Patterns and controls of ecosystem function in longleaf pine – wiregrass savannas.
I. Aboveground net primary productivity

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Abstract: Longleaf pine – wiregrass (*Pinus palustris* Mill. – *Aristida stricta* Michx.) woodlands occupy sites ranging from deep, xeric sandhills to the edge of wetlands in the southeastern United States. Aboveground net primary productivity (ANPP) of the overstory and understory were determined for three replicate sites of three site types (xeric, intermediate, and wet–mesic) that span a wide environmental gradient. In addition, soil moisture (at 30 and 90 cm) and N mineralization (in situ buried bag incubations) were measured through an annual cycle. Longleaf pine – wiregrass ecosystems varied by nearly twofold in ANPP across complex gradients. Overstory and understory and total (overstory and understory) ANPP were positively correlated to soil moisture at 30 and 90 cm. The proportion of understory ANPP relative to the total ANPP did not increase across the environmental gradient as predicted by hypotheses that invoke niche differentiation in rooting habits of grasses and trees. Contrary to expectations, cumulative net N mineralization was negatively related to soil moisture. All ANPP estimates were significantly and negatively related to cumulative N-mineralization. Further work is needed to explore the mechanisms by which soil moisture regulates productivity across space, time, and for individual species. Additional experimentation through resource addition would allow for investigations into multiple resource limitations and how resource limitations vary depending on gradient position.

Résumé : La forêt claire de pin des marais et aristide des pinèdes (*Pinus palustris* Mill. – *Aristida stricta* Michx.) occupe, dans le sud-est des États-Unis, des sites répartis depuis des collines de sable profond sec jusqu'au bord des milieux humides. Les auteurs ont déterminé la productivité primaire nette épigée (PPNÉ) de l'étage dominant et du sous-étage dans trois répliques de trois types de sites (sec, intermédiaire et humide–mésique) couvrant un gradient environnemental étendu. En plus, ils ont mesuré l'humidité du sol à 30 et 90 cm et la minéralisation de l'azote (en utilisant in situ des sacs d'incubation enfouis) pendant un cycle annuel complet. La PPNÉ des écosystèmes de pin et aristide varie, le long d'un gradient complexe, presque du simple au double. La PPNÉ de l'étage dominant, du sous-étage et totale (étage dominant et sous-étage) est corrélée positivement avec l'humidité du sol à 30 et 90 cm. La proportion de la PPNÉ du sous-étage, par rapport à la PPNÉ totale, n'augmente pas le long du gradient environnemental, tel que prédit par les hypothèses qui font appel à la différenciation des niches quant à la forme d'enracinement des herbes et des arbres. Contrairement à l'attente, la minéralisation cumulative nette d'azote est reliée négativement à l'humidité du sol. Tous les estimés de la PPNÉ sont corélés, de façon significative et négative, avec la minéralisation cumulative de l'azote. D'autres travaux sont nécessaires pour explorer les mécanismes par lesquels l'humidité du sol règle la productivité dans l'espace, dans le temps et des différentes espèces. Une expérimentation additionnelle, par l'addition de ressources, permettrait d'étudier plusieurs facteurs limitatifs et la façon dont ces facteurs limitatifs varient en fonction de la position par rapport au gradient.

[Traduit par la rédaction]

Introduction

Net primary productivity (NPP) is perhaps the most fundamental characteristic of terrestrial ecosystems. Understanding how productivity is regulated across the landscape is among the most pressing issues in terrestrial ecology (Aber and Melillo 1991). Although considerable work has been done that quantifies productivity patterns and their controls for various forests (Keyes and Grier 1981; Nadelhoffer et al. 1985; Gholz et al. 1991; Gower et al. 1992; Reich et al. 1997) and grasslands (Coupland 1979; Long and Hutchin 1990; Long et al. 1992; Knapp et al. 1993), relatively less attention has been paid to landscape-scale variation in productivity of savanna systems (McPherson 1997). This is particularly true for longleaf pine – wiregrass (*Pinus palustris* Mill. – *Aristida stricta* Michx.) ecosystems in the U.S. Southeast. To date, no study has documented patterns in net primary productivity of longleaf pine – wiregrass woodlands or investigated their controls.

Longleaf pine – wiregrass ecosystems once dominated the Coastal Plain region of the southeastern United States (Ware

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et al. 1993); however, these forests presently occupy a much smaller proportion of the landscape than historically (Noss 1989). Recently, interest has increased in conserving the remaining longleaf pine stands as well as restoring longleaf pine ecosystems on a portion of the sites that they once occupied because of the importance of longleaf pine – wiregrass ecosystems both from a regional biological conservation view and their economic value (Landers et al. 1995). These forests are distinguished ecologically by the wide variety of sites that they occupy (Peet and Allard 1993), their dependence on fire, as well as the large number of additional disturbances that act at various scales in time and space to mold their structure and function (Michener et al. 1998). By virtue of the wide variety of site types and the interaction of site and disturbance, these communities are among the most floristically diverse temperate ecosystems recorded in the literature (Walker and Peet 1983). Understanding the complex feedback mechanisms among disturbance, site resources, and productivity is essential for guiding ecosystem management (Christensen et al.1996) and restoration efforts (Ewel 1987).

