SUNFLOWER AND BIOMASS SORGHUM PHOTOSYNTHESIS RESPONSE TO CO₂ ENRICHMENT

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ABSTRACT

Carbon dioxide concentration is expected to increase to 500-1000 ppm by 2100 according to the ecological and social scenarios of IPCC. In this context, the aim of the study was twofold, namely to assess and to compare the sunflower and biomass sorghum photosynthesis responses to CO₂ enrichment at leaf scale, as well as the related interactions with other physiological determinants. We wanted to test if an enrichment of [CO₂] led to a better exploitation of resources (water and radiation) and if there were any differences as regards the performance of the two crops.

In order to evaluate the effect of the CO₂ enrichment at leaf scale, both crops (sunflower and biomass sorghum) were cultivated in Southern Italy under the same conditions. The results obtained showed that an increased concentration from 370 (ambient) to 760 μmol mol⁻¹ of CO₂ led to: (i) an improvement in the net photosynthesis rate (e.g. more than 60% in the case of sunflower and more than 110% in the case of sorghum); (ii) lower values for the stomatal conductance, up to 7% in the case of sunflower and 12% for sorghum compared to the ambient carbon dioxide concentration; (iii) water saving (due to the transpiration loss) equal to 0.074 L of water per m⁻² of leaf surface h⁻¹ for sunflower and 0.063 L of water per m⁻² of leaf surface h⁻¹ for sorghum.

In addition, a higher photosynthesis activity coupled with a lower water loss, led to improved instantaneous water use efficiency (WUE). Specifically, doubling the ambient CO₂ concentration, the WUE reached 10.56 mg CO₂ g H₂O⁻¹ in the case of sunflower (4.36 mg CO₂ g H₂O⁻¹ at ambient CO₂) and 14.07 mg CO₂ g H₂O⁻¹ for biomass sorghum (7.67 mg CO₂ g H₂O⁻¹ at ambient CO₂).

Key words: sorghum, sunflower, instantaneous water use efficiency, net assimilation rate, leaf gas exchange, CO₂ enrichment.

INTRODUCTION

According to the projections of the Intergovernmental Panel on Climate Change (IPCC, 2007) the atmospheric carbon dioxide concentration [CO₂] will increase to 500-1000 ppm by 2100.

Carbon dioxide has a central role for the plant metabolism, affecting growth and implicitly the chemical and physiological processes. Therefore, an increase of CO₂ availability for the photosynthesis leads to an overall improvement of plant growth and biomass accumulation.

In the case of C₃ plants, the fixation of CO₂ occurs through the Calvin cycle, or C₃ cycle, which provides the link with the ribulose-1,5-diphosphate and is catalyzed by the Rubisco enzyme; this enzyme can add to ribulose CO₂ or O₂, which compete for the active site for the enzyme.

C₃ plants, both under hot and drought conditions, close their stomata to limit the water loss. When stomata are closed, CO₂ concentration in the leaves air spaces falls. This triggers the phenomenon of photorespiration, with substrate oxidation without energy gain, decreasing in the same time the efficiency for the fixation of C.

The C₄ plants overcome the photorespiration process through a particular mechanism; the leaves of these plants have the Kranz anatomy with two types of cells: mesophill and bundle sheath around the vascular bundles. In the mesophill, CO₂ is added to the phosphoenolpyruvate, reaction catalyzed by PEP carboxylase, which has a greater affinity for CO₂ than Rubisco. In the
bundle sheath the oxaloacetate releases the CO2, starting the Calvin cycle. In this site the concentration of CO2 is much greater than that of O2, reducing the photorespiration and increasing the efficiency for the fixation of C.

Under elevated [CO2] the rates of photosynthesis of C3 plants are enhanced (Acoc and Allen, 1985; Chen et al., 1995; Ainsworth, 2008), whereas contrasting results are reported for C4 plants. Under well watered conditions, some studies reported that elevated [CO2], affected positively leaf photosynthesis (Le Cain and Morgan, 1998; Ziska et al., 1999) of C4 plants, while other researches have indicated the increase in photosynthesis activity only in dry conditions (Adam et al., 2000). Other authors underlined that photosynthesis rate PN was not affected significantly (Chen et al., 1995; Rogers et al., 1983) when [CO2] increased.

