

Water table depth affects productivity, water use, and the response to nitrogen addition in a savanna system

Chelcy R. Ford, Robert J. Mitchell, and Robert O. Teskey

Abstract: We investigated annual aboveground net primary productivity (ANPP) and transpiration (E) of the dominant plant life forms, longleaf pine (*Pinus palustris* Mill.) trees and wiregrass (*Aristida stricta* Michx.), in a fire-maintained savanna. Experimental plots spanned a natural hydrologic gradient (xeric and mesic site types) mediated by soil moisture (θ) and water table depth (WTD), and received additions of either 0 or 100 kg N·ha⁻¹·year⁻¹. Low rates of ANPP (1.3–2.2 Mg·ha⁻¹) and annual E (108–380 mm) were observed in these communities. WTD and N addition explained 95% of the variation in community ANPP, whereas site type and WTD explained 83% of variation in community E . Between tree and grass life forms, longleaf pine ANPP was more coupled to WTD than wiregrass. For any given leaf area supported, ANPP of longleaf pine increased linearly with increasing water use and decreasing WTD. The longleaf pine ANPP response to N addition was greater in sites with high water use compared with those with low water use, indicating that this savanna system is colimited by nutrient and water availability and that water table depth plays a role in regulating savanna productivity.

Résumé : Nous avons étudié la productivité primaire nette de la partie aérienne (PPNA) et la transpiration (E) annuelles des espèces végétales dominantes (pin des marais (*Pinus palustris* Mill.) et aristide des pinèdes (*Aristida stricta* Michx.)) dans une savane maintenue par le feu. Les parcelles expérimentales couvraient un gradient hydrique naturel (types de station xérique et mésique), engendré par la teneur en eau du sol (θ) et la profondeur de la nappe phréatique (PNP), et ont reçu des amendements de 0 ou 100 kg N·ha⁻¹·an⁻¹. Nous avons observé de faibles taux annuels de PPNA (1,3 à 2,2 Mg·ha⁻¹) et de E (108 à 380 mm) dans ces communautés. La PNP et l'amendement en N ont expliqué 95 % de la variation de la PPNA de la communauté alors que le type de station et la profondeur de la NP ont expliqué 83 % de la variation de la E de la communauté. Considérant la différence entre les espèces végétales herbacée et arborescente, la PPNA du pin des marais était davantage reliée à la PNP que l'était celle de l'aristide des pinèdes. Pour toutes les valeurs de surface foliaire, la PPNA du pin des marais augmentait linéairement avec une augmentation de l'utilisation de l'eau et une diminution de la PNP. La réaction de la PPNA du pin des marais à l'amendement en N était plus prononcée dans les stations caractérisées par une grande utilisation de l'eau comparativement aux stations où il y avait une faible utilisation de l'eau. Ce résultat indique que ce système de savane est limité conjointement par la disponibilité en nutriments et en eau et que la profondeur de la nappe phréatique joue un rôle régulateur sur la productivité de la savane.

[Traduit par la Rédaction]

Introduction

Savannas contribute disproportionately to global diversity but also face increasing demands from land use; thus, understanding how savanna structure regulates ecological function is critical to developing sustainable management (Grace et

al. 2006; Scholes and Archer 1997; Young and Solbrig 1993). Savannas account for nearly 15% of the global land surface area (Kimmins 1987), and cover as much as 50×10^6 ha in North America (McPherson 1997). They are also socioeconomically important in providing fuel, fiber, and food (McPherson 1997) from the tropics to temperate climates. Notwithstanding their importance, they have received less scientific attention globally than other physiognomic types (e.g., forest and prairies) (Harris 1980; Walker 1987), particularly in temperate regions (Jose et al. 2006; McPherson 1997). Moreover, few studies have investigated how the dominant plant life forms in savannas interact with resource availability to regulate net primary productivity (NPP) and how NPP varies across the landscape (but see Eamus et al. 2001).

Multiple limitations on ecosystem productivity, particularly nitrogen (N) and water, are recognized generally (Chapin et al. 1987), and there is evidence suggesting that both N and water availability constrain NPP in savannas (Scholes and Archer 1997). For example, in temperate oak savanna communities, Reich et al. (2001) found that

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aboveground NPP (ANPP) and soil N availability were positively correlated. However, Mitchell and others (1999) reported that ANPP of a longleaf pine (*Pinus palustris* Mill.)–wiregrass (*Aristida stricta* Michx.) savanna was negatively related to rates of N mineralization but positively related to soil moisture. This indicates that access to water, more so than N availability, may be the principal factor limiting productivity in savanna systems.

Access to water has been shown to vary by life form in savannas. Previous studies have shown that savanna trees and grasses can have spatially distinct functional rooting zones, with deeply rooted trees accessing deep, stable water resources, and cooccurring grasses relying more on transient soil water resources (Dodd et al. 1998; Ludwig et al. 2003, 2004; Moreira et al. 2003; Smith et al. 1997; Weltzin and McPherson 1997). Although these differences in rooting depths are likely to be generalized across all savanna systems (Jackson et al. 1996), their implications for aboveground function are also likely dependent on the water table position. For example, if the water table depth exceeds the rooting depth of both trees and grasses, competition between the life forms for soil water may ensue. Furthermore, how the two life forms respond to N resources will likely interact with water availability. With greater access to water resources and, hence, greater stomatal conductance to water vapor and CO₂, productivity should increase with increased N resources. Conversely, limited access to water may produce a lessened response to N availability.

