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The reflection of deciduous forest communities in leaf litter: implications for autochthonous litter assemblages from the fossil record

Robyn J. Burnham, Scott L. Wing, and Geoffrey G. Parker

Abstract.—To assess the degree to which forest litter reflects the source forest, three 1-ha plots of temperate deciduous forest were mapped and litter accumulating in these forests was sampled. Identity, position, and diameter of all stems 2 cm or larger diameter at breast height are known for each forest. Composition of the leaf litter is governed by two key factors: (1) abscised leaves are deposited primarily on the forest floor directly underneath the canopy that produced them, and (2) the leaf mass of a species is highly correlated with its stem cross-sectional area. These factors produce autochthonous litter samples that correspond closely in composition to the forest within a circle of canopy-height radius or less. Even relatively small litter samples (350 leaves) consistently contained all the common species in the local area. However, the rarer tree species were seldom recovered in the litter samples. Correlation coefficients for litter mass and basal area by species are typically over .80.

These observations have three important implications for interpreting autochthonous compression-fossil assemblages. First, approximate relative abundances of locally dominant and subdominant forest taxa can be obtained from relatively small samples of autochthonous compression-fossil assemblages. Second, representation of rare forest species, even in large fossil samples, will be fortuitous. For this reason, complete species lists and consistent estimates of richness cannot be derived directly from most existing samples of autochthonous compression-fossil assemblages. Third, the strong tendency for leaves to fall beneath the canopy of the tree that sheds them suggests that properly sampled autochthonous fossil leaf assemblages may yield information on crown size of individual trees and the spatial distribution of individuals and species, aspects of vegetational structure that have been thought accessible only in well-preserved “fossil forests” with standing trunks.

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Introduction

Three goals of plant paleoecology are to clarify the composition, species richness, and spatial structure of past vegetation. Reconstructions of forest vegetation generally have been attempted only for exceptionally well-preserved “fossil forests” consisting of in situ trunks or trunk casts (Gastaldo 1983, 1987; Wnuk and Pfefferkorn 1984; DiMichele and DeMaris 1987; DiMichele and Nelson 1989). More common are the well-preserved, autochthonous compression-fossil assemblages (Chaney 1938; Spicer and Hill 1979; DiMichele and Phillips 1985; Gastaldo 1986; Taggart 1988). These assemblages frequently have been studied from floristic or taxonomic

perspectives, but rarely are they used to infer the ecological roles of their component species, or to understand the spatial structure of the original vegetation (see Hickey 1980; Wing 1984).

The objective of the research reported here is to reveal the qualitative and quantitative relationships between forest litter and the forest from which it is derived. One aspect of this objective is simply to determine which attributes of the forest and of the litter to measure. Another is to reveal the size of the area that contributes litter to a particular collection site. Understanding these relationships is prerequisite to knowing which forest features can be inferred reliably from fossil

leaf floras. The fidelity with which temperate litter reflects its source forest indicates the confidence that can be placed in paleoecological reconstructions. Perfect reflection of a forest in its litter would yield accurate information on tree species richness, density of individuals, canopy height, relative importance of different species, diversity of life forms, and population distribution of taxa. We focused on modern temperate deciduous forests in which total woody-plant species richness is relatively low and in which litter fall is complete and synchronous. The research is distinct from previous plant taphonomic studies (Spicer 1981; Scheihing and Pfefferkorn 1984; Spicer and Wolfe 1987; Burnham 1989; Gastaldo 1989) in that detailed quantitative descriptions of the modern forests are used to interpret the patterns of autochthonous leaf-litter presence and abundance on the forest floor.

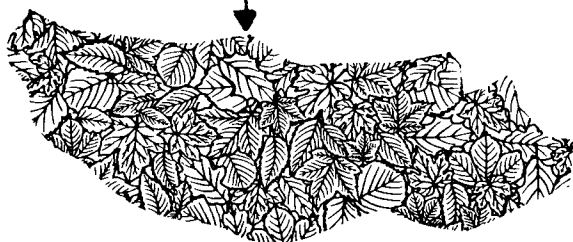
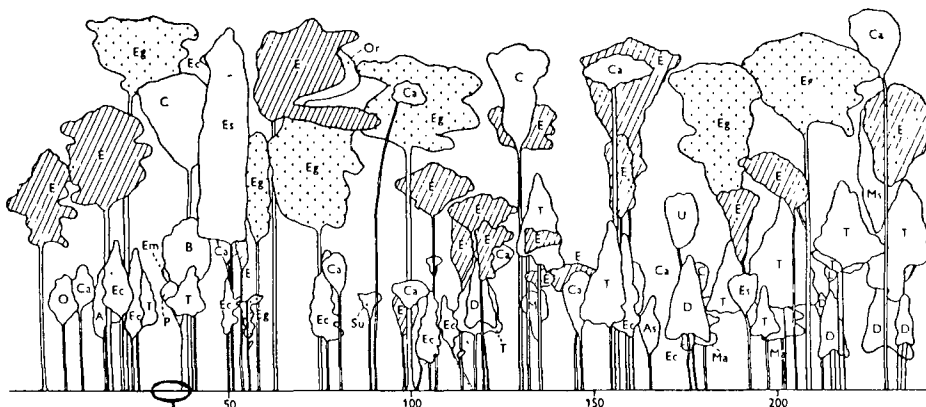
The roots of quantitative plant taphonomy (the study of the incorporation of plant parts into sediments) can be traced to the work of Chaney on the modern redwood forest of northern California and its relationship to the Tertiary Bridge Creek flora of central Oregon (Chaney 1924, 1925). Chaney used data from over 20,000 fossil specimens (largely vegetative) from the Bridge Creek flora to estimate the numbers of individual source-tree species for the fossil flora. The estimations were based on the relationship between *leaf number* and *stem number* in the modern redwood forests, which gave disappointingly low correlation coefficients, averaging .44 (Chaney 1924: p. 138). From these relations, Chaney inferred the number of individuals of the dominant taxa in the fossil flora in a relative sense. Many of the subsequent studies of plant taphonomy have focused on transport processes and the environment of deposition in which plant material is found (Spicer 1981, 1989; Scheihing and Pfefferkorn 1984; Ferguson 1985; Gastaldo 1986, 1989; Carpenter and Horowitz 1988). These studies have investigated the potential for preservation in temperate and tropical settings including lacustrine, fluvial, and estuarine environments. Recently, Spicer and Wolfe (1987) related modern transported plant remains to vegetation zones in a conifer-

dominated fluvial-lacustrine basin. Still, Chaney's original, implicit question of the relationship between the quantitative representation of litter in the fossil record and the forest from which it came was not addressed, despite an earlier emphasis on quantifying collections of fossil plants for inferring ecological relationships (Scott 1977; Spicer and Hill 1979; DiMichele and Phillips 1985).

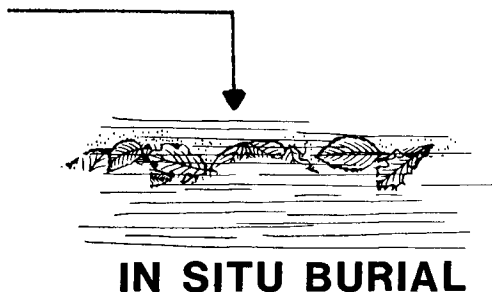
Clues to the representation of the forest in litter accumulations could come from data compiled on modern forest biomass and productivity (see, e.g., Klinge and Rodrigues 1968; Woods and Gallegos 1970; van Schaik and Mirmanto 1985; Rawat and Singh 1989). With few exceptions, however (Kunkel-Westphal and Kunkel 1979; Turnbull and Madden 1983; Carpenter and Horowitz 1988), these studies are concerned primarily with *total* litter mass and nutrient cycling and either they do not categorize foliage mass by species (Klinge and Rodrigues 1968; Bongers et al. 1988; Dantas and Phillipson 1989) or they do not provide detailed information on the position of trees in the source forest (Goulter and Allaway 1979; Kunkel-Westphal and Kunkel 1979; Mayack et al. 1989). A recent study by Parker et al. (1989) is one of the first to investigate litter-source forest relationships on a per-species basis, although the motivation was not for paleoecological analysis.

