

## Seasonal variation in competitive effect on water stress and pine responses

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Plant mixtures were established that differed in both proportion and density of loblolly pine (*Pinus taeda* L.), sweetgum (*Liquidambar styraciflua* L.), and broomsedge (*Andropogon virginicus* L.). Soil moisture availability to the pine seedlings was quantified every 2 weeks by measuring predawn xylem pressure potentials. Temporal variation in pine water potential was accounted for by a water stress integral approach. Cumulative water stress integral values were calculated over four overlapping periods, from May to June, May to July, May to August, and May to September and compared with the mean seedling stem volume index at each period to determine competitive responses at the whole plant scale. Diurnal measures of stomatal conductance were taken each month to compare competitive responses at the leaf scale. In addition, environmental and plant responses that may control stomatal behavior were quantified. The pine water stress integral was strongly influenced by competing vegetation after the onset of a period of drought in early summer. The correlation between the water stress integral and pine growth increased after a significant drying period, accounting for more than half of the variation in stem volume index at the end of the first growing season. Stomatal conductance was also influenced by competition, with competitive effects more evident during times of drought. Conductance was most often related to bulk leaf water potential, which in turn was related to competitive effects on soil moisture availability. Vapor pressure deficit also influenced stomatal conductance, but this was largely unrelated to competitive effects.

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Nous avons planté du pin à encens (*Pinus taeda* L.), du liquidambar d'Amérique (*Liquidambar styraciflua* L.) et du barbon de Virginie (*Andropogon virginicus* L.) en mélanges de proportions et de densités différentes. La disponibilité en eau pour les plants de pin a été évaluée aux deux semaines au moyen de mesures de potentiel hydrique pré-aube. Ces mesures ont servi au calcul de l'intégrale de stress hydrique. Les valeurs cumulatives d'intégrale de stress hydrique ont été calculées pour quatre périodes avec chevauchement, de mai à juin, de mai à juillet, de mai à août et de mai à septembre, puis comparées à l'indice moyen de volume de tige des semis à chaque période afin de déterminer la réponse de la plante entière à la compétition. Des mesures mensuelles de conductance stomatique ont servi à l'évaluation de la réponse foliaire à la compétition. Nous avons aussi quantifié les facteurs environnementaux et les réponses de la plante qui pourraient influencer le comportement des stomates. L'intégrale de stress hydrique des pins a été très affectée par la présence de compétition végétale au cours d'une sécheresse au début de l'été. La corrélation entre l'intégrale de stress hydrique et la croissance des pins s'est accrue après une période significative de sécheresse, expliquant plus de 50% de la variation de l'indice de volume de tige à la fin de la première saison de croissance. La conductance stomatique a aussi été affectée par la compétition, ces effets étant plus évidents pendant les périodes de sécheresse. La conductance était souvent reliée au potentiel hydrique foliaire, lui-même relié à l'effet de la compétition sur la disponibilité en eau. La conductance était aussi influencée par le déficit atmosphérique de pression de vapeur, mais cet effet était indépendant de l'effet de la compétition.

[Traduit par la rédaction]

### Introduction

Competition has been described as a two part process: (i) the effect of competitors on resource levels, and (ii) the response of the target plants to the level of available resources (Goldberg 1990). This perspective views resources (water, light, and nutrients) as intermediaries through which plants interact. Plant response to resources can be seen in growth rates, physiological activity (i.e., stomatal conductance), and reproductive output (Kramer 1983). Goldberg (1990) argues that for competition to occur, both the effect and response components must be significant. Thus, resolution of

controversies about the types of environments under which competition is an important determinant of individual fitness and community structure, or the types of resources driving competitive relationships will depend on trends in both the magnitude of resource depletion and the degree of resource limitation to plant development (Goldberg 1990).

Goldberg's conceptual model of competition provides a sound perspective from which the mechanisms of competition can be viewed. Few studies, however, have attempted to separate competitive effects from responses (Goldberg 1990). Competitive effects on resources can vary in time and space; thus, some means of integrating resource availability is required to relate spatial and temporal patterns in

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competitive effects to responses. Recently, a water stress integral approach was suggested as a means of relating variation in competitive effects on soil moisture to competitive responses (Mitchell et al. 1993). Secondly, temporal variation in competitive responses has not been investigated. In addition, competitive responses may vary with respect to effects. For instance, survival responses to competition may be different from that of growth. Responses at the scale of the whole plant may differ from competitive responses at the leaf scale (i.e., stomatal conductance). Yet little work has addressed multiple responses of plants to competition.

Soil moisture is one of the most limiting resources to loblolly pine (*Pinus taeda* L.) productivity in the southeastern United States (Kramer 1983). Increased conifer growth following the control of herbaceous and (or) woody competitors has also been well documented for the southeastern United States (Nelson et al. 1981; Knowe et al. 1985; Bacon and Zedaker 1987; Glover et al. 1989; Britt et al. 1990, 1991; Miller et al. 1991) and elsewhere throughout the world (Walstad and Kuch 1987; Nambiar 1990). Frequently, increased pine growth associated with decreased competition is attributed to decreased competition for soil moisture (Carter et al. 1984; Zutter et al. 1986; Byrne et al. 1987; Allen et al. 1990); yet, the extent to which this is true has not been quantified. Furthermore, past experiments have largely relied on repeated efforts to eliminate competition, either mechanically (hoeing) or chemically (herbicide). Typically, silvicultural practices only reduce levels of competitors rather than eliminating them, frequently resulting in complex associations of multiple life forms (i.e., various grasses, other herbaceous plants, shrubs, sprouting hardwoods, etc.; see Fredericksen et al. 1991).