The fire-maintained, longleaf pine–wiregrass systems of the southeastern United States are characterized by a grass–herbaceous understory layer dominated by wiregrass, and an overstory of longleaf pine. Longleaf pine savanna systems occur across a range of soil water availability determined by soil texture, topography, and water table depth (Mitchell et al. 1999). These systems also vary in productivity across hydrologic gradients and are likely to be limited by both water and N (Wilson et al. 1999). The objectives of this study were to examine ANPP and transpiration (*E*) of mesic and xeric longleaf pine–wiregrass communities and to investigate the effect of N addition on ANPP and *E* on mesic and xeric sites. We also examined the degree to which ANPP and *E* were coupled and whether this relationship varied with differences in site water availability or N addition. We hypothesized the following: (i) ANPP increases with increasing water resources and with N addition; (ii) within life forms, longleaf pine ANPP is more coupled to water table dynamics than wiregrass, decreasing as water table depth increases; and (iii) the ANPP response to N addition will depend on the level of water availability or *E*.

Materials and methods

Site description and experimental design

This experiment was conducted between January 2002 and May 2003 at the Joseph W. Jones Ecological Research Center in southwestern Georgia, USA, which contains 6000 ha of naturally regenerated, second-growth, longleaf pine–wiregrass communities managed with prescribed burning every 2–5 years. The community structure is an over-

story canopy of longleaf pine, a subcanopy and shrub layer of oaks (*Quercus geminata* Small, *Quercus laevis* Walt., *Quercus stellata* Wang., and *Quercus virginiana* Mill.), and an understory dominated by wiregrass (Table 1).

Using a land classification system (Goebel et al. 1997), we selected four replicate plots, 2 ha in area, in mesic and xeric sites across the landscape (henceforth whole plot). Mesic sites are poorly drained because of a clay-textured lens that decreases water infiltration into deeper soil layers, whereas xeric sites have excessively well-drained, deep, sand-textured soils. Within each 2 ha replicate plot, we established two, 1 ha plots for the fertilization treatment (henceforth split plot). The broadcast N fertilization treatment, totaling 100 kg N·ha⁻¹ year⁻¹ of dry ammonium nitrate, was applied to one randomly chosen 1 ha plot, and the other 1 ha plot served as an unfertilized control. Fertilizer was applied three times during the study in May 2002, August 2002, and January 2003 at 60%, 20%, and 20%, respectively, of the annual total treatment based on annual variation in net N mineralization. Differences in the length of time since last burn existed among the sites: four plots were burned in January 2002, two plots were burned in 2001, and two plots were burned in 2000.

An open-field weather station onsite measured ambient air temperature, relative humidity, solar radiation, and precipitation (models HMP35C, LI200SA, and TES25; Campbell Scientific, Inc., Logan, Utah),³ and a datalogger (CR10X; Campbell Scientific, Inc.) recorded values every 15 min. During the study period, 24 h mean air temperatures ranged from 30.2 to –3.6 °C. The frost-free period extended approximately 8 months. Annual precipitation (March to March) was 1623 mm (1310 mm long-term annual mean), all occurring as rain, and showed no distinct seasonal pattern in frequency or amount.

Soil moisture and groundwater table depth were measured in each plot throughout the study. Piezometer wells were installed in 2001 to monitor weekly groundwater table depths and fluctuations (Slope Indicator, Mukilteo, Wash.). Soil moisture content in the 0–30 cm soil layer (*θ*) was measured monthly in each site type and treatment combination throughout the study using time domain reflectometry (model 1502-B, Tektronix, Inc., Beaverton, Ore.).

Productivity measurements

We determined annual ANPP for the oaks, pines, and wiregrass in all plots. These three plant types represent >95% of the total standing biomass in similar xeric and mesic sites (R. Mitchell, unpublished data); thus, we defined community-level ANPP as the sum of oak, pine, and wiregrass ANPP. All trees >5 cm in diameter at 1.3 m above the ground were tagged and surveyed for diameter at the initiation and termination of the study. Tree ANPP was estimated by summing annual biomass increment, which was calculated using site- and species-specific allometric equations (Mitchell et al. 1999), and annual leaf mass production. Leaf litter traps (0.25 m²) were randomly located in each split plot (*n* = 7 mesic sites, *n* = 5 xeric sites). Litter was collected every 2 weeks (in autumn) or monthly, sorted by species, weighed, and converted to leaf area index (LAI)

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Table 1. Canopy and subcanopy stand characteristics of all replicate plots in 2001 before treatments were applied ($n = 8$).

Site type	Plant group	Density (stems·ha ⁻¹)	Aboveground biomass (Mg·ha ⁻¹)	Basal area (m ² ·ha ⁻¹)
Mesic	Oak	6 (1)	3.29 (0.47)	0.57 (0.08)
	Pine	205 (16)	115.28 (3.50)	14.59 (0.48)
	Total	209 (16)	118.54 (3.29)	15.15 (0.45)
Xeric	Oak	59 (7)	7.27 (0.66)	1.25 (0.11)
	Pine	54 (3)	32.10 (2.02)	4.05 (0.23)
	Total	113 (8)	39.37 (1.43)	5.30 (0.13)

Note: Values are means with SEs given in parentheses. Before treatment application, total standing tree biomass did not differ between control and fertilized split plots ($t = 1.32$, $P = 0.23$).

using species-specific leaf mass–area relationships (S. Pecot, unpublished data; Donovan et al. 2000). Pine LAI was estimated as annual leaf area collected and doubled given the 2 year retention time of longleaf pine needles.