The processes of plant fossilization can be viewed as involving three steps: (1) abscission/accumulation; (2) transport/mixing; and (3) burial (fig. 1). The research reported here concerns only the pattern of plant-part distribution and abundance following the first step: abscission/accumulation. Obviously, many plant-fossil assemblages have been transported and cannot be interpreted solely in light of the biases introduced at step one. We have focused on the initial step in fossilization, nevertheless, for two reasons. First, there *do* exist plant-fossil deposits in which plants are preserved in their initial spatial pattern following abscission and accumulation (e.g., some volcanic deposits [Burnham and Spicer 1986], and some swamp deposits [Wing 1984; Wnuk and Pfefferkorn 1984, 1987; DiMichele and DeMaris 1987; Gastaldo 1987;

SOURCE FOREST

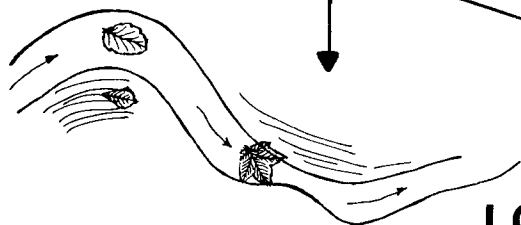


LITTER ACCUMULATION



IN SITU BURIAL

TRANSPORT AND MIXING



LONG AND

SHORT DISTANCE

FIGURE 1. Three steps in the process of plant taphonomy. Litter accumulation in situ produces autochthonous assemblages. The amount of subsequent transport controls whether the deposits have greatest similarity to local or to regional source floras. Burial of the assemblage before degradation produces a high-quality fossil flora.

TABLE 1. Western Triangle one-hectare stand summary.

Species	No. stems	Relative stem no.	Basal area (m ²)	Relative basal area	No. stems > 10 cm
<i>Liriodendron tulipifera</i>	90	7.43	9.594	27.53	88
<i>Quercus falcata</i>	29	2.39	7.125	20.45	29
<i>Fagus grandifolia</i>	509	42.03	6.887	19.76	115
<i>Quercus rubra</i>	40	3.3	4.119	11.82	39
<i>Q. alba</i>	16	1.32	2.748	7.89	16
<i>Carya</i> (2 species)	42	3.47	1.783	5.12	32
<i>Liquidambar styraciflua</i>	22	1.82	1.076	3.09	8
<i>Acer rubrum</i>	56	4.62	0.491	1.41	16
<i>Nyssa sylvatica</i>	62	5.12	0.234	0.67	5
<i>Pinus virginiana</i>	2	0.17	0.184	0.53	2
<i>Ilex opaca</i>	141	11.64	0.172	0.49	1
<i>Cornus florida</i>	96	7.93	0.167	0.48	2
<i>Carpinus caroliniana</i>	91	7.51	0.151	0.43	3
<i>Quercus michauxii</i>	1	0.08	0.083	0.24	1
<i>Amelanchier arborea</i>	3	0.25	0.018	0.05	1
<i>Ulmus americana</i>	1	0.08	0.007	0.02	0
<i>Fraxinus</i> sp.	2	0.17	0.007	0.02	0
<i>Prunus serotina</i>	2	0.17	0.002	0.01	0
<i>Vaccinium corymbosum</i>	3	0.25	0.001	<0.01	0
<i>Vitis</i> sp.	1	0.08	<0.001	<0.01	0
<i>Celtis</i> sp.	1	0.08	<0.001	<0.01	0
<i>Juniperus virginiana</i>	1	0.08	<0.001	<0.01	0
Totals	1211	99.99	34.849	100.01	358

DiMichele and Nelson 1989]). In addition, once the abscission/accumulation step is clarified for many forest types, the wealth of data accumulating on steps 2 and 3 (Scheihing and Pfefferkorn 1984; Spicer and Greer 1986; Gastaldo et al. 1989; Spicer 1989) can be integrated to give a much broader framework within which to evaluate plant-fossil deposits, both taxonomically and paleoecologically.

Location and Description of Research Plots

Three forest communities were described and quantitatively compared to the accumulated leaf litter on the forest floor. The sites were chosen to represent plant heterogeneity typical of eastern temperate forests. The sites were nearly flat. The stem-map data for all plots are archived at the Smithsonian Environmental Research Center at Edgewater, Maryland. The following forest terms are used.

Diameter at breast height (dbh): diameter of tree stem as measured at 1.4 m above the ground
Basal area: total stem cross-sectional area, measured at breast height (1.4 m above ground level), units are m² ha⁻¹;

Source forest: standing forest of living trees ≥ 2 cm dbh in the mapped plot

Species importance value: percentage of stems + percentage of total forest basal area (by species): sums to 200

Leaf-deposition area: area over which leaves are deposited, both beneath and beyond the source tree

Litter-reflection radius: the radius of the forest circle with the greatest similarity to a collection of leaves from a single site at the center of that circle

Western Triangle, Maryland.—The Western Triangle (WT) hectare plot is located at 5–10 m above sea level on the grounds of the Smithsonian Environmental Research Center at Edgewater, Maryland. The forest is a *Quercus* spp.–*Fagus grandifolia*–*Liriodendron tulipifera* assemblage with a maximum canopy height of 37 m and has been undisturbed for about 120 yr. All the tree species in the hectare are deciduous angiosperms except *Ilex opaca*, *Pinus virginiana*, and *Juniperus virginiana*. The predominant understory tree species are *I. opaca*, *Cornus florida*, and saplings of *F. grandifolia*. There are relatively few forest-floor perennials, although *Viburnum dentatum*, *Vac-*

TABLE 2. Battle Creek one-hectare stand summary.

Species	No. stems	Relative stem no.	Basal area (m ²)	Relative basal area	No. stems >10 cm dbh
<i>Taxodium distichum</i>	146	19.97	42.25	75.08	151
<i>Acer rubrum</i>	319	43.64	11.66	20.72	212
<i>Ulmus americana</i>	36	4.92	1.38	2.46	22
<i>Platanus occidentalis</i>	3	0.41	0.30	0.53	3
<i>Fraxinus</i> sp.	5	0.68	0.28	0.5	5
<i>Liriodendron tulipifera</i>	10	1.37	0.12	0.21	5
<i>Carpinus caroliniana</i>	27	3.69	0.08	0.15	3
<i>Rhus radicans</i>	14	1.92	0.05	0.09	2
<i>Asimina triloba</i>	70	9.58	0.04	0.08	0
<i>Ilex opaca</i>	19	2.6	0.03	0.06	0
<i>Vitis</i> sp.	9	1.23	0.02	0.03	0
<i>Viburnum dentatum</i>	31	4.24	0.01	0.02	0
<i>Nyssa sylvatica</i>	2	0.27	0.01	0.02	1
<i>Cornus florida</i>	6	0.82	0.01	0.02	0
<i>Ilex verticillata</i>	12	1.64	0.01	0.01	0
<i>Parthenocissus quinquefolium</i>	2	0.27	0.01	0.01	0
<i>Cornus stricta</i>	9	1.23	0.01	0.01	0
<i>Viburnum prunifolium</i>	5	0.68	<0.01	<0.01	0
<i>Alnus serrulata</i>	1	0.14	<0.01	<0.01	0
<i>Quercus rubra</i>	1	0.14	<0.01	<0.01	0
<i>Prunus serotina</i>	3	0.41	<0.01	<0.01	0
<i>Lindera benzoin</i>	1	0.14	<0.01	<0.01	0
Totals	731	99.99	56.27	100	404

cinium corymbosum, and various ferns are locally abundant. Summary statistics of this 1-ha forest plot are recorded in table 1.

Battle Creek, Maryland.—The Battle Creek (BC) hectare plot is located at sea level on the grounds of the Battle Creek Cypress Sanctuary south of Prince Frederick, Maryland. The forest is a *Taxodium distichum*–*Acer rubrum* swamp with a canopy height of about 35 m. *Ilex opaca* is the only woody evergreen within the mapped hectare, although conifers are present elsewhere within the sanctuary boundaries. Common understory trees are *Asimina triloba* and *Cornus stricta*. The most common shrub is *Viburnum dentatum*. The forest floor has extensive patches of *Saururus cernuus* and *Impatiens capensis*. The stand characteristics for the 1-ha forest plot are summarized in table 2.

Mountain Lake, Virginia.—The plot at Mountain Lake (ML) is located at about 1100 m elevation near the Mountain Lake Biological Station in southwestern Virginia. Three hectares of forest were mapped in 1982 and 1983 (Bonan 1984) and were recensused in 1988. The stand characteristics for a circular study area of about 1 ha (area = 11,310 square m; radius of circle, 60 m) are summarized in table

3. A *Quercus* spp.–*Acer rubrum* forest occupies the site with a maximum canopy height of about 19 m. All tree species are deciduous, except *Tsuga canadensis* and *Kalmia latifolia*. The predominant understory species are *Castanea dentata*, *Acer pensylvanicum* and *Amelanchier arborea*. Few perennial forest-floor plants are present; however, there are dense patches of ferns and *Vaccinium corymbosum* on the plot.

