

Foliar litter position and decomposition in a fire-maintained longleaf pine – wiregrass ecosystem

Joseph J. Hendricks, Carlos A. Wilson, and Lindsay R. Boring

Abstract: Foliar litter position and decomposition were assessed in longleaf pine (*Pinus palustris* Mill.) – wiregrass (*Aristida beyrichiana* Trin. & Rupr.) woodlands during a 3-year burn interval. Position assessments revealed 57.7 and 67.4% of foliar litter was elevated in wiregrass crowns 1 and 2 years, respectively, following burning. Decomposition assessments revealed soil-surface mass loss decay constants (range 0.097–0.282) similar to those measured in comparable pine forests. However, elevated longleaf pine and wiregrass litter exhibited decay constants (0.052 and 0.074, respectively) 50% lower than corresponding soil-surface rates and among the lowest values in the literature. With the exception of wiregrass, which did not exhibit an immobilization of the nutrients (N, P, Ca, K, and Mg) assessed, foliar litter exhibited either extensive P immobilization with minimal N immobilization or minimal, short-lived immobilization of N, P, or both N and P. The percentage of original N and P remaining after 3 years varied widely among the soil surface (N range 6.3–56.3%; P range 3.4–204.7%) and elevated (N range 76.8–94.9%; P range 52.0–99.2%) litter. These results suggest that fire regimes typically employed in longleaf pine – wiregrass woodlands may balance N losses via volatilization with P limitations via litter immobilization.

Résumé : La position et la décomposition de la litière de feuilles ont été évaluées dans des forêts de pin des marais (*Pinus palustris* Mill.) et d'aristide bleutée (*Aristida beyrichiana* Trin. & Rupr.) au cours d'un intervalle de 3 ans entre deux feux. L'étude de la position révèle que respectivement 57,7 et 67,4% de la litière foliaire se retrouve dans la cime de l'aristide bleutée 1 et 2 ans après un feu. L'étude de la décomposition révèle que les constantes de décomposition qui traduisent la perte de masse à la surface du sol (0,097–0,282) sont semblables à celles qui ont été mesurées dans des forêts comparables de pin. Cependant, la litière surélevée de pin des marais et d'aristide bleutée ont des constantes de décomposition (respectivement 0,052 et 0,074) 50% plus faibles que les taux correspondants à la surface du sol et parmi les plus faibles rapportées dans la littérature. À l'exception de l'aristide bleutée qui n'immobilise pas les nutriments (N, P, Ca, K et Mg) mesurés, la litière de feuille immobilise soit beaucoup de P et peu de N, soit peu de N, de P ou de N et de P pendant de courtes périodes. Après 3 ans, les pourcentages initiaux de N et P encore présents varient beaucoup selon que la litière se trouve à la surface du sol (N varie de 6,3–56,3%; P varie de 3,4–204,7%) ou au-dessus du sol (N varie de 76,8–94,9%; P varie de 52,0–99,2%). Ces résultats indiquent que le régime de feux normalement utilisé dans les forêts de pin des marais et d'aristide bleutée peut contrebalancer les pertes de N par volatilisation mais peut causer des carences en P à cause de l'immobilisation dans la litière.

[Traduit par la Rédaction]

Introduction

Longleaf pine (*Pinus palustris* Mill.) – wiregrass (*Aristida beyrichiana* Trin. & Rupr.) woodlands are considered to be one of the most threatened ecosystems in North America (Noss 1989; Ware et al. 1993). Prior to European settlement, this ecosystem type covered over 30×10^6 ha primarily in the Coastal Plain Region of the southeastern United States (Christensen 1977). However, a variety of anthropogenic disturbances have since reduced the areal coverage of this ecosystem to approximately 2% of its original extent (Simberloff 1993). Currently, there is a strong and growing

interest in the management and restoration of longleaf pine woodlands for both ecological and economic reasons (Walker and Peet 1983; Clewell 1989; Noss 1989; Landers et al. 1995; Drew et al. 1998). Gaining an improved understanding of the controls on the structure and function of longleaf pine – wiregrass woodlands is critical for the development of ecologically sound management regimes and restoration strategies for these ecosystems (Aber and Melillo 1991; Sharitz et al. 1992; Loreau 1994).

Fire is an integral component of longleaf pine – wiregrass woodlands (Christensen 1987; Clewell 1989; Landers et al. 1995). While it has long been recognized that these ecosystems evolved under the influence of fire and require regular burning to persist, there is a need for a more basic understanding of fire controls on multiple resource limitations in these ecosystems, which now rarely burn naturally (see Robbins and Myers 1992). This problem has taken on added significance, since several recent studies allege that the prescribed burning regimes commonly employed in longleaf pine – wiregrass woodlands and similar ecosystem types (i.e., dormant season burning on 1- to 3-year intervals used primarily to reduce fuel loading and enhance game popula-

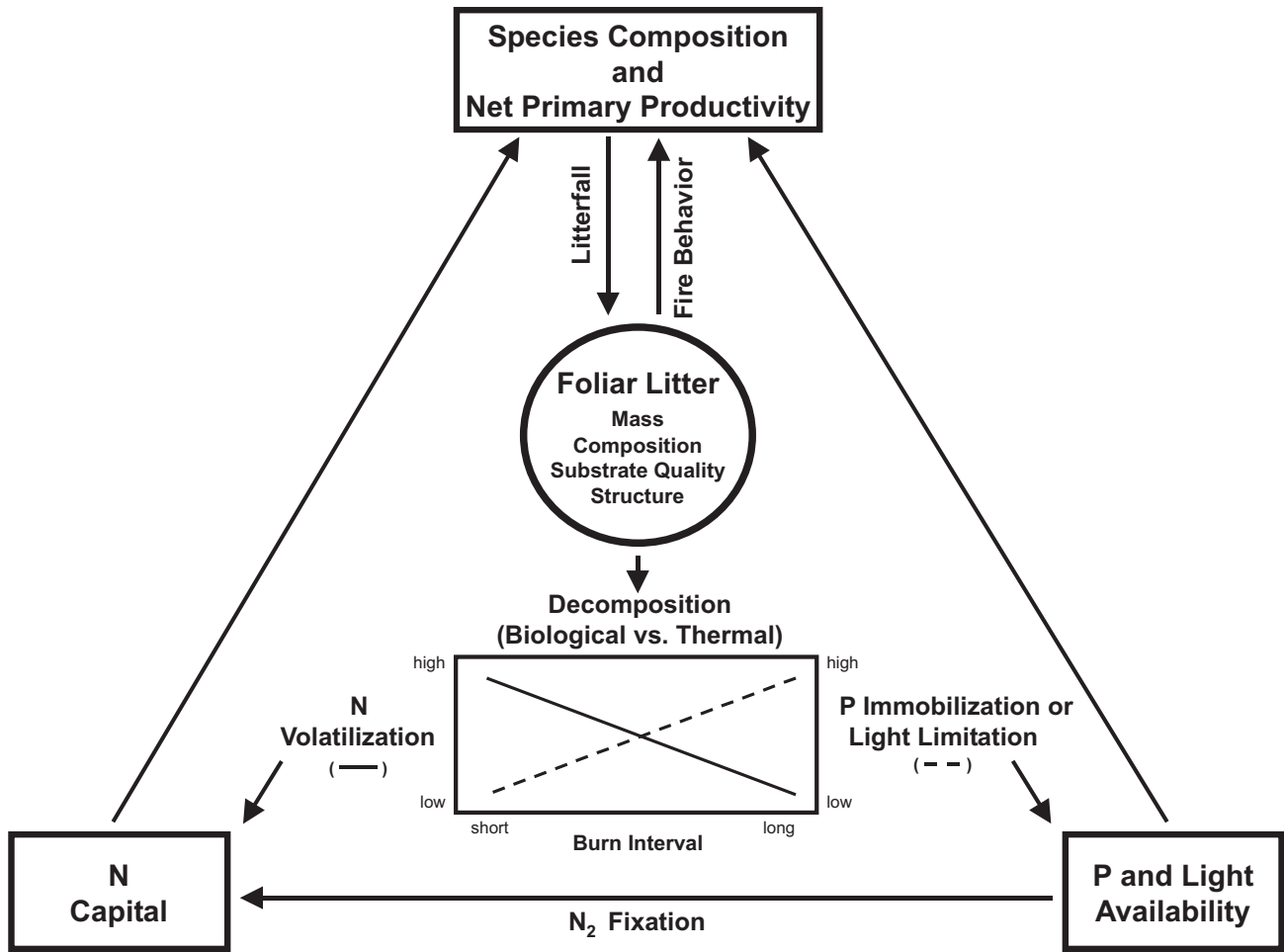
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Fig. 1. Schematic diagram illustrating how the relative influence of biological versus thermal litter decomposition (note that the increase in the burn interval duration denotes a progressive increase in the relative influence of biological litter decomposition) may influence the resource (N, P, and understory light) availability, net primary productivity, and species composition of longleaf pine – wiregrass ecosystems.



tions) could have deleterious impacts on the long-term productivity and stability of these systems (Christensen 1987; Bell and Binkley 1989; Zahner 1989; Binkley et al. 1992; Blair 1997; Wright and Hart 1997).