Little is known about pine seedling responses to gradients in competition with multiple life forms. Competitive responses of conifers using quantitative approaches that vary the proportion and density of competitors have only recently been reported (Shainsky and Radosevich 1991; Perry et al. 1993). Since only a few reports have attempted to quantify resources across gradients in competition (Goldberg 1990; Shainsky and Radosevich 1992), our understanding of the mechanisms of competition is limited. Thus, the primary objective of this study was to determine the influence of gradients in broomsedge (*Andropogon virginicus* L.), sweetgum (*Liquidambar styraciflua* L.), and pine density on the water relations and competitive responses (i.e., pine growth and stomatal responses) of pine seedlings throughout the first growing season. A secondary objective was to examine the relationship in pine growth response by an integrated measure of water stress. The final objective was to examine the degree to which stomatal conductance patterns were related to competitive effects (such as soil moisture availability or light) rather than variables not directly affected by competitive structure (e.g., vapor pressure deficit).

## Methods

### Study site

The study site was located at Auburn University's E.V. Smith Research Center, near Shorter, Ala. Soils are of the Malbis series (fine-loamy, siliceous, thermic, Typic Hapludults), which are representative of soils found in the Upper Coastal Plain in Alabama. Average annual precipitation is approximately 134 cm. The site has an average slope of >1%. The area was in row crop production during the 20-year period prior to the establishment

of this study, and was last used for this purpose in 1987. After laying fallow during 1988, the site was chisel plowed to break up any plow pan created by past agricultural practices. The area was sprayed with glyphosate (4.5 kg/ha) in early September 1988, disked in October, and then fumigated with 98% methyl bromide and 2% chloropicrin to control weeds.

### Experimental design and installation

An experiment was established as a complete factorial arrangement of loblolly pine and sweetgum at 0, 1, 2, and 4 plants/m<sup>2</sup> and broomsedge at 0, 4, and 16 plants/m<sup>2</sup>, yielding a total of 48 treatments. Each treatment was replicated four times, occurring once per block in a randomized complete block design. Owing to personnel constraints, only three blocks were used for this study; however, the same three blocks were used for all measurements throughout the study.

Treatment plots measured 488 × 902 cm and were divided into 44 subplots, each 122 × 82 cm (1 m<sup>2</sup>). Each subplot had 24 potential planting locations (the total number of individuals in the highest density treatment), with each location approximately 20 cm from adjacent locations. Within each subplot, the number of plants of each species, as dictated by treatment, were randomly assigned planting locations.

Sweetgum regeneration on harvested sites is usually of sprout rather than seed origin, and broomsedge is often present at the time of pine outplanting. Thus, these species were established in the following manner. In December 1988, sweetgum seedlings (1-0 stock, root collar diameter 6.0–10.0 mm) from a seed source in the Upper Coastal Plain of Alabama were planted. In February and March 1989, broomsedge seedlings were excavated from nearby natural stands, individual seedlings separated, and 2 or 3 seedlings were planted per designated planting location. The sweetgum and broomsedge plants were allowed to grow in 1989. During this time, they were irrigated on two occasions, and plots were hand weeded to ensure maximum survival. Though survival was good (>90%), a supplemental planting of broomsedge was made in May 1989. In December 1989, sweetgum and broomsedge were cut 5 and 10 cm, respectively, above the groundline. At the time of cutting, sweetgum survival was greater than 99% and broomsedge survival exceeded 95%. During 1990, these plants sprouted and grew with the newly planted loblolly pine. Bare-root loblolly pine seedlings from half-sib seed from an improved Upper Coastal Plain parent (1-0 stock, root collar diameter 4.0–6.0 mm) were planted in February 1990.

### Data collection

Predawn xylem water potential ( $\Psi_{PD}$ ) measurements were taken approximately every 2 weeks from early May through late September 1990. Predawn xylem water potential was measured on individual fascicles of loblolly pine using the pressure chamber method (Scholander et al. 1964). Measurements were taken from the most recent, fully developed flush of growth between 01:00 and 04:00 h CDST. Three seedlings per plot were randomly selected at each measurement date. Predawn pine xylem water potential measurements of loblolly pine fascicles were conducted on the 18 treatments resulting from the factorial combination of loblolly pine at 2 and 4 plants/m<sup>2</sup>, sweetgum at densities of 0, 2, and 4 plants/m<sup>2</sup>, and broomsedge at 0, 4, and 16 plants/m<sup>2</sup>.

Basal diameter and total height were measured on eight randomly selected pines in each treatment plot beginning in early March and continuing monthly through early September (Perry et al. 1993). The stem volume index for each seedling was calculated by multiplying the cross-sectional area at the base by the height.

Stomatal conductance (*g*), air temperature, leaf temperature, relative humidity, and photon flux density were measured with a LI-COR 1600 steady-state porometer. Six treatments, consisting of the factorial arrangement of loblolly pine at 2 plants/m<sup>2</sup>, sweetgum at 0 and 2 plants/m<sup>2</sup>, and broomsedge at 0, 4, and 16

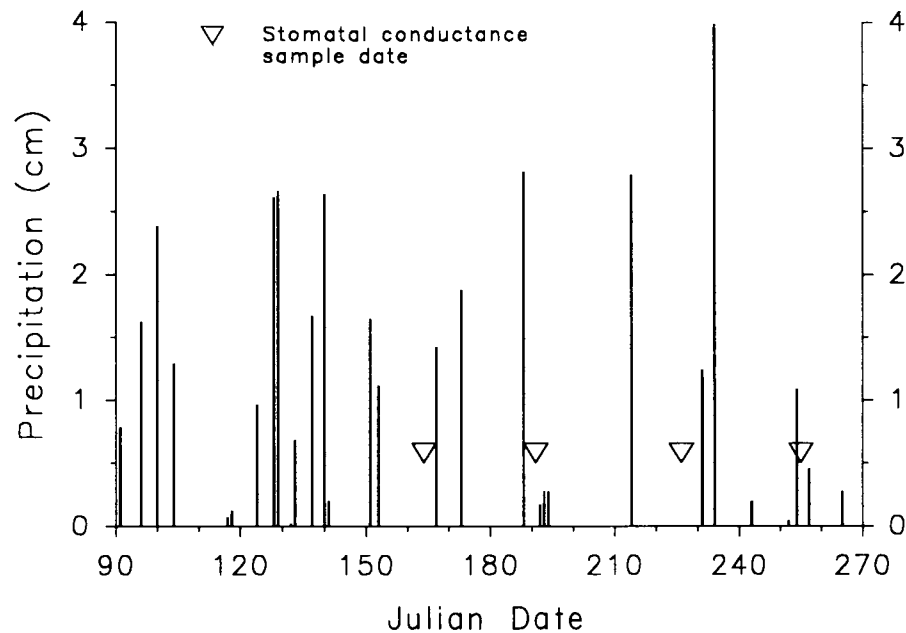


FIG. 1. Timing of diurnal stomatal conductance measurements with respect to precipitation events.

