Testing the “source–sink” hypothesis of down-regulation of photosynthesis in elevated \([\text{CO}_2]\) in the field with single gene substitutions in \(\text{Glycine max}\)

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Abstract

Acclimation of photosynthesis to elevated atmospheric carbon dioxide concentration was tested in lines of soybean (\(\text{Glycine max}\)) that differed by single genes that altered either the capacity to nodulate or growth habit (determinate or indeterminate growth). Both genetic changes provided, within a uniform genetic background, a test of the “source–sink” hypothesis that down-regulation of photosynthesis in elevated carbon dioxide is a result of inability to form sufficient “sinks” for the additional photosynthate. Plants were grown under ambient and elevated [CO\(_2\)] (550 \(\mu\)mol mol\(^{-1}\)) in the field, using free air gas concentration enrichment (FACE). Mutation of the determinate cultivar, Elf, to an indeterminate form did not result in increased responsiveness to elevated [CO\(_2\)]. This may reflect a large sink capacity in the selection of determinate cultivars. In elevated [CO\(_2\)] only the determinate isoline of the indeterminate cultivar (Williams-dt1) and the non-nodulating genotype showed down-regulation of photosynthesis. This resulted from decreases in apparent \(v_{\text{c,max}}\) and maximum rate of electron transport \(J_{\text{max}}\). Increase in total non-structural carbohydrate (TNC) content, which is often correlated with down-regulation of photosynthesis, in Williams-dt1 was 80% greater in elevated [CO\(_2\)] than in ambient [CO\(_2\)] controls, compared to 40% in the indeterminate line. The results from mutations of the Williams line are consistent with the hypothesis that genetic capacity for the utilization of photosynthate is critical to the ability of plants to sustain increased photosynthesis when grown at elevated [CO\(_2\)].

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1. Introduction

The CO\(_2\) concentration of the atmosphere ([CO\(_2\)]) is predicted to rise from its present 370 to 550 \(\mu\)mol mol\(^{-1}\) by the middle of this century (IPCC, 2001). For 

\(C_3\) plants this will substantially increase potential

\(A\) because the oxygenase reaction of Rubisco will be inhibited and because carboxylation velocity will increase, since Rubisco is not CO\(_2\) saturated in the present atmosphere (Drake et al., 1997). However, this increased potential is rarely realized fully in the long-term, due to down-regulation of photosynthetic capacity. Much circumstantial evidence, primarily from studies in enclosed environments, suggests that this

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down-regulation results from inadequate “sink” capacity. “Sink” is defined as the parts of the plant that at a given stage of development are utilizing photosynthetic product for growth and development. Under such conditions non-structural carbohydrates will accumulate and, possibly through increased hexose cycling within the leaf, expression of genes coding for the photosynthetic apparatus is suppressed resulting in decreased photosynthetic capacity; most notably a decrease in the amount of Rubisco (reviewed: Sheen, 1994; Drake et al., 1997; Moore et al., 1999). The issue has broader implications than atmospheric change, since it also concerns the question of whether increasing photosynthetic capacity through genetic manipulation may be translated into increased productivity. While many studies have inferred “sink” limitation as the cause of down-regulation of photosynthesis with growth at elevated [CO₂], single gene mutations providing defined alteration of sink capacity have not been used to test this hypothesis.

Soybean (Glycine max (L.) Merr) provides a model C₃ species for such a study. Growth habit (determinate or indeterminate growth) and the ability to assimilate atmospheric N₂ through the symbiotic association with Bradyrhizobia affect “sink” capacity and are significantly associated with reported variation in photosynthetic capacity in soybean growing areas (American Soybean Association, 2001), and allows the crop to be grown in one of the world’s most productive soybean growing areas (American Soybean Association, 2001). In these cases, however, there are multiple and undefined genetic differences between cultivars and thus differences in down-regulation are not necessarily the result of differences in sink-size. Further, most studies have used controlled environments or enclosures, which could also restrict the response to elevated [CO₂]. A survey of the 111 prior studies of the effects of elevated [CO₂] on soybean showed that the average increase in yield in large pots (>9 dm³) was only one-third of that when grown in the field (Ainsworth et al., 2002a). The significance of genetic restrictions on sink capacity to acclimation is therefore most appropriately evaluated under field conditions, without restriction of rooting volume.