Mechanistically, burning influences the species composition, vegetation structure, resource availability, and net primary productivity of longleaf pine – wiregrass woodlands, which, in turn, influence the quantity and quality of fuels in the ground cover and, thus, the behavior and intensity of subsequent burn events (Wilbur and Christensen 1983; Christensen 1987; Clewell 1989) (Fig. 1). Central to this complex feedback system is the understory necromass or litter that serves as the primary fuel source for the fire and contains potentially large pools of carbon (C) and nutrients that may be altered in form and availability by fire (Hough 1982; Gilliam 1988). In particular, fire has a major impact on the cycling of nitrogen (N) and phosphorus (P), which are potentially colimiting to net primary productivity in these woodlands (Walker and Peet 1983; Christensen 1987; O’Connell 1988; Gillon et al. 1995) and are among the most immobile elements in litter (Hough 1982; Gilliam 1988). Nitrogen has a relatively low volatilization temperature (Raison et al. 1985; Binkley et al. 1992; Ojima et al. 1994; Gillon et

al. 1995), thus N in litter that is not biologically mineralized (i.e., converted to ammonium, NH_4^+ , and transferred to the soil) is generally thermally mineralized (i.e., converted to molecular nitrogen, N_2 , and transferred to the atmosphere) during the regular burn events and lost from the ecosystem (DeBell and Ralston 1970; O’Connell 1988). In contrast, while P may be volatilized in the most intense understory fires (i.e., $>800^\circ\text{C}$), most burns are cooler, and this element is generally transformed to more readily available inorganic forms by fire and retained in the ecosystem (Raison et al. 1985; Binkley et al. 1992; Gillon et al. 1995). Thus, the degree of biologically mediated decomposition prior to burning (i.e., the fire interval duration) may dictate the type and degree of nutrient limitation in these systems; relatively frequent burning may increase P mineralization and availability while reducing the C and N capital, whereas less frequent burning may conserve C and N while reducing P availability via litter immobilization. Consequently, an improved understanding of the patterns and controls of biologically mediated foliar litter mass loss and nutrient dynamics is essential to more accurately assess and predict the impact of various burning regimes on resource availability in longleaf pine – wiregrass woodlands.

While foliar litter decomposition has been studied extensively in temperate forests and grasslands (Aber et al. 1990; Seastedt et al. 1992; Aerts 1997), the patterns and controls of litter decomposition have not been assessed in longleaf pine – wiregrass woodlands, which generally differ in structure, function, and composition from other temperate biomes (Fig. 1) (Drew et al. 1998; Mitchell et al. 1999). For example, longleaf pine – wiregrass woodlands are among the most floristically rich of all temperate forests (Walker and Peet 1983; Drew et al. 1998; Hains et al. 1999; Kirkman et al. 2001), and, consequently, may exhibit a broader range of foliar litter substrate quality (i.e., tissue chemical characteristics, such as nutrient concentrations, as well as the form and concentration of C compounds, which influence decomposition rates; Berg 1986; Lohmus and Ivask 1995) among species. Also, the relatively open longleaf pine overstory may have a major impact on the microclimate and, thus, decomposition dynamics of the litter in the ground cover (Mitchell et al. 1999). In addition, N mineralization rates measured in this ecosystem type ($7.8 \pm 1.3 \text{ kg N}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ (mean \pm SD); Wilson et al. 1999) are among the lowest reported for terrestrial ecosystems in North America (see Scott and Binkley 1997), and N limitations may be compounded or superseded by P limitations in these Coastal Plain soils (Walker and Peet 1983; Gholz et al. 1985; Christensen 1987). Furthermore, longleaf pine – wiregrass woodlands generally occur at the warmer extreme of the temperate region.

The primary objective of this study was to assess the patterns and controls of foliar litter decomposition in longleaf pine – wiregrass woodlands during a 3-year, fire-free period, which is typically the longest burn interval employed in the management of remnant stands (Landers et al. 1995). The specific objectives were to (i) assess the position of foliar litter (i.e., on the soil versus elevated in wiregrass crowns) in the ground cover of longleaf pine – wiregrass woodlands, (ii) determine the influence of foliar litter position on litter mass loss patterns and nutrient dynamics, and (iii) compare the patterns and controls of foliar litter mass loss and nutrient dynamics in longleaf pine – wiregrass woodlands with a more general, conceptual model of litter decomposition dynamics developed for temperate biomes.

Methods

Study sites

Foliar litter position and decomposition dynamics in longleaf pine – wiregrass ecosystems were assessed at the Joseph W. Jones Ecological Research Center at Ichauway, in Baker County, Georgia. Ichauway is on the Karst Dougherty Plain located in the Lower Coastal Plain and Flatwood Province of southwestern Georgia (McNab and Avers 1994). The climate for this region is characterized as humid subtropical with a mean annual precipitation of 131 cm distributed evenly throughout the year, and mean daily temperatures ranging from 21 to 34°C in summer and from 5 to 17°C in winter (Goebel et al. 1997).

The longleaf pine – wiregrass ecosystems at Ichauway have been maintained using understory prescribed burning (average return interval of 2 or 3 years) since the 1930s. The woodlands are characterized by a monotypic overstory of

longleaf pine and a dense understory dominated by wiregrass but including numerous other species of perennial grasses, forbs, and hardwood sprouts (Goebel et al. 1997; Drew et al. 1998). The sites selected for this study had soils classified as Psammentic Kandiodults or Grossarenic Kandiodults, which have been generally characterized as somewhat excessively drained soils consisting of loamy sands over sandy loams occurring on upland terraces with undulating (2%) slopes. The study sites correspond to ecosystem type 12 in a site classification system of the property based on soil type, landscape position, and vegetation described by Goebel et al. (1997).

The foliar litter position assessments were conducted in the ground cover of two type 12 longleaf pine – wiregrass woodlands; one of the sites had approximately 1 year of litter accumulation (i.e., a 1-year-old ground cover), whereas the other had 2 years of litter accumulation (i.e., a 2-year-old ground cover). The patterns and controls of foliar litter decomposition were assessed in four type-12 longleaf pine – wiregrass sites that were burned in February approximately 10 months prior to the study initiation so that the litterbag deployment the following December would coincide with the natural first-year litter deposition following burning.

Litter position assessments

In December 1994, 15 sample plots (each 0.75 m²) were randomly established in the understory of the longleaf pine – wiregrass woodlands with 1- and 2-year-old ground covers for the foliar litter position assessment. The litter in each plot was sampled by first collecting the pine needles elevated in the wiregrass crowns above the soil surface. Live and dead wiregrass tillers that were not in contact with the soil were then cut at ground level and returned to the laboratory where they were sorted into vitality classes (i.e., live and dead; wiregrass tillers were considered to be dead if greater than 90% was brown and appeared senescent). Following the removal of the “elevated” litter, the litter in contact with the soil or “soil surface” litter was harvested and returned to the laboratory where it was sorted into species and vitality classes. The litter samples from each plot were dried at 70°C to a constant mass, weighed, ground using a SPEX 8000-D mixer mill (SPEX Industries, Inc., Edison, N.J.), and subsampled for ash determination (500°C for 5 h) to express all litter estimates on an ash-free, dry-mass basis (Jones 1984).