Forest Mapping and Litter Collection

At WT and BC, trees were located on a coordinate grid to within at least 0.5 m accuracy using a triangulation mapping system and coordinate-determining program designed by M. Kabel (National Museum of Natural History, Smithsonian Institution). Each hectare plot was divided into 25 20 × 20 m cells. All trees were identified and assigned a unique identifying number. Their dbh and the distance to the two closest corner points of their cell were measured. The map position of each tree was obtained using triangulation with the two corner points. At ML, a grid of tapes was laid out in a 10 × 10 m network, and tree coordinates were read directly off the tapes. Numbering of trees and dbh recording followed the same methods as at WT and BC.

TABLE 3. Mountain Lake 1.13-hectare stand summary.

Species	No. stems	Relative stem no.	Basal area (m ²)	Relative basal area	No. stems >10 cm dbh
<i>Quercus rubra</i> + <i>velutina</i>	162	8.69	10.50	30.15	148
<i>Q. alba</i>	125	6.71	7.88	22.62	117
<i>Q. prinus</i>	87	4.67	6.23	17.89	87
<i>Acer rubrum</i>	385	20.65	5.50	15.80	217
<i>Amelanchier arborea</i>	241	12.93	1.78	5.10	67
<i>Carya</i> sp.	47	2.52	0.54	1.54	18
<i>Castanea dentata</i>	439	23.55	0.52	1.50	2
<i>Robinia pseudo-acacia</i>	12	0.64	0.51	1.47	11
<i>Quercus coccinea</i>	5	0.27	0.50	1.45	5
<i>Magnolia acuminata</i>	16	0.86	0.34	0.97	8
<i>Acer pensylvanicum</i>	269	14.43	0.29	0.82	6
<i>Tsuga canadensis</i>	11	0.59	0.15	0.43	5
<i>Ilex montana</i> v. <i>ambigua</i>	15	0.80	0.03	0.08	0
<i>Prunus serotina</i>	5	0.27	0.02	0.07	0
<i>Rhododendron calendulaceum</i>	32	1.72	0.02	0.07	0
<i>Hamamelis virginiana</i>	6	0.32	0.01	0.02	0
<i>Betula lenta</i>	1	0.05	0.01	0.01	0
<i>Kalmia latifolia</i>	4	0.21	0.01	0.01	0
<i>Nyssa sylvatica</i>	2	0.11	<0.01	0.01	0
Totals	1864	100	34.85	100	691

Litter was collected in 21 wooden bushel baskets (average aperture, 1450 cm²) at the WT and BC plots. Hectare plots were subdivided into 25 20 × 20 m subplots. Nine baskets were placed in the center 20 × 20 m subplot, with interbasket distances of 5 m minimum. The additional 12 baskets were placed in the central 40 × 40 m of the hectare, with minimum interbasket distances of 5 m. At ML, 18 such baskets were placed in a stratified random design within a 60 × 110 m area in the center of the mapped plot. The data

from one basket at Mountain Lake were deleted from the data set because the basket overturned during the collecting season. At Mountain Lake, some tree species were not clearly distinguishable by their leaves in the litter; therefore, the two species of *Carya* (*C. glabra* and *C. tomentosa*) were lumped, and two of the five species of *Quercus* (*Q. rubra* and *Q. velutina*) were lumped. Litter was collected from all baskets biweekly, sorted, counted, and weighed by species and organ (leaf, fruits and seeds, flowers). Here the focus is on only

TABLE 4. Litter summary: Western Triangle. Values are annual per-basket averages; weights are grams dry weight; frequency represents proportion of all baskets in which species is found as litter.

Species	Frequency	Mean leaf no.	% Leaf no.	Mean leaf weight	% Leaf weight
<i>Quercus falcata</i>	100.0	65.43	17.92	17.61	27.44
<i>Liriodendron tulipifera</i>	100.0	61.48	16.84	16.56	25.80
<i>Fagus grandifolia</i>	100.0	131.04	35.88	11.62	18.11
<i>Quercus rubra</i>	100.0	11.38	3.12	5.81	9.05
<i>Q. alba</i>	100.0	23.57	6.45	5.35	8.34
<i>Carya</i> spp.	100.0	20.00	5.48	3.27	5.10
<i>Liquidambar styraciflua</i>	85.7	6.29	1.72	1.89	2.94
<i>Acer rubrum</i>	81.0	4.48	1.23	0.65	1.01
<i>Carpinus caroliniana</i>	71.4	28.38	7.77	0.61	0.95
<i>Cornus florida</i>	85.7	4.19	1.15	0.41	0.64
<i>Nyssa sylvatica</i>	33.3	1.71	0.47	0.23	0.36
<i>Pinus virginiana</i>	85.7	4.95	1.36	0.07	0.11
<i>Quercus michauxii</i>	9.5	0.10	0.03	0.05	0.08
<i>Ilex opaca</i>	9.5	0.19	0.05	0.03	0.05
<i>Vaccinium corymbosum</i>	38.1	1.95	0.53	0.02	0.03
<i>Amelanchier arborea</i>	4.8	0.05	0.01	0.00	0.00
Totals		365.19	100.00	64.18	100.00

TABLE 5. Battle Creek litter summary. Values are annual per-basket averages; weights are grams dry weight; frequency represents proportion of baskets in which species is found as litter.

Species	Frequency	Mean leaf no.	% Leaf no.	Mean leaf weight	% Leaf weight
<i>Taxodium distichum</i>	100.0	1782.00	88.63	46.23	64.54
<i>Acer rubrum</i>	100.0	133.10	6.62	16.93	23.64
<i>Rhus radicans</i>	100.0	41.00	2.04	4.39	6.13
<i>Ulmus americana</i>	90.5	7.90	0.39	1.16	1.62
<i>Parthenocissus quinquefolium</i>	95.2	22.00	1.09	0.86	1.20
<i>Viburnum dentatum</i>	66.7	13.20	0.66	0.48	0.67
<i>Liriodendron tulipifera</i>	57.1	1.86	0.09	0.35	0.48
<i>Fraxinus</i> sp.	14.3	2.57	0.13	0.33	0.46
<i>Asimina triloba</i>	33.3	1.38	0.07	0.28	0.39
<i>Quercus rubra</i> *	23.8	0.52	0.03	0.26	0.36
<i>Platanus occidentalis</i>	9.5	0.24	0.01	0.15	0.21
<i>Cornus stricta</i>	23.8	3.10	0.15	0.07	0.10
Unidentified monocot†	14.3	0.66	0.03	0.05	0.07
<i>Quercus falcata</i> *	14.3	0.14	0.01	0.03	0.04
<i>Liquidambar styraciflua</i> *	14.3	0.19	0.01	0.02	0.03
<i>Saururus cernuus</i> †	9.5	0.14	0.01	0.01	0.02
<i>Quercus alba</i> *	4.8	0.05	<0.01	0.01	0.01
<i>Pinus virginiana</i> *	4.8	0.05	<0.01	<0.01	0.01
<i>Nyssa sylvatica</i>	4.8	0.05	<0.01	<0.01	0.01
<i>Itea virginica</i> †	4.8	0.29	0.01	<0.01	<0.01
<i>Viburnum prunifolium</i>	4.8	0.10	0.01	<0.01	<0.01
<i>Ilex verticillata</i>	4.8	0.05	<0.01	<0.01	<0.01
<i>Fagus grandifolia</i> *	4.8	0.05	<0.01	<0.01	<0.01
<i>Prunus serotina</i>	4.8	0.05	<0.01	<0.01	<0.01
Totals		2010.69	100	71.63	100

* Woody plant not present on plot.

† Woody plant present on plot but too small for census.

the leaf component of the litter because the reproductive parts were relatively few in number and temporally very variable, creating a very unreliable reflection of the forest stem community. Raw data on reproductive-organ abundance and distribution in the litter is available from the first author on request. At Battle Creek, *Taxodium distichum* shoots were counted as individual leaf equivalents. Because the counts of *T. distichum* were so high (e.g., 1750 per basket), all the shoots in one basket were counted, weighed, and the mean shoot mass used to derive leaf number for all the other baskets. The average litter abundance and mass data per basket per species are presented in tables 4, 5, and 6 for each forest hectare.

Results

Qualitative Comparisons of Litter and Source Forest

Western Triangle.—Of the 22 species represented at WT, 16 (73%) were represented in the 21 litter samples. The 16 species present in the litter accounted for 99.97% of the basal

area of the source forest (fig. 2). Furthermore, all species found as litter were present in the tree census of the forest. Total yearly leaf-litter mass was 44,303 g/ha.

Individual baskets contained 9–13 species (41%–59% of the species list for the source forest), consistently representing over 90% of the forest basal area (fig. 3). A bootstrap analysis of the basket-collection data produces a curve (fig. 4) indicating that eight baskets (roughly 2900 leaves) are required to obtain 94% of all species found as leaves in the litter (99.9% of the basal area of the source forest).