Isogenic soybean lines that vary by a single gene altering either growth habit or nodulating capacity provide an opportunity to test how acclimation of photosynthesis to elevated [CO₂] is affected by “sink-strength” (Nakamura et al., 1999). Indeterminate soybean cultivars continue growth after flowering (Hoeft et al., 2000), while determinate cultivars have a shorter flowering period and mainstem growth is approximately 80% complete once flowering has begun (Lin and Nelson, 1988). By restricting vegetative growth after flowering, the determinate growth may potentially limit the size of the sink for carbon. Root nodules are strong sinks for carbohydrate (Walsh et al., 1987); the respiratory rate of a nodulated root system may be an order of magnitude greater than that of an equivalent non-nodulated root system (Vessey et al., 1988). Therefore, the absence of root nodules should accentuate the potential for carbohydrate feedback under elevated [CO₂] (Arnone and Gordon, 1990). A large “sink” capacity has been suggested as a critical factor for maximizing plant production in elevated [CO₂] (Drake et al., 1997). This hypothesis has been examined by comparing different species or cultivars within a species with obvious differences in storage organ sizes (Ziska and Bunce, 1995, 2000; Ziska et al., 2001). In this study, the response of soybean lines to elevated [CO₂] is examined in an open-air, field environment within the soybean free air gas concentration enrichment (SoyFACE) experiment. SoyFACE is located in central Illinois, in one of the world’s most productive soybean growing areas (American Soybean Association, 2001), and allows the crop to be grown
in the field under elevated [CO$_2$] without alteration of microclimate. Specifically, this study tests the following predictions in the field: (a) determinate forms of indeterminate cultivars and non-nodulating lines grown at elevated [CO$_2$] will show a decrease in \textit{in vivo} Rubisco activity (Sage, 1994; Drake et al., 1997; Rogers and Humphries, 2000); (b) acclimation of determinate and indeterminate genotypes will correlate to increased total non-structural carbohydrate (TNC) (Drake et al., 1997; Rogers et al., 1998). Inability to nodulate is likely to have most effect at the beginning of flowering, before pod formation starts. At this time canopy development is complete, but the major sink, i.e. the pod, has not been initiated. Determinate growth habit is likely to have most effect during pod-filling. Effects on photosynthesis were therefore investigated at the start of flowering for non-nodulating mutants and during pod-filling for lines that differ in stem termination. In each case the mutant was compared with the germplasm from which it was developed.

2. Methods

2.1. Site description and plant material

The study was conducted at the soybean free air gas concentration enrichment facility in Champaign, IL, USA (40°02′N, 88°14′W, 228 m above sea level). The SoyFACE facility, situated on 32 ha of Illinois farmland, consisted of four blocks, each containing two 20 m diameter octagonal plots. The soil is a Drummer (fine-silty, mixed, Typic Endoaquoll), which is very deep and formed from loess and silt parent material deposited on the till and outwash plains. No fertilizer was added to the soybean crop, according to standard regional agronomic practice. Measurements for this study were made from 22 to 27 July 2001 and from 23 to 26 August 2002. The mean minimum and maximum temperature for the 2001 measuring period were 20.3 and 29.8°C, respectively, and 19.2 and 28.4°C for 2002. The average relative humidity was 85.0%, total precipitation was <0.001 mm for the 2001 measuring period, compared to 85.7% and 0.03 mm for the 2002 measuring period. Within each block, one plot was at current ambient [CO$_2$] of 370 μmol mol$^{-1}$ and one plot was fumigated to an elevated [CO$_2$] of 550 μmol mol$^{-1}$, using the FACE design of Miglietta et al. (2001). The plots were separated by at least 100 m, which has been demonstrated sufficient to minimize cross-contamination of CO$_2$ (Lewin, 1992). In 2001, the actual [CO$_2$] averaged across the growing season and four soybean plots was 548.6 μmol mol$^{-1}$. One-minute averages of [CO$_2$] within the plots were within ±10% of the 550 μmol mol$^{-1}$ target 86% of the time. In 2002, the mean elevated [CO$_2$] in the FACE plots was 551.8 μmol mol$^{-1}$, and 1 min averages of [CO$_2$] were within 10% of the target 85% of the time (Tim Mies, personal communication). Each plot was divided into 52 1.9 m × 1.9 m subplots. Soybeans were planted on 27 May 2001 and 1 June 2002. One side of each ring (26 subplots) was planted with a common soybean cultivar together with the rest of the field. The other side of each ring was planted with a range of genotypes including those described in Table 1 and included for this study. Each genotype occupied the same position in each ring. NNS is a non-nodulating mutant of Williams that was found in a population mutagenized with NMU. This line carries two recessive genes ($rj_5$ and $rj_6$) that condition the non-nodulation response (Pracht et al., 1993). L85-2029 is a backcrossed-derived, determinate isolate of Williams, an indeterminate variety, and L81-4274 is a backcrossed-derived indeterminate isolate of the determinate Elf cultivar (Bernard et al., 1991). Seed was obtained from the USDA Soybean Germplasm Collection in Urbana, IL.