Wiregrass ANPP was determined by destructively subsampling circular plots (1 m diameter area in November 2002 before the first killing frost. Five (xeric sites) and seven (mesic sites) subplots were harvested, and biomass was pooled across the subplots for each split plot. Wiregrass biomass was sorted into live (produced in the current year) and dead (retained dead foliage from previous years) tissue categories, dried, and weighed. Biomass was converted to wiregrass projected leaf area using specific leaf area (SLA, cm² area·g mass⁻¹). We sampled 25 wiregrass blades in each site type and treatment. Because SLA did not differ by site type or treatment, SLA data were pooled across treatments ($R^2 = 0.85$, $F = 90.57$, $P < 0.001$, $y = 24.27x$). Total live leaf area measured in the subplots was then scaled to the entire plot.

Transpiration measurements

We determined whole plant water use (i.e., transpiration) of trees using thermal dissipation (TD) probes (Granier 1985). A random location within each split plot was chosen, and sap flux density (v , g H₂O·m⁻² sapwood⁻¹·s⁻¹) was monitored in the five nearest trees (because of cable length constraints). In xeric sites, both longleaf pine and oak trees were monitored, whereas only longleaf pine trees were monitored in mesic sites because of the low frequency of oak therein (Table 1). Each tree monitored had two sets of TD probes installed at 1.3 m stem height at least 90° apart. We constructed 2 cm long Granier-style TD probes (Granier 1985), with single thermocouples at 1 cm. The TD probes were insulated with foam blocks and reflective insulation. Dataloggers (Campbell Scientific Inc. & Wescor Inc., Logan, Utah) on each plot queried probes every 10 min and compiled 1 h means. Two replicate probe readings per tree were averaged. Probes were routinely replaced throughout the monitoring period if null, out of range, or negative readings were recorded or if probes were physically damaged. Each tree was monitored from May 2002 to May 2003.

At the end of the monitoring period, sapwood areas (A_{sw}) were determined. For oak, dye was injected into the xylem at sensor height to help identify the active xylem. If the oak sapwood radius was less than 2 cm, a corrected temperature

difference was calculated according to Clearwater et al. (1999). For longleaf pine, A_{sw} was estimated from one increment core taken from each tree near the location of the probes. Heartwood can be visually identified in longleaf pine as dark red, resinous xylem.

To scale v to sap flow (F , g H₂O·s⁻¹), we characterized the radial distribution of v on similar trees (Ford et al. 2004). The values of F were scaled to the whole-plot level by assuming that the mean F computed from sampled trees represented F of all trees in the plot. Whole-plot F was estimated separately for pines and oaks by computing the ratio of the mean basal area (A_B) of all the trees in the plot to the mean A_B of the trees measured. This measurement was finally scaled to plot-level pine and oak transpiration (E_c , mm) based on plot area.

Sap flux measurements are not feasible in wiregrass, and there were no previous measurements of wiregrass transpiration reported. To estimate annual wiregrass water use (i.e., transpiration), we constructed a model driven by photosynthetically active radiation (PAR), θ , and vapor pressure deficit (D). We used ambient air temperature to calculate saturation vapor pressure (e_s) according to Lowe (1977). Actual vapor pressure (e_a) was calculated from fractional relative humidity and $e_s \times D$ was calculated as the difference between e_s and e_a . We assumed that open-field D approximated understory D .

To estimate understory PAR, we measured the fraction of light reaching the understory in each split-plot by measuring PAR along 11–24 transects at 1 m height throughout the split plot on cloudless days in the spring (LI191; LI-COR Inc., Lincoln Neb.). This was used to scale the weather station open-field radiation sensor measurements (LI200; LI-COR Inc.) after converting them to PAR (Campbell and Norman 1998). We also measured PAR (LI190; LI-COR Inc.) at one open spatial point at 30 cm height every 15 min throughout the study in each mesic whole plot for comparison with the weather station radiation measurements.

We modeled daily θ using an exponential decay function:

$$[1] \quad \theta = \theta_{\max} \times e^{-k \times \text{DSR}} + \epsilon$$

where θ_{\max} is the maximum soil moisture content, $-k$ is a coefficient representing water lost from the 0–30 cm soil layer, and DSR is days since last rainfall event. A relationship between DSR and measured θ was developed for each site type and treatment combination using the GLM pro-

cedure (version 9.1; SAS Institute Inc., Cary, N.C.) on log-transformed data. Relationships differed by site type ($P < 0.01$) but not treatment ($P = 0.99$); thus, we pooled data across treatment and developed one equation between DSR and measured θ for each site type using the NLIN procedure in SAS software (xeric: $\theta_{\max} = 9.22$, $k = -0.16$, $P < 0.001$, $R^2 = 0.97$; mesic: $\theta_{\max} = 14.20$, $k = -0.09$, $P < 0.001$, $R^2 = 0.94$). Approximate R^2 was calculated as $1 - (\text{residual sum of squares}/\text{uncorrected total sum of squares})$.

The response of wiregrass transpiration per unit leaf area (E_L , $\text{mmol H}_2\text{O}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) to understory PAR, D , and θ was modeled using a normalized function reducing maximum leaf-level transpiration rate (E_{\max}) (Jarvis 1976; Reed et al. 1976). Six wiregrass plants adjacent to the xeric and mesic sites were excavated and maintained in the greenhouse to determine E_{\max} under ideal conditions and to develop relationships between wiregrass E_L and PAR, D , and θ . E_L was measured under varying levels of PAR and D at field capacity (LI-COR 6400; LI-COR Inc.), and then E_L was measured under saturating light ($2000 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) while varying levels of θ . One function was fit to each environmental variable and then combined as

$$[2] \quad E_L = E_{\max} \left[fE_{\max} \left(\frac{\text{PAR}}{\text{PAR} + k_p} \right) \right] \times \left[fE_{\max} \left(\frac{\theta}{\theta + k_d} \right) + \theta \times k_s \right] (fE_{\max} \times D)$$

