SHORT-TERM CHANGES IN LOBLOLLY PINE WATER CONDUCTANCE AND PHOTOSYNTHETIC CAPACITY FROM FERTILIZER SOURCE AND STRAW HARVESTING

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ABSTRACT

Organic matter removal associated with intensive straw harvesting in loblolly pine (*Pinus taeda* L.) plantations has the potential to alter tree water regimes and photosynthetic capacity. Fertilization done to remedy nutrient removals from straw harvesting, as well as the type of fertilizer, likewise has potential to change water regimes and photosynthetic capacity of these plantations. In 2008 and 2009, conductance, light-saturated photosynthesis, and intrinsic water use efficiency were measured seasonally in a loblolly pine plantation in north central Louisiana in response to: (1) a non-raked, non-fertilized control treatment, (2) annual straw raking for seven years, (3) annual straw raking for seven years and five years of inorganic fertilizer application, and (4) annual straw raking for seven years and five years of organic fertilizer (poultry litter) application. Precipitation was comparable to or exceeded regional averages throughout the study period. Conductance in spring was greater in response to poultry litter application than to all other treatments. Both fertilization treatments were associated with lower photosynthetic capacity in summer relative to the control treatment. No differences in intrinsic water use efficiency were observed in response to treatments.

INTRODUCTION

Pine straw is commonly used in the southeast U.S. as a landscaping material in residential, urban, and industrial settings (Minogue and others 2007). Pine straw production supplements income from conventional forest products (Minogue and others 2007, Wolfe and others 2005). Pine straw is a large component of the forest floor in loblolly pine plantations (Kinerson and others 1977), and the presence of this organic matter in part determines soil water availability and temperature (Attiwill and Adams 1993). Blazier and others (2008) found that soil available water holding capacity was reduced by annual pine straw harvesting. Excessive removal of organic matter without soil amendment in plantations in which pine straw is frequently harvested could potentially reduce tree water uptake and use as well.

Nutrient amendments are often used in southern pine plantations to replenish macro- and micronutrients removed by pine straw raking (Morris and others 1992). Both inorganic and organic fertilizers such as poultry litter have been used to supply nutrients and increase productivity of southern plantations in which pine straw is harvested (Blazier and others 2008, Chastain and others 2007). Poultry litter is a by-product of poultry production and consists of chicken manure, feed waste, and bedding materials such as rice hulls, peanut hulls, or pine shavings. Amending southern pine plantations with poultry litter may prove beneficial in replacing not only nutrients but also organic matter removed during pine straw raking. The additional organic matter added to the soil may benefit growth by increasing porosity and reducing the impacts of compaction, thereby improving water availability to the trees (Blazier and others 2008).

Both nutrient and water regimes in loblolly pine plantations are important to productivity and tree growth (Green and Mitchell 1992, Samuelson and others 2008). Removal of organic matter in stands in which pine straw is harvested and subsequent fertilization with inorganic or organic fertilizer may alter the water regimes as well as photosynthetic capacity of loblolly pine that govern its productivity. Understanding of the effects of straw raking and fertilizer source on the water regimes and photosynthetic capacity of loblolly pine is needed to develop ecologically sustainable management practices, but research on these issues is limited. The objectives of this study were to determine the effects of annual straw harvesting, fertilization, and fertilizer source on stomatal water conductance, photosynthetic capacity, and intrinsic water use efficiency of loblolly pine.

METHODS

The study site was located at the LSU AgCenter Calhoun Research Station in north central Louisiana (32° 30’ 48” N, 92° 20’ 53” W). The study was established in two loblolly pine plantations located within 0.5 km of each other. The

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plantations were planted in winter 1990 at a spacing of 4.9 m x 1.8 m. Prior to tree establishment the two areas had been managed as a bermudagrass (*Cynodon spp*.) pasture. In 2000, the stands were thinned to 618 trees/ha. The soil mapping unit at this study site is an Ora-Savannah association (Matthews and others 1974). This association is composed of loamy soils that are nearly level to gently sloping, medium acid to very strongly acid, and low in natural fertility. These soil series are primarily classified as fine loamy, mixed, siliceous, thermic, Typic Fragiudults (Matthews and others 1974). The climate in Ouachita Parish is mild, humid subtropical with high rainfall occurring in the winter and spring followed by dry weather in the summer and autumn. Average annual temperature is 21° C, and average rainfall is 128 cm (Matthews and others 1974). Ice storms passed through Ouachita Parish in December 1998 and January 2001, with minimal damage occurring in the study stands.