2.2. Photosynthetic gas exchange

Measurements of leaf CO$_2$ and water vapor exchange were performed on Williams and Williams-NN (non-nodulating) during the flowering growth phase from 22 to 27 July 2001 as the first experiment, and on Williams, Williams-dt1, Elf, and Elf-Dt1 during pod-filling, from 23 to 26 August 2002 as the second

Table 1

<table>
<thead>
<tr>
<th>Genotype</th>
<th>Denoted in text as</th>
<th>Nodulation</th>
<th>Growth habit</th>
</tr>
</thead>
<tbody>
<tr>
<td>Williams</td>
<td>Williams-NN</td>
<td>Nodulating</td>
<td>Indeterminate</td>
</tr>
<tr>
<td>L85-2029</td>
<td>Williams-dt1</td>
<td>Non-nodulating</td>
<td>Indeterminate</td>
</tr>
<tr>
<td>Elf</td>
<td>Elf-Dt1</td>
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<td>Elf-Dt1</td>
<td>Nodulating</td>
<td>Determinate</td>
</tr>
</tbody>
</table>
Typically three to four leaves per cultivar per ring were sampled for gas exchange analysis from every plot for each experiment. The response of assimilation (A) to intercellular CO₂ concentration (c_i) provides an in vivo measurement of Vc max and Jmax. The objective was to infer changes in the underlying photosynthetic capacity of leaves. Transient decrease in water potential, decrease in chloroplast inorganic phosphate concentration, and decrease in maximum photosystem II efficiency can all occur after a few hours of sunlight, and may all alter the A/c response. To avoid this complication, gas exchange analysis was conducted on leaves, sampled pre-dawn with petioles cut under water, and then kept immersed in water. Leaves were maintained in low light prior to measurement. Leaves were sampled from the upper canopy. Rates of photosynthesis measured on leaves, sampled in this way, equaled or exceeded those measured in situ, suggesting that this procedure did not lower photosynthetic capacity.

Water vapor and carbon dioxide fluxes were measured with a portable open gas-exchange system, incorporating an infrared gas analyzer (LI-6400, Li-Cor, Lincoln, NE, USA). A and stomatal conductance to water vapor (g_s) were calculated in response to changes in c_i according to the method of von Caemmerer and Farquhar (1981).

Photosynthesis was initially induced, on transfer to the measurement photon flux density (1250 μmol m⁻² s⁻¹) at the growth [CO₂]. The leaf cuvette [CO₂] was reduced stepwise to 50 μmol mol⁻¹ and then increased stepwise to an upper concentration of 1200–1400 μmol mol⁻¹. Ten or 11 points were measured to construct each A/cᵢ curve. Leaf temperature was maintained at 25 °C with a vapor pressure deficit in the air of the cuvette of 1.25 ± 0.3 kPa.

