb strata.—Total biomasses, including both above- and below-ground organs, for the herb strata were 396, 1,881 and 542 kg/ha in oak, fen, and swamp, respectively (Table 7). Aerial biomasses only are listed in Tables 8 and 9 to retain consistency with tree data which are for shoots only. The weight of subterranean organs can be calculated by subtracting production figures (aerial shoots) from total biomass for most species in Table 7.

Herb-strata production figures were 150, 489, and 180 kg/ha in oak, fen, and swamp, respectively.

TABLE 6. Aerial biomass and annual production of the tall shrub strata^a

Forest	Dead wood	Living wood	Foliage	Total live biomass	Annual production
Oak (kg/ha)	138	162	50	212	58
(kcal/ha x 10 ⁻⁴)	62	72	20	92	24
Fen (kg/ha)	60	223	58	281	65
(kcal/ha x 10 ⁻⁴)	27	100	24	124	26

^aThe only species were *Corylus americana* in the oak forest and *C. cornuta* in the fen.

Production of herbaceous species was calculated simply as the weight and energy content of the aerial shoots. Low-shrub production (*Vaccinium angustifolium* and *Gaultheria procumbens*) was calculated as the sum of current twigs and leaves. Caloric coefficients can be calculated from the production column in calories in Table 7.

Herb production data correspond roughly with light-penetration data. Geometric means of light penetrating to the 1-m level were 3.9%, 9.3%, and 2.1% of maximum in oak, fen, and swamp forests, respectively. Ratios of these values in the same order are 0.42/1.0/0.23 compared with herb shoot ratios of 0.31/1.0/0.37. Geometric means of light at the ground level were 2.4%, 1.8%, and 1.6% of maximum for oak, fen, and swamp, respectively. In spite of differences in ecosystem structure, nearly equal amounts of light are reflected or absorbed by each ecosystem as a whole.

Because of the manner in which biomass and production were calculated from density and average plant weights, results are averages of two halves of each study area so that *n* = 2. Standard errors for herb production of 71, 118, and 53 kg/ha for oak, fen, and swamp, respectively, were high, reflecting both low *n* and the highly variable distribution of herb cover.

Nearly all herbaceous species in this study were perennials and some proportion of shoot growth was produced at the expense of underground storage organs. The method used was therefore accurate if the energy debt to the underground organs had been repaid at the time of clipping (maximum shoot biomass). Judging from the shrunken appearance of herbs after fruiting, one might suspect that the resorption of nutrients and energy may not be completed until well after the shoots reach maximum biomass. If this is true, production by the herbaceous layer was overestimated by this method, and actual production lies between maximum shoot biomass and herbaceous litter. As an example, the range for the oak forest lies between 150 kg/ha maximum biomass and 97 kg herbaceous litter. Such a range, though broad in itself, does not represent a significant error in total community production (Tables 8 and 9).

Total community biomass and production.—

TABLE 7. Total biomass and annual aerial production for herbaceous and low shrub species

Species ^a	Biomass (kg/ha)			Annual production (kg/ha)			Annual production (kcal/ha x 10 ⁻⁴)		
	Oak	Fen	Swamp	Oak	Fen	Swamp	Oak	Fen	Swamp
<i>Galium boreale</i>	2.7			1.9			0.76		
<i>Uvularia sessilifolia</i>	5.1	1.8		1.8	0.6		0.81	0.29	
<i>Anemone quinquefolia</i>	3.3	0.6		1.2	0.2		0.51	0.09	
<i>Gaultheria procumbens</i>	13.8	2.9		3.6	0.7		0.17	0.35	
<i>Vaccinium angustifolium</i>	49.8	11.9		7.0	1.7		3.25	0.78	
<i>Aster macrophyllus</i>	36.1	7.6		14.3	0.3		5.97	1.26	
<i>Pteridium aquilinum</i>	56.1	23.0		30.8	16.6		13.12	7.06	
<i>Carex pensylvanica</i>	92.1	37.5		54.7	24.1		23.24	9.87	
<i>Oryzopsis asperifolia</i>	4.6	7.1		3.9	6.4		1.66	2.66	
<i>Osmunda claytoniana</i>	83.9	785.2		14.7	151.8		6.40	66.92	
<i>Poa pratensis</i>	8.4	0.6	0.9	4.5	0.3	0.5	1.88	0.12	0.20
<i>Brachyelytrum erectum</i>		6.7			4.5			1.79	
<i>Geranium maculatum</i>		8.3			2.1			0.80	
<i>Clintonia borealis</i>	0.3	4.4	0.9	0.2	2.4	0.5	0.07	0.96	0.21
<i>Parthenocissus inserta</i>	23.0	12.2	18.7	4.6	2.6	4.6	1.83	1.00	1.72
<i>Maianthemum canadense</i>	0.8	4.0	1.2	0.3	1.4	0.4	0.11	0.61	0.18
<i>Aralia nudicaulis</i>	14.2	6.6	26.5	5.5	2.4	9.4	2.42	1.02	4.08
<i>Trientalis borealis</i>	1.0	0.2	1.3	0.6	0.1	0.8	0.25	0.05	0.34
<i>Arisaema atrorubens</i>	0.2	9.6	7.5	0.1	4.8	3.1	0.03	2.00	1.33
<i>Viola incognita</i>	0.7	0.9	5.7	0.5	0.6	4.0	0.18	0.22	1.47
<i>Scutellaria lateriflora</i>		0.4			0.1			0.06	
<i>Impatiens capensis</i>		8.3	0.8		7.8	0.8		3.17	0.32
<i>Onoclea sensibilis</i>		42.0	11.7		23.9	6.0		8.97	2.49
<i>Carex pedunculata</i>		58.5	16.6		41.9	11.8		17.65	4.93
<i>Osmunda cinnamomea</i>		508.8	90.4		87.3	17.5		38.13	7.44
<i>Circaea alpina</i>		0.9	1.0		0.7	0.9		0.31	0.36
<i>Poa palustris</i>		1.3	1.2		1.0	0.9		0.42	0.39
<i>Athyrium filix-femina</i>		285.7	283.5		83.2	81.8		34.10	32.71
<i>Galium triflorum</i>		0.1	0.2		0.1	0.2		0.04	0.08
<i>Rubus pubescens</i>		11.1	16.4		6.4	9.0		2.61	3.67
<i>Osmunda regalis</i>		11.1	2.9		1.3	0.5		0.59	0.22
<i>Dryopteris spinulosa</i>		12.4	30.3		4.5	12.0		1.96	5.18
<i>Dryopteris thelypteris</i>		6.1	5.2		5.3	2.1		2.16	0.86
<i>Mitella nuda</i>		2.9	13.0		1.7	8.2		0.66	3.10
<i>Lycopus uniflorus</i>		0.2	1.6		0.2	1.4		0.08	0.58
<i>Carex leptalea</i>			0.4			0.3		0.01	0.14
<i>Cornus canadensis</i>			1.3			0.6			0.26
<i>Fragaria virginiana</i>			3.0			2.3			0.90
Pteridophyte subtotal	140.0	1,674.3	424.0	45.5	373.9	119.9	19.52	159.90	48.90
Monocotyledon subtotal	111.5	131.5	28.7	65.5	87.4	17.5	27.80	36.38	7.38
Dicotyledon subtotal	144.6	75.1	89.5	39.2	27.7	42.2	16.85	12.50	16.88
Total ^b	396.1	1,880.9	542.2	150.2	489.0	179.6	64.17	208.78	73.16