Litter decomposition: tissue selection, collection, and processing

The litter types used in this decomposition assessment represented the dominant species of the major taxonomic guilds in type-12 longleaf pine – wiregrass ecosystems, provided a broad range in tissue substrate quality, and facilitated the comparison of results with those from other studies. In addition to longleaf pine, slash pine (*Pinus elliottii* Engelm.) and chestnut oak (*Quercus prinus* L.) were the representative tree species. Slash pine is a natural component of more hydric longleaf pine – wiregrass communities and has been used in other foliar decomposition studies conducted in the Coastal Plain Region of the southeastern United States (Gholz et al. 1985; Polglase et al. 1992). Chestnut oak, which is not native to longleaf ecosystems,

provided a median litter substrate quality type representative of oaks in the understory and served as a common litter type with the Long-term Intersite Decomposition Experiment (LIDET 1995). In addition to the three tree species, four herbaceous species common in the understory of these systems were selected as well: wiregrass, blackberry (*Rubus* spp.), bracken fern (*Pteridium aquilinum* (L.) Kuhn), and the N₂-fixing legume, goat's rue (*Tephrosia virginiana* (L.) Persoon) (Hiers 1999).

In the fall of 1994, approximately 2 kg of freshly senescent (i.e., tissues that had not been leached by rainfall) foliar litter were collected for each species. Longleaf pine and the understory species litter were collected in several sites classified as type 12 longleaf pine – wiregrass ecosystems (Goebel et al. 1997). Slash pine was obtained from a more hydric longleaf pine – wiregrass community and chestnut oak was collected at the Coweeta Hydrologic Laboratory near Franklin, N.C. Tree litter was collected using large perforated sheets of plastic placed under representative individuals. Wiregrass litter was acquired by raking the dead tillers from individual crowns (1 year of growth) in early fall and collecting senescent tillers following the first killing frost of the season. Blackberry, bracken fern, and goat's rue litter were obtained by hand picking senescent foliage (i.e., tissue that had changed color and was easily removed from the stem).

The foliar litter of each species was air-dried in the laboratory to a constant mass. Following homogenization of each litter type, subsamples were taken to determine air-dry to oven-dry (70°C) conversion factors. Subsequently, 256 litterbags were constructed for both longleaf pine and wiregrass, and 128 litterbags were constructed for each of the remaining six species. Each litterbag consisted of approximately 10 g of air-dry tissue enclosed in a fiberglass screen (2-mm mesh size) bag with a numbered metal tag attached to the corner. (Note that the dimensions of the litterbags varied by species such that the vertical layering of the leaf tissues in the litterbags was similar to the leaf litter layering on the soil surface for 1 year of litterfall in the natural systems.) The initial air-dry mass, calculated oven-dry mass, species, plot location, and identification number were recorded for each litterbag prior to deployment in the field.

Litter decomposition: field incubations

Within each of the four longleaf pine – wiregrass ecosystems selected for the decomposition assessments, four 5 × 5 m plots were randomly located yielding a total of 16 plots for the study. In late fall of 1995, eighty litterbags were placed in each plot: 64 positioned on the soil surface (hereafter referred to as “soil surface” samples) and 16 positioned above the soil surface (hereafter referred to as “elevated” samples) in wiregrass crowns. Soil surface samples were established by locating eight tether cords, each of which contained one litterbag per species, among the understory vegetation. Elevated samples were established by staking eight litterbags per species of longleaf pine and wiregrass within wiregrass crowns in the perimeter of the plot. One randomly selected tether cord (i.e., one soil surface litterbag per species) and one elevated litterbag for both longleaf pine and wiregrass were collected immediately after establishment to assess mass loss resulting from handling. This set

served as the initial sample. Subsequent sets of litterbags were collected in the same manner 58, 145, 365, 422, 513, 751, and 1122 days following establishment.

Litter decomposition: sample analysis

Following collection, litterbags were immediately returned to the laboratory where residual tissues were meticulously cleaned (i.e., brushed to remove soil particles), oven-dried (70°C) to a constant mass, weighed, ground using a SPEX 8000-D mixer mill, and subsampled for ash determination (500°C for 5 h) to express all mass, C-fraction, and nutrient indices on an ash-free, dry-mass basis (Jones 1984). Residual litter C-fraction concentrations including “extractives” (i.e., more readily decomposable C compounds consisting of nonpolar constituents, such as fats, oils, waxes, and polar constituents, such as nonstructural carbohydrates and polyphenols removed using a two-stage extraction in dichloromethane and boiling water, respectively), “acid-soluble” structural components (i.e., moderately decomposable C compounds consisting primarily of cellulose and hemicellulose removed using a two-stage digestion in 72% and 2.5% sulfuric acid, respectively), and “acid-insoluble” structural components (i.e., highly recalcitrant C compounds consisting of lignin and other highly reduced compounds, such as suberin, cutin, and tannin protein complexes which are the residual of the two-stage sulfuric acid digestion minus ash mass) were assessed using a modification of the forest products serial digestion technique (Ryan et al. 1990). Tissue C and N concentrations were determined with a Perkin-Elmer Model 240B CHN analyzer (Norwalk, Conn.). Tissue P concentrations were assessed using method No. 10-115-01-1-c developed for a Lachat flow injection analyzer (Lachat Instruments, Inc., Milwaukee, Wis.). In addition, tissue calcium (Ca), magnesium (Mg), and potassium (K) concentrations were determined by atomic absorption spectroscopy using a Perkin Elmer 5100 PC following wet digestion of ground samples in sulfuric acid (Parkinson and Allen 1975).

Data and statistical analysis

Student's *t* tests were used to assess differences between soil surface and elevated litter mass estimates as part of the litter position assessments, and between soil surface and elevated litter mass loss and nutrient concentrations for longleaf pine needles and wiregrass tillers as part of the litter decomposition assessments (Steel et al. 1997). ANOVA analyses were used to assess differences ($P < 0.05$) in litter mass loss, C-fraction concentrations, and nutrient concentrations among species and sample dates for the seven litter types incubated on the soil surface as part of the decomposition assessment. If differences existed, Tukey's HSD (honest significant difference) means separation test was used to determine which means differed significantly.

Preliminary assessments revealed that the mass loss data for the soil surface and elevated litter types were best described using the standard exponential decay model: $y = e^{-kt}$, where y is the percentage of the initial mass remaining, k is the decay constant, and t is the time of decomposition in days (Steel et al. 1997). The decay constant (k) was determined statistically for each litter type, and simple linear regression analyses were used to determine if there were

significant linear relationships between the derived k constants and the initial substrate quality indices for the seven litter types incubated on the soil surface, which may be used to predict mass loss rates based on initial litter substrate quality indices (Aber et al. 1990). In addition, simple linear regression analyses were used to determine if there were significant inverse-linear relationships between the percent mass remaining and the nutrient concentrations for the seven soil-surface litter types. In turn, the slopes of the inverse-linear nutrient functions were regressed against initial substrate-quality indices to develop equations that predict litter nutrient dynamics based on initial litter chemistry indices.

Results

Litter position

The assessment of litter position in the understory of type-12 longleaf pine – wiregrass ecosystems revealed that the majority of foliar necromass was elevated above the soil surface in the crowns of wiregrass bunches (Table 1). Elevated litter, which consisted almost exclusively of longleaf pine needles and wiregrass tillers, accounted for 57.7 and 67.4% of the total litter standing stock in 1- and 2-year-old ground covers, respectively. Consequently, the proportion of litter positioned on the soil surface decreased from 42.3 to 32.6% between the younger and older ground covers. Longleaf pine needles and wiregrass tillers also were the dominant soil-surface litter components; the other foliar litter components, largely composed of small leaves from legumes and other forb species, cumulatively represented only 1.1 and 2.9% of the total litter standing stock in 1- and 2-year-old vegetation, respectively (Table 1).

Litter mass loss dynamics

Foliar litter percent mass remaining for the seven species incubated on the soil surface were best described using standard exponential decay functions (Fig. 2). The derived k values over the 3-year span of this study ranged from 0.097 to 0.282 for slash pine needles and blackberry leaves, respectively. With the exception of the day 58 sample date, blackberry percent mass remaining was significantly lower than those measured for the other six litter types decomposing on the soil surface. In contrast, longleaf pine and slash pine needle percent mass remaining were consistently higher than the other litter types (significantly different from all species except chestnut oak on the day 58, 365, 422, and 513 sample dates and goat's rue on the day 1122 sample date). After 3 years of decomposition, blackberry leaves had only 3.9% mass remaining, whereas longleaf pine and slash pine had 25.1 and 27.2% mass remaining, respectively.