where E_L and E_{\max} ($12.4 \text{ mmol H}_2\text{O}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) are as previously defined and k_p , k_d , and k_s are constants (185.1, 0.56, and 0.004, respectively). The fraction of maximum transpiration rate, fE_{\max} , was determined for each environmental variable (PAR, 0.706; θ , 0.755; D , 0.232). Functions for PAR and θ were fit using nonlinear iterative estimation, and the function for D was fit using least-squares linear regression (SigmaPlot, version 8.02; SYSTAT, Inc., Chicago, Ill.). All functions and parameters were significant ($\alpha = 0.05$). Estimated wiregrass E_L was evaluated against actual E_L measured in the field during May, the peak period of wiregrass transpiration—the slope of the estimated versus observed E_L regression line was not significantly different from unity ($F = 2.86$, $P = 0.15$, slope = 0.85, $R^2 = 0.95$). Measurements of air temperature and leaf temperature also did not differ during this time (paired t test, $t = -1.08$, $P = 0.31$).

Leaf-level responses were scaled to the plot on an hourly time step. We estimated the fraction of annual leaf area (fLA) present in each plot over time from wiregrass leaf elongation rates (Parrott 1967). Wiregrass E_L rates were multiplied by the estimated fLA in the plot, then scaled to a hectare level, and converted to millimeters. This was assumed to represent transpiration of the understory layer. The sum of pine, oak, and wiregrass transpiration was assumed to represent whole-plot transpiration (E).

Statistical analyses

Pretreatment (before fertilization) differences in standing tree biomass between fertilized and control split plots were made using a paired t test (Table 1). We analyzed ANPP, E , and LAI as response variables. Two additional response variables analyzed were water use efficiency (WUE, esti-

mated as the ratio of ANPP to E), and growth efficiency (estimated as the ratio of ANPP to LAI). Posttreatment differences in all response variables were analyzed as a split-split-plot design with three fixed factors. Site type, with two levels (mesic and xeric), was the whole-plot factor. Treatment, with two levels (fertilized and control), was the split-plot factor. Plant group, with two factors (pine and wiregrass), was the split-split plot factor. Oaks were not included in the plant group comparison because species of oak are not consistent between site type, and no oaks were present in two of the four mesic site replicates. However, community-level comparisons always included contributions by oaks. We used the MIXED procedure (SAS version 8; SAS Institute Inc., Cary N.C.), with the whole-plot and split-plot errors specified as random effects, to test for the main effects and their interactions on response variables. A post hoc means separation among split-plot factors was performed if necessary. To determine the effect of water table depth on response variables, linear models were fit using the MIXED procedure, allowing and testing for different intercepts for main effects and slopes for main effect interactions with annual minimum water table depth.

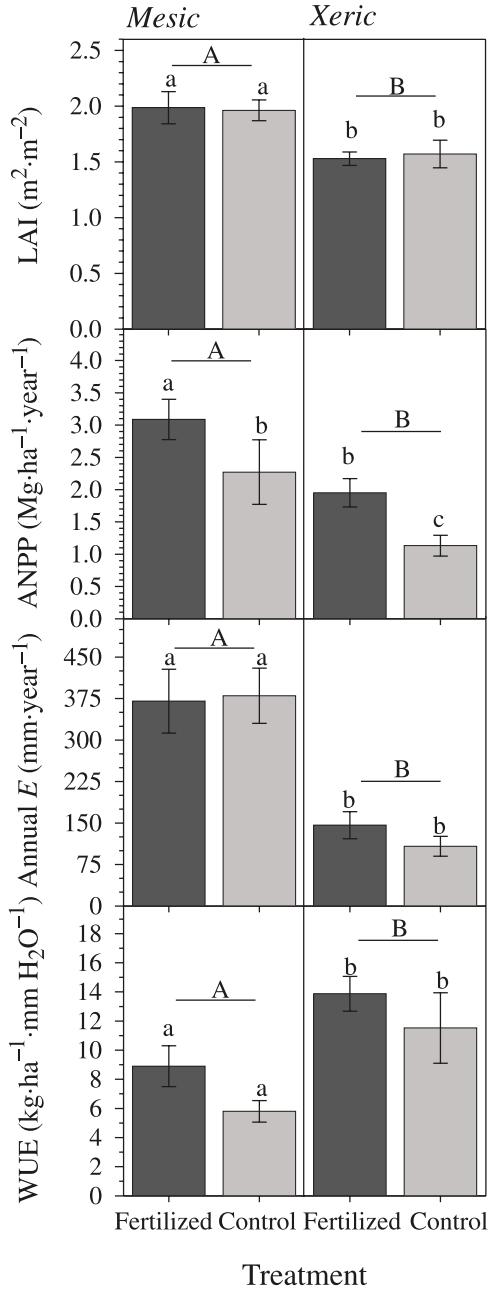
Results

ANPP increased with increasing water resources (i.e., site type and water table depth) and with N addition, confirming our first hypothesis (Fig. 1). Soil moisture was consistently lower in xeric sites compared with mesic sites ($7.4\% \pm 0.1\%$ (mean \pm SE) vs. $11.3\% \pm 0.1\%$, $P < 0.01$) and did not differ significantly in either site with fertilization ($P = 0.21$). Water table depths among the sites varied from <1 m to almost 10 m (data not shown), but there was more variation in water table depths among replicate sites than between site types ($P = 0.71$). ANPP of mesic sites was greater than that of xeric sites ($P = 0.03$). The mean ANPP (averaged across the control and fertilized treatment) of the mesic sites was $2.6 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ as opposed to $1.5 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ for the xeric sites. Fertilizer treatments significantly increased ANPP by an average of 54% on both mesic and xeric sites ($P < 0.01$) (Fig. 1). Differences in ANPP were greater between fertility treatments than site types, whereas LAI followed the opposite trend. LAI was 25% greater on mesic sites compared with the xeric sites, while fertilization had no effect on LAI ($P = 0.91$).

