Tree Physiology 25, 191–200

Radiation-use efficiency and gas exchange responses to water and nutrient availability in irrigated and fertilized stands of sweetgum and sycamore

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Received January 29, 2004; accepted June 4, 2004; published online December 1, 2004

Summary We investigated how water and nutrient availability affect radiation-use efficiency (ε) and assessed leaf gas exchange as a possible mechanism for shifts in ε. We measured aboveground net primary production (ANPP) and annual photosynthetically active radiation (PAR) capture to calculate ε as well as leaf-level physiological variables (light-saturated net photosynthesis, A_{sat}; stomatal conductance, g_s; leaf internal CO_2 concentration, C_i; foliar nitrogen concentration, foliar [N]; and midday leaf water potential, Ψ_{leaf}) during the second (2001) and third (2002) growing seasons in sweetgum (*Liquidambar styraciflua* L.) and sycamore (*Platanus occidentalis* L.) stands receiving a factorial combination of irrigation and fertilization at the Savannah River Site, South Carolina. Irrigation and fertilization increased PAR capture (maximum increase 60%) in 2001 and 2002 for both species and annual PAR capture was well correlated with ANPP (mean $r^2 = 0.77$). A decreasing trend in ε was observed in non-irrigated stands for sweetgum in 2001 and for sycamore in both years, although this was only significant for sycamore in 2002. Irrigated stands maintained higher gas exchange rates than non-irrigated stands for sweetgum in 2001 and for sycamore in both years, although foliar [N] and Ψ_{leaf} were generally unaffected. Because C_i decreased in proportion to g_s in non-irrigated stands, it appeared that greater stomatal limitation of photosynthesis was associated with decreased A_{sat}. On several measurement dates for sweetgum in 2001 and for sycamore in both years, ε was positively correlated with gas exchange variables (A_{sat}, g_s, C_i) (r ranged from 0.600 to 0.857). These results indicate that PAR capture is well correlated with ANPP and that gas exchange rates modified by irrigation can influence the conversion of captured light energy to biomass.

Keywords: fertilization, intercepted radiation, irrigation, Liquidambar styraciflua, photosynthesis, Platanus occidentalis.

Introduction

Radiation interception and the efficiency with which it is used to produce photosynthate play a major role in the growth of forest stands. A linear relationship between net primary production (NPP) or aboveground net primary production (ANPP) and the interception of photosynthetically active radiation (PAR) occurs for many species over a broad range of resource availabilities (e.g., Cannell et al. 1987, 1988, Landsberg and Wright 1989, Dalla-Tea and Jokela 1991, McCrady and Jokela 1998, Balster and Marshall 2000, Will et al. 2001). This relationship was first described by Monteith (1977), and the slope of the relationship is commonly referred to as radiation-use efficiency (ε). Radiation-use efficiency represents the integration of all photosynthetic and respiratory processes (Medlyn 1998) and is a simple yet robust variable describing growth (Sinclair and Muchow 1999).

Radiation-use efficiency may be affected by site conditions (e.g., fertility, climate, water availability) and by cultural practices (e.g., thinning, fertilization and irrigation). Several studies have shown that drought stress may decrease ε in forest stands (Cannell et al. 1987, Phillips and Riha 1993, Harrington and Fownes 1995), without offering an explanation for the reduction. However, Phillips and Riha (1993), who calculated ε based on ANPP, suggested that drought might have increased partitioning of biomass to roots, thereby decreasing ε. In a spacing trial of *Acacia koa* A. Gray, higher stand density resulted in more rapid water depletion and lower ε as a result of decreased stomatal conductance (Meinzer et al. 1996). A study with *Eucalyptus* *regnans* F. J. Muell. found that, at one site, thinning had no effect on ε, whereas at another site, thinning increased ε, a result the authors attributed to the extra belowground resources and irradiance made available by thinning (West and Osler 1995).

Several studies have shown increases in ε of forest stands in response to fertilization (Landsberg and Wright 1989, Wang et al. 1991, Raison and Myers 1992, Balster and Marshall 2000). Wang et al. (1991) hypothesized that the increase in ε resulted from a combination of increased photosynthetic rates, leaf area development and aboveground carbon allocation. Likewise, several modeling analyses of forest stands predict that ε is related to foliar nitrogen concentration (foliar [N]) (Kirschbaum et al. 1994, Medlyn 1996, Sands 1996). However, other studies on *E. globulus* Labill. (Linder 1985) and *Pinus taeda* L. and *P. elliottii* Engelm. (Dalla-Tea and Jokela 1991) found no effect of nitrogen fertilization on ε, leading the authors to conclude that the fertilization-induced increase in growth was solely a result of enhanced foliar development and light interception.

Because ε represents the integration of gas exchange processes (Medlyn 1998), it follows that resource-mediated shifts in gas exchange likely play a role in the conversion of captured radiation to biomass. In general, hardwood species have higher photosynthetic rates than conifers (Teskey et al. 1994) and tend to be more responsive to changes in resource availability (Reich et al. 1995, Ripullone et al. 2003). Several studies have shown positive effects of irrigation (e.g., Ibrahim et. al. 1998, Wang et al. 1998, Rieger et al. 2003) and fertilization (e.g., Clearwater and Meinzer 2001, Cordell et al. 2001) on gas exchange rates of broadleaf deciduous species.

Using intensively managed sweetgum (*Liquidambar styraciflua* L.) and sycamore (*Platanus occidentalis* L.) stands, the objectives of this study were to: (1) determine the effects of irrigation and fertilization on PAR capture and its relationship with ANPP; and (2) examine leaf gas exchange as a potential mechanism underlying the changes in ε. We hypothesized that fertilization increases ε by increasing photosynthetic capacity, which in turn is associated with increased foliar [N]. We also hypothesized that irrigation increases ε by reducing episodes of stomatal closure associated with reduced water availability. Although several modeling analyses have quantified the potential drivers of ε (e.g., Linder 1985, McMurtrie et al. 1994, Landsberg et al. 1996, Medlyn 1998), none have compared gas exchange measurements directly with changes in ε for forest stands.

