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Author(s): J. Patrick Megonigal, Frank P. Day and Jr.

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ORGANIC MATTER DYNAMICS IN FOUR SEASONALLY FLOODED FOREST COMMUNITIES OF THE DISMAL SWAMP¹

J. PATRICK MEGONIGAL AND FRANK P. DAY, JR.

Division of Wetlands Ecology, Savannah River Ecology Laboratory,
Drawer E, Aiken, South Carolina 29801; and Department of Biological Sciences,
Old Dominion University, Norfolk, Virginia 23529

ABSTRACT

Budgets of organic matter dynamics for plant communities of the Great Dismal Swamp were developed to summarize an extensive data base, determine patterns of biomass allocation, transfer and accumulation, and make comparisons with other forested wetlands. Aboveground net primary production on the flooded sites ($1,050\text{--}1,176\text{ g m}^{-2}\text{ yr}^{-1}$) was significantly greater than on a rarely flooded site ($831\text{ g m}^{-2}\text{ yr}^{-1}$). Estimates of belowground net primary production were comparable to aboveground production on flooded sites ($824\text{--}1,221\text{ g m}^{-2}\text{ yr}^{-1}$). However, productivity was nearly three times greater belowground than aboveground on the rarely flooded site ($2,256\text{ g m}^{-2}\text{ yr}^{-1}$). Aboveground productivity in Dismal Swamp forests is relatively high compared to other forested wetlands. This is attributed to the timing and periodic nature of flood events. Fine root turnover is shown to be an important source of soil organic matter. Estimates indicate that roots contribute about 60% of the annual increment to soil organic matter. Leaf litter contributes 6–28% and wood debris contributes 5–15%. Comparisons with other forested wetlands suggest that detritus accounts for greater than half of the total organic matter (living + dead) in many wetland systems.

THE BIOGEOCHEMICAL CYCLES of freshwater forested wetlands are unique among forested ecosystems. Flooding leads to predictable and dramatic changes in the solubility and chemical reactivity of important soil nutrients (Gambrell and Patrick, 1978) and influences rates of elemental import, export, storage, and processing (Kuenzler et al., 1980; Brinson, Lugo, and Brown, 1981). Secondary production in wetlands and associated aquatic systems is intimately related to organic matter and nutrient processing rates (Benke, 1984). Certain aspects of organic matter dynamics, such as litterfall and decay rates, have been the subject of many ecosystem level studies at a variety of freshwater forested wetland sites. However, there have been comparatively few

efforts at an ecosystem level synthesis of all the major storage and transfer rates on a given site. Such studies provide valuable insight into patterns of productivity, storage, and mass balance which are often overlooked in less complete investigations (Vogt, Grier, and Vogt, 1986). We present a synthesis of several studies on organic matter dynamics in the Great Dismal Swamp, Virginia. These data permit between-site comparisons of net primary production, above- and belowground detrital transfer rates, and the annual contribution of various litter sources to soil organic matter from various litter sources. In addition, patterns of organic matter storage in Dismal Swamp forests are compared with other freshwater forested wetlands.

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STUDY SITES—The Great Dismal Swamp occurs on 85,000 ha of the Atlantic coastal plain in southeastern Virginia and northeastern North Carolina. The Suffolk escarpment is the artesian head of an aquifer that underlies the swamp's eastward sloping surface (Lichtler and Walker, 1979). Water movement is thought to be quite slow and in a southeasterly direction, except through the numerous ditches that dissect the swamp's surface. Hydroperiod is highly dependent on annual patterns of precipitation; flooding generally occurs during the winter and spring. During periods of low rainfall the water table can drop $>1\text{ m}$ below the

TABLE 1. Selected features of four long-term research sites in the Great Dismal Swamp

Feature	Cedar	Cypress	Maple-gum	Mixed hardwoods
Relative basal area for canopy dominant (%) ^a	56	47	33 (maple) 45 (gum)	51
Age range of canopy dominant (yr) ^b	33–101	47–113	38–103	39–109
Months flooded ^c	4	6	6	0
Maximum flooding depth ^c (cm)	20	21	17	—
Soil pH (range) ^c	3.3–4.4	4.5–5.5	4.3–5.6	3.2–4.9
Soil organic matter ^d	84.7%	3.7%	13.6%	2.4%
Soil type ^d	Medisaprist	Fluvaquent	Fluvaquent	Ochraqult
Water-retaining capacity ^e	734%	—	501%	83%

^a From Dabel and Day (1977).^b From Train and Day (1982).^c From Day (1982).^d From J. Rule and T. Matthews (unpublished data). Unweighted average to 40 cm.^e From Levy and Walker (1979) WRC (%) = (saturated wt. – oven-dry wt.)/oven-dry wt. × 100.

soil surface. Mean annual precipitation is 117 cm, with a low in August of 7 cm and a high in April of 15 cm. The mean annual temperature is 15 C.

The Dismal Swamp is a patchwork of vegetation and soil types. Data used in this study were collected from four long-term study sites which represent the more extensive plant communities (Gammon and Carter, 1979). The sites differ in dominant vegetation, soils, and hydroperiod (Table 1). Three sites are periodically flooded; one is rarely flooded. Two sites support coniferous canopy dominants (Atlantic white cedar [*Chamaecyparis thyoides*] and cypress [*Taxodium distichum*]), and two support hardwood species (maple-gum [*Acer rubrum*-*Nyssa aquatica*] and oak species [*Quercus* spp.]). Atlantic white cedar (herein referred to as cedar) occurs on an acid peat while the others occur on mineral soils (Bandle and Day, 1985). More detailed descriptions of the vegetation, soils, and history of these sites are found in Dabel and Day (1977), Gomez and Day (1982), and Bandle and Day (1985).