The variation in photosynthesis rate is not the only effect due to [CO2] enrichment. Some other effects can be mentioned, namely: (i) the stomatal closure in response to the elevated level of [CO2] (Mott, 1990) which reduces the stomatal conductance (gS; Knapp et al., 1994); ii) transpiration (E) decreases for both C3 and C4 plants (Mott, 1988; Assmann, 1999; Wand et al., 1999), although with different magnitude between species with different photosynthetic carbon pathways.

In response to [CO2] enrichment, different paths for C3 and C4 plants have been noticed; the differences in photosynthetic activity have an impact on the final biomass accumulation and, on average, the growth stimulation is about 40-44% in the case of C3 plants and 22-33% for C4 plants, doubling the values for current [CO2] (Poorter, 1993; Wand et al., 1999).

The analyzed data from previous research studies showed that photosynthetic behaviours of both C3 and C4 species are driven by different variables other than [CO2]. This cannot furnish univocal response according to climatic condition, soil type and crop management. For instance in sunflower, Garofalo and Rinaldi (2015) indicated as the water stress lowered Pn up to 61% compared to the well watered plants, according to the drought timing. Therefore, impacts of climate change in stimulating photosynthetic activity could change according to the environmental conditions and, on the same site, to crop management. The reduction of the erratic effect of these variables, lead to a more accurate evaluation of different photosynthesis patterns between C3 and C4 species.

The study of the effects of [CO2] enrichment on plants, may involve morphological and productive traits, and/or physiological aspects at leaf scale. Research regarding the changes of vegetative habitus of crop has been carried out through the free air CO2 enrichment (FACE) or open top chamber (OTC). In FACE system, a given perimeter of cultivated field is bounded by a set of pipes emitting a continuous flow of CO2 to maintain a steady prefixed value of [CO2]. Being an open system, the demand for CO2 is high, affecting the operating costs of the system and under extreme wind conditions, [CO2] on plants can undergo substantial changes. To overcome these issues, in OTC system, the crop usually is grown in pots and placed in a chamber with specific size and covering material as fiberglass, polycarbonate or Plexiglas. OTC system has the advantage of simplicity, cheapness, easiness of installation and a better control of [CO2]. However the covering layer of the OTC system also has some disadvantages, such as: the higher temperature than the outside, altered radiation and humidity that affects the crop physiology and growth (D’Andrea and Rinaldi, 2010). Finally, in the OTC systems, the [CO2] is established at the beginning of the experiment, thus the crop response is univocal; for this reason the “crop response curve” at different levels of [CO2] is not achievable.

To partially overcome these issues, the infrared gas analyzer (IRGA) on crop grown under normal field conditions can be used. With this portable and friendly instrument, the physiological aspects of the plant at leaf level, such as transpiration, photosynthesis and stomatal conductance can be analyzed, by imposing different [CO2] concentrations. Obviously, with this system, any direct assessment of morphological changes in response to different [CO2] at field scale cannot be performed. However, the
physiological data obtained with IRGA can be implemented in the crop growth model, photosynthetically-based (de Reffye et al., 1999; Fournier et al., 2003; Prusinkiewicz, 2004; Gayler et al., 2008; Génard et al., 2008; Evers et al., 2010), in order to check trends of crop growth in response to \( \text{CO}_2 \) changing.

In this paper we present the experimental results of a study that has considered sunflower (a C\(_3\) plant) and biomass sorghum (C\(_4\) plant). Both crops were grown under the same conditions. The main aim of the study was to assess and to compare the response of photosynthesis and the corresponding interactions to future carbon dioxide enrichment at leaf scale; more specifically we wanted to test if there are different performances of the two crops, as regards a better exploitation of \([\text{CO}_2]\) availability and improvement in future resources use efficiency.

**MATERIAL AND METHODS**

The research was carried out at the experimental farm of the Council for Agricultural Research and Economics - Research Unit for Cropping Systems in Dry Environments, in Foggia (lat. 41° 8’ 7” N; long. 15° 83’ 5” E, alt. 90 m a.s.l.), Southern Italy, in 2010.