Materials and methods

Study site

This study was conducted in the northern portion of the Savannah River Site, a National Environmental Research Park (33°23′ N, 81°40′ E) in the Upper Coastal Plain of South Carolina. Mean annual temperature is 20 °C and mean annual precipitation is 1190 mm, but extended droughts often occur during the growing season. The soil is a loamy, siliceous, semiactive, thermic Grossarenic Paleudult (Blanton series, USDA Soil Classification System). The study site was in agricultural use until the 1950s, when it was converted to forest land. Fertilizer was not used in the management of previous stands. The eastern half of the 40-ha study site previously supported an 11-year-old loblolly pine (*P. taeda*) plantation, whereas the western half supported a 35-year-old longleaf pine (*Pinus palustris* Mill.) plantation, both of which were harvested in 1999. In the summer of 1999, the site was cleared of large debris and small debris was pulverized and incorporated into the soil with an RS-500 Reclaimer/Stabilizer (CMI, Oklahoma City, OK). The site was disked and winter rye planted for erosion control in the fall of 1999. Dolomite lime was applied at a rate of 3.4 Mg ha^{-1} to obtain a soil pH of 6.5.

In spring 2000, the study site was planted at 1333 trees ha^{-1} (2.5 × 3 m spacing) with five taxa: *L. styraciflua* (sweetgum), *P. occidentalis* (sycamore), *P. taeda* (loblolly pine) and two *Populus deltoides* Bartr. (eastern cottonwood) clones. In this study, we focused on sweetgum and sycamore. One-year-old bare-root sweetgum (MeadWestvaco family WV340) and sycamore (MeadWestvaco orchard run) seedlings were planted. The design of the experiment was a 2 × 2 factorial combination of irrigation (no irrigation versus irrigation) and fertilization (no fertilization versus fertilization). Three 0.22-ha plots per taxa and treatment combination were installed in a randomized complete block design. Before bud break each year, oxyfluorfen was applied for pre-emergent weed control. Glyphosate was applied directly as needed (2–3 times year^{-1}) to maintain complete interspecific competition control. During the 2000 and 2001 growing seasons, 3 cm water week^{-1} was applied for 26 weeks, which was considered to be equivalent to or greater than the evaporative demand. In 2002, irrigation applications fluctuated between weeks to meet evaporative demand, which was calculated from on-site meteorological measurements (Van Bavel 1966), and averaged 1.9 cm week^{-1} for 26 weeks of treatment. Sweetgum was supplied with 40 kg ha^{-1} N, 18 kg ha^{-1} P and 33 kg ha^{-1} K in 2000 and 2001, and 80 kg ha^{-1} N, 35 kg ha^{-1} P and 66 kg ha^{-1} K in 2002. Sycamore received 40 kg ha^{-1} N, 18 kg ha^{-1} P and 33 kg ha^{-1} K in 2000, 80 kg ha^{-1} N, 35 kg ha^{-1} P and 66 kg ha^{-1} K in 2001, and 120 kg ha^{-1} N, 53 kg ha^{-1} P and 99 kg ha^{-1} K in 2002. The nutrient increases between years were intended to meet the increasing nutrient demand of the growing plantations. Sycamore received more nutrients than sweetgum in proportion to its faster initial growth rate. All nutrients were applied through drip irrigation tubes as 7:7:7 (N:P:K) with micronutrients (0.22% B, 0.01% Cu, 0.05% Mn, 0.001% Mo and 0.03% Zn). For a more detailed description of the study site and the experimental setup, see Coleman et al. (2004).

Aboveground net primary production

Estimates of ANPP were based on data from five biomass harvests, three made during December (2000, 2001 and 2002) and two during September (2001 and 2002). Dormant season woody biomass was determined from December harvests and peak leaf biomass from September harvests. Sycamore was measured during each harvest, whereas sweetgum was measured in each September harvest and in the December 2001 harvest. At each biomass harvest, four to six trees representative of the range of tree diameters were selected per treatment and cut at the groundline. Trees were divided into thirds (upper, middle and lower stem) and separated into leaf (September), branch and stem components. For the December 2000 and 2001 and the September 2001 and 2002 harvests, stem, branch and leaf components were placed in bags and oven-dried at 60 °C to constant dry mass. In December 2002, green mass of the stem sections was determined in the field. A 10-cm disk was taken from each section and the green mass/dry mass ratio was determined to calculate dry mass of the entire section. The relationship between individual biomass components (i.e., stem, branch and leaves) and groundline diameter (2000 and 2001) or diameter at breast height (DBH) (2002) was determined to obtain species- and treatment-specific diameter–biomass relationships.

Before each December harvest, groundline diameter or DBH was measured on trees in the measurement plot (54 trees per plot). Biomass for each component was calculated with allometric regression equations and scaled to the hectare. When averaged over all species and treatments, diameter explained more than 90% of the variation in biomass. For the September harvests, groundline diameter or DBH was measured on the six trees (subplot) in the center of each plot. Based on the relationship between September and December diameters for the subplot, diameters were estimated for the measurement plot during September 2001 (groundline) and 2002 (DBH) to scale leaf biomass to the plot level.

