

A COMPARISON OF LITTER PRODUCTION IN YOUNG AND OLD
BALDCYPRESS (*TAXODIUM DISTICHUM* [L.] STANDS
AT CADDO LAKE, TEXAS

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Abstract.—Aboveground primary productivity for cypress forests was assessed from measurements of litter production in two age groups and in two hydrological regimes (standing water and free-flowing). Caddo Lake, located in northeast Texas on the Texas-Louisiana border, offered a unique study site since it is dominated by extensive stands composed entirely of *Taxodium distichum* (L.) Rich. (baldcypress) in different age groups. Young stands (approximately 100 years old) are found along the shoreline and on shallow flooded islands. Old stands (~150 to 300 years old) are found in deeper water where they were continuously flooded. Litter production over three years from October 1998 to September 2001 was measured. Litter consisting of leaves, twigs, bark, reproductive parts, and *Tillandsia usneoides* (L.) L. (Spanish moss) was collected monthly using 0.5 m² floating traps. Tree diameters were measured within 200 m² circular plots in each stand. The young stands supported densities greater than 2,000 stems/ha and a mean stand basal area of 72.3 m²/ha, whereas old stands supported lower densities of about 500 stems/ha but with a similar mean stand basal area of 73.3 m²/ha. There was a significant difference between old and young stands for overall yearly litter production, averaging about 670 g/m²/yr in the young stands and 460 g/m²/yr in the old stands. Leaves and twigs were significantly greater in the young stands, while reproductive parts were higher in old stands. Litter collections between years or hydrological regimes were not significantly different.

Litter production is useful in ecological assessments of ecosystem function and health for determining the aboveground primary productivity. Primary productivity may be influenced by factors such as hydrological regime and nutrient content, where productivity was compared for bottomland forests in stagnant floodwaters or long-term inundated areas and forests in free-flowing or seasonally-flooded areas. Productivity, litter production, and nutrient levels were associated as functions of differences in flooding regime (Conner et al. 1981; Gomez & Day 1982). Diverse

Florida cypress systems subjected to various water flows and nutrients were examined in Brown (1981) and compared with other studies; nutrient-enriched cypress domes in still water had higher productivity than flowing water stands. Specific stem densities and basal areas are not necessarily associated with certain hydrological regimes. Brown et al. (1979) showed high stem densities and basal areas associated with inundated areas. Gomez & Day (1982) reported the converse where litter production in frequently-flooded stands at Dismal Swamp, Virginia, exceeded other periodically flooded or stagnant water ecosystems, such as the flowing water (periodically flooded) ecosystems of Lac des Allemands Swamp in Louisiana (Conner & Day 1976; Conner et al. 1981), very-slowly flowing cypress ecosystems at Okefenokee Swamp, Georgia (Schlesinger 1978) or in Illinois (Mitsch et al. 1977), and seasonally-flooded alluvial swamps in North Carolina (Brinson et al. 1980). Mitsch et al. (1991) likewise ascertained a definite pattern of progressively higher to lower litter production along a light-to-heavy flooded gradient in Kentucky. Litter production was also greater in a regularly drained crayfish pond and natural swamp area than in an impounded area at Barataria Basin, Louisiana (Conner & Day 1992). Brown & Peterson (1983), however, reported no significant differences in litter production for mixed-species bottomland forests in Illinois for flowing water and in stagnant floodwaters.

Past studies focused on hydrological regimes and they were conducted in mixed-species forests of undetermined age or of predominantly old or young growth stands only. Conner & Day (1976) suggested that maturity of trees may be a factor influencing overall biomass productivity or litter production. They studied two highly-diverse ecosystems of second-growth young stands of less than 30 years for the bottomland hardwoods (23 woody species) and between 50 and 95 years old for cypress swamps (nine woody species). The standing biomass of cypress swamps was twice that of younger bottomland hardwoods. Although average litter production was not significantly different between these two

ecosystems, Conner & Day (1976) observed that the sparse, larger trees of the cypress swamp yielded more litter than dense younger bottomland hardwoods collectively.