Battle Creek.—Of the 22 species on the BC plot, 68% were present in the 21 litter collections. Like the samples from WT, these 15 species accounted for 99.8% of the basal area of the source forest (fig. 2). Six species found in the litter were not present in the hectare, and three other species found in the litter were present on the plot but under the 2-cm diameter limit of the tree census. Total yearly leaf-litter mass was 49,414 g/ha.

Individual baskets contained 5–11 species (23%–46% of the species list of the source for-

TABLE 6. Litter summary: Mountain Lake. Values are annual basket averages; weights are grams dry weight; frequency represents proportion of baskets in which species is found as litter.

Species	Frequency	Mean leaf no.	% Leaf no.	Mean leaf weight	% Leaf weight
<i>Quercus rubra</i> / <i>velutina</i>	100.0	37.12	16.41	13.97	27.96
<i>Q. alba</i>	100.0	51.18	22.63	12.79	25.59
<i>Acer rubrum</i>	100.0	74.12	32.77	10.15	20.31
<i>Quercus prinus</i>	94.1	19.76	8.74	6.26	12.53
<i>Q. coccinea</i>	87.5	8.71	3.85	3.53	7.06
<i>Amelanchier arborea</i>	94.1	20.65	9.13	1.2	2.40
<i>Castanea dentata</i>	58.8	2.59	1.15	0.62	1.24
<i>Carya</i> spp.	70.6	4.82	2.13	0.59	1.18
<i>Acer pensylvanicum</i>	58.8	2.47	1.09	0.55	1.10
<i>Magnolia acuminata</i>	47.1	0.76	0.34	0.14	0.28
<i>Rhododendron calendulaceum</i>	5.9	0.29	0.13	0.06	0.12
<i>Robinia pseudo-acacia</i>	23.5	2.94	1.30	0.06	0.12
<i>Prunus serotina</i>	29.4	0.71	0.31	0.05	0.10
<i>Vaccinium corymbosum</i> *	5.9	0.06	0.03	<0.01	<0.01
Totals		226.18	100	49.97	100

* Woody plant on plot but too small for 2-cm dbh census.

est), representing over 95% of the forest basal area (fig. 5). A bootstrap analysis of the basket-collection data produces a curve (fig. 4) showing that eight baskets most commonly represent 71% of the litter species list, which collectively represent 95% of the basal area.

Mountain Lake.—Of the 19 tree species that can be identified unequivocally by their dispersed leaves, 13 are present in the 17 litter collections (68% of the species list of the source forest), representing stems that include 99.3% of the forest basal area (fig. 2). All species found in the litter collectors, with the exception of *Vaccinium corymbosum*, were present in the tree census of the central 11,310 square m. *Vaccinium corymbosum* stems fell below the 2-cm diameter size limit. Total yearly leaf-litter mass was 33,516 g/ha.

Individual baskets contain 7–11 species (37%–58% of the species list for the source forest), representing over 93% of the basal area in almost all cases (fig. 6). A bootstrap analysis of the basket collections produces a curve (fig. 4) showing that eight baskets represent 93% of the forest species found in the litter samples. These species make up 99.2% of the basal area of the forest.

Quantitative Relationships

Determination of Best Attributes for Forest Reflection.—One objective of the research was to determine which quantitative attributes of forest and litter are most highly correlated with one another. In this section the descrip-

tive attributes of forest and leaf litter are analyzed to determine the attributes that are most closely correlated. The source-forest attributes employed for quantitative comparisons are: stem basal area, stem density, and stem importance value. All possible pairwise comparisons of the forest and litter attributes were investigated with linear regression to determine which provided the overall closest fit between forest community and leaf community (table 7). For these comparisons, all tree species in a circle of radius 30 m around the baskets were used, rather than only those species actually landing in one or more of the baskets. Regressions were not forced through the origin; thus, a perfect correspondence between litter and forest would generate a plot of taxa with slope of 1.0, intercept of 0, and a correlation coefficient of 1.0. The results presented in table 7 show the maximum fit between litter communities and the source-forest communities. The best-fit solutions for individual species are generally congruent with these results.

The comparisons between stem basal area and leaf mass come close to a 1:1 correspondence (slope of 1) and have a consistently high r^2 value (table 7). Results using stem-importance values are often very similar to those using basal area. However, because the importance value is a combination variable (which can be constituted in many ways), the simpler basal-area value was chosen for use in all subsequent analyses as a summary of

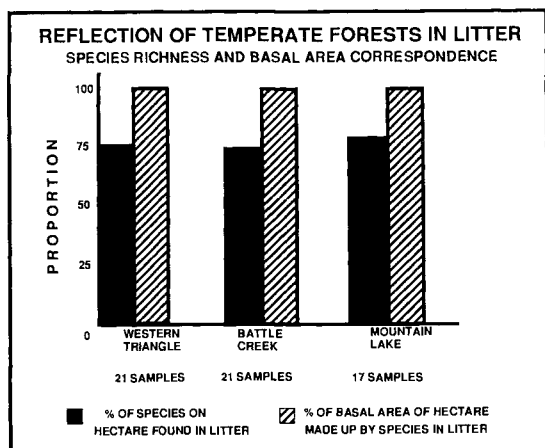


FIGURE 2. Representation of 1-ha forest plots by litter samples. *Black bars*, The proportion of species on the hectare that were in the litter samples. *Lined bars*, The proportion of the total basal area of the hectare accounted for by those species found in the samples.

the forest. Thus, all subsequent quantitative analyses reported here are based on comparisons between litter-leaf mass and source-forest basal area.

Quantitative Reflection of Forest in the Litter.—Two means of comparison of the quantitative data were employed: linear regression and dominance-diversity profiles.

Simpler Linear Regression. First, basket averages were regressed on total source forest. It

is assumed that a high correspondence of basal area and litter ($r \approx 1.0$, slope ≈ 1.0 , intercept ≈ 0), indicates that the litter reflects the forest with greater fidelity.

In addition to assessing similarities of average basket samples to the entire hectare, we analyzed *single-basket* reflection of the source forest using simple linear regression. For these analyses, the litter from individual baskets was compared to several forest "circles" centered on the basket, increasing in 5-m radial increments starting at 5 m. For each radius, a new value was calculated for the proportion of the total basal area taken up by each species.

Dominance Order. The similarity of the species rank order of abundances between the leaf-litter and the source-forest stems is presented in figures 9, 11, and 13. The closer the order of abundance, the closer the correspondence between the litter and the source forest.

Western Triangle.—At WT, regression of the litter-basket mass average on the source-forest stem-basal area yields a high correlation ($r^2 = .98$, $p \ll .01$; fig. 7). Although this value gives a good impression of the correspondence between the source forest and the *average* basket taken from the central area, a single basket can deviate significantly from

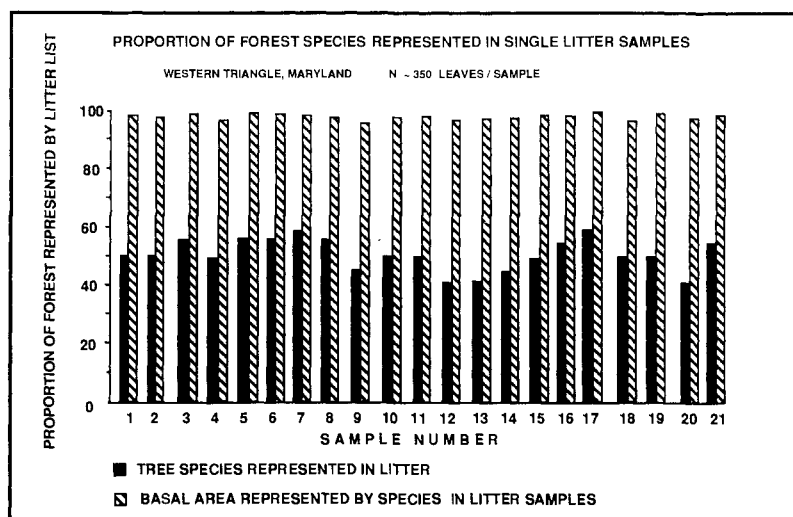


FIGURE 3. Comparisons of individual litter samples with stand characteristics at Western Triangle, Maryland. *Black bars*, The proportion of species on the hectare that were found in particular baskets. *Lined bars*, The proportion of the total basal area of the hectare accounted for by those species found in the samples.

the average values and probably reflects an area much smaller than the entire surrounding hectare. However, the correlation coefficient between single baskets and the entire source hectare is high, ranging from .59 to .94. To determine the area from which a single basket collected leaves from the forest, basket accumulations were individually compared to forest areas circumscribed by circles of increasing radii. The r^2 values rise with increasing area and then level off at a radius of 20–25 m (1257–1963 square m) at values of .81–.96 (fig. 8).

