

Chapter 10

Effects of Elevated Carbon Dioxide and Drought Stress on Agricultural Crops

Jong Ahn Chun, Sanai Li, and Qingguo Wang

10.1 Introduction

The atmospheric CO₂ concentration has increased exponentially from about 280 ppm at the beginning of the industrial revolution to about 380 ppm today, and is expected to double preindustrial levels during this century (Keeling and Whorf 2001). The increase in atmospheric CO₂ concentrations may contribute to climate change including changes in precipitation patterns and evapotranspiration (Kruijt et al. 2008; Long et al. 2004; Schneider 2001). This climate change may increase in the risks of drought in many areas (Bates et al. 2008).

Seasonal variability in rainfall is one of the crucial factors contributing to variations of crop yields (Hu and Buyanovsky 2003). Approximately 40 % of the world land surface was covered by arid and semiarid areas, where drought stress is a main limiting factor for the conventional rain-fed agriculture (Gamo 1999). In some areas of the world, water supply is already a limiting factor for agricultural production (Penning de Vries et al. 1995). Climate change and variability will impose significant impacts on agricultural productivity by altering precipitation pattern, rising temperature, and carbon dioxide.

Climate change would influence the hydrological cycle and water resource availability, suggesting that it has an impact on crop productivity (Evans 1996). Climate change can accelerate the hydrological cycle through altering rainfall, evapotranspiration, and the intensity and frequency of extreme climate events such as floods and droughts (Watson et al. 1996). Under future climate, the potential and actual evapotranspiration possibly increase by the rising temperature (Riedo et al. 2001). The agricultural production is likely to be greatly impacted by a decrease in soil moisture and an increase in the possible extreme events such as droughts and floods

J.A. Chun (✉) • S. Li • Q. Wang

Climate Change Research Team, Department of Climate Research, APEC Climate Center,
12 Centum 7-ro, Haeundae-gu, Busan 48058, Republic of Korea
e-mail: jachun@apcc21.org

caused by combined effects of rising CO₂ concentrations and temperatures (Chiotti and Johnston 1995). It is therefore important to know how drought and elevated CO₂ will affect crop growth, development, water use, and productivity.

There is continued interest in how agricultural crops will respond to future CO₂, since CO₂ is an essential substrate for photosynthesis and limits the rate of photosynthesis in many crops at current conditions. Generally, plants sense and respond to elevated CO₂ through increased photosynthesis and reduced stomatal conductance. All other effects are derived from these two fundamental responses (Long et al. 2004). Elevated CO₂ stimulates photosynthesis and reduces the opening of plant stomata, contributing to a decrease in plant transpiration. As a result, plants growing in elevated CO₂ conditions will improve water use efficiency (WUE, the ratio of rate of carbon assimilation to the rate of transpiration).

There are two main plants categorized into C₃, C₄, or C₃–C₄ intermediate plants according to the spatial distribution of pathways of CO₂ fixation within leaf tissues, and as crassulacean acid metabolism (CAM) plants with a temporal distribution (Freschi and Mercier 2012). C₃ plants represent over 95 % of the Earth plant species, mainly growing in cool and wet climate areas. C₄ and CAM plants occur in hot and dry climatic conditions. Elevated CO₂ concentrations will, in general, lead to increased photosynthesis and decreased transpiration in C₃ plants. Agricultural crops with a C₃ photosynthetic pathway often exhibit greater assimilation responses than those with a C₄ pathway due to differences in CO₂ use during photosynthetic procedures (Amthor 1995; Rogers et al. 1997).

It is widely known that drought is the single most critical threat to world food security. Because the world's water supply is limiting, future food demand for rapidly increasing population pressures is likely to further aggravate the effects of drought (Somerville and Briscoe 2001). Under water stress conditions, photosynthesis decreases through direct effects, as the decreased CO₂ availability caused by diffusion limitations through the stomata and the mesophyll (Flexas et al. 2004, 2007; Warren 2008) or the alterations of photosynthetic metabolism (Lawlor and Cornic 2002). These water stress conditions can arise as secondary effects, namely oxidative stress, and feedback regulation by end-product accumulation (Nikinmaa et al. 2013).

The purpose of this review is to provide: (1) an overview of physiological processes including photosynthesis and transpiration of agricultural crops under elevated CO₂ and drought stress and (2) summary of recent research on those crop responses to elevated CO₂ and drought stress based on field experiments and crop modeling studies.

10.2 Physiological Processes Under Elevated CO₂ and Drought Stress

10.2.1 Photosynthesis

Two key processes occur in photosynthesis: light-dependent reactions and light-independent (or dark) reactions. In the former reactions, light energy is converted into adenosine triphosphate (ATP) and nicotinamide adenine dinucleotide phosphate

hydrogen (NADPH), and O_2 is released. In the latter reactions, the enzyme Ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO) captures atmospheric CO_2 and releases three-carbon sugars by utilizing ATP and NADPH.

