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


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 CO₂ (460 or 750 ppm CO₂ mol⁻¹), soil N (40 or 400 kg N ha⁻¹ yr⁻¹), and water (“adequate” and “drought”). Elevated atmospheric CO₂ concentration increased photosynthesis, tended to decrease stomatal conductance, and increased water-use efficiency (WUE). Although soil resource availability influenced gas exchange parameters, it generally did not affect the magnitude or direction of the response to CO₂ concentration. However, significant interactions among treatment variables were observed for plant shoot growth potential. In seedlings grown with high N, a positive growth response to elevated atmospheric CO₂ increased whole-plant water use resulting in lower shoot plant water stress, despite increased leaf-level WUE; however, under low N conditions the lack of a growth response to elevated CO₂ reduced whole-plant water use, decreased water stress severity, and increased WUE. Photosynthetic response to CO₂ 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 CO₂ 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 CO₂ 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 CO₂ in the atmosphere is increasing at an unprecedented rate (Houghton et al., 1990) and plants will be directly affected by this rise in CO₂. In general, studies have shown positive effects of CO₂ enrichment on plants including increased growth and WUE (Rogers and Dahlman, 1993; Allen and Amthor, 1995; Wittmer, 1995) and, although more variable, increased rates of photosynthesis (Chaves and Perreira, 1992; Amthor, 1995). However, the majority of CO₂ 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 CO₂ 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 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 Aikart, 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 optimum continuum and are often found on soils with low N availability; therefore, understanding how availability of differing soil resources affect plant response to CO₂ is also critical in predicting future productivity of southern pine forests. Prior et al. (1997) reported that a growth response to elevated atmospheric CO₂ was observed for longleaf pine growing under high, but not low, N conditions; in contrast, however, plants exposed to water stress showed a

Abbreviations: R, root to shoot ratio; WUE, water-use efficiency; Fv/Fm, photosynthesis, Ω, stomatal conductance; XIP, xylem pressure potential.

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greater relative growth response to elevated CO₂ than did their adequately-watered counterparts. This may suggest fundamentally different mechanisms by which availability of soil resources interact with atmospheric CO₂ concentration to affect plant growth, which may be reflected by plant photosynthetic responses.

Soil fertility may influence plant photosynthetic response to CO₂ via control of sink/source relationships and photosynthetic acclimation through time (Greeninger et al., 1996). However, N may also interact with water in regulating photosynthetic response to CO₂. Nitrogen fertility may also influence plant WUE (Green and Mitchell, 1992), but in a fundamentally different way than elevated CO₂. Elevated CO₂ generally increases stomatal conductance (gs) which increases leaf-level WUE (Tolley and Strain, 1984; Wray and Strain, 1986; Hollinger, 1987) and suggests elevated CO₂ may provide a mechanism for moderation of drought stress. High N increases WUE by increasing P, disproportionately more than gₛ (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 (RS) such that plants are predisposed to drought stress, while elevated CO₂ tends to increase RS 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 CO₂ 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 CO₂ 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 placed (three per container) in 45.2-l plastic containers filled with coarse sandy soil (pH 5.1) of very low fertility (Copes et al., 1980). Seedlings were exposed to ambient (~285 μmol CO₂ mol⁻¹) or elevated (~730 μmol CO₂ mol⁻¹) atmospheric CO₂ beginning 30 May, 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, CO₂ supply, and CO₂ monitoring/dispensing systems have been previously described for this study site (Mitchell et al., 1993). Nitrogen treatments, slightly modified from those described by Bazzaz and Mao (1991), consisted of either 40 or 400 kg N ha⁻¹ yr⁻¹ applied at 3-m intervals (sulfate 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 near-limiting 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 10-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 h using a pressure bomb (Scholander et al., 1965). Individual containers received enough water to return them to field capacity weights when gravimetric measurements indicated the appropriate water 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 h following determination of new field capacity weights. Average needle xylem pressure potentials immediately prior to watering were ~3.6 and ~1.3 MPa for seedlings in the adequately-watered and water-stressed treatments, respectively. Use of deionized water ensured that fertility treatments were not affected by water treatments. Treatments were arranged in a split-plot design; CO₂ 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 CO₂ 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-strained containers received no water after 20 July. Gas exchange measurements were made twice weekly (total of 5) throughout the 1994 growing season on one randomly selected seedling (on each date, measurements were concluded before 0900 and 1000 h EDT to avoid diurnal effects) using a CIraS-I portable infrared gas analyzer (PP Systems, Haverhill, MA). Measurement CO₂ concentrations were equivalent to those in the open top chamber under assessment. Instantaneous leaf level WUE (μmol CO₂ mmol⁻¹ H₂O) was calculated.