The study design was a randomized complete block design with a one-way treatment structure and four levels of pine straw harvesting and fertilizer regime treatments. The four treatment regimes were replicated twice within a 1-ha block in each stand, with stand as the blocking factor. Treatments were applied to 0.08-ha plots which were separated by a 3-m buffer to ensure independence of treatments. The regime treatments were: (1) a control treatment of no straw raking and no fertilization (CONTROL), (2) pine straw raking without fertilization (RAKE), (3) pine straw raking with annual application of diammonium phosphate and urea (RAKE-IN), and (4) pine straw raking with an annual application of poultry litter (RAKE-PL).

Pine straw raking began in fall 2000, with straw harvests occurring annually thereafter. Pine straw was collected in February, August, and November each year by tractor-drawn hay rakes and balers operated by a commercial pine straw harvest contractor. Understory vegetation in raked plots was controlled with glyphosate applied once in August 2003 at a rate of 1.2 L active ingredient/ha. All coarse and fine woody debris and vegetative matter was removed and windrowed by hand prior to raking but left on site. Average annual production was 173 bales/ha, with an average bale weight of 11.3 kg. Fertilizer applications in the RAKE-IN and RAKE-PL treatments began in April 2003 and were conducted annually thereafter. For the RAKE-IN treatment, 308 kg/ha of urea and 280 kg/ha of diammonium phosphate were applied each spring. The fertilizers applied for the RAKE-IN treatment supplied N and P at 193 kg/ha/year and 129 kg/ha/year, respectively. For the RAKE-PL treatment it was assumed that the poultry litter had N and P concentrations of 3 percent, and dry litter was applied at a rate of 7.7 Mg/ha in order to provide N and P equivalent to that of the RAKE-IN treatment.

Gas exchange was measured to determine light-saturated photosynthesis (Amax) and stomatal conductance (Gs). Measurements were taken on needles from the upper, mid, and lower branch positions of the crown seasonally: summer (August 2008), late fall (December 2008), winter (February 2009), and spring (May 2009). Dominant trees with well-developed crowns and absent of disease, insect, drought, or ice damage were selected for sampling. Branches from one tree from each plot were excised with a 12-gauge shotgun. The same trees were sampled each season. Measurements were taken in an open-system configuration with a CI-340 Photosynthesis System (CID Inc., Camas, WA, USA). The cuvette of the analyzer was operated under ambient CO_2 concentrations, and saturating light (photosynthetically active radiation of 1800 µmol/m^2/s) was applied so that photosynthesis was maximized throughout the measurement period. When branches were detached, they were placed upright in a container of water at ambient temperature and measured within 5 minutes to optimize accuracy during measurement (Blazier and others 2004). Nine needles (three fascicles) from the first flush of current-year foliage were placed into the leaf chamber of the gas analyzer. The CI-340 Photosynthesis System calculated Amax and Gs based on the gas exchange parameters (relative humidity, air temperature, leaf temperature, and atmospheric pressure) directly measured with the instrument. Intrinsic water use efficiency (WUE) was then calculated by dividing Amax by Gs (Cregg and others 2000).

During the study period, daily precipitation was measured by a tipping-bucket rain gauge located at the Calhoun Research Station as part of the Louisiana Agriclimatic Information System. Daily precipitation was summed for each month from July 2008 through June 2009. The historical monthly potential evapotranspiration (PET) for the Calhoun Research Station was developed from 30-year monthly averages of air temperature and day length collected at the station (Thornthwaite 1948).