plants/m<sup>2</sup> were measured for these parameters on each of three seedlings for each species on each plot. These individuals were measured at three times throughout the day (9:00, 12:00 and 14:00 solar time). Because of the number of measurements involved, each block was measured on a separate day. Diurnal leaf water potential ( $\Psi_1$ ), and  $\Psi_{PD}$  measurements were taken on the same individuals on which stomatal conductance was measured. Measurement periods were June 13–15, July 10–12, August 14–16, and September 11–13. The order that treatments were measured within a block was randomized independently for each period. July and September measurements were taken when soil moisture was high, less than 3 days following a rain of 2 cm or more, while June and August measurements were taken when soil moisture was low, 10 or more days following a rain of only 3 mm or less (Fig. 1).

#### Data analysis

To derive an estimate of plant water stress through time, water stress integral (WSI) was calculated from the predawn xylem water potential measurements using the equation described by Myers and Landsberg (1988):

$$WSI = \left| \sum_{i=0}^{i=t} (\Psi_{i,i+1} - c) \right|$$

where  $\Psi_{i,i+1}$  is the mean predawn water potential over any interval,  $i, i+1$ , of  $n$  days in length,  $c$  is the maximum (least stressed) predawn water potential measured over the duration of the experiment, and  $t$  is the number of intervals. Water stress integral was calculated over four overlapping periods (from the beginning of May to early June, May to July, May to August, and May to mid-September). The relationship between WSI and the calculated pine stem volume index at the end of each of these four periods was examined using linear and hyperbolic models.

Repeated measures analysis of variance (Moser et al. 1990) was performed on WSI with date as the repeated factor, and on stomatal conductance and diurnal  $\Psi_1$  at each date using the measurement period as the repeated factor. Stomatal conductance was regressed as a function of combinations of  $\Psi_1$ ,  $\Psi_{PD}$ , vapor pressure deficit (VPD), and photon flux density (PFD) at the leaf surface (as well as squared terms for each of these factors) as independent variables for each measurement period. Vapor pressure deficit (VPD) was calculated from temperature and relative humidity using the equation of Goff and Gratch (1946) to

obtain saturated vapor pressures. All repeated measures analysis of variance and regressions were performed using the general linear models, nonlinear regression, and regression procedures of SAS (SAS Institute Inc. 1988).

#### Results

Pine water stress integral (WSI) was influenced by sweetgum ( $P = 0.0003$ ) and broomsedge ( $P = 0.0021$ ) density, as well as by date (Table 1). Differences among treatments were not evident in early June but were apparent by early July (Fig. 2). By the end of the first growing season, mean WSI ranged from 59.3 MPa-days for pine only to 94.3 MPa-days for pine with 16 broomsedge and four sweetgum. Pine stem volume index (SVI) was not correlated with pine WSI in early June (Fig. 3). However, by early July, a hyperbolic relationship between pine SVI and WSI was observed ( $R^2 = 0.44$ ). The strength of the relationship between pine SVI and WSI increased marginally through early August ( $R^2 = 0.50$ ) into mid-September ( $R^2 = 0.54$ ).

Stomatal conductance was influenced by the time of day for all dates measured (Table 2, Fig. 3). Stomatal conductance was more sensitive to the presence of competitors when soil moisture was low (mid-June and mid-August) than on dates with higher soil moisture (mid-July) (Table 2, Figs. 1, 4, and 5). Stomatal conductance decreased with sweetgum and broomsedge on the June 13–15 and August 14–16 measurements. No effect of either species was detected on July 10–12 or September 11–13. Conductance was most often correlated with  $\Psi_1$  (Table 3). Vapor pressure deficit, quantum level, and  $\Psi_{PD}$  were also related to  $g$ . In general,  $g$  increased as photon flux density and  $\Psi_{PD}$  increased, and decreased as VPD increased. The strength of these relationships, however, varied by date and time of day (Table 3).

Xylem water potential varied diurnally for all dates (Table 4, Fig. 5), although on July 10–12 a nonsignificant trend was observed ( $P = 0.0714$ ). The effect of associated vegetation on pine  $\Psi_1$  differed by date (Table 4). Neither sweetgum nor broomsedge resulted in a significant decrease in pine  $\Psi_1$  at the June 13–15 or July 10–12 measurement.