Each 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 photographically using a Licor LI-3000 area meter (Li-Cor, Lincoln, NE). Root to shoot ratio (RS) was determined for dry weights (oven-dried at 45°C) of harvested seedlings. Destructive data were totaled for each seedling and averaged for each container prior to analysis.

Data were analyzed using the unstrructured 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 ≤ 0.05 level.

RESULTS

Elevated atmospheric CO₂ increased Pₚ, tended to reduce gₛ and, thus, dramatically increased WUE throughout the water stress cycle (Table 1); however, the reduction in gₛ was significant only during the early phase of the water stress cycle. WUE across the water stress cycle, Pₚ for pine grown with elevated CO₂ 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.

<table>
<thead>
<tr>
<th>Variable</th>
<th>CO2 Concentration</th>
<th>N Fertility regimen</th>
<th>H2O Stress regimen</th>
<th>Adequate</th>
<th>Stressed</th>
<th>Pr &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>350</td>
<td>720</td>
<td>P0 &gt; P1</td>
<td>40</td>
<td>400</td>
<td>P0 &gt; P1</td>
</tr>
<tr>
<td></td>
<td>205</td>
<td>150</td>
<td>0.040</td>
<td>5.84</td>
<td>8.41</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>207</td>
<td>152</td>
<td>0.020</td>
<td>6.45</td>
<td>9.37</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>210</td>
<td>130</td>
<td>0.000</td>
<td>5.43</td>
<td>6.62</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>214</td>
<td>135</td>
<td>0.000</td>
<td>7.18</td>
<td>8.62</td>
<td>&lt;0.001</td>
</tr>
<tr>
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<td>217</td>
<td>140</td>
<td>0.000</td>
<td>5.81</td>
<td>8.12</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>230</td>
<td>155</td>
<td>0.022</td>
<td>104.12</td>
<td>76.3</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>230</td>
<td>135</td>
<td>0.000</td>
<td>107.6</td>
<td>62.2</td>
<td>0.002</td>
</tr>
<tr>
<td></td>
<td>235</td>
<td>145</td>
<td>0.000</td>
<td>94.6</td>
<td>51.2</td>
<td>0.010</td>
</tr>
<tr>
<td></td>
<td>240</td>
<td>150</td>
<td>0.000</td>
<td>93.3</td>
<td>54.4</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>245</td>
<td>155</td>
<td>0.000</td>
<td>70.2</td>
<td>29.0</td>
<td>0.004</td>
</tr>
<tr>
<td></td>
<td>250</td>
<td>160</td>
<td>0.000</td>
<td>2.52</td>
<td>8.43</td>
<td>&lt;0.001</td>
</tr>
<tr>
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<td>252</td>
<td>145</td>
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<td>2.44</td>
<td>4.86</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>254</td>
<td>140</td>
<td>0.000</td>
<td>2.46</td>
<td>4.86</td>
<td>&lt;0.001</td>
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<tr>
<td></td>
<td>256</td>
<td>135</td>
<td>0.000</td>
<td>2.46</td>
<td>4.87</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>258</td>
<td>130</td>
<td>0.000</td>
<td>2.39</td>
<td>4.87</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>260</td>
<td>125</td>
<td>0.000</td>
<td>0.66</td>
<td>0.07</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>202</td>
<td>180</td>
<td>0.000</td>
<td>0.62</td>
<td>0.59</td>
<td>0.006</td>
</tr>
<tr>
<td></td>
<td>204</td>
<td>170</td>
<td>0.000</td>
<td>0.67</td>
<td>0.72</td>
<td>0.007</td>
</tr>
<tr>
<td></td>
<td>206</td>
<td>160</td>
<td>0.000</td>
<td>0.65</td>
<td>0.77</td>
<td>0.003</td>
</tr>
<tr>
<td></td>
<td>208</td>
<td>150</td>
<td>0.000</td>
<td>0.63</td>
<td>0.87</td>
<td>0.008</td>
</tr>
</tbody>
</table>