METHODS—An extensive data base on organic matter dynamics in the Great Dismal Swamp was summarized in budget format. Most standing stocks and rates of flux were measured directly on the sites. These included above- and belowground biomass; aboveground net primary production; belowground net primary production on the maple-gum site; leaf, branch, and wood litter standing stocks; leaf, branch, and wood litterfall rates; leaf litter and root necromass decay rates; red maple branch and bole decay rates; and soil organic matter standing crop (Table 2). There were no data available on bole mortality rates. Three groups of tree taxa were distinguished on each site: 1) the dominant species, 2) red maple and

3) other species. Some calculations distinguished between fine (<3 mm) and course roots. Parameters were quantified for each category on each site and are detailed in Appendix 1. After calculations were made, some of the data were lumped for ease of presentation.

Aboveground net primary production was determined for stems >2.54 cm dbh using species specific diameter increments and mean tree regression equations (Dabel and Day, 1977). Annual increments were based on published vernier tree band data (Day, 1985) and unpublished tree ring data (Train and Day, unpublished manuscript). Leaf production was assumed to equal leaf standing stock for deciduous species and leaf litter production for evergreen species (250 g m⁻² yr⁻¹ for cedar). Production of other understory vegetation was assumed to be negligible.

Some parameter estimates were based on literature sources or certain reasonable assumptions. The percentage of total bole or branch biomass in each species category was used to partition wood litter standing stocks among the three groups. Cedar wood litter was increased to 50% of the wood litter standing stock to account for the unusually high mortality rate of this species on our sites. Leaf litter 01 and 02 standing stocks represent yearly maxima and were partitioned among the species categories based on unpublished data from Day's (1979) study of litter accumulation in the Dismal Swamp. Further details on the percentages and assumptions used for dividing standing crops or fluxes among species categories are available in Megonigal (1986).

Bole and branch decay rates for red maple were used for gum, other species, and oaks. The exceptionally slow decay of cedar and cypress wood was accounted for by multiplying the maple wood decay rate by the ratio of decay rates for cedar (or cypress) leaf litter and maple

TABLE 2. *Methods used to estimate the parameters of the organic matter budgets. See the Methods section for more detail*

Parameter	Method	Citation
Leaf, branch, and bole standing crop	Diameter-mass regressions	Day and Dabel, 1978
Leaf 01, leaf 02, branch, and bole litter standing crop	Forest floor harvest	Day, 1979
Total root standing crop	Pit harvests	Montague and Day, 1980
Live/dead root ratios	Core sampling ^a	Symbula and Day, in press
Branch and bole production	Diameter increment and regressions	Day, 1985; Dabel and Day, 1977
Root production	Serial root cores ^b	Symbula and Day, in press
Leaf and small wood litter fall	Litter baskets	Gomez and Day, 1982
Leaf litter decay	Litter bags	Day, 1982
Root necromass decay	Litter bags ^c	Tupacz, unpublished data
Maple branch decay	Prewieghed maple branches	Day, 1982
Maple bole decay	Prewieghed maple boles ^d	Day, unpublished data
All transfers to SOM	Mass balance	See Methods section

^a Annual average of lateral root biomass and necromass from 10 soil-root cores (7 cm diameter to a depth of 40 cm) taken from the maple-gum site at one month intervals from May 1983 to April 1984. Cores were located by stratified-random sampling.

^b Calculated from monthly estimates of root biomass and necromass using the Wiegert-Evans' model (1964). Root decomposition rates for the model were measured at 10 and 30 cm depths using 1 mm mesh litter bags retrieved at 2–2.5 month intervals.

^c Mass loss from root litter bags (1 mm mesh) after 351 days in the field. Bags were filled with air-dried roots harvested from each site. Litter bags were about 4 cm wide and 40 cm long so that decay estimates are effectively integrated over a 40 cm depth.

leaf litter. This correction was made separately for boles and branches on the cedar and cypress sites.

Bole and branch decay rates were determined using unconfined samples and therefore represented both mineralization and fragmentation losses. Harmon et al. (1986) reported two studies that separated these factors, one on *Abies balsamea* and the other on *A. concolor*. They showed fragmentation to be 63 and 55% of total weight loss, respectively. We multiplied total wood decay losses by 40% for an estimate of mineralization rate. Leaf and root litter decay rates were assumed to be entirely mineralization losses because they were determined using 1 mm mesh litter bags.

The rate at which surface litter is incorporated into soil organic matter (SOM) is rather difficult to quantify. However, given the litter standing crop and its decay rate and assuming the litter standing crop is relatively constant, transfer rates can be calculated by mass balance. Mass balance was used to calculate rates of transfer from the leaf litter 01 to the leaf litter 02 layer, from leaf litter 02 to SOM and from fine root necromass to SOM.

A rough estimate of wood litter to SOM transfer was made given the reasonable assumption that the woody litter layer is also at steady-state (Bormann and Likens, 1979). Woody litter inputs were estimated as 1.5% of the wood biomass on a site (Waring and Schlesinger, 1985). The difference between wood

mortality and mineralization was the amount transferred to SOM. Steady-state is an unreasonable assumption for the cedar site because of the relatively high mortality rate of cedar trees. Therefore, the transfer rate determined for the cypress site was applied to the cedar site.

Total lateral root standing stocks reported by Montague and Day (1980) were multiplied by a live root : dead root ratio to estimate the fraction in each of those categories. The ratio was based on mean annual lateral root biomass and necromass data from the maple-gum site (Symbula and Day, in press). Separate estimates were made for fine and coarse roots (Symbula and Day's fine root category was ≤ 5 mm); the ratios were 0.67 and 0.69, respectively.

Root production was estimated as the product of total root biomass and a production: biomass ratio. The ratio (1.12) was based on estimates of fine root net primary production and mean annual fine root biomass for the maple-gum site (Symbula and Day, in press). We considered the fine root production estimate ($439 \text{ g m}^{-2} \text{ yr}^{-1}$) conservative because it was based on statistically significant changes in root biomass over time.

