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ScienceDirect
Forest Ecology and Management 234 (2006) 60–77
Forest Ecology and Management
www.elsevier.com/locate/foreco

Litterfall in the hardwood forest of a minor alluvial-floodplain

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Received 3 March 2006; received in revised form 15 June 2006; accepted 16 June 2006

Abstract

Within mature deciduous forests, annual development of foliar biomass is a major component of aboveground net primary production and nutrient demand. As litterfall, this same foliage becomes a dominant annual transfer of biomass and nutrients to the detritus pathway. We report litterfall transfers of a mature bottomland hardwood forest in a minor alluvial-floodplain within the middle Coastal Plain physiographic province of central Louisiana, USA. Climate is humid subtropical. Floodplain forests of minor alluvial-streams may account for nearly half the remaining acreage of bottomland forests in the Southeastern USA and differ markedly from those of major alluvial-rivers and deep-water swamps. For a 3-year period, litterfall magnitude, components, leaf species, and timing were monitored by monthly collection of materials from litterfall collectors. Variations in litterfall transfers across 10 study-plots and their relationships to forest parameters are evaluated. Mean transfers of total litterfall, leaf fall, reproductive structures, fine wood, and other litterfall were 816, 512, 130, 98, and 76 g m^{-2} $year^{-1}$, respectively. *Quercus pagoda* Raf., *Q. nigra* L., and *Liquidambar styraciflua* L. accounted for an average of 49% of annual leaf fall, with 11 tree species and canopy vines accounting for 94% of total annual leaf fall. A total of 38 species and genera contributed to total leaf fall. Variation in total litterfall and leaf fall transfers across the alluvial bottom were related to size of overstory trees and their species composition. Higher and more consistent mass transfers of reproductive structures were observed than previously reported for upland hardwood stands.

Keywords: Litterfall; Leaf fall; Reproductive structures; *Liquidambar styraciflua*; *Quercus pagoda*; Bottomland hardwoods; Minor alluvial floodplain; Southeastern USA

1. Introduction

Pre-European settlement, the forested areas of major alluvial-floodplains (Mississippi and other major rivers) and deep-water swamps were immense; however, these forests have largely been lost to agricultural and other non-forest uses. Hodges (1998), based on available data, estimated that forests growing on minor alluvial-floodplains represented over half the remaining acreage of wetland forests in the Southeastern USA. Moreover, minor alluvial-floodplains differ significantly from major alluvial-floodplains in ways beyond stream size and floodplain width. In major alluvial-floodplains, commonly termed major bottoms, flooding reflects regional weather events, is predominantly overbank and of long duration, commonly lasting one-to-several months and into the growing season. In contrast, minor bottoms flood frequently but with flashy events, lasting only one-to-several days. Flooding in minor bottoms is most common in the winter and early spring, with flooding during the growing season a relatively rare event. In minor bottoms, flooding is of both overbank and riparian origins (adjacent hill-slope processes and lower order streams). Geomorphically, major bottoms typically have broad, fluvially generated, features reflecting the flooding regime, sediment sources and bottomland shape. By comparison, in minor bottoms, geomorphic features are narrower, spatially compressed between the stream and adjacent upland toe-slopes. Minor streams often add to the apparent compression and complexity by meanders that abruptly cross the entire

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doi:10.1016/j.foreco.2006.06.026

floodplain. Soils in minor bottoms, reflecting local sediment sources and fluvial geomorphology, are spatially more variable than in major bottoms, especially with regard to soil phases and depths (Boyd et al., 1998; Hodges, 1998; Stanturf and Schoenholtz, 1998).

In a mature forest, leaf tissue production is the dominant component of aboveground net primary productivity and a major source of mineral nutrient demand (Conner and Day, 1992). Litterfall (or the subset leaf fall) has thus been used as an indicator of primary productivity and is recognized as a major path of carbon and mineral nutrient transfer (Cole and Rapp, 1981; Megonigal and Day, 1988; Conner and Day, 1992; Megonigal et al., 1997). In this paper we report the litterfall transfers in a mature bottomland hardwood forest of a minor alluvial-floodplain. We evaluate the magnitude, major components, and seasonality of litterfall and describe the species composition of the leaf fall component. Variation in litterfall across the bottomland is evaluated in relation to overstory stand parameters and species presence.

For many of the world's major forest types, litterfall transfers have been repeatedly measured under varying stand ages, conditions, and successional stages. Litterfall magnitude, its components, and associated nutrients have been compared and interpreted from a variety of perspectives such as material and energy fluxes within ecosystems or as an indicator of ecosystem productivity (e.g., Bray and Gorham, 1964; Jordan and Murphy, 1978; Meentemeyer et al., 1982; Vitousek, 1982; Vogt et al., 1986). Forested wetlands from the Southeastern USA were touched upon lightly or omitted altogether from most early review papers. Their absence, in part, was due to a lack of early studies and the objectives of the reviewers but may also have reflected the varied and sometimes inexplicable impacts on productivity of the wetland forests' inundation regimes.

In the last three decades, interest in litterfall transfers within wetland forests in the Southeastern USA has greatly increased. Summaries by Shure and Gottschalk (1985), Conner et al. (1990), Conner and Day (1992), Conner (1994), and Conner and Buford (1998) cite litterfall transfers from 47 forested wetlands as reported in 25 articles. Studies by Megonigal et al. (1997), Burke et al. (1999), and Busbee et al. (2003) report annual litterfall from an additional 24 wetland stands. Though this array of studies has addressed a variety of questions, most studies have been of deep-water wetlands (Conner and Day, 1992; Conner, 1994) or major alluvial-floodplains. Although a significant and dramatic segment of these wetland forests, they are not the only wetland forests. As outlined by Shepard et al. (1998), forest wetlands in the Southeastern USA are diverse and, depending on study purposes and investigators' interests, have been divided into 7–10 wetland types and, in one case, zones with scores of community types (Wharton et al., 1982). Messina and Conner (1998) recognized nine wetland-forest types: deep-water swamps, major alluvial-floodplains, minor alluvial-floodplains, pocosins and Carolina bays, mountain bogs, cypress domes, wet flatwoods, and mangroves.

2. Methods

2.1. *The study area*

This study was located within the middle Coastal Plain physiographic province on the alluvial floodplain of an upper segment of the Iatt Creek watershed. The site (31°43′30″N, 92°38′W) is in the Kisatchie National Forest, approximately 16-km northwest of Williana, Louisiana, USA. The study area is approximately 345 ha in size and varies in width from 550 to 1000 m with an overall length of approximately 5000 m. An upstream watershed area of about 195 km^2 drains into the study area.

Within the study area, the floodplain of Iatt Creek is dominated by a network of streams and sloughs. Flooding and meandering of the channels have created natural levees adjacent to the streams and varying patterns of ridge and swale topography across the floodplain. The channel of Iatt Creek is deeply incised, requiring an over 4-m water depth for overbank flooding. From the surrounding uplands, the largest lower-order streams cross the bottom and flow directly into Iatt Creek. However, most upland streams discharge within the bottom into lesser channels that parallel Iatt Creek for some distance before flowing into the creek. These paralleling streams are primarily separated from Iatt Creek by natural levees.

The study area lies within the subtropical division of the continental humid temperate ecoregion or domain (Bailey, 1998). Normal annual temperature (30 year) is 17.9 °C with normal precipitation of 1508 mm $year^{-1}$ (Anonymous, 2002). The forest is mixed bottomland hardwood at least 68–74 years in age with scattered older individuals. The floodplain was logged in the early 1900s with some selective cutting in the late 1950s, primarily of scattered pine. The adjacent uplands are dominated by loblolly (*Pinus taeda* L.) and shortleaf (*Pinus echinata* Mill.) pines.

Soils in the floodplain are mapped as the Guyton series, which are fine silty, siliceous, thermic Typic Glossaqualfs, derived from geologically recent local alluvium deposited over Pleistocene sediments (Boyd et al., 1998). Commonly, the soils are poorly drained silt loams to silty clay loams, but within the study area, depth and texture of recent alluvium varies with surface topography and distance from stream channels. Natural levees with slightly higher elevations and silt loam to very fine sandy loam textures are at least moderately well to somewhat poorly drained (personal observation). The surrounding uplands are dominated by fine textured Ultisols with moderately poor internal drainage that primarily support pine-hardwood forests.

2.2. *Study plots*

Starting from a random point, seven parallel line-transects were established on 500-m intervals at right angles to the central axis of the floodplain. Each transect line, the study area perimeter, and central baseline were marked with numbered steel stakes at 61-m intervals. The location and elevation of each stake were determined by a closed survey using a Topcon Total Station (Topcon Positioning Systems, Livermore, CA, USA). Survey was done by surveying staff, USDA Forest Service, Kisatchie National Forest. At 122-m intervals, on each transect line, we established 0.1-ha plots (20 m × 50 m). An inventory of all trees $\geq$7.6 cm DBH (diameter at breast height, DBH, measured at 1.4-m above the ground) and subsequent use of cluster analysis techniques (SAS Institute, 1994) indicated that over three-quarters of the 47 plots were dominated by sweetgum (*Liquidambar styraciflua* L.) or sweetgum and cherrybark oak (*Quercus pagoda* Raf.) (Gardiner et al., 1996). Blue beech (*Carpinus caroliniana* Walt.) and blackgum (*Nyssa sylvatica* var. *sylvatica* Marsh.) were the most common mid- and understory trees. From these 2 dominant stand types, we randomly selected 10 plots for more detailed study of productivity and nutrient cycling processes.

2.3. Stand measurements

For the 10 intensive study plots, DBH and height were determined for all trees $\geq$2.5-cm DBH. Diameters were measured annually and heights biennially. Height of each tree was measured twice using a Criterion 400 (Laser Technology Inc., Centennial, CO, USA) from two perspectives at least 45° apart, at distances from the tree greater than its height. Similarly, basal diameters and heights of all saplings taller than 1.4 m and <2.5-cm DBH were measured annually. Sapling height was measured using a standard height pole. Basal diameter was measured using a digital caliper, the average of two readings taken at 90° apart.

2.4. Soil water table

At each of the 10 intensive study plots, the soil water table, to a depth of about 1.8 m, was measured every 2 h by use of an automated capacitance-based sensor (WL80, Remote Data Systems, Wilmington, NC, USA). Sensors were housed in a perforated well-casing, 7.6-cm i.d., with the casing's upper 60 cm sealed with a 3 mm-thick rubber wrap.

2.5. Litterfall collections

Five fine-litterfall collectors were placed in each plot. The basket-shaped collector had a 4560-cm^2 circular opening formed by a steel hoop. A mesh basket approximately 50-cm deep was sewn to the circular hoop. The mesh basket was made from common window screen (woven fiberglass, coated with polyethylene) and had 1.5-mm openings. The steel hoop was supported by three steel-posts at a height of 1.4 m above the ground. Collectors were elevated to minimize impacts of frequent winter-floods. Posts did not extend above the collector opening. Some loss of seed and fruit to rodents and birds did occur. Due to trap height above ground, herbaceous and small-sapling litterfall transfers were essentially excluded from the collections.

Litterfall was collected at least monthly from July 1995 to July 1998. From October through December 1996 litterfall was collected every 2 weeks. Sampling intervals also varied somewhat due to weather, flooding, and available work force. Litterfall was separated into five components: leaves, fine-wood and bark, reproductive structures, animal detritus, and "other" litter materials. Reproductive structures included aborted, immature, and mature seeds, seed-containing structures (e.g., cones, acorn caps, the husk and nut from *Carya* spp.), their fragments and, primarily in the spring, flowering structures. Fine-wood and bark material was defined as all collected bark, regardless of size, and branches whose maximum diameter was <1 cm. Leaf fall was further sorted by plant species. Insects dominated the animal component. "Other" litterfall referred to fragments too small to be identified by eye. All mass values are reported on an oven-dried (70 °C) basis.