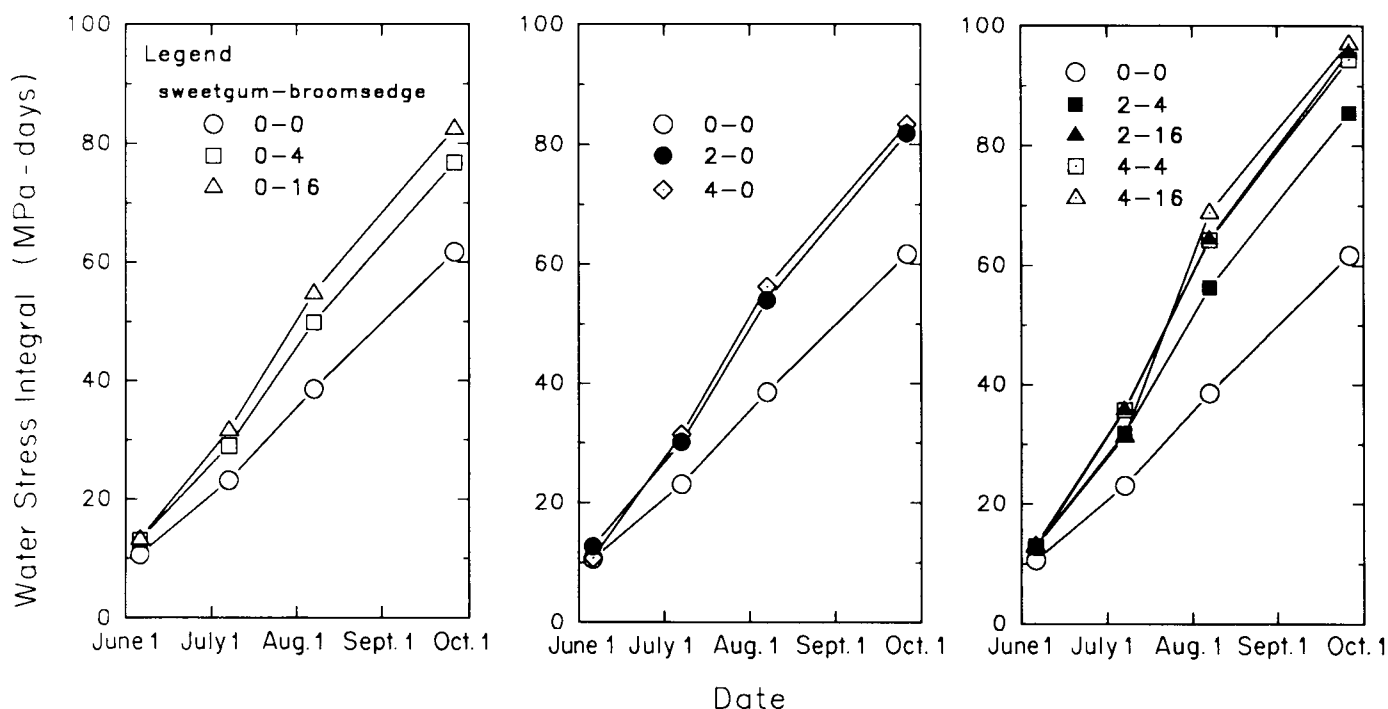


FIG. 2. Cumulative loblolly pine water stress integral (WSI) through the first growing season. Treatment codes indicate the level (plants/m<sup>2</sup>) of sweetgum and broomsedge, respectively (sweetgum–broomsedge).

TABLE 1. Analysis of loblolly pine water stress integral throughout the growing season in a 3 × 3 × 3 factorial of densities of loblolly pine (*Pinus taeda*), sweetgum (*Liquidambar styraciflua*), and broomsedge (*Andropogon virginicus*)

Source of variation <sup>a</sup>	df	Wilks' $\lambda^b$	MS	F	P > F
B	2		803.20	4.39	0.0201
P	1		147.90	0.81	0.3749
L	2		1917.81	10.48	0.0003
P × L	2		200.65	1.10	0.3455
A	2		1362.02	7.45	0.0021
P × A	2		14.96	0.08	0.9217
L × A	4		71.07	0.39	0.8154
P × L × A	4		58.90	0.32	0.8613
Error	34		182.94		
D	3	0.0085 (32)		1242.51	0.0001
D × B	6	0.5055 (64)		4.34	0.0010
D × P	3	0.8698 (32)		1.80	0.2096
D × L	6	0.4824 (64)		4.69	0.0005
D × P × L	6	0.9000 (64)		0.58	0.7472
D × A	6	0.6679 (64)		2.39	0.0384
D × P × A	6	0.9410 (64)		0.33	0.9193
D × L × A	12	0.6363 (85)		1.32	0.2230
D × P × L × A	12	0.7525 (85)		0.80	0.6461

<sup>a</sup>P, *Pinus taeda*; L, *Liquidambar styraciflua*; A, *Andropogon virginicus*; B, block; D, date.

<sup>b</sup>Wilks'  $\lambda$  is a multivariate test (error degrees of freedom are given in parentheses) applied to the repeated measures factor, date.

Measurements taken on August 14–16, however, revealed a decrease in pine  $\Psi_1$  owing to sweetgum ( $P = 0.0097$ ; Fig. 5). Pine  $\Psi_1$  at the September 11–13 measurement decreased with both broomsedge ( $P = 0.0209$ ), and sweetgum ( $P = 0.0552$ ).

### Discussion

Although several studies have reported that competition among early successional competitors and conifers is often

related to moisture stress (Nelson et al. 1981; Carter et al. 1984; Zutter et al. 1986; Byrne et al. 1987; Allen et al. 1990; Morris et al. 1993), few have attempted to relate competitive effects on soil moisture to competitive responses (sensu Goldberg 1990). Competitive effects on resources, particularly soil moisture, vary spatially and temporally. Mitchell et al. (1993) reported complex patterns in soil moisture across levels of competition. They noted a positive association between density of competitors and increas-