CO_2 and soil water considerably influence the process of photosynthesis in most plants by altering stomatal regulation, the ultrastructure of the organelles, concentration of various pigments and metabolites. A great number of research found that the plant photosynthetic rates were greatly enhanced under elevated CO_2 in the short-term (Radmer and Kok 1977; Witter 1979), and these increases were likely to be more moderate due to various feedback responses and constraints in the long-term (Kramer 1981). There was a significant and marked increase in photosynthesis of C_3 plants (Norby et al. 1999; Ainsworth and Long 2005), but there were significant differences between species and cultivars. In C_3 plants, the maximum carboxylation rate and the maximum rate of electron transport were also significantly reduced at elevated CO_2 . There was a significant increase in photosynthesis of C_4 crops, as an indirect effect resulting through the mitigation of drought stress due to reduced stomatal conductance (Ghannoum et al. 2000). Increases in photosynthesis in sorghum and maize were associated with improved water status or were limited to periods of low rainfall where drought stress was likely ameliorated at elevated CO_2 (Leakey et al. 2004; Kimball 2006).

Photosynthetic responses to water stress are highly complex. These effects vary according to the intensity and duration of progression of the water stress as well as with the leaf age and the plant species and at different time scales in relation to plant development (Lawlor and Cornic 2002; Flexas et al. 2004). Both stomatal and non-stomatal limitations to photosynthesis are important. Photosynthesis acclimation under drought indirectly affects photosynthesis. This acclimation will help to maintain plant water status and therefore photosynthesis. Osmotic compounds that build up in response to water stress will lead to restoration of cellular homeostasis and detoxification.

10.2.2 Stomatal Conductance

The regulation of leaf stomatal conductance is a key phenomenon in plants for photosynthesis and transpiration (Medici et al. 2007). One of the most consistent responses of plants to elevated CO_2 is a reduction in stomatal conductance (Ainsworth and Long 2005). However, the responses are significantly different among species and cultivars. As an exception, Ellsworth (1999) reported that *Pinus taeda* guard cells appear to be insensitive to elevated CO_2 . The decrease in stomatal conductance may be largely determined by stomatal aperture rather than density. Ainsworth and Rogers (2007) found that a decrease in the density is statistically insignificant through a meta-analysis of stomatal density responses to elevated CO_2 .

Guard cells sense intercellular CO_2 rather than at the leaf surface. Stomatal conductance responses to elevated CO_2 may vary according to the duration of plants grown in elevated CO_2 . In the short term, stomatal aperture generally decreases in response to high CO_2 . In the long-term, stomatal conduction may acclimate to ele-

vated CO₂. Ball et al. (1987) reported that stomatal conductance would decrease in response to elevated CO₂. Medlyn et al. (2001) found that stomatal conductance only in water-stressed *Phillyrea angustifolia* was acclimated to elevated CO₂ in six tree species. However, there is little evidence that stomatal conductance independently acclimates to elevated CO₂ for *Lolium perenne* grown at 600 μmol mol⁻¹ (Leakey et al. 2006a, b).

The magnitude of the effect of elevated CO₂ on stomatal conductance varies considerably with environmental factors (Medlyn et al. 2001; Leakey et al. 2006a, b). There is generally a smaller effect of elevated CO₂ on stomatal conductance under water stress (Leakey et al. 2006a, b). For example, there was no significant change in stomatal conductance at elevated CO₂ in *Liquidambar styraciflua* when vapor pressure deficit was high (Herrick et al. 2004). For long-term water stress, stomatal conductance will be much less reduced in elevated CO₂ compared to ambient conditions (Leakey et al. 2006a, b). A small decline in stomatal conductance may have protective effects against water stress, by less transpiration rate and improving plant water use efficiency.

Under water-stress conditions, the first response of plants is the stomatal closure to prevent the water loss due to transpiration to maintain the photosynthesis at low water availability (Pan et al. 2011). The stomata closure under water stress generally occurs due to decreased leaf turgor or water potential and low humidity atmosphere along with root-generated chemical signals (Chaves et al. 2009). The stomata closure is caused mainly by the action of a plant hormone, abscisic acid (ABA). High ABA level can cause an increase in cytosolic Ca²⁺ and activation of plasma membrane-localized anion channels (Kohler and Blatt 2002). This causes potassium efflux, guard cell depolarization, loss of guard cell volume and turgor, high water production, and finally the stomata closure (Wang et al. 2012).