^aSpecies are arranged in an approximate continuum from upland to swamp based chiefly on density data.

^bThe following species were recorded in quadrats but were too rare or small to warrant estimation of biomass and production. Those principally in the oak forest were *Amphicarpa bracteata*, *Apocynum androsaemifolium*, *Diervilla lonicera*, *Equisetum sylvaticum*, *Helianthus giganteus*, *Smilacina stellata*, *Aquilegia canadensis*, and *Rubus idaeus*. Those principally in the fen were *Viola pallens*, *Gaylussacia baccata*, *Ribes triste*, *Trillium cernuum*, *Rhus radicans*, and *Ribes hirtellum*. Those principally in the swamp forest were *Caltha palustris*, *Botrychium virginianum*, *Coptis groenlandica*, *Corallorhiza trifida*, *Dryopteris disjuncta*, and *Lysimachia thysifolia*.

Aboveground biomass totals for oak, fen, and swamp forests were 125, 99, and 160 mt/ha, respectively (Table 8). The tree strata accounted for over 99% of biomass in each forest; shrub strata contributed 0.2% and 0.3% in the oak and fen forests; herb strata contributed 0.1%, 0.5%, and 0.1% in oak, fen, and swamp forests, respectively.

These total biomass estimates fall into the low range of Smoky Mountain forest values (Whittaker 1966), are higher than the 66 mt/ha value for the Long Island oak pine forest (Whittaker and Woodwell 1969), and are less than the 164 mt/ha value for an Anoka Sand Plain oak forest in the vicinity of this study area (Ovington et al. 1963).

Aboveground net production totals for oak, fen, and swamp forests were 8.9, 7.1 and 10.3 mt/ha, respectively (Table 8). Production was slightly more evenly distributed among strata than was biomass. The tree strata accounted for 97.7%, 92.2%, and 98.3% of the total in oak, fen, and swamp, respectively, compared with over 99% for biomass in all three forests. The shrub layers contributed 0.6% and 0.9% in oak and fen, respectively, and the herb layer contributed 1.7%, 6.9%, and 1.7% of oak, fen, and swamp production, respectively (Table 9). As expected from physiognomic appearance, production was most evenly distributed among strata in the fen.

TABLE 8. Synopsis of radiation, biomass, production, and detritus data for the oak, marginal fen, and cedar swamp forests in terms of weight and energy

Item	Weight in kg/ha			Energy in kcal/ha x 10 ⁻⁴		
	Oak	Fen	Swamp	Oak	Fen	Swamp
Solar radiation						
Annual total	R ₀			1,214,580		
Growing season total	R ₁			734,710		
Annual visible	R ₂			522,269		
Growing season visible	R ₃			315,925		
Living, aboveground biomass						
Tree layer	124,273	98,075	159,406	56,932	44,370	73,959
Tall shrub layer	212	281		92	124	
Herb layer	150	489	180	64	209	73
Total	(B) 124,635	98,845	159,586	57,089	44,702	74,032
Total foliage	(G) 3,637	4,407	7,941	1,706	1,979	3,725
Net, aboveground primary production						
Tree layer	8,700	6,512	10,139	1,846	1,110	1,659
Tall shrub layer	58	65		24	209	
Herb layer	150	489	180	64	209	73
Total	(P) 8,908	7,066	10,319	4,110	3,149	4,747
Litter fall						
Tree-shrub layers	4,574	4,115	4,881	2,208	1,909	2,374
Herb layer	97	299	112	40	122	45
Total	(L) 4,671	4,414	4,993	2,248	2,031	2,419
Detritus						
L layer	7,010	5,160	4,890	3,119	2,362	2,312
F layer	5,590	3,730	2,320	1,584	1,498	1,049
H layer ^a	52,580	313,980	910,150	22,647	166,806	445,939
Total forest floor	(F) 65,180	322,870	917,360	27,350	170,660	449,300
Dead trees and branches	10,651	4,017	3,883	4,879	1,837	1,810
Dead shrubs and branches	138	60		62	27	
Total detritus	(D) 75,969	326,947	921,243	32,291	172,524	451,110

^aCalculated on an ash-free basis because of very high ash contents. H-layer values are therefore slightly underestimated because ash contents of other materials are included in dry weights.

These production totals fall into the low to intermediate range of totals for Smoky Mountain forests (Whittaker 1966) and bracket the Long Island oak-pine forest (8.6 mt/ha) (Whittaker and Woodwell 1969) and the Anoka Sand Plain oak forest (8.2 mt/ha) (Ovington et al. 1963).