Frequently burned longleaf pine woodlands are characterized by an open canopy monotypic overstory with a grass-dominated understory. Both longleaf pine and wiregrass, the dominant grass in many undisturbed, fire-maintained longleaf pine ecosystems, have attributes that enhance persistence in fire-dominated landscapes and encourage frequent fire (Clewell 1989). These ecosystems are found throughout a wide range of sites in which fire has been maintained, ranging from xeric, deep sands where scrub oaks (predominately turkey oak, *Quercus laevis* Walt.) are codominants (Christensen 1988; Jacqmain et al. 1999) to the edge of wetlands in which slash pine (*Pinus elliottii* L.) is found with longleaf pine (Christensen 1988; Ware et al. 1993; Goebel et al. 1997).

Although it is widely recognized that longleaf pine – wiregrass communities occupy a wide complex ecological gradient, it is unknown how patterns in resource availability and productivity are regulated across the gradient. Walter (1971) proposed that niche differentiation in rooting habits of grasses and trees with deep taproots should result in predictable patterns in productivity across landscapes. Walter's two-layer hypothesis predicts that productivity of deep-rooted trees should be relatively greater on deep soils with low water holding capacity than shallow rooted grasses, and grasses should increase in NPP disproportionately on shallow soils underlain by an impervious, heavy-textured subsurface soil horizon (Scholes and Archer 1997). Findings supporting the supposition that grasses and woody plants access different soil moisture pools have been reported for shrub steppe communities (Lee and Lauenroth 1994; Sala et al. 1989; Soriano and Sala 1983) and tree savannas (Hesla et al. 1985; Johnson and Tothill 1985; Knoop and Walker 1985; Scarpe 1992). Longleaf pine is a deep tap rooted species (Wahlenberg 1946), and wiregrass roots are largely confined to the surface soil (Satterson and Vitousek 1984). Moreover, longleaf pine – wiregrass sites vary from deep sands to wetlands in which heavy-textured, subsurface horizons impede drainage and result in frequently perched water tables at or near the soil surface (Goebel et al. 1997); thus, such sites provide an opportunity to test this prediction. However, the extent that soil moisture rather than fertility is a major determinant of productivity has not been assessed for this ecosystem.

In addition to moisture, soil fertility has been shown to regulate productivity of forests (Reich et al. 1997). Particularly for southern pine forests, N is the most common limiting nutrient (Pritchett and Smith 1975; Vose 1988; Vose and Allen 1988); however, little is known with respect to the direction or magnitude in the variability of N availability across longleaf pine gradients. Soil moisture has been suggested to be positively correlated with N mineralization across some landscapes by directly increasing populations and activities of soil microbes (Zak et al. 1986) and indirectly by affecting the amount and quality of organic matter inputs to the soil (Aber and Melillo 1982; Melillo et al. 1982; Vitousek 1982; Hendricks et al. 1997). Although the complex environmental gradient that longleaf pine – wiregrass communities occupy is often referred to as a hydrologic gradient, the extent that productivity may be related to variation in soil N availability has not been investigated. Albaugh et al. (1998) reported that loblolly pine (*Pinus taeda* L.) was influenced by N fertility (fertilization) to a much greater extent than soil moisture (irrigation) on deep, excessively well-drained sands. Gholz et al. (1991) also reported that slash pine aboveground productivity on a somewhat poorly drained flatwood site was influenced more by fertilization than soil moisture. Although these two studies span the range of sites that longleaf pine ecosystems occur, the extent that longleaf pine – wiregrass productivity follows similar patterns is not known.

The objective of this work was to quantify aboveground productivity of longleaf pine – wiregrass woodlands, soil moisture, and N mineralization across a complex environmental gradient from deep sandy xeric sites to the longleaf wiregrass sites that boarder wetlands. We hypothesized that (*i*) productivity varies among sites proportionally to soil moisture availability throughout the landscape, but because of differences in root habit, surface soil moisture will be more closely related to understory productivity (especially wiregrass), while variation among sites in subsurface soil moisture should be more closely related to variation in overstory aboveground net primary productivity (ANPP); and (*ii*) N availability should increase as moisture increases and, thus, also be positively correlated to patterns in productivity. However, N-mineralization will explain a greater proportion of the variation in productivity among sites due to overriding nutrient limitations.

Methods

Site description

The study site is located at Ichauway, a 115 km^2 preserve located in the Coastal Plain of southwestern Georgia, U.S.A. The climate for this region is characterized as humid subtropical (Christensen 1981), with an average annual precipitation of 131 cm, which is evenly distributed throughout the year. Mean daily temperatures range from 21 to 34°C in summer and from 5 to 17°C in winter (Goebel et al. 1997). Ichauway is located within the Dougherty Plain physiographic region (Hodler and Schretter 1986) in the Gulf Coastal Plain Province described by Walker and Coleman (1987) or the Lower Coastal Plain and Flatwoods (LCPF) section (Plains and Wiregrass Plains subsections) described by McNab and Avers (1994). The LCPF section is a karst landscape, characterized by flat, weakly dissected alluvial deposits over Ocala Limestone (Hodler and Schretter 1986). Parent materials are marine and continental sand and clay deposits formed during the Mesozoic and Cenozoic eras (Keys et al. 1995).

