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Longleaf Pine Photosynthetic Response to Soil Resource Availability and Elevated Atmospheric Carbon Dioxide

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ABSTRACT

Gas exchange responses during a drought cycle were studied in longleaf pine (*Pinus palustris* Mill.) seedlings after prolonged exposure to varying levels of atmospheric CO_2 (≈365 or ≈730 μmol CO_2 mol^{-1}), soil N (40 or 400 kg N ha^{-1} yr^{-1}), and water ("adequate" and "stressed"). Elevated atmospheric CO_2 concentration increased photosynthesis, tended to decrease stomatal conductance, and increased water-use efficiency (WUE). Although soil resource availability influenced gas exchange measurements, it generally did not affect the magnitude or direction of the response to CO_2 concentration. However, significant interactions among treatment variables were observed for plant xylem pressure potential. In seedlings grown with high N, a positive growth response to elevated atmospheric CO_2 increased whole-plant water use resulting in more severe plant water stress, despite increased leaf-level WUE; however, under low N conditions the lack of a growth response to elevated CO_2 reduced whole-plant water use, decreased water stress severity, and increased WUE. Photosynthetic response to CO_2 was greatest in the high N treatment at the beginning of the drought cycle, but diminished as water stress increased; however, plants grown with low N showed greater photosynthetic responses to CO_2 later in the drought cycle. Therefore, plant gas exchange rates interact with growth response in determining the severity of water stress under drought and, thus, the ability of elevated atmospheric CO_2 to ameliorate the effects of drought and allow plants to maintain increased rates of photosynthesis may be influenced by the availability of other resources, such as N and water.

The concentration of CO_2 in the atmosphere is increasing at an unprecedented rate (Houghton et al., 1990) and plants will be directly affected by this rise in CO_2. In general, studies have shown positive effects of CO_2 enrichment on plants including increased growth and WUE (Rogers and Dahlman, 1993; Allen and Amthor, 1995; Wittwer, 1995) and, although more variable, increased rates of photosynthesis (Chaves and Pereira, 1992; Amthor, 1995). However, the majority of CO_2 research has focused on crops under optimal growth conditions, rather than on native plants under limiting soil resources (Ceulemans and Mousseau, 1994; Amthor, 1995), despite the fact that natural terrestrial ecosystems are often limited by suboptimal levels of soil resource availability (e.g., N and water).

Understanding how forest species respond to this CO_2 buildup, and to potential associated climatic changes, is critical for predicting changes in stand structure and growth (McGuire and Joyce, 1995), which is particularly important due to the long-lived nature of trees and the economic and ecological values of forests. Coastal plain forests of the southeastern USA were once dominated by nearly pure stands of longleaf pine with a diverse understory plant community (Peet and Allard, 1993). The longleaf pine savanna ecosystem now occupies only 2% of its former range, a loss comparable to or exceeding that of most endangered communities throughout the world (Noss, 1989).

Longleaf pine forests currently occupy sites at the more xeric end of the moisture continuum and are often found on soils with low N availability; therefore, understanding how availability of differing soil resources affect plant response to CO_2 is also critical in predicting future productivity of southern pine forests. Prior et al. (1997) reported that a growth response to elevated atmospheric CO_2 was observed for longleaf pine growing under high, but not low, N conditions; in contrast, however, plants exposed to water stress showed a

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Abbreviations: R/S, root to shoot ratio; WUE, water-use efficiency; P_n, photosynthesis; g_s, stomatal conductance; XPP, xylem pressure potential.

greater relative growth response to elevated CO_2 than did their adequately-watered counterparts. This may suggest fundamentally different mechanisms by which availability of soil resources interact with atmospheric CO_2 concentration to affect plant growth, which may be reflected by plant photosynthetic responses.

Soil fertility may influence plant photosynthetic response to CO_2 via control of sink/source relationships and photosynthetic acclimation through time (Groninger et al., 1996). However, N may also interact with water in regulating photosynthetic response to CO_2. Nitrogen fertility may also influence plant WUE (Green and Mitchell, 1992), but in a fundamentally different way than elevated CO_2. Elevated CO_2 generally increases photosynthesis (P_n) and tends to reduce stomatal conductance (g_s) which increases leaf-level WUE (Tolley and Strain, 1984; Wray and Strain, 1986; Hollinger, 1987) and suggests elevated CO_2 may provide a mechanism for moderation of drought stress. High N increases WUE by increasing P_n disproportionately more than g_s (Green and Mitchell, 1992); thus, high N may or may not moderate plant response to drought through increased WUE. Furthermore, high N may increase leaf area and decrease root to shoot ratio (R/S) such that plants are predisposed to drought stress, while elevated CO_2 tends to increase R/S and have little effect on leaf area in pines (Prior et al., 1997).