2.6. Litterfall and stand parameters

Relationships between a tree's foliar biomass and total tree mass or stem-volume dimensions have been frequently developed (Landsberg, 1986). To determine if differences among plots in litterfall or its components were related to differences in stand

Table 1
Stand attributes for the Iatt Creek study site estimated from the 10 (0.1 ha) bottomland hardwood plots investigated in this study

Stand age (years)	68–74[a]		
	Mean	S.D.	Range
Diameter breast height[b] (cm)			
All trees > 2.5 cm DBH	20.6	3.1	14.9–23.9
All trees > 10 cm DBH	36.1	6.2	26.4–50.5
All trees > 30.5 m tall	60.5	7.8	46.5–71.4
Tree height[b] (m)			
All trees > 2.5 cm DBH	11.5	1.7	9.2–14.4
All trees > 10 cm DBH	22.3	3.3	17.7–29.9
All trees > 30.5 m tall	36.8	1.8	34.9–40.0
Stand density[b] (stems ha^{-1})			
All trees > 1.4 m tall	2720	1641	1210–6040
All trees > 2.5 cm DBH	1019	231	720–1500
All trees > 10 cm DBH	317	77	220–480
All trees > 30.5 m tall	88	31	40–140
Basal area at DBH[b] (m^2 ha^{-1})			
All trees > 2.5 cm DBH	33.8	9.1	23.2–50.2
All trees > 10 cm DBH	32.4	8.7	21.4–48.0
All trees > 30.5 m tall	25.0	8.7	14.8–45.0
Size parameter: BAH[c] (m^3)	11.2	3.4	6.1–16.7
Weather parameters[d]			
Mean annual temperature (°C)	17.8		17.7–17.9
Annual precipitation (mm year^{-1})	1463		1235–1608

[a] Age based on increment cores taken from dominant and co-dominant ring-porous trees. Cores were taken just above butt swell, approximately 0.75 m above the ground. Actual tree age may be 10–15 years older.

[b] Dimensions indicate minimum dimension considered and reflect all individuals greater than the stated minimum. Reported means, standard deviations, and ranges are based on plot means or totals, $n = 10$.

[c] The size parameter [(tree Basal Area at DBH) × (total tree height)], was determined for each tree >30.5 m tall. Mean BAH values were then calculated for each plot. Mean and range of sample sizes for individual plot means was one-tenth the stand density value (stems ha^{-1}) for trees >30.5 m tall, reported above.

[d] Mean annual weather parameters were based on 3-years of data collected using an on-site weather station.

size or biomass, a stand size parameter, based on individual-tree basal area and height, was developed. For each tree >30.5 m in height, the product of its basal area (BA, m^2) and height (H, m) was calculated with means (BAH) determined on a per-study-plot basis. To gain insight about possible relationships between the species composition of stands and annual leaf fall or other litterfall components, the fractions of total plot basal area (BAFrt) contributed by *L. styraciflua* (BAFrt$_{L.\ styraciflua}$) and all *Quercus* spp. (Appendix A) (BAFrt$_{Quercus}$) were also determined for each of the study plots.

2.7. Weather monitoring

A meteorological station was established in an adjacent opening (clearcut). In the opening, wind speed and direction, air temperature and relative humidity (at 3 m), incoming total solar and photosynthetically active radiations, soil temperature at 5-, 25-, 50-, and 100-cm depths, and rainfall were continuously monitored (DataLoggers Inc., Logan, UT, USA).

3. Results

All plots support mature closed canopy forests (Table 1). Variation among plots, in basal area and stand density, in part reflects the presence of secondary creeks or sloughs that cross some plots, depressional sloughs, and old canopy gaps (caused by falling trees) that have since filled in with advance regeneration. Precipitation and water table fluctuations are outlined in Fig. 1; note the unusually dry winter of 1995–1996. Rainfall for November 1995 through March 1996, 318 mm, was 55% below the 30-year normal for this period (Anonymous, 2002) and 51 and 61% below the respective 1996–1997 and 1997–1998 winter (November through March) totals for our study (Fig. 1).

3.1. Litterfall components

Annually, litterfall normally has two peak-periods of transfer (Fig. 2). A small spike occurs in spring (March and April) during bud burst and flowering, with a slow rise in transfers during the summer months. The dominant peak is the period from September through December and early January. On average, 71% of annual litterfall is transferred in this period, with only 10% of total annual litterfall in the 2-month spring period. Overall, leaves are the dominant litterfall component; however, in the spring spike, "other fine materials" account for 39% of total transfer and fine-wood and bark fragments an additional 26%. In the autumn through early winter period, leaves and reproductive structures account for, on average, 74 and 16% of total litterfall, respectively. Throughout the study

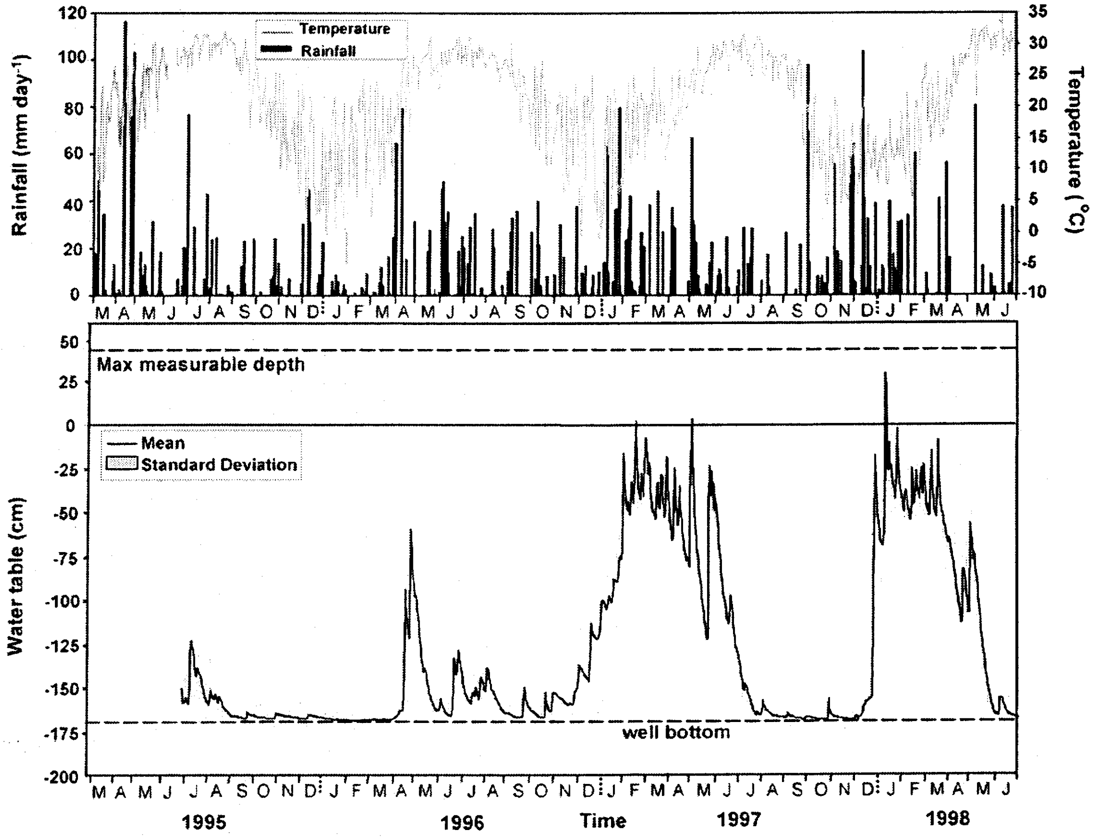

Fig. 1. Fluctuations in temperature, precipitation and mean water-table depths for the Iatt Creek Study area, during the study period (July 1996–1998). For water table daily mean and standard deviation values $n = 10$. Daily rainfall and temperature data prior to July, 1995 are from the cooperative weather station, Winnfield 2W, 19 km north of the study area (Southern Regional Climate Center, Office of the State Climatologist, Louisiana State University, Baton Rouge, LA).

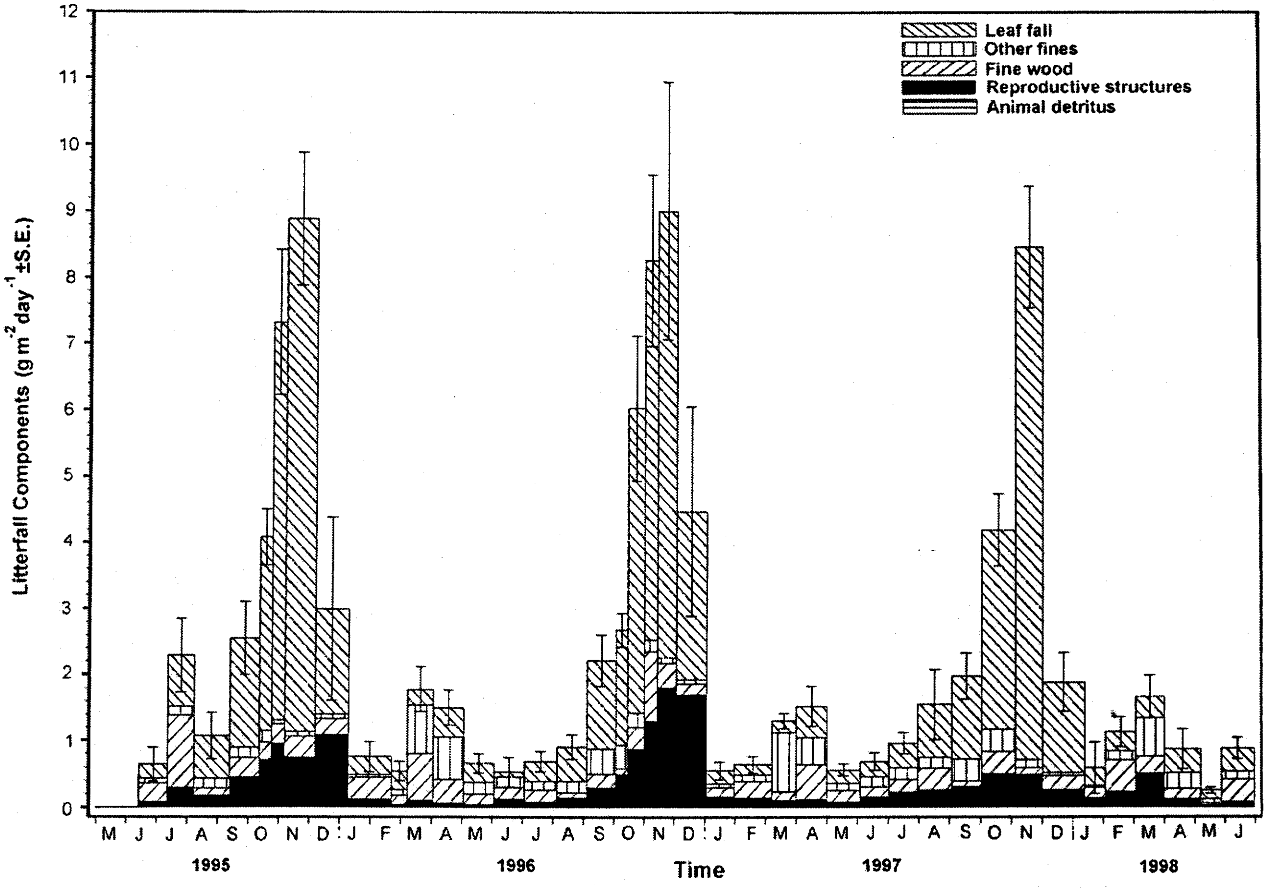

Fig. 2. Time trends in mean daily transfer rates for total litterfall and litterfall components. Bar width varies with the length of the collection period. Standard error terms are for total daily transfers, during respective collection periods, $n = 10$.

period the animal detritus component of litterfall mass (Fig. 2) remains at trace levels.