The dominance-diversity profiles of species in litter and forest communities are shown in figure 9. Litter rank order has been rearranged where necessary to allow single species comparisons. Dominance-diversity curves for litter and for stems are quite similar. The source-forest curve shows a slightly more concave profile, reflecting the lesser importance of "intermediate" species (neither abundant nor rare) in the forest relative to the litter. Among the eight most important taxa, the order of two species was transposed (*Liriodendron/Q. falcata*), representing a reflection "error" of 2% and 7%, respectively.

Battle Creek.—The litter average of 21 baskets is highly correlated with basal-area values from the source forest ($r^2 = .94$; $p < .01$). Single baskets deviated somewhat from the r^2 value for the mean (.79–.94). The similarity between single litter collections and forest (fig. 10) was often high at a radius of only 10 m surrounding the basket. A few baskets showed an r^2 value pattern similar to that at Western Triangle, rising up to about 15–20 m from the basket, then stabilizing at $r^2 = .90$ –.94.

The dominance-diversity profiles of litter and tree species of the source forest are shown in figure 11. The dominance-diversity patterns for litter and stems are very similar. The litter and source forest are dominated by *T. distichum* and *A. rubrum*. Species less important than these dominants are not similarly ranked between the two communities. However, differences in dominance-diversity profiles occur because of species that together account for only 2.6% of the basal area and 11.9% of the litter mass. Thus, differences be-

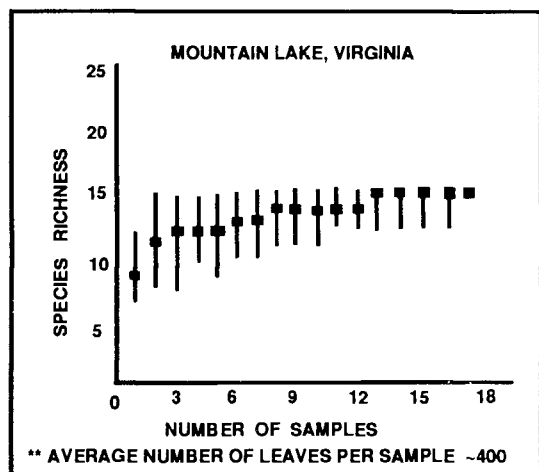
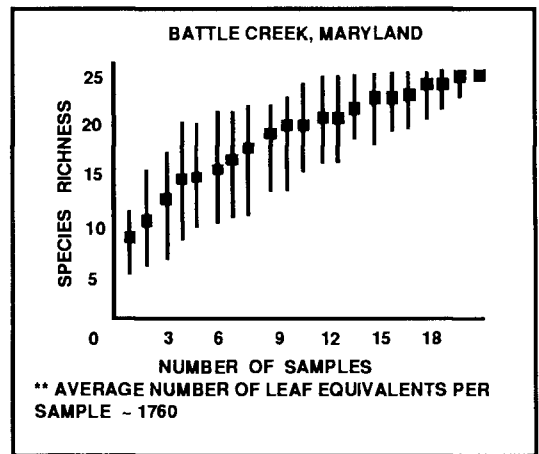
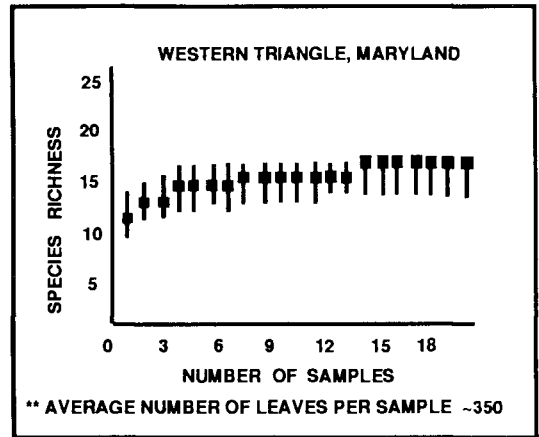


FIGURE 4. Bootstrap analysis (with species replacement) of species richness with increasing number of litter samples from three temperate-forest hectares. Vertical lines, Range of species richness recovered with 200 iterations. Forest richness values: WT, 22; BC, 22; ML, 19. Litter richness values: WT, 16; BC, 24; ML, 13.

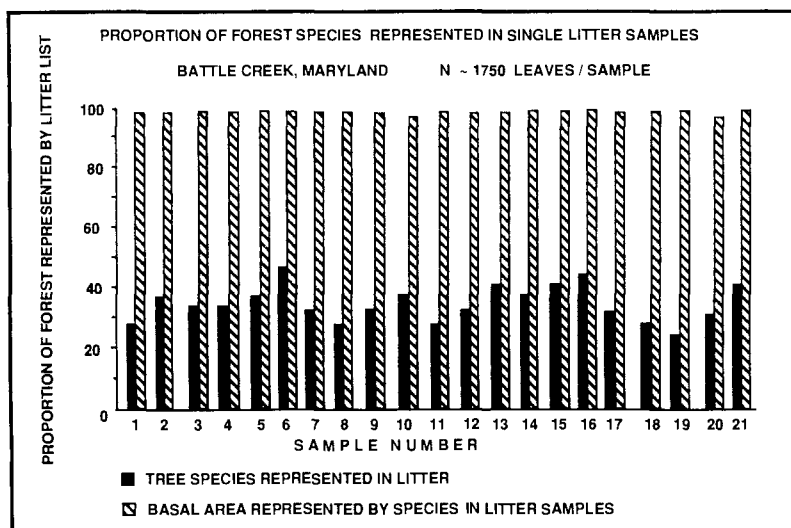


FIGURE 5. Single-basket comparisons of individual litter samples with stand characteristics at Battle Creek, Maryland. *Black bars*, The proportion of species on the hectare that were found in particular baskets. *Lined bars*, The proportion of the total basal area of the hectare accounted for by those species found in the samples.

tween litter and basal-area ranking are due to rare species in the source forest. The most notable reflection errors are the two vines, *Parthenocissus* and *Rhus* which make up 6.1% and 1.2%, respectively, of the litter mass but only .09% and .01% of the source-forest basal area.

Mountain Lake.—The average litter mass of the 17 baskets is highly correlated ($r^2 = .94$) with basal area of the full forest area (radius = 70 m). Single-basket correlation with a forest area of about 1 ha is generally less than the pooled average ($r^2 = .64-.94$).

We used forest areas with radii up to 50 m to compare the mapped forest at ML to the litter. The r^2 value increases from 5 m and generally stabilizes between 10 and 20 m (fig. 12). The peak r^2 value is quite variable ($r = .69-.96$).

The dominance-diversity profiles of the litter average and basal area of species in the source forest are shown in figure 13. The sequence of the first seven taxa is similar; these taxa make up the top 95% of the basal area and leaf mass. The rarer taxa are considerably scrambled in order and, indeed, rank order

TABLE 7. Regression coefficients for comparisons of litter and forest attributes.

	Litter attributes								
	Leaf number			Leaf weight			Leaf area		
	r^2	Slope	Intercept	r^2	Slope	Intercept	r^2	Slope	Intercept
Western Triangle									
Stem number	.55	.74	.04	.26	.53	.07	.28	.61	.05
Stem importance value	.79	.96	-.00	.74	.96	-.01	.72	1.05	-.04
Stem basal area	.67	.76	.05	.94	.94	.01	.90	1.01	-.01
Battle Creek									
Stem number	.14	.83	-.01	.37	.87	.00		not calculated	
Stem importance value	.55	1.08	-.03	.76	.98	.00		not calculated	
Stem basal area	.88	1.03	.01	.88	.86	.03		not calculated	
Mountain Lake									
Stem number	.23	.77	.03	.10	.65	.04	.12	.65	.04
Stem importance value	.62	.99	-.01	.53	.99	-.02	.50	.93	-.01
Stem basal area	.72	.88	.03	.85	.96	.00	.72	.88	.02

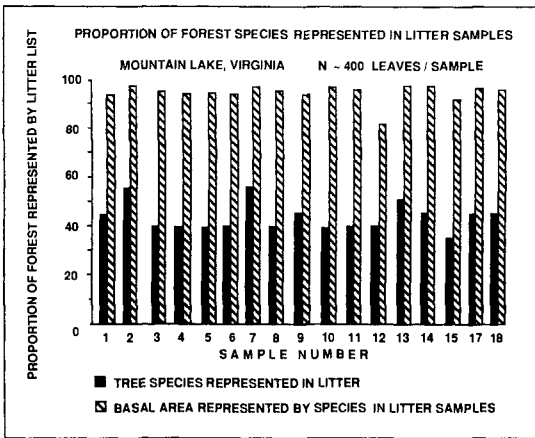


FIGURE 6. Single-basket comparisons of individual litter samples with stand characteristics at Mountain Lake, Virginia. *Black bars*, The proportion of species on the hectare that were found in individual baskets. *Lined bars*, The proportion of the total basal area of the hectare accounted for by those species found in the samples.

is quite variable from basket to basket. Dominance-diversity curves have similar patterns, showing that the dominance pattern is faithfully represented in the leaf litter. Although the dominance-diversity plot indicates that the *exact* relative percentage importance of the rare species cannot be read from the litter, the taxa that are source-forest dominants are clear litter dominants (*Quercus rubra/velutina*, *Q. alba*, *Q. prinus*, *Acer rubrum*), and species that are subdominants (*Amelanchier arborea*, *Castanea dentata*, and *Q. coccinea*) are clear subdominants in the dominance-diversity profiles.