Community water use and WUE patterns also differed on mesic and xeric sites (Fig. 1). Patterns of E reflected the patterns of LAI, and E values were three times higher on mesic sites than on xeric sites. Fertilization treatments had no effect on annual transpiration on either site type ($P = 0.74$). The greater production per unit water use on the xeric sites compared with the mesic sites resulted in the former having 72% greater WUE compared with the latter ($P = 0.02$). WUE did not differ significantly with fertilization treatment ($P = 0.11$) despite ANPP significantly increasing and water use remaining constant with added N.

With minimum annual water table depth as a covariate in the linear model, the effects of fertilization and minimum annual water table depth explained 95% of the variation in the ANPP among all sites (Fig. 2). Site type did not explain any additional variability beyond what water table depth and

Fig. 1. Mean leaf area index (LAI), aboveground net primary productivity (ANPP), transpiration (*E*), and water use efficiency (WUE) for fertilized and control mesic and xeric site types. Bars are the sum of mean oak, pine, and wire grass values, and the error bars are SEs. Different capital letters denote significant differences among whole plots. Different lowercase letters denote significant differences among split plots and whole plots.



fertilization explained. The main effect of fertilization was significant; the fertilized linear model had a significantly different intercept than the control linear model ($P < 0.01$), but slopes did not differ ($P = 0.59$).

The values of *E* also declined within site types as minimum annual water table depth increased (Fig. 3). With minimum annual water table depth as a covariate in the linear model, the effects of site type and minimum annual water table depth explained 83% of the variation in the *E* among

Fig. 2. ANPP as a function of minimum annual water table depth. Points represent the total ANPP (sum of pine, oak, and wiregrass) for each fertilized (solid line, $y = 3.48 - 0.00256x$) and unfertilized (broken line, $y = 2.66 - 0.00256x$) split plot. Intercepts of lines are significantly different ($P < 0.01$), but slopes are not ($P = 0.59$); the model explains 95% of variation in ANPP.

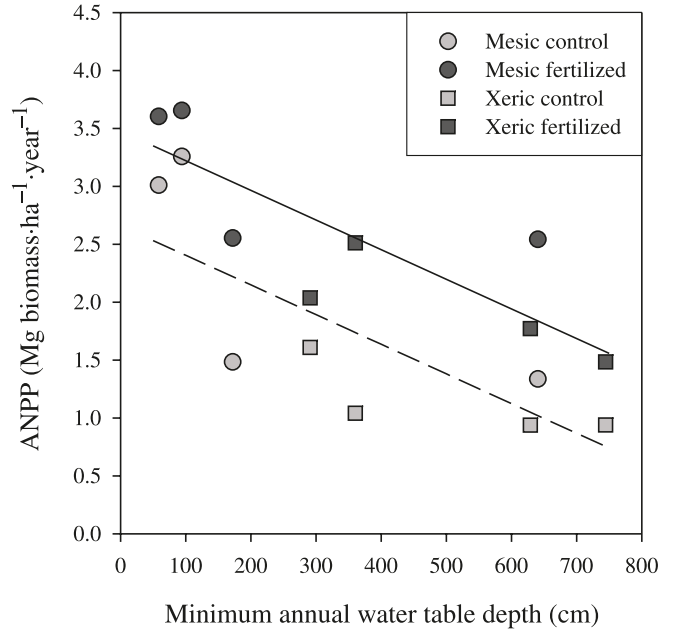


Fig. 3. Annual transpiration (*E*) as a function of minimum annual water table depth for each site type. Points represent the total *E* (sum of pine, oak, and wiregrass) for each mesic (solid line, $y = 423.71 - 0.20x$) and xeric (broken line, $y = 228.91 - 0.20x$) split plot. Intercepts of lines were significantly different ($P < 0.001$), but slopes were not ($P = 0.39$); the model explained 83% of variation in *E*.

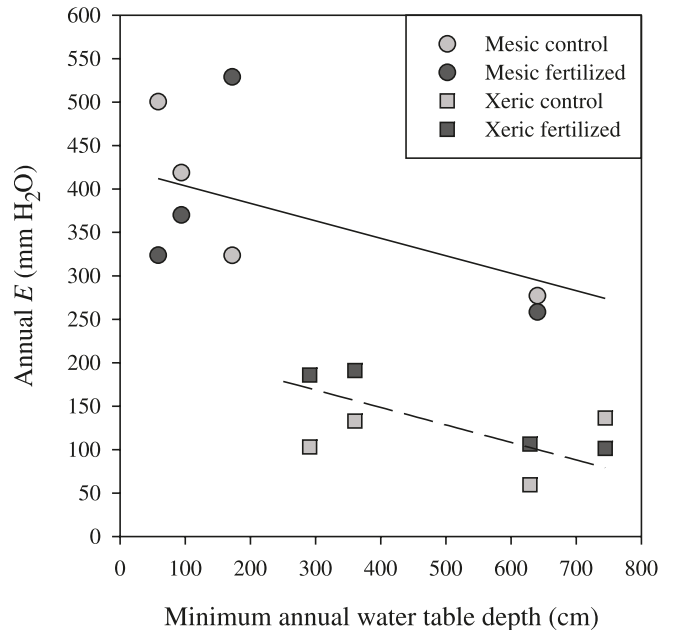


Fig. 4. Mean LAI, ANPP, *E* and WUE by the two plant groups measured for fertilized (heavily shaded bars) and control (lightly shaded bars) mesic and xeric sites. Error bars are SEs. Different capital letters denote significant differences between treatments. Different lowercase letters denote significant differences between plant life forms within a treatment.