Root mortality data from Symbula and Day (in press) were used to estimate root turnover. A mortality:biomass ratio was determined for fine and coarse roots (1.05 and 1.55, respectively), averaged, and compared with the pro-

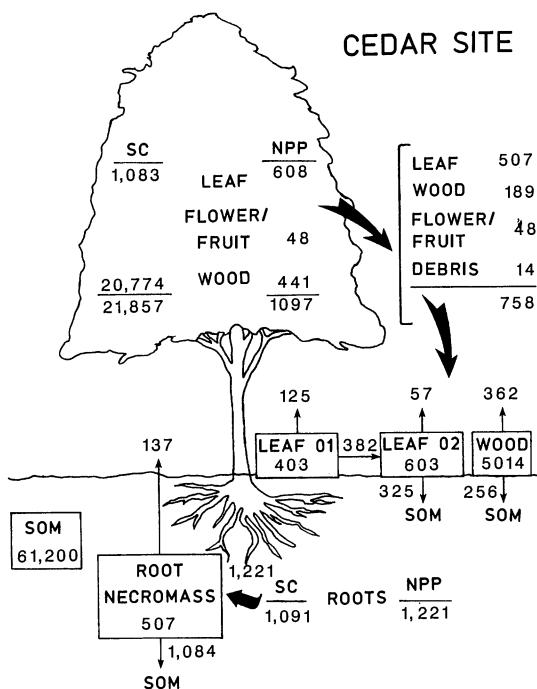


Fig. 1. Organic matter budgets for a cedar forest community in the Great Dismal Swamp. Upward-oriented arrows represent mineralization losses, arrows between boxes represent mass transfer, SC = standing crop, NPP = net primary production, and SOM = soil organic matter. The bracket indicates litterfall fluxes. Wood litterfall is for small stems only (Gomez and Day, 1982) and was not used to calculate wood litter to soil organic matter transfer rates (see text). The 01 leaf litter is largely undecomposed while the 02 leaf litter has undergone considerable decomposition.

duction:biomass ratio determined earlier. Because the ratios were quite close, root mortality was assumed to equal root production.

Bulk densities of study site soils were determined in order to calculate SOM mass (40 cm depth). Undisturbed soil cores were taken from each site at depths that correspond to major shifts in % SOM (Megonigal, 1986). Cores were dried at 110 C to constant mass. Analysis of Variance (ANOVA) and Duncan multiple range tests were used to test for differences in production. Total belowground standing crops were compared with *t* tests. Further details on the methods are in Table 2.

RESULTS—Standing crop and net primary production—Wood standing crop was significantly greater at the cypress site than at the other three sites ($F = 3.47$, $P = 0.026$); there were no significant differences in wood standing crop among the other three sites. Total root standing stocks were significantly greater on

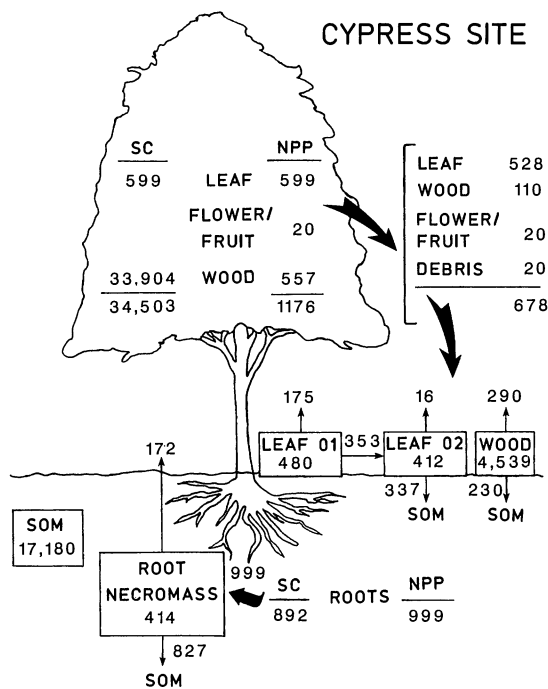


Fig. 2. Organic matter budgets for a cypress forest community in the Great Dismal Swamp. Details as in Fig. 1.

the mixed hardwood site ($2,905 \text{ g m}^{-2}$; $P \leq 0.01$) than on the flooded sites ($1,086\text{--}1,594 \text{ g m}^{-2}$).

Aboveground net primary production (AGNPP) was greatest on the periodically flooded sites (Fig. 1–4). Wood production on flooded sites was significantly greater than at the rarely flooded site ($F = 6.90$, $P \leq 0.01$). Leaf production (standing crop for deciduous species) did not differ significantly among deciduous communities. Our estimate of leaf production at the cedar site was not included in the ANOVA because it was based on litterfall rates (rather than litter standing crop). However, this estimate ($608 \text{ g m}^{-2} \text{ yr}^{-1}$) approximated those of the cypress and maple-gum sites (599 and $583 \text{ g m}^{-2} \text{ yr}^{-1}$). The data indicated that differences in AGNPP were due to variation in wood production. Belowground net primary production was comparable to AGNPP at the flooded sites ($824\text{--}1,221 \text{ g m}^{-2} \text{ yr}^{-1}$) but was nearly three times greater than AGNPP at the mixed hardwood site. Total productivity (above- + belowground) was greatest at the mixed hardwood site.