Discussion

The results presented above show that untransported, undecayed forest leaf litter faithfully reflects the location and relative abun-

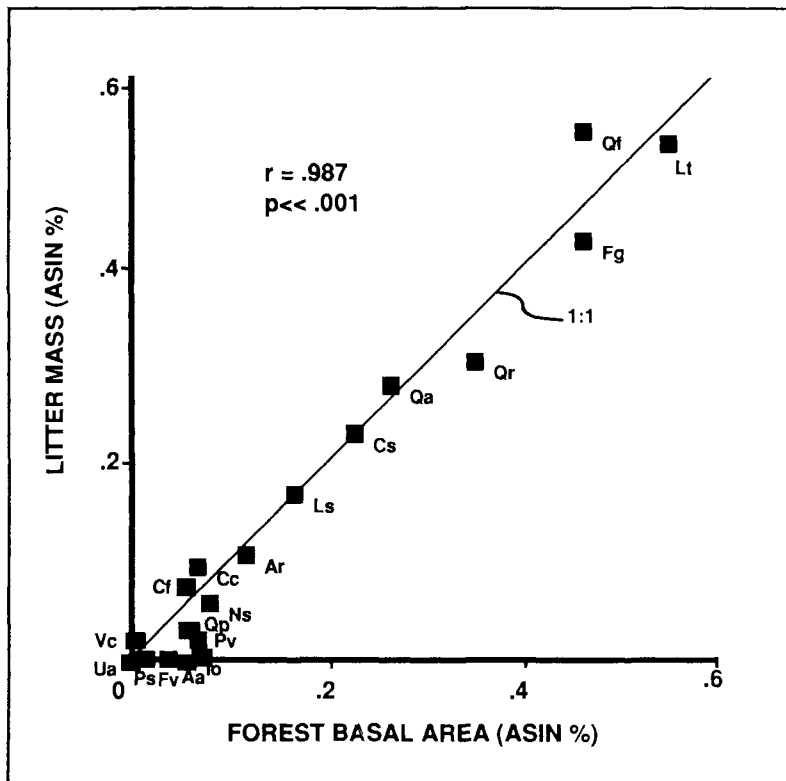


FIGURE 7. Correlation of litter-mass and stem-basal-area values at Western Triangle, Maryland. Litter values represent 21 basket averages per species, and source forest is all trees larger than 2 cm dbh ($r^2 = .94$, $p \ll .001$). Percentage values of litter and forest are arcsin transformed. [Qf, *Quercus falcata*; Lt, *Liriodendron tulipifera*; Fg, *Fagus grandifolia*; Qr, *Quercus rubra*; Qa, *Quercus alba*; Cs, *Carya* spp.; Ls, *Liquidambar styraciflua*; Ar, *Acer rubrum*; Cc, *Carpinus caroliniana*; Cf, *Cornus florida*; Qp, *Quercus prinus*; Pv, *Pinus virginiana*; Io, *Ilex opaca*; Aa, *Amelanchier arborea*; Fv, *Fraxinus velutina*; Ps, *Prunus serotina*; Ua, *Ulmus americana*; Vc, *Vaccinium corymbosum*.

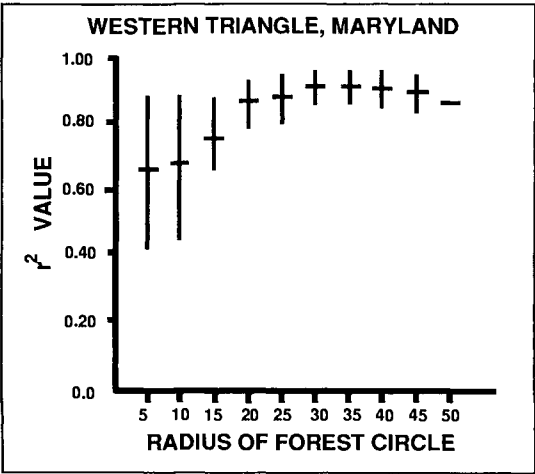


FIGURE 8. Effect of increasing forest area on litter-forest correspondence. Horizontal bars, Mean values (r^2) of correlation of litter samples with increasing areas of forest at Western Triangle, Maryland. Vertical bars, ± 1 SD. $N = 21$.

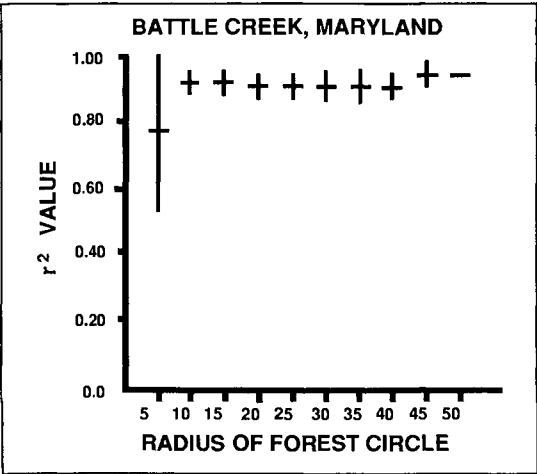


FIGURE 10. Effect of increasing forest area on litter-forest correspondence. Horizontal bars, Mean values (r^2) of correlation of litter samples with increasing areas of forest at Battle Creek, Maryland. Vertical bars, ± 1 SD. $N = 21$.

dance of common tree species in temperate forests. Leaf litter falls almost directly under the canopy that produced it. In addition, the masses of the individual species in the leaf litter are highly correlated with the source-tree basal area. The implications of these findings for sampling and interpreting the plant fossil record are discussed below. The first

section pertains to effects relevant to the first phase of fossilization: abscission/accumulation. All fossil assemblages pass through this phase; therefore, the biases introduced in this phase are the minimum distortion that will be present in all fossil assemblages. The second section addresses biases introduced during subsequent phases of preservation of an

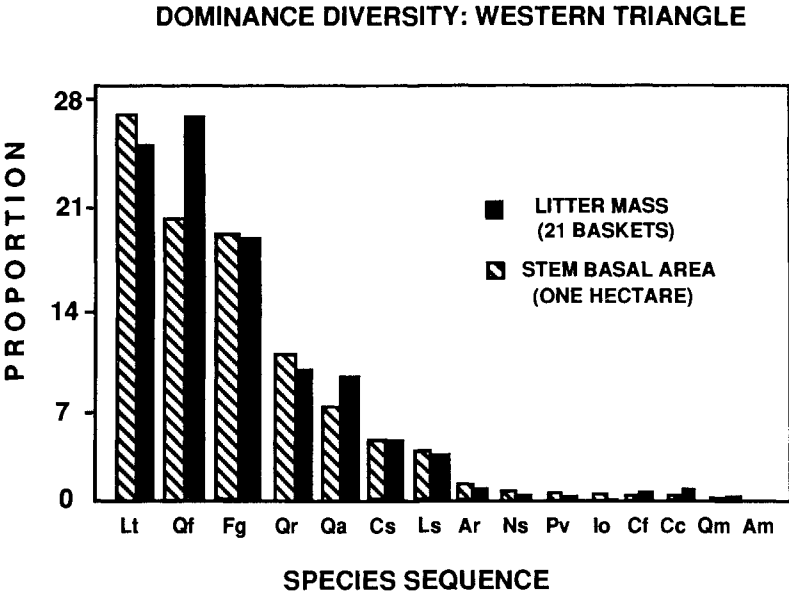


FIGURE 9. Dominance-diversity profiles for litter and forest at Western Triangle, Maryland. See figure 11 for abbreviations.