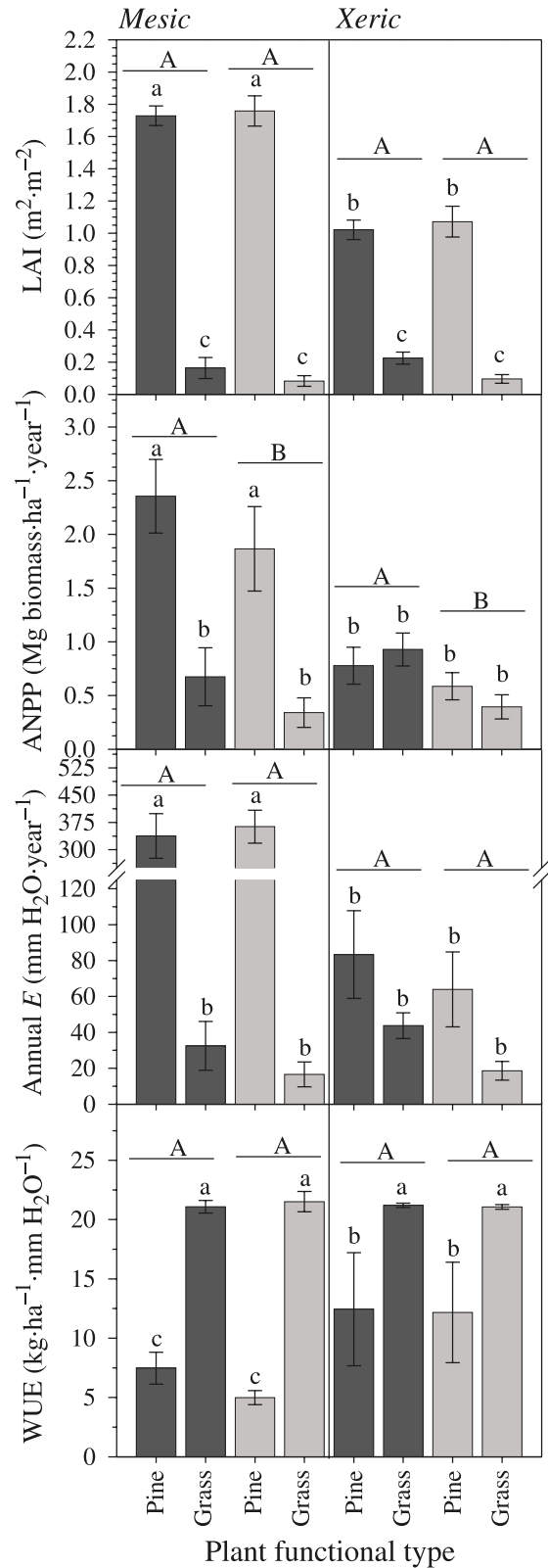
all sites. The main effect of site type was significant; the xeric linear model had a significantly different intercept than the mesic linear model ($P < 0.01$), but slopes did not differ ($P = 0.39$).

The productivity, leaf area, and transpiration of longleaf pine and wiregrass varied by site type and in their response to fertilization treatments (Fig. 4). In all sites and fertilization treatments, pine LAI was greater than that of wiregrass. Pine productivity and LAI were significantly greater in mesic sites compared with xeric sites ($P < 0.01$). In xeric sites, pine and wiregrass productivities were similar, although wiregrass production exceeded pine by 19% in the fertilized sites. The greater LAI on mesic sites compared with xeric sites was largely due to longleaf pine LAI. Pine LAI on mesic sites was nearly double that on xeric sites, whereas wiregrass LAI was comparable (30% greater on xeric sites). Fertilization increased ANPP of wiregrass (98% and 135%, respectively, for mesic and xeric sites) more than was observed for pine (26% mesic and 33% xeric).

Pine transpiration patterns were similar to LAI and ANPP. Pines transpired more than fourfold the amount of water on mesic sites than on xeric sites (Fig. 4). On xeric sites, wiregrass transpiration was an important component of the total community water use, and was one-third to one-half that of pine *E*, on control and fertilized plots, respectively. In contrast, on mesic sites, wiregrass transpiration was only about 7% that of the pines in both control and fertilized treatments. WUE of wiregrass was over twofold higher than that of pines. WUE of xeric site pines was greater than that of mesic pines (12.3 vs. 6.2 $\text{kg}\cdot\text{ha}^{-1}\cdot\text{mm}^{-1}$, $P = 0.05$).

Across the landscape, as annual minimum water table depth decreased, pine productivity decreased, but wiregrass productivity did not (Fig. 5). This evidence supported our second hypothesis. With minimum annual water table depth as a covariate in the linear model, the effects of life form and minimum annual water table depth explained 75% of the variation in ANPP among all nonfertilized sites. The main effect of life form was significant; the longleaf pine linear model had a significantly different intercept than the wiregrass linear model ($P < 0.01$). The effect of minimum annual water table depth was also significant ($P < 0.01$). The slope of the longleaf pine model was negative and significantly different than zero ($P < 0.01$), whereas the slope of the wiregrass linear model was not different than zero ($P = 0.62$).