The percent mass remaining for longleaf pine and wiregrass litter elevated above the soil surface in wiregrass crowns also exhibited exponential decay functions (Fig. 2). The derived decay constants for elevated longleaf pine needles and wiregrass tillers (0.052 and 0.074, respectively) were 54 and 53% lower, respectively, than the decay constants measured for corresponding tissues decomposing on the soil surface. The percent mass remaining for the elevated litter types were significantly higher than the corresponding soil-surface litter on each sample date. After 3 years of decomposition, longleaf pine and wiregrass litter elevated in

Table 1. Foliar litter mass positioned on the forest floor and elevated in wiregrass crowns for 1- and 2-year-old understory ground covers.

Litter type	Litter position	
	Forest floor (g)	Elevated (g)
One-year-old ground cover		
Longleaf pine needles	241.7 (16.8)	267.1 (24.4)
Wiregrass tillers	27.5 (4.5)	109.7 (11.5)
Other litter	7.5 (1.3)	—
Total	276.7	376.8
Two-year-old ground cover		
Longleaf pine needles	169.1 (12.3)	276.5 (25.3)
Wiregrass tillers	47.2 (3.9)	214.9 (22.8)
Other litter	21.1 (2.4)	—
Total	237.4	491.4

Note: Values are means of 15 plots, with SD given in parentheses.

wiregrass crowns had 55.0 and 41.8% mass remaining, respectively, compared with 25.1 and 16.6% mass remaining, respectively, for the corresponding litter incubated on the soil surface.

Foliar tissues exhibited two distinct C-fraction mass loss patterns over the 3-year span of the study (Fig. 3). Blackberry, bracken fern, goat's rue, and wiregrass displayed the more typical sequential degradation of extractable, acid-soluble, and acid-insoluble C fractions. In contrast, the three tree species differed substantially from the other litter types in that the degradation of the three C fractions generally occurred concurrently (Fig. 3). While litter position altered the absolute mass loss rates of longleaf pine and wiregrass tissues, it did not affect the C-fraction mass loss patterns of these tissues in the groundcover.

The seven soil-surface litter types selected for this study provided a broad range of tissue substrate quality (Table 2). When the initial substrate-quality indices were regressed against their corresponding derived decay constants, blackberry was a consistent outlier exhibiting mass loss rates that were higher than predicted based on most substrate-quality indices (Fig. 4). When blackberry was excluded, regressions using more conventional C/N and acid-insoluble C/N (i.e., lignin/N) substrate quality indices yielded R^2 values of 0.65 and 0.71, respectively. However, the strongest relationship was derived using the initial P concentration which yielded a R^2 of 0.82 with blackberry excluded. Other substrate-quality indices yielded substantially lower coefficients of determination, notably the lignocellulose index (Melillo et al. 1989) which yielded R^2 values of 0.06 and 0.02 with and without blackberry excluded, respectively (data not shown).

Litter nutrient dynamics

With the notable exception of wiregrass, which did not exhibit a net immobilization of the five nutrients (i.e., Ca, K, Mg, N, and P) assessed in this study in the soil surface or elevated position, the foliar litter types used in this study were generally characterized by P and (or) N immobilization (Fig. 5). The six tissue types incubated on the soil surface that exhibited net nutrient immobilization may be generally classified by either (i) extensive, prolonged P immobilization and minimal, short-lived N immobilization (longleaf pine,

Fig. 2. Percent mass remaining through time for the five litter types incubated only on the soil surface (left panel) and the longleaf pine and wiregrass litter incubated on both the soil surface (SS) and elevated (ELEV) in wiregrass crowns (right panel). Values are means, and error bars are SEs.

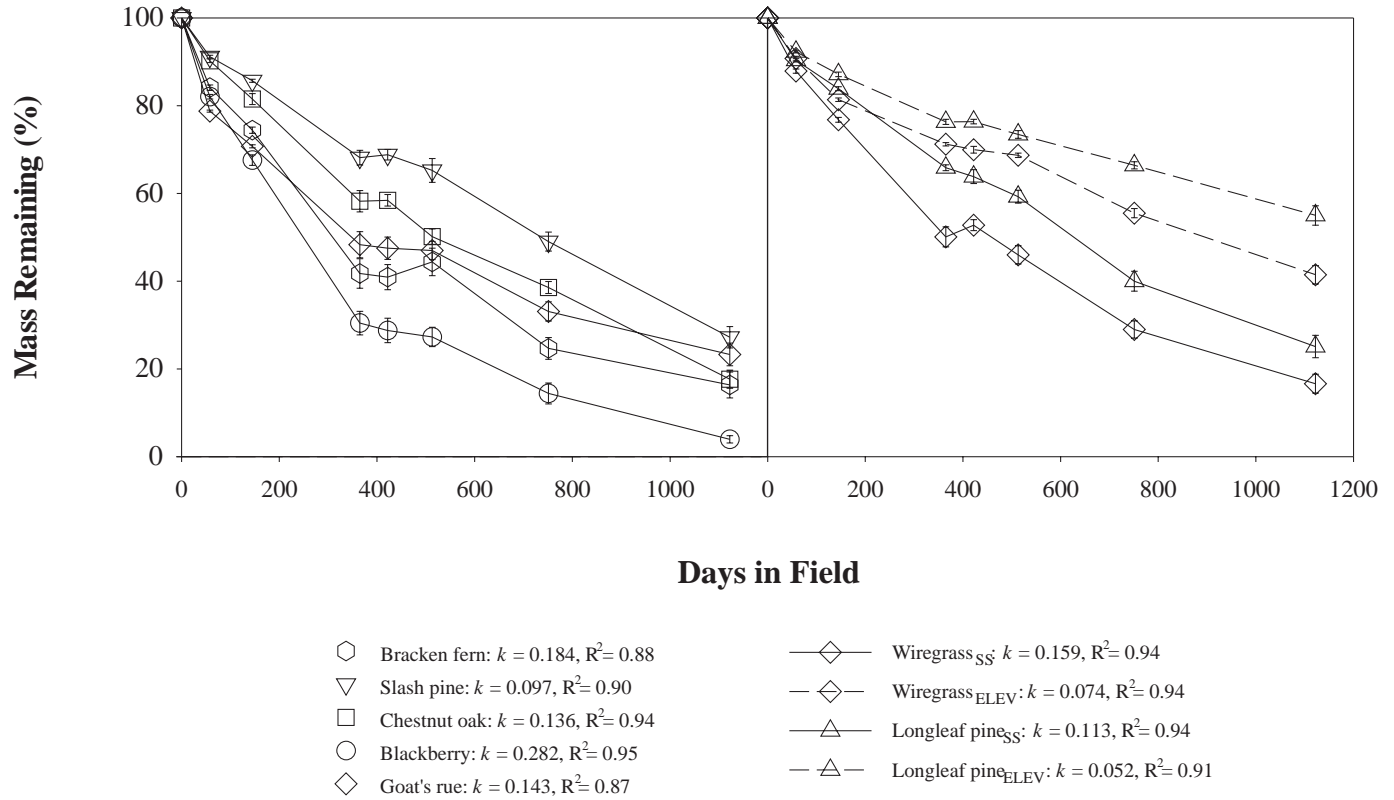


Table 2. Initial substrate quality (%) indices for the seven foliar litter types used in this study.

Litter type	C	N	P	Extractable C	Acid-soluble C	Acid-insoluble C	Acid-insoluble C/N
Blackberry	49.52 (0.14)	0.90 (0.01)	0.056 (0.002)	65.6 (1.4)	20.4 (0.9)	14.7 (0.5)	16.3
Bracken fern	46.29 (0.09)	1.15 (0.01)	0.081 (0.003)	27.6 (2.4)	29.6 (1.1)	37.0 (1.2)	32.2
Chestnut oak	51.82 (0.12)	0.69 (0.01)	0.021 (0.002)	46.1 (2.7)	24.5 (1.9)	30.9 (0.7)	44.8
Goat's rue	49.52 (0.31)	1.78 (0.01)	0.052 (0.002)	43.3 (2.5)	25.0 (1.8)	31.8 (1.6)	17.9
Longleaf pine	51.66 (0.22)	0.35 (0.01)	0.017 (0.001)	34.2 (2.2)	33.0 (1.2)	31.3 (1.5)	89.4
Slash pine	52.38 (0.38)	0.34 (0.01)	0.006 (0.000)	29.9 (0.9)	31.6 (1.1)	37.9 (0.9)	111.5
Wiregrass	47.56 (0.07)	0.53 (0.01)	0.035 (0.001)	51.9 (2.2)	36.3 (1.2)	10.1 (1.7)	19.1

Note: Values are means with SD given in parentheses.

slash pine, chestnut oak) or (ii) minimal, short-lived immobilization of N (bracken fern), P (goat's rue), or both N and P (blackberry). While these six soil-surface litter types did immobilize other nutrients assessed in this study (i.e., Ca, K, and Mg), the relative rates of immobilization for these nutrients did not exceed those for N or P on any sample date (Figs. 3 and 5).