Within the prolonged autumn through early winter period, the rate of total litterfall increased rapidly in October, reaching a maximum in mid- to late-November, then dropping sharply in the December to early January period (Fig. 2). Timing and rates of total litterfall reflected the timing of senescence and the frequency and timing of collections. The highest reported rate, 9.1 g m^{-2} day^{-1}, was for the 19-day period 14 November to 3 December 1996 (Fig. 2). The preceding 14-day collection period had a mean daily transfer rate of 8.2 g m^{-2} day^{-1}. The time weighted transfer rate for the entire 33-day period was 8.7 g m^{-2} day^{-1}. For approximately the same 30-day periods in 1995 and 1997, daily transfer rates were 8.6 and 8.2 g m^{-2} day^{-1}, respectively, illustrating general similarity during the 3-year period, the potential averaging effect of longer collection periods, and the potential for brief periods of higher transfer rates.

Standard errors of total litterfall transfers, for a collection period, reflect variation in litterfall across the study area (Fig. 2). Variation in standard errors through time also reflects forest composition, phenology, variable disturbance, and length and timing of measurement periods. For example, relative to similar time periods in other years, the highest standard errors for total litterfall (Fig. 2) are from collections made in late October through December 1996. In 1996, collections during October and November are more frequent; thus, in part, the standard errors reflect the detection of temporal variation among plots in time when litter fell. Yet, illustrating total litterfall's complexity, the highest standard error for this 1996 period, is for the longer December through early January collection period when mean rate of total litterfall is only half that of the preceding November collection. The higher variance in the December 1996 collection, and earlier months also reflects that year's higher transfers of reproductive structures and its high variability among plots; similarly, the relatively low standard errors in the fall and early winter of 1997–1998 reflect the 60–70% drop in transfers of reproductive structures during that time.

Mean total litterfall transfers for the three collection-years were 870, 820, and 759 g m^{-2} year^{-1} with respective mean leaf fall transfers of 548, 487, and 502 g m^{-2} year^{-1} accounting for an average of 63% of total transfers (Fig. 3). However, variability among plots in total annual litterfall was not primarily due to variability in leaf fall. Box plots (Fig. 3) were used to describe the variation among plots of annual transfers for total litterfall and its components. Although annual transfers of reproductive structures had much lower medians and means than respective leaf fall transfers, their interquartile ranges were as-great-as leaf fall's, and the influences of their high outliers

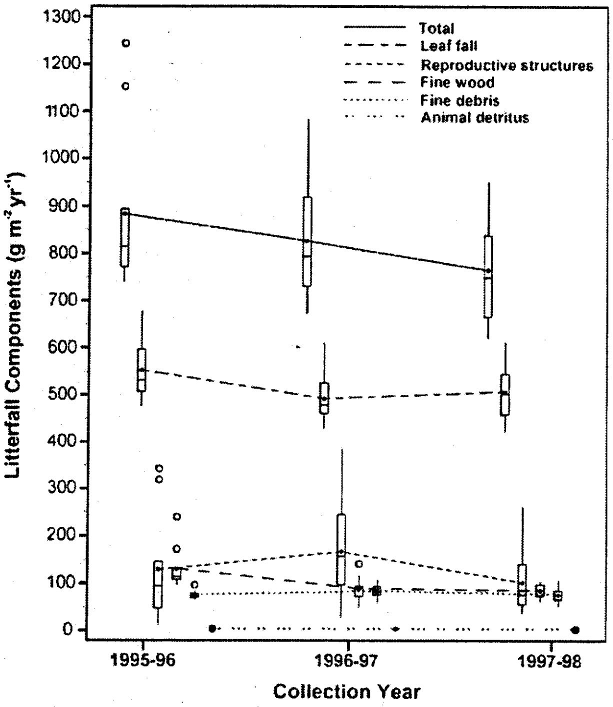

Fig. 3. Box and whisker plots of annual litterfall transfers for the three collection-years, $n = 10$. The box contains the middle 50% of the ranked data points. The upper edge of the box marks the 75th percentile of the data set with the lower marking the 25 percentile. Within the box, the horizontal line marks the median for the entire data set. The difference between the 75th and 25th percentiles (termed the upper and lower quartiles) is the interquartile range. The two vertical lines or whiskers extend from the box to the lowest and highest data points within 1.5-times the interquartile range. The outlier ("○") data points are directly above their respective 1.5 interquartile ranges. The coded lines connect the mean annual transfer values ("●") and identify the components.

and/or upper whisker values on total litterfall were evident. Similarly, for bark and fine-woody materials, the two high outliers in 1995–1996 and one in 1996–1997 added to observed variability in total litterfall.

3.2. *Leaf fall species*

Leaf fall was sorted into species or species groups and data were presented as mean daily transfers (Fig. 4). A complete listing of the species identified in leaf fall is given in Appendix A. Included in Fig. 4 were the leaf fall transfers of the 11 tree species or genera that individually had mean annual leaf fall transfers of at least 8.9 g m^{-2} year^{-1}. Also included were the three other leaf fall groups: canopy vines (Appendix A), other identified leaf species, and unidentified leaf fragments. The 11 tree species and canopy vines accounted for an average of 94% of annual leaf fall transfers; 8 species or genera contributed to the canopy vine component; 20 species contributed to the category "other identified leaf fall".

During the peak period of autumn leaf fall, *Quercus* species and *L. styraciflua* accounted for an average of 59% of total leaf fall (Fig. 4). *Q. pagoda* and *L. styraciflua* were the prominent leaf fall species, averaging 1.49 and 1.79 g m^{-2} day^{-1}, respectively, together accounting for 43% of mean November transfers. During the same period, *Quercus* species contributed 2.74 g m^{-2} day^{-1} or 36% of mean leaf fall.

In this primarily deciduous forest, the peak periods of autumn leaf fall accounted for much of the annual transfer; yet, through the late August through February period, timing of leaf fall varied among species and perhaps years. Significant *L. styraciflua* leaf fall began in August (Fig. 4), exceeding total *Quercus* leaf fall through September and October with *Quercus* species higher in late November and December. The pattern is best shown in the more frequently collected autumn of 1996, when *L. styraciflua* transfers reached a peak mean rate of 1.87 g m^{-2} day^{-1} for the first-half of November and declined to 1.27 g m^{-2} day^{-1} for the second-half. In contrast, mean *Quercus* spp. leaf fall was 1.68 and 2.76 g m^{-2} day^{-1} during the same respective periods, and in December, *Quercus* spp. averaged 1.76 g m^{-2} day^{-1} while *L. styraciflua* leaf fall plummeted to 0.13 g m^{-2} day^{-1}.

Comparing individual oak species, *Q. pagoda,* with its strong peak in November, clearly dominated the overall *Quercus* leaf fall. In contrast, *Q. nigra*, for the 4 months of October through January (Fig. 4), had mean leaf fall rates of 0.24, 0.38, 0.46, and 0.10 g m^{-2} day^{-1}, respectively. Though it had a lower overall autumn transfer rate, *Q. nigra*'s protracted period of leaf fall is characteristic of the species. In December, *Q. nigra* nearly equaled or exceeded leaf fall rates of *Q. pagoda*; in the January through early February period *Q. nigra* was the predominant leaf fall species.

Leaf fall patterns of *Q. michauxii* and *Q. shumardii* varied among years. In November 1995 and 1997, mean transfers of *Q. michauxii* were 0.56 and 0.45 g m^{-2} day^{-1}, respectively, at least four times greater than the species' mean daily October and December leaf fall rates. However, in 1996, the late November transfer averaged 0.31 g m^{-2} day^{-1} with a mean December rate of 0.33 g m^{-2} day^{-1}. Similarly, *Q. shumardii* leaf fall rates, in November 1995 and 1997, were also at seasonal maximums of 0.12 and 0.11 g m^{-2} day^{-1}, respectively, with lower rates in October and December. However, early and late November 1996 means were 0.12 and 0.08 g m^{-2} day^{-1}, respectively, with the December 1996 mean of 0.16 g m^{-2} day^{-1}. During the autumn period, most of the above differences in leaf fall transfers are matters of timing, not of total seasonal mass transfers.

In our study, leaf fall of *Carya* spp. included five species: *C. cordiformis* (Wang.) K. Koch, *C. glabra* (Miller) Sweet, *C. tomentosa* (Poiret) Nuttall, *C. glabra* var. *hirsuta* (Ashe) Ashe-(*C. leiodermis* Sarg.), and *C. aquatica* (Michaux f.) Nuttall. The most common *Carya* leaf fall was from *C. glabra* var. *hirsuta. Carya* was a significant part of leaf fall within the study area; during its peak period of leaf fall, average daily rates equalled or exceeded all *Quercus* species except *Q. pagoda* (Fig. 4). Leaf fall from *Carya* reached a peak mean rate in November; in early November 1995, it averaged 0.49 g m^{-2} day^{-1}, with a mean of 1.00 g m^{-2} day^{-1} in the period from mid-November to early December. Similarly, in early November 1996, *Carya* leaf fall averaged 0.46 g m^{-2} day^{-1} with a late November average of 0.92 g m^{-2} day^{-1}. In both years, December leaf fall for this species group was near trace levels.

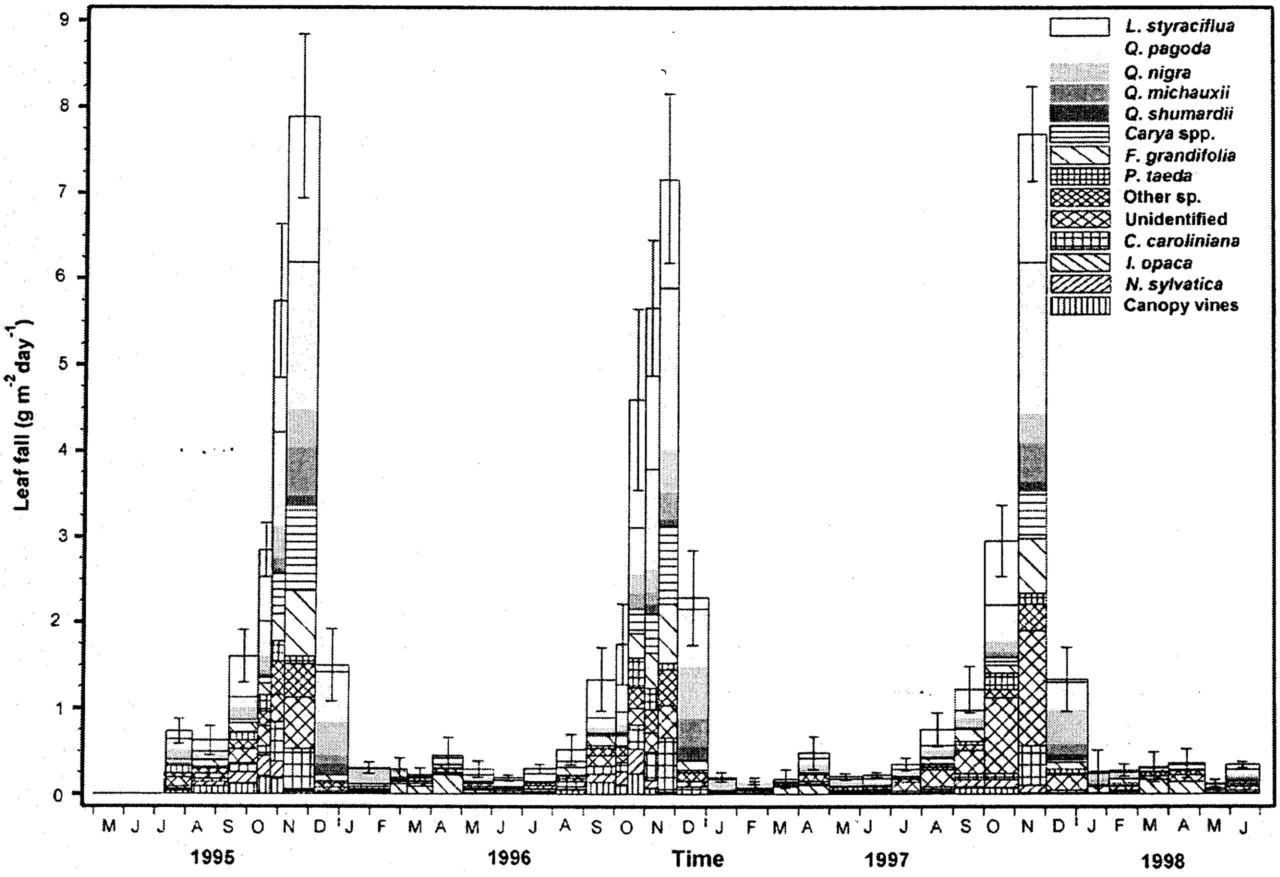

Fig. 4. Time trends in mean daily transfer rates for total leaf fall and dominant species leaf falls. Histogram bar width varies with the length of the collection period. Standard error terms are for total daily transfers, during respective collection periods, $n = 10$.