Ecological site classification: soils and vegetation

We selected study sites with soils of three drainage classes encompassing the range of soil moisture conditions of longleaf pine – wiregrass ecosystem types at Ichauway: (*i*) excessively well drained; (*ii*) somewhat excessively drained; and (*iii*) somewhat poorly drained. The excessively well-drained sites occur on upland sand ridges of undulating slopes of 3–4% and have deep, sandy soils, with no argillic horizon, i.e., no significant accumulation of clay within 300 cm. These soils are Typic Quartzipsamments with a water-holding capacity (in the upper 300 cm) of approximately 18 cm water per metre of soil. The somewhat excessively drained sites occur on upland terraces with undulating slopes of 2% and have soils classified as Psammentic Kandiudults or Grossarenic Kandiudults. These soils are loamy sands over sandy loams, with a depth to argillic horizon approximately 150 cm. The water holding capacity of these sites is 28 cm water per metre of soil. The somewhat poorly drained sites occur on upland terraces with soils classified as Aquic Arenic Kandiudults. These soils are sandy loam over sandy clay loam or clay on nearly level slopes with a water holding capacity of 40 cm water per metre of soil. An argillic horizon is present within 50 cm of the soil surface. Hereafter, we refer to the excessively well drained sites as xeric, the somewhat excessively well drained sites as intermediate, and the somewhat poorly drained sites as wet–mesic.

The xeric, intermediate, and wet–mesic sites correspond to ecosystem types 13, 12, and 9, identified by a recent ecosystem classification of Ichauway, based on landscape position, soil type, and vegetation (Goebel et al. 1997). The vegetation of these sites is maintained with frequent prescribed fire with a return interval of 1–5 years, depending on moisture conditions and fuel accumulation. Xeric ecosystems are dominated by open stands of longleaf pine and scrub oaks: the dominant oak, turkey oak occurs in all the aboveground strata. Intermediate ecosystems are characterized by longleaf pine as a dominant overstory species and by bluejack oak (*Quercus incana* Bartr.) and sand post oak (*Quercus margaretta* Ashe) occurring only as understory components. The somewhat poorly drained ecosystems are characterized by the single dominant longleaf pine in the overstory with *Diospyros virginiana* L. occurring frequently in the understory. Dense ground cover at all sites is dominated by the perennial grass, wiregrass with numerous species of other perennial grasses and forbs also present (Goebel et al. 1997).

Study design

The three longleaf pine ecosystem types included in this study span the range of soil moisture conditions found at Ichauway and are similar to the range in soil types throughout the southwestern Georgia – northern Florida region. We selected three replications of each of the three ecological site types (n = 9). Plot size ranged from 0.47 to 1.31 ha (mean 0.66 ha) so that at least 55 pine trees were located in each plot. Ten subplots were randomly located within each stand based on basal area. To locate sampling subplots, a 5-m grid was established across each plot and pine basal area measurements (BAF 5) were made at the intersection of the grids. The distribution of pine basal area was then divided in 20 percentile rankings, and two randomly selected locations was chosen from each percentile ranking, yielding 10 subplots per plot. All sites were burned in March 1994.

Net nitrogen mineralization and soil moisture measurements

Nitrogen (N) availability was estimated for a 12-month period (June to June) using in situ buried bag incubations of the mineral soil in each of the 10 subplots (Eno 1960). Soil samples were collected from the top 10 cm in each subplot at the beginning of the incubation cycle, sieved at the laboratory, and subsampled for estimation of initial pools of inorganic N as well as soil moisture content. Four aliquots were drawn from each sample, placed in gas-permeable, plastic bags and buried (to 10 cm) in their original subplot location within a 24-h period. After an incubation cycle of 28–35 days samples were retrieved, composited by subplot, and treated in the same manner as the initial soil samples. All soils were extracted with 2 M KCl (10 g : 25 mL) by vigorous agitation on a mechanical shaker for 15 min followed by centrifugation for an additional 15 min period. The supernatant for each sample was then carefully drawn off and frozen until inorganic N analyses could proceed. Ammonium (NH_4^+) and nitrate (NO_3^-) concentrations were analyzed colorimetrically on a Lachat Flow Injection analyzer (Lachat Instruments, Inc., Milwaukee, Wis.). Ammonium N was analyzed by the indophenol-blue method and nitrate N was reduced to nitrite using a Cd column and the determined by diazotiation (Keeney and Nelson 1982; Lachat Instruments Inc. 1992, 1997). Net nitrogen mineralization was then calculated by subtracting the initial from the final pools of extractable inorganic N.

Soil moisture was measured using time domain reflectometry as described by Topp et al. (1980). Two sets of stainless steel rods (30 and 90 cm length) were inserted vertically in the soil in all subplots. Soil moisture was quantified using a Techtronix cable tester every 2 weeks throughout the study period (June 1995 – June 1996).