Forest floor organic matter—The cedar and cypress sites had the greatest accumulations of organic matter on the forest floor, mainly because of the wood litter component, which ac-

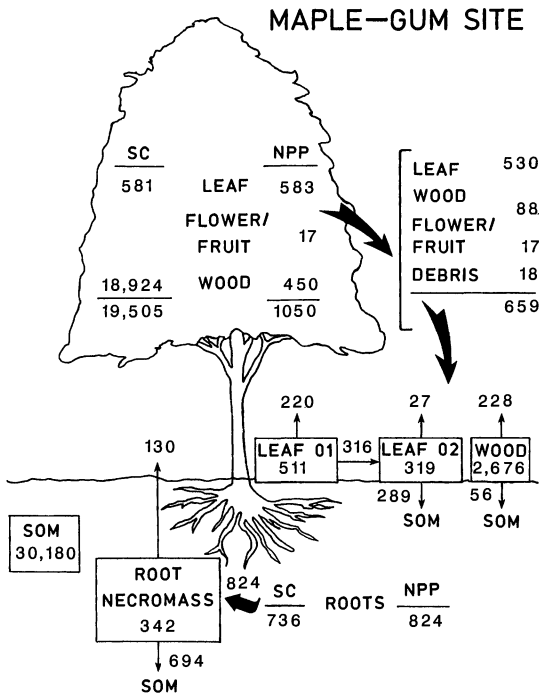


Fig. 3. Organic matter budgets for a maple-gum community in the Great Dismal Swamp. Details as in Fig. 1.

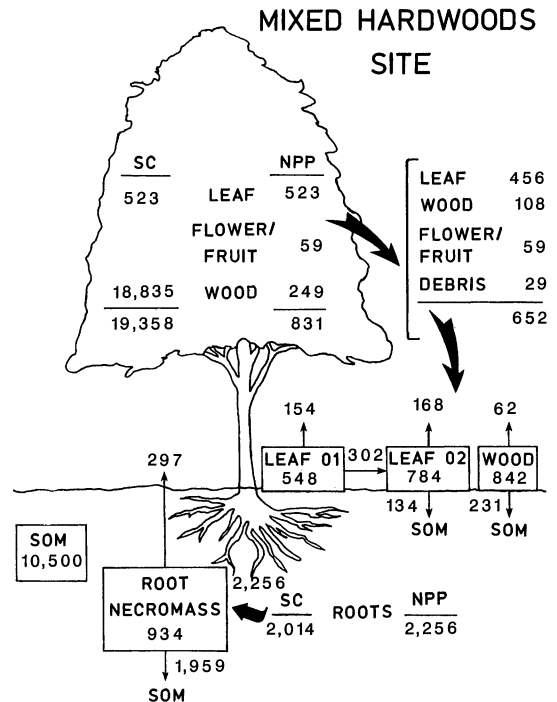


Fig. 4. Organic matter budgets for a mixed hardwood community in the Great Dismal Swamp. Details as in Fig. 1.

counted for 83 and 76% of the total (Day, 1979). Wood litter accumulation was lowest at the mixed hardwood site. Total leaf litter differed significantly at all sites ($P \leq 0.01$). The 02 soil layer at the mixed hardwood site was significantly greater than at the other deciduous sites ($P \leq 0.01$). This layer was not measured on the cedar site due to frozen conditions (Day, 1979).

Soil organic matter—Accumulations of soil organic matter (SOM) were greatest at the cedar and maple-gum sites. The cedar site had four times the SOM of the cypress site, twice that of the maple-gum site and six times the amount at the mixed hardwood site.

Estimates of litter 01 to litter 02 transfer rate could not be analyzed statistically but appeared comparable for all sites (range: 302–382 $\text{g m}^{-2} \text{yr}^{-1}$). Estimates of transfer from the 02 litter pool to SOM were similar among flooded sites (range: 289–337 $\text{g m}^{-2} \text{yr}^{-1}$) and were twice the estimate for the mixed hardwoods site (134 $\text{g m}^{-2} \text{yr}^{-1}$).

Transfer from wood to SOM was similar for the cedar and cypress sites (256 and 230 $\text{g m}^{-2} \text{yr}^{-1}$) because they had similar wood litter standing crops and the cypress transfer rate coefficient was used for the cedar site estimate (see Methods). Wood transfer to SOM was four times greater at the mixed hardwood site (231

$\text{g m}^{-2} \text{yr}^{-1}$) than at the maple-gum site (56 $\text{g m}^{-2} \text{yr}^{-1}$) despite nearly identical wood mortality rates. This was a direct result of relatively rapid decay rates on the maple-gum site and the mass balance assumption.

DISCUSSION—*Net primary production and standing crop*—Wetland productivity is tightly coupled to hydrology and nutrient regime. Periodically flooded wetlands are more productive than those which are either continuously inundated or drained (Mitsch and Ewel, 1979). Floodplain forests are generally more productive than slow-water or still-water systems (Conner and Day, 1976; Brinson et al., 1981; Brown, 1981) largely because of nutrient subsidies associated with water inputs other than precipitation. Mitsch, Dorge, and Wiemoff (1979) showed that P inputs from precipitation were relatively minor compared with inputs from a nearby river during a flood event. Schlesinger (1978) attributed low production in the ombrotrophic Okefenokee cypress swamp forest to continuous flooding and low nutrient inputs. Thus, the percentage of water coming from precipitation is an important determinant of wetland productivity.

Little is known about hydrologic inputs to the Dismal Swamp. Lichtler and Walker (1979) estimated that $117 \times 10^6 \text{ m}^3 \text{yr}^{-1}$ of upland

runoff enters the swamp annually. Rainwater inputs can be estimated by multiplying average rainfall and the areal extent of the swamp. Using values in Lichtler and Walker (1979), precipitation contributes about $1,090 \times 10^6 \text{ m}^3 \text{ yr}^{-1}$ or 90% of the water input. This estimate does not account for interception by drainage ditches or ground water inputs. By comparison, precipitation is 70–90% of water inputs to the Okefenokee Swamp (Rykiel, 1984).