Sycamore ANPP for the 2001 and 2002 growing seasons was calculated as (September leaf biomass + December woody biomass) – previous December woody biomass. For sweetgum, the only December woody biomass estimates were from 2001. To estimate December 2000 woody biomass, groundline diameters from December 2000 were entered into the biomass equations determined for 2001. Although this may have introduced error, the magnitude of the error was small because the December 2000 biomass was relatively small, i.e., 18% of the 2001 biomass. Therefore, even with an unrealistically large 20% error in estimating 2000 biomass, only a 3% error in ANPP estimates would result. For estimates of December 2002 sweetgum woody biomass, measurements of December 2002 DBH were entered into biomass equations determined for September 2002. Although this may have introduced error if stem taper or branch biomass for a given DBH changed between September and December 2002, the error would have been small because DBH increased less than 6% between September and December. Once these estimates were obtained, sweetgum ANPP was determined as described for sycamore.

Intercepted photosynthetically active radiation and ε

Intercepted photosynthetically active radiation (IPAR) was measured between 1000 and 1600 h on cloudless days every 30–60 days during the 2001 (five measurements) and 2002 (seven measurements) growing seasons with a Sunscan canopy analysis system (Delta-T, Cambridge, U.K.). Percent intercepted radiation was calculated based on the ratio between incident radiation and the mean of 50 subsamples beneath the canopy (IPAR = 1 – canopy transmittance/incident radiation). Because zenith angle has a large effect on radiation interception, IPAR was corrected to a standard angle of 30° from zenith with empirically derived equations. To develop these zenith angle correction equations, hourly measurements were made in one representative block in 2001 (June 18) and in every plot in 2002 (July 19). From these measurements, regression equations were derived ($\text{IPAR} = a + b(\text{zenith angle})^2$) for each species and treatment combination. A 30° angle from zenith was chosen as the standard sun angle because radiation interception at 30° was a good representation of mean radiation interception when integrated across a day.

Interpolation between measurement dates provided estimates of daily percent IPAR. Bud break was monitored and determined to be March 19, 2001, and March 22, 2002, for sweetgum and March 28, 2001, and April 4, 2002, for sycamore. Based on empirical observations, it was predicted that leaf abscission would be completed by December 15 for both years and species. Because there was no measurement after September 7, 2001, leaf abscission was assumed to begin on October 31, 2001, for PAR capture calculations. No such assumptions were made in 2002, because measurements were conducted in mid-October 2002. Solar energy data from an on-site weather station (Campbell Scientific, Logan, UT) were used to convert percent daily interception to annual energy capture values (percent daily interception × incoming daily radiation = daily energy capture). All values of energy capture were multiplied by 0.5 to convert total energy capture to PAR capture (Monteith 1970). Radiation-use efficiency was calculated by dividing ANPP by annual PAR capture.

Gas exchange

Light-saturated net photosynthesis (A_{sat}), stomatal conductance (g_s) and leaf internal CO_2 concentration (C_i) were measured four times each growing season between 0900 and 1600 h with an LI-6400 infrared gas analyzer (Li-Cor, Lincoln, NE) with an attached cuvette that controlled irradiance, temperature, CO_2 concentration and water vapor. On each measurement date, three subsamples were collected (i.e., three rounds of sampling per date) and averaged to balance within-day fluctuations. On randomly selected trees, sample leaves were chosen from the upper half of the canopy where they were exposed to full sunlight for a portion of the day. All measurements were made under light-saturated conditions (1600 $\mu\text{mol m}^{-2}\text{ s}^{-1}$) and at about ambient CO_2 concentration (370 $\mu\text{mol mol}^{-1}$). Temperature (22–37 °C, 2001; 23–37 °C, 2002) and leaf to air vapor pressure deficit (VPD) (0.75–4.2 kPa, 2001; 0.88–5.7 kPa, 2002) were maintained close to ambient conditions, but were held constant within each sampling round for a given block. Following measurement, each leaf was plucked and kept on ice until placed in an oven to dry at 70 °C. After drying, samples were ground to a fine powder with an 8000-D mixer mill (Spex Certiprep, Metuchen, NJ) and analyzed for foliar [N] with an NA 1500 nitrogen/carbon analyzer (CE Elantech, Lakewood, NJ). Concurrent with gas exchange measurements, midday leaf water potential (Ψ_{leaf}) was measured with a pressure chamber (PMS Instruments, Corvallis, OR) on a leaf in a similar canopy position to the leaf used for gas exchange measurements.

Statistical analysis

We analyzed IPAR and all leaf-level measurements (i.e., A_{sat}, g_s, C_i, foliar [N] and Ψ_{leaf}) with a 2 × 2 factorial analysis of variance (ANOVA) (irrigation and fertilization), with date added as a split-plot factor and each species and year analyzed separately. Radiation-use efficiency, a variable calculated at the end of each year, did not include date as a factor and therefore was analyzed by a 2 × 2 factorial ANOVA. Relationships between annual PAR capture and ANPP, and leaf-level physiological measurements and ε, were assessed by regression analysis.

Results

Intercepted photosynthetically active radiation and ε

Sweetgum In the 2001 growing season, irrigation increased IPAR ($P = 0.05$). Although fertilization with irrigation resulted in the greatest IPAR, the main effect of fertilization and the interaction between fertilization and irrigation were not significant (Figure 1). In 2002, both irrigation ($P = 0.005$) and fertilization ($P = 0.002$) increased IPAR. Canopy growth was substantial between 2001 to 2002. In the combined treatment, the maximum IPAR was about 30% in 2001 and the corresponding value for 2002 was nearly 70%.

Annual IPAR was well correlated with ANPP for 2001 and 2002 (Figure 2). In 2002, values of ε were greater than in 2001 (Figure 3) as a result of an upward shift in the y-intercept of the relationship (Figure 2). There was no significant effect of treatment on ε for either year (Figure 3).