To characterize the influence of the treatments on tree nutrition, foliage samples were collected from the upper-mid portion of tree crowns in December 2007 from three dominant or codominant trees of good form and vigor per plot using a 12-gauge shotgun. Ten needle fascicles were taken from the first flush of current-year foliage in the excised branches. All sampled fascicles were pooled for each plot, so each plot was represented by one composite sample. Concentrations of N, P, K, S, B, Ca, Cu, Fe, Mg, Mn, and Zn were then analyzed. Nitrogen was analyzed by dry combustion (Nelson and Sommers 1996) with a Leco CN analyzer (Leco, Inc., St. Joseph, MI, USA). All other nutrients in the foliage samples were determined by nitric acid digestion followed by analysis with ICP spectrometry (Zarcinas and others 1987) on a Thermo-Jarrell Enviro II (Thermo-Jarrell Ash, Inc., Franklin, MA).

All gas exchange variables (Amax, Gs, WUE) were analyzed with the SAS System program using a repeated measures mixed model (PROC MIXED; SAS Inc.) that included block, season, and the interaction of block and season as random effects and treatment, crown position, and the interaction of treatment and crown position as fixed effects. An autoregressive correlation structure was used for the repeated measures analysis. All nutrient variables were analyzed with a model that contained block, treatment, and the interaction of block and treatment as fixed effects. When an ANOVA indicated significant treatment effects, treatment means were calculated using the LSMEANS procedure and separated by the DIFF and SLICE options. The DIFF option provided multiple comparisons of treatment means by invoking t-tests to determine significant differences between all possible treatment combinations. The SLICE option, which was used to investigate treatment main effects when significant 2-way interactions were found, provided t-tests of treatment means in which the effect of one treatment was evaluated at each level of another treatment. An alpha of 0.10 was used for all data analyses.

RESULTS AND DISCUSSION

Significant season x treatment interactions were found in the analyses of Amax and Gs (Table 1). In August 2008, Amax of the CONTROL and RAKE treatments were greater than those of both fertilization treatments. Among all foliage nutrients tested, only S and P were affected by treatments (Table 2). The RAKE-PL treatment had greater P concentrations than the unfertilized treatments. Interestingly both fertilizer treatments had greater S than the non-fertilized treatments, and the RAKE-PL treatment led to greater loblolly pine foliage S concentrations than the RAKE-IN treatment. Foliage S concentrations of the CONTROL treatment were below foliage S critical values, so the site was likely deficient in S (Allen 1987, Jokela and others 1991). Increased foliage S of the RAKE-IN treatment may have been due to increased uptake capacity as a result of the N and P applied as part of this treatment regime. Increased foliage S of the RAKE-PL treatment was likely because of the S supplied by the poultry litter as well as improved uptake capacity as a consequence of the other nutrients supplied by the poultry litter. The increases in tree foliage S nutrition as a result of the fertilizer treatments may have contributed to the short-term lower Amax of the trees observed in August 2008, because studies of S-enriched plants have revealed reductions in net photosynthesis (Black and Unsworth 1979).

Stomatal conductance of the RAKE-PL treatment in May 2009 was greater than that of all other treatments (Table 1). Similar increases in Gs during the spring with poultry litter additions were found by Tyler and others (1993) in outdoor container- grown *Hemerocallis* spp. in North Carolina. Tyler and others (1993) found that Gs increased with rate of poultry litter application and the greater Gs was attributed to increased soil water-holding capacity, available water, and nutrients with the addition of poultry litter. In a concurrent study at the Calhoun study site, Ellum (2010) found that the RAKE-PL treatment had higher soil organic matter concentrations than all other treatments. This increased organic matter may have contributed to the greater Gs observed in response to this treatment in May 2009. This effect of poultry litter on Gs was likely most pronounced in May 2009 among all sampling periods because litter had been applied two weeks before measurement occurred. Intrinsic WUE was unaffected by treatments, which was likely due to the sufficient precipitation of the study period. In all months of sampling, precipitation exceeded PET (Figure 1).

CONCLUSIONS

During a study period characterized by sufficient precipitation, there were no persistent effects of straw raking on Amax, Gs, and WUE. Lower Amax in fertilized treatments than in non-fertilized treatments was observed in summer. In a measurement period within two weeks of poultry litter application, greater Gs was found in response to litter application. The short-term increase in Gs in response to litter application was likely due to water retention by the litter.