Biomass relationships among forests follow the ratios of 0.78/0.62/1.0 in the order of oak, fen, and swamp. Production ratios, given in the same order, parallel biomass closely (0.86/0.68/1.0). Both biomass and production decrease in the order of swamp > oak > fen. Because biomass and production correlate, biomass-to-production ratios (Table 9) are similar (14.0, 14.0, and 15.4 for oak, fen, and swamp, respectively). These ratios suggest that the swamp supported the most biomass or structural organization per unit of energy fixed (Margalef 1963). Biomass-to-production ratios for a variety of Smoky Mountain forests range from 8.9 to 51.5, and for xeric heaths range from 11.0 to 20.7 (Whittaker 1966). The ratio for the Long Island oak-pine forest is 7.7 (Whittaker and Woodwell 1969).

Foliage weights vary by ratios of 0.46/0.56/1.0 for oak, fen, and swamp, respectively. Differences in foliage weights represent a major structural differ-

ence between the three forests. The major contributor to this variation was *Thuja occidentalis* for which the weight of foliage was far out of proportion to basal area (Table 1), or to biomass (Table 2) compared with deciduous species. Production-to-foliage ratios for oak, fen, and swamp are 2.45, 1.60, and 1.30, respectively, inversely corresponding with an increase of *Thuja* in the tree strata. Conifers have higher foliage weights and somewhat higher productivities than deciduous trees in general in the same environments (Whittaker 1966, Satoo 1970).

The ratios of production to chlorophyll may vary from the production-to-foliage ratio. Ovington and Lawrence (1967) indicated that large amounts of chlorophyll exist in branches of oak trees, perhaps as much as 37-70% of leaf chlorophyll during the summer months.

Basal area, a fundamental measure of forest structure, roughly parallels biomass and production. The ratios for basal area among oak, fen, and swamp forests, respectively, are 0.63/0.59/1.00 (Table 1). Ratios for biomass and production for forests given in the same order are 0.78/0.62/1.00 and 0.86/0.68/1.00. Biomass per unit basal area appears to be higher in the oak and fen forests in comparison with

TABLE 9. Ratios for interpreting the structure and function of the oak, marginal fen, and cedar swamp forests in terms of efficiencies, production, biomass, and energy flow and accumulation in detritus (The ratios and symbols are derived from data in Tables 2, 6, 7, and 8 and are presented in terms of both weight and energy.)

Ratio	Weight basis			Energy basis			
	Oak	Fen	Swamp	Oak	Fen	Swamp	
Biomass distribution							
Tree layer/B	0.997	0.992	0.999	0.997	0.992	0.999	
Bole wood/tree biomass	0.744	0.661	0.656	0.744	0.667	0.659	
Bole bark/tree biomass	0.098	0.080	0.076	0.096	0.076	0.076	
Old branch wood and bark/tree biomass	0.128	0.216	0.214	0.126	0.214	0.210	
Current twigs/tree biomass	0.002	0.002	0.002	0.002	0.002	0.002	
Foliage/tree biomass	0.028	0.039	0.049	0.028	0.039	0.049	
Fruits/tree biomass	0.0003	0.001	0.003	0.0004	0.001	0.003	
Shrub layer/B	0.002	0.003	—	0.002	0.003	—	
Old stems/shrub biomass	0.726	0.769	—	0.740	0.786	—	
Current twigs/shrub biomass	0.038	0.025	—	0.039	0.024	—	
Foliage/shrub biomass	0.236	0.206	—	0.221	0.190	—	
Herb layer shoots/B	0.001	0.005	0.001	0.001	0.005	0.001	
Production distribution							
Tree layer/P	0.977	0.922	0.983	0.978	0.925	0.985	
Lateral bole wood and bark/tree production	0.465	0.376	0.352	0.459	0.381	0.355	
Lateral branch wood and bark/tree production	0.100	0.137	0.162	0.098	0.138	0.160	
Current twig and fruits/tree production	0.041	0.046	0.082	0.040	0.047	0.086	
Current foliage/tree production	0.395	0.441 ^a	0.404 ^a	0.403	0.434 ^a	0.399 ^a	
Shrub layer/P	0.006	0.009	—	0.006	0.008	—	
Current twigs/shrub production	0.138	0.108	—	0.150	0.113	—	
Foliage/shrub production	0.862	0.892	—	0.850	0.887	—	
Herb layer/P	0.017	0.069	0.017	0.016	0.066	0.015	
Production-biomass ratios							
Biomass/production	B/P	13.991	13.989	15.465	13.890	14.196	15.597
Production/foliage	P/G	2.449	1.603	1.299	2.409	1.591	1.274
Production efficiencies							
Annual efficiency (total)	P/R ₀				0.0034	0.0026	0.0039
Growing season efficiency (total)	P/R ₁				0.0056	0.0043	0.0064
Annual efficiency (visible)	P/R ₂				0.0078	0.0062	0.0091
Growing season efficiency (visible)	P/R ₃				0.0130	0.0099	0.0150
Detritus ratios							
Litter/biomass	L/B	0.037	0.045	0.031	0.039	0.045	0.033
Litter/production	L/P	0.524	0.625	0.484	0.547	0.645	0.509
Litter/forest floor	L/F	0.072	0.014	0.005	0.082	0.012	0.005
Forest floor/biomass	F/B	0.523	3.266	5.748	0.479	3.818	6.069
Forest floor/production	F/P	7.317	45.693	89.900	6.654	54.195	94.657
Forest floor/litter	F/L	13.954	73.147	183.729	12.166	84.028	185.738
Forest floor/detritus	F/D	0.858	0.988	0.996	0.847	0.989	0.996
Detritus/biomass	D/B	0.610	3.308	5.773	0.566	3.859	6.093

^aAssuming current foliage in *Thuja occidentalis* is approximately 35% of total foliage.

the swamp. As described earlier, the high taper in *Thuja* boles led to a low bole volume relative to basal area. Since a large proportion of biomass and production is contributed by boles (Table 9), such a variation in tree form in the swamp could be a major cause of an overestimate in production based on basal area alone, a fact well recognized in forestry.