The response of A to c_i was fit via the model of Farquhar et al. (1980) using maximum likelihood regression to predict Vc max and Jmax (Sigmaplot, Jandel Scientific, Erkrath, Germany), as described in Ainsworth et al. (2002b). Vc max was determined from points below the inflexion of the A/cᵢ plot and Jmax was determined from values above the inflexion.

2.3. Carbohydrate analysis

Leaf disks for carbohydrate analysis were collected on 30 August 2002 from 14:00 to 15:30 p.m. Leaf disks (3.14 cm²) were sampled in the field, immediately frozen in liquid N, and stored at −80 °C. Ethanol-soluble carbohydrates were extracted from ground leaf tissue in six overnight incubations in 90% (v/v) ethanol at 60 °C. The six overnight incubations were necessary to recover >98% of the ethanol-soluble carbohydrate fraction. Bulk ethanol-soluble carbohydrate content was determined using the phenol-sulfuric acid assay described by Dubois et al. (1956). Following ethanol incubations, starch was extracted from ground leaves using 32% (v/v) perchloric acid as described by Farrar (1993) and assayed as described above.

2.4. Statistical analysis

The experimental design was a split-plot with [CO₂] as the main plot factor and cultivar as the split-plot factor (n = 4 blocks). A mixed model ANOVA (PROC MIXED, SAS Institute, 1996) was used for statistical analysis of gas exchange variables and leaf carbohydrate data. Each pairing of cultivar and its mutant was analyzed independently. Pre-planned comparisons of means were analyzed with linear contrasts.

3. Results

3.1. Nodulation

The light-saturated rate of photosynthesis (A_sat) was increased by 29% in elevated [CO₂] in Williams (P < 0.05). In sharp contrast, it was not affected by [CO₂] in Williams-NN when measured during flowering in 2001 (Table 2). The photosynthetic capacity of Williams-NN was significantly reduced under elevated [CO₂]. Vc max was reduced by 29% (P < 0.05) and Jmax was reduced by 18% (P < 0.05). Again by contrast, the photosynthetic potential of Williams was unaffected (Table 2). The ratio of Vc max/Jmax was not significantly altered by growth at elevated [CO₂] in either Williams or Williams-d/l (Table 2).

3.2. Stem termination

There was no difference in photosynthetic capacity between Williams-d/l (the determinate Williams isolate), and Williams, or between Elf-d/l (the
indeterminate Elf isoline) and Elf under ambient [CO₂], suggesting that differences in sink capacity were insufficient to induce changes at the current [CO₂] but were at elevated [CO₂]. For three of the four genotypes (Elf, ELF-Dt1, and Williams), there was no difference in A₉₅₀ of plants grown in control and elevated [CO₂], when compared at a common measurement [CO₂] (Table 3). However, A₉₅₀ of Williams-dt1 grown at elevated [CO₂] was significantly less than A₉₅₀ of control-grown plants, when both lines were measured at a common [CO₂] (550 μmol mol⁻¹). This implies a loss of photosynthetic capacity with growth at elevated [CO₂]. Analysis of the A/RI response of Williams-dt1 revealed that this resulted from significantly lower V₉₅ₐₓ with growth at elevated [CO₂] (Fig. 1). The decreased V₉₅ₐₓ and J₉₅ₐₓ (data not shown) in the Williams-dt1 eliminated any increase in photosynthesis by elevated [CO₂], such that photosynthesis of the plants grown and measured at elevated [CO₂] equaled that of those grown and measured at ambient [CO₂]. This contrasts sharply with Williams where plants grown and measured at elevated [CO₂] showed a significant ca. 30% increase (Table 3). There was a consistent reduction in the ratio of V₉₅ₐₓ/J₉₅ₐₓ in elevated [CO₂] for both Williams and Williams-dt1; however the reduction in the ratio was not significant for the Elf and Elf-Dt1 genotypes (Fig. 2, Table 4).