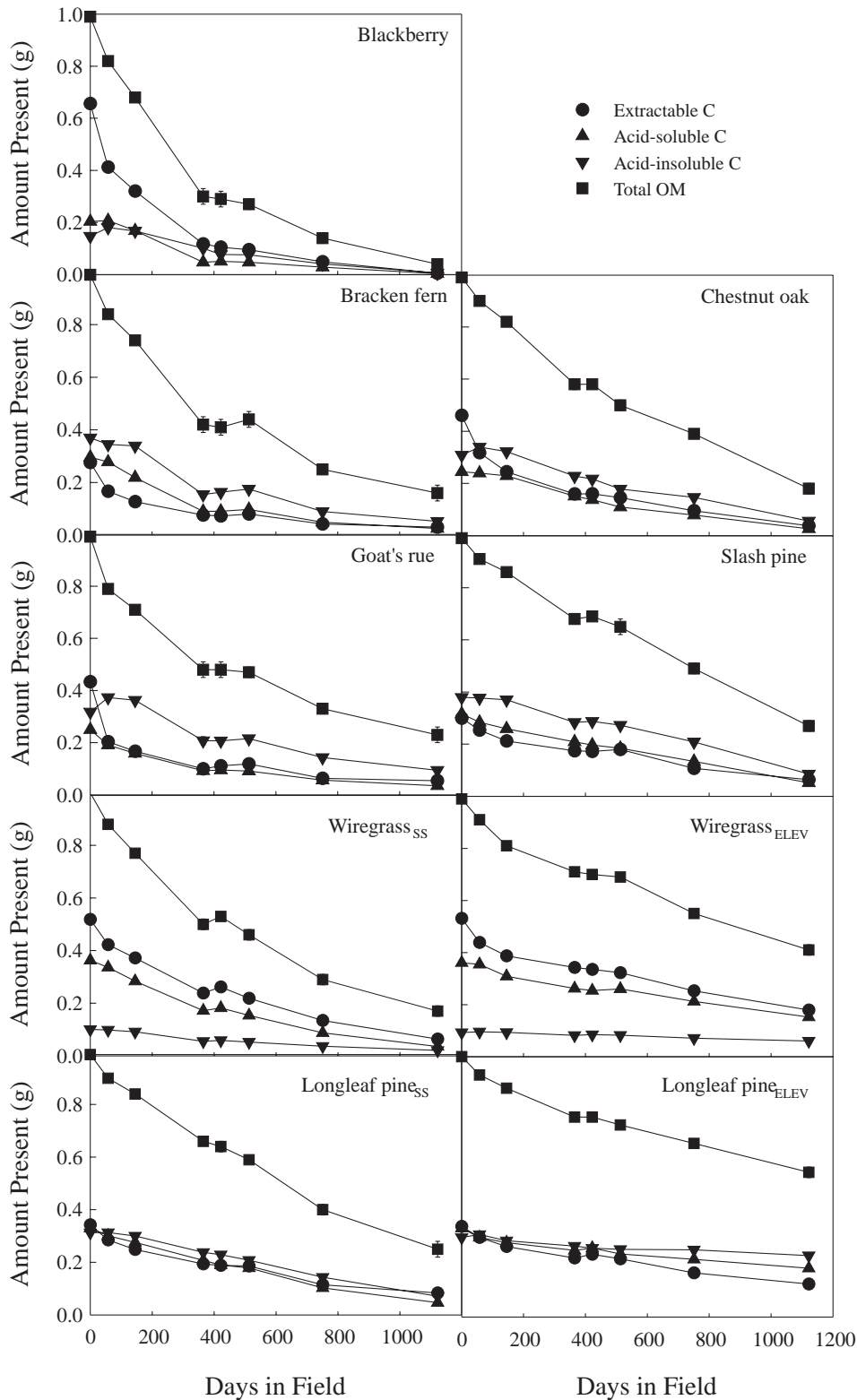
The litter for the three tree species exhibited prolonged P immobilization which peaked on day 513 of decomposition (121.1 ± 10.6 , 141.7 ± 22.4 , and $299.8 \pm 34.2\%$ of original P for longleaf pine, chestnut oak, and slash pine, respectively) for each species. Slash pine litter remained in a net immobilization phase after approximately 3 years of decomposition ($204.7 \pm 34.6\%$ of original P remaining). In contrast, longleaf pine and chestnut oak litter exhibited a net mineralization of P by the day 1122 sample date. The onset of P immobilization in longleaf pine and chestnut oak litter did

not coincide with the onset of acid-insoluble C fraction degradation (Figs. 3 and 5).

Nitrogen was immobilized by all of the tissue types incubated on the soil surface except wiregrass and goat's rue litter (Fig. 5). For the five litter types that did exhibit N immobilization, tissue N content generally peaked on day 58 (range of 103.6 ± 3.0 to $107.2 \pm 1.3\%$ of original N for slash pine needles and bracken fern fronds, respectively) before entering a net mineralization phase by day 365 for each litter type except longleaf pine needles, which peaked at $104.5 \pm 2.1\%$ of original N on day 422 of decomposition before entering a net mineralization phase. The onset of net N mineralization generally coincided with the onset of acid-insoluble C fraction disappearance (Fig. 3).

While most litter types initiated net N mineralization within the first year of decomposition, mineralization rates thereafter varied widely among the tissues (Fig. 5). After

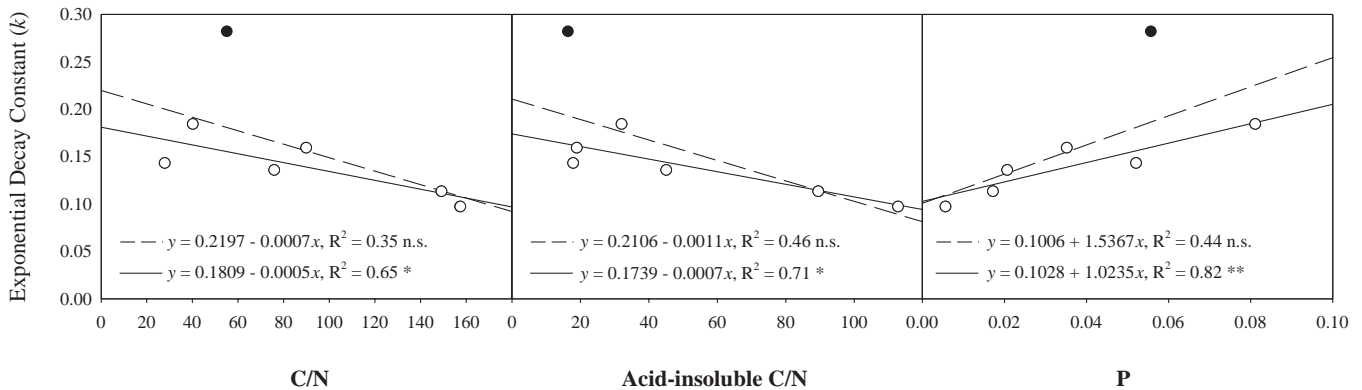
Fig. 3. Carbon-fraction mass loss patterns through time for each litter type. Each C fraction was standardized to 1 g, and values are mean absolute amount present on each collection date. Error bars are SEs.



3 years of decomposition, the percentage of original N remaining in the tissues ranged from 6.3 to 56.3% for blackberry leaves and slash pine needles, respectively (Fig. 5). The percentage of original N remaining in the tissues was strongly and inversely correlated with the initial P concen-

tration (correlation coefficients of -0.83 , -0.83 , and -0.80 after 1, 2, and 3 years of decomposition, respectively). Furthermore, with the exception of the tree litter types that exhibited prolonged P immobilization, N and P mineralization rates for the soil-surface litter types over the 3-year period

Fig. 4. Exponential decay constants versus selected initial substrate quality indices for the seven litter types incubated on the soil surface. Linear functions, coefficients of determinations, and probability values are provided for regressions run with (broken line) and without (solid line) blackberry included (ns, not significant; *, $P < 0.05$; **, $P < 0.01$; and ***, $P < 0.001$).



were strongly and positively correlated (correlation coefficients of 0.86, 0.98, 0.99, and 0.99 for wiregrass, bracken fern, blackberry, and goat's rue, respectively).