Productivity measurements

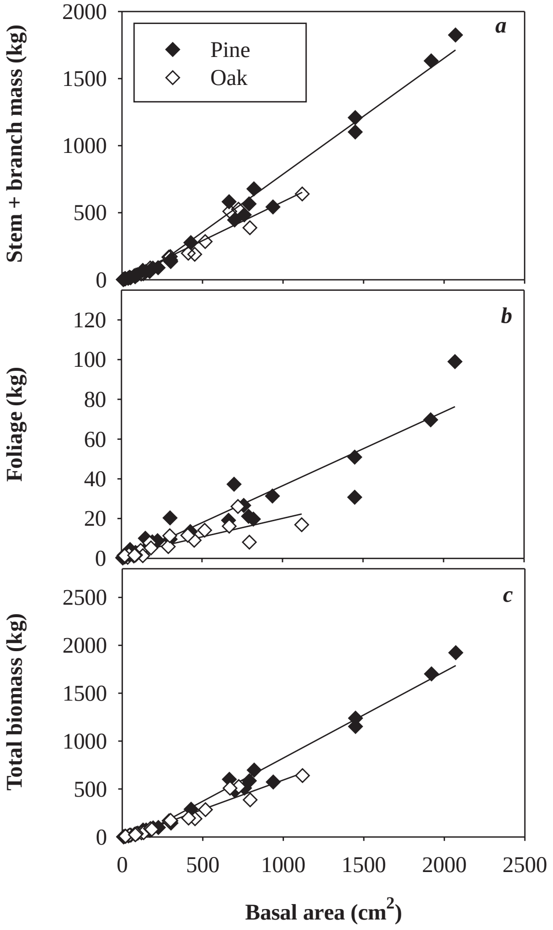
Aboveground biomass of longleaf pine and turkey oak were determined by constructing allometric equations from trees cut from areas adjacent to the study plots. Trees were selected to span the range in diameters found on the study sites. Selected trees were cut at groundline, and their height and DBH was recorded. The distance from the base of the tree to each branch, e.g., branch height was recorded. Each branch was severed from the bole and the branch length and diameter and fresh mass were recorded (±0.1 g). To convert fresh mass to dry mass for branches one branch from the lower third, middle third, and upper third of the canopy was randomly selected and dried to constant mass at 70°C. Foliage was separated by age-class (for pine) and fresh mass (±0.01 g) was determined. Foliage subsamples were taken for each age-class on each branch to determine fresh and dry mass conversion. After all branches were removed, the stem was cut into 1- to 2-m sections and weighed to the nearest 0.1 kg using a 100-kg capacity spring scale. Basal disks were cut from each section, and the ratio of fresh mass to dry mass was determined. Allometric equations and fitted lines using basal area as the independent variable are presented in Table 1 and Fig. 1, respectively. These equations explained 98% of the variation in aboveground biomass for pines and 97% for oaks. In addition, this approach was able to account for 93 and 90% of first-year and second-year needle biomass, respectively, and 84% of the variation in oak leaf biomass. Biomass increment was determined by calculating the change in aboveground wood production based on basal area increment and adding biomass of first-year needle production for pine and total leaf production for oaks for each tree. Five-year basal area growth was determined for pines and oaks in study plots by extracting an increment core in the summer of 1995 and growth estimated for 1989–1993. These increment cores also allowed determination of tree ages.

Table 1. Allometric equations for pine and oaks used in estimation of ANPP.

	b_0	b_1	SE	N	$P > F$	R^2
Pinus palustris						
First-year foliage		0.0221	0.0012	23	0.0001	0.93
Second-year foliage		0.0145	0.0010	23	0.0001	0.90
Total foliage		0.0366	0.0020	23	0.0001	0.94
Stem/branches	–77.0701	0.8640	0.0246	23	0.0001	0.98
Total biomass	–77.6939	0.9011	0.0250	23	0.0001	0.98
***Quercus* spp.**						
Total foliage		0.0211	0.0020	20	0.0001	0.84
Stem/branches		0.5614	0.0228	20	0.0001	0.96
Total biomass		0.5825	0.0237	20	0.0001	0.97

Nota: Data were collected in July–August 1995 and 1996, Baker County, Georgia. Mass values (kg) are regressed against basal area (cm^2).

Fig. 1. Combined stem and branch mass (*a*), total foliage (first- and second-year needles for pine) (*b*), and total biomass (*c*) as a function of basal area for 23 pines and 20 oaks used in developing allometric equations for the study. Data are from trees adjacent to the study plots and span the environmental gradient. No significant difference with respect to site was detected in the dependent variables. Equations fitted with simple linear regression are given in Table 2.



Sites differed in density and age of pines and oaks (Table 2). Mean pine age varied across sites with average age of xeric and wet–mesic sites 56 and 51 years old, respectively. Longleaf pine on intermediate sites averaged approximately 20 years older than those on the xeric or wet–mesic sites; however, Stoll et al. (1994) reported that age differences of a much greater magnitude than we observed had only marginal influences on pine growth. While some site differences were observed with respect to tree age, stand establishment probably came from the same stand replacement harvesting approximately 70 years ago (Palik and Pederson 1996). These age differences may reflect differences in the time of height growth initiation from the grass stage. The extent that observed age differences are significant determinants of longleaf pine growth cannot be assessed in this work and awaits future study. Presumably, rare older pines most likely were unmerchantable stems left after the harvest (Fig. 2). Oaks were codominant on the xeric site (347 trees/ha) but insignificant at the other two sites (1 or 2 trees/ha). They also tended to be younger than pines on average, although a few oaks greater than 130 years old were observed.