Elevated [CO₂] significantly increased leaf ethanol-soluble carbohydrate content by 20%, starch content by 120%, and total non-structural carbohydrate content by 58% (Fig. 3, Table 4). Ethanol-soluble carbohydrates were increased by growth in elevated [CO₂] in the two determinate lines, Elf and Williams-dt1 but not in the two indeterminate lines, Elf-Dt1 and Williams. While all genotypes grown at elevated [CO₂] had significant increases in starch and TNC, Williams-dt1 had the greatest absolute levels of TNC (Fig. 3). When grown at elevated [CO₂], TNC was significantly greater in determinate Williams-dt1 than in indeterminate Williams (P < 0.1).

4. Discussion

Acclimation of photosynthesis to elevated [CO₂] in soybean has previously been described as complex, inconsistent, and difficult to understand (Xu et al., 1994). Soybean has been described as a species that shows no photosynthetic acclimation (Ziska et al., 2001), moderate reduction in Rubisco activity (Vu et al., 1997), and substantial reduction in Rubisco (Moore et al.,...
Fig. 1. The maximum rate of RuBP-saturated carboxylation in vivo \( (V_{\text{c,max}}) \pm 1 \text{ S.E.} \) (A) Williams isogenic pair: Williams and Williams-dt1; (B) Elf isogenic pair: Elf and Elf-Dt1. Soybeans were grown at ambient \([\text{CO}_2]\) (white bars) and elevated \([\text{CO}_2]\) (black bars), and measured during pod-filling in August 2002 \((n = 4 \text{ blocks})\). Abbreviations for cultivars are listed in Table 1. Pre-planned comparisons of \([\text{CO}_2]\) treatments within genotypes were performed using contrast statements. \(^* P < 0.05\).

The range of reported responses likely stems from differences in \([\text{CO}_2]\) treatment levels, nutrient conditions, rooting volumes, and multi-allelic differences between varieties. In this study, acclimation of photosynthesis was studied for the first time under open-air elevation of \([\text{CO}_2]\) without any restriction of rooting volume and, for the first time, using isolines with traits directly affecting “sink” capacity, i.e. nodulation and stem termination. Significant acclimation of photosynthesis was apparent only in the non-nodulating, Williams-NN, and the determinate Williams-dt1, both derived by single gene mutations of the nodulating indeterminate Williams (Table 2, Fig. 1). This is consistent with the expectation that acclimation only
occurs when sink capacity is lowered (Rogers et al., 1996, 1998; Drake et al., 1997; Morgan et al., 2001). Down-regulation of photosynthesis in Williams-dt1 corresponded to a significant increase in leaf TNC, as would be expected with decreased sink capacity. Such an increase in TNC has been phenomonologically linked to acclimation of photosynthesis and decreased $V_{\text{c,max}}$ (Xu et al., 1994; Rogers et al., 1998; Isopp et al., 2000). Williams-dt1 was developed from the indeterminate variety Williams with a single gene substitution (dt1). Elf is also a determinate variety, yet by contrast to Williams-dt1 did not show any loss of photosynthetic capacity with growth at elevated [CO$_2$]. The disparity between those two determinate
Table 4
Statistical analysis of effects of [CO$_2$] on photosynthetic parameters of determinate and indeterminate genotypes