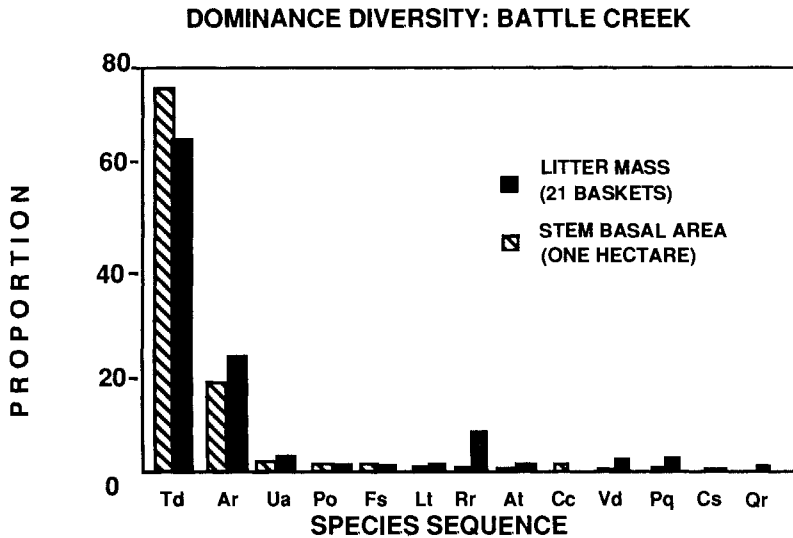


FIGURE 11. Dominance-diversity profiles for litter and forest at Battle Creek, Maryland. Td, *Taxodium distichum*; Ar, *Acer rubrum*; Ua, *Ulmus americana*; Po, *Platanus occidentalis*; Fs, *Fraxinus* sp.; Lt, *Liriodendron tulipifera*; Rr, *Rhus radicans*; At, *Asimina triloba*; Cc, *Carpinus caroliniana*; Vd, *Viburnum dentatum*; Pq, *Parthenocissus quinquefolium*; Cs, *Cornus stricta*; Qr, *Quercus rubra*.

autochthonous leaf assemblage, and problems specific to sampling fossils.

Litter-Forest Relationships

Area of Forest Reflected by Single Samples.—The small size of leaf-deposition areas is implied by the small radii at which litter samples show their maximum similarity to the surrounding forest (figs. 8, 10, 12) and has been confirmed by direct measurement of leaf-deposition areas of individual trees with different canopy heights and leaf sizes in different forest types (Ferguson 1985; Parker and Burnham unpublished observation). A single litter sample of about 350 leaves has greatest similarity to the forest within 10–25 m of the sample site, an area of approximately 300–2000 m². Smaller areas of forest (e.g., circles of 5-m radius) have a lower similarity to the sample because many leaves are derived from trees outside the circle. Larger areas (e.g., circles of 50-m radius) have a lower similarity to the sample because large circles include trees whose leaves are unlikely to appear in the sample. Similarity of litter samples to the surrounding forest does not decline substantially with increasing area if the forest is highly homogeneous, as in most samples from WT and ML (figs. 8, 12).

The size of the area that has maximum similarity to the litter sample (the reflection radius) is influenced primarily by two factors: the height of the forest and the species richness-spatial heterogeneity of the forest. Taller trees with larger canopies shed leaves farther from their trunks, increasing the area over which their leaves can be sampled. Litter samples from species-rich or spatially heteroge-

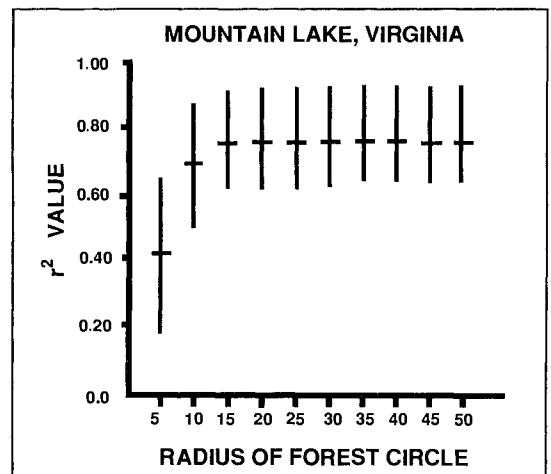


FIGURE 12. Effect of increasing forest area on litter-forest correspondence. Horizontal bars, Mean values (r^2) of correlation of litter samples with increasing areas of forest at Mountain Lake, Virginia. Vertical bars, ± 1 SD. $N = 17$.

DOMINANCE DIVERSITY: MOUNTAIN LAKE

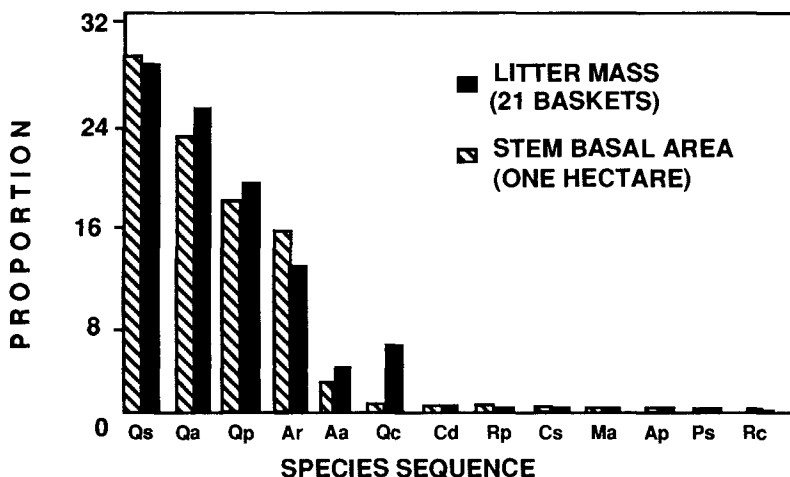


FIGURE 13. Dominance-diversity profiles for litter and forest at Mountain Lake, Virginia. Qs, *Quercus velutina* and *Quercus rubra*; Qa, *Quercus alba*; Qp, *Quercus prinus*; Ar, *Acer rubrum*; Aa, *Amelanchier arborea*; Qc, *Quercus coccinea*; Cd, *Castanea dentata*; Rp, *Robinia pseudoacacia*; Cs, *Carya* sp.; Ma, *Magnolia acuminata*; Ap, *Acer pensylvanicum*; Ps, *Prunus serotina*; Rc, *Rhododendron calendulaceum*.

neous forests will reflect a small area because forest composition changes rapidly away from the sample area. Yet, as shown here, in relatively homogeneous forests, correlation (r value) of single litter samples with the hectare of source forests is generally .80–.95.

Fossil samples, censused quantitatively—each sample consisting of about 350 leaves, and samples separated by about 10 m—should be of the right size and separation to reconstruct forest heterogeneity. Species-rich fossil assemblages, or those derived from low-statured forests, should be sampled at closer intervals; more homogeneous assemblages can be sampled at greater intervals.

Recovering Relative Abundances of Tree Species.—The strong positive correlation between the basal area of a species and the litter mass it produces allows considerable accuracy in reproducing the basal areas of the common forest species (those making up more than 10% of the leaf flora: figs. 9, 11, 13). At the WT site, the rank order of the two dominant species is reversed in the litter samples, but this occurs because the basal-area proportions of the two species are very similar. The results from the three temperate-forest plots reported here are consistent with those from relatively low diversity, subtropical, floodplain forests (Burnham 1989).

Evidence from this study suggests that autochthonous leaf-fossil assemblages derived from forests with fairly low diversity and heterogeneity can be sampled with single, small (~350 leaves) collections and produce reconstructions of the relative importance of the dominant and codominant species in the local forest area of about 300–2000 m². Greater numbers of samples increase the confidence and area over which dominance can be assessed.

Distribution of Species and Size of Individuals.—Compositional variation in autochthonous leaf-fossil assemblages along lateral transects has been noted and related to local environmental gradients and depositional effects (see, e.g., Hickey 1980; Wing 1984; Burnham 1989). These studies did not explore the potential for inferring canopy size of the distribution of individuals from leaf assemblages, although this has been done with in situ fossil trunks (DiMichele and DeMaris 1987; DiMichele and Nelson 1989).

The results reported here for autochthonous litter deposits suggest that, because leaves fall almost directly to the ground, litter preserves information on the breadth of individual canopies and the spatial distributions of individuals and species. If it is isolated from conspecific individuals, a tree's

canopy size can be estimated from the dimensions of the leaf-deposition area. In groups of closely spaced samples (e.g., 5–10 m apart), the distribution of the leaves may indicate its growth form. Leaves of large, common trees are abundant and ubiquitous in all samples (high mean, low coefficient of variation [CV]). Leaves of large rare trees are abundant in one or a few samples (moderate mean, high CV). Leaves of small, rare trees occur as one or two specimens in few samples (low mean, high CV). Leaves of small, common trees are moderately abundant in all samples (moderate mean, low CV). Clumps of small trees are difficult to distinguish from isolated larger trees, but theoretically the leaf-deposition area for a clump of small trees should attenuate more rapidly because the leaves disperse less in falling to the ground (Burnham and Wing 1989).

In order to maximize the potential for recovering information on canopy size and distribution of individuals, samples should be considerably closer together than the probable canopy height of the vegetation. Sample sizes of about 350 leaves are sufficient to recover the leaves of proximal trees.