10.2.3 Rubisco Activity and Content

Rubisco is usually fully active and carbamylated at current CO₂ under steady-state high light conditions (von Caemmerer and Quick 2000). Under elevated CO₂ conditions, photosynthesis increases; there is an increasing demand for ATP and control of photosynthesis shifts from being limited by Rubisco to being limited by the capacity for ribulose-1,5-bisphosphate (RuBP) regeneration (Farquhar et al. 1980; von Caemmerer and Quick 2000). Reductions in the ATP:ADP ratio lead to a reduction in activase activity. The reductions in Rubisco activation state have been reported under elevated CO₂ (Cen and Sage 2005).

One of the most prominent effects of water stress is the stomata closure, which leads to a lower concentration of intercellular CO₂, which in turn causes deactivation of Rubisco (Mumm et al. 2011). Medrano et al. (1997) observed that water deficit conditions reduced the initial and total Rubisco activity, but it did not decrease the overall amount of Rubisco per unit of leaf area in subterranean clover (*Trifolium subterraneum*). Marques and Arrabica (1995) reported that Rubisco activity in *Setaria sphacelota* declined slightly under moderate water stress, but substantially

under severe water stress. Using transgenic tobacco plants, Gunasekera and Berkowitz (1993) showed that a 68 % decrease in Rubisco activity did not hamper photosynthesis under water-limited regimes. They concluded that drought stress may affect any of the steps involved in the regeneration of RuBP rather than Rubisco itself.

10.3 Effects of Elevated CO₂ and Drought Stress on Crops

It is widely known that elevated CO₂ concentrations contribute to the increases of crop photosynthetic exchange rates (CER) and yield by decreasing photorespiration. This response of C₃ plants to elevated atmospheric CO₂ is higher than that of C₄ plants (Sage and Monson 1999). Increases in the growth of C₃ plants under doubled atmospheric CO₂ concentrations are approximately 40–45 %, while the growth of C₄ plants under doubled atmospheric CO₂ concentrations increases by 10–20 % (Ghannoum et al. 2000).

The water relations for most plants exhibit improved under-elevated CO₂, and showed less transpiration by inducing the partial stomatal closure. Studies have shown that elevated CO₂ reduces transpiration for both C₃ (Allen et al. 1994; Prior et al. 1991) and C₄ (Chaudhuri et al. 1986) plants. Using stem flow gauges under elevated CO₂, Dugas et al. (1997) reported the reduction in whole-plant transpiration for both soybean (C₃) and sorghum (C₄) crops.

The reduction in transpiration under elevated CO₂, coupled with increased photosynthesis, can contribute to increase in WUE (Baker et al. 1990; Sionit et al. 1984). Kimball and Idso (1983) analyzed 46 observations for transpiration and over 500 observations for economic yield, and suggested a doubling of WUE for a doubling of CO₂ concentrations. Under elevated CO₂, C₄ plants show a smaller response to elevated CO₂ than C₃ plants. However, both C₃ and C₄ plants show reduced transpiration. These results indicate that WUE should be primarily controlled by transpiration in C₄ plants, whereas both photosynthesis and transpiration are important in C₃ plants (Acock and Allen 1985).

Obviously, water-stressed plants have lower relative water content than non-stressed ones. For example, exposure of wheat and rice plants to drought stress substantially decreased the leaf water potential and transpiration rate (Siddique et al. 2001). Nerd and Nobel (1991) suggested that during drought stress, total water contents of *Opuntia ficusindica* cladode were decreased by 57 %. In another study on *Hibiscus rosasinensis*, transpiration, stomatal conductance, and WUE were declined under drought stress (Egilla et al. 2005). Abbate et al. (2004) reported that under limited water supply, WUE of wheat was greater than in well-watered conditions due to stomatal closure to reduce the transpiration under water stress conditions. Lazaridou and Koutroubas (2004) concluded that WUE of clover (*Trifolium alexandrinum*) was increased due to decreased transpiration rates and leaf area. In studies on *Artemisia tridentata* (DeLucia and Heckathorn 1989) and *Medicago sativa* (Lazaridou et al. 2003), drought stress increased WUE mainly due to a decrease in stomatal conductance with increasing water deficit.

Given the fact that elevated CO₂ can reduce transpiration, it has been suggested that this might partially ameliorate the effects of drought (Bazzaz 1990) and allow plants to maintain increased photosynthesis. This has frequently been observed (Acock and Allen 1985; Sionit et al. 1981; Prior et al. 1991). It has been suggested that under elevated CO₂ whole-plant water use may be differentially affected as a result of leaf area index (LAI) or plant size, although instantaneous WUE is increased. Allen (1994) reported that higher LAI could counter balance the reduction in water use. Jones et al. (1985) showed that increase in WUE was greater for plants with a lower LAI than higher LAI.