In 1997, the basic pattern for *Carya* leaf fall was similar to prior years, but peak transfer rate was 40% below that of earlier years. Though, in one plot, there was some mortality of *Carya*, the decline in leaf fall more likely reflected difficulty in sorting leaf fall collected during the November 1997 period. Sorting *Carya* leaf fall was difficult because senescing *Carya* leaflets tended to blacken and curl while on the tree, creating a fragile senescent leaf that became more fragile when oven-dried; moreover, in 1997 some samples were inadvertently compressed prior to sorting. The November 1997 decline in *Carya* leaf fall corresponds with a doubling in mass of unidentified leaf fragments relative to previous years (Fig. 4).

Leaf fall from *Fagus grandifolia* Ehrhart was noticeable in August, increased slightly in September, and reached a peak rate of 0.69 g m^{-2} day^{-1} in mid- to late-November before dropping to approximately 0.10 g m^{-2} day^{-1} in December (Fig. 4). Despite the visually apparent tendency of *F. grandifolia* to retain foliage on lower branches and saplings, its leaf fall was not a significant component of late season leaf fall mass. In part, this discrepancy between visual appearance and mass transfer is because *F. grandifolia*'s leaf area per-unit-mass is 80% higher than *Quercus* spp. and *L. styraciflua* (unpublished data).

Mature *P. taeda* L. were scattered across the Iatt Creek study area; their period of peak needle fall occurred in late October and early November. The 1995 mean late-October needle fall was 0.20 g m^{-2} day^{-1}, which rose to a mean of 0.24 g m^{-2} day^{-1} in early November. The mean rate then declined to 0.09 g m^{-2} day^{-1} for the remainder of November. Similarly, in 1996, mean leaf fall for the last half of October was 0.34 g m^{-2} day^{-1}, which declined to a mean of 0.25 g m^{-2} day^{-1} for the first 2 weeks of November and dropped to 0.07 g m^{-2} day^{-1} for the final 2 weeks of the month. In 1997, reflecting the longer collection periods, mean transfer for October was 0.19 g m^{-2} day^{-1} with a drop to a mean of 0.13 g m^{-2} day^{-1} for the month of November.

The most common understory species (Appendix A) in leaf fall collections was *C. caroliniana*. Occupying similar sites and canopy position, *Ostrya virginiana* (Miller) K. Koch was also present but less common. Senescent leaves of *O. virginiana* were combined with *C. caroliniana* because it was not possible to readily differentiate between senescent leaves of the two species; for brevity the composited-species group will be referred to as *C. caroliniana*. Significant *C. caroliniana* leaf fall of 0.09 g m^{-2} day^{-1} began in September and continued at near the same rate for October. In the 1995 and 1996 collection years, mean rates of transfer increased sharply during the early weeks of November and reached maximum rates of 0.48 and 0.63 g m^{-2} day^{-1}, respectively, in the latter part of the month.

Similarly, in 1997 the mean rate for November was 0.45 g m^{-2} day^{-1}. For all years, mean December rates were <0.1 g m^{-2} day^{-1}.

In our study, *N. sylvatica* var *sylvatica* was predominantly found in the mid- or understory. The species is known for its early leaf senescence. Leaf fall of *N. sylvatica* var *sylvatica* having begun in late August, appeared to reach its peak in October and essentially end by mid-November. Differences among years appeared to reflect timing and length of collection periods.

Ilex opaca Aiton, *Symplocus tinctoria* (L.) L'Her, and *Magnolia grandiflora* L. were the three broadleaf-evergreens visually evident in the study area. Of these species, only *I. opaca* was included as a separate species (Fig. 4). Within this bottomland site, *I. opaca* varied from a waist-high shrub to trees exceeding 15 m in height. As with other broadleaf evergreens in this study, peak *I. opaca* leaf fall occurred in the spring (March and April; Fig. 4) when transfers averaged 0.12 and 0.15 g m^{-2} day^{-1}, respectively.

The canopy vine group included seven species and one genus grouping (Appendix A). The highest transfers were from *Vitis rotundifolia* Michaux. Considered together, vine leaf fall began in August and extended through November. The *Vitis* spp. appeared especially sensitive to late summer and early fall water deficits, initiating early leaf fall in response. Vine leaf fall in August ranged from 0.05 to 0.07 g m^{-2} day^{-1}, rose to 0.12–0.14 g m^{-2} day^{-1} in September, and tended to reach a maximum mean rate of 0.2 to 0.24 g m^{-2} day^{-1} near the end of October (Fig. 4). Though not dominant over broad areas of bottomland, their leaf fall rates illustrate the potential importance of vine leaf area, a component of canopy leaf area that is often simply ignored.

In Fig. 4, patterns of mean daily leaf fall through time, are shown with standard error bars for total leaf fall in a collection period. In Fig. 5, for the dominant individual species, box plots are used to examine annual leaf fall transfers and their variability among plots. As expected, annual leaf fall means of a species generally reflect the daily rates during their periods of high autumn transfer (Fig. 4). However, their large interquartile ranges, 3/2 interquartile whiskers, and relative positions of medians and means illustrate the wide difference in annual species leaf fall across the bottomland (Fig. 5). For the dominant species, *L. styraciflua*, *Q. pagoda*, and *Q. nigra*, transfer rates were 103.0, 94.2, and 44.9 g m^{-2} year^{-1}, respectively; however, their upper whiskers extended to include mean 3-year highs of 235.0, 220.0, and 101.9 g m^{-2} year^{-1}, respectively, with low whiskers extending to near zero.

The potential significance of a species that, for the entire study area, has a lower mean leaf fall is also evident (Fig. 5). *Carya* spp. and *F. grandifolia*, respectively, have 3-year mean outliers of 112 and 161 g m^{-2} year^{-1}, that are 3.5- to over 4 times greater than the study means and medians. In these outlier sites, *Carya* spp. and *F. grandifolia* account for, respectively, one-fifth and one-third of total annual leaf fall.

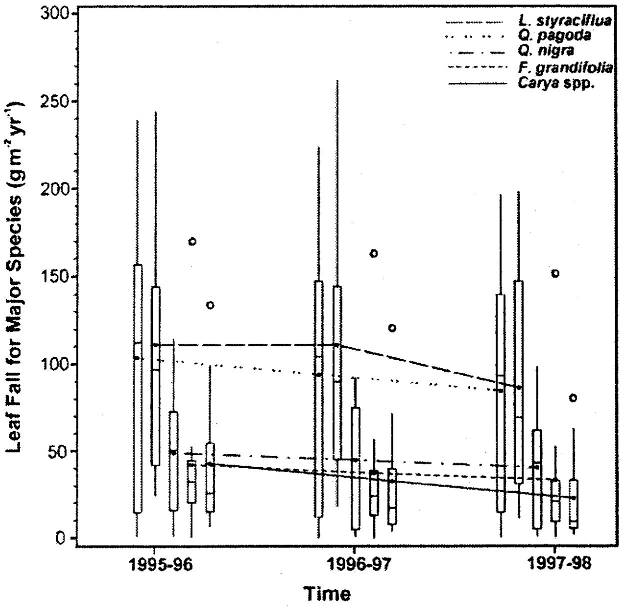

Fig. 5. Box and whisker plots of annual leaf fall by species or species group for the three collection-years, $n = 10$. Within the box, the horizontal line marks the median for the entire data set. Whiskers extend from the box to the lowest and highest data points within 1.5-times the interquartile range. The outlier ("○") data points are directly above their respective 1.5 interquartile ranges. Coded lines identify the leaf species and connect the mean annual transfer values ("●"). Box and whisker plots are outlined in greater detail in Fig. 3 caption.

For *L. styraciflua* and *Q. pagoda*, the highest leaf fall (Fig. 5) was 270 g m^{-2} year^{-1} with the lesser values for these dominant species ranging from 210 to 250 g m^{-2} year^{-1}. Though these values demonstrate the strength of a species presence on a site, mean total leaf fall for the 3-year period was 512 g m^{-2} year^{-1} with a minimum 1-year transfer of 423 g m^{-2} year^{-1}; thus, total leaf fall was the product of more than a single species. On the 10 plots, no single species, during the 3 years, accounted for more than 46% of total annual leaf fall (Table 2). The *L. styraciflua* and *Q. pagoda*, respectively, averaged 19.5 and

Table 2
Percentages of mean annual leaf fall transfers contributed by species and species groups

Species	Percent of total annual leaf fall		
	Mean	S.E.	Range
Liquidambar styraciflua	19.5	4.0	3.8–40.3
Quercus spp.	35.3	7.0	4.7–65.5
Q. pagoda	19.7	5.1	0.1–45.7
Q. nigra	9.5	2.4	0.1–23.2
Q. michauxii	4.3	1.5	0.1–16.4
Q. shumardii	1.8	1.0	0.0–9.3
Fagus grandifolia	7.7	3.1	0.1–33.6
Carya spp.	6.1	1.9	0.8–20.0
Carpinus caroliniana	5.7	0.8	2.0–11.2
Pinus taeda	3.5	1.8	0.0–18.1
Nyssa sylvatica var. *sylvatica*	2.1	1.0	0.1–10.5
Ilex opaca	2.1	0.8	0.0–8.0
Vines	2.1	0.3	0.7–3.7
Other species	5.1	1.1	1.0–11.3
Unidentified leaf fragments	10.8	0.9	8.1–15.4

Values are based on plot means, $n = 10$, for the 3-year study period.

19.7% of total leaf fall but respective ranges, across the study plots, were 3.8–40.3 and 0.1–45.7% (Table 2). Mean percentages and their ranges support the differences in species importance across the study area that were suggested by box and whisker plots (Fig. 5).

The dominant overstory species, during the 3-year period, accounted for 344 g m^{-2} $year^{-1}$ of leaf fall, approximately 68% of the total leaf fall (Fig. 6). The other overstory species (Fig. 6), although including leaves from as-many-as nine tree species, contributed a mean of only 34.5 g m^{-2} $year^{-1}$. Despite their obvious presence in stem numbers, the mid- and understory species contributed only, on average, 61.0 g m^{-2} $year^{-1}$ of leaf fall, or as little as 12% of total annual leaf fall. The unidentified leaf fragments accounted for 6% of total leaf fall in the first 2 years, but jumped to nearly 20% in the third year; although other species groups were impacted, the mean increase in unidentified fragments was primarily at the expense of leaf fall from the dominant overstory species (Fig. 6), especially *Carya* spp. (Fig. 4).