Sycamore In 2001, both irrigation ($P = 0.02$) and fertilization ($P = 0.04$) increased IPAR (Figure 1). The combination of these treatments, however, yielded no additional increase in IPAR. The non-additive effect of fertilization and irrigation resulted in a statistical interaction ($P = 0.06$). In 2002, both irrigation and fertilization increased IPAR (irrigation, $P = 0.0004$;

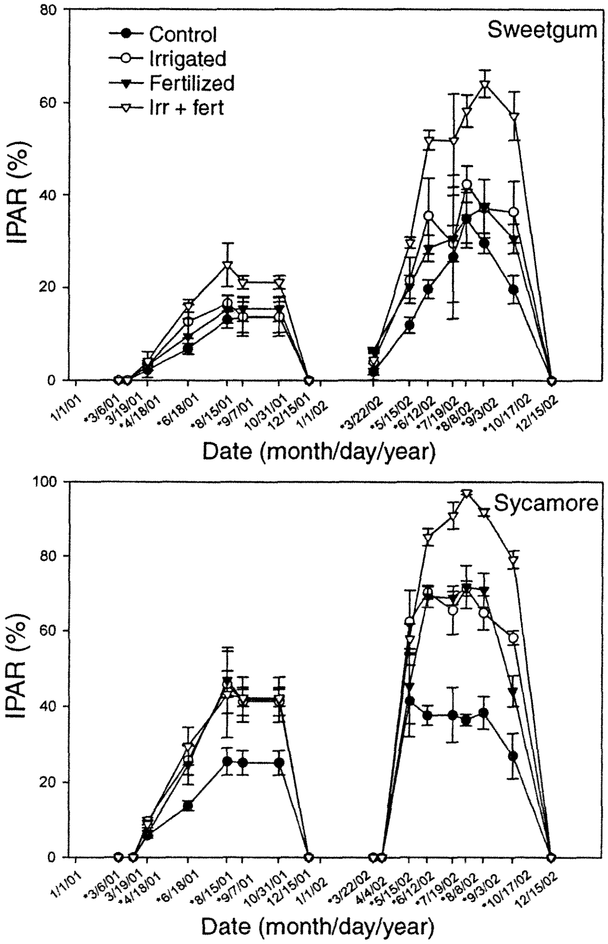

Figure 1. Intercepted photosynthetically active radiation (IPAR) at each sampling date in the 2001 (second) and 2002 (third) growing seasons for sweetgum and sycamore. Bars represent ± 1 SE. Dates indicated with an asterisk represent actual measurement dates. Abbreviations: Irr + fert = irrigation and fertilization.

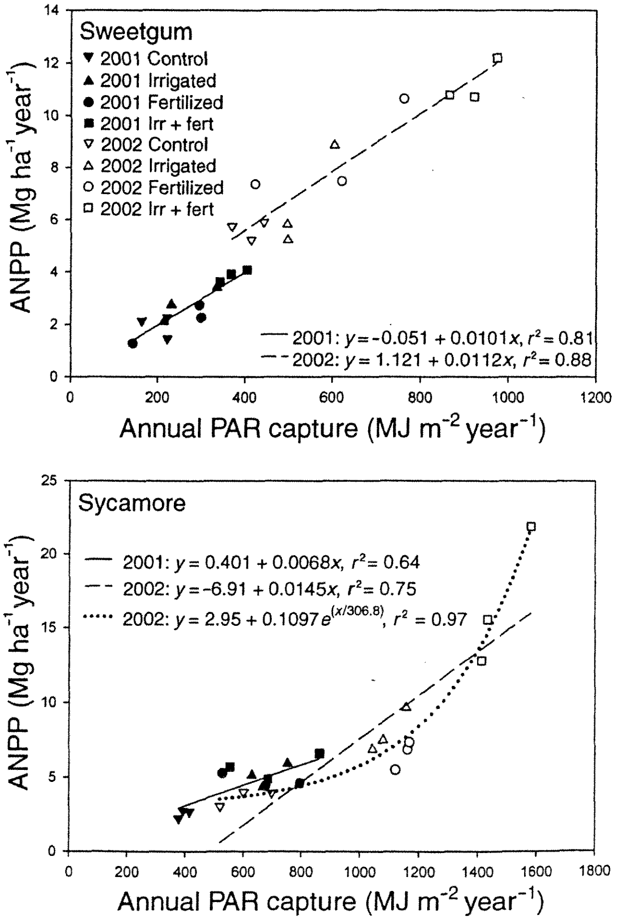

Figure 2. Relationship between annual photosynthetically active radiation (PAR) capture and aboveground net primary production (ANPP) in the 2001 (second) and 2002 (third) growing seasons for sweetgum and sycamore. Regression equation and corresponding r^2 value are included for each relationship. Abbreviations: Irr + fert = irrigation and fertilization.

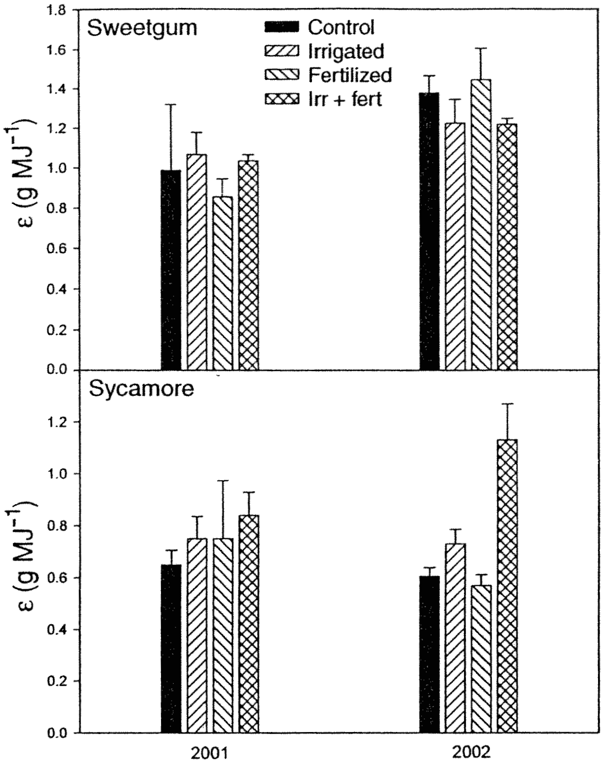

Figure 3. Radiation-use efficiency (ε) in the 2001 (second) and 2002 (third) growing seasons for sweetgum and sycamore. Bars represent ± 1 SE. Abbreviations: Irr + fert = irrigation and fertilization.

