Journal of Plant Physiology 168 (2011) 1909–1918

Contents lists available at ScienceDirect

Journal of Plant Physiology

journal homepage: www.elsevier.de/jplph

Elevated CO_2 increases water use efficiency by sustaining photosynthesis of water-limited maize and sorghum

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ARTICLE INFO

Article history:
Received 31 January 2011
Received in revised form 13 May 2011
Accepted 15 May 2011

Keywords:
Biomass
Canopy gas exchange
C_4 photosynthesis
Drought stress
Elevated CO_2
Maize
Sorghum
Water use efficiency

ABSTRACT

Maize and grain sorghum seeds were sown in pots and grown for 39 days in sunlit controlled-environment chambers at 360 (ambient) and 720 (double-ambient, elevated) μmol mol^{-1} carbon dioxide concentrations [CO_2]. Canopy net photosynthesis (PS) and evapotranspiration (TR) was measured throughout and summarized daily from 08:00 to 17:00 h Eastern Standard Time. Irrigation was withheld from matched pairs of treatments starting on 26 days after sowing (DAS). By 35 DAS, cumulative PS of drought-stress maize, compared to well-watered plants, was 41% lower under ambient [CO_2] but only 13% lower under elevated [CO_2]. In contrast, by 35 DAS, cumulative PS of drought-stress grain sorghum, compared to well-watered plants, was only 9% lower under ambient [CO_2] and 7% lower under elevated [CO_2]. During the 27–35 DAS drought period, water use efficiency (WUE, mol CO_2 Kmol^{-1} H_2O), was 3.99, 3.88, 5.50, and 8.65 for maize and 3.75, 4.43, 5.26, and 9.94 for grain sorghum, for ambient-[CO_2] well-watered, ambient-[CO_2] stressed, elevated-[CO_2] well-watered and elevated-[CO_2] stressed plants, respectively. Young plants of maize and sorghum used water more efficiently at elevated [CO_2] than at ambient [CO_2], especially under drought. Reductions in biomass by drought for young maize and grain sorghum plants were 42 and 36% at ambient [CO_2], compared to 18 and 14% at elevated [CO_2], respectively. Results of our water stress experiment demonstrated that maintenance of relatively high canopy photosynthetic rates in the face of decreased transpiration rates enhanced WUE in plants grown at elevated [CO_2]. This confirms experimental evidence and conceptual models that suggest that an increase of intercellular [CO_2] (or a sustained intercellular [CO_2]) in the face of decreased stomatal conductance results in relative increases of growth of C_4 plants. In short, drought stress in C_4 crop plants can be ameliorated at elevated [CO_2] as a result of lower stomatal conductance and sustaining intercellular [CO_2]. Furthermore, less water might be required for C_4 crops in future higher CO_2 atmospheres, assuming weather and climate similar to present conditions.

Introduction

The global atmospheric carbon dioxide concentration ([CO_2]), presently at about 385 μmol CO_2 mol^{-1} air, may surpass 700 μmol mol^{-1} before the end of this century (Solomon et al., 2007). A rise in atmospheric [CO_2] and other greenhouse-effect gases is expected to cause changes in global climate, including increases in air temperatures and shifts in regional scale rainfall patterns, which could result in decreased soil water availability in some areas of the world (Schneider, 2001; Long et al., 2004). The rise in atmospheric [CO_2], together with the potential global warming and changes in precipitation, will likely cause substantial economical and ecological impacts on agricultural systems.

The present atmospheric [CO_2] limits growth of C_3 crop plants, which show responses to elevated [CO_2] via reduced photorespiration and enhanced photosynthetic rates, thereby increasing their growth and yield. Research on plant responses to rising atmospheric [CO_2] and climate changes has primarily focused on C_3 species, advancing our understanding of processes underlying C_3 plant acclimation and responses to projected rises in atmospheric [CO_2] and variations in climate (Bowes, 1993; Long et al., 2004). In contrast, responses of C_4 plants to future elevated atmospheric

Abbreviations: DAS, days after sowing; DOY, day of year; NADP-ME, nicotinamide adenine dinucleotide phosphate-malic enzyme; PEP, phospho-enol pyruvate; PPFD, photosynthetic photon flux density; PS, canopy photosynthesis; RuBP, ribulose 1,5-bisphosphate; TR, evapotranspiration; WS, water stressed; WUE, water use efficiency; WW, well watered.