Despite the commonality of soil resource limitations in natural terrestrial ecosystems, particularly longleaf pine forests of the southeastern USA, few investigations have tested the extent to which photosynthetic response to CO_2 is regulated by resource limitations or examined the potential for differences among varying soil resources (e.g., N vs. water). The objective of this study was to evaluate gas exchange responses to elevated CO_2 for longleaf pine seedlings grown under two levels of both N and water availability and determine the potential for these soil resources to vary in the manner in which they regulate photosynthetic response.

MATERIALS AND METHODS

One-year-old, nursery-grown longleaf pine seedlings from an open-pollinated seed source were graded to a uniform size and planted (three per container) in 45-L plastic containers filled with a coarse sandy medium (pH 5.1) of very low fertility (Cope et al., 1980). Seedlings were exposed to ambient ($\approx$365 μmol CO_2 mol^{-1}) or elevated ($\approx$730 μmol CO_2 mol^{-1}) atmospheric CO_2 beginning 30 Mar. 1993 in an open top chamber system (Rogers et al., 1983b). Open top chambers were fitted with clear Teflon film covers to exclude rainfall. The chambers, CO_2 supply, and CO_2 monitoring/dispensing systems have been previously described for this study site (Mitchell et al., 1995). Nitrogen treatments, slightly modified from those described by Bazzaz and Miao (1993), consisted of either 40 or 400 kg N ha^{-1} yr^{-1} applied at 3-mo intervals (sulfur coated urea; 38–0–0) initiated at planting. Foliar N levels resulting from these treatments have been previously reported (Runion et al., 1997). Other nutrients were maintained at nonlimiting levels (Prior et al., 1997). Two water stress treatments (target maximum values of −0.5 and −1.5 MPa pre-dawn xylem pressure potential (XPP) for each drought cycle) were initiated after a 19-wk establishment period. At initiation of water-stress treatments, all containers were flooded with water, allowed to drain overnight, and weighed; these weights were taken as field capacity values. Gravimetric measurements were correlated with pre-dawn XPP, measured on excised needles (one per treatment per chamber) at each weighing for 1 mo using a pressure bomb (Scholander et al., 1965). Individual containers received enough water to return them to field capacity weight when gravimetric measurements indicated the appropriate stress level had been achieved; xylem pressure potentials continued to be taken a minimum of once a month as a check on gravimetric readings. New field capacity values were determined after the November 1993 harvest and midway through the second growing season (July 1994) to compensate for changes in plant mass; xylem pressure potential was measured at each weighing for 1 mo following determination of new field capacity weights. Average needle xylem pressure potentials immediately prior to watering were −0.6 and −1.3 MPa for seedlings in the adequately-watered and water-stressed treatments, respectively. Use of deionized water ensured that fertility treatments remained unaffected by water treatments. Treatments were arranged in a split-plot design; CO_2 treatments (main plots) were randomly assigned to chambers within each of four replicates (total of eight chambers). Nitrogen and water stress treatments (subplots) were randomly assigned, in a 2 by 2 factorial design, to a total of 16 containers within each chamber. Container locations within each chamber were re-randomized monthly.

On 20 July 1994 (following 16 mo of CO_2 exposure and 19 drought stress cycles) all containers were watered to field capacity; a water stress cycle was then initiated and continued until 5 August. Adequately-watered containers were watered four times (every 3–4 d) during this period; water-stressed containers received no water after 20 July. Gas exchange measurements were made twice weekly (total of 5) throughout this drought cycle on one randomly selected plant per treatment per chamber. Pre-dawn XPP was determined on excised needles (one per treatment per chamber) prior to each gas exchange measurement using a pressure bomb. Stomatal conductance (mmol H_2O m^{-2} s^{-1}) and photosynthesis (μmol CO_2 m^{-2} s^{-1}) were measured as quickly as possible in the morning (on each date, measurements were concluded between 0900 and 1000 h EDT to avoid diurnal effects) using a CIRAS-1 portable infrared gas analyzer (PP Systems, Haverhill, MA). Measurement CO_2 concentrations were equivalent to those in the open top chamber under assessment. Instantaneous leaf-level WUE (μmol CO_2 mmol^{-1} H_2O) was calculated.

One container from each treatment in each chamber was destructively harvested in November 1994, 20 mo after initiation of the study. Foliar surface area of harvested seedlings was determined photometrically using a LiCor LI-3100 area meter (Li-Cor, Lincoln, NE). Root to shoot ratio (R/S) was determined from dry weights (oven dried at 55°C) of harvested seedlings. Destructive data were totaled for each seedling and averaged for each container prior to analysis.