Recovering Species Composition and Richness from Fossil Samples.—A single collection of 350 leaves contained, on the average, only 40%–50% of the tree species in the surrounding hectare of a temperate deciduous forest. The variability in the proportion of species recovered in single samples (23%–59%, figs. 3, 5, 9) is high but appears to depend on the type of forest from which the samples are derived. Litter from spatially homogeneous forests shows a lower degree of variability and thus higher potential for use in fossil assemblages. Single samples are of questionable value in extrapolating forest richness unless forest type can be determined (Burnham et al. 1990).

The proportion of species recovered increases with larger numbers of samples (fig. 4), but even as many as 20 samples recovered only about 70% of the tree species mapped in the surrounding hectares. The bootstrap analyses show that in the two homogeneous forests with about 20 arborescent species per hectare (WT and ML), 12–15 samples recovered about 70% of the tree species present. At BC, where an ecotone crossed one edge of the

plot, the bootstrap analysis demonstrates that, although 12–15 samples recover 70% of the flora mapped on the plot, another 8 species are found in samples that are not mapped on the plot. This potentially raises the total species number that would be assessed on such a plot and does a poor job of reflecting the target hectare. Thus, extreme caution must be taken with heterogeneous forests because estimation of species richness for a given area is profoundly affected by the heterogeneity of the site in which the samples lie.

Under the favorable conditions in this study (e.g., low number of tree species, low heterogeneity, moderately tall canopy, and synchronous abscission), many samples were required to recover 70% of the tree species on the hectare. More diverse or heterogeneous forests, or those with more trees of small stature, would have to be sampled even more intensively to detect the same proportion of species. This kind of sampling has rarely if ever been attempted for fossil assemblages. Because sampling techniques for most published fossil floras have been inadequately documented, extreme caution should be used in placing biological interpretations on patterns of diversity changes in megafloras (Lidgard and Crane 1990). The results suggest that, for autochthonous fossil assemblages, a great sampling effort is necessary to recover a large proportion of the original forest diversity of an area as large as a hectare. Replicate samples are required to determine the correct multiplier to apply to any fossil plant assemblage to derive original species richness. A recommended sampling regime for fossil deposits is to determine first the site variability with respect to species number within a 20–30 m transect. Low site-to-site variability would indicate that single samples of 350 leaves represent 40%–60% of the total species list for temperate forests. Much larger groups of samples (12–15 samples; 4200–5200 leaves) can consistently recover 70% of the species. Depending on the accuracy desired for the study, these conversion factors can be employed to extrapolate to forest species richness. Conversely, for heterogeneous forests or in sedimentary deposits that cross ecotonal boundaries, extreme caution must be taken to ensure that reconstructed species richness is

indicative of the defined source forest. Further work in heterogeneous and species-rich forests is underway to clarify the extrapolations that may be made for deposits derived from such forests (Burnham in preparation). Clearly, the preceding recommendations are *minimal* procedures to be taken to reconstruct fossil source forests because the baseline data are derived from unmixed, untransported assemblages.

Effect of Growth Forms.—Different plant species devote varying proportions of their biomass to leaves versus stems, creating a less precise correlation between stem-basal area and any measure of leaves. Only woody plants are considered here and, of those, only the liana (woody vines) leaf-measures consistently overestimate basal area. At BC, *Rhus radicans* leaves account for an average of approximately 2% of leaf number and 6% of leaf weight per sample, but most of the stems are small, the 14 stems accounting for .09% of the total basal area of the hectare. This high leaf-to-stem ratio reflects the basic growth form of vines and lianas, which rely on trees for support (Putz 1983, 1990). There are many very small stems of *Rhus* in the forest; however, these stems are much smaller than the 2-cm diameter limit measured for this study. Although the abundance of liana leaves in the litter leads to an inaccurate assessment of their stem-basal area, it is an accurate representation of their photosynthetic area relative to tree species and thus a good measure of their importance in the vegetation. Lianas could not be distinguished from trees by the distribution of their leaves in the litter, implying that recognition of vines and lianas in fossil assemblages will have to be based on morphological features or systematic affinity.

Additional Problems in Interpreting Fossil Leaf Assemblages

Many autochthonous compression-fossil assemblages are modified from the original forest-floor litter by several processes. The effect of these processes on the information preserved in the leaf assemblage, and on how paleobotanical sampling should be carried out in light of these effects, is discussed below.

Generally, the processes that operate to modify forest litter before its preservation as an essentially autochthonous leaf accumulation do not seem likely to erase patterns created during the initial phase of abscission and accumulation.

Redistribution of Leaves after Abscission.—Surface winds do not significantly redistribute leaves on the forest floor (Ferguson 1985; but see Scheihing 1980 with respect to open areas). Moving water is a highly effective transporter of leaves (see, e.g., Spicer 1980, 1989; Ferguson 1985) but transported assemblages can be recognized by primary bedding features and grain size of the enclosing matrix, or by folding and abrasion of the leaves.

Counting Fossil Leaves.—The litter-forest comparisons in this study were based on leaf mass because it was the litter measure most highly correlated with basal area on all three plots. Leaf mass cannot be obtained for fossils, but leaf area appears to be a good proxy (table 8), even though leaf density (area/mass) varies substantially among species (Ferguson 1985). This relationship was investigated here only for temperate deciduous forests. However, an estimate of leaf areas from fossil leaves can be obtained by multiplying the number of leaf fragments of a species (counting only fragments larger than half of one leaf to preclude counting the same leaf twice) by the average area of the whole leaf specimens for that species. Leaf area was derived in an analogous fashion in this study and was highly correlated with basal area (table 8). Further factors could be introduced to correct for differences in leaf density (e.g., seasonally deciduous vs. evergreen leaves) if that is found to be necessary by further modern forest studies. Differences in leaf density frequently can be detected in fossil assemblages by textural or cuticular differences.

Leaf Decay.—Decay rates of leaves of different species vary widely (Spicer 1981; Ferguson 1985), but given the relatively high degree of preservation required to identify fossil leaves, it is probable that the assemblages that are collected and studied have not been heavily degraded. Studies of leaf decay have demonstrated that leaf mass can de-

crease dramatically over periods of less than one year, but the appearance and identifiability of leaves changes more slowly, at least in the absence of mechanical abrasion or macroinvertebrate detritivores that quickly destroy the leaves (Ferguson 1985). Where decay has significantly affected the composition of fossil assemblages, it should be observable in the form of differential preservation of fine details as well as from different degrees of fragmentation. Because substantial degradation can occur over the approximately 2-month period of leaf fall in temperate forests, some care must be taken to account for differential degradation of species on the forest floor during the period of accumulation.

Conclusions

In situ forest litter was investigated because it has undergone the *minimal* modification that could be expected between a living forest and a fossil leaf assemblage. It contains the most information about the forest from which it is derived. Simple, synchronously deciduous forests were studied, with only 20–25 homogeneously distributed tree species per hectare. These conditions provided the framework for the question, "What is the most information we can hope to extract from the plant fossil record?"

Comparisons of leaf litter and standing vegetation under these conditions show that several characteristics of the forest can be inferred from the litter: relative abundance of species making up more than 10% of the stem-basal area, local spatial variation in species composition and abundance, and, possibly, canopy size of individual trees. Crude estimates of total species richness can be approximated from relatively small samples, providing that the heterogeneity of the litter can be determined.

Although the composition of most fossil litter deposits probably is modified before deposition and preservation, in situ litter is a reasonable analogue for some kinds of autochthonous fossil leaf assemblages (Hickey 1980; Wing 1984). Interaction between the timing of leaf abscission and the timing of sedimentation may be an important, though

as yet uninvestigated, source of bias in the composition of autochthonous fossil leaf assemblages.

This investigation of the initial step in the formation of autochthonous fossil leaf assemblages leads to the following recommendations for sampling and analyzing data from the plant fossil record.

1. An individual sample of 350 to 400 leaves will probably recover most of the species that could have shed leaves onto the sample site. Additional effort should be put into increasing sample number.

2. It is well worth recording relative abundances of the species present, because a reasonable estimate of the dominance of taxa in the local vegetation can be derived from these records. The relative number of leaves can be converted easily to relative leaf areas, a good predictor of relative stem-basal area.

3. Differences in species composition and abundance among samples from the same bed may well reflect the original heterogeneity in the forest vegetation and the leaf-deposition areas of individual trees.

4. Samples spaced about 10 m apart are the right scale to recover patterns of local forest heterogeneity. Intersample distances of about 5 m are probably more suitable for recovering information on canopy size of individuals.

5. Total species richness is difficult to estimate unless replicate samples are made and the environment of growth is known. Studies of the plant fossil record that rely on smaller sample sizes should focus on other features of paleoforests such as dominance, heterogeneity, and growth form. These features can be estimated at least as accurately as total species richness.

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