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doi:10.1016/j.jplph.2011.05.005

[CO_2] and interactions of elevated [CO_2] with unfavorable climate change factors are still uncertain (Leakey et al., 2006). Plants of the C_4 photosynthetic pathway have a CO_2-concentrating mechanism that overcomes limitations of low atmospheric [CO_2] and high photorespiration and possesses a near-saturating photosynthetic capability at current atmospheric [CO_2]. Henceforth, a rise in atmospheric [CO_2] will theoretically have a limited direct impact on C_4 photosynthesis. Nevertheless, a number of C_4 crop plants express a positive response to elevated growth [CO_2], although to a smaller extent compared to C_3 plants (Kimball, 1993; Poorter et al., 1996).

Although C_4 plants represent less than 4% of angiosperm species, their ecological and economic significance is important (Brown et al., 2005). On a global basis, up to one-third of terrestrial productivity is provided by C_4 plants. For many tropical countries, human food and livestock feed is primarily based on C_4 monocots, among which maize, sorghum, and millet are the most important (Brown, 1999). Understanding responses of such economically valuable C_4 crop plants to future rises in atmospheric [CO_2] and changes in the ecological environment is a challenging opportunity for global climate change impacts research.

The objective of the present study was to measure the interactive impacts of elevated [CO_2] and water-limiting conditions on canopy photosynthetic CO_2 uptake, canopy transpiration, and growth of maize and grain sorghum plants during early vegetative stages of growth. The primary hypothesis was that the effects of elevated [CO_2] would make substantial quantifiable improvements in photosynthetic CO_2 uptake responses and water use efficiency under water-limiting conditions. A secondary hypothesis was that differences exist in these two C_4 monocots, both being nicotinamide adenine dinucleotide phosphate-malic enzyme (NADP-ME) subtypes, in their photosynthesis, water use efficiency, and biomass accumulation response to elevated [CO_2] and drought.

Materials and methods

Plant material and growth conditions

Maize (*Zea mays* L. cv. Saturn Yellow) and grain sorghum (*Sorghum bicolor* L. cv. DeKalb 28E) seeds were sown on September 14, 2007 (day of year, DOY, 257), and plants were grown for 39 days (until October 23, DOY 296) in eight sunlit, controlled-environment growth chambers (Soil-Plant-Atmosphere-Research, or SPAR, units) located outdoors in Gainesville, Florida. These plant growth and canopy gas exchange measurement systems were based on the design of Jones et al. (1984). The chambers were 2 m × 1 m in cross section and 1.5 m high, with a 1 m high × 2 m wide × 0.4 m thick extension on the south-facing door with a trapdoor access that permitted a person to work in the chamber with minimal loss of air. The aluminum frame was covered with transparent polyethylene telephthalate "Sixlight" film (Taiyo Kogyo Co., Tokyo, Japan), which transmits about 88% of solar photosynthetic photon flux density (PPFD). All chambers received the same solar radiation throughout the course of the experiment. Each chamber was attached to a soil bin (2 m × 1 m in area and 0.60 m deep). Soil (Kendrick fine sand topsoil, a loamy, siliceous, hyperthermic Arenic Paleudult) filled the bins to 0.60 m. Because this experiment was conducted with potted plants to achieve water-stress quickly, white ground cloth was used to cover the leveled soil surface to provide a stable plane for plastic pots and a barrier to minimize soil evaporation. Twenty-five cm diameter plastic pots that were 22 cm deep, painted white to reduce solar heating, were filled with 4 kg Sta-Green planting mix and 100 g Osmocote (19–6–12 as N–P–K) were added. Eight seeds were sown at 2 cm depth in each pot. Eighteen pots were placed in each chamber, 72 pots in four chambers for maize and 72 pots in four chambers for grain sorghum. Plants were grown at daytime [CO_2] of 360 (ambient) or 720 (double-ambient) μmol mol^{-1}.