Data were analyzed using the unstructured model in the repeated measures analysis with the Mixed procedure of the Statistical Analysis System (SAS Institute, 1996). Error terms appropriate to the split-plot design were used to test the significance of main effects and their interactions. Differences were considered significant at the $P \leq 0.05$ level.

RESULTS

Elevated atmospheric CO_2 increased P_n, tended to reduce g_s, and, thus, dramatically increased WUE throughout the water stress cycle (Table 1); however, the reduction in g_s was significant only during the early phase of the water stress cycle. When averaged across the water stress cycle, P_n for pines grown with elevated CO_2 was 46% higher than for those grown in ambient

Table 1. Main treatment effects for photosynthesis, stomatal conductance, water-use efficiency, and xylem pressure potential of longleaf pine seedlings through a drought stress cycle.

Variable†	CO_2 Concentration			N Fertility regime			H_2O Stress regime		
DOY‡	365	720	Pr > F§	40	400	Pr > F	Adequate	Stress	Pr > F
	μmol mol^{-1}			kg ha^{-1} yr^{-1}					
P_n									
203	6.18	8.17	0.046	5.94	8.41	<0.001	6.39	7.97	0.012
207	3.92	6.28	0.021	4.83	5.37	0.397	5.34	4.86	0.448
210	5.59	7.41	0.080	6.38	6.62	0.792	7.17	5.83	0.156
214	6.55	9.90	0.002	7.83	8.62	0.065	9.35	7.09	<0.001
217	4.39	7.06	0.004	6.28	5.18	0.112	7.25	4.21	<0.001
g_s									
203	105.2	75.2	0.022	104.2	76.3	0.031	82.8	97.6	0.231
207	98.2	64.5	0.007	101.6	61.2	0.002	82.8	80.0	0.800
210	76.8	66.1	0.442	91.6	51.2	0.010	84.7	58.1	0.071
214	74.6	72.1	0.666	92.3	54.4	<0.001	94.2	52.5	<0.001
217	53.8	45.4	0.525	70.2	29.0	0.004	72.5	26.8	0.002
WUE									
203	2.47	4.83	<0.001	2.44	4.86	<0.001	3.59	3.71	0.621
207	1.80	4.26	<0.001	2.08	3.98	<0.001	2.81	3.24	0.086
210	2.91	4.95	<0.001	2.96	4.90	<0.001	3.67	4.19	0.260
214	2.66	4.43	<0.001	2.47	4.62	<0.001	3.13	3.96	0.002
217	2.24	3.76	<0.001	2.39	3.61	<0.001	3.04	2.97	0.789
XPP									
203	−0.49	−0.47	0.936	−0.48	−0.48	0.880	−0.44	−0.52	0.020
207	−0.68	−0.69	0.952	−0.55	−0.83	0.006	−0.52	−0.86	0.001
210	−0.80	−0.91	0.687	−0.72	−0.99	0.017	−0.54	−1.17	<0.001
214	−0.84	−0.92	0.757	−0.79	−0.97	0.063	−0.61	−1.15	<0.001
217	−0.92	−1.09	0.635	−0.87	−1.14	0.008	−0.60	−1.41	<0.001

† Variables: P_n = photosynthesis (μmol CO_2 m^{-2} s^{-1}); g_s = stomatal conductance (mmol H_2O m^{-2} s^{-1}); WUE = water use efficiency (μmol CO_2 mmol H_2O^{-1}); XPP = xylem pressure potential (MPa); levels for the water stress regimes refer to target maximum xylem pressure potential values of −0.5 and −1.5 MPa for Adequate and Stress, respectively.

‡ DOY's (day of year) correspond to sample dates of 22, 26, 29, July and 2 and 5, August, respectively.

§ Probability of a greater *F* value calculated, using appropriate error terms for the split-plot design, under Mixed procedure of SAS. Values are from data averaged across a drought stress cycle.