The soil is a vertisol of alluvial origin, Typic Calcixeret, (Soil Taxonomy 10\(^{th}\) ed., USDA 2010), silty-clay with the following characteristics: organic matter, 2.1%; total N, 0.122%; NaHCO\(_3\) extractable P, 41 ppm; NH\(_4\)O Ac-extractable K\(_2\)O, 1598 ppm; pH (water), 8.3; field capacity water content, 0.396 m\(^3\) m\(^{-3}\), permanent wilting point water content, 0.195 m\(^3\) m\(^{-3}\), available soil water, 202 mm m\(^{-1}\). The local climate is „accentuated thermo-Mediterranean as classified by FAO-UNESCO Bioclimatic Maps (1962), with daily temperatures below 0 °C in the winter and above 40 °C in the summer. Annual rainfall (average 550 mm) is mostly concentrated during the winter months, while only 101 mm of precipitation/rainfall is recorded, on average, during sorghum crop cycle (1\(^{st}\) May - 15\(^{th}\) August).

Biomass sorghum (Sorghum bicolor L., hybrid BIOMASS 133) and sunflower (Helianthus annuus L., hybrid SANBRO) were sown at first ten-day of May (25 and 7.5 plants per m\(^2\) for sorghum and sunflower, respectively) and the harvest occurred at flowering for sorghum (first ten-day of August) and at maturity for sunflower (beginning of September). As pre-sowing fertilization 2 q ha\(^{-1}\) of diammonium phosphate was supplied to the crops. Both crops were cultivated in well watered conditions, supplying the water consumed by the crop, each time the crop evapotranspiration (ETc), calculated multiplying the reference evapotranspiration with FAO–Penman–Monteith method (ETc; Allen et al., 1998) by the crop coefficient (kc; Garofalo et al., 2011), reached 60 mm.

Rainfall recorded during the crop growing cycle was 59.2 mm; total water supplied to the crops resulted equal to 452 and 338 mm for sorghum and sunflower, respectively. ETc was 706 mm for sorghum and 446 mm for sunflower.

Leaf gas exchange rates and associated parameters were measured on two new fully expanded leaves during the vegetative phase of three plants randomly chosen in the field, in the upper part of the canopy exposed to full sunlight, using a Photosynthesis System LCpro+, Portable Infrared Gas Analyzer (ADC, BioScientific Ltd., Hoddesdon, Herts, UK). Three measurements for each leaf were recorded automatically every 2 min., after changing the \([\text{CO}_2]\) in the leaf chamber, to ensure a steady-state condition for the gas exchange flow.

The \([\text{CO}_2]\) in the leaf chamber (c\(_{ref}\)) was increased step by step, starting with 370 (ambient), followed by: 450, 580, 680 and 760 µmol mol\(^{-1}\).

The light units (the diode array contains blue LED’s at 470 nm and red ones at 660 nm) upper the jaw enclosing the leaf, were used to ensure a constant irradiance replicating the sunlight during the midday (PAR; 1566 µmol m\(^{-2}\) sec\(^{-1}\)).

The chamber cooler was set to avoid the increase of the temperature in the jaw up to 10°C from the ambient.

The measurements were carried out in the same three days for both crops: 30 days (juvenile phase; Jph), 60 days (full canopy expansion; Fph) and 90 days (beginning of
RESULTS AND DISCUSSION

1. Comparison between C\textsubscript{3} and C\textsubscript{4}: ambient [CO\textsubscript{2}]

The growth phase had effect on P\textsubscript{N} and the other measured parameters, with different pathway for C\textsubscript{3} and C\textsubscript{4} plants, as shown in Table 1. For sunflower, P\textsubscript{N} resulted higher in the first and second sampling, whereas in Sph the photosynthetic activity was almost halved. After the maximum leaf expansion, the sink activity decreased, and therefore, the demand for the photosynthetates was lower, hence for the net photosynthesis rate. In Fph, g\textsubscript{s} decreased by 22%, this may be explained by the high temperatures of this period (July), compared to the coldest period during the juvenile phase (May - June). As a consequence of the decline of g\textsubscript{s}, E also decreased by 24%, compared to the values recorded during juvenile period and initial senescence period.

According to the results, C\textsubscript{i} cannot be linked to the stomatal conductance, resulting statistically similar during all the measurements. This confirms that as plant matures, the capability of leaves to fully exploit the intercellular [CO\textsubscript{2}] is reduced. This leads to lower values for P\textsubscript{N} and in the same time keeps similar concentration for C\textsubscript{i}, despite the reduction of flow of CO\textsubscript{2} into the leaves, driven by the stomatal closure.