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Isogenic pair</th>
<th>[CO$_2$] (1), $F$, $P$</th>
<th>Genotype (3), $F$, $P$</th>
<th>[CO$_2$] × genotype (3), $F$, $P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$A_{sat}$ (growth [CO$_2$])</td>
<td>Williams/Williams-dt1</td>
<td>23.30, &lt;0.01</td>
<td>3.31, 0.08</td>
<td>6.11, &lt;0.01</td>
</tr>
<tr>
<td></td>
<td>Elf/EIlf-Dt1</td>
<td>22.30, &lt;0.01</td>
<td>0.21, 0.65</td>
<td>&lt;0.01, 0.99</td>
</tr>
<tr>
<td>$V_{c,\text{max}}$</td>
<td>Williams/Williams-dt1</td>
<td>13.88, 0.01</td>
<td>2.06, 0.20</td>
<td>2.08, 0.20</td>
</tr>
<tr>
<td></td>
<td>Elf/EIlf-Dt1</td>
<td>0.43, 0.54</td>
<td>0.39, 0.57</td>
<td>0.03, 0.87</td>
</tr>
<tr>
<td>$J_{\text{max}}$</td>
<td>Williams/Williams-dt1</td>
<td>0.77, 0.41</td>
<td>&lt;0.01, 0.95</td>
<td>7.2, 0.04</td>
</tr>
<tr>
<td></td>
<td>Elf/EIlf-Dt1</td>
<td>1.57, 0.26</td>
<td>0.15, 0.75</td>
<td>0.48, 0.51</td>
</tr>
<tr>
<td>$V_{c,\text{max}}/J_{\text{max}}$</td>
<td>Williams/Williams-dt1</td>
<td>25.59, &lt;0.01</td>
<td>1.11, 0.33</td>
<td>0.57, 0.48</td>
</tr>
<tr>
<td></td>
<td>Elf/EIlf-Dt1</td>
<td>2.44, 0.15</td>
<td>0.66, 0.44</td>
<td>&lt;0.01, 0.95</td>
</tr>
<tr>
<td>Ethanol-soluble CH$_2$O</td>
<td>Williams/Williams-dt1</td>
<td>5.07, 0.04</td>
<td>2.26, 0.16</td>
<td>0.75, 0.40</td>
</tr>
<tr>
<td></td>
<td>Elf/EIlf-Dt1</td>
<td>10.03, 0.02</td>
<td>11.16, 0.02</td>
<td>0.72, 0.43</td>
</tr>
<tr>
<td>Starch</td>
<td>Williams/Williams-dt1</td>
<td>19.55, &lt;0.01</td>
<td>0.76, 0.42</td>
<td>1.82, 0.23</td>
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<tr>
<td></td>
<td>Elf/EIlf-Dt1</td>
<td>113.99, &lt;0.01</td>
<td>11.16, 0.02</td>
<td>0.72, 0.43</td>
</tr>
<tr>
<td>TNC</td>
<td>Williams/Williams-dt1</td>
<td>22.72, &lt;0.01</td>
<td>2.15, 0.17</td>
<td>2.33, 0.15</td>
</tr>
<tr>
<td></td>
<td>Elf/EIlf-Dt1</td>
<td>67.71, &lt;0.01</td>
<td>0.04, 0.86</td>
<td>0.22, 0.66</td>
</tr>
</tbody>
</table>

Analysis of variance of photosynthetic and leaf carbohydrate parameters measured in 2002, for plants grown at ambient [CO$_2$] (370 µmol mol$^{-1}$) and elevated [CO$_2$] (550 µmol mol$^{-1}$). A mixed model ANOVA with [CO$_2$] as the main plot factor and genotype as the split-plot factor was used for each isogenic pair.

lines may lie in the fact that Elf was developed as a determinate variety, Elf, although much shorter than Williams, was selected to be highly productive by producing nearly as many pods on branches as on the main stem (Beaver et al., 1985), thereby avoiding “sink” limitation (Kilgore-Norquest and Sneller, 2000). For determinate cultivars to be competitive it is likely that breeders will select lines with sufficient potential for pod formation to avoid “sink” limitation. While intraspecific variation in the response of photosynthesis to elevated [CO$_2$] in soybeans has been reported previously (Ziska and Bunce, 1995; Ziska et al., 1998, 2001; Nakamura et al., 1999), these studies were not performed under open-air conditions nor did they compare isogenic lines. When determinate and indeterminate cultivars of various isolines are compared, there are multi-allelic differences. This prevents ascribing differences in [CO$_2$] response purely to growth habit (Robinson and Wilcox, 1998). By using single gene changes, this study has demonstrated that preventing nodulation and restricting main stem growth produce acclimation of photosynthesis to elevated [CO$_2$]. However, the reciprocal conversion of the determinate Elf variety to indeterminate did not result in an up-regulation of photosynthesis in elevated [CO$_2$].

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