Density data for the three forests show poor relationships with biomass and production. Ratios for density among oak, fen, and swamp, respectively, are 0.53/1.00/0.82. Although density, biomass, and production have roughly the same relationships in comparisons of oak and swamp forests, density seems to be inversely related to production in the fen where

a high proportion of stems are small alders (*Alnus rugosa*). Since tree size, biomass, and production are roughly proportional within certain age limits, and since average tree size and density are usually inversely related, such a result is not surprising. If the numerous, small alders are subtracted from all three forest densities, density ratios are altered to 0.72/0.83/1.00 for oak, fen, and swamp, respectively, an improvement over the original ratios, but still a poor relationship with biomass or production.

All of these interpretations of differences between forests are confounded by the fact that comparisons are not only between structurally contrasting types, but also between forests of different ages. Different

ages do not necessarily signify proportionally different degrees of maturity because the respective dominant species may have quite dissimilar developmental times. Thus, although it is twice as old, the cedar swamp may not be twice as mature in terms of productivity changes over a complete developmental sequence.

Caloric data.—Data in Tables 8 and 9 are given in energy as well as mass units. Because caloric coefficients vary little among plant materials, differences between caloric values and weight values in Table 8 are generally proportional, and energy ratios in Table 9 are basically similar to weight ratios. Some differences in Table 9 reflect fundamental differences in caloric content of certain fractions. These lead to regular deviations in ratios based on mass to ratios based on energy.

The weighted caloric coefficients for foliage tissues (4.690, 4.484, 4.690 kcal/g for oak, fen, and swamp, respectively) are higher than those for fractions comprising production (4.613, 4.452, 4.600) in all three forests. This factor leads to slight decreases in production-to-foliage ratios in changing from weight to energy units. Similarly, the weighted caloric coefficient for fractions involved in production (4.613) is higher than that for biomass in general (4.580) in the oak forest. The reverse is true in the fen and swamp (4.452 vs. 4.522 and 4.600 vs. 4.639). These differences cause the changes in ratios involving production and biomass which are unique to each forest. The fact that weighted caloric coefficients for foliage are higher than for biomass or production fractions also creates appropriate changes from mass to energy ratios involving litter, production, and biomass.

Discrepancies between mass and energy ratios involving forest floors are chiefly caused by the use of ash-free weight for the H layer (see footnote Table 9). This leads to disproportionately high energy contents of H layer material, thereby distorting these ratios.

Where caloric coefficients may be compared with those of Ovington and Lawrence (1967), they vary by no more than 3%.

Efficiencies.—Efficiencies of energy transformation are provided in four of the many ways which are found in the literature (e.g., Botkin and Malone 1967) (Table 9). Because all three forests received equal amounts of sunlight, denominators for efficiency ratios are identical and ratios are proportional to, and merely reflect differences in, net annual production. Since the numerators are very small in comparison to the denominators, there is little absolute difference between efficiencies in the three forests (Table 9).

The most conservative and least ambiguous of these efficiency ratios is based on total annual radiation which gives values of approximately 0.3%. If

only 43% of total annual radiation is considered as visible light (Szeicz 1966) and therefore involved in photosynthesis, efficiencies rise to 0.8%.

Efficiency may be calculated by considering only radiation impinging during the growing season. This can be done by ignoring possible photosynthesis occurring in bark tissue, and in this case, photosynthesis occurring in *Thuja* during the arbitrary non-growing season. The period of time used for seasonal efficiency calculations (5 months) approximates the growing season, but may be somewhat longer than the frost-free season. Trees of this study area have some degree of resistance to frost damage so the frost-free season is not as meaningful as it is for herbaceous ecosystems. More than one-half the annual solar radiation occurs during the growing season, so seasonal efficiencies are less than double annual efficiencies, falling in the order of 0.5%. If only visible light is considered over the growing season, efficiencies rise to the order of 1.3%.

Since efficiencies are proportional to production, the forests are ranked swamp > oak forest > marginal fen in this regard. If the growing season total of visible light is further reduced by the percentage penetrating to the forest floor, efficiencies for oak, fen, and swamp are changed only slightly to 1.33%, 1.02%, and 1.52%.

Interpretation of these efficiencies is limited because only aboveground production is included in the numerator. Comparison of efficiencies among ecosystems is of the greatest value when the ecosystems are highly dissimilar in some fundamental respect; otherwise productivity data are more useful. Efficiency data from contrasting systems such as oceans or grasslands generally entail total production and therefore are not exactly comparable with the efficiency ratios given here.

If 20% (Bray 1963) is used as a rough estimate of the ratio of root to shoot production, then total production in oak, fen, and swamp, respectively, would be 10.7, 8.5 and 12.4 mt/ha. This estimate would therefore yield efficiencies 20% higher than each of the efficiencies described for aerial production alone. Root production may actually vary widely from 20% of shoot estimates. Root biomass, and therefore production, may be as low as 15% in wetland species and as high as 30% in upland species. The root-to-shoot ratio for biomass of oaks in the Long Island oak-pine forest was 52%, but a more conservative 35% was used for a production estimator by Whittaker and Woodwell (1969). The use of 20% for estimating root production in the forests of this study probably underestimates oak forest efficiencies and overestimates fen and swamp efficiencies.