WUE was influenced by the trend of P\textsubscript{N} and E. Indeed, the highest value for WUE was recorded at full canopy expansion, due to the greatest net photosynthetic rate, while the lowest WUE was observed at Jph, because of the greatest transpiration rate of the young leaves.

The pathway of P\textsubscript{N} influenced the Q\textsubscript{Y}, the latter showing comparable values during the active growth of plants (16.7 μmol mmol\textsuperscript{-1}) as well a lower value at the beginning of senescence.

Table 1. Net photosynthesis rate and associated parameters for sunflower and sorghum during the crop growing cycle at ambient [CO\textsubscript{2}]

<table>
<thead>
<tr>
<th>Crop</th>
<th>Phase</th>
<th>P\textsubscript{N}</th>
<th>g\textsubscript{s}</th>
<th>E</th>
<th>C\textsubscript{i}</th>
<th>WUE</th>
<th>Q\textsubscript{Y}</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>(μmol m\textsuperscript{-2} s\textsuperscript{-1})</td>
<td>(μmol m\textsuperscript{-2} s\textsuperscript{-1})</td>
<td>(μmol m\textsuperscript{-2} s\textsuperscript{-1})</td>
<td>(μmol mol\textsuperscript{-1})</td>
<td>(μmol CO\textsubscript{2} mmol\textsuperscript{-1} H\textsubscript{2}O)</td>
<td>(μmol mmol\textsuperscript{-1})</td>
</tr>
<tr>
<td>Sunflower</td>
<td>Jph</td>
<td>24.11 a</td>
<td>0.93 a</td>
<td>6.78 a</td>
<td>236</td>
<td>3.56 b</td>
<td>15.6 a</td>
</tr>
<tr>
<td></td>
<td>Fph</td>
<td>27.69 a</td>
<td>0.73 ab</td>
<td>6.37 a</td>
<td>218</td>
<td>4.36 a</td>
<td>17.7 a</td>
</tr>
<tr>
<td></td>
<td>Sph</td>
<td>17.92 b</td>
<td>0.48 b</td>
<td>5.21 b</td>
<td>247</td>
<td>3.45 ab</td>
<td>11.6 b</td>
</tr>
<tr>
<td></td>
<td>Avg.</td>
<td>23.24 a</td>
<td>0.71 a</td>
<td>6.12 a</td>
<td>234</td>
<td>3.79 b</td>
<td>14.8 a</td>
</tr>
<tr>
<td>Sorghum</td>
<td>Jph</td>
<td>25.84 b</td>
<td>0.29 b</td>
<td>4.20 ab</td>
<td>134 b</td>
<td>6.07 b</td>
<td>16.5 b</td>
</tr>
<tr>
<td></td>
<td>Fph</td>
<td>35.98 a</td>
<td>0.38 a</td>
<td>4.97 a</td>
<td>113 b</td>
<td>7.67 a</td>
<td>23.0 a</td>
</tr>
<tr>
<td></td>
<td>Sph</td>
<td>19.62 b</td>
<td>0.23 ab</td>
<td>3.71 b</td>
<td>161 a</td>
<td>5.63 b</td>
<td>12.5 b</td>
</tr>
<tr>
<td></td>
<td>Avg.</td>
<td>26.57 a</td>
<td>0.30 b</td>
<td>4.25 b</td>
<td>136 b</td>
<td>6.23 a</td>
<td>17.3 a</td>
</tr>
</tbody>
</table>

Abbreviations: Jph = juvenile phase; Fph = full canopy expansion; Sph = beginning of senescence; P\textsubscript{N} = leaf photosynthetic rate; g\textsubscript{s} = stomatal conductance; E = leaf transpiration rate; C\textsubscript{i} = sub-stomatal [CO\textsubscript{2}]; WUE = instantaneous water use efficiency; Q\textsubscript{Y} = instantaneous quantum yield.

Different behaviour was observed for sorghum, more specifically the best performances of the analyzed parameters (excepting C\textsubscript{i}) were observed at Fph. In this
phase the higher temperatures and drought conditions, led to defensive mechanisms of plants by reducing the transpiration. The C₄ crops due to the lower Cᵣ, stomatal conductance and consequently leaf transpiration, suffer less under the heat stress or drought condition (Vitkauskaitė and Venskaitytė, 2011) showing an advantage in term of Pₑ and WUE over C₃ plants. Again, the advantage of sorghum is referring to the full canopy expansion period.