Aboveground productivity of the understory was quantified by sequential destructive harvests (0.75-m^2 plots) in July and November 1995. Plots were sampled from each subplot. All herbaceous vegetation was destructively harvested, and woody plants were included in the understory if stem diameter at ground level was 1 cm or smaller. Harvested plants were sorted into wiregrass (live and dead), other grasses, legumes, other forbs, ferns, woody plants, and dead herbaceous plant tissue. Sorted plant materials were then dried and weighed. The November 1995 harvest was conducted several weeks prior to the first killing frost. Understory productivity was determined by the change in live standing crop plus increases in dead plant material plus estimates of decomposed material (L.R. Boring, unpublished data) since last sampling period.

Statistical analysis

Differences among sites in aboveground productivity were determined using analysis of variance (three site types and three replications) (SAS Institute Inc. 1990). A statistically significant difference was noted at $\alpha = 0.05$ or less (LSD test). Soil moisture was averaged across all dates and N-mineralization was summed for the year. Aboveground productivity was regressed against resource availability using simple linear regression.

Results

ANPP varied across the gradient, but the magnitude of variation in productivity depended on the structural component (Fig. 3). Pine growth on a stand basis was strongly depressed on the xeric sites averaging approximately 1.50 $Mg \cdot ha^{-1} \cdot year^{-1}$. In part, this reduction in pine productivity was due to lower pine density and oaks occupying a dominant overstory component. When oak and pine ANPP is viewed

Table 2. Site diagnostics of the study sites, with ranges in parentheses.

	Age	DBH (cm)	Density (no./ha)	Total height (m)	Soil moisture capacity (g/cm^3)
Xeric					0.042
Quercus spp.	43 (10–132)	10.16 (5–56.6)	347	7.23 (2.1–18)	
Pinus palustris	56 (7–204)	22.77 (5.2–49.6)	65	13.60 (4.8–25.2)	
Intermediate					0.082
Oaks	33 (26–39)	8.75 (8.3–9.2)	2	5.80 (5.6–6)	
Pines	73 (42–102)	34.19 (7.4–56.4)	128	23.26 (6.5–30)	
Wet–mesic					0.108
Quercus spp.[a]	42	11.30	1	8.22	
Pinus palustris	51 (19–166)	23.49 (6.1–50.7)	234	19.63 (6.9–30.6)	

Note: Data are from Baker County, Georgia.

[a] There was only one observation at the wet–mesic site.

Fig. 2. Age structure of the overstory on the study sites. Note the greater proportion of oaks observed on the xeric site.

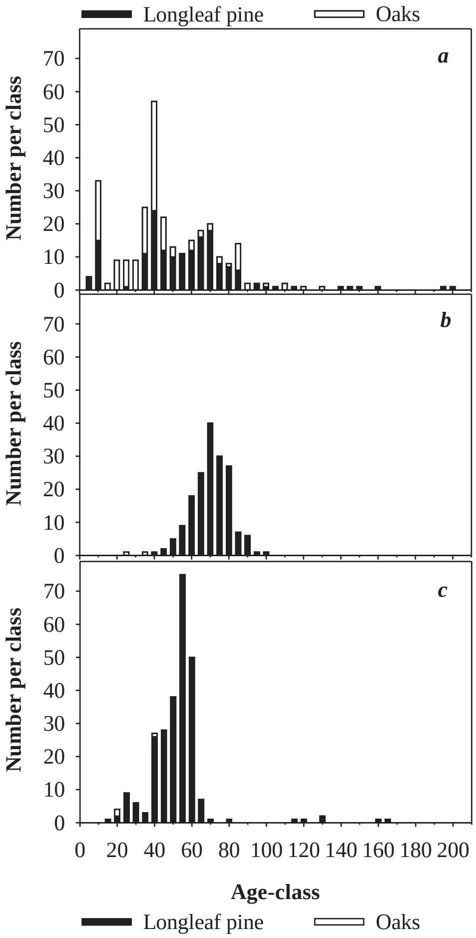
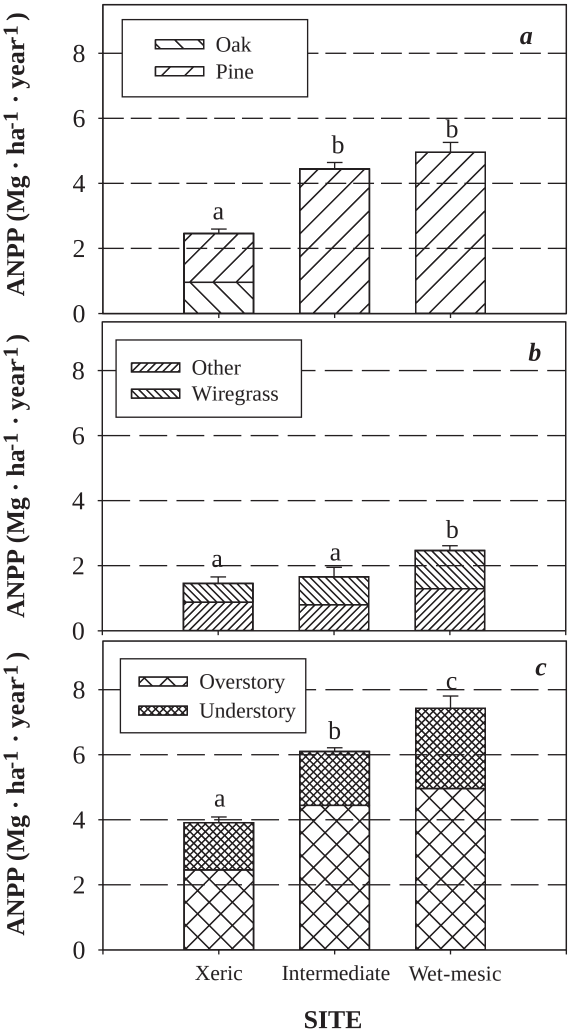