Energetics and species structure.—Production data by individual species within an ecosystem provide

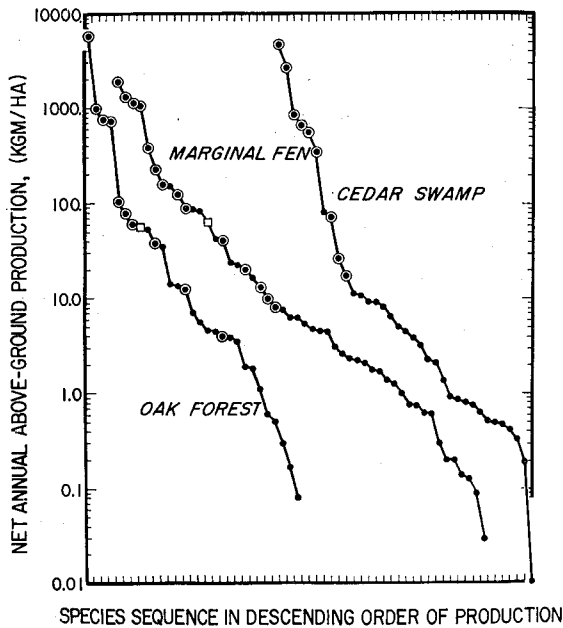


FIG. 2. Dominance-diversity curves for the oak forest, marginal fen, and cedar swamp. All but very small or rare species are registered according to their rank in aboveground, net production (abscissa) and amount of production (ordinate). Large, open circles indicate tree species (Table 2), squares indicate tall shrubs, and small, closed circles represent low shrubs or herbaceous species (Table 7).

an opportunity to examine plant community structure in terms of the distribution of a common function, primary production, among the component plant populations of the community. Such an analysis is made with dominance-diversity curves (Whittaker 1965b) constructed from data in Tables 2, 6, and 7 (Fig. 2). These curves combine floristic richness (the richness component of diversity) with the distribution of function and, presumably, resources among species (the equitability component of diversity). Although difficult to describe with a single index value, these curves effectively portray much about the structure of plant communities. Caution should be observed in examining these curves because the logarithmic ordinate tends to obscure the concentration of dominance in the top species of the sequence.

The oak forest dominance-diversity curve may best be described as three linear line segments. The upper, and steepest, segment includes the top five species. The second, with the lowest slope, includes 15 intermediates, and the third includes nine species distributed to produce an intermediate slope. The first segment consists of dominant and subdominant tree species and has the least equitability in terms of distribution of production among species. To a greater degree than found in either of the other forests, dominance is concentrated in one species. *Quer-*

cus ellipsoidalis contributes 75% of the basal area and 66% of primary production in this forest. All of the community attributes controlled by canopy species are, to a large degree, held by one species in the oak forest, rendering the forest particularly susceptible to significant alteration if that species were seriously damaged. This is a real possibility on the sand plain since oak wilt (*Ceratocystis fagacearum* [Bretz] Hunt) is currently a problem (Anderson and Anderson 1963) and has decimated entire stands of *Quercus ellipsoidalis* (personal observation). Subdominance is rather closely shared by four tree species in the 1,000-100 kg/ha range. The lowest of these, *Amelanchier* sp., is actually a subcanopy species. The second line segment in the oak forest curve includes a variety of growth forms including incidental canopy trees, a subcanopy species (*Ostrya virginiana*), a tall shrub and a low shrub, ferns, and herbaceous angiosperms. The third segment is quite linear and consists of rare or small-sized herbaceous species. Together, these two groups contribute most of the floristic richness but only 4% of production.

The most numerous species (50) were assessed for production in the fen giving it the lowest slope among the curves of Fig. 2. This community showed an unusually even distribution of dominance among the top four species, *Fraxinus nigra*, *Alnus rugosa*, *Thuja occidentalis*, and *Acer rubrum*. Whereas one species contributed 66% of production in the oak forest, the top species in the fen contributed only 27% and the top four combined contributed 77%. Below the fourth species the curve is rather concave, indicating increasingly even distribution of production among a wide range of species of all growth forms. Below 2 kg/ha the curve becomes convex as species, all herbaceous, become increasingly rarer.

The dominance-diversity curve for the swamp is similar to that of the fen, especially in the lower portions. There are two dominant species, *Thuja occidentalis* and *Betula papyrifera*. The top species, *Thuja*, contributes 65% of total basal area but only 46% of production. Together, *Thuja* and *Betula papyrifera* contribute 73% of production in the swamp. A cluster of four subdominants follows these species, including representatives of the fen, plus occasional, but large individuals of *Betula lutea* and *Larix laricina*. In the swamp, as in the oak forest, there are clear demarcations in production between the dominants, subdominants, and other species. Among the lesser species, the curve becomes concave, then convex producing a slight sigmoid character similar to that of the fen curve.

Sigmoid curves are characteristic of communities of intermediate diversity, but individualistic variations occur which may result from special historical or competitive circumstances (Whittaker 1965b). Very diverse communities have sigmoid curves with

moderate slopes throughout. Communities of rigorous environments or low species diversity produce linear curves approximating a geometric series (Whittaker 1965b). Among the three forests of this study, sigmoid tendencies exist but are not marked, so that from the point of view of curve shape, these communities fall between linear and sigmoid, or low and intermediate diversity types. On the basis of overall slope, the marginal fen possesses the greatest diversity, especially in the canopy dominants.

Several single-value indices expressing the evenness of distribution of some common parameter among species are available (Whittaker 1965b, McIntosh 1967). Evenness or equitability indices have been calculated for the forests with the expression:

$$J = H / \log_2 s,$$

where J = equitability, H = average bits of information per individual, and s = number of species (Pielou 1966). Equitability based on production values of Tables 2, 6, and 7 for oak, fen, and swamp forests, respectively, are 0.366, 0.559, and 0.435.

Single indices of community complexity may be calculated from a number of possible indices (McIntosh 1967). Diversity indices based on the data used in Fig. 2 were calculated by the Brillouin (1962) expression:

$$H = \frac{1}{N} \log_2 \frac{N!}{N_1! N_2! \dots N_s!},$$

where H = bits of information/unit, N = total number of units, and s = total number of species. This index assesses both the number of species per unit area (richness) and the evenness of distribution of production or some other parameter among species (equitability). This expression, rather than the Shannon-Wiener formula, was used here on the basis of sampling difficulties occurring in patchy communities and the attendant impossibility of gaining true estimates of proportions required by the Shannon-Wiener expression (Pielou 1966). Data were multiplied by 10 so all values were integers. The resulting indices for the oak, fen, and swamp were 1.778, 3.154, and 2.212.

On the basis of floristic richness, dominance diversity curves, equitability, the Brillouin expression, and the distribution of production among strata (Table 9), the forests may be ranked fen > swamp > oak forest in terms of decreasing complexity.