In addition, the mixed forest species stands in these studies can influence overall stand litter production. Stands with multiple species were noted in Conner & Day (1976), but litter was not differentiated by species in their study. Litter was sorted by species groups in Brown (1981) and Deghi (1977). Gomez & Day (1982) offer a comprehensive separation of litter production by four to six dominant species in four forest types at the Great Dismal Swamp, Virginia, that included a cypress swamp. Since dissimilar species will exhibit different litter production phenologies (Burns & Honkala 1990a; 1990b), the monthly or yearly patterns of overall stand litter production can be subsequently affected. Thus, a selection of forest stands with fewer species may help control for confounding litter production effects of diverse species.

A monotypic tree species ecosystem would aid research to examine the influence of multiple species on primary litter production. Furthermore, ecosystems with discrete age stands would allow maturity of stands to be also studied as a factor in litter production. Caddo Lake is a naturally-occurring permanent lake of 10,200 ha in Texas (Fig. 1), and is a locale uniquely dominated by baldcypress (*Taxodium distichum*) with different age stands. There are distinct water depth areas present in the lake that include deep water (>1.5 m) without baldcypress, deep water (1–1.5 m) with older baldcypress stands, and shallow water (<0.5 m) with baldcypress stands. Most of Caddo Lake was formed by the “Great Raft”, a 266-km log jam on the Red River and Atchafalaya River. The Great Raft accreted around 1100 AD and was cleared by Henry Shreve from 1832 to 1839 (Triska 2008). Presently, the water level at Caddo Lake is controlled by a weir (66.3 m MSL), constructed in 1971 on the Louisiana side of the lake. Water levels are also affected by releases from Lake O’ the Pines reservoir, located about 26 km upstream on Big Cypress Bayou.

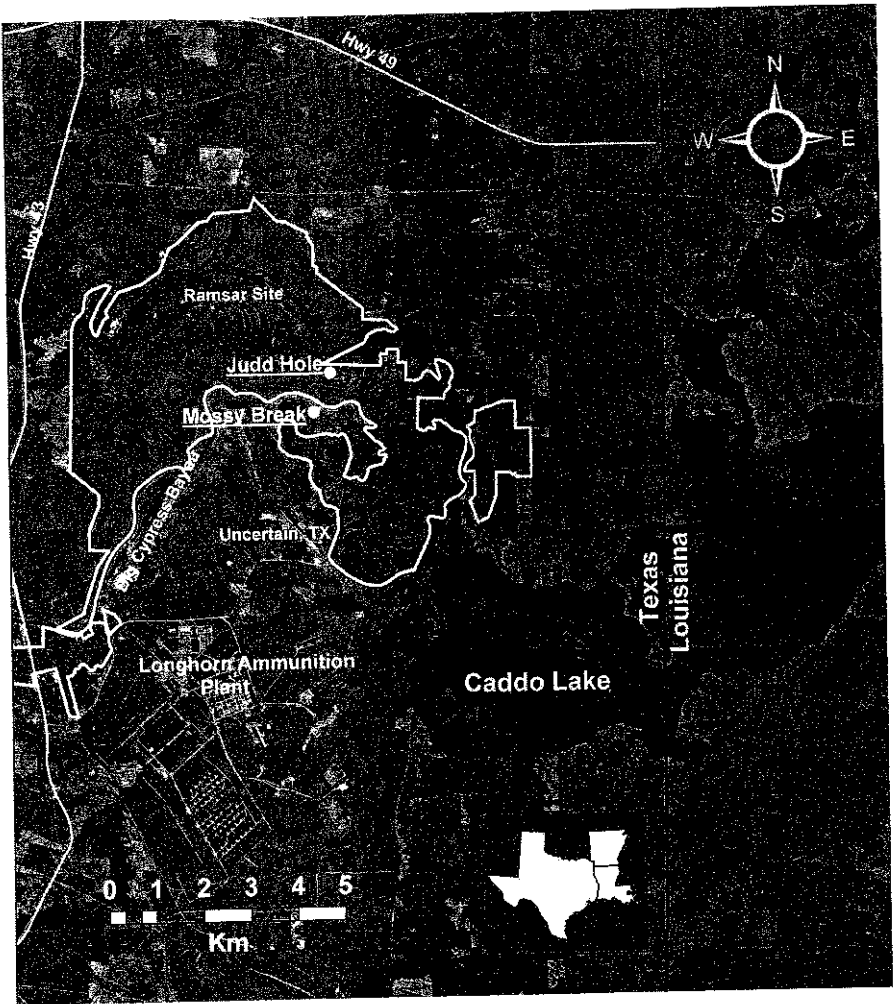


Figure 1. Map of Caddo Lake, Texas. The Ramsar Wetland Site boundary is delineated by the white line. Inset map shows approximate location of study area. Mossy Break and Judd Hole are indicated with white dots. The Texas side of Caddo Lake contains most of the baldcypress stands while the Louisiana side is deeper with more open water.