CO2 (P = 0.009), was reduced from 81.7 to 64.7 mmol H2O 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 CO2 concentration (Fig. 1 and 2). Thus, interactions of CO2 with other treatment variables were generally not significant. However, a significant CO2 × X interaction for WUE was observed wherein the magnitude of increase due to elevated CO2 was greater for plants grown in high, relative to low, N (Fig. 1). A significant CO2 × water interaction for P0 was also observed to be due to

![Fig. 1. Interactions of CO2 with soil nitrogen (N) on photosynthesis (P0), stomatal conductance (gS), 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 CO2 treatments.](image-url)
a difference in magnitude, that is, the increase due to elevated CO₂ was greater for plants grown with ade-
quate water, relative to water stress (Fig. 2). Significant N × water and CO₂ × 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 interac-
tions. 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, CO₂, which resulted in a significantly lower XPP for high N plants under elevated CO₂ when subjected to water stress (Table 2).

Under adequately-watered conditions, XPP was unaf-
fected by CO₂ and N (Fig. 3) \(g\), also was not significantly affected by atmospheric CO₂ concentration, although it tended to be numerically lower under elevated CO₂ throughout the water stress cycle (Fig. 4). In contrast, P, (Fig. 3) and WUE (Fig. 4) were generally higher under elevated CO₂ for plants grown with adequate water. Effects of CO₂ on gas exchange measurements tended to occur regardless of N level; however, differ-
ences between CO₂ 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 CO₂; for plants grown with ambien-
t CO₂, N treatment level did not affect XPP (Fig. 3). Although CO₂ concentration significantly affected XPP only in high N plants as the final measurement, the pattern of response to CO₂ varied dramatically between the two N treatments. In plants grown with high N, XPP was lower under elevated CO₂, but XPP for low N plants was consistently higher under elevated CO₂, indicating that low N plants were never stressed to the extent of high N plants, particularly under elevated CO₂. This differential pattern of XPP response to the water stress treatment influenced P, 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 CO₂ exposure and on leaf area (LA) and root to shoot ratio (R/S) from plants destructively harvested after 20 mo of CO₂ exposure.

<table>
<thead>
<tr>
<th>Soil N</th>
<th>Water stress</th>
<th>CO₂</th>
<th>XPP</th>
<th>Pr &gt; T</th>
<th>LA (m²)</th>
<th>Pr &gt; T</th>
<th>R/S</th>
<th>Pr &gt; T</th>
</tr>
</thead>
<tbody>
<tr>
<td>40</td>
<td>Adequate</td>
<td>365</td>
<td>-0.55</td>
<td>0.079</td>
<td>0.41</td>
<td>0.85</td>
<td>1.01</td>
<td></td>
</tr>
<tr>
<td>40</td>
<td>Adequate</td>
<td>365</td>
<td>-0.55</td>
<td>0.879</td>
<td>1.77</td>
<td>&lt;0.001</td>
<td>0.98</td>
<td></td>
</tr>
<tr>
<td>40</td>
<td>Stress</td>
<td>305</td>
<td>-0.69</td>
<td>0.096</td>
<td>0.26</td>
<td>0.63</td>
<td>0.10</td>
<td></td>
</tr>
<tr>
<td>40</td>
<td>Stress</td>
<td>305</td>
<td>-0.69</td>
<td>0.056</td>
<td>0.63</td>
<td>0.008</td>
<td>0.74</td>
<td></td>
</tr>
<tr>
<td>40</td>
<td>Adequate</td>
<td>720</td>
<td>-0.67</td>
<td>0.23</td>
<td>0.82</td>
<td>1.68</td>
<td>1.04</td>
<td></td>
</tr>
<tr>
<td>40</td>
<td>Adequate</td>
<td>720</td>
<td>-0.67</td>
<td>0.637</td>
<td>1.67</td>
<td>&lt;0.001</td>
<td>0.96</td>
<td></td>
</tr>
<tr>
<td>40</td>
<td>Stress</td>
<td>720</td>
<td>-0.72</td>
<td>0.091</td>
<td>0.82</td>
<td>&lt;0.001</td>
<td>1.04</td>
<td></td>
</tr>
<tr>
<td>40</td>
<td>Stress</td>
<td>720</td>
<td>-0.72</td>
<td>0.091</td>
<td>0.82</td>
<td>&lt;0.001</td>
<td>1.04</td>
<td></td>
</tr>
</tbody>
</table>