CO_2 ($P = 0.009$), g_s was reduced from 81.7 to 64.7 mmol H_2O m^{-2} s^{-1} ($P = 0.072$), and WUE increased by more than a factor of 1.8 ($P < 0.001$). Soil resource availability tended to influence gas exchange measurements but not the magnitude or direction of the response to CO_2 concentration (Fig. 1 and 2), thus, interactions of CO_2 with other treatment variables were generally not significant. However, a significant $CO_2 \times$ N interaction for WUE was observed wherein the magnitude of increase due to elevated CO_2 was greater for plants grown in high, relative to low, N (Fig. 1). A significant $CO_2 \times$ water interaction for P_n was also observed to be due to

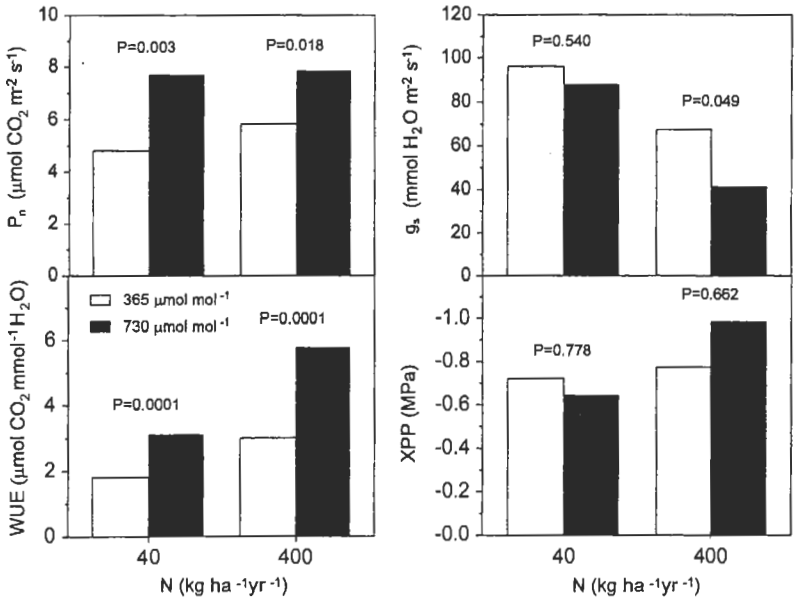

Fig. 1. Interactions of CO_2 with soil nitrogen (N) on photosynthesis (P_n), stomatal conductance (g_s), water-use efficiency (WUE), and xylem pressure potential (XPP). Data are averaged across five measurements made during a drought stress cycle. *P* values located above each set of bars refer to differences between CO_2 treatments.

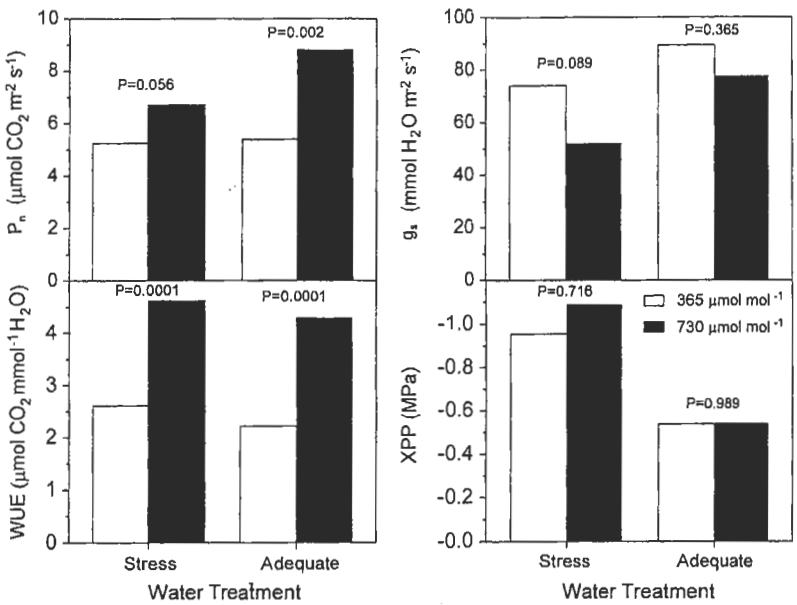

Fig. 2. Interactions of CO_2 with plant water stress on photosynthesis (P_n), stomatal conductance (g_s), water-use efficiency (WUE), and xylem pressure potential (XPP). Data are averaged across five measurements made during a drought stress cycle. *P* values located above each set of bars refer to differences between CO_2 treatments.

a difference in magnitude, that is, the increase due to elevated CO_2 was greater for plants grown with adequate water, relative to water stress (Fig. 2). Significant N × water and CO_2 × N × water interactions were also observed for XPP. These results are taken from a single water stress cycle within a long-term study and plants were not of equal size at initiation of the drought cycle; therefore, XPP responses are the result of both direct and indirect (those mediated through long-term changes in plant growth) effects of treatments and their interactions. In the water stress treatment, XPP was decreased in high N plants, possibly due to increases in leaf area (water demand) or decreases in R/S (water supply). In addition, the magnitude of the increase in leaf area or decrease in R/S was greater for plants grown under elevated, compared with ambient, CO_2 which resulted in a significantly lower XPP for high N plants under elevated CO_2 when subjected to water stress (Table 2).