Preservation of this natural lake was undertaken by The Nature Conservancy in 1992, when it purchased 3,200 ha of Caddo Lake and then donated the land to the Texas Parks and Wildlife

Department (Texas Parks and Wildlife Department 2008). In 1993, this area was declared a Wetland of International Importance under the Ramsar Convention (Texas Parks and Wildlife Department 2008). Although the lake is dominated by baldcypress only, the area surrounding Caddo Lake supports about 120 woody and over 300 herbaceous plant species, as well as 450 species of animals (fish, amphibians, reptiles, birds, and mammals), of which 44 are threatened or endangered (Sierra Club 2000's).

Although baldcypress can cohabitate with species such as *Nyssa biflora* Walter (swamp tupelo) or *Nyssa aquatica* L. (water tupelo) (Brandt & Ewel 1989), Caddo Lake contains exclusive baldcypress stands of relatively younger (about 100 years) and older trees (150 to 300 years in age) (Keeland et al. 1997). Caddo Lake also has two main hydrological regimes, standing water and free-flowing. This study examined differences in forest characteristics and litter production between the young and old stands in two water flow regimes for a monotypic species (baldcypress) at Caddo Lake over multiple yearly time periods. Three specific objectives were tested: (1) to determine whether litter production varied from year to year and monthly, (2) to determine whether litter production differed between standing and free-flowing hydrological regimes, and (3) to determine whether litter production differed between young and old cypress stands.

METHODS

Litter was collected at Caddo Lake, Texas, over a 36-month period (October 1998 through September 2001). Sites were selected from two hydrological scenarios of standing water and free-flowing, each with homogeneous stands of young or old trees. Sites were accessible by motor boat or canoes, and then by hip waders.

Study sites.—The Judd Hole and Mossy Break sites are located in the northwest quadrant of Caddo Lake in Texas (Fig. 1). These sites are approximately 3 km apart and were selected for diverse

water flow characteristics. Judd Hole is a natural backwater swamp, while Mossy break is in a flow-through area. Soils at both sites have large amounts of organic material and clay (Wilson 2003), but Mossy Break has sand that was observed to accumulate along the canal. The young and old stands at Mossy Break are separated by a constructed canal that frequently overflows and allows water to move freely and swiftly through this site. The baldcypress stands of Judd Hole are naturally separated by deep water. The young stand at Judd Hole is on a small island (< 2 ha) surrounded by deep water, while the young stand at Mossy Break is a contiguous area (~4 ha) which grades into a bottomland hardwood swamp. The Judd Hole and Mossy Break sites are also hydrologically connected so that water depths are assumed similar despite being physically separated by distance. The age stands within these sites are homogeneous without any apparent advanced regeneration.

Free-floating litter traps (0.5 m^2) were randomly placed in young and old stands at the two sites. Litter traps were square and constructed of a 2.5 by 15.2 cm pressure-treated wood frame mounted on a rectangular, 10.2 cm pvc pipe float. The inside of the trap was lined with aluminum screen and an additional layer of nylon screen to help reduce the tendency of an item to bounce out of the litter trap. Ten litter traps were placed in each of the young and old stands at each site for a total of 40 litter traps. The traps were tethered to live baldcypress trees which allowed them to be free-floating and track fluctuations in water level. Monthly water levels were obtained from U.S. Army Corps of Engineers water level records at the Caddo Lake weir (Fig. 2) and are concomitant with season and rainfall events occurring within the watershed.

Litter was collected from each trap mid-monthly. Litter was sorted by component (leaves, twigs, bark, Spanish moss, and reproductive parts) and dried at 60°C to a constant weight. Reproductive litter parts consisted of baldcypress male and female cones, as well as scales/seeds.