1 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; 616 atmospheric CO₂ concentration in ppm CO₂ mol⁻¹. Data for XPP are averaged across five measurements made during a single drought stress cycle.

2 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) and pre-dawn xylem pressure potential (XPP) for longleaf pine seedlings at five treatment dates throughout a drought cycle as affected by interactions between CO2 and soil N. Asterisks above the graphed lines indicate significant differences (P ≤ 0.05) between CO2 treatments under high N (comparing filled symbols), while those below the lines indicate differences under low N (comparing open symbols). Elevated CO2 tended to increase P in high N plants only in the absence of water stress, while differences for low N plants became significant as stress increased. Elevated CO2 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.

At the beginning of the drought cycle (i.e., no water stress), higher P in response to CO2 addition was greatest in the high N treatment; however, as water stress increased, differences between CO2 treatments decreased. In contrast, plants grown with low N showed increased P in response to added CO2 later in the drought cycle. For plants under water stress, elevated CO2 reduced g, early in the cycle in both N treatments (Fig. 4). Similar to plants under adequately-watered conditions, elevated CO2 tended to increase WUE regardless of N conditions for plants under water stress and differences between CO2 treatments were larger for plants grown with high N. However, in contrast to the adequately-watered treatment, this increased WUE under elevated CO2 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 CO2 enrichment is a significant increase in photosynthesis of C3 plants, a fact readily apparent from the CO2 literature (Rogers et al., 1983; Wullschleger, 1989; Long and Drake, 1992; Allen and Amthor, 1995; Amthor, 1995; En arms et al., 1995; Tissue et al., 1995). In this experiment, longleaf pine seedlings were exposed to twice ambient concentrations of CO2 for 16 mo and, in the high resource treatment (i.e., high N and adequate water), P increased 56% under elevated CO2 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 CO2 interacts with soil resource availability to influence plant P, however, the manner in which these resources interact with CO2 may differ. In general, plants grown under ambient CO2 decrease P when placed under water stress, while elevated CO2 alleviates this stress (to some degree), allowing plants to maintain higher P (Hsuiher et al., 1984; Corroy et al., 1986; Liang and Maruyama, 1995). Even in cases where water stress was severe enough to reduce P of elevated CO2-grown plants, high CO2-water-stressed plants maintained P, rates equivalent to ambient CO2-adequately-watered plants, again suggesting amelioration of water stress (Groninger et al., 1996). In contrast, elevated CO2 may not alleviate nutrient stress and both P (Corroy et al., 1986) and N (Tissue et al., 1995; Curtis et al., 1994) limitations have been reported to dampen or negate elevated CO2-induced increases in P. However, some researchers have observed increased P under high CO2 even under conditions of low fertility (Nobis and O’Neill, 1991); although, this may be due in part to P, acclimation induced by small pot size (Acp,
1991; Thomas and Strain, 1991). Groninger et al. (1996) found that P, increased in sweetgum (Liquidambar styr-
aciflua L.) but decreased in loblolly pine in response to
high N; however, response of P, to CO, was not influ-
enced by N in either species. We observed that longleaf
pine P, response to CO, was also rarely influenced by
either N or water stress (elevated CO, grown seedlings
tended to have higher P, under both N and water treat-
ments); 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, concentration. Curtis et al. (1994) suggested that,
although nutrient or water stress clearly influences the
magnitude of CO, response, the stimulation of P, by
elevated CO, is rarely fully eliminated; results from this
study support this suggestion. However, if N is insuffi-
cient for growth (Pritchard et al., 1997), additional C from
increased P, may accumulate and disrupt needle chloro-
plant integrity (Pritchard et al., 1997) and, thus, nega-
tively impact plant health.