Primary production on the Anoka Sand Plain

Primary production on the Anoka Sand Plain has received substantial study. Thus an opportunity is provided for comparison of other ecosystems with the three forests of this study. An array of ecosystems studied in Cedar Creek Natural History Area is portrayed with aboveground biomass and produc-

tion estimates in Fig. 3. This figure illustrates a typical arrangement of ecosystem types in response to topographic variation ranging from open lakes to upland prairies, savannas, and oak forests, and back down to conifer swamps on former lake basins.

The prairie-savanna-oak woodland sequence described by Ovington et al. (1963) represents a successional series, since without burning, the prairies are invaded by woody species and savannas are converted to oak woodlands. Fires maintained the first two types in the past where soil characteristics and exposure to chronic fires permitted. Today, prairie and savanna types are maintained at Cedar Creek Natural History Area by controlled burning programs.

The prairie-savanna-oak woodland sequence shows an increase in productivity, but not in proportion to the much larger increase in biomass. Biomass-to-production ratios for aboveground parts are 1.03, 6.36, and 20.06 for prairie, savanna, and woodland, respectively. Thus production is increased at great cost in terms of organic matter and energy stored in the structure of the system. However, the sequence represents a gradient of greater maturity and conservation in the sense of amount of biomass supported per unit of production (Margalef 1963).

Production by the prairie ecosystem is rather low, both in relation to other similar vegetation of the sand plain and to other prairies. Two early stages of old-field succession, one dominated by *Setaria glauca* and another dominated by *Aristida basiramea*, had net production values of 1.2 t/ha. A more advanced old field, dominated by *Sorghastrum nutans* and approximating a tall-grass prairie, produced 1.6 t/ha (Bray, Lawrence, and Pearson 1959). Thus all three successional related old fields produced substantially more than the little-disturbed prairie of Ovington et al. (1963) (0.9 t/ha). Comparable data by workers in other prairies are also substantially higher (Hadley and Kieckhefer 1963, Kucera, Dahlman, and Koelling 1967, Hadley and Buccos 1967). The unusually low productivity of the prairie studied by Ovington et al. may have been caused by the particularly poor soil qualities at that site, which is on dunal sand rather than glacial outwash (Ovington et al. 1963). Textural analyses of prairie and savanna soils I collected at 7.5-, 15.0-, and 22.5-cm depths showed averages of 93.4% sand, 4.6% silt, and 0.7% clay. There was very little difference between sites or depths. In comparison, averages of samples from the same depths in the oak forest of Ovington et al. were 87.0% sand, 10.2% silt, and 1.8% clay.

Data for the oak woodland described by Ovington et al. are particularly valuable because their woodland is similar in age to the oak forest of this study and provides a basis for comparing data. Data on species composition are limited. Apparently the

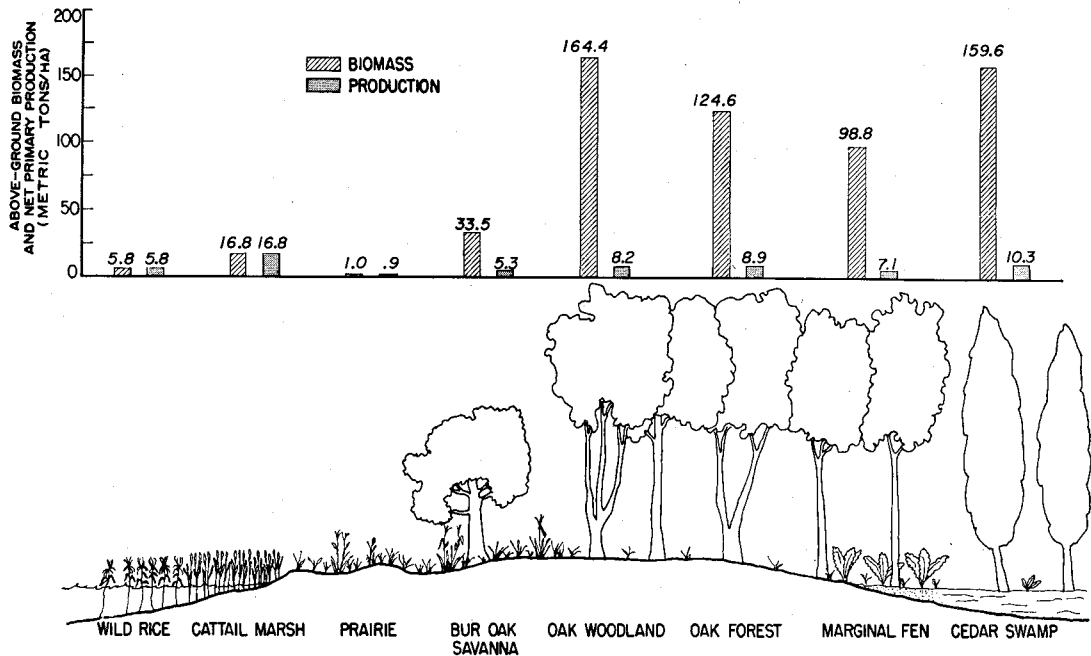


FIG. 3. A semidiagrammatic profile of natural ecosystems of the Anoka Sand Plain together with estimates of their aboveground biomass and annual net production. Data for the wild rice and cattail systems are from Bray, Lawrence, and Pearson (1959); data for the prairie, savanna, and oak woodland are from Ovington, Heitkamp, and Lawrence (1963).

woodland was dominated by *Quercus rubra*, but these individuals may have been hybrids, to some degree, with *Q. ellipsoidalis*. Production data compare remarkably well (8.2 t/ha for the Ovington et al. forest vs. 8.9 t/ha), but biomass data diverge substantially (164.4 vs. 124.6 t/ha). The reason for the disparity in biomass may lie in structural differences. Density in the Ovington et al. woodland was much lower than in the oak forest of this study (799 vs. 1,788 stems/ha), while its basal area was nearly equal (25 compared with 26.5 m²/ha). The Ovington et al. woodland therefore had fewer but larger trees indicating possible higher biomass, but not necessarily more production.