fertilization, $P = 0.0002$), and the combined treatment effects were additive (Figure 1). In 2001, IPAR reached a maximum of about 55%, whereas in 2002, 97% of radiation was captured, representing essentially full canopy closure.

There was a good correlation between annual PAR capture and ANPP for both years, although in 2001, the relationship appeared to be driven largely by the low values of the control treatment (Figure 2). For the 2002 growing season, the relationship had exponential properties—the coefficient of determination increased substantially when an exponential function was fit to the data. The curvilinearity of the relationship indicated more efficient aboveground biomass production per unit of radiation capture with the combination of irrigation and fertilization treatments. This is corroborated by the large synergistic effect of irrigation and fertilization on ε in 2002 (Figure 3). Although irrigation ($P = 0.005$) and fertilization ($P = 0.06$) significantly increased ε, these effects (particularly for fertilization) were driven by the large interaction between irrigation and fertilization ($P = 0.03$).

Gas exchange

Sweetgum During the August and October 2001 sampling dates, A_{sat} was lower for non-irrigated trees than for irrigated tree plots, resulting in a significant interaction between sampling date and irrigation (Figure 4, Table 1). Stomatal conductance exhibited similar relative decreases associated with lack

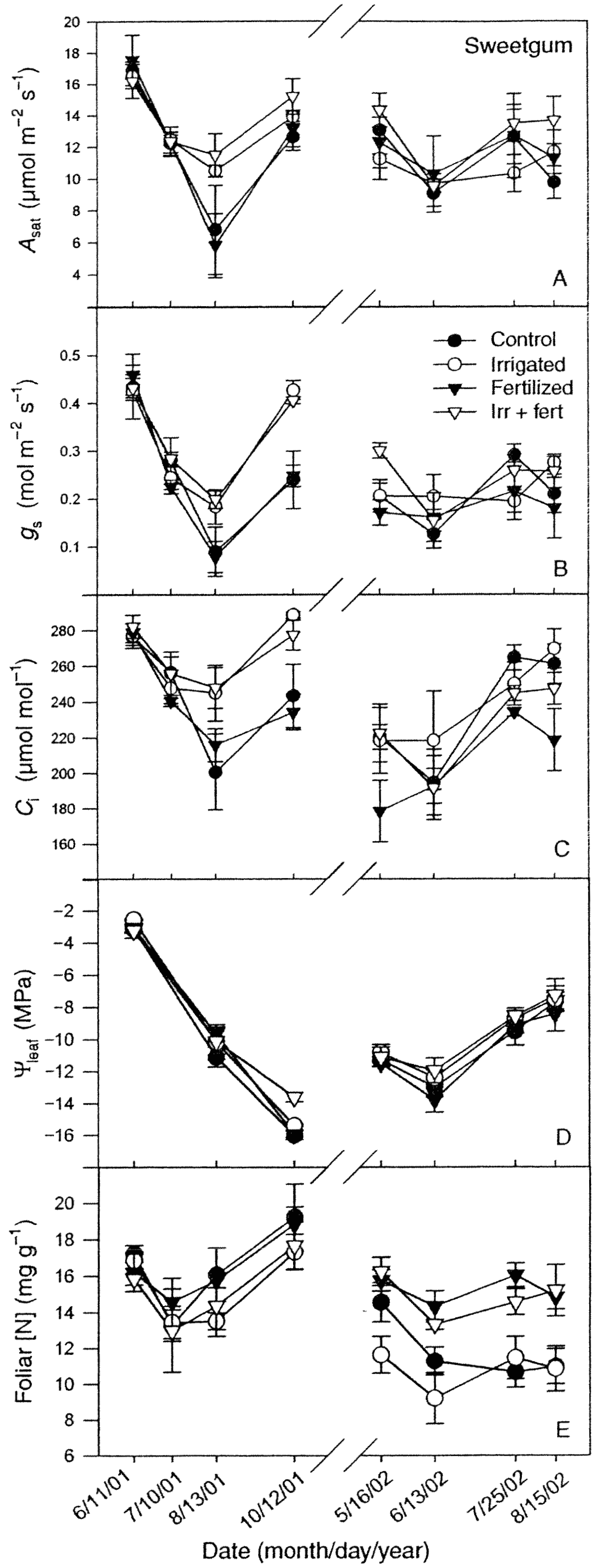

Figure 4. Light-saturated net photosynthesis (A_{sat}), stomatal conductance (g_s), leaf internal CO_2 concentration (C_i), leaf water potential (Ψ_{leaf}) and foliar nitrogen concentration (foliar [N]) for sweetgum on each of the measurement dates in the 2001 (second) and 2002 (third) growing seasons. Bars represent ± 1 SE.

Table 1. Statistical summary ($P > F$) of ANOVA for irrigation (Irr) and fertilization (Fert) effects (whole plot factors) for four measurement dates (split plot factor) during 2001 (second) and 2002 (third) growing seasons. Abbreviations: A_{sat} = light saturated net photosynthesis; g_s = stomatal conductance; C_i = leaf internal CO_2 concentration; [N] = nitrogen concentration; and Ψ_{leaf} = leaf water potential.