Fig. 3. ANPP of the understory (*a*), overstory (*b*), and total (*c*) across an environmental gradient in Baker County, Georgia. Bars indicate least significant differences (α = 0.05), and bars with different letters are significantly different.



in aggregate, approximately 2.45 Mg·ha^{-1}·year^{-1} was observed for the xeric site. ANPP of overstory pines did not differ statistically (P = 0.11) between the intermediate and wet–mesic site (4.44 and 4.96 Mg·ha^{-1}·year^{-1} for the intermediate and wet–mesic sites, respectively). Understory productivity was least in the xeric site (0.57 and 1.45 Mg·ha^{-1}·year^{-1} for wiregrass and total understory, respectively) and greatest in the wet–mesic (1.18 and 2.47 Mg·ha^{-1}·year^{-1} for wiregrass and total understory, respectively). Intermediate sites did not significantly differ in understory ANPP from xeric sites but were significantly less than that of the wet–mesic sites. Total productivity (overstory plus understory) on the wet–mesic site was 90% greater than that found on xeric sites (7.43 vs. 3.91 Mg·ha^{-1}·year^{-1}), with the average productivity of the intermediate sites 56% greater

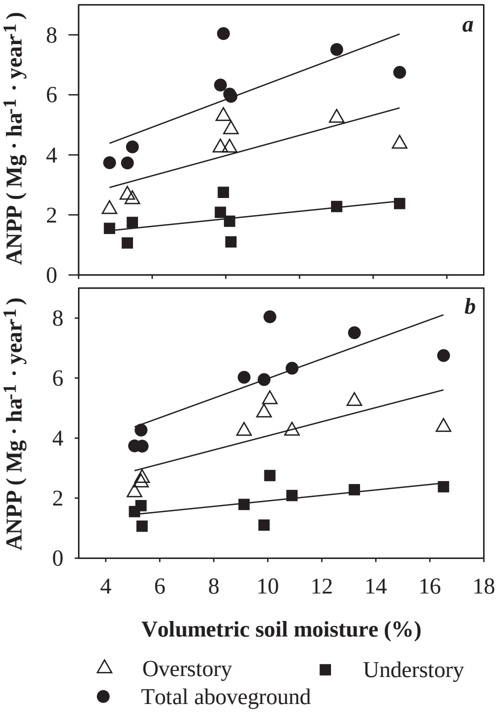


Fig. 4. ANPP of understory, overstory, and total aboveground mass as a function of soil moisture at 30 (*a*) and 90 cm (*b*) depth. Lines are fitted using simple linear regression. Equations for Fig. 4*a* (understory, overstory, and total, respectively) are: $y = 0.4041 + 0.1256x$ ($R^2 = 0.33$, $P = 0.1050$, $SE_y = 0.0674$ Mg·ha^{-1}·year^{-1}), $y = 0.610 + 0.337x$ ($R^2 = 0.55$, $P = 0.0229$, $SE_y = 0.116$ Mg·ha^{-1}·year^{-1}), $y = 1.223 + 0.462x$ ($R^2 = 0.58$, $P = 0.0164$, $SE_y = 0.147$ Mg·ha^{-1}·year^{-1}). Equations for Fig. 4*b* (understory, overstory, and total, respectively) are: $y = 0.997 + 0.091x$ ($R^2 = 0.38$, $P = 0.0771$, $SE_y = 0.091$ Mg·ha^{-1}·year^{-1}), $y = 1.721 + 0.235x$ ($R^2 = 0.58$, $P = 0.0166$, $SE_y = 0.075$ Mg·ha^{-1}·year^{-1}), $y = 2.717 + 0.326x$ ($R^2 = 0.64$, $P = 0.0100$, $SE_y = 0.093$ Mg·ha^{-1}·year^{-1}).

than that of the xeric sites. Wiregrass ANPP was relatively constant in proportion of understory productivity among the three sites (approximately 49% of understory productivity). The greatest proportion of understory productivity to total productivity was observed in the xeric site, probably as a result of the low overstory productivity (60, 38, and 50% for xeric, intermediate, and wet–mesic sites, respectively).