We found support for our third hypothesis that the ANPP response to N addition will depend on the level of *E*. For longleaf pines across all site types, ANPP per unit LAI (i.e., growth efficiency) increased linearly as water use increased (Fig. 6) and as annual minimum water table depth decreased (data not shown). With access to water and, thus, greater transpiration, the magnitude of the ANPP response to fertilization also increased (Fig. 6), more so for xeric sites than



mesic sites. The intercepts of the linear regressions were significantly different for control and fertilized plots ($P = 0.012$), and the slopes (1.64 vs. 1.99) also differed significantly ($P = 0.018$). This indicated not only that fertilization increased ANPP per unit LAI (different intercepts), but also

Fig. 5. ANPP of the dominant life forms across all nonfertilized sites with respect to minimum annual water table depth: longleaf pine (solid line, $y = 2212.85 - 2.64x$) and wiregrass (broken line, $y = 481.85 - 0.30x$). The slopes and intercepts differed significantly ($P = 0.003$, $P < 0.001$, respectively), and the model explained 75% of variance in data.

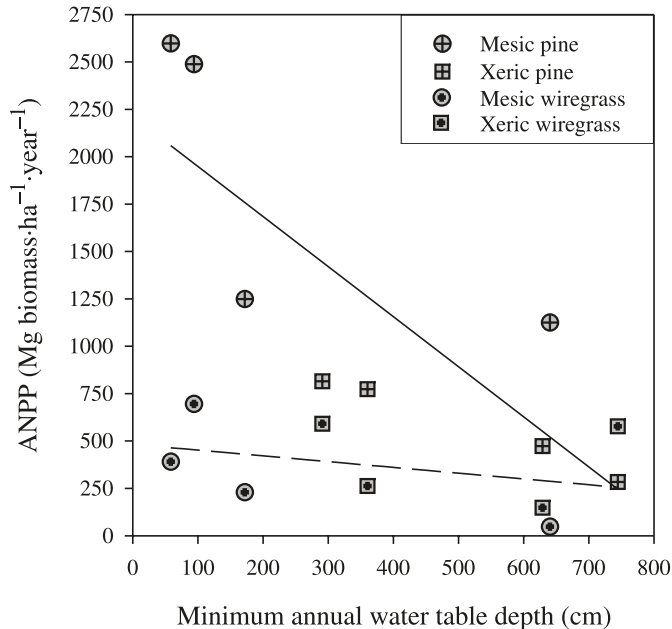
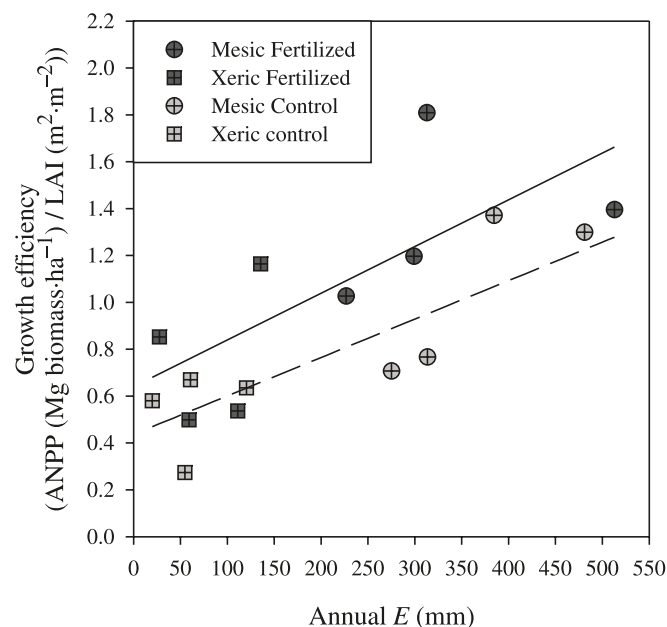


Fig. 6. Growth efficiency as a function of annual water use (E) for the longleaf pine component in each fertilized and control plot. Fertilized (solid line, $y = 0.6405 + 0.00199x$) and control (broken line, $y = 0.4366 + 0.00164x$) slopes and intercepts differed significantly ($P = 0.018$, $P = 0.012$, respectively); the model explained 65% of variance in data.



that further increases occurred on sites that had shallower water tables and high water use (different slopes). For wiregrass, no relationship between ANPP per unit LAI, N addition, and water resources was found.

Discussion

We predicted greater productivity at the whole-system scale as water and N resources increased in this savanna system. At the community level, water table depth and N addition explained much of the variation in ANPP. Mean ANPP for these longleaf pine–wiregrass communities ranged from 1.1 to 2.3 Mg·ha⁻¹·year⁻¹ on unfertilized xeric and mesic sites, respectively. These values are low relative to those reported for pine- and hardwood-dominated forests in this region (Bolstad et al. 2001; Martin and Jokela 2004; McNulty et al. 1996), which range from 2 to 11.8 Mg biomass·ha⁻¹·year⁻¹. However, this level of ANPP is similar to seasonally dry Australian savannas (Chen et al. 2003), dry tropical savannas (Grace et al. 2006), and temperate oak savannas (Reich et al. 2001). Consistent with our predictions, sites with greater soil moisture (mesic) had about four times greater ANPP than sites with lower soil moisture (xeric sites). Differences in ANPP between mesic and xeric sites were largely influenced by longleaf pine, both in terms of the number of pines and the rate of pine productivity.

LAI differences among sites were consistent with patterns of ANPP, in contrast to N, which did not affect LAI (Fig. 1). LAI in this system was comparable with other temperate savannas in North America (Baldocchi et al. 2004; Reich et al. 2001). Sites with lower soil moisture content, lower water-holding capacity, and higher hydraulic conductivity (e.g., xeric sites) had lower LAI compared with sites with higher soil moisture, higher water-holding capacity, and lower hydraulic conductivity (e.g., mesic sites). This is consistent with many studies that have shown that site water balance constrains leaf area development (Gholz 1982; Grier and Running 1977; Vose et al. 1994). Increases in growth in fertilized sites were not accompanied by increases in LAI. This is in contrast with rapid LAI responses to N addition reported for faster growing southern pines such as loblolly pine (*Pinus taeda* L.) and slash pine (*Pinus elliotii* Engelm.) (Teskey et al. 1994; Vose et al. 1994). This suggests a greater change in photosynthetic capacity of individual leaves in response to N availability in longleaf pine than was found in either loblolly (Munger et al. 2003) or slash (Teskey et al. 1994) pines.