Under adequately-watered conditions, XPP was unaffected by CO_2 and N (Fig. 3); g_s also was not significantly affected by atmospheric CO_2 concentration, although it tended to be numerically lower under elevated CO_2 throughout the water stress cycle (Fig. 4). In contrast, P_n (Fig. 3) and WUE (Fig. 4) were generally higher under elevated CO_2 for plants grown with adequate water. Effects of CO_2 on gas exchange measurements tended to occur regardless of N level; however, differences between CO_2 treatments were generally of a larger magnitude and more frequently significant for plants grown with the high level of soil N.

Under water-stressed conditions, high N plants had lower XPP (i.e., more stress) than low N plants when grown under elevated CO_2; for plants grown with ambient CO_2, N treatment level did not affect XPP (Fig. 3). Although CO_2 concentration significantly affected XPP only in high N plants at the final measurement, the pattern of response to CO_2 varied dramatically between the two N treatments. In plants grown with high N, XPP was lower under elevated CO_2, but XPP for low N plants was consistently higher under elevated CO_2 indicating that low N plants were never stressed to the extent of high N plants, particularly under elevated CO_2. This differential pattern of XPP response in the water stress treatment influenced P_n throughout the drought cycle

Table 2. Effects of treatment variables† on xylem pressure potential (XPP) of longleaf pine seedlings taken during a drought stress cycle after 16 mo of CO_2 exposure and on leaf area (LA) and root to shoot ratio (R/S) from plants destructively harvested after 20 mo of CO_2 exposure.

Soil N	Water stress	CO_2	XPP	Pr > T‡	LA (m^2)	Pr > T	R/S	Pr > T
40	Adequate	365	−0.55		0.41		1.20	
400	Adequate	365	−0.53	0.879	1.73	<0.001	0.81	0.004
40	Stress	365	−0.89		0.26		1.01	
400	Stress	365	−1.02	0.261	0.60	0.008	0.74	0.041
40	Adequate	730	−0.57		0.23		1.08	
400	Adequate	730	−0.52	0.637	1.67	<0.001	0.90	0.147
40	Stress	730	−0.72		0.19		1.39	
400	Stress	730	−1.46	<0.001	1.05	<0.001	1.08	0.021

† Treatment variables are: Soil N = soil nitrogen in kg ha^{-1} yr^{-1}; water stress levels refer to target maximum xylem pressure potential values of −0.05 and −1.5 MPa for Adequate and Stress, respectively; and atmospheric CO_2 concentration in µmol CO_2 mol^{-1}. Data for XPP are averaged across five measurements made during a single drought stress cycle.

‡ Probability of a greater value for the T statistic calculated, with appropriate error terms for the split-plot design, using the unstructured model of the repeated measures analysis under the Mixed procedure of SAS for the difference between N treatments.