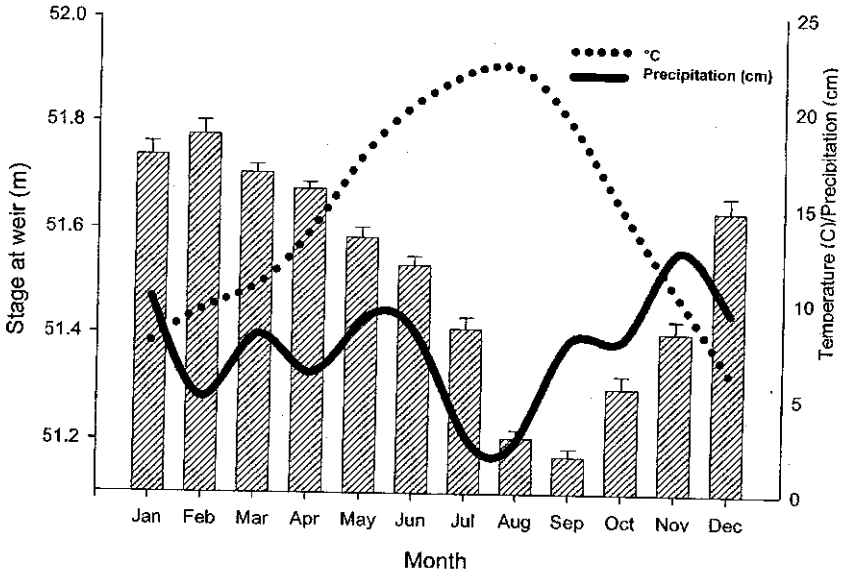


Figure 2. Monthly averages (with SE bars) of water level (m), temperature ($^{\circ}\text{C}$), and precipitation (cm) from January 1998 to December 2000. Water levels are from unpublished U.S. Army Corps of Engineers data from the Caddo Lake weir. Precipitation and temperature are derived from ClimVis NOAA website East Texas data.

Each baldcypress stand was sampled once in 1998 to measure diameter at breast height (dbh) per tree at 1.37 m and above the buttress, in 200 m^2 circular plots centered at a tree with an attached litter trap. Basal area was calculated from the dbh.

Statistical analyses.—Monthly averages were calculated across all traps per age stand within each site, and were summed for three 12-month yearly totals beginning in October 1998. The use of a repeated measures analysis of variance was not justifiable and not applied because the likelihood ratio test was not significant for selecting repeated measure models and the three yearly totals as time periods were not correlated with each other. Instead, analysis of variance was applied to the yearly total litter production

Table 1. Stem density and basal area for live baldcypress trees in young and old stands at Mossy Break and Judd Hole sites of Caddo Lake, Texas.

Site	Density (stems/ha)		Basal Area (m ² /ha)	
	Young	Old	Young	Old
Mossy Break	2050	437	72.6	72.1
Judd Hole	2037	512	72.0	74.6
Combined	2043	475	72.3	73.3

responses (overall and per litter component separately), testing for differences among time periods, age stand types, and sites, as per Gomez & Day (1982). Monthly litter differences were compared between sites and stand types using *t* tests. The level of significance was $\alpha = 0.05$. All analyses were performed using SAS, version 8, SAS Institute Inc. (1999).

RESULTS

Live stem densities for young stands (>2000 stems/ha) were four times greater than in old stands (~500 stems/ha) (Table 1). Basal areas, however, were alike (72.0–74.6 m²/ha) in both age stands at the Mossy Break and Judd Hole sites (Table 1).

Leaves comprised about 64% of the total litter production, followed by reproductive parts (13%), twigs or Spanish moss (10%), and bark (3%). Monthly patterns followed natural leaf fall in the late autumn and winter months and reproductive parts in winter and spring, whereas patterns of other litter components were more variable and usually resulted from disturbances to the trees (Fig. 3).

Year was not significantly different for litter collection (Table 2). The amount that litter fluctuated yearly was not more than 10%. Despite the fact that the Judd Hole site is a backwater area and the Mossy Break site is a flow-through area, there were no significant differences between these hydrological sites for any litter component except Spanish moss (Table 2: $P = 0.0202$).