3.3. *Litterfall and stand attributes*

The preceding results illustrated variation among plots in leaf fall of given species or species groups. We found no significant relationship ($R^2 = 0.001$, $P < 0.866$) between total leaf fall and total basal area of the study plots. However, there was a solid positive relationship between the annual leaf fall of individual species, by plot and year, and their respective species basal areas (Fig. 7). Using a quadratic model, a significant relationship ($R^2 = 0.79$, $n = 332$; Fig. 7a) was found for all data points with >0.1 m^2 basal area ha^{-1} ($n = 332$). For the 11 species with highest mean leaf fall, a similar relationship was found between mean species-leaf fall and mean species-basal area ($R^2 = 0.96$, $n = 11$; Fig. 7b). In both analyses, the rate of increase in species leaf fall, with increasing species basal area, dropped sharply at the higher basal areas and was near zero at the maximum species basal area.

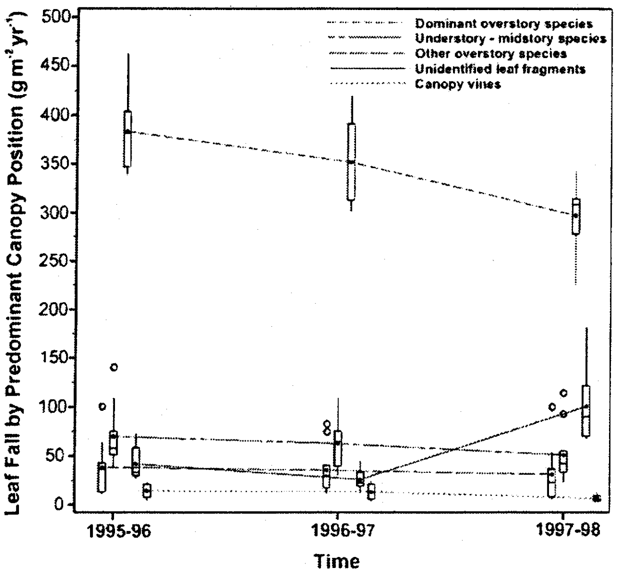

Fig. 6. Box and whisker plots of annual leaf fall transfers by canopy position or species groups for the three collection-years, $n = 10$. Within the box, the horizontal line marks the median for the entire data set. Whiskers extend from the box to the lowest and highest data points within 1.5-times the interquartile range. The outlier (○) data points are directly above their respective 1.5 interquartile ranges. Coded lines identifying the leaf fall groups, connect the mean annual transfer values (●). See Appendix A for list of species in each position. Components of box and whisker plots are outlined in greater detail in Fig. 3, caption.

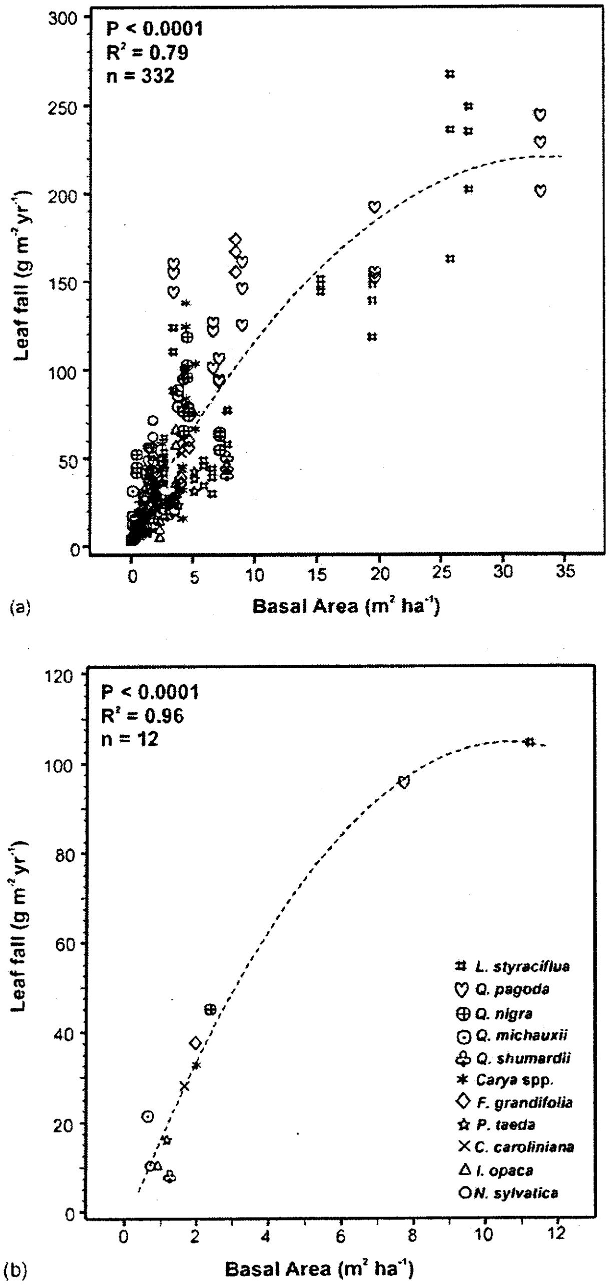

Fig. 7. Relationship between species annual leaf fall and the basal area of the species on a study plot. (a) Considers all species, plots, and years and (b) presents the mean leaf fall by mean basal area (all plots and years) for the dominant species. Each data point had at least 0.1 m^2 ha^{-1} basal area for the indicated species. The legend in (b) applies to both graphs. In (a), the '●' marks data points for the less common unlisted species.

Table 3
Relationships between annual total litterfall or litterfall components and stand attributes

Component = BAH × BAFrt × year		Litterfall component	Component = BAH × BAFrt × year	
Model: $R^2 = 0.50$, $P < 0.001$		Total litterfall	Model: $R^2 = 0.47$, $P < 0.003$	
BAH	<0.0007		BAH	<0.0009
$\mathrm{BAFrt}_{L.\ styraciflua}$	NS		$\mathrm{BAFrt}_{Quercus}$	NS
Year	<0.048		Year	NS
Model: $R^2 = 0.48$, $P < 0.021$		Non-(wood and bark)	Model: $R^2 = 0.47$, $P < 0.0024$	
BAH	< 0.0005		BAH	<0.0005
$\mathrm{BAFrt}_{L.\ styraciflua}$	NS		$\mathrm{BAFrt}_{Quercus}$	NS
Year	NS		Year	NS
Model: $R^2 = 0.79$, $P < 0.0001$		Leaf fall	Model: $R^2 = 0.82$, $P < 0.0001$	
BAH	<0.0001		BAH	<0.0001
$\mathrm{BAFrt}_{L.\ styraciflua}$	<0.0001		$\mathrm{BAFrt}_{Quercus}$	<0.0001
Year	<0.0003		Year	<0.0001
Model: $R^2 = 0.37$, $P < 0.018$		Reproductive structures	Model: $R^2 = 0.39$, $P < 0.011$	
BAH	NS		BAH	NS
$\mathrm{BAFrt}_{L.\ styraciflua}$	<0.006		$\mathrm{BAFrt}_{Quercus}$	<0.0033
Year	NS		Year	NS
Model: $R^2 = 0.52$, $P < 0.0007$		Fine-wood and bark	Model: $R^2 = 0.56$, $P < 0.0003$	
BAH	<0.050		BAH	<0.042
$\mathrm{BAFrt}_{L.\ styraciflua}$	<0.040		$\mathrm{BAFrt}_{Quercus}$	<0.013
Year	<0.001		Year	<0.0007

Model: litterfall = BAH × BAFrt × year. BAH = plot mean for the parameter tree basal area times height for all trees >30.5 m tall. BAFrt = decimal fraction of total stand basal area (trees >2.5 cm at DBH) occupied by the subscript-identified species or species group. Year refers to the class variable collection year. Litterfall components are as defined in the methods. NS = non-significant at the $P < 0.05$ level, $n = 30$.

Significant relationships were found between all litterfall components and stand parameters. The model: litterfall component mass = BAH × $\mathrm{BAFrt}_{dominant\ species}$ × year (Table 3) was significant for all litterfall components with R^2 ranging from 0.37 to 0.82 (Table 3 and Fig. 8), though model parameters differed in significance among litterfall components (Table 3). For annual total and non-woody litterfall the BAH parameter was significant, but we did not detect a significant relationship with BAFrt parameters, and the class variable year was only significant ($P < 0.048$) in the model: total litterfall = BAH × $\mathrm{BAFrt}_{L.\ styraciflua}$ × year. Total litterfall and non-woody litterfall both increased as the BAH factor increased (Fig. 8a and b). For leaf fall and fine wood all model parameters were significant. Leaf fall, with R^2 values of 0.79 and 0.82 (Table 3), increased with increasing BAH (Fig. 8c) and $\mathrm{BAFrt}_{L.\ styraciflua}$ (Fig. 9a), respectively, but declined with increasing $\mathrm{BAFrt}_{Quercus}$ (Fig. 9b). Fine wood increased with increasing BAH (Fig. 8d) and $\mathrm{BAFrt}_{Quercus}$ (Fig. 9e) but declined with increasing $\mathrm{BAFrt}_{L.\ styraciflua}$ (Fig. 9f). The model detected a significant but weak to moderate relationship ($R^2 = 0.37$ and 0.39) for mass transfers of reproductive structures, but only the BAFrt parameters were significant (Table 3). Reproductive mass increased with increasing $\mathrm{BAFrt}_{Quercus}$ (Fig. 9c) and declined with increasing $\mathrm{BAFrt}_{L.\ styraciflua}$ (Fig. 9d).

4. Discussion

4.1. Study site and forest stands

Variations in water table depths and short-duration flood events (Fig. 1) were as expected for minor alluvial-floodplains (Hodges, 1998). Higher soil water tables and more frequent flood events in January, February, and March reflected weather patterns during this period and antecedent soil moisture levels, both on the alluvial floodplain and the contributing watershed. Flood events, beyond initial weeks of the growing season, were minimal because of high evapotranspiration and resulting soil moisture draw-down in the watershed.

Because of watershed size, number and magnitude of flood events were relatively closely linked to annual variability in local weather patterns (Fig. 1). In the winter preceding the litterfall study, field crews were forced out of the study area by floods no-fewer-than five times. These floods were of short duration, with major overbank flooding lasting 5 days or less. In contrast, during the first winter of the litterfall study, though soils were moist, there was no flood event and soil water tables were not near the surface. In subsequent winters, water tables were often near the surface and there were flood events; however, the higher flooding frequency that we encountered while establishing the Iatt Creek study area was not repeated.