Year	Main effect	df	A_{sat}	g_s	C_i	Foliar [N]	Ψ_{leaf}
Sweetgum							
2001	Block	2					
	Irrigation	1	0.06	0.001	0.003	0.07	0.06
	Fertilization	1	0.68	0.91	0.95	0.87	0.16
	Irr × fert	1	0.75	0.47	0.76	0.98	0.83
	Error 1	6					
	Date	3	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
	Irr × date	3	0.004	0.0008	0.007	0.62	0.18
	Fert × date	3	0.90	0.94	0.54	0.72	0.23
	Irr × fert × date	3	0.76	0.50	0.62	0.73	0.12
	Error 2	24					
2002	Block	2					
	Irrigation	1	0.72	0.20	0.33	0.51	0.007
	Fertilization	1	0.22	0.95	0.12	0.01	0.62
	Irr × fert	1	0.44	0.37	0.50	0.80	0.25
	Error 1	6					
	Date	3	0.008	0.007	< 0.0001	0.0004	< 0.0001
	Irr × date	3	0.39	0.13	0.44	0.50	0.82
	Fert × date	3	0.89	0.66	0.66	0.57	0.92
	Irr × fert × date	3	0.43	0.05	0.16	0.19	0.80
	Error 2	24					
Sycamore							
2001	Block	2					
	Irrigation	1	0.08	0.009	0.02	0.19	0.25
	Fertilization	1	0.28	0.96	0.31	0.91	0.28
	Irr × fert	1	0.55	0.54	0.94	0.30	0.63
	Error 1	6					
	Date	3	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
	Irr × date	3	0.14	0.14	0.01	0.19	0.63
	Fert × date	3	0.62	0.04	0.52	0.004	0.45
	Irr × fert × date	3	0.36	0.87	0.20	0.17	0.14
	Error 2	2					
2002	Block	2					
	Irrigation	1	0.004	0.0009	0.04	0.58	0.05
	Fertilization	1	0.80	0.96	0.58	0.0008	0.05
	Irr × fert	1	0.05	0.03	0.20	0.29	0.40
	Error 1	6					
	Date	3	< 0.0001	< 0.0001	< 0.0001	0.06	< 0.0001
	Irr × date	3	0.13	0.70	0.52	0.68	0.66
	Fert × date	3	0.02	0.004	0.01	0.03	0.08
	Irr × fert × date	3	0.33	0.67	0.95	0.18	0.93
	Error 2	24					

of irrigation (Figure 4, Table 1). Because C_i was also lower in non-irrigated trees, the lower photosynthetic rates in the non-irrigated plots compared with the irrigated plots were probably a result of greater stomatal limitation. Irrigation caused Ψ_{leaf} to be less negative, although this effect occurred mainly in October 2001. Irrigation reduced foliar [N] (annual means of 15.2 and 16.4 mg g^{-1} for irrigated and non-irrigated plots, respectively). In the 2002 growing season, gas exchange variables and foliar [N] showed little response to irrigation. Irrigation, however, increased Ψ_{leaf} ($P = 0.06$; Figure 4). Fertilization had no affect on leaf gas exchange in either 2001 or 2002 (Figure 4, Table 1). Fertilization significantly increased foliar [N] in 2002, but not in 2001.

The later season measurements in 2001, A_{sat}, g_s and C_i were positively correlated with ε (Table 2). In general, reductions in leaf-level gas exchange in non-irrigated trees were associated with lower ε. In 2002, leaf-level variables were uncorrelated with ε (Table 2).

Sycamore In 2001, patterns of sycamore gas exchange variables were similar to those of sweetgum (Figure 5). Like

Table 2. Correlation coefficients (r) for linear regressions between radiation-use efficiency and leaf-level variables (A_{sat} = light saturated net photosynthesis; g_s = stomatal conductance; C_i = leaf internal CO_2 concentration; foliar [N] = foliar nitrogen concentration; and Ψ_{leaf} = leaf water potential) for the 2001 (second) and 2002 (third) growing seasons. Asterisks indicate significance at $\alpha = 0.05$.

Year	Date	A_{sat}	g_s	C_i	Foliar [N]	Ψ_{leaf}
Sweetgum						
2001	Jun 11	0.152	0.401	0.138	−0.010	0.239
	Jul 10	−0.110	0.071	0.118	0.158	0.000
	Aug 13	0.760 *	0.765 *	0.446	−0.089	−0.055
	Oct 12	0.387	0.654 *	0.687 *	0.089	−0.329
	Mean	0.613 *	0.801 *	0.600 *	0.063	−0.176
2002	May 16	0.055	−0.045	−0.190	0.394	−0.063
	Jun 13	0.333	0.045	−0.063	0.505	0.138
	Jul 25	0.499	0.432	−0.122	0.400	0.375
	Aug 15	0.292	0.148	0.055	0.235	−0.155
	Mean	0.414	0.232	−0.095	0.430	0.098
Sycamore						
2001	Jun 11	0.286	0.190	0.182	−0.089	0.071
	Jul 10	−0.499	−0.046	0.138	0.383	0.000
	Aug 13	0.583 *	0.678 *	0.592 *	0.607 *	0.022
	Oct 12	−0.026	0.509	0.490	0.055	−0.195
	Mean	0.373	0.515	0.549	0.373	−0.055
2002	May 16	0.425	0.777 *	0.508	0.313	−0.311
	Jun 13	0.696 *	0.760 *	0.501	0.122	0.010
	Jul 25	0.554	0.585 *	0.474	0.404	−0.313
	Aug 15	0.420	0.578 *	0.359	0.463	−0.288
	Mean	0.725 *	0.857 *	0.624 *	0.365	−0.311

sweetgum, sycamore A_{sat} decreased without irrigation later in the growing season as a result of the positive effect of irrigation on g_s and C_i (Figure 5, Table 1). Fertilization did not affect A_{sat} or C_i in 2001. A significant interaction occurred between fertilization and date for both g_s and foliar [N] because of slightly higher values associated with fertilization on the October sampling date.