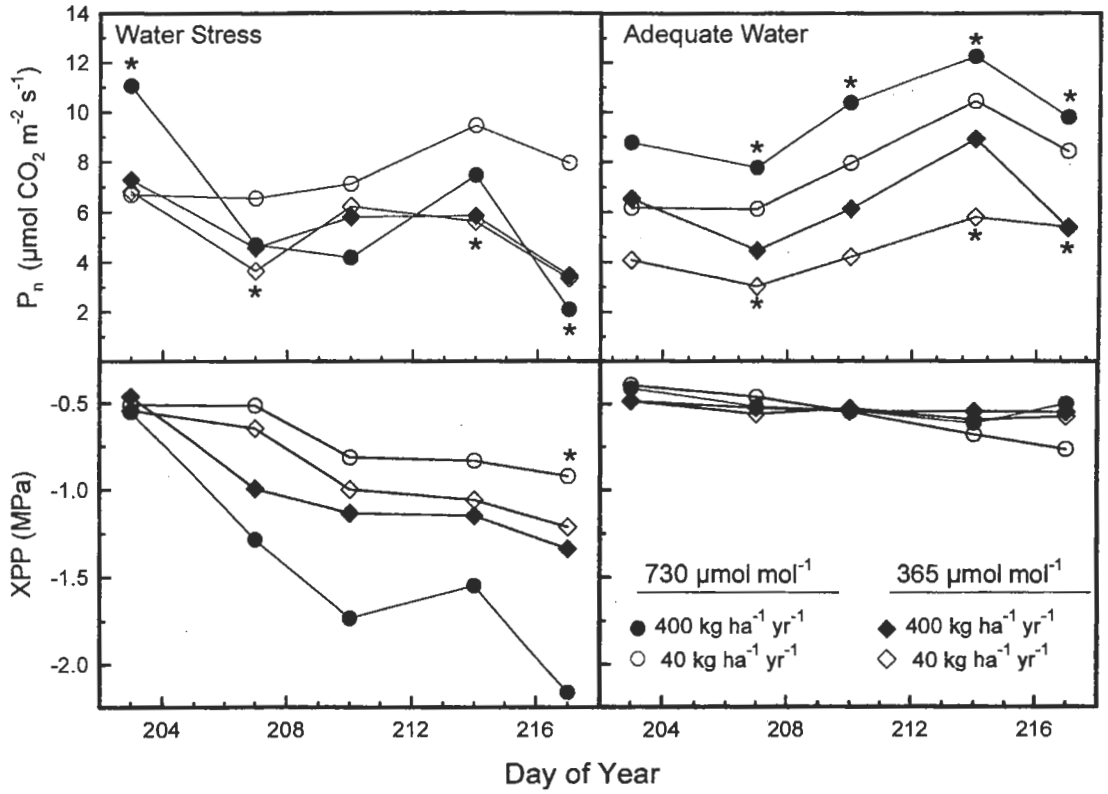

Fig. 3. Photosynthesis (P_n) and pre-dawn xylem pressure potential (XPP) for longleaf pine seedlings at five measurement dates through a drought cycle as affected by interactions between CO_2 and soil N. Asterisks above the graphed lines indicate significant differences ($P \leq 0.05$) between CO_2 treatments under high N (comparing filled symbols), while those the below the lines indicated differences under low N (comparing open symbols). Elevated CO_2 tended to increase P_n in high N plants only in the absence of water stress, while differences for low N plants became significant as stress increased. Elevated CO_2 resulted in lower XPP for stressed plants grown with high N throughout most of the drought cycle, while this reduction was not observed for low N plants.

(Fig. 3). At the beginning of the drought cycle (i.e., no water stress), higher P_n in response to CO_2 addition was greatest in the high N treatment; however, as water stress increased, differences between CO_2 treatments decreased. In contrast, plants grown with low N showed increased P_n in response to added CO_2 later in the drought cycle. For plants under water stress, elevated CO_2 reduced g_s early in the cycle in both N treatments (Fig. 4). Similar to plants under adequately-watered conditions, elevated CO_2 tended to increase WUE regardless of N conditions for plants under water stress and differences between CO_2 treatments were larger for plants grown with high N. However, in contrast to the adequately-watered treatment, this increased WUE under elevated CO_2 diminished at the end of the water stress cycle for plants grown with high, but not low, N (Fig. 4).

DISCUSSION

Woodward (1992) states that the best documented and repeatable response to atmospheric CO_2 enrichment is a significant increase in photosynthesis of C_3 plants, a fact readily apparent from the CO_2 literature (Rogers et al., 1983a; Wittwer, 1985; Long and Drake, 1992; Allen and Amthor, 1995; Amthor, 1995; Eamus et al., 1995; Tissue et al., 1995). In this experiment, longleaf pine seedlings were exposed to twice ambient concentrations of CO_2 for 16 mo and, in the high resource treatment (e.g., high N and adequate water), P_n increased 56% under elevated CO_2 which is similar to increases reported for other tree species (see reviews by Eamus and Jarvis, 1989; Long and Drake, 1992; Mousseau and Saugier, 1992; Ceulemans and Mousseau, 1994).

Research has shown that elevated CO_2 interacts with soil resource availability to influence plant P_n; however, the manner in which these resources interact with CO_2 may differ. In general, plants grown under ambient CO_2 decrease P_n when placed under water stress, while elevated CO_2 alleviates this stress (to some degree), allowing plants to maintain higher P_n (Huber et al., 1984; Conroy et al., 1986; Liang and Maruyama, 1995). Even in cases where water stress was severe enough to reduce P_n of elevated CO_2-grown plants, high CO_2/water-stressed plants maintained P_n rates equivalent to ambient CO_2/adequately-watered plants, again suggesting amelioration of water stress (Groninger et al., 1996). In contrast, elevated CO_2 may not alleviate nutrient stress and both P (Conroy et al., 1986) and N (Tissue et al., 1993; Curtis et al., 1994) limitations have been reported to dampen or negate elevated CO_2-induced increases in P_n. However, some researchers have observed increased P_n under high CO_2 even under conditions of low fertility (Norby and O'Neill, 1991); although, this may be due in part to P_n acclimation induced by small pot size (Arp,