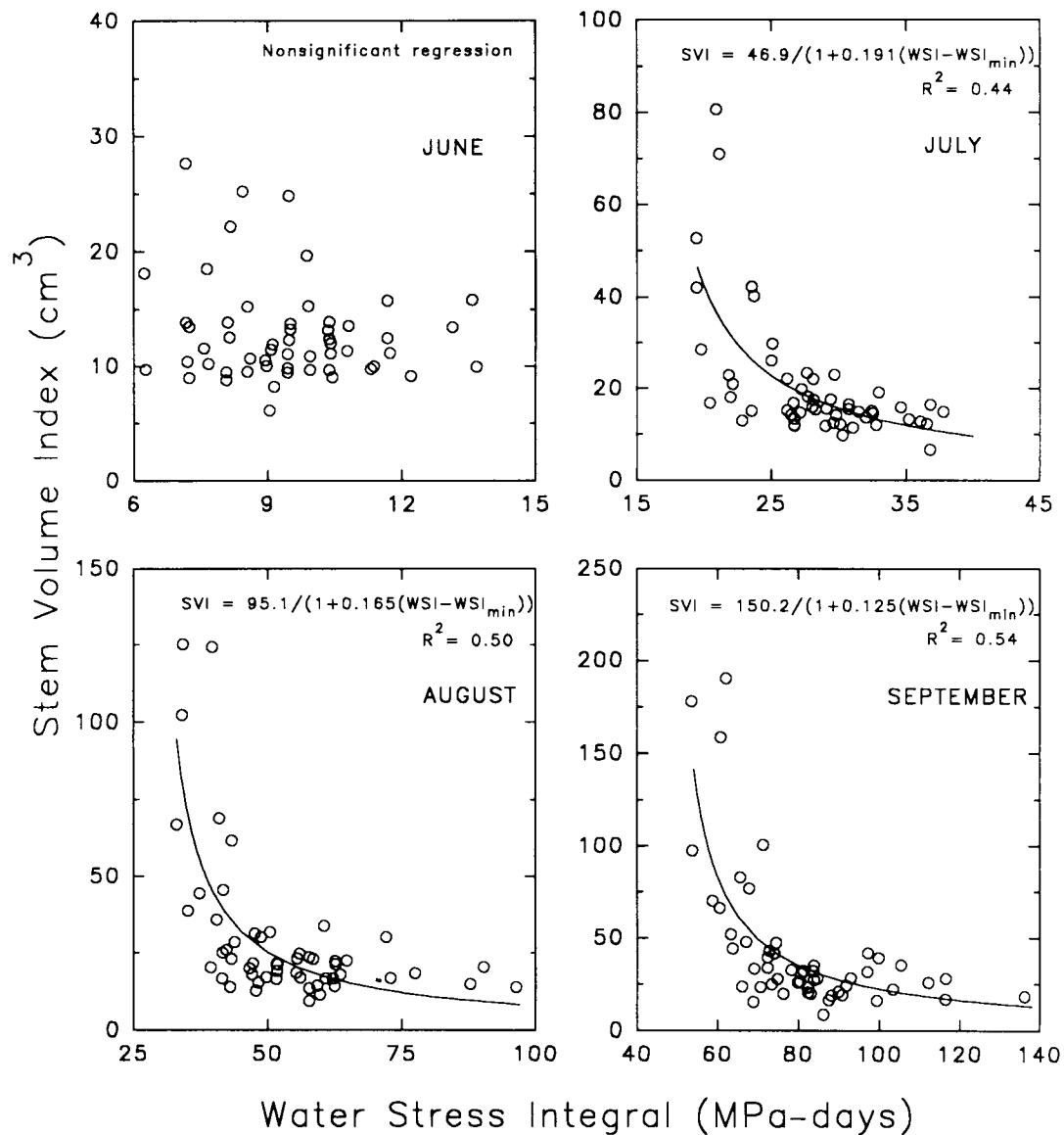


FIG. 3. Relationship between loblolly pine stem volume index and cumulative water stress integral (WSI) by month during the growing season.

TABLE 2. Results of analysis of variance ( $P$ -values) for diurnal stomatal conductance of loblolly pine

Source of variation <sup>a</sup>	df	$P$ -value			
		June	July <sup>b</sup>	August	September
Block	2	0.6894	0.1335	0.5232	0.9344
L	1	0.0047	0.8947	0.0164	0.9901
A	2	0.0550	0.9242	0.0522	0.0836
Linear	1	0.0222	0.7708	0.0245	0.0555
Quadratic	1	0.4712	0.8082	0.3306	0.2176
L × A	2	0.9361	0.8092	0.1883	0.6544
H	2	0.0012	0.0063	0.0003	0.0026
H × B	4	0.7933	0.4022	0.2739	0.5706
H × L	2	0.4738	0.7811	0.3177	0.7809
H × A	4	0.9102	0.3124	0.1923	0.4434
H × L × A	4	0.8894	0.7984	0.7460	0.3352

<sup>a</sup>L, *Liquidambar styraciflua*; A, *Andropogon virginicus*; B, block; H, hour.

<sup>b</sup>Analysis based on two blocks owing to missing data (df block = 1, hour × block = 2).

ing soil moisture in the surface horizon, attributing the relationship to increased infiltration and reduced evaporation. Deeper portions of the solum showed the opposite trend (i.e., reduced soil moisture with increasing density of competitors).

Predawn xylem water potential is a good indicator of overall plant water status and reflects soil water potential throughout the rooting zone (Kramer 1983). Lowering of  $\Psi_{PD}$  can occur with increasing drought (Schulze and Hall 1982) or can result from increased competition for soil moisture (Nelson et al. 1981). Nelson et al. (1981) found that during an extended drying period, herbaceous vegetation in unweeded plots resulted in pine  $\Psi_{PD}$  of  $-1.5$  MPa, while plots with 50% and greater herbaceous control averaged nearly  $-0.5$  MPa. Although reductions in  $\Psi_{PD}$  of this magnitude were not observed in the present study, the presence of broomsedge commonly reduced pine  $\Psi_{PD}$  by 0.1–0.8 MPa, with the effect becoming stronger as the time since the last rain increased. Reductions in loblolly pine  $\Psi_{PD}$  due to sweetgum were of similar magnitude and pattern. The

TABLE 3. Regression coefficients of statistically significant independent variables used to characterize stomatal conductance at each measurement period ( $n=18$ )

Date	Hour	Intercept	Model parameters								
			$\Psi_{PD}$	$\Psi_{PD}^2$	$\Psi_1$	$\Psi_1^2$	VPD	VPD <sup>2</sup>	PFD	PFD <sup>2</sup>	$R^2$
June 13–15	9:00	306.3			493.0	223.5					0.40*
	12:00	563.2			580.4	175.3	-35.6		0.049		0.86***
	14:00	109.2		98.6	79.6					$1.3 \times 10^5$	0.62**
July 10–12	9:00	197.7			34.1		-53.1				0.62**
	12:00 <sup>a</sup>										— <sup>b</sup>
	14:00 <sup>a</sup>										—
Aug. 14–16	9:00	107.7			138.1	45.3					0.87***
	12:00	-2070.5			13.6		870.7	-90.3			0.59**
	14:00	83.5			21.0		-8.1				0.42*
Sept. 11–13	9:00	-1716.4	406.1	292.9			2374.9	-723.9			0.51*
	12:00										—
	14:00										—

NOTE: Variables considered were predawn leaf xylem water potential ( $\Psi_{PD}$ ), leaf xylem water potential at time of measurement ( $\Psi_1$ ), vapor pressure deficit (VPD), photon flux density (PFD), and quadratic term for each of the aforementioned factors.  $R^2$ , coefficient of determination.