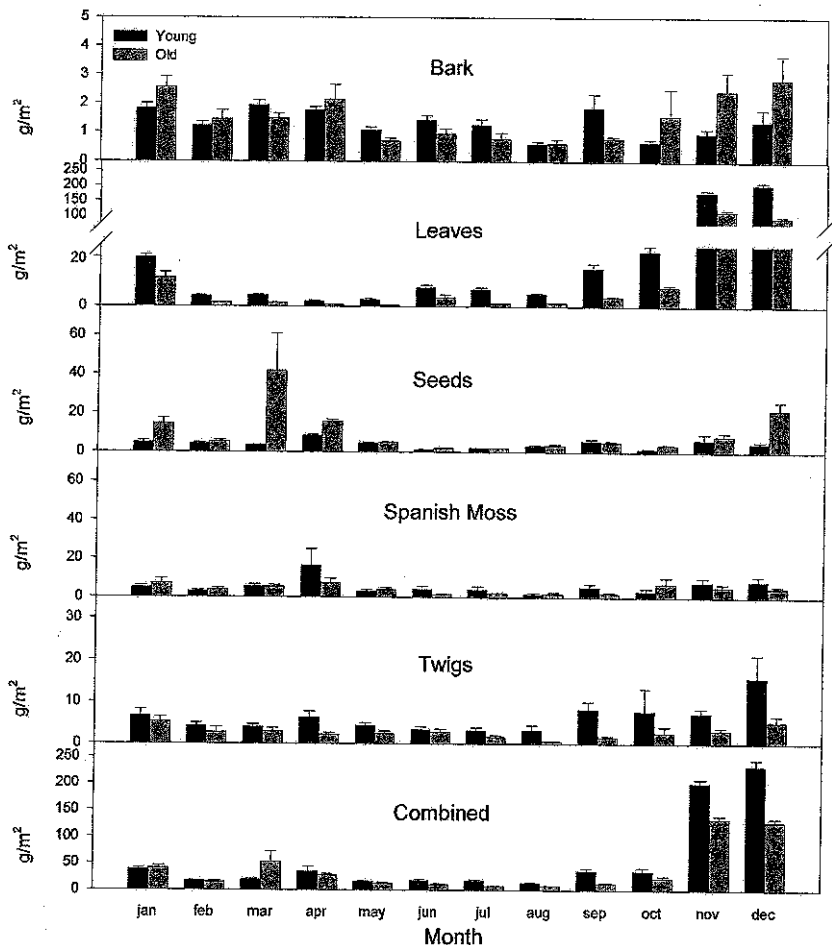


Figure 3. Monthly averages ($\text{g/m}^2/\text{month}$) over three years (October 1998 to September 2001) for each litter component and combined litter collected at Caddo Lake, TX. Note scaling: bark is $1/10^{\text{th}}$ the weight of reproductive parts, twigs, and Spanish moss, whereas leaves are 10 times greater. Standard error bars are included.

There were significant differences between the young and old stands for most litter components (Table 2). Young stands produced 1.5 times more combined litter than old stands ($P =$

Table 2. Yearly sums of litter collected at Caddo Lake, Texas, are presented as $g/m^2/year$, where time period 1 is October 1998 - September 1999, time period 2 is October 1999 - September 2000, and time period 3 is October 2000 - September 2001. Mossy Break and Judd Hole have been abbreviated to the first word. Data are presented for the main effects of time period, site, and stand, followed by the combination of site with stand.

		Litter Component					
		Combined	Bark	Leaves	Reproductive	Spanish moss	Twigs
Time	1	605	20	375	99	71	40
	2	525	13	345	54	46	67
	3	568	18	357	74	56	63
Site	Mossy	579	18	380	78	40	62
	Judd	553	16	338	73	75	52
Stand	Young	673	14	468	47	63	80
	Old	460	19	249	104	53	34
Site- Stand	Mossy-Young	695	14	509	34	42	95
	Mossy-Old	462	22	251	121	39	29
	Judd-Young	650	15	428	59	83	65
	Judd-Old	457	17	248	87	67	38

0.0011), where there was significantly twice as much leaf and twig litter in young than old stands ($P = 0.0002$ and $P = 0.0032$, respectively). In contrast, the old stands produced twice the amount of reproductive litter than the young stands ($P = 0.0077$). Bark and Spanish moss litter did not statistically differ between stands.