The predominant forest stand types of the Iatt Creek study site are representative of minor bottoms in the Southeastern USA. Dominant litterfall species (Figs. 4 and 5) have been classified as intermediate (e.g., *L. styraciflua*, *Q. nigra*) to intolerant (e.g., *Q. michauxii*, *Q. pagoda*, *N. sylvatica* var. *sylvatica*) of more than brief periods of inundation (Hodges, 1994; Meadows and Stanturf, 1997). Gemborys and Hodgkins (1971), working with small-stream bottoms in the Coastal Plain province of southwestern Alabama, developed a moisture-regime index for species that agrees well with the species found in our study plots (Fig. 4 and Appendix A). Similarly, applying a five-zone classification of wetlands (Wharton et al., 1982;

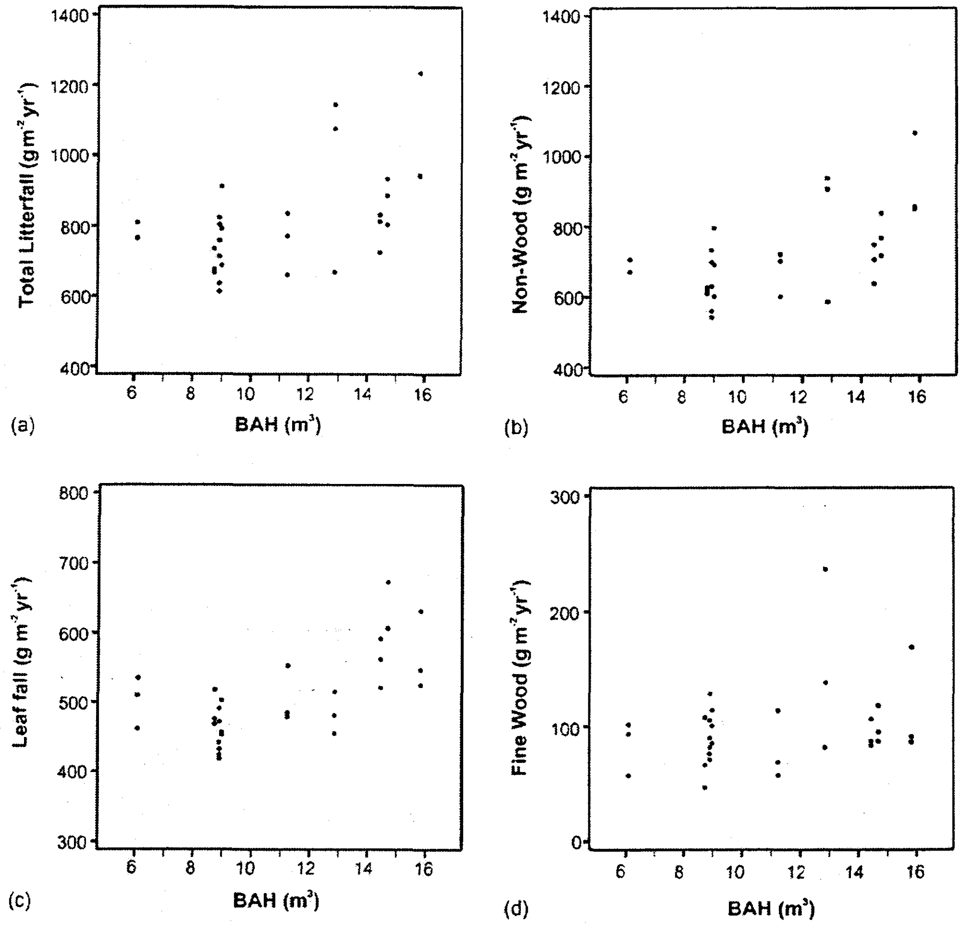

Fig. 8. Relationships between yearly total litterfall or litterfall components and stand size parameter, BAH. As defined in the study methods and noted in Table 3, for each plot, BAH is the mean of the product, individual tree BAsal area times total tree height for all trees >30.5 m tall.

Conner et al., 1990; Taylor et al., 1990) to the Iatt Creek study area places the study site primarily in zone V (e.g., *Q. pagoda*) with some forest in the more hydric zone IV (e.g., *L. styraciflua*) (Conner et al., 1990). The four zones, applicable to wetland forests (II–V), are based on a flooding or "anaerobic" gradient (Conner et al., 1990). Zone IV typically has inundation or saturation from 1 to 2 months of the year, usually during the winter but extending into the growing season. Zone V is described as having flooding for only brief periods during the growing season and water table dropping well below the surface by late summer, a condition apparent in our study area (Fig. 1).

4.2. Annual litterfall transfers

For the 3-year study period, annual litterfall, for Iatt Creek study plots, averaged 817 g m^{-2} year^{-1} (range 687–1040 g m^{-2} year^{-1} among plots) (Fig. 3), 48% above the global mean (550 g m^{-2} year^{-1}) for warm-temperate forests reported by Bray and Gorham (1964) and 68% above the mean (487 g m^{-2} year^{-1}) for warm-temperate broadleaf deciduous forests reported by Vogt et al. (1986). These reviews included few, if any, wetland forests from the Southeastern USA. Mean total litterfall in the Iatt Creek study was 83% above the mean (446 g m^{-2} year^{-1}, range 63–724 g m^{-2} year^{-1}, $n = 34$) for the natural wetland-forests summarized by Conner (Conner et al., 1990; Conner, 1994); however, these forests, although in the Southeastern USA, included primarily deep-water swamps and major alluvial-floodplains. The Iatt Creek study was 43% above mean total litterfall (570 g m^{-2} year^{-1}, range 422–720 g m^{-2} year^{-1}, $n = 13$) for a group of wetland forests that included less hydric sites (Brinson et al., 1980; Brown and Peterson, 1983; Shure and Gottschalk, 1985; Conner et al., 1993; Jones et al., 1996; Burke et al., 1999) and 49% above the mean (548 g m^{-2} year^{-1}, range 336–902 g m^{-2} year^{-1}, $n = 21$) for a cross-section of Southeastern USA hardwood and coniferous forests compiled by Clawson et al. (2001). Comparing the above means and ranges it was evident that, on average, total litterfall in the Iatt Creek study area was high, but the overlap in ranges showed our estimates were within reason.

4.3. Litterfall components

In mature forests, total litterfall is a dominant parameter in the estimation of net primary productivity and a basic measure of material entering the detritus pathway. Still, total annual litterfall, considered alone, can obscure similarities and

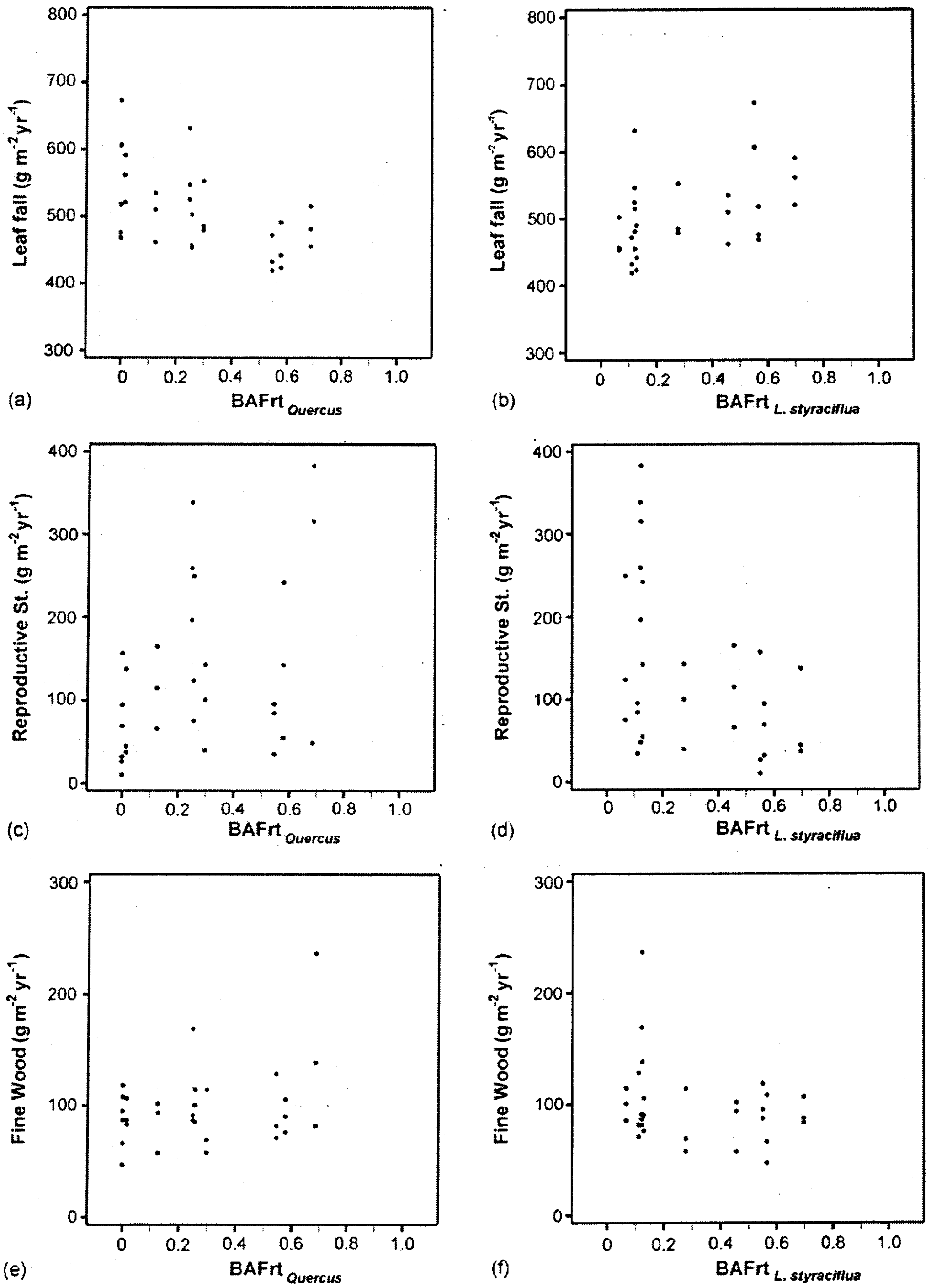

Fig. 9. Relationships between annual transfers of leaf fall, reproductive structures, fine-wood and bark and the factors $\mathrm{BAFrt}_{Quercus}$ and $\mathrm{BAFrt}_{L.\ styraciflua}$, the decimal fractions of total plot basal area accounted for by *Quercus* spp. and *L. styraciflua*, respectively.

differences among stands. In our study, although leaf fall (Fig. 3) accounted for the majority of total litterfall it was not the primary cause of variability in litterfall among plots; transfers of reproductive structures and the fine-wood and bark component were more variable (Fig. 3).

Studies of wetland forests have identified up to 15 litterfall components (e.g., Brinson et al., 1980; Jones et al., 1996; Megonigal et al., 1997) with choice of components reflecting research objectives, the known, expected, or assumed significance of specific components, and pragmatic limits of what can be sorted. In Iatt Creek, we sorted litterfall into five components: leaf fall, fine-wood and bark, reproductive structures, fine debris, and animal detritus. As noted earlier, the fifth component, animal detritus, was consistently at trace levels. The four significant components averaged 512, 98, 130, and 77 g m^{-2} $year^{-1}$, respectively, and accounted for, respectively, 63, 12, 16, and 9% of total litterfall. By comparison, for seven wetland-forest stands, whose litterfall components could be similarly grouped, component transfers averaged 481, 112, 51, and 33 g m^{-2} $year^{-1}$, respectively, and 71, 16, 8, and 5% of total transfers (Bell et al., 1978; Brinson et al., 1980; Gomez and Day, 1982). Leaf fall, in both, is the major single component of total litterfall. However, in the Iatt Creek study, although average total litterfall (817 g m^{-2} $year^{-1}$) was 140 g m^{-2} $year^{-1}$ (21%) higher than the mean (677 g m^{-2} $year^{-1}$) of the above seven stands, leaf fall averaged only 31 g m^{-2} $year^{-1}$ (6%) higher. Examining the non-leaf fall components, fine-wood and bark litterfall in the Iatt Creek study averaged 13% or 14 g m^{-2} $year^{-1}$ below the mean of the seven cited forests whereas average reproductive litterfall and fine debris transfers were, respectively, 2.5- and 2.3-times or 79 and 44 g m^{-2} $year^{-1}$ greater in our study. Net differences in non-leaf components accounted for 78% of the difference in total litterfall means.

Comparing stands in which litterfall had been divided into at least leaf and non-leaf litterfall components does not alter the above pattern. For 17 bottomland forests, litterfall and leaf fall means were, respectively, 684 and 502 g m^{-2} $year^{-1}$ with leaf fall accounting for an average of 74% of total litterfall (Bell et al., 1978; Brinson et al., 1980; Gomez and Day, 1982; Brown and Peterson, 1983; Shure and Gottschalk, 1985; Cuffney, 1988; Clawson et al., 2001). Mean total litterfall in Iatt Creek averaged 19% higher than the above mean total litterfall, but mean leaf fall (512 g m^{-2} $year^{-1}$) was similar to the above leaf fall mean. Leaf fall in the 17 stands ranged from 58 to 85% of total litterfall (S.D. 8.6%). The potential importance of the non-leaf fall transfers again appeared evident.