Longleaf pine – wiregrass ecosystems differed in average N mineralization and mean soil water content across sites. Xeric sites had the lowest soil moisture content but the greatest net N-mineralization rates. Wet sites had the highest soil water content and showed the least net N-mineralization rates. Intermediate sites were intermediate in both resources. Overstory, understory, and total ANPP was positively correlated with soil moisture (Fig. 4) and negatively correlated with annual net N-mineralization (Fig. 5).

Discussion

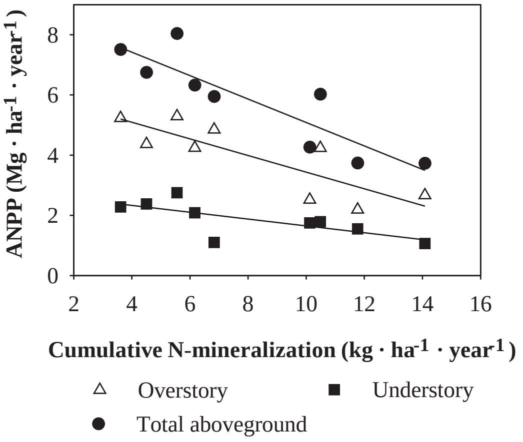


Fig. 5. ANPP of understory, overstory, and total aboveground mass as a function of cumulative N-mineralization for longleaf pine forests in Baker County, Georgia. Lines are fit using simple linear regression. Equations for understory, overstory, and total aboveground are $y = 2.781 - 0.113x$ ($R^2 = 0.51$, $P = 0.030$, $SE_y = 0.0419$ Mg·ha^{-1}·year^{-1}), $y = 6.198 - 0.276x$ ($R^2 = 0.70$, $P = 0.005$, $SE_y = 0.0689$ Mg·ha^{-1}·year^{-1}), and $y = 8.979 - 0.389x$ ($R^2 = 0.79$, $P = 0.001$, $SE_y = 0.0768$ Mg·ha^{-1}·year^{-1}),

Longleaf pine – wiregrass ANPP patterns varied strongly across a complex environmental gradient characteristic of this ecosystem. Productivity was lowest for both pine and wiregrass on deep excessively drained sandhill ecosystems; however, oak ANPP was substantial only on these xeric sites. The low productivity of the components that engender pyrogenicity to this ecosystem (longleaf pine and wiregrass) may explain the ability of oaks to persist on dry sites. Longleaf pine density was lowest on xeric sites, a typical characteristic of many of the second-growth longleaf pine ecosystems on sandhills (Christensen 1987; Ware et al. 1993). In addition to the low density of pine and spatial discontinuity in pine litterfall, wiregrass productivity was significantly reduced. The reduction in wiregrass productivity may be related to low soil moisture availability directly inhibiting growth but also high soil disturbance rates by fossorial herbivores (pocket gophers and gopher tortoise) and the slow recovery of vegetation on these sites after disturbance (personal observation). The diminished ANPP coupled with the discontinuity of pyrogenic fuels may result in more patchy fires and allow oaks to grow to a fire-safe size (Jacqmain et al. 1999).

Although considerable research has been published that reports ANPP of closed-canopy conifer stands in the temperate (average of approximately 10 Mg·ha^{-1}·year^{-1}) or subtropical (20 Mg·ha^{-1}·year^{-1}) region (Gholz et al. 1994), fewer data are available for open-canopy savannas. This is the first report of ANPP in open-canopy longleaf pine savannas that span the range of sites common to this ecosystem. Pine. ANPP in this study varied from slightly greater than 1.5 Mg·ha^{-1}·year^{-1} on xeric sandhills to almost 5.0 Mg·ha^{-1}·year^{-1} for the most wet–mesic sites in this study. When oaks were added to pines, overstory ANPP almost doubled on the xeric sites. These ANPP values are considerably less than those reported for young loblolly pine plantations (Albaugh et al. 1998) on sandhill sites (mean ANPP of 6.96 Mg·ha^{-1}·year^{-1} over a 3-year period) and by Gholz et al.

(1991) for slash pine plantations on wet flatwood sites (3-year average of 8.1 $\mathrm{Mg \cdot ha^{-1} \cdot year^{-1}}$). Although these differences may be species-specific or age-related, the open-canopy habit of natural longleaf pine forests is most likely the greatest difference between overstory pine productivity in these systems and those of young plantations. Biomass production potential is closely related to the ability to intercept light (Cannell 1989; Linder 1987). The open-canopy of longleaf pine savannas allows for a considerable amount of light to reach a robust understory. Moreover, understory productivity varies considerably across the complex longleaf pine – wiregrass gradient and is less than that reported from comparable grasslands. Knapp et al. (1993) reported that tallgrass prairie productivity varied twofold across a across a range of hill slope positions (mean ANPP over a 2-year period was 3 $\mathrm{Mg \cdot ha^{-1} \cdot year^{-1}}$ on dry sites and 6 $\mathrm{Mg \cdot ha^{-1} \cdot year^{-1}}$ on wet sites). Long et al. (1992) reported on NPP for grasslands of the tropics and subtropics and found that ANPP values ranged from 4.5 $\mathrm{Mg \cdot ha^{-1} \cdot year^{-1}}$ in a savanna in Kenya to greater than 70 $\mathrm{Mg \cdot ha^{-1} \cdot year^{-1}}$ for a tropical grassland in the floodplain of the Amazon. Differences in ANPP among grasslands is largely due to temperature and moisture (Sala et al. 1989; Knapp et al. 1993); however, wiregrass savannas experience higher average temperature, longer growing seasons, and more precipitation than North American tallgrass prairies but tend to have lower production.