Irrigation was applied to pots early each morning via a timed, automated drip system. Excess water drained from holes in the pots through the ground cloth into the soil bin below. Volumetric soil water content (v/v, %) of each pot was measured every 2–3 days with a TH_2O soil moisture probe attached to a HH2 moisture meter (Delta-T Devices Ltd., Cambridge, UK). Measurements were made in five pots of each chamber every 2–3 days prior to initiating the water stress treatment and every 1–2 days after initiating the water stress treatment. Some plant roots were able to grow through the holes in the pots through the ground cloth into the soil below. Quantitative evapotranspirational water use was not based on pot soil water measurements, but on mass balance of condensate described in the following section. Nighttime [CO_2] buildup in each chamber was limited by venting for 13 min each hour. The chamber air temperatures were controlled by an algorithm that provided a sinusoidal wave mode during the daytime, and decay function during the nighttime (Pickering et al., 1994; Allen et al., 2003). All chambers were controlled to a daytime maximum/nighttime minimum air temperature regime of 30/20 °C from sowing to final plant harvest. Dewpoint temperatures followed a similar pattern with daytime maximum/nighttime minimum values of 18/12 °C.

Plants emerged at 5 days after sowing (DAS) for both crops. The plants were thinned on DAS 12 and again on DAS 19 to a final population of 35, 33.5, 34, and 33.5 plants m^{-2} for maize treatments of 360 μmol mol^{-1} well watered (WW), 360 μmol mol^{-1} water stressed (WS), 720 μmol mol^{-1} WW, and 720 μmol mol^{-1} WS, respectively, and 34, 34.5, 34, and 33.5 plants m^{-2} for grain sorghum treatments of 360 μmol mol^{-1} WW, 360 μmol mol^{-1} WS, 720 μmol mol^{-1} WW, and 720 μmol mol^{-1} WS, respectively. On October 10, 2007 (26 DAS) drought stress was begun by withholding drip irrigation in the pots for four chambers, one each of maize and grain sorghum plants exposed to either ambient or elevated [CO_2]. Pots in the control group (four chambers) continued to receive water.

Details of chamber environmental control systems for air temperature, dewpoint temperature, and daytime [CO_2] have been reported (Allen et al., 2003; Prasad et al., 2003). Incoming PPFD, μmol photon m^{-2} s^{-1}) was measured with a sensor (Model Li-190 quantum sensor, LI-COR Biosciences, Lincoln, NE, USA) on-site at a height of 5 m above ground.

Gas exchange measurements

Every 5 min, CO_2 flux density per unit land area in each SPAR chamber was computed from CO_2 mass balance. Likewise, water flux density was computed every 5 min from condensate that dripped from the cooling coil in each SPAR chamber air handler unit. Canopy net photosynthesis (PS) as net mol CO_2 uptake m^{-2} and evapotranspiration (TR) as Kmol H_2O condensate m^{-2} were summed from 08:00 to 17:00 h Eastern Standard Time (EST) each day from 11 to 39 DAS for each chamber using the system as reported previously (Baker et al., 1997). This 9-h period was selected to center around true solar time (mean of about 12:25 h EST for Gainesville) and to avoid early morning and late afternoon periods when PS values were small. The [CO_2] in each chamber was measured continuously with a dedicated infrared gas analyzer (Ultramat 22P, Siemens, Hagenau, France). Daytime [CO_2] in each chamber was maintained from a compressed CO_2 gas cylinder through 300 sccm (standard cm^3 min^{-1}) mass flow controllers (Model 5850i, Brooks Instrument, Hatfield, PA, USA) located at each chamber. The mass flow controller also functioned as a mass flow meter.