Megonigal et al. (1997), for 32 wetland-forest stands, divided litterfall into woody and non-woody components and equated "leaf litter" to all non-woody litter assuming that "flowers, fruits, and seeds, typically account for <10% of all non-woody litterfall total." Stands were classified as wet ($n = 9$), intermediate ($n = 17$), or dry ($n = 6$), based on water-table depth during the growing season. Mean non-woody transfers for the wet, intermediate, and dry sites were 429, 688, and 716 g m^{-2} $year^{-1}$, respectively. Accepting the assumption that 90% of non-woody litterfall is leaf fall, then mean leaf fall at Iatt Creek was higher than on their wet sites and well below the means for intermediate and dry sites. If, conversely, the comparison is based on a literal interpretation of sorting guidelines the average non-woody litterfall in the Iatt Creek site, 719 g m^{-2} $year^{-1}$, is slightly above the high mean of the drier wetland-forests which have water table depths similar to our stands. These comparisons again illustrate that components other than leaf fall are significant components of litterfall and better drained or drier bottomland forests are often more productive.

The noted high transfers of reproductive structures (130 g m^{-2} $year^{-1}$) appear reasonable for our study site and species. Comparing annual transfers of reproductive mass, Brinson et al. (1980) reported a 2-year average of 100 g m^{-2} $year^{-1}$ in reproductive structures within a *N. aquatica* dominated forest. Peterson and Rolfe (1982) measured a reproductive mass transfer of 179 g m^{-2} $year^{-1}$ in a good seed-year in an *Acer saccharinum* Marsh. dominated stand. Pregitzer and Burton (1991) found, for five mature *A. saccharinum* dominated stands, mean reproductive litterfall was 89.2 g m^{-2} $year^{-1}$, with a range of 30.6–161.7 g m^{-2} $year^{-1}$ that accounted for 6.2–33.8% of total litterfall (Pregitzer and Burton, 1991). Bell et al. (1978) reported reproductive masses increased from 48 g m^{-2} $year^{-1}$ in a floodplain *A. saccharinum* forest to 135 and 192 g m^{-2} $year^{-1}$ in respective transitional and upland stands; increases were credited to increasing dominance of heavy-seeded *Q. umbricaria* Michx., *Q. alba* and *Carya* spp. and improved internal soil drainage. Similarly, Clawson et al. (2001) reported that mass of reproductive structures and its fraction of total litterfall increased on a moisture gradient in a bottomland hardwood forest, moving from poorly to intermediate and somewhat poorly drained soils. In their study, basal area of *Quercus* spp. increased from 5% of total in the poorly drained site to 51 and 68% of total basal area in the intermediate and somewhat poorly drained sites, respectively (Clawson et al., 2001).

For 2 years, in the Iatt Creek plots, we found a significant relationship between reproductive mass transfers and plot basal area of *Quercus* and *Carya* species (Fig. 10). There was not a significant relationship in the third year when mean reproductive mass was lowest, and plots, with the highest *Quercus* and *Carya* basal areas, transferred below average masses of reproductive structures (Fig. 10). High reproductive mass transfers of 300–400 g m^{-2} $year^{-1}$ (Fig. 10) for the highest individual plots appear plausible as compared to acorn yields in good seed-years for the upland oaks *Q. rubra* L. and *Q. alba* L. (Beck, 1977). We acknowledge that the high annual transfers, in

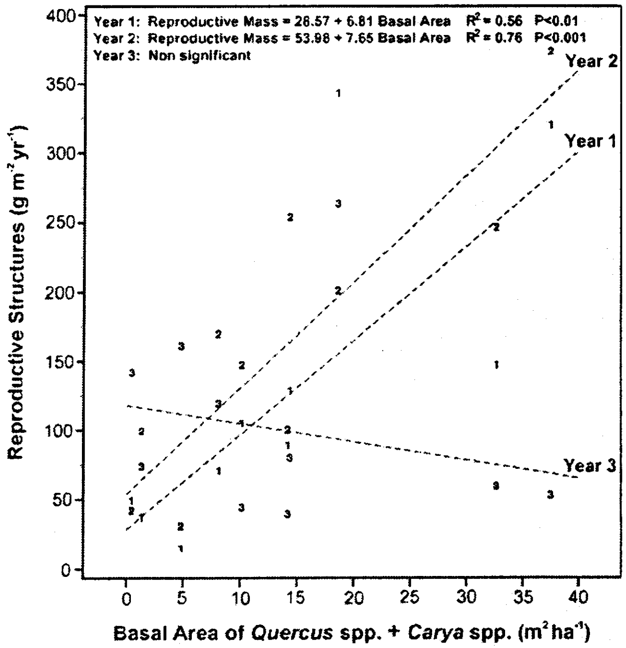

Fig. 10. Variation among years in relationships between the annual mass transfers of reproductive structures and combined stand basal areas of *Quercus* spp. and *Carya* spp. within the Iatt Creek Study area. Data points marked by collection years.

some plots and sample years, may partially reflect a chance higher estimate caused by the clustered temporal dispersal patterns of these relatively heavy fruits (Gomez and Day, 1982); however, it appears that our sampling methods did detect differences between species among years (Fig. 10). Moreover, if chance placement and limited numbers of litterfall collectors did result in higher estimates of reproductive structures in some plots and collection years, they also likely resulted in lower estimates in other plots and collection years; therefore, the mean transfers of reproductive structures for the study area are reasonable.

It may seem odd we did not detect a significant collection year effect (Table 3) for annual transfers of reproductive structures (Fig. 10). Though average reproductive mass differed numerically among years, the plots did not all show the same relative pattern of reproductive mass transfer across the three collection-years (Fig. 10). The lack of consistency in relative mass production across all plots may reflect species differences among plots as well as variation among individual trees within the same species and stand in their individual, year-to-year, seed production patterns (Beck, 1977; Greenberg, 2000).

Our results suggest that reproductive mass, although difficult to quantify, potentially plays a significant role in material transfers and net primary productivity in bottomland hardwood forests. This potential is increased for stands dominated by mature trees of heavy-fruited genera such as *Quercus* and *Carya* (Fig. 10). Anecdotal evidence for Southeastern bottomland hardwoods does suggest that fruiting is more regular than reported for upland species and sites (e.g., Beck, 1977; Healy et al., 1999; Greenberg, 2000); for example, we observed that *Carya* spp. and to a lesser extent *Q. nigra* produced significant mass of reproductive structures on a near annual basis.

It is important to recognize that yearly significant mass transfers of reproductive structures are not in conflict with the reported cyclic or erratic occurrence of heavy seed or regeneration crops in *Quercus* and other hardwoods. When focused on regeneration or seed production, only mature viable seeds are counted; if weighed, non-viable seed, acorn caps, cones, husks, and flowering structures are excluded from estimates of seed production (Beck, 1977; Greenberg and Parresol, 2000).

Litterfall's fine debris vary with age and species composition of the forest, season, rainfall amounts and intensities, mesh size of collector screens, and protocols for laboratory sorting. Two peaks occurred in our study; the spring peak in fine debris (Fig. 2) generally reflected transfer of bud scales and fragments of flowering structures but was also affected by the leaf herbivory and associated frass and fragment production by *Heterocampa manteo* (Doubleday) and other insect larvae. Having two generations in Southeastern hardwood forests, *H. manteo* larvae produced significant frass in March and April, shortly after bud burst, and again in late summer and autumn (September and October, Fig. 2). In addition to frass, fine debris transferred in the autumn contained fine bark and other debris seemly related to leaf senescence, seed dissemination, and return of intense rain storms after a common period of dry weather in late summer.

Rates of woody litterfall (fine-wood and bark) in the Iatt Creek stands, like fine-debris transfers, reflected biological and environmental factors and the study's collection and sorting protocols. Mean fine-wood and bark transfer was slightly lower in the Iatt Creek study than the mean of the seven wetland-forest stands noted above (Bell et al., 1978; Brinson et al., 1980; Gomez and Day, 1982). In part, the lower transfer was likely due to our exclusion of branches with a maximum diameter >1 cm. Larger-diameter transfers were measured in a separate study and are not reported here.

In litterfall the significance of large-diameter wood depends on the species present, tree maturity and size, and storm events during the study period. Peterson and Rolfe (1982) reported leaf fall dropped to 35% of total litterfall for 1 year because of a two-fold increase in branchfall caused by an ice storm, as well as a large spring-seed-crop. The following year, the leaf fall percentage returned to the more expected 70%. Conner and Day (1976) noted the impact of a hurricane on litterfall, but in a later study reported no relationship to storm patterns in a 4-year study within three wetland-forests (Conner and Day, 1992). The limitations in measuring large-diameter debris in collectors designed for leaf fall were recognized by Conner et al. (1993) when they noted that one large limb, falling across two leaf fall collectors, doubled their annual estimate of woody litterfall.

4.4. Litterfall seasonal patterns

We noted two peaks in litterfall transfers, the small spring peak in March and April and the dominant autumn–winter transfer period from late August through early January. We have considered the timing and magnitudes of leaf fall for an array of species and species groups (Fig. 4). The late November period of peak total leaf fall reflects the maximum transfer rate for *Quercus* species and a high rate for *L. styraciflua*, which reached a peak transfer rate in early to mid-November (Fig. 4). Due primarily to the high rates of transfers by the several *Quercus* species, leaf fall remained high through December, then declined sharply from late December to early January. Leaf fall by *L. styraciflua* exceeded that of *Quercus* from August through October, before the two species began their peak period of transfer in November. The somewhat protracted leaf fall period and heavier early leaf fall transfers of *L. styraciflua* may be related to morphological and physiological differences between its early leaves, which are preformed in the terminal bud, and late leaves that are formed from primordia laid down later in the growing season during sustained growth (Zimmermann and Brown, 1971; Brown and Sommer, 1992). Alternatively, the litterfall pattern of *L. styraciflua* may reflect differences between sun and shade leaves or a response to autumn drought stress.

Other studies in Southeastern USA bottomland forests have similarly illustrated the effect of species composition on timing of leaf fall. Brinson et al. (1980) found that within a mature alluvial-swamp forest with leaf fall dominated by *N. aquatica* (96%), leaf fall began in August and reached a maximum in October; less than 15% of total leaf fall occurred in November. In our study (Fig. 4), *N. sylvatica* var. *sylvatica*, along with the vine species group, were among the first species to begin dropping leaves, with transfers essentially completed by the end of October. Shure and Gottschalk (1985) found that the period of autumn leaf fall was more protracted; transfer rates peaked later as one moved from forests dominated by *Fraxinus pennsylvanica* and *N. sylvatica* var. *biflora* to stands that, in a manner somewhat similar to ours, were dominated by *L. styraciflua* and *Q. nigra*. Conner and Day (1992) and Lockaby and Walbridge (1998) similarly noted that the autumn period of litterfall began in September and ended in January, but *Nyssa* spp. lost their leaves early and *T. distichum* much later. Conner and Day (1992) also noted that on slightly less hydric sites, *A. rubrum* and *Fraxinus* spp. were more common than *N. aquatica* and the first species to drop leaves.