The highest value for Pₑ, recorded at maximum canopy expansion, could be explained by the characteristics of C₄ leaves at different development stages. Indeed, Ghannoum et al. (2000), reported that young C₄ leaves have C₃-like characteristics (similar value for Pₑ during Jph, both for sorghum and sunflower) and the cell-specific accumulation of photosynthetates begins later (with the initiation of veins in monocotiledones and dicotiledones). As consequence, in the fully expanded leaves, the photosynthetic rate resulted greater than 39% as compared to the young leaves (and higher than sunflower), whereas in Sph the photosynthetic rate was halved compared to Fph. Indeed, in the last part of the growing cycle, suberization of leaf tissue reduced the gₛ and, consequently, the transpiration of leaves (Ghannoum et al., 2000). This led to a lower capability of the leaf mesophill for the photosynthesis process, explaining a higher [CO₂] in the sub-stomatal cavity despite a lower CO₂ flow into the leaf (consequent to the stomatal closure).

As for Pₑ, Qᵥ also resulted higher in Fph and lower during the last part of the growing cycle, with a maximum difference of 44% between the two phases.

At ambient [CO₂], the overall path for Pₑ resulted statistically similar for C₃ and C₄ plants, although the intercellular CO₂ to be allocated to the photosynthesis process was lower in sorghum than in the sunflower. Indeed, in the case of C₃ plants, Rubisco enzyme involved in photosynthesis is also implicated in the uptake of CO₂, whereas for C₄ plants, the delivery of CO₂ to the Rubisco is assigned to the PEP Carboxylase. This means a faster and more efficient processing of carbon dioxide for C₄ than C₃ crops, allowing a lower CO₂ accumulation in the leaf tissues before to being processed by the photosynthesis. This entails also a shorter time for the stomatal opening of C₄ compared to C₃ species, for the same amount of CO₂ gain for photosynthesis.

As result, the lower gₛ recorded for sorghum during all the measurements (0.41 mol m⁻² s⁻¹ less than sunflower), led to a water saving (due to transpiration), equal to 31% compared to sunflower.

From these measurements a better value for the WUE emerged in the case of C₄ compared to C₃ plants, with an overall improved performance of 64%.

The instantaneous quantum yield efficiency resulted slightly higher in sorghum than in sunflower, namely an increase of 13%.

2. Comparison between C₃ and C₄: enriched [CO₂]

The analysis of the behaviour of C₃ and C₄ plants in response to CO₂ enrichment, was carried out during the measurements at maximum canopy development (Fph), corresponding to the maximum Pₑ both for sorghum and sunflower.

The increase of [CO₂] at leaf scale, determined significant increment of Cᵣ, both for C₃ and C₄ plants. Indeed, doubling the cₑ from the current value, also the sub-stomatal [CO₂] resulted almost double in the case of sorghum and more than double in the case of sunflower (Figure 1a), indicating the capability of plants to capture CO₂ to the atmosphere, proportionally to its increment.

Despite the rate of the carbon sap in the leaf tissue was similar for sorghum and sunflower, the final gain in term of Pₑ resulted quite dissimilar. With cₑ ranging between 370 and 580 μmol mol⁻¹, C₄ plants kept the advantage in term of Pₑ; more specifically the Pₑ oscillated between 0.097 and 0.09 μmol mol⁻¹ per μmol mol⁻¹ of cₑ greater than 18% compared to C₃ plants (Figure 1b). With further increases in cₑ, the photosynthetic gap between C₃ and C₄ plants rapidly closed, to vanish completely at 760 μmol mol⁻¹.

At the highest level of cₑ, the values of Pₑ were comparable between sorghum and sunflower (58.57 μmol m⁻² s⁻¹, on average). However, under different [CO₂] (starting from
ambient and then doubling the $\text{[CO}_2\text{]}$), the gain in term of $P_N$ varies, resulting 76% greater in the case of C$_3$ compared to C$_4$ species.

In our study, sorghum achieved the saturation for $P_N$ (58.71 μmol m$^{-2}$ s$^{-1}$), when the $C_i$ doubled the initial sub-stomatal $\text{[CO}_2\text{]}$ (Figure 2), confirming the results of Ziska and Bunce (1997) with saturation for $P_N$ in sorghum, at 220 μmol mol$^{-1}$ of $C_i$.