The four wetland systems range from graminoid littoral systems to forests (Fig. 3). These physiognomic contrasts are reflected in a broad range of biomass in this group (5.8 to 159.6 t/ha). This range in biomass is not, however, paralleled by production values. In fact, the cattail system with relatively low biomass showed the highest productivity of all the ecosystems studied on the sand plain (16.8 t/ha) (Bray et al. 1959). Outstanding production by similar marsh ecosystems has also been cited by Westlake (1963).

Production by wild rice (5.8 t/ha) is only 34% of cattail marsh production but 82% of the marginal fen. Production in the total wild rice system was likely to have been seriously underestimated because significant quantities of organic compounds are lost to the pelagic zone from the macrophyte-epiphyte

complex (Wetzel and Allen 1971). Such losses could not be measured by the harvest method used by Bray et al. (1959); but, if included, would bring production even closer to that of the marginal fen (1.1 t/ha).

Production (7.1 mt/ha) and biomass (98.8 mt/ha) for the marginal fen are the lowest among the four forests studied, due, in part, to the difficult conditions for large trees in the wet substratum. The wet, shallow rooting zone permits a high frequency of windthrow, thereby preventing establishment of large trees and a complete tree cover. Furthermore, the exceptionally low bole-diameter growth among fen trees in the last 10–15 years suggests that a change in the water table may have disrupted the system. The average annual precipitation has declined slightly since 1950 after a rather wet decade (Baker, Haines, and Strub 1967), and substantial water-table alterations have been documented for the area in the 1930's and 40's (Buell, Buell, and Reiners 1968).

The cedar swamp had the second highest productivity and biomass of all the systems shown in Fig. 3. It was also the oldest and the most completely stocked forest in terms of basal area (Table 1) and light-penetration data.

In summary, three major points emerge from this comparison of sand-plain ecosystems. First, a 171-fold range in aboveground biomass exists among the systems examined thus far. Productivity, however, varies only 18-fold. Second, although biomass data for the three forests described in this study seem

rather low in comparison with the only available example (the oak woodland of Ovington et al. 1963), productivity data are consistent with data on that oak woodland and other sand-plain ecosystems. Third, two classes of ecosystems exist in terms of biomass and production relations: the graminoid type with low biomass-to-production ratios (1.0, 1.0, 1.03 for wild rice, cattail, and prairie systems, respectively), and forest types with very high biomass-to-production ratios (20.1, 14.0, 14.0, and 15.5 for oak woodland, oak forest, fen, and swamp, respectively). The only transitional type for which data are available is the savanna with a biomass-to-production ratio of 6.4.

Comparison of data with a regional predictor for production.—Data on Anoka Sand Plain ecosystems provide an opportunity to examine variation in production among native ecosystems in relation to a regional predictor based on environmental factors. Rosenzweig (1968) described such a predictor with his empirical model for net aboveground productivity based on actual evapotranspiration (AET). The rationale for the use of AET as a predictor lies in its integration of solar energy and water availability. It is limited to mature communities because of variation in productivity through successional time. It is also restricted to ecosystems on well-drained soils.

Predicted net, annual aboveground production for upland sites of the Anoka Sand Plain is 8.7 mt/ha (Rosenzweig, *personal communication*). This prediction is based on a correlation of a broad array of mature ecosystems with the AET of their respective regions, and on an estimate of AET for east-central Minnesota derived from climatological data.

Production of upland systems in Fig. 3 as percentages of the prediction are 11 for prairie, 60 for savanna, 94 for oak woodland, and 102 for the oak forest. The close relation of both oak forest production estimates to the predicted value is gratifying and somewhat surprising because more water than usual is lost from the rooting zone through deep percolation on the Anoka Sand Plain. As a result, AET is probably less than estimated on the basis of precipitation and thermal data. Nutrients might also be expected to be limiting due to excessive drainage and low cation-exchange capacity of sandy soils, contributing further to relatively low production. Therefore, it might be expected that primary production would be overestimated by the predictive equation. The similarity of predicted and observed values might be due to the relative youth of the two forests, and it is possible that their productivity will be less in more mature states.

The low productivities of the prairie (0.9 mt/ha) and savanna (5.3 mt/ha) ecosystems relative to both Rosenzweig's standard and the higher productivities

of the oak forests might be ascribed to their poorer dunal soils compared with the outwash soils of the oak forests. If AET could be estimated by direct measurements rather than meteorological data, AET might be much lower than estimated, and a revised prediction might meet actual production figures. A related factor may be the superior ability of oak trees compared with prairie plants to exploit the capillary fringes of the generally high water table of the sand plain. Although some upland grasses, notably *Andropogon gerardi*, do have deep root systems (Weaver 1954), most cover in the prairie in question consisted of species with relatively shallow root systems (Ovington et al. 1963). If oaks are superior to local prairie herbs in this respect, this would account for the higher production in the savanna where 63% of the production was contributed by the scattered trees.

Rosenzweig's predictive model is designed for ecosystems on well-drained soils and therefore cannot be compared with results from wetland systems. If potential evapotranspiration is substituted for AET, the new predicted value, 9.3 mt/ha, is intermediate between the fen (7.1 mt/ha) and swamp (10.3 mt/ha) values, but unrelated to the graminoid wetland systems.

In summary, an empirical prediction based on simple meteorological data matched measured productivity for upland oak forests within 10% even though these forests are not mature. Production totals of other native upland communities are substantially lower than this value, presumably because of their inability to fully exploit energy and water resources of the region. This inability may be based on local site variations or structural constraints imposed by periodic fires.

The role of detritus in forest structure and function

Energy flow in detritus.—The weight and energy of litter fall and of accumulated detritus are tabulated in Table 8. These data have been more fully analyzed by Reiners and Reiners (1970). Odum and de la Cruz (1963) reviewed evidence for the importance of detritus in energy-flow patterns of many systems and some of the characteristics of detritus-based ecosystems. The detritus pathway is likely to be preeminent in most terrestrial ecosystems and may be most exaggerated in forest ecosystems.