Despite apparently low nutrient inputs, Dismal Swamp forests are more productive (aboveground; Fig. 1–4) than seven still-water sites reported in Brown and Peterson (1983) and are comparable to a Louisiana floodplain swamp (Conner and Day, 1976). Flooding in the Dismal Swamp occurs mainly during winter months when trees are dormant. Although water may be standing on the flooded sites at bud break, it has normally begun to draw down and does not persist far into the most active part of the growing season. Wet, but aerobic, soil conditions during this period may stimulate productivity (Day, 1984). Productivity may also be enhanced by seasonal pulses of decay and nutrient release caused by alternate periods of drying and flooding (Gomez and Day, 1982). Periodic flooding and, in particular, the timing of periodic floods contribute to the relatively high productivity of Dismal Swamp forests. A more definitive study of water relations in this system is needed to determine the extent to which upland runoff and groundwater inputs contribute to the overall hydrologic budget. These sources of water may also be significant sources of nutrients.

Belowground production on the flooded sites is similar in magnitude to a *Liriodendron* forest in Tennessee ($900 \text{ g m}^{-2} \text{ yr}^{-1}$; Harris, Kinerson, and Edwards, 1977) and within the range reported by McClaugherty, Aber, and Melillo (1984) for a mixed hardwood forest in Massachusetts ($540\text{--}1,140 \text{ g m}^{-2} \text{ yr}^{-1}$). Root production on the mixed hardwood site is larger in comparison because of a large root standing stock. However, our estimate includes production of coarse lateral roots where other studies do not. Because coarse roots are less dynamic than fine roots, the application of a fine root production ratio to total belowground biomass probably overestimated belowground production.

Soil organic matter—SOM serves as a nutritive substrate for microorganisms and influences biologically mediated soil processes such as reduction-oxidation reactions and the availability, cycling and transformation of nutrients (Anderson and Coleman, 1985; Schi-

mel, Coleman, and Horton, 1985). The suitability of SOM as a carbon or energy source can vary depending on nitrogen, holocellulose and lignin content (Berg, 1986). Therefore, it is important to consider the sources of tissues that contribute to SOM. Our estimates indicate that roots contribute about 60% of the organic matter in Dismal Swamp soils (cedar: 65%, cypress: 59%, maple-gum: 67% and mixed hardwoods: 84%). The percentage is highest for the mixed hardwood site which has the greatest root standing crop and the lowest accumulation of forest floor detritus. The magnitude of these estimates is consistent with reports from other systems. Harris, Santantonio, and McGinty (1979) estimated that root turnover accounted for 70% of the organic matter returned to the soil in an upland forest. Further calculations show that if coarse root production ($> 3 \text{ mm}$) was overestimated by 50%, the contribution of roots to soil carbon is still about 50% for flooded sites (range 46–55%) and 76% for the rarely flooded mixed hardwood site. Fine roots alone (assuming no turnover of coarse roots) would contribute one-third of the annual soil carbon increment on flooded sites and two-thirds on the mixed hardwood site. Thus, root turnover is certainly an important component of soil carbon dynamics.

Large contributions of carbon to soils from fine roots is due in part to rapid turnover rates. However, it is also important to consider the environment of deposition. Roots are in direct contact with the soil at death; and transport into the mineral horizon is not a requisite step for incorporation into SOM. Colonization by microbial decomposers may be more rapid belowground. Flooding has a particularly important influence on the environment of root deposition because of its control on decomposition rates.

Soils of the mixed hardwood site are relatively dependent on roots as a source of soil organic matter (Fig. 4). Turnover in the aboveground litter layers is slow on this site; turnover time of the O2 leaf litter layer is about 2.6 years compared with 1.0–1.6 years on the flooded sites. In addition, mass balance considerations suggest that a relatively small percentage of annual turnover in the O2 layer is incorporated into the soil on the rarely flooded (mixed hardwood) site (cedar: 54%, cypress: 82%, maple-gum 91% and mixed hardwoods: 17%). Perhaps processes that incorporate organic matter into soils on the flooded sites do not operate efficiently on the rarely flooded stand. For example, winter flood waters may serve as a means of vertical transport.

Leaf litter contributes 6–28% of annual in-

TABLE 3. Accumulations of biomass and detritus in forested wetlands and the distribution of organic matter among the biomass and detrital subsystems. Soil organic matter was adjusted to reflect a 40 cm depth when peat accumulations exceeded 40 cm. N W cedar = northern white cedar and A W cedar = Atlantic white cedar. References are 1) Schlesinger, 1978, 2) Reiners, 1972, 3) Reader and Stewart, 1972, 4) Duever, Carlson, and Riopelle, 1984, 5) Nessel and Bayley 1984, and 6) this study. Values are Mg/ha. The "other" category includes shrubs, herbs, epiphytes, and fruit biomass

Stand type	Biomass					Detritus					Detritus to total mass ratio	System total	Ref.
	Wood	Leaf	Root	Other	Total	Wood	Leaf	Root	SOM	Total			
Wetland sites													
Cypress	298.2	2.3	—	6.1	306.6	51.7 ^a	—	—	400.0 ^b	451.7	0.60	758.3	1
N W Cedar	151.2	7.8	—	1.0	160.0	3.9	7.2	—	520.1 ^c	531.2	0.77	691.2	2
Hardwood fen	94.1	3.9	—	2.3	100.3	4.1	8.9	—	314.0	327.0	0.77	427.3	2
Spruce bog	44.5 ^d	—	22.8	—	67.3	—	—	—	306.5 ^e	306.5	0.82	373.8	3
Cypress strand (large trees)	603.3	3.5	38.4	1.3	646.5	11.2	11.2	—	657.6 ^f	680.0	0.51	1,326.5	4
Cypress strand (small trees)	234.2	4.9	42.2	1.2	282.5	8.1	12.9	—	361.7 ^g	382.7	0.58	665.2	4
Cypress dome ^h (sewage treated)	284.3	6.5	135.4	—	426.2	26.9	16.3	—	553.5	596.7	0.58	1,022.9	5
A W Cedar	207.7	10.8	10.9	2.3 ⁱ	231.7	50.1	10.1	5.1	612.0	677.3	0.75	909.0	6
Cypress	339.0	6.0	8.9	0.4	354.3	45.4	8.9	4.1	171.8	230.2	0.39	584.5	6
Maple-gum	189.2	5.8	7.4	0.9	203.3	26.8	8.3	3.4	301.8	340.3	0.63	543.6	6
Upland sites associated with forested wetlands													
Mixed hard-woods	188.4	5.2	20.1	1.5	215.2	8.4	13.3	9.3	105.0	136.0	0.39	351.2	6
Oak forest	120.8	3.4	—	0.7	124.9	10.8	12.6	—	52.6	76.0	0.38	200.9	2

^a Above-water dead wood only.