In contrast to sweetgum, sycamore showed a large response to irrigation in the 2002 growing season (Figure 5). As in the 2001 season, decreases in A_{sat} occurred in conjunction with lower g_s and greater stomatal limitation (lower C_i) in the non-irrigated stands. Although fertilization increased foliar [N], there was no consistent effect of fertilization on gas exchange (Figure 5, Table 1). However, a significant interaction between fertilization and date for the gas exchange variables occurred, primarily because of large decreases in gas exchange values of trees in the fertilized only treatments between the first and second sampling dates. Both irrigation and fertilization caused Ψ_{leaf} to be less negative in 2002.

In 2001, A_{sat}, g_s, C_i and foliar [N] were significantly correlated with ε for the August sampling date, although correlations were not significant when averaged over the season (Table 2). For 2002, however, overall means for A_{sat}, g_s and C_i were each positively correlated with ε (Table 2). The strongest correlation occurred for g_s, with individual correlations significant for each measurement date. These correlations were driven by irrigation, because trees receiving water had higher ε and gas exchange rates.

Discussion

We investigated how resource availability affects ε and measured gas exchange under ambient conditions as a possible mechanism. The effects of high temperature, high VPD, time of day and soil water were all integrated within the multiple sampling rounds and dates. Although this integration may decrease the precision and ability to test for differences in photosynthetic capacity, it is an appropriate and robust approach for exploring ongoing differences in photosynthetic rate that might affect ε.

The increases in IPAR associated with fertilization and irrigation corroborate many previous studies, showing that increased nutrient and water availability, whether inherent to the site or culturally manipulated, increase canopy size and therefore IPAR (e.g., Vose and Allen 1988, Colbert et al. 1990, Dalla-Tea and Jokela 1991, Stoneman et al. 1997, Kuers and Steinbeck 1998, Osorio et al. 1998, Will et al. 2002, Li and Wang 2003). Likewise, a positive linear correlation between IPAR or PAR capture and biomass growth has been found previously (e.g., Monteith 1977, Cannell et al. 1988, Dalla-Tea and Jokela 1991, West and Osler 1995, McCrady and Jokela 1998, Will et al. 2001). Another study, however, found an exponential relationship between IPAR and stem volume production for fertilized and unfertilized stands of *Pseudotsuga menziesii* (Mirb.) Franco (Balster and Marshall 2000), similar to our findings for sycamore ANPP in 2002. Balster and Marshall (2000) hypothesized that the exponential nature of the re-

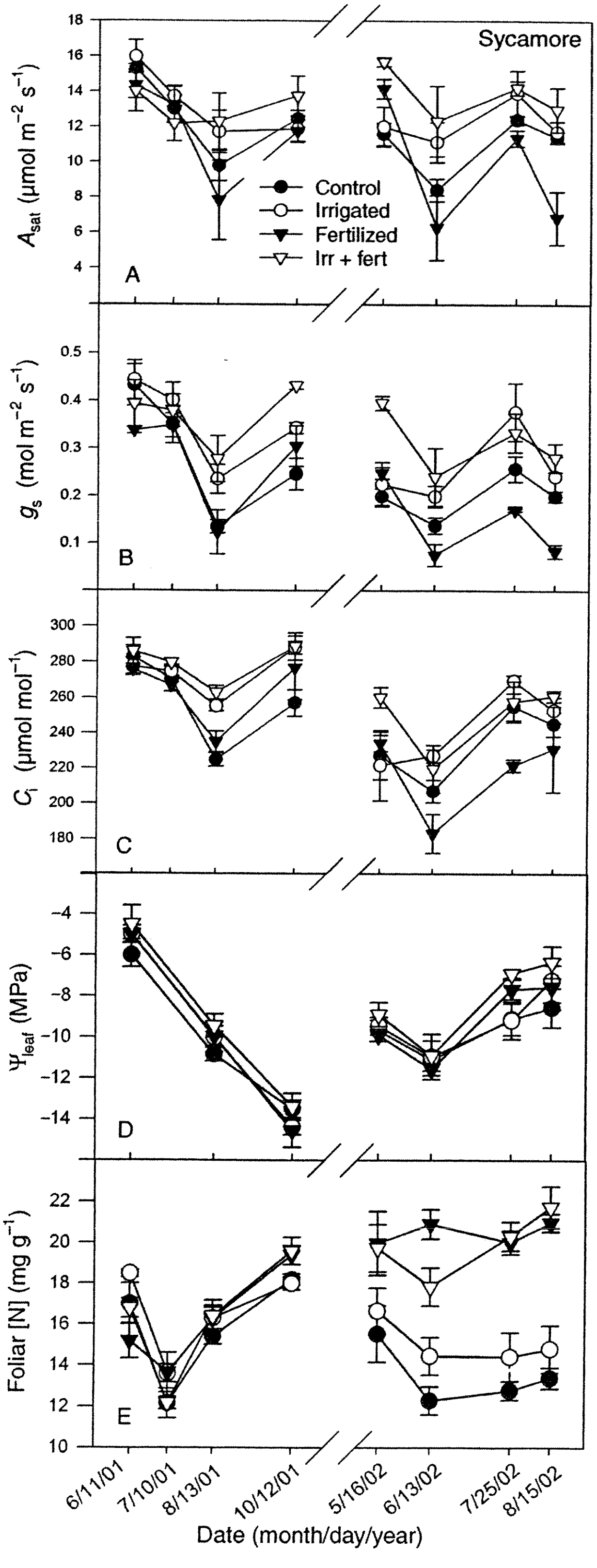

Figure 5. Light-saturated net photosynthesis (A_{sat}), stomatal conductance (g_s), leaf internal CO_2 concentration (C_i), leaf water potential (Ψ_{leaf}) and foliar nitrogen concentration (foliar [N]) for sycamore on each of the measurement dates in the 2001 (second) and 2002 (third) growing seasons. Bars represent ± 1 SE.