Within both sites, young stands produced substantially more combined, leaf, and twig litter ($P = 0.0133$, $P = 0.0011$, and $P = 0.0362$, respectively) (Table 2). The young stands in Judd Hole had more Spanish moss ($P = 0.0480$). Old stands exceeded young stands in reproductive litter ($P = 0.0328$).

There were no significant monthly differences between the hydrological sites for the combined litter collection in young or old stands, and there were no significant site differences in any litter component, except for reproductive parts in young stands ($P =$

0.0012) and for Spanish moss in old stands ($P = 0.0162$). There were, however, significant differences in litter production between age stands, where young baldcypress stands produced higher monthly combined, leaf, and twig litter than old baldcypress stands ($P = 0.0213$, $P = 0.0020$, and $P = 0.0087$, respectively). Since there were no general statistical differences in sites, monthly data averaged over three years are presented as pooled over sites by age stand (Fig. 3).

DISCUSSION

This study determined the relationship of baldcypress stand age with litter production at Caddo Lake. There were significant stand age differences for litter components except bark. Young baldcypress stands produced about twice the amount of litter than old baldcypress stands. Based on field observations, young stands of baldcypress trees had potentially a greater number of limbs that support more leaves affecting leaf litter production; whereas old baldcypress trees had relatively sparse number of limbs supporting fewer leaves. The amount of reproductive litter, however, was twice greater in the old stands than young stands, suggesting that the enhanced reproductive capability of baldcypress may be associated with maturity since there were 77% fewer baldcypress trees in the old stands than young stands.

Total annual litter production values at Caddo Lake were within the overall litter production range of baldcypress ecosystems between 300 and 600 g/m² (Deghi et al. 1980). The Caddo Lake study showed no significant differences in hydrological regimes for litter collection (579 g/m² in flow-through vs. 553 g/m² in backwater). Two other studies also showed no significant differences in hydrological regimes: 574 g/m² in better-drained vs. 620 g/m² in standing water (Conner & Day 1976), and 607 g/m² in flow-through vs. 650 g/m² in still water (Brown & Peterson 1983). Conner & Day (1992), however, reported significantly higher litter production for better-drained sites versus stagnant sites (579 g/m² in seasonally-flooded > 401–405 g/m² in slowly-flowing > 293 g/m²

in impounded areas.) There are also examples of low total litter production values in still-water ecosystems, such as at Okefenokee Swamp, GA (328 g/m², Schlesinger [1978]) and a cypress swamp in Illinois (348 g/m², Mitsch et al. [1977]). Mitsch et al. (1991) reported low baldcypress litter production in slowly-flowing, permanently-flooded waters at Henderson Sloughs, KY (253 g/m²).

Percentages of litter components are compared with other litter studies. At Caddo Lake, leaves represented 64% of yearly litter collected, with 70% in young stands and 54% in old stands. The reproductive parts comprised of 13% of the total litter, with higher production by old stands (23%) as compared to young stands (7%).

For baldcypress forest studies with comparable average age similar to young stands at Caddo Lake, the percentages of leaf production were often higher and reproductive parts lower. In young cypress ecosystems of Florida (~40 to 120 yrs of age), leaf litter of cypress species accounted for about 85%–95% of the total cypress litter production for most sites (Brown 1981). The Florida sewage-enriched pond cypress dome (~40 yrs old) in the Deghi (1977) study had a similar percentage of leaf litter (70%) as in the Caddo Lake study, but a higher proportion of cypress reproductive parts (15%) influenced by increased nutrient inputs (Brown 1981). Litter of baldcypress at the Prairie Creek floodplain forest (~90 yrs old) near Gainesville, Florida consisted of more leaves (82%) but similar percentages of reproductive parts (7%) as in Caddo Lake (Brown 1981). For the natural, non sewage-treated pond cypress dome (~120 yrs old) at Austin Cary Forest, Florida, leaves represented 85% of the litter but reproductive parts were lower at 2% (Deghi 1977). Similarly, 78% of the litter was leaves and only 3% was reproductive parts for baldcypress (70–95 yrs old) in the Great Dismal Swamp, Virginia (Gomez & Day 1982).