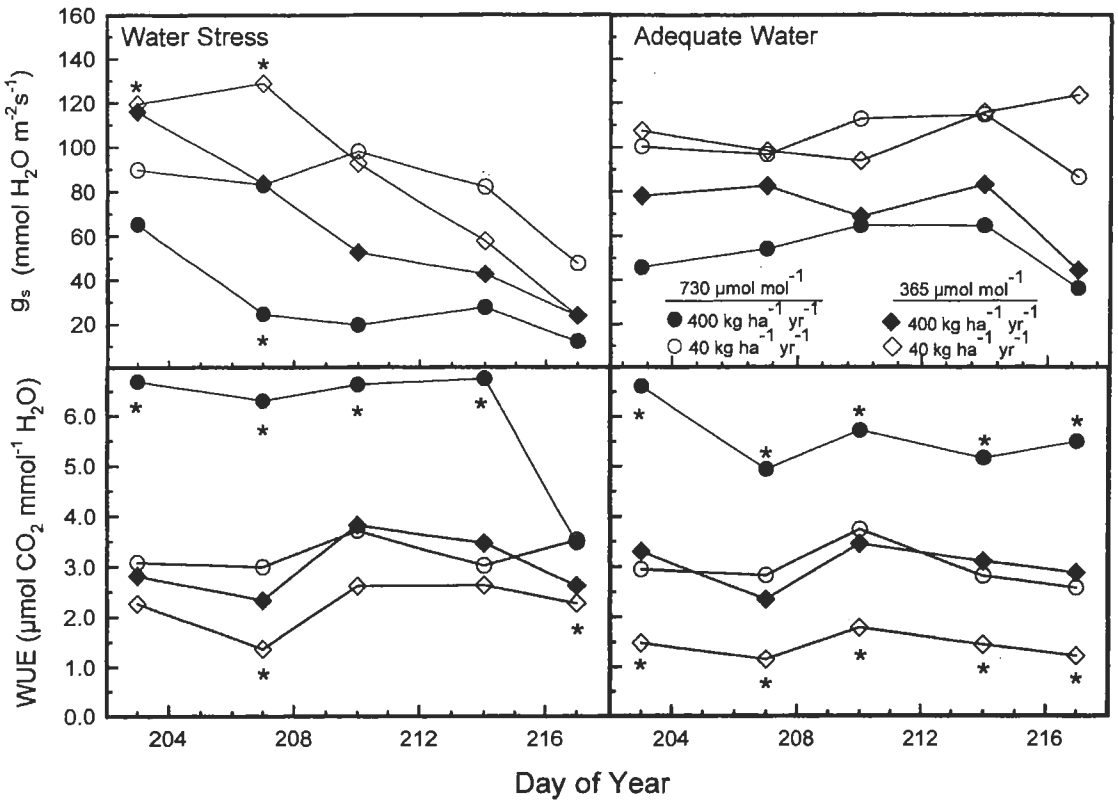

Fig. 4. Stomatal conductance (g_s) and water-use efficiency (WUE) for longleaf pine seedlings at five measurement dates through a drought cycle as affected by interactions between CO_2 and soil N. Use of asterisks is the same as in Fig. 3. Elevated CO_2 tended to decrease g_s under water stress early in the stress cycle. Elevated CO_2 tended to increase WUE regardless of N and water conditions, although differences between CO_2 treatments tended to be larger for plants grown with high N. This increase diminished at the end of the drought cycle for plants grown with high N.

1991; Thomas and Strain, 1991). Groninger et al. (1996) found that P_n increased in sweetgum (*Liquidambar styraciflua* L.) but decreased in loblolly pine in response to high N; however, response of P_n to CO_2 was not influenced by N in either species. We observed that longleaf pine P_n response to CO_2 was also rarely influenced by either N or water stress (elevated CO_2-grown seedlings tended to have higher P_n under both N and water treatments); so, although soil resource availability influenced gas exchange measurements, it rarely had a significant effect on the magnitude or direction of the response to CO_2 concentration. Curtis et al. (1994) suggested that, although nutrient or water stress clearly influences the magnitude of CO_2 response, the stimulation of P_n by elevated CO_2 is rarely fully eliminated; results from this study support this suggestion. However, if N is insufficient for growth (Prior et al., 1997), additional C from increased P_n may accumulate and disrupt needle chloroplast integrity (Pritchard et al., 1997) and, thus, negatively impact plant health.