^b Based on an unadjusted peat depth of 2.9 m.

^c Based on an unadjusted peat depth of 0.7 m; Reiners and Reiners, 1970.

^d Includes leaf biomass.

^e Based on an unadjusted peat depth of 1.9 m.

^f Bulk density was assumed to be 0.41 g/m³ and organic matter 40.1% based on the peat horizon of a North Florida cypress strand (Lugo, Nessel, and Hanlon, 1984).

^g Peat depth at the strand edge calculated to equal 0.22 m from figure 32.4 in reference 4.

^h Based on figure 26.7 and table 26.7.

ⁱ Herb and shrub data from Day and Dabel (1978); fruit and flower data from Gomez and Day (1982).

crements to SOM. This component (like fine root necromass) is relatively dynamic compared with wood litter. While many studies have investigated the nutrient dynamics associated with leaf litter decay in wetlands, and the factors controlling it (Brinson et al., 1981; Day, 1982), its importance to overall ecosystem dynamics has rarely been addressed.

The ecology of wood debris in terrestrial ecosystems has received little attention in comparison to leaf litter. Harmon et al. (1986) showed that wood debris is important to N and P cycling in some systems, as a long term source of energy and nutrients and as plant and animal habitat. Its importance as a source of SOM on our study sites is relatively minor, on an annual basis, compared with fine roots. Despite large accumulations of wood debris in Dismal Swamp forests, wood litter contributes just 5–17% of the annual SOM increment. Fallen

branches and logs are only in partial contact with the soil surface; this can have a negative effect on their moisture content and rate of decomposition (Harmon et al., 1986). By the time wood litter has decomposed to the point that it can be incorporated into SOM, much of its original mass has already been lost to mineralization.

The transfer of mass from dead leaves, wood, and roots to SOM was calculated as the difference between inputs and mineralization losses under the assumption of steady-state conditions. Mineralization losses were calculated as the product of mean annual standing crop and annual decay rate. An alternative approach is to multiply the annual mass input to a detrital component by the annual decay rate. By this method, the contribution to SOM is 42–75% for roots, 12–27% for leaves, and 13–35% for wood. The relative importance of leaf,

wood, and root litter to SOM is essentially the same by either approach.

These conclusions apply only to the most recent accumulations of SOM. As a given annual increment to the SOM pool ages, the relative proportions of wood, leaf, and root tissue change depending on their decomposability. A recent modeling effort concluded that wood, leaf, and root tissue comprise 62, 8, and 15% of the *steady-state* SOM pool of a *Pinus silvestris* forest (Ågren and Bosatta, 1987). Thus, further research may show that roots and leaves are most important to the labile (and most nutritious) fraction of the forest SOM pool while wood is most important to the recalcitrant fraction.

Total detritus accumulations—Detrital accumulations constitute a large part of the energy and nutrient stores of forested ecosystems. Unfortunately, few studies report data that allow detailed comparisons of organic distribution among the components of a forested wetland; bottomland hardwood and riverine forests are particularly underrepresented (Table 3). Harmon et al. (1986) found just 8 such studies for temperate terrestrial sites.

Detrital accumulations often account for greater than half of the total organic matter (living + dead) in forested wetlands (Table 3), particularly those with large peat accumulations. By comparison, temperate upland forests often have greater than half of the total organic matter tied up in biomass (Grier and Logan, 1977; Harmon et al., 1986). Schlesinger (1977) estimates that, on a worldwide basis, detritus accounts for 45% of the total organic matter in temperate forests, 36% in tropical forests, 62% in boreal forests and 91% in swamps and marshes. However, there are numerous exceptions for both upland and wetland systems. Detrital dominance in wetlands is due to large accumulations of soil carbon (Schlesinger, 1977). One would predict detritus-dominated systems to have relatively slow turnover times for organic matter and nutrients.

The cypress site is biomass-dominated due to large amounts of wood biomass and low SOM (Table 3). Yet budget calculations suggest that total input and output to soils on the site are comparable to other flooded sites in the ecosystem. The large accumulation of biomass (as opposed to necromass) on this site may turn over very slowly because of the longevity of cypress. If this is the case, development of a large detritus component may re-

quire a relatively long period of time. Belowground dynamics have been shown to be important in the development of SOM; perhaps production and turnover of root mass is less rapid than estimated. Export of detritus via surface water runoff is assumed to be unimportant in this low gradient, slow-flowing system. The leaf litter estimates, which represent peak values (December and January collections; Day and Dabel, 1978), would overestimate the annual standing stock if there is export during the flood season. In this case, our mass balance estimate of leaf litter to SOM transfer would be high.

Mass balance studies often serve to illustrate where research is lacking. Most of the simplifying assumptions required for this study relate to detrital dynamics. Future research on the detrital cycles of forested systems should focus on the chemical nature and dynamics of root tissues because they are a primary organic component of the rooting environment. Soil organic matter dynamics (e.g., decay rates) are also poorly understood and deserve increased attention. Models based on the organic matter budgets presented here have been developed and offer additional insight into system dynamics (Megonigal, 1986).