The lower production of understory communities in longleaf pine savannas compared with other grasslands is likely to be due to competition between trees and the understory (Scholes and Archer 1997). The negative effect of trees on grasses may result from shading and root competition or through nonuptake effects on resources (sensu Goldberg 1990), such as interception of rain by the canopy (Scholes and Archer 1997). Generally, tree-removal studies have shown a negative exponential relationship between tree abundance and understory productivity (Burrows et al. 1990; Walker et al. 1986; Pressland 1975). Similar relationships in grass productivity and tree abundance have been reported for studies that use natural variation in tree density (Scholes and Archer 1997). A significant finding of our study was that the most productive grasslands were on sites with the greatest pine density, i.e., the wet–mesic sites. This apparent paradox may be explained by soil factors influencing the shape of the negative hyperbolic relationship between overstory abundance and understory productivity (sensu Zutter et al. 1998). More mechanistic investigations are needed to partition variation in site resources, rainfall patterns, and overstory structure as controls on productivity of wiregrass communities in longleaf pine savannas.

Although the range in environmental conditions in which longleaf pine occurs is often described as a hydrologic gradient, the degree that nutrients vary in concert or opposition to soil moisture throughout the landscape is not well known (Christensen 1987). Jacqmain et al. (1999) reported that soil cations increased as moisture increased across a range of longleaf pine sites, but potentially mineralizable N and extractable P decreased as soil moisture increased. In a companion study (see Wilson et al. 1999), in situ net N mineralization was found to be negatively correlated with average soil moisture. Differences among sites in N availability appear to be regulated by both differences in microclimate and quality of organic matter inputs to the detritus system (Wilson et al. 1999).

Although recent reports have suggested that gradients in southern pine forest productivity may be more nutrient limited than water limited (Albaugh et al. 1998; Gholz et al. 1991), our results suggest that control of longleaf pine productivity throughout a natural gradient appears to be limited by soil moisture. Nitrogen has been thought to be the primary nutrient limiting coniferous forests of the southeastern United States (Vose 1988; Vose and Allen 1988). Recent reports suggest that loblolly pine growing on deep sandhill sites increased ANPP 13% when irrigated and 85% when N nutrition was maintained high (1.3 times foliar values; other nutrients were balanced). Gholz et al. (1991) found that N fertilization enhanced productivity of a 22-year-old slash pine plantation on a wet flatwood site, but they could not find leaf water potential or photosynthetic response to variation in soil moisture. Reich et al. (1997) reported that N-mineralization rate was strongly and positively correlated with ANPP of forests in Minnesota and Wisconsin regardless of variation in age or forest type. In addition, Walker and Peet (1983) report strong increases in wiregrass understory biomass when fertilized. These reports and the low annual N-mineralization rate of the surface soil all would lead to a conclusion that the longleaf pine systems reported here should be N limited. In fact, these ecosystems may be limited by multiple resources (Seastedt and Knapp 1993). The negative correlation of N and ANPP should not be overstated in importance. This result may stem from two features of N availability with respect to soil water. First and foremost, N was arrayed throughout the landscape in a diametrically opposed fashion with respect to soil moisture. Secondly, N variance throughout the landscape was low; N mineralization rates on all sites are among the least reported for North American forests (Wilson et al. 1999). Thus, the soil moisture signal seemingly dominates productivity patterns. Although we do not present data for phosphorus (P), extractable P and net N mineralization were strongly correlated with each other throughout the landscape in a similar fashion as reported by Jacqmain et al. (1999). Also, extractable P was negatively correlated with productivity (unpublished data).

Soil moisture was related to growth of overstory and understory in similar ways. The prediction that understory productivity would be more closely tied to surface soil moisture values and variation in overstory productivity would be more fully explained by deeper sources of moisture was also not supported by our findings. For savannas of shallow-rooted grasses and deep-rooted trees, Walter (1971) predicts that the proportion of total productivity in grasses should increase as sites increase in moisture. We report that no consistent pattern in the proportional productivity of the understory may suggest that little niche differentiation in access to soil water is evident in longleaf pine – wiregrass savannas.

Certainly data presented in this study point to landscape controls on soil moisture as a major regulator of productivity, but understanding how soil water availability regulates temporal, spatial, and species-specific differences in water relations is needed to more fully understand how those controls are manifested throughout the landscape. Furthermore, investigations that manipulate resource availability, particularly at each extreme in the gradient, would shed further light on the mechanisms that regulate productivity of these savannas. Investigations into tree–grass interactions and the manner in which sites regulate those interactions are needed to more fully predict productivity of these savannas. Lastly, regulation of belowground productivity has not been reported. These investigations would provide greater insight into the patterns reported in this study.

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