Leaf fall from numerous overstory species contributed relatively small amounts to the spring peak. The potential impact of succession and increased dominance of broadleaf evergreen species on timing of litterfall transfers is suggested by *I. opaca*, which was the dominant single species in the spring leaf fall period. At present, *I. opaca* and *Symplocos tinctoria* (L.) L'Her. are the most common broadleaf evergreens in the under- and mid-story layers with *M. grandiflora* L. less common, but occurring in all canopy positions. If our bottomland forest remains undisturbed and develops into a shade-tolerant *F. grandifolia–M. grandiflora* community, then late-spring leaf fall, the normal period of leaf senescence for *M. grandiflora*, would become more significant, if not a dominant period of litterfall. Similarly, the timing of reproductive mass transfers could be affected by changes in species composition. *Acer rubrum* is a common understory and mid-story species in our study and a dominant component of some wetland forests (Peterson and Rolfe, 1982; Brown and Peterson, 1983; Mitsch et al., 1991). A shift from dominance by *Quercus* and *Carya* species to *A. rubrum* could lead to a shift from autumn to spring peaks in transfer of reproductive litterfall.

An area's climate and frequent or infrequent weather events such as freezing weather, hail, drought, severe winds, hurricanes or ice storms influence the timing and duration of litterfall. For example, between year differences in time of the first severe freeze altered overall leaf fall timing and transfer rates in a riverine bottomland forest in Illinois (Bell et al., 1978). In the Iatt Creek study area's humid subtropical climate, the timing of spring and autumn litterfall peaks appears more in synchrony with changes in day length, warmer or cooler temperatures, and associated physiological processes than freezing weather events (Kozlowski and Pallardy, 1997). Nevertheless, the 50% probability for the first severe autumn freeze (−2.2 °C) is late November (Vega et al., 1994), which coincides with the peak autumn period of leaf fall (Fig. 2) and the 50% probability for the last spring freeze (0.0 °C) is mid-March, near the initiation of flowering and bud burst. In our study area, late spring freezes are known to damage or destroy flowers and associated seed crops but seldom do severe damage to foliage and terminal buds. The increased fine debris and fine branch fall during the spring (Fig. 2) appear related to high intensity storms common to the area during this period (e.g., Rice et al., 1997).

4.5. Annual leaf fall transfers by species

The observed variability in the species composition of total leaf fall was a reflection of the species richness within plots and variation in species composition among study plots (Figs. 3 and 5 and Table 2). As previously noted, the two dominant species, *L. styraciflua* and *Q. pagoda* averaged, respectively, 19.5 and 19.7% of total leaf fall and ranged from less than 5 to 40.3 and 45.7%, respectively. Contributions of multiple species to leaf fall appear common in bottomland sites that are mesic but not inundated for prolonged periods and not inundated well into the growing season (Dabel and Day, 1977; Brinson et al., 1980; Conner et al., 1993). Forests that are inundated for prolonged periods may illustrate the opposite extreme. For example, Brinson et al. (1980) reported that a 30-year-old alluvial-swamp forest was dominated by the inundation tolerant *N. aquatica*, which accounted for 96% of all leaf fall. Although this high level of single species dominance may be extreme, it is not uncommon to see leaf fall dominated by *N. aquatica* or *N. sylvatica* var. *biflora* and *T. distichum* in deep-water wetlands (Lockaby and Walbridge, 1998; Clawson et al., 2001; Busbee et al., 2003).

Considering species groups or genera, less inundated forests also may exhibit dominance by single species or an association of similar species; Gomez and Day (1982) noted that leaf fall in four communities within the Great Dismal Swamp (VA, NC, USA), was dominated by *Quercus* spp. that accounted for 72–75% of total leaf fall transfers. Other associated species included *P. taeda*, *Carya* spp., *F. grandifolia*, *N. sylvatica* var. *sylvatica*, *I. opaca*, and *C. caroliniana*. In the Iatt Creek plots, *Quercus* spp. together accounted for as much as 65.5% of total annual leaf fall, but reflecting the diversity seen among plots, also dropped to as low as 4.7% with a mean of only 35.3% (Table 2).

The lack of understory development is relatively common for deep-water swamps (e.g., Brinson et al., 1980). Yet, even within swamp forests, a mid- or understory may develop on ridges and transition sites and contribute to leaf fall (Conner et al., 1981); Conner et al. (1993) report that 40% of leaf fall came from flood-tolerant shrub species on one such site. Though not of comparable flooding tolerance, species within the Iatt Creek study that we classified as being predominantly in the mid- and understory layers accounted for about 12% of total leaf fall (Fig. 6). In our study area, the contribution of understory species to leaf fall appears to reflect a balance between a mature dense overstory and the presence of canopy gaps caused by tree mortality, sloughs, and stream channels.

4.6. Relationships with stand parameters

The lack of significant relationship between total leaf fall and total stand basal area was noted in our results and is as expected. In closed canopy stands, basal area alone is generally not a good estimate of leaf area (Waring and Schlesinger, 1985). Stand leaf area and resulting annual leaf fall normally reach a maximum at crown closure and, barring major disturbance, remain at a quasi-equilibrium through the stand's life span, in balance with a site's water balance or other limiting factor (Waring and Schlesinger, 1985).

The significant relationships between a species's annual leaf fall and its basal area (Fig. 7a and b) support this interpretation. For an individual species (Fig. 7a), the initial steep rise in annual leaf fall with increasing species basal area is a measure of that species presence in the community. When a species has a relatively high basal area and associated leaf fall on a plot, then the influence of site water balance on closed canopy leaf area becomes evident. Within this high species basal area region, increases in individual species basal areas would normally be associated with modest to negligible increases or decreases in annual species leaf fall.

We used the BAH factor (Table 3) as a stand or community size parameter, which appeared reasonable because the study plots were of similar age, well-stocked, and dominated by broadleaf deciduous species. Total litterfall transfers and most components of litterfall increased as the BAH factor increased (Table 3 and Fig. 8) suggesting higher litterfall is part of a larger more productive deciduous hardwood site. The patterns of decreasing leaf fall with increasing oak dominance (i.e., greater $\mathrm{BAFrt}_{Quercus}$; Fig. 9a and c) and increasing leaf fall with increasing $\mathrm{BAFrt}_{L.\ styraciflua}$ might be a reflection of *L. styraciflua* occupying the better sites. However, we found no relationship between BAH and either BAFrt factor, which suggests that the increasing $\mathrm{BAFrt}_{Quercus}$ was perhaps reflecting a more open and diverse stand or, alternatively, the differences in leaf fall might be due to differences in growth and leaf production (carbon allocation) by *Quercus* species as compared to *L. styraciflua*. Most *Quercus* species exhibit a burst of growth in the spring producing leaves preformed in the year's terminal bud and then form another over-wintering terminal bud. In contrast, *L. styraciflua* follows a similar burst of growth and expansion of preformed leaves by typically entering a second period of growth in which neoformed leaves are produced (Zimmermann and Brown, 1971; Brown and Sommer, 1992). This allows *L. styraciflua* to have a prolonged period of leaf production and potentially for the stand to have a higher annual leaf fall as the $\mathrm{BAFrt}_{L.\ styraciflua}$ within the stand increases.

The BAH factor was not significant in the estimation of reproductive mass; this was not unexpected due to the differences in mass of reproductive structures produced by different species or species groups (Table 3). The increase in mass of reproductive transfers with increasing $\mathrm{BAFrt}_{Quercus}$ and decreasing $\mathrm{BAFrt}_{L.\ styraciflua}$ (Fig. 9c and d) is also consistent with differences in the reproductive structures normally produced by these species. The winged seeds of *L. styraciflua* are very small and the mature dry capsule (3–4 cm diameter) is mostly hollow and not nearly the individual mass or density of *Quercus* spp. fruit, cap, and husk. In a normal seed year, differences in number of seeds produced would not easily negate these differences (Kormanik, 1990; Olson, 1974).

5. Summary

Total litterfall and leaf fall transfers within the studied mature bottomland hardwood forest are at the high end of reported annual transfers for bottomland forests and, in general, temperate deciduous forests. Leaf fall, reflecting the winter flash flooding regime of a minor alluvial-floodplain, has a greater diversity of contributing species than deep-water swamps and other bottomland forests flooded well into the growing season. The temporal pattern of leaf fall reflects the phenology of the species present and the forest environment. Variations in annual litterfall and litterfall components across the study area were significantly related to apparent site quality and dominance of a species or genus group. Although leaf fall is the dominant single component of litterfall, the potential contribution of other components, specifically mass of reproductive structures, is also evident. In minor alluvial-bottoms, mass transfers of reproductive structures appear higher and more consistent than reported for many upland forests, especially for stands dominated by heavy-seeded genera such as *Quercus* and *Carya* species. A higher reproductive mass is not in conflict with the reported infrequency of good "seed" or "reproduction" years in bottomland forests; mass transfers of reproductive structures include far more than nuts and viability varies greatly among years and species. Spatial diversity and temporal patterns of litterfall reflect species composition and may change according to successional or disturbance trends, climate change, or both.

Acknowledgments

We gratefully acknowledge the support of staff from Center for Bottomland Hardwoods Research, especially, Kristi Wharton, Al Brazzel, Kenney Caraway, Melissa Breland, Angelia DeLaughter, Heidi Whitlach, Billy H. McDonnieal (deceased), and Mike Worsham. We thank the Kisatchie National Forest and especially the staff of the Winn Ranger District for their positive attitude, cooperation, and support. Their actions and supportive attitudes were critical to the success of this study and remain a positive aspect of our continuing research. The constructive reviews of Tom Dell, Brian Lockhart, Dave Haywood, Margaret Devall, and two anonymous reviewers added significantly to this manuscript. With regard to Billy McDonnieal, his field expertise and leadership, sense of humor, well-delivered one-liners, patience, and sometimes exasperating mind-set were critical to the initial layout of much of this study area. He is remembered with respect and a smile. This research was supported by the USDA, Forest Service, Southern Research Station with additional support from the USGS, Biological Sciences Division.

Appendix A

Leaf fall species found in litterfall collections made in the bottomland hardwood forest within the Iatt Creek Study Area. For tree species, canopy position refers to the vertical canopy position in which a species was most commonly found. The overstory species were also classified according to how common or dominant a species was. The less common were termed "other overstory".

Appendix A (*Continued*)

Scientific name	Predominant canopy position			
	Dominant overstory	Other overstory	Midstory–understory	Canopy vine
Acer rubrum L.			x	
Anisostichus capreolata (L.) Bureau				x
Arundinaria gigantea (Walter) Muhl.			x	
Asimina triloba (L.) Dunal			x	
Berchemia scandens (Hill) K. Koch				x
Carpinus caroliniana Walter			x	
Carya spp.	x			
Celtis laevigata Willd.			x	
Cornus florida L.			x	
Fagus grandifolia Ehrhart	x			
Fraxinus pennsylvanica Marshall		x		
Gleditsia triacanthos L.		x		
Halesia diptera Ellis			x	
Hamamelis virginiana L.			x	
Ilex decidua Walter			x	
Ilex opaca Aiton			x	
Liquidambar styraciflua L.	x			
Lonicera japonica Thunberg				x
Magnolia grandiflora L.			x	
Melia azedarach L.			x	
Nyssa sylvatica var. *sylvatica* Marshall		x		
Ostrya virginiana (Miller) K. Koch			x	
Parthenocissus quinquefolia (L.) Planchon				x
Pinus taeda L.	x			
Platanus occidentalis L.		x		
Prunus caroliniana Aiton			x	
Prunus serotina Ehrhart			x	
Quercus michauxii Nuttall	x			
Quercus nigra L.	x			
Quercus pagoda Raf.	x			
Quercus shumardii Buckley	x			
Smilax spp. L.				x
Symplocos tinctoria (L.) L'Her.				
Taxodium distichum (L.) Richard			x	
Tilia americana L.		x		
Toxicodendron radicans (L.) Kuntze				x
Ulmus americana L.			x	
Ulmus alata Michaux			x	
Vitis rotundifolia Michaux				x
Vitis spp.				x
Vines other				x

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