Longleaf pine and wiregrass litter elevated in wiregrass crowns exhibited significantly lower N and P mineralization rates than corresponding tissues decomposing on the soil surface (Fig. 5). Elevated and soil surface wiregrass litter differed significantly in the percent N remaining on day 365 and consistently thereafter, whereas the percent P remaining differed significantly between the two positions only on the last two sample dates. The percent N and P remaining in longleaf pine litter incubated in the two positions differed significantly only on the last sample date. After 3 years of decomposition, the percentage of original N remaining in soil surface and corresponding elevated litter was 51.2 ± 6.1 versus $94.9 \pm 3.5\%$ for longleaf pine and 28.6 ± 2.9 versus $76.8 \pm 2.5\%$ for wiregrass. Likewise, the percentage of original P remaining in soil surface and corresponding elevated litter was 66.7 ± 9.3 versus $99.2 \pm 5.1\%$ for longleaf pine and 24.8 ± 4.5 versus $52.0 \pm 4.1\%$ for wiregrass after 3 years of decomposition (Fig. 5).

The seven soil-surface and two elevated litter types used in this study exhibited the standard inverse-linear relationship between the percent mass remaining and tissue N concentration (Fig. 6). However, inverse-linear relationships between percent mass remaining and tissue P or acid-insoluble C-fraction concentrations were not significant for any litter type. The coefficients of determination for the N relationship increased significantly for four litter types (0.70, 0.92, 0.96, and 1.0 for goat's rue, bracken fern, blackberry, and chestnut oak, respectively) when the point from the last sample date was eliminated from the analysis. (Note that this is consistent with other reports which indicate that the inverse-linear relationship between percent mass remaining and N concentration holds until there is approximately 20% mass remaining; see Aber et al. 1990.) Despite the strong species-specific relationships, the slopes of these functions were not strongly correlated with any of the initial substrate quality indices assessed in this study (Table 2) possibly because of the relatively narrow range in slopes among litter types (Fig. 6).

Discussion

While foliar litter decomposition has been studied exten-

sively in temperate forests and grasslands (Aber et al. 1990; Seastedt et al. 1992; Aerts 1997), the patterns and controls of litter decomposition have not been assessed in longleaf pine – wiregrass woodlands, which exhibit compositional and structural characteristics of both forest and grassland ecosystems and generally occur at the warmer extreme of the temperate region (Fig. 1) (Drew et al. 1998; Mitchell et al. 1999). The litter position assessments conducted as part of this study revealed that 57.7 and 67.4% of the total litter standing stock in 1- and 2-year-old ground covers, respectively, decompose in the crowns of wiregrass bunches (Table 1). While sites with more than 2 years of litter accumulation were not assessed in this study, the 2-year-old ground cover was approaching crown closure, and it may be hypothesized that litter immobilization in older ground covers will be comparable with or greater than that measured for the 2-year-old system.

Litter mass loss dynamics

The mass loss rates for tissues incubated on the soil surface of longleaf pine – wiregrass woodlands were comparable with or greater than those reported for other pine forest types growing on sites with similar soils and (or) climatic regimes. After 1 year of decomposition, mass loss for tissues incubated on the soil surface in longleaf pine – wiregrass woodlands ranged from 31.9 to 69.6% for slash pine needles and blackberry leaves, respectively (Figs. 2 and 3). In comparison, 1-year mass loss reported for loblolly pine (*Pinus taeda* L.) and slash pine ranged from 15 to 27% for needles incubated on the forest floor of their respective forest types in the southeastern United States (Jorgensen et al. 1980; Gholz et al. 1985; Polglase et al. 1992).

In addition to these intraregional comparisons, chestnut oak (i.e., the common litter type used in this study and LIDET; LIDET 1995) mass loss measured in the longleaf pine – wiregrass woodlands was comparable with or substantially higher than those measured in the 27 LIDET study sites spanning from the arctic tundra to tropical rainforests (LIDET 1995). The percent mass remaining for chestnut oak after the first, second, and third year of decomposition in longleaf pine – wiregrass woodlands (58.2 ± 2.4 , 38.6 ± 1.4 , and $17.6 \pm 2.1\%$, respectively) were most similar to those measured in the temperate deciduous forests at the Harvard Forest Long-Term Ecological Research Site in Massachu-

Fig. 5. Nutrient net immobilization and mineralization patterns through time for the five litter types incubated only on the soil surface (left panels) and the longleaf pine and wiregrass litter incubated on both the soil surface (SS) and elevated (ELEV) in wiregrass crowns (right panels). Values are means, and error bars are SEs.