\*,  $P < 0.05$ ; \*\*,  $P < 0.001$ ; \*\*\*,  $P < 0.0001$  (model  $R^2$ ).

<sup>a</sup> $n = 12$  owing to missing data for one block.

<sup>b</sup>Measurement periods with no parameters listed were measured, but no significant model was found.

decrease in water potential with increasing density of competitors may be directly attributed to their effects on soil moisture, but also may be indirectly related to decreased rate of root extension into deeper portions of the soil which had greater water availability. As aboveground growth is reduced by competition, root extension also decreases. Thus, the variation in pine size observed among the treatments (as much as an order of magnitude difference in stem volume between pine alone and the greatest competition treatments) may affect the location of resource acquisition (e.g., larger plants may access deeper soil zones first). Further work on the phenology, distribution, and resource acquisition of roots in various competitive environments is needed. However, water stress integral collapses this variation in soil moisture throughout the root system of the plant and through time (Myers and Landsberg 1988; Mitchell et al. 1993), and thus, complex patterns in water stress due to competitive effects can be related to responses.

In addition to long-term changes in plant water status,  $\Psi_1$  also varied diurnally. Xylem water potential was greatest at the predawn measurement and decreased throughout the day as potential evapotranspiration increased, with little or no recovery observed by 14:00. This decrease in  $\Psi_1$  through the day was coupled with a decrease in  $g$ . Both decreased plant water status and depressed conductance were associated with increased competitor density. Thus, competition appears to affect growth, at least in part, owing to stomatal effects.

A correlation between  $\Psi_1$  and  $g$  has been found in many studies (Sands and Mulligan 1990; Schulze 1986; Pallardy and Kozlowski 1979); however, the debate over whether this is a causal relationship continues. Recent evidence refutes the claim that bulk leaf water status regulates  $g$ . Sands and Mulligan (1990), in a root removal study, found that  $g$  was reduced before any change in leaf water status was observed. Gollan et al. (1986) found that the curve expressing  $g$  as a function of leaf  $\Psi_1$  could be shifted about 0.8 MPa by changing whole plant transpiration when plants were exposed to different vapor pressure deficits under drying soil conditions. While the relationship between  $g$  and leaf  $\Psi_1$  varied, the response of  $g$  to extractable soil water

TABLE 4. Results of analysis of variance (p-values) for diurnal xylem water potential of loblolly pine

Source of variation <sup>a</sup>	df	P-value			
		June	July <sup>b</sup>	August	September
Block	2	0.0905	0.2351	0.0389	0.0324
L	1	0.0914	0.6992	0.0097	0.0552
A	2	0.3239	0.7620	0.2859	0.0209
Linear	1	0.1439	0.4841	0.1446	0.0067
Quadratic	1	0.9472	0.9531	0.5719	0.8459
L × A	2	0.9350	0.6743	0.8154	0.6382
H	2	0.0001	0.0714	0.0001	0.0001
H × B	4	0.0378	0.2380	0.0284	0.0300
H × L	2	0.8188	0.4961	0.3767	0.8783
H × A	4	0.4513	0.7820	0.3584	0.1126
H × L × A	4	0.0394	0.9815	0.2627	0.7820

<sup>a</sup>L, *Liquidambar styraciflua*; A, *Andropogon virginicus*; B, block; H, hour.

<sup>b</sup>Analysis based on two blocks owing to missing data (df for block = 1, hour × block = 2).

remained constant. The idea that stomatal aperture is controlled by a signal from the root based on soil water status has been widely accepted (Bates and Hall 1981; Schulze 1986; Turner 1986; Davies et al. 1990; Davies and Zhang 1991).

On dates where no significant differences in  $g$  were found among competition treatments (July 10–12 and September 11–13), only the morning measurement periods revealed a relationship between stomatal conductance and any measured parameter (i.e., predawn  $\Psi_1$ , diurnal  $\Psi_1$ , light, or VPD). During the July 10–12 measurements, the morning (09:00) measurement period showed significant relationships between  $\Psi_1$  ( $P = 0.0475$ ) and VPD ( $P = 0.0010$ ) and  $g$  (Table 3). The September 11–13 measurements showed relationships between  $g$  and  $\Psi_{PD}$ , VPD, and the squared terms for these variables. Stomatal closure with increases in VPD has been observed in numerous experiments (Grantz 1990; Schulze and Hall 1982; Pallardy and Kozlowski 1979). Decreases in PFD have also been found to decrease stomatal aperture