The still-water baldcypress swamps at Okefenokee Swamp, Georgia, had undisturbed remnant forest stands with canopy trees that were 120-200 yrs old (Schlesinger 1978). The yearly amount

of leaves (223 g/m^2) was similar to backwater old stands at Caddo Lake (248 g/m^2) (Table 2). Because of the lower amount of total litter production (328 g/m^2), leaves at Okefenokee Swamp represented a higher percentage (68%) of the total litter production but reproductive parts (10%) was lower than Caddo Lake.

The Caddo Lake study presents detailed monthly patterns of each litter component corresponding with the phenology of baldcypress (Burns & Honkala 1990a) (Fig. 3). Total litter production monthly patterns concurred with basic monthly patterns observed for baldcypress in the Dismal Swamp (Gomez & Day 1982) and in Lac des Allemands swamp in Louisiana (Conner et al. 1981). Leaf fall showed a distinctive pattern primarily from November to December, with gradual elevated amounts in September, October, and January. At Caddo Lake reproductive parts fell primarily in spring after female cones developed and matured during the autumn and male cones matured during the winter. Bark represents a very small fraction of litter and was relatively constant throughout the year with slightly lower quantities during the warmer months. Twig litter was lowest in the baldcypress active growing season and highest from autumn to winter.

Spanish moss comprised 10% of the total yearly litter produced at Caddo Lake and its yearly litter production of 58 g/m^2 was similar to that found by Schlesinger et al. (1975) at 65 g/m^2 collected at Okefenokee Swamp, Georgia. Because baldcypress is considered high in nutrients that leach from its leaves, the Spanish moss biomass is directly associated with nutrient availability (Schlesinger 1977). Furthermore, there was a positive correlation ($r = 0.83$) between the amount of bark and Spanish moss collected in litter traps. Spanish moss, an epiphyte, may anchor under bark or entwine in twigs of the baldcypress and fall with the shedding bark or breaking twigs.

In general, litter collection methods varied among other studies. The sampling designs were often for a single year with uneven sampling times (increased autumn collections to weekly or biweekly, then monthly or longer afterwards). Multiple yearly collections at Caddo Lake confirmed no statistical differences among typical years similarly as in the 2-year study of Megonigal et al. (1997) or in the 4–5 year study undertaken by Conner & Day (1992).

Traps were generally smaller and varied greatly in other studies, and usually numbered 5–15 per site/area, such as the use of stationary traps (0.25 m^2) (Brown 1981), wooden bushel baskets (0.11 m^2) at $\sim 1.4 \text{ m}$ above water level (Schlesinger 1978), stationary litterboxes (0.25 m^2) at 1.5 m above ground level (Mitsch et al. 1991), randomly-located 0.25 m^2 nylon-screen traps at 1 m above ground level (Megonigal et al. 1997), or stationary aluminum-screen baskets (0.25 m^2) elevated above maximum flood levels (Gomez & Day 1982). In addition, Gomez & Day (1982) have acknowledged that their sampling systems were better designed for leaves and not adequate for reproductive or other litter parts. Larger traps (1 m^2 baskets with mesh bottoms) that floated or were attached to fenceposts above floodwater were used in mixed species studies (Brown & Peterson 1983), and 1 m^2 boxes with mesh bottoms fitted on 1 m long legs above flood waters were used by Conner & Day (1992). At Caddo Lake, larger floating traps (with an improved design) tethered exclusively to baldcypress, along with consistent monthly measurements over several years, is believed to assure more accurate annual collections of baldcypress litter.

In conclusion, there were significant differences found in litter production between young and old baldcypress stands at Caddo Lake, Texas. Young stands produced about twice the amount of litter than old stands, with the majority as leaves, whereas old stands produced relatively more reproductive parts. Since age has been shown to be an important factor in litter production at Caddo

Lake, consideration should be given to determining stand age using methods such as tree-ring analysis, and selecting multiple stands with age diversity in litter production studies.

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