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Table 1—Light-saturated photosynthetic rate (Amax) and stomatal conductance (Gs) of loblolly pine in north central Louisiana in response to no fertilization and no raking of pine straw (CONTROL), annual pine straw raking initiated in 2000 (RAKE), annual pine straw raking initiated in 2000 and annual application of urea and diammonium phosphate initiated in 2003 (RAKE-IN), and annual pine straw raking initiated in 2000 and annual application of poultry litter initiated in 2003 (RAKE-PL). For each variable, means within each column differ at $P < 0.10$.

Treatment	Date			
	August 2008	December 2008	February 2009	May 2009
Amax (μmol/m^2/s)				
CONTROL	4.58 a	1.88 a	0.43 a	2.37 a
RAKE	3.97 a	1.05 a	1.81 a	1.83 a
RAKE-IN	1.99 b	0.70 a	0.78 a	1.64 a
RAKE-PL	1.73 b	2.07 a	1.43 a	2.66 a
Gs (mmol/m^2/s)				
CONTROL	0.44 a	0.22 a	1.37 a	1.00 b
RAKE	0.14 a	0.03 a	0.85 a	0.35 b
RAKE-IN	0.33 a	0.09 a	1.70 a	0.38 b
RAKE-PL	0.11 a	0.46 a	0.85 a	2.99 a

Table 2—Foliar nutrient concentrations of loblolly pine in north central Louisiana in response to no fertilization and no raking of pine straw (CONTROL), annual pine straw raking initiated in 2000 (RAKE), annual pine straw raking initiated in 2000 and annual application of urea and diammonium phosphate initiated in 2003 (RAKE-IN), and annual pine straw raking initiated in 2000 and annual application of poultry litter initiated in 2003 (RAKE-PL). For each nutrient, means within each row differ at P < 0.10

Nutrient	Treatment			
(mg/kg)	CONTROL	RAKE	RAKE-IN	RAKE-PL
N	14633 a	14470 a	18850 a	19413 a
P	1260 b	1303 b	1375 ab	1443 a
K	3528 a	3467 a	3755 a	3895 a
S	985 c	1048 c	1158 b	1255 a
Ca	1630 a	1588 a	1653 a	2055 a
Mg	803 a	973 a	745 a	855 a
B	11 a	14 a	14 a	21 a
Cu	3 a	3 a	4 a	3 a
Fe	37 a	37 a	37 a	35 a
Mn	365 a	315 a	369 a	406 a
Zn	32 a	37 a	32 a	41 a

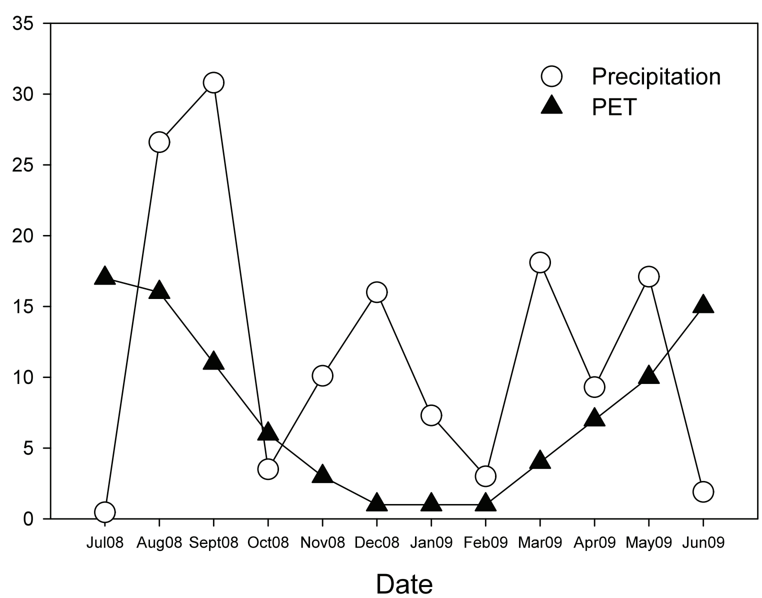

Figure 1—Average monthly precipitation at the LSU AgCenter Calhoun Research Station during the study period and Thornthwaite potential evapotranspiration based on 30-year climatic data collected at the station.