Data for the forests of this study lend support to this belief. On a weight basis, material falling to the forest floor as detritus represented 3.7%, 4.5%, and 3.1% of the aboveground biomass and 52.4%, 62.5%, and 48.4% of net primary production of the oak, fen, and swamp, respectively. The remaining half of production is divided between long-term storage in the still-growing forests and the grazing pathway. Grazing losses have never been fully assessed

in forests. Aboveground losses include consumption of foliage by chewing insects, losses of cell sap to piercing-sucking insects, and losses of buds and fruits to birds and mammals. Only the first type has been measured on an entire ecosystem basis to my knowledge. Whittaker and Woodwell (1969) estimated leaf loss to chewing insects at 3.7% of aboveground production. Bray (1964) estimated similar losses from Ontario forests to range from 1.5% to 2.5% of aboveground production. Perhaps the highest recorded loss through leaf consumption was 13.1% of leaf weight on *Quercus petraea* by *Tortrix viridiana* under epidemic conditions (Carlisle, Brown, and White 1966). If we assume that leaf production is 33% of aboveground net production, this loss amounts to 4.3% of aboveground production. Still, these losses are trivial relative to errors of estimate for forest energetics. Because no estimates of leaf consumption were made in this work, some of the losses to the grazing pathway have, in effect, already been subtracted from net primary production. If they could be determined, they would be added to totals given in Table 8. Of course some grazing was still likely to have occurred after late August or early September, the time in which the forests were sampled. Such losses would not be added to totals given here but would be diverted from biomass storage, or more likely, from detritus.

It is conceivable that considerable grazing may occur on roots, so that if total production could be tabulated, the grazing fraction might be larger than presently suspected. Furthermore, underground losses might detract not only from subterranean biomass, but shoot growth as well.

Accumulated detritus.—The accumulation of detritus in the forest floor represents an energy and nutrient storage pool, a habitat for many kinds of heterotrophs, and a substratum for plants. The size of the accumulated detritus pool is a function of detrital input, successional time, and decomposition rate (Olson 1963). Decomposition rate is, in turn, a function of the nature of the detrital material, temperature, and moisture content (Reiners 1968). One of the principal structural differences between the three forests of this study was the size and turnover rates of forest floors (Reiners and Reiners 1970). The mass and energy content increased markedly downslope in these forests (65, 323, and 917 mt/ha), whereas detrital inputs were approximately equal (Table 8). Thus turnover times (forest floor/input) for all components of forest floors increased from oak to fen to swamp (14, 73, 184 years for total weight). They also represented 7, 46, and 90 years of aboveground production at current rates. Forest floors were 52%, 327%, and 575% of the respective biomasses of the oak, fen, and swamp.

A large amount of detritus in the form of dead

tree branches and boles and dead shrubs was found in all three forests but especially in the oak forest. This represented 8.6%, 4.1%, and 2.4% of living, aboveground biomass and 14.2%, 1.2%, and 0.4% of total detritus in oak, fen, and swamp forests, respectively. The sum of forest floor and dead wood (defined as detritus in Table 8) was 61%, 331%, and 577% of living biomass in the oak, fen, and swamp forests, respectively.

From these figures detritus clearly composes a major parameter of all three forests from both structural and functional points of view. Of course, accumulated detritus is maximized in wetland forests, such as the marginal fen and cedar swamp, where muck and peat have accumulated. For some purposes these deposits might not be defined as forest floors, but as organic soils or even geological deposits. These organic accumulations were collectively treated as forest floors in this study because forest floor humus and muck or peat were not clearly separated in the field, and because of the desirability to lump certain functions of a soil and more surficial layers (Reiners 1968).

The detritus pathway and system steady state.—About half of net primary production currently follows the detritus pathway in all three forests, and in the fraction of production utilized by heterotrophs, about 90% is probably utilized via the detritus pathway.

If these forests were permitted to develop to full steady states in terms of ecosystem photosynthesis and respiration, net production would theoretically be equaled by heterotroph respiration (Whittaker and Woodwell 1969). If the division of primary production distributed between grazing and detritus pathways were to remain the same in maturity, litter fall would eventually represent approximately 90% of net primary production. Litter inputs for oak, fen, and swamp forests, respectively, are 52%, 62%, and 48% of net production. These percentages are underestimates because they do not include tree-fall. Sporadic and highly dispersed tree-falls can add significant amounts to detrital input over long terms. But according to these data, the marginal fen is the closest to steady state and the cedar swamp the least mature—a conclusion contrary to one drawn on the basis of ages of the forests. Two factors may be responsible for these conflicting conclusions. First, the high ratio of litter to production in the fen is distorted upward because some litter fall is contributed by swamp and oak forests. Fen litter is exported to these forests as well, but since litter fall is heavier in oak and swamp than in the fen, the net movement is into the fen (Reiners and Reiners 1970). Such a contribution to fen litter fall would have to amount to 17% of the present total, however, to reduce the percentage of litter to 52% of production, the level

estimated for the oak forest. The second factor is that dominance of a conifer in the swamp may lead to misleading comparison with predominately deciduous forests. *Thuja occidentalis* has a lower turnover of this foliage via litter fall than deciduous species. As a result, the litter-fall-to-production ratios of the swamp will be lower due to functional attributes of *Thuja* alone. This characteristic of tree form and function should be considered whenever estimates of maturity based on litter fall/production are compared between forest types.

ACKNOWLEDGMENTS

The author wishes to thank Mrs. Robert Shoemaker and the undergraduates of the University of Minnesota who assisted in the field and laboratory. Appreciation is expressed to Dr. William H. Marshall, Director of Cedar Creek Natural History Area, for his cooperation, and to Dr. George M. Woodwell, Brookhaven National Laboratory, for suggestions pertaining to the manuscript. My wife, Norma, was invaluable in all stages of the project. This study was made financially possible through National Science Foundation Grants GB-3636 and GB-7148.

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