LITERATURE CITED

- ÅGREN, G. I., AND E. BOSATTA. 1987. Theoretical analysis of the long-term dynamics of carbon and nitrogen in soils. *Ecology* 68: 1181–1189.
- ANDERSON, D. W., AND D. C. COLEMAN. 1985. The dynamics of organic matter in grassland soils. *J. Soil Water Conserv.* 40: 211–216.
- BANDLE, B. J., AND F. P. DAY. 1985. Influence of species, season, and soil on foliar macronutrients in the Great Dismal Swamp. *Bull. Torrey Bot. Club* 112: 146–157.
- BENKE, A. C. 1984. Secondary production of aquatic insects. In V. H. Resh and D. M. Rosenberg [eds.], *The ecology of aquatic insects*, 289–322. Praeger, New York.
- BERG, B. 1986. Nutrient release from litter and humus in coniferous forest soils—a mini review. *Scand. J. For. Res.* 1: 359–369.
- BORMANN, F. H., AND G. E. LIKENS. 1979. *Pattern and process in a forested ecosystem*. Springer-Verlag, New York, Heidelberg, Berlin.
- BRINSON M. M., A. E. LUGO, AND S. BROWN. 1981. Primary productivity, decomposition and consumer activity in freshwater wetlands. *Annual Rev. Ecol. Syst.* 12: 123–161.
- BROWN, S., AND D. L. PETERSON. 1983. Structural characteristics and biomass production of two Illinois bottomland forests. *Amer. Midl. Naturalist* 110: 107–117.
- . 1981. A comparison of the structure, primary productivity, and transpiration of cypress ecosystems in Florida. *Ecol. Monogr.* 51: 403–427.
- CONNER, W. H., AND J. W. DAY. 1976. Productivity and

- composition of a bald cypress-water tupelo site in a Louisiana swamp. *Amer. J. Bot.* 63: 1354-1364.
- DABEL, C. V., AND F. P. DAY. 1977. Structural comparisons of four plant communities in the Great Dismal Swamp, Virginia. *Bull. Torrey Bot. Club* 104: 352-360.
- DAY, F. P. 1985. Tree growth rates in the periodically flooded Great Dismal Swamp. *Castanea* 50: 89-93.
- . 1984. Biomass and litter accumulation in the Great Dismal Swamp. In K. C. Ewel and H. T. Odum [eds.], *Cypress swamps*, 386-392. University Presses of Florida, Gainesville.
- . 1982. Litter decomposition rates in the seasonally flooded Great Dismal Swamp. *Ecology* 63: 670-678.
- . 1979. Litter accumulation in four plant communities in the Great Dismal Swamp, Virginia. *Amer. Midl. Naturalist* 102: 281-289.
- , AND C. V. DABEL. 1978. Phytomass budgets for the Great Dismal Swamp ecosystem. *Virginia J. Sci.* 29: 220-224.
- DUEVER, M. J., J. E. CARLSON, AND L. A. RIOPELLE. 1984. Corkscrew Swamp: a virgin cypress strand. In K. C. Ewel and H. T. Odum [eds.], *Cypress swamps*, 334-348. University Presses of Florida, Gainesville.
- GAMBRELL, R. P., AND W. H. PATRICK, JR. 1978. Chemical and microbiological properties of anaerobic soils and sediments. In D. D. Hook and R. M. M. Crawford [eds.], *Plant life in anaerobic environments*. Ann Arbor Science Publishers, Ann Arbor, MI.
- GAMMON, P. T., AND V. CARTER. 1979. Vegetation mapping with seasonal color infrared photographs. *Photogrammetric Engineering & Remote Sensing*. 45: 87-97.
- GOMEZ, M. M., AND F. P. DAY. 1982. Litter nutrient content and production in the Great Dismal Swamp. *Amer. J. Bot.* 69: 1314-1321.
- GRIER, C. C., AND R. S. LOGAN. 1977. Old growth *Pseudotsuga menziesii* communities of a western Oregon watershed: Biomass distribution and production budgets. *Ecol. Monogr.* 47: 373-400.
- HARMON, M. E., J. F. FRANKLIN, F. J. SWANSON [AND OTHERS]. 1986. Ecology of coarse woody debris in temperate ecosystems. *Advances Ecol. Res.* 15: 133-302.
- HARRIS, W. F., R. S. KINERSON, JR., AND N. T. EDWARDS. 1977. Comparison of belowground biomass of natural deciduous forests and loblolly pine plantations. *Pedobiologia* 17: 369-381.
- , D. SANTANTONIO, AND D. MCGINTY. 1979. The dynamic belowground ecosystem. In R. H. Waring [ed.], *Forests: fresh perspectives from ecosystem analysis*, 119-129. Oregon State University Press, Corvallis.
- KUENZLER, E. J., P. J. MULHOLLAND, L. A. YARBRO, AND L. A. SMOCK. 1980. Distributions and budgets of C, P, Fe, and Mn in a floodplain swamp ecosystem (UNCWRRI-80-157). Water Resources Research Institute, University of North Carolina, Chapel Hill.
- LEVY, G. F., AND S. W. WALKER. 1979. Forest dynamics in the Dismal Swamp of Virginia, 101-126. In P. W. Kirk [ed.], *The Dismal Swamp*. University Press of Virginia, Charlottesville, VA.
- LICHTLER, W. F., AND P. N. WALKER. 1979. Hydrology of the Great Dismal Swamp, Virginia-North Carolina. In P. W. Kirk [ed.], *The Great Dismal Swamp*, 140-168. University Press of Virginia, Charlottesville.
- LUGO, A. E., J. K. NESSEL, AND T. M. HANLON. 1984. Root distribution in a north-central Florida cypress strand. In K. C. Ewel and H. T. Odum [eds.], *Cypress swamps*, 279-285. University Presses of Florida, Gainesville.
- MCCLAUGHERTY, C. A., J. D. ABER, AND J. M. MELILLO. 1984. Decomposition dynamics of fine roots in forested ecosystems. *Oikos* 42: 378-386.
- MEGONIGAL, J. P. 1986. Organic matter budgets and models for four plant communities in the Great Dismal Swamp. M.S. thesis, Old Dominion University, Norfolk, VA.
- MITSCH, W. J., C. L. DORGE, AND J. R. WIEMHOFF. 1979. Ecosystem dynamics and a phosphorus budget of an alluvial cypress swamp in southern Illinois. *Ecology* 60: 1116-1124.
- , AND K. C. EWEL. 1979. Comparative biomass and growth of cypress in Florida wetlands. *Amer. Midl. Naturalist* 101: 417-426.
- MONTAGUE, K. A., AND F. P. DAY. 1980. Belowground biomass of four plant communities of the Great Dismal Swamp, Virginia. *Amer. Midl. Naturalist* 103: 83-87.
- NESSEL, J. K., AND S. E. BAYLEY. 1984. Distribution and dynamics of organic matter and phosphorus in a sewage enriched cypress swamp. In K. C. Ewel and H. T. Odum [eds.], *Cypress swamps*, 262-278. University Presses of Florida, Gainesville.
- READER, R. J., AND J. M. STEWART. 1972. The relationship between net primary production and accumulation for a peatland in southeastern Manitoba. *Ecology* 53: 1024-1037.
- REINERS, W. A. 1972. Structure and energetics of three Minnesota forests. *Ecol. Monogr.* 42: 71-94.
- , AND N. M. REINERS. 1970. Energy and nutrient dynamics of forest floors in three Minnesota forests. *J. Ecol.* 58: 497-519.
- RYKIEL, E. J., JR. 1984. Okefenokee Swamp watershed: water balance and nutrient budgets. In K. C. Ewel and H. T. Odum [eds.], *Cypress swamps*, 374-385. University Presses of Florida, Gainesville.
- SCHIMEL, D. S., D. C. COLEMAN, AND K. A. HORTON. 1985. Soil organic matter dynamics in paired rangeland and cropland toposequences in North Dakota. *Geoderma* 36: 210-214.
- SCHLESINGER, W. H. 1978. Community structure, dynamics and nutrient cycling in the Okefenokee cypress swamp-forest. *Ecol. Monogr.* 48: 43-65.
- . 1977. Carbon balance in terrestrial ecosystems. In R. F. Johnson [ed.], *Annual Rev. Ecol. Syst.* 8: 51-81.
- SYMBULA, M., AND F. P. DAY. In press. Evaluation of two methods for estimating belowground production in a freshwater swamp forest. *Amer. Midl. Naturalist*.
- TRAIN, E., AND F. P. DAY. 1982. Population age structure of tree species in four plant communities in the Great Dismal Swamp, Virginia. *Castanea* 47: 1-16.
- VOGT, K. A., C. C. GRIER, AND D. J. VOGT. 1986. Production, turnover, and nutrient dynamics of above- and belowground detritus of world forests. *Advances Ecol. Res.* 15: 303-377.
- WARING, R. H., AND W. H. SCHLESINGER. 1985. *Forest ecosystems*. Academic Press, New York.
- WIEGERT, R. G., AND F. C. EVANS. 1964. Primary production and the disappearance of dead vegetation on an old field in southeastern Michigan. *Ecology* 45: 49-62.