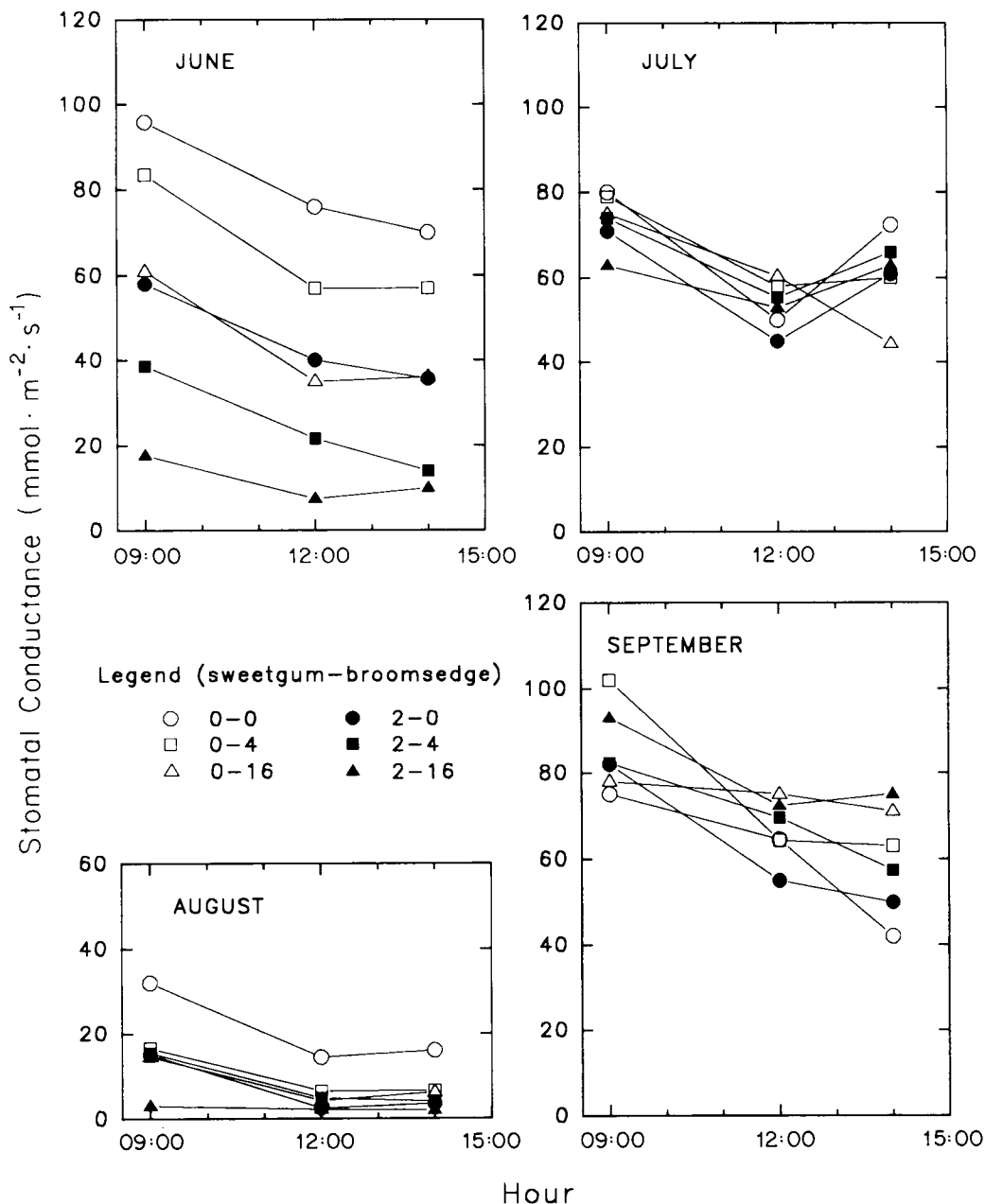


FIG. 4. Diurnal stomatal conductance by sample date for loblolly pine at 2 plants/m<sup>2</sup> grown in six combinations of sweetgum and broomsedge. Treatment codes indicate level (plants/m<sup>2</sup>) of sweetgum and broomsedge, respectively (sweetgum-broomsedge).

(Schulze and Hall 1982; Küppers 1984; Pallardy and Kozlowski 1979). At all but two measurement periods in which  $\Psi_1$  was significant by related to  $g$ , either VPD or both VPD and PFD were also significantly related to  $g$  (Table 3). The exception to this occurred on the June 13-15 and August 14-16 morning measurements, when  $\Psi_1$  was the only factor correlated with  $g$ . Contrary to the theory that soil moisture availability regulates  $g$ ,  $\Psi_{PD}$  (which reflects available soil water status) was significantly related to stomatal conductance at only two measurement periods. Running (1976) reported a relationship between  $\Psi_{PD}$  and maximum daily  $g$ . Although the maximum measured  $g$  (morning measurement) was related to  $\Psi_{PD}$  on only one date in our study, there was a general relationship between  $\Psi_{PD}$  and maximum  $g$  across all dates (data not presented). This indicates that, for field-grown loblolly pine,  $g$  was not controlled by

soil moisture levels alone, but was more closely related to bulk leaf water status which reflects a dynamic relationship between soil moisture availability, transpirational demand, and resistance to water flow between the soil-plant-atmosphere continuum.

Water deficits are often responsible for reduced shoot growth (Davies and Zhang 1991; Bradford and Hsiao 1982) and changes in root:shoot ratios (Goldberg and Fleetwood 1987). Hanson and Hitz (1982) discuss possible mechanisms through which water deficits affect plant metabolism, both stomatal and nonstomatal. Decreases in growth without decreased  $g$  were reported by Saab and Sharp (1989), which suggests moderate water deficits can disrupt certain metabolic processes which affect plant growth without a reduction in  $g$ . In the present study, competition affected plant water status, stomatal conductance and growth. As few as four