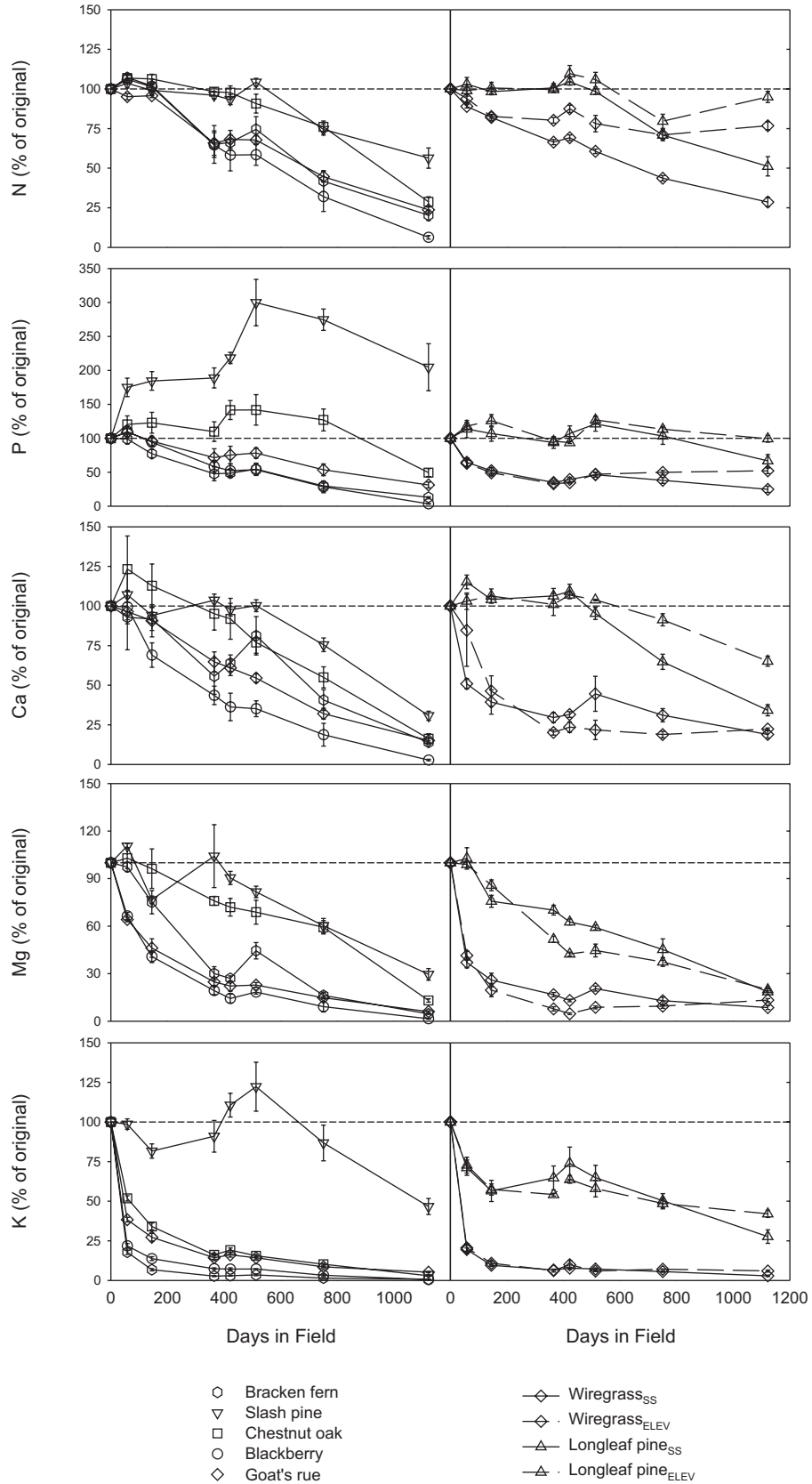
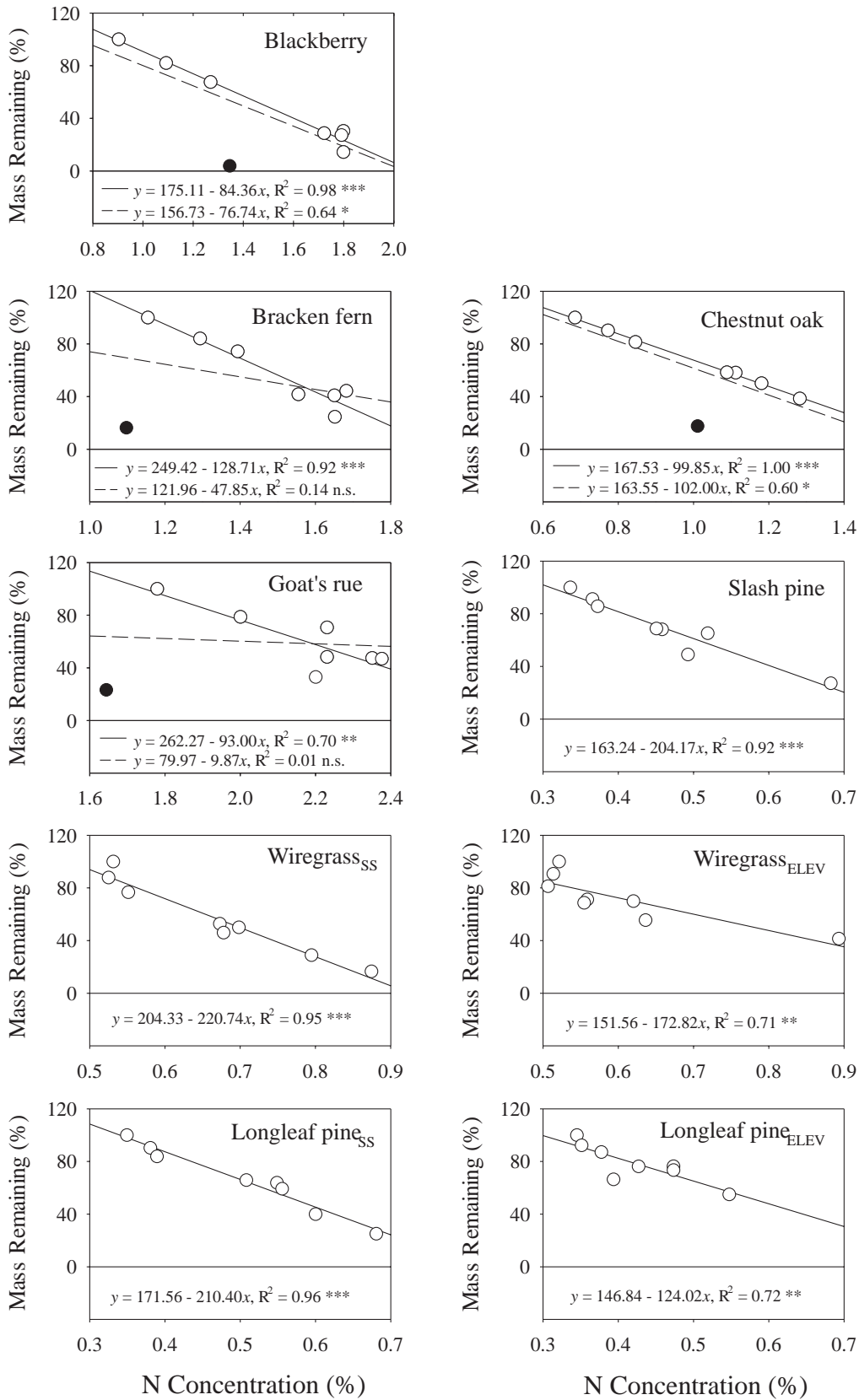


Fig. 6. Inverse-linear relationships between the percent mass remaining and the nitrogen concentration of tissues through time for each litter type. Linear functions, coefficients of determinations, and probability values are provided for regressions run with (broken line) and without (solid line) the last sample date (solid circles) included (ns, not significant; *, $P < 0.05$; **, $P < 0.01$; and ***, $P < 0.001$).



setts (60.7 ± 6.0 , 35.9 ± 13.8 , and $14.8 \pm 8.3\%$, respectively) and the tropical rainforests at the La Selva Biological Station in Costa Rica (62.3 ± 1.6 , 34.1 ± 6.5 , and $28.1 \pm 7.9\%$, respectively) (Figs. 2 and 3). It should be noted that while the chestnut oak litter for this study and the LIDET study were collected from the same location, the results are not statistically comparable, since the tissues for the two studies were collected in different years. However, the differences in mass loss rates between the longleaf pine – wiregrass woodland sites reported here and the LIDET sites were likely conservative, since the initial substrate quality of the chestnut oak litter used in this study (e.g., N = 0.69% and acid insoluble C/N = 44.8; Table 2) was lower than that of the chestnut oak litter used in the LIDET study (e.g., N = 0.86% and acid insoluble C/N = 27.3).

While litter mass loss rates on the soil surface of the longleaf pine – wiregrass woodlands were comparable with or greater than those measured in a wide range of terrestrial biomes, the majority of litter in these ecosystems decomposes above the soil-surface in wiregrass crowns where mass loss decay constants (0.052 and 0.074 for longleaf pine and wiregrass, respectively) were approximately 50% lower than corresponding soil-surface rates and among the lowest values reported in the literature (Fig. 2) (Bruhn 1980; Hart et al. 1992; Monleon and Cromack 1996; Aerts 1997). The significant reduction in mass loss rates for elevated litter compared with soil-surface litter with the same initial substrate quality may be attributed to reduced contact with decay organisms in the soil and (or) alteration of the litter microclimate. Although these ecosystems received moderate amounts of precipitation during this study, elevated foliar litter likely experienced more extreme drying cycles because of high intercepted solar radiation at these lower temperate latitudes, the relatively open overstory canopy structure, and low moisture buffering capacity in wiregrass crowns (Landers et al. 1995; Mitchell et al. 1999; Wilson et al. 1999). This significant reduction in mass loss rates for litter elevated above the soil surface was consistent with patterns observed in temperate grassland ecosystems (Seastedt et al. 1992). In addition to having a substantial impact on fuel loading and fire behavior in these systems, the resulting accumulation of litter should influence the microclimate and resource availability in the understory (Seastedt et al. 1992). In particular, the potential impact of litter position and mass loss rates in the regulation of nutrient fluxes prior to thermal mineralization is important in these fire-maintained systems.

Litter nutrient dynamics

Phosphorus appeared to be the most limiting nutrient to the microbial decomposers in longleaf pine – wiregrass woodlands. Initial P concentration was the tissue substrate quality index most strongly correlated with the mass loss decay constants (Fig. 4). Also, P was the most strongly immobilized nutrient in the three tissues (i.e., foliage of the tree species) that exhibited extensive and prolonged immobilization (Fig. 5). The pronounced immobilization of P is consistent with the results for big bluestem (*Andropogon gerardii* Vitman) decomposing in tallgrass prairie (Koelling and Kucera 1965; Seastedt 1988), slash pine needles decomposing in older stands in central Florida (Gholz et al. 1985), as well as foliage decomposing in subtropical and tropical for-

ests (O'Connell 1988; Vitousek et al. 1994; Hobbie and Vitousek 2000).

While P appeared to be the overriding limiting nutrient, N also appeared to be limiting as evidenced by (i) N immobilization in five of the seven species decomposing on the soil surface (Fig. 5); (ii) the slow rate of N mineralization relative to P mineralization from the wiregrass litter (Fig. 5); and (iii) the inverse-linear relationship between the percent mass remaining and the N concentration of tissues, which is indicative of rate limiting resources (Fig. 6) (Berg and McClaugherty 1987, 1989; Aber et al. 1990). In addition, N limitations may have been at least partially alleviated by inputs via atmospheric deposition, which added an estimated $7.9 \text{ kg N} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$ to this ecosystem (unpublished data that is consistent with total N deposition rates measured in Southern Commercial Forests Research Cooperative Monitoring Sites summarized by Allen and Gholz (1996)) (Aerts and De Caluwe 1997). Collectively, these results suggest that P and N were colimiting to decomposition which is consistent with previous reports that these nutrients were colimiting to net primary production in comparable ecosystems (Koelling and Kucera 1965; Gholz et al. 1985; Christensen 1987; Seastedt 1988).