APPENDIX 1. *The data used to construct organic matter budgets broken down by species group and size class. These data and those in the methods section provide all the information necessary to reconstruct the budgets. Standing crops and rates are g m⁻² and g m⁻² yr⁻¹; decay rates are yr⁻¹*

Parameter	Species	Cedar	Cypress	Maple-gum	Mixed hardwood
Leaf biomass	Dominant	725	112	269	287
	Maple	131	164	192	53
	Others	227	323	120	183
Bole biomass	Dominant	8,363	16,749	7,331	9,283
	Maple	3,420	5,072	5,120	1,488
	Others	5,724	8,817	3,130	5,026
Branch biomass	Dominant	1,229	449	1,545	1,696
	Maple	749	960	1,101	308
	Others	1,289	1,857	698	1,034
Root biomass	<3 mm diam.	402	297	250	670
	>3 mm diam.	689	595	486	1,344
Leaf litter 01	Dominant	165	206	247	303
	Maple	168	137	133	50
	Others	70	137	131	195
Leaf litter 02	Dominant	312	244	145	444
	Maple	137	42	115	92
	Others	154	126	59	248
Bole litter	Dominant	2,370	2,392	1,198	434
	Maple	872	725	836	69
	Others	1,498	1,248	508	235
Branch litter	Dominant	137	24	62	58
	Maple	46	51	44	11
	Others	91	99	28	35
Root necromass	<3 mm diam.	198	147	123	330
	>3 mm diam.	309	267	219	604
Bole production	Dominant	168	226	192	101
	Maple	140	64	119	10
	Others	60	207	62	99
Branch production	Dominant	29	5	38	17
	Maple	30	12	25	2
	Others	14	43	14	20
Leaf litter 01 decay loss	Dominant	0.288	0.279	0.478	0.255
	Maple	0.332	0.418	0.374	0.425
	Others	0.294	0.444	0.399	0.289
Leaf litter 02 decay loss	Dominant	0.082	0.018	0.092	0.252
	Maple	0.075	0.077	0.090	0.057
	Others	0.138	0.068	0.071	0.204
Bole litter decay loss	Dominant	0.173	0.112	0.216	0.174
	Maple	0.184	0.138	0.216	0.174
	Others	0.184	0.138	0.216	0.174
Branch litter decay loss	Dominant	0.197	0.162	0.164	0.263
	Maple	0.210	0.200	0.164	0.263
	Others	0.210	0.200	0.164	0.263
Root necromass decay loss	All sizes	0.270	0.415	0.381	0.318