lationship between stem volume growth and IPAR was the result of greater partitioning of biomass to stem relative to roots at high resource availabilities. For sycamore in our study, preliminary analyses indicate that the relative biomass partitioned above ground increased with irrigation and fertilization and may have contributed to the curvilinearity of the relationship between radiation capture and ANPP. For sweetgum, which exhibited a linear relationship between radiation capture and ANPP, no treatment effects were apparent on the biomass partitioned to root relative to shoot.

Our estimates of ε are based on three replications which may be insufficient for identifying treatment differences in some cases. Even so, our results indicated a trend of increasing ε with irrigation for sweetgum and sycamore in 2001 and a significant increase in ε for sycamore during 2002 resulting from irrigation and the combined effects of irrigation and fertilization. These results concur with previous studies showing increases in ε with increasing resource availability (e.g., Landsberg and Wright 1989, Wang et al. 1991, Raison and Myers 1992, Harrington and Fownes 1995, Balster and Marshall 2000).

Irrigation had a positive effect on gas exchange variables (A_{sat}, g_s and C_i) for sweetgum in 2001 and for sycamore in both years, probably reflecting total rainfall of 661 and 536 mm for 2001 and 2002, respectively, each about half the rainfall received in an average year. The irrigation effects were observed primarily in the August and October measurements, the hottest (August) and driest part of the year. Additionally, leaf area is greater later in the season, resulting in greater potential demand for water. Because specific leaf area was not significantly affected by treatments, treatment effects on gas exchange results were similar whether expressed on an area or mass basis. Similar decreases in photosynthetic rates in non-irrigated stands relative to irrigated stands have been reported by others (Murthy et al. 1996, Ibrahim et al. 1998, Wang et al. 1998, Jose et al. 2003, Rieger et al. 2003). In our study, irrigation had a small positive effect on midday Ψ_{leaf} in some cases; however, the relatively larger stomatal response indicates that trees were compensating for lower soil water content primarily by reducing transpirational water loss.

Because we did not measure A–C_i curves, we were unable to quantify the extent to which decreases in A_{sat} in the non-irrigated stands resulted from increased stomatal limitation. However, because C_i decreased in conjunction with g_s and A_{sat} in non-irrigated stands, stomatal limitation played a role. The alternative, i.e., that A_{sat} decreased as a result of a down-regulation in photosynthesis, would have caused either an increase in C_i as CO_2 was consumed at a lower rate from the intercellular air space, or no change in C_i as the stomata closed in proportion to decreased photosynthetic demand for CO_2.

Unlike irrigation, fertilization had no effect on gas exchange even though it increased foliar [N] of both species in 2002. Although similar results have been reported (e.g., Ibrahim et al. 1998, Samuelson et al. 2001, Maier et al. 2002, Munger et al. 2003), many studies have shown a positive link between foliar [N] from fertilization and photosynthetic rate (e.g., Chandler and Dale 1995, Murthy et al. 1996, Samuelson 1998, Wang et al. 1998, Clearwater and Meinzer 2001, Cordell et al. 2001, Jose et al. 2003, Ripullone et al. 2003). Failure to find a fertilization effect during the 2002 growing season when foliar [N] increased in response to fertilization may have been associated in part with limitations to photosynthesis imposed by ambient environmental conditions. Fertilization may have had a positive influence on carboxylation efficiency (Cordell et al. 2001, Lai et al. 2002) or electron transport capacity (Clearwater and Meinzer 2001, Maroco et al. 2002), but we did not measure these parameters. Although fertilization did not increase leaf-level gas exchange, enhanced stand growth was probably a result of increased leaf area index and radiation capture (Linder 1985, Dalla-Tea and Jokela 1991, Munger et al. 2003). Similarly, much of the positive growth response of the irrigated stands was probably related to increases in canopy size.

In conclusion, we hypothesized that fertilization would increase ε by increasing A_{sat} and that irrigation would increase ε by maintaining g_s during hot and dry periods. The first hypothesis was not supported by the data, because fertilization had no effect on A_{sat} under ambient conditions or any significant main effect on ε. Irrigation, however, increased g_s and A_{sat} for sweetgum in 2001 and for sycamore in both years, and these increases were correlated to increased ε, providing support for the second hypothesis. Radiation-use efficiency integrates the response of the whole tree throughout the growing season. In contrast, gas exchange entailed leaf-level measurements limited to several days within each growing season. Consequently, we cannot quantify the effect of gas exchange on ε. Rather, the gas exchange measurements and their correlation to ε serve as periodic assessments of whether a mechanistic relationship exists between the efficiency of aboveground biomass growth and leaf-level rates of net carbon gain.

Overall, our data indicate that, although PAR capture is the primary driver of ANPP, shifts in the relationship between PAR capture and ANPP can occur in response to changing resource availabilities. In particular, irrigation increased the efficiency of converting radiation to biomass, with reduced stomatal limitation probably playing a role. The results highlight the importance of supplemental water and are well suited for integration into process models that incorporate soil water availability.

Acknowledgments

This research was funded by SRWC (Short-Rotation Woody Crops Cooperative), Plum Creek Timber Co., USDA Forest Service and the D.B. Warnell School of Forest Resources, University of Georgia.

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