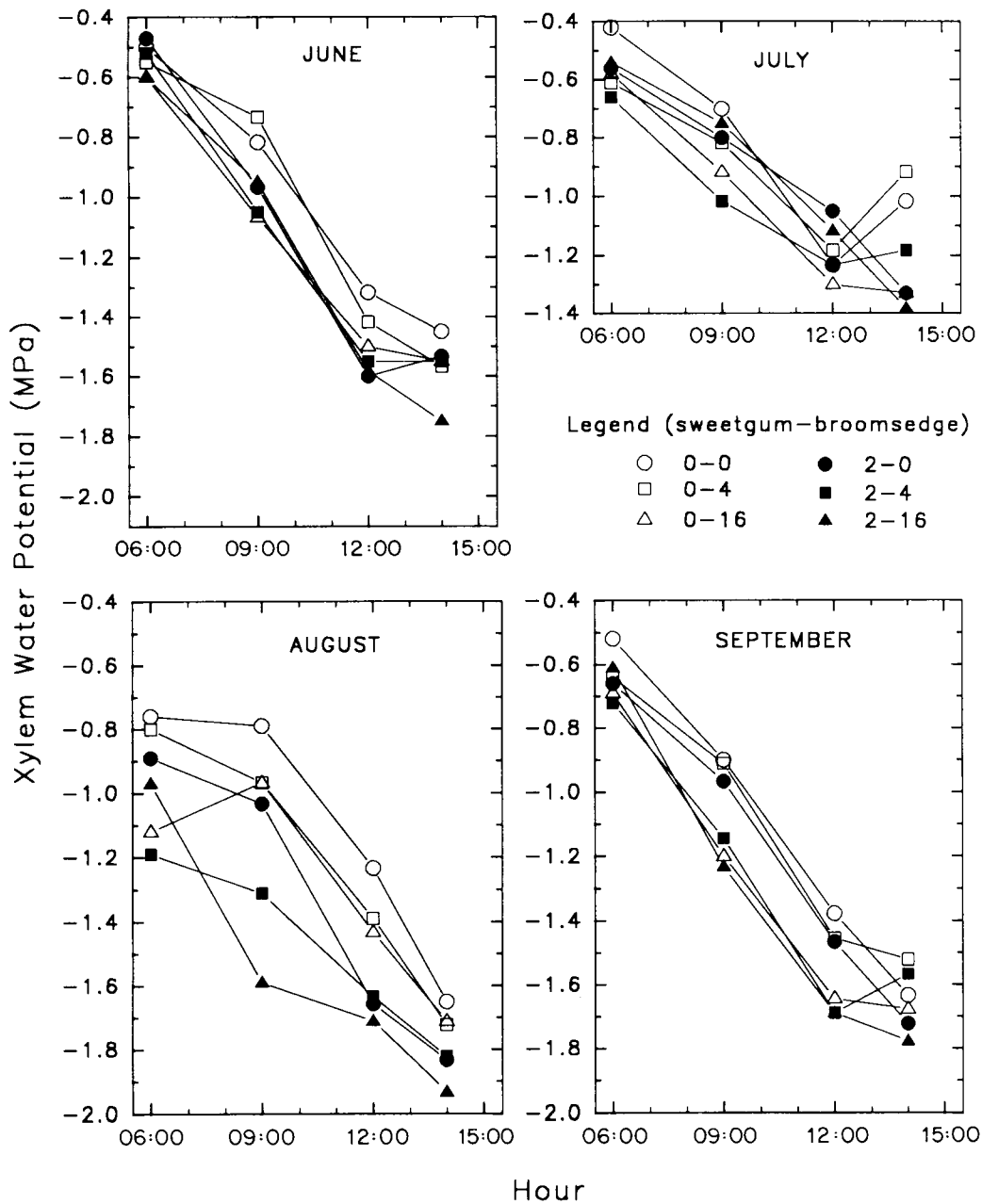


FIG. 5. Diurnal leaf xylem water potential by sample date for loblolly pine at 2 plants/m<sup>2</sup> grown in six combinations of sweetgum and broomsedge. Treatment codes indicate level (plants/m<sup>2</sup>) of sweetgum and broomsedge, respectively (sweetgum-broomsedge).

broomsedge plants per square meter reduced WSI, stomatal conductance, and growth, which indicates a relatively low threshold of competitive injury. However, investigations that use lower densities of competitors are needed to more precisely define the threshold of competition, and the degree that it may differ among responses (stomatal responses versus growth).

Furthermore, competitive thresholds may also be influenced by patterns in establishment. Growth of pine was affected by both sweetgum and broomsedge to a greater extent in the present study than that reported by Morris et al. (1993). The major difference in the two studies was that in the present study competitors were established 1 year prior to the pine (as is common on pine regeneration sites) while Morris et al. (1993) established all three species at the same time. This may suggest that resource preemption is an impor-

tant mechanism that structures competitive relationships in these types of communities. Thus, models such as those by Tilman (1988), which ignore timing of establishment, may not be suitable for mechanistically representing competitive effects and responses in systems in which resource preemption is important. Perhaps individually based, spatially explicit, and resource-mediated models may provide greater promise in depicting important mechanisms of competition for these communities (Mou et al. 1993; Pacala et al. 1993).

As water status of a plant is an important determinant for growth and development, the relationship between WSI and growth is not surprising. Shainsky and Radosevich (1992) found significant linear relationships between relative growth rate and  $\Psi_{PD}$  on a single date for both Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and red alder (*Alnus rubra* Bong.). The use of WSI to relate the complex pat-

terns inherent in soil moisture availability in field environments to competitive responses appears to be useful in relating competitive effects to responses. In our study, a negative hyperbolic relationship was observed between pine WSI and pine SVI as early as July of the first growing season, with the strength of the relationship increasing only slightly as the season progressed. It should be noted that pine growth was more strongly related to competitor density (Perry et al. 1993) than WSI. This may have been due to water stress occurring prior to the beginning of our sampling in (early May). An alternative explanation of the superiority of competitor density in accounting for variation in SVI is that other factors may be influencing competitive responses in addition to water stress. Competitor density may be more inclusive of total resource use by competitors, hence, accounts for more of the variation in SVI. The density model fails, however, to examine the mechanisms involved in competition.

In summary, after a significant drought, competitive growth response of pine was related to competitive effects on pine water stress. This response was observed rapidly, pine SVI was not related to WSI in early June, but was strongly related to WSI in July. Stomatal conductance was influenced by competition treatments, and was also related to bulk leaf water potential. Competitive effects on pine water status, and responses (both stomatal conductance and growth) were affected by competitive densities as low as four broomsedge plants per square metre.

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