The P immobilization potential of longleaf pine needles (in both the soil surface and elevated positions) coupled with the significant reduction in P mineralization from wiregrass tillers decomposing in the elevated position ($52.0 \pm 4.1\%$ of original P versus $24.8 \pm 4.5\%$ for corresponding soil-surface litter after 3 years of decomposition) suggest that the necromass in the ground cover may be a relatively strong P sink. This, in turn, may adversely affect nutrient mineralization and net primary production both directly, since P is an apparent limiting nutrient, and indirectly, since P may influence key N cycling processes. For example, the percentage of original N remaining after 3 years of decomposition varied widely among litter types (range of 6.3 to 56.3% for blackberry leaves and slash pine needles, respectively) and was strongly and inversely correlated with the initial P concentrations in the tissues (correlation coefficients of -0.83 , -0.83 , and -0.80 after 1, 2, and 3 years of decomposition, respectively). Also, N-mineralization rates among the three tissues with relatively high initial N concentrations were strongly and positively correlated with P-mineralization rates (correlation coefficients of 0.99, 0.98, and 0.99 for blackberry, bracken fern, and goat's rue, respectively). In addition, P availability may limit the symbiotic N_2 -fixation activity by native herbaceous legumes that have been hypothesized to play important N-replacement roles in these regularly burned ecosystems (Boring et al. 1988, 1991; Hendricks and Boring 1992, 1999). Phosphorus controls on the input and availability of N indicate that fire regimes that reduce the availability of N and P relative to microbial demand may promote the establishment of a positive feedback between litter substrate quality and nutrient availability (Mooney and Gulmon 1982; Kellman 1984; Gholz et al. 1985; Aerts and De Caluwe 1997). This positive feedback may further exacerbate nutrient limitations in these inherently oligotrophic ecosystems, thereby emphasizing the importance of developing quantitative models of litter mass loss and nutrient dynamics to more rigorously evaluate burning regimes in longleaf pine – wiregrass woodlands.

Models of mass loss and nutrient dynamics

Biologically mediated foliar litter decomposition in temperate biomes has been widely studied and is generally characterized by a two-phase conceptual model (Aber and Melillo 1982; Berg 1986, 2000; McClaugherty and Berg 1987; White et al. 1988; Aber et al. 1990; Couteaux et al. 1995; Aerts 1997). Phase one is described by a relatively constant fractional mass loss regulated primarily by microclimate and secondarily by litter substrate quality controls on microbial activity. During this phase, extractive and acid-soluble C molecules are consumed by microbes resulting in the net immobilization of limiting nutrients, most notably N (Berg 1986; Aber et al. 1990). In contrast, phase two is characterized by substantially lower mass loss rates as the residual acid-insoluble C compounds are slowly degraded (McClaugherty and Berg 1987). The onset of phase two is generally marked by the net mineralization or release of previously limiting nutrients from the litter as microbial populations become more energy limited by the recalcitrant acid-insoluble C substrate. A critical question for assessing and predicting the impact of various fire regimes in longleaf pine – wiregrass ecosystems is whether these general patterns and controls of biologically mediated foliar litter decomposition occur in fire-maintained longleaf pine – wiregrass woodlands, which differ in structure, function, composition, and climate from the majority of ecosystems used to develop this model.

While blackberry, bracken fern, goat's rue, and wiregrass decomposition dynamics were generally consistent with the general two-phase model, the mass loss and nutrient dynamics for the three tree species differed from the model in three basic ways. First, as previously noted, P immobilization in the tree foliar litter was more extensive and prolonged than N immobilization (Fig. 5). Second, the C-fraction mass loss patterns for the three tree species differed substantially from the other litter types in that the degradation of the three C fractions generally occurred concurrently as opposed to the more typical sequential degradation of extractable, acid-soluble, and acid-insoluble C fractions (Fig. 3). Finally, the onset of P mineralization among the foliar litter of the three tree species was not mechanistically linked to the onset of acid-insoluble C-fraction degradation as commonly reported for the mineralization of limiting nutrients (i.e., N) in temperate ecosystems (Figs. 3 and 5) (Berg and McClaugherty 1987, 1989). Although it is not possible to clearly identify why the tree foliar litter exhibited different C-fraction mass loss and nutrient dynamics than the herbaceous litter decomposing in the same microsites, the tree litter did have the lowest initial P concentrations of the litter types used in this study suggesting that tissue substrate quality influenced microbial activity and (or) composition (i.e., bacterial vs. fungal) in these woodlands (Table 2) (Berg 1986; Couteaux et al. 1995; Aerts 1997).

Although existing models for temperate biomes may not adequately describe tissue mass loss and nutrient patterns for the suite of tissues used in this study, the results may be used to modify and (or) develop quantitative models of necromass and nutrient dynamics in the ground cover of longleaf pine – wiregrass woodlands. The generalized relationships between litter exponential decay constants (k) and initial substrate quality indices (Fig. 5) may be used to pre-

dict the litter mass in the ground cover through time. In turn, the species-specific inverse-linear relationships between the percent mass remaining and tissue N concentrations (Fig. 6) may be used to estimate the N capital in the litter for different burn intervals. While the lack of significant inverse-linear relationships between percent mass remaining and tissue P concentrations precludes model predictions of litter P concentrations through time, this element is generally transformed to more readily available inorganic forms by fire and retained in the ecosystem (Raison et al. 1985; Binkley et al. 1992; Gillon et al. 1995).

Implications for fire and ecosystem management

The results of this study qualitatively suggest that the operational fire regimes (i.e., burning on 1- to 3-year intervals) typically employed in remnant longleaf pine – wiregrass woodlands may balance N losses via volatilization with P (and understory light) limitations via litter accumulation and immobilization. The relatively rapid mineralization of N and P from litter with high initial nutrient concentrations (e.g., blackberry, bracken fern, and goat's rue) indicates that much of the N in these tissues (importantly including fixed legume N) will be mineralized and conserved in the ecosystem even under short burn intervals. On the other hand, the low mineralization potential of relatively nutrient poor litter (e.g., longleaf pine needles and wiregrass tillers particularly in the elevated position) after 3 years of decomposition suggests that large nutrient pools will be immobilized during most operational burn intervals. However, employing longer or suppressed burn intervals to conserve the C and N in these tissues may have adverse effects on ecosystem structure and function via (i) greater fuel accumulation that may amplify fire intensity and produce negative forest impacts (Landers et al. 1995), (ii) greater immobilization of P which may limit decomposition, N mineralization, and productivity in these sites (Gholz et al. 1985), (iii) lower light availability in the understory which may reduce ground cover net primary productivity, and perhaps even flowering and reproduction (Seastedt et al. 1992), and (iv) decreased N_2 fixation (due to light and (or) P limitations) by native herbaceous legumes (Hains et al. 1999; Hendricks and Boring 1999). Others have also reported enhanced establishment of fire-intolerant oak species (*Quercus* spp.) in the mid- and over-story of fire-suppressed longleaf pine woodlands, which may promote the succession of these sites to other types of ecosystems (Kellman 1984; Jacquemain et al. 1999).

This study was conducted in type-12 longleaf pine – wiregrass ecosystems that are intermediate site types within a broad gradient of longleaf pine – wiregrass woodlands (i.e., ranging from xeric sandhills to the edge of wetlands) exhibiting patterns of moisture availability and aboveground net primary productivity that are inversely correlated with N and P availability indices (see Goebel et al. 1997; Mitchell et al. 1999; and Wilson et al. 1999). Thus, additional studies are warranted to assess the relative influences and interactions of microclimate and nutrient availability on litter decomposition dynamics across this complex resource availability gradient with particular emphasis on P controls and variation due to litter position in the ground cover. These studies of internal nutrient cycling dynamics should be coupled with assessments of nutrient fluxes into (e.g., N_2

fixation, atmospheric deposition, and fertilization) and out of (e.g., volatilization, denitrification, leaching, and harvesting) these ecosystems to more fully evaluate the effects of various fire regimes on the structure and function of longleaf pine – wiregrass woodlands.

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