Decreased g, under high CO, (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 im-
portant under future climate change scenarios. How-
ever, increases in leaf area (i.e., under high N) might
compensate for reduced leaf-level g, and result in similar
or greater, whole-plant water use. Therefore, this poten-
tial for alleviation of drought stress via decreased g, 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, on stomata
can override the effects of light, water stress triggers
stomatal closure and can override both CO, and light.
This is supported by the present study in that elevated
CO, significantly decreased g, 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, in combination with in-
creased P, are also of interest to plant scientists due to
potential impacts on WUE. Increased instantaneous,
leaf-level WUE under elevated CO, as we observed, has
been commonly reported (Rogers et al., 1983a; Morison,
1985; Eamus and Jarvis, 1989; Norby and O'Neill, 1991;
Liang and Maryama, 1995); however, it has been sug-
gested that drought stress and nutrient deficiency are
likely to moderate this response (Mousseau and Saugier,
1992). Although previously reported CO, induced in-
creases in WUE under high fertility (Norby and O'Neill,
1991) and water stress (Liang and Maryama, 1995)
were observed, the fact that interactions of these re-
sources with CO, on WUE tended to be of magnitude
rather than rank suggests their moderating effect on
WUE response to CO, may be minimal.

In this study, high N as well as elevated CO, increased
WUE of longleaf pine seedlings and we suggested that
these increases may occur in fundamentally different ways (i.e., that elevated CO2 increases WUE by increasing Pn and reducing g, while high N increases WUE by increasing Pn, disproportionately more than g), this is not supported by our data. High N did increase Pn (particularly under adequate water), but also tended to decrease g, g was only influenced by elevated CO2 early in the growing season, and high CO2 had a much stronger effect on Pn (particularly under adequate water). However, the constipation that elevated CO2 ameliorates the effects of hypoxia (e.g., 1990) and low plant growth maintains increased Pn, while high N does not, may still be valid. Increased N availability resulted in decreased XPP of water-stressed leaves, 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 CO2 concentration on water stress intensity was dependent on N availability. In seedlings grown with high N, a positive growth response to elevated CO2 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 CO2 (Prior et al., 1997) combined with somewhat lower g, reduced whole-plant water use and decreased water-stress severity.

Data from this study indicate that leaf-level g, interacts with growth response in determining the severity of water stress under drought conditions. Other things remaining constant, decreases in g, with elevated CO2 will ameliorate water stress intensity and allow increased Pn; however, increased growth can easily overcome these positive effects. When growth responses to increased temperature (N and/or CO2) availability occur, more water is used by the large plant and more severe stress can occur, implying no changes in resources availability or efficiency of acquisition. Therefore, our data indicate that, while increased Pn and WUE may be maintained under low-N environments (such as that where longleaf pine normally inhabit), this might not be the case for longleaf pine growing under high N availability, when growth response to elevated atmospheric CO2 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 in place, 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 CO2 tend to increase belowground allocation (Prior et al., 1997; Rusanin et al., 1997). Therefore, although the exact nature of the relationship of growth response with Pn and WUE in plants in the field may vary from that observed in this container study, it will, again, depend on interactions of elevated CO2 with soil resource availability.

Increased Pn, of longleaf pine seedlings under varying levels of both N and water may reflect the plasticity of this species observed in nature. How coupled with other potential benefits (e.g., resistance to insects, disease, and fire), may make longleaf pine an attractive species given rising CO2 and changing climate. However, to predict plant responses to future climate change, leaf-level measurements of Pn, g, 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 CO2 effects may be overestimated (Morison, 1985; Emanuel, 1995). Although data from the present study do not address large tree or mature forests, they may be relevant for seedling establishment during regeneration which is of critical importance to forest productivity and biodiversity.

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