Some authors (Taiz and Zeiger, 1991; von Caemmerer et al., 1997) reported that for C$_4$ plants, the saturation for $P_N$ is reached near the current $\text{[CO}_2\text{]}$ level, with a small improvement in term of net photosynthetic rate, as a consequence of the increase of $\text{[CO}_2\text{]}$. In the case of C$_3$ plants, the saturation for $P_N$ (similar to the C$_4$ plants) is reached by doubling the current $\text{[CO}_2\text{]}$.

On the other hand, several studies (Wand et al., 1999; Ziska et al., 1999) have shown that saturation of photosynthesis for C$_4$ species is achieved at a higher level of $\text{[CO}_2\text{]}$ than the current one, especially when crops are in well watered regimes.

For C$_3$ species, the saturation is reported to be achieved at levels of intercellular $\text{[CO}_2\text{]}$ higher than in the case of C$_4$ plants. In soybean, the plateau of $P_N$ is reached close to 500 μmol mol$^{-1}$ of $C_i$ (Sims et al., 1998). Also for rice, Makino et al. (1994) indicated a significant increment in $P_N$ when the intercellular CO$_2$ pressure raises from 49 to 395 μmol mol$^{-1}$ and then stabilized close to 444 μmol mol$^{-1}$.

Specifically for sunflower, in our study, we observed that $P_N$ was saturated when $C_i$ reached 500 μmol mol$^{-1}$, a lower value if compared with that (close to 800 μmol mol$^{-1}$) reported by Makino and Mae (1999) for the same crop.

So, both for C$_3$ and C$_4$ species, the saturation point for $P_N$, requires defined level of $C_i$, that in this research, resulted halved in sorghum compared to sunflower.

Figure 3a shows that a rise of the $\text{[CO}_2\text{]}$ level in the leaf chamber, declines the $g_s$. Moreover, when $c_{ref}$ equals 760 μmol mol$^{-1}$, $g_s$ decreased by 7% compared to ambient $\text{[CO}_2\text{]}$ in the case of sunflower, and by 12% compared to ambient $\text{[CO}_2\text{]}$ for sorghum.

CO$_2$ enrichment leads to a decrement in $g_s$ both for C$_3$ and C$_4$ plants, with a magnitude that varies according the studies reported in
the literature. Thus, in a review of Ainsworth and Rogers (2007), it has been shown that in FACE experiments, the decrease of \( g_s \) could oscillate between 20 and 30% in the case of C\(_3\) crops, as well between 19 and 39% for C\(_4\) crops, when the [CO\(_2\)] passed from 366 to 567 \( \mu \text{mol mol}^{-1} \).

As regards the open top chamber experiments, Chen et al. (1995) found that \( g_s \) passed from 1.73 to 0.89 mol m\(^{-2}\) s\(^{-1}\) in the case of sunflower and from 0.64 to 0.18 mol m\(^{-2}\) s\(^{-1}\) in corn, when the environmental [CO\(_2\)] rose from 350 ppm to 700 ppm.

For sunflower, Maddaluno et al. (2011) reported that the plants grown in water stress condition, reduced the \( g_s \) by 62% compared to well watered plants, when the [CO\(_2\)] was set to 760 \( \mu \text{mol mol}^{-1} \).

However, climatic condition affects the physiological response of crops to [CO\(_2\)] enhancement, especially when vapour pressure deficit condition is low; the crop tends to emphasize the effect of enriched [CO\(_2\)] on stomatal closure (Wullschleger et al., 2002).

Moreover, the growth under low N and drought, exacerbates the decrease of \( g_s \) when the plants are submitted to the increase of [CO\(_2\)], with magnitude almost doubled on the stomatal closure, compared to optimal growth conditions (Ainsworth and Long, 2005).

From these data, we can emphasize that between \( g_s \) and the [CO\(_2\)] enrichment there is an inverse relationship; crop management and pedoclimatic conditions could also impact highly on the relative magnitude. The small variation for \( g_s \) observed in this study, can be explained by the crop management, targeted to reduce the water and nitrogen stress for plants.