Patterns in ANPP among sites were accompanied by variation in WUE. WUE of these communities was greater than other southeastern, forested systems (e.g., 50 mg C·g H₂O⁻¹ vs. 45 mg C·g H₂O⁻¹ for oak–hickory forest) (Webb et al. 1978). WUE differed among sites at the community scale with xeric sites being more efficient than mesic sites. The increase in WUE was due to both an increase in wiregrass dominance and also to longleaf pine having greater WUE in the xeric sites compared with the mesic sites ($P = 0.04$). The wiregrass rate of production per unit of water lost was greater than that of longleaf pine ($P < 0.01$). This is likely a result of inherent differences in WUE that result from differences in carbon assimilation (e.g., C4 vs. C3 in wiregrass

and pine, respectively). WUE for longleaf pine in our sites was approximately twofold greater than that reported for loblolly pine (24–37 mg C·g H₂O⁻¹ for longleaf pine vs. 10–12 mg C·g H₂O⁻¹ for loblolly pine) (Sun et al. 2000).

We also hypothesized that tree productivity would decrease as water table depth increased. Consistent with our hypothesis, tree production declined on nonfertilized sites as the water table depth increased across the landscape; however, wiregrass production did not. Although we predicted that grass production would be greater on sites with higher soil moisture, wiregrass productivity was similar between sites with differing soil moisture. This could have been influenced by the high WUE of wiregrass or by the differences in light environment in the xeric and mesic sites types limiting wiregrass production. The fraction of light reaching wiregrass in the mesic sites averaged 0.55 ± 0.05 compared with 0.78 ± 0.03 in the xeric sites.

The decline in ANPP of longleaf pine as water table depth decreased suggests that rooting depth, or root density with depth, may have been insufficient to effectively utilize water in deeper soil layers. The fine root distribution of longleaf pine in this system has been documented to extend down to 2 m (Addington et al. 2006). Other reports of excavated root systems of mature longleaf pines growing on deep sandy soils show that taproots can extend to at least 4 m and that thick cordlike roots extend deeper than 4 m (Heyward 1933). This observation suggests that, although some longleaf pine roots are likely to extend beyond 2–3 m, root density distribution at these depths may be insufficient in capacity to affect whole plant water use. In this case, the role of these deep roots may be to influence root survival in the upper soil layers (e.g., hydraulic redistribution) rather than to promote additional aboveground growth.

Previous studies have shown that savanna trees and grasses can utilize different sources of water within the soil profile (Dodd et al. 1998; Smith et al. 1997; Weltzin and McPherson 1997) and that the root systems of savanna trees can redistribute a portion of deep water resources to shallow, drier soil layers (Ludwig et al. 2003, 2004; Moreira et al. 2003). These observations are likely to be generalized across all savanna systems (Walter 1971, 1973); however, they are also likely dependent on the water table position. Our results point towards the importance of soil moisture storage in regulating savanna ANPP. If the groundwater table drops below the rooting zones of the trees and grasses, both trees and grasses must rely on, and compete for, soil moisture. For example, at our sites when precipitation events occurred, less soil moisture was held in xeric-site soils compared with mesic-site soils (18 vs. 40 cm·m⁻¹) and for a shorter duration (hydraulic conductivity 49.8 vs. 5.3 cm·h⁻¹) (Addington et al. 2006). Because less soil moisture was available in the xeric sites, in general, less ANPP, transpiration, and LAI were observed compared with the mesic sites.

For any amount of leaf area supported, longleaf pine ANPP increased linearly as water use increased and as water table depths became shallower (data not shown). We found that this relationship was similar regardless of whether longleaf pines were growing in xeric or mesic sites. This was consistent with the results of Addington et al. (2006), who found that, on nonfertilized xeric and mesic sites, pines had similar canopy conductance because of differences in the

ratios of sapwood area to leaf area and root area to leaf area, which were both higher in xeric compared with mesic pines. Our data also suggest that trees growing on shallow water tables have a greater ability to supply water to the foliage, thereby increasing production per unit leaf area. Although the relationship was weak, the greater increase in ANPP per unit LAI for fertilized sites that had high water use indicates that photosynthetic capacity and stomatal conductance may have been higher on these sites, thus affecting the potential ANPP response to N addition.

In conclusion, we found that 95% of the variation in ANPP could be explained by differences in water table depth and N fertilization. Our data emphasize that savanna systems are likely colimited by nutrient and water availability. A positive growth response to N fertilization was seen across the mesic and xeric sites suggesting that they were all N limited. In addition, we found that water table depth and soil water availability were both important drivers of ANPP in these savannas and are likely to be so in other savanna plant communities as well. Longleaf pine trees provided the majority of the community ANPP, especially when the minimum annual water table depth was less than 2–3 m deep. Particularly interesting was the fact that tree ANPP declined linearly with increasing water table depth. This suggests that, as water table depth increased, the trees were increasingly unable to effectively utilize groundwater. Ultimately, at water table depths >2–3 m, the grass and trees may have been competing mostly for the same soil water resource. This opens the possibility that, in other savanna communities sometimes, trees and grasses are direct competitors for water and sometimes not, depending on water table depth and rooting effectiveness of the trees.

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