Decreased g_s under high CO_2 (Rogers et al., 1983a; Morison, 1985; Eamus, 1991; Allen and Amthor, 1995) implies decreased water use, and possible amelioration of drought stress, which may become increasingly important under future climate change scenarios. However, increases in leaf area (i.e., under high N) might compensate for reduced leaf-level g_s and result in similar or greater, whole-plant water use. Therefore, this potential for alleviation of drought stress via decreased g_s will depend on plant growth response and on the severity and length of the stress. It has been suggested (Murray, 1995) that, while effects of elevated CO_2 on stomata can override the effects of light, water stress triggers stomatal closure and can override both CO_2 and light. This is supported by the present study in that elevated CO_2 significantly decreased g_s until the middle of the water stress cycle, which was the same point at which the effect of water stress became significant.

Implications of altered g_s, in combination with increased P_n, are also of interest to plant scientists due to potential impacts on WUE. Increased instantaneous, leaf-level WUE under elevated CO_2, as we observed, has been commonly reported (Rogers et al., 1983a; Morison, 1985; Eamus and Jarvis, 1989; Norby and O'Neill, 1991; Liang and Maruyama, 1995); however, it has been suggested that drought stress and nutrient deficiency are likely to moderate this response (Mousseau and Saugier, 1992). Although previously reported CO_2-induced increases in WUE under high fertility (Norby and O'Neill, 1991) and water stress (Liang and Maruyama, 1995) were observed, the fact that interactions of these resources with CO_2 on WUE tended to be of magnitude rather than rank suggests their moderating effect on WUE response to CO_2 may be minimal.

In this study, high N as well as elevated CO_2 increased WUE of longleaf pine seedlings and we suggested that

these increases may occur in fundamentally different ways (i.e., that elevated CO_2 increases WUE by increasing P_n and reducing g_s, while high N increases WUE by increasing P_n disproportionately more than g_s); this is not supported by our data. High N did increase P_n (particularly under adequate water), but also tended to decrease g_s; g_s was only influenced by elevated CO_2 early in the water stress cycle, while CO_2 had a much stronger affect on P_n (particularly under adequate water). However, the contention that elevated CO_2 ameliorates the effects of drought (Bazzaz, 1990) and allow plants to maintain increased P_n, while high N does not, may still be valid. Increased N availability resulted in decreased XPP of water stressed plants, indicating an exacerbation of water stress. This increased stress was most likely due to the fact that growth of fertilized seedlings was sufficient to increase whole-plant water use. The effect of elevated atmospheric CO_2 concentration on water stress intensity was dependent on N availability. In seedlings grown with high N, a positive growth response to elevated CO_2 increased whole-plant water use resulting in more severe water stress, despite increased WUE. However, under low N conditions, the lack of a growth response to elevated CO_2 (Prior et al., 1997) combined with somewhat lower g_s, reduced whole-plant water use and decreased water-stress severity.

Data from this study indicate that leaf-level g_s interacts with growth response in determining the severity of water stress under drought conditions. Other things remaining constant, decreases in g_s with elevated CO_2 will ameliorate water stress severity and allow increased P_n; however, increased growth can easily overcome these positive effects. When growth responses to increased resource (N and/or CO_2) availability occur, more water is used by the larger plant and more severe stress can occur, assuming no changes in resource availability or efficiency of acquisition. Therefore, our data indicate that, while increased P_n and WUE may be maintained under low-N environments (such as those that longleaf pine normally inhabit), this might not be the case for longleaf pine growing under high N availability, when growth response to elevated atmospheric CO_2 may increase water stress due to greater whole-plant water use. However, plants grown in a more natural environment (as opposed to containers) might have a larger root system and, thus, increased access to soil water so that the increased water stress observed here would likely be diminished or delayed until water became more limiting; nonetheless, when water becomes limiting, larger plants will experience increased stress. Plants grown under high fertility tend to allocate less growth belowground, while those grown under elevated CO_2 tend to increase belowground allocation (Prior et al., 1997; Runion et al., 1997). Therefore, although the exact nature of the relationship of growth response with P_n and WUE for plants in the field may vary from that observed in this container study, it will, again, depend on interactions of elevated CO_2 with soil resource availability.

Increased P_n of longleaf pine seedlings under varying levels of both N and water may reflect the plasticity of this species observed in nature and, when coupled with other potential benefits (e.g., resistance to insects, disease, and fire), may make longleaf pine an attractive species given rising CO_2 and changing climate. However, to predict plant responses to future climate change, leaf-level measurements of P_n, g_s, and WUE must be scaled up to the whole plant and canopy to take into account considerations of differences in plant size and, thus, the importance of reported CO_2 effects may be overestimated (Morison, 1985; Eamus, 1991). Although data from the present study do not address large trees or mature forests, they may be relevant for seedling establishment during regeneration which is of critical importance to forest health and productivity.

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