However, to a small decrement for the stomatal conductance, corresponds a significant reduction in the leaf transpiration, equal to 15 and 22% for sunflower and...
sorghum, respectively (Figure 3b). This means water saving due to reduced E, equal to 0.074 and 0.063 L of water per m² of leaf surface h⁻¹ for sunflower and sorghum, respectively. For sorghum, it can be considered a mean value for the leaf area index from the juvenile to beginning of senescence phase, equal to 5.9 m² m⁻² (Rinaldi and Garofalo, 2011) and 4.6 m² m⁻² for sunflower (Goksoy et al., 2004), as well a day light length for both crops equal to 10 hours. This means a water saving during the whole crop grown equal to 393 and 261 mm for sorghum and sunflower, respectively.

The larger PN and the lower transpiration rate, observed at higher level of [CO₂] resulted in a greater WUE (Figure 3c). The sunflower was the crop that mostly took advantage by [CO₂] enrichment, more specifically the WUE increased by 141%, doubling the current [CO₂], whereas the increment for sorghum was 83%.

For C₃ species, such as cotton, Reddy et al. (1995) reported an increment in WUE at 700 μmol mol⁻¹ [CO₂] equal to 100%, whereas for sunflower, Chen et al. (1995) underlined that the improvement in instantaneous water use efficiency resulted of 90%, a percentage not so dissimilar to that for corn (97%) when [CO₂] passed from 350 to 700 μmol mol⁻¹.

However, the advantage in term of WUE seemed to be due mainly to a better exploitation of water availability (hence, the PN) rather than a lower water requirement, or reciprocal of water use efficiency. The latter was 54% for sorghum and 41% in sunflower at doubled c_ref.

If improvement in PN is reported for the well watered conditions, in water stress condition, especially for C₃ plants, different studies showed that drought condition negatively impacts on photosynthesis and accelerates the photorespiration rate by stomatal closure in C₃ plants, reducing the activity of key enzymes in C metabolism (Maroco et al., 2002) and down-regulation of photosynthetic apparatus by low C availability (Tourneux and Peltier, 1995).

However, even for C₄ species, water stress causes the reduction in plant transpiration through stomatal closure; transpiration may be lower up to 61% comparing well watered and stressed plants, but with no adverse effects on WUE (Garofalo and Rinaldi, 2013).

Finally, the path for Qᵥ, resulted quite similar for both species (Figure 3d). The gain in term of Qᵥ, was slightly higher in sorghum than sunflower up to 580 μmol mol⁻¹ [CO₂], but above this concentration, the gap resulted null and the final gain was equal to 14.5 and 19.6 μmol mmol⁻¹ for sunflower and sorghum, respectively.

CONCLUSIONS

This research study assessed the gas exchanges and associated parameters at leaf scale, in response to [CO₂] enrichment for C₃ (sunflower) and C₄ (biomass sorghum) crops in well watered conditions. The main findings of the experiment were that for any increment of [CO₂] lower or equal to 300 μmol mol⁻¹ to the ambient value, the PN greatly improved in the case of C₄ crop. With further increase of carbon dioxide, the C₃ plants retrieved this gap or, pushing the [CO₂] beyond 760 μmol mol⁻¹ may have even better performances.

However, the increase of [CO₂], as predicted by the future climate scenarios, will be accompanied by raise of temperature and less rainfall. In these conditions, the C₄ plants through the abatement of the stomatal conductance and leaf transpiration, combined with a faster intercellular CO₂ processing, could fit better to the changing environmental conditions than C₃ species, enhancing leaf PN and growth via increases in C₃ improvements of shoot water relations and increases in leaf temperature. Indeed for C₃ species, adverse climatic issues (high temperatures, drought) together with [CO₂] enrichment, may cause an excessive stomatal closure by increasing the rate of photorespiration.

However, as underlined from our study, in well watered conditions, the increases in carbon dioxide concentration led to an improvement in plant carbon assimilation and processing, by: (i) increasing the PN, (ii) reducing the water transpired by the plants and (iii) improving the water use efficiency and quantum yield. These effects were more pronounced for the C₄ plants at the initial increases of [CO₂], indicating a better
flexibility, compared to the C₃ species, in the environmental short term CO₂ enrichment. However, optimal cropping management could exploit the higher carbon availability also for C₃ plants and, as reported, these species may be more efficient compared to C₄ species, especially in the long term carbon dioxide enrichment.

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