Elevated CO₂ intends to increase photosynthesis through raising the CO₂ gradient between the atmosphere and the inside of leaves, and consequently improve its conversion into carbohydrates (Rosenzweig and Hillel 1998). The impacts of elevated CO₂ on crop yield may vary among different experimental studies due to differences in experimental methods and its corresponding environmental conditions. The free-air CO₂ enrichment (FACE) showed that crop yield of C₃ plants such as rice, wheat, cotton, and sorghum increased by about 17–20 % at 550 ppm (Long et al. 2004; Ainsworth and Long 2005). On the other hand, the glasshouse and growth chamber experiments showed an 18–23 % increase in crop yield (Amthor 2001; Tubiello et al. 2007), and the response of crops to elevated CO₂ is slightly higher than the FACE results. Under elevated CO₂, increases in the number of grains per plant and the harvest index lead to an increase in crop yield (Wu et al. 2004). However, the CO₂ fertilization effect may be limited by some severe environmental stress, such as temperature, rooting volume, light, nutrient, and drought (Batts et al. 1997; Arp 1991; Kramer 1981).

The impacts of drought on crop depend on the magnitude of water stress and the developmental stages (Sau and Mínguez 2000). The negative impacts of drought are more severe during some moisture-sensitive phenological stages (Nesmith and Ritchie 1992). In the early growth stages, extreme water stress can postpone sowing of crop and affect seed germination (Hu and Buyanovsky 2003). From emergence to double ridge stages, drought stress can significantly affect the leaf expansion of crops (Acevedo et al. 1971). The leaf expansion rate of wheat is expected to be greatly reduced when the extractable soil water is smaller than 50 % (Meyer and Green 1980, 1981). During the pre-anthesis stage, the number of kernels per spike of wheat can be greatly reduced by drought stress (Fischer 1980). This result can be explained by considering that the number of kernels per spike largely contributed to grain yield particularly under drought conditions (García del Moral et al. 2003). Shpiler and Blum (1991) found that the grain yield of wheat showed the most sensitivity to moisture deficit during double ridge to anthesis stages due to the substantial effect of water deficit on both spikelet number and kernels per spike. However, van Herwaarden et al. (1998) reported that the grain yield of wheat was mostly impacted by the moisture deficit after anthesis. The different conclusions may be resulted from the differences in crop varieties, field management, and climatic conditions. In addition, crop development can also be accelerated by soil moisture deficit during anthesis (Simane et al. 1993). During the grain filling period, grain weight can be greatly decreased by drought stress mainly through accelerating senescence

rates and shortening growth duration (Hochman 1982). These results suggest that efficacious adaptation strategies can be provided by focusing on the most moisture-sensitive stages.

10.4 Interactive Effects of Elevated CO₂ and Drought Stress on Crops

The interaction of elevated CO₂ and water on crop growth has been studied. The water use of C₄ crops under elevated CO₂ decreases by reducing stomatal conductance without an increase in photosynthesis (Morison 1993; Leakey et al. 2006a, b; Long et al. 2006). Loomis and Lafitte (1987) reported that large changes in the supplies of CO₂ and water little affected corn growth. An increase in WUE was found regardless of water supply (Surano and Shinn 1984). Prior et al. (2010) reported that elevated CO₂ significantly increases WUE, suggesting better soil moisture conservation at elevated CO₂.

In an outdoor growth chamber study conducted by Chun et al. (2011), some points (denoted as “breaking points”) from high to low rates of soil water uptake were observed in the bottom depth (between 0.625 and 0.85 m from the surface), indicating a decrease in water availability. The breaking points were earlier under ambient CO₂ than under elevated CO₂, suggesting that the depletion of the easily available water occurred later under elevated CO₂ than under ambient CO₂.

The effects of elevated atmospheric CO₂ concentrations on plants under drought are complex. Plants reduce transpiration by closing stomata, but this substantially reduces photosynthetic rates. However, elevated CO₂ enhances photosynthetic rates in C₃ plants. If the photosynthesis-stimulating effect of elevated CO₂ is greater than the reduction in photosynthesis from drought-induced stomatal closure, the overall effects of CO₂ and water stress will be positive. Otherwise, the overall effects will be negative. Morgan et al. (2004) observed that the relative photosynthetic benefits of elevated CO₂ are generally greater in more arid environments in large-scale studies. Numerous studies have shown that increasing CO₂ may benefit photosynthesis and survival during droughts of moderate duration, while the negative effects may overwhelm the benefits of elevated CO₂ where droughts become more severe. Elevated CO₂ caused a smaller reduction in evapotranspiration under water stress and different species have different responses to elevated CO₂ under water stress conditions. Reddy et al. (2000) found that there was no reduction in evapotranspiration for cotton; however, Hunsaker et al. (2000) reported 4 % reduction in evapotranspiration for wheat.

Elevated CO₂ can alleviate drought stress and improve crop yields by improvement of water use efficiency under higher CO₂ concentrations (Allen et al. 1998; Makino and Mae 1999; Maroco et al. 1999). In the Free-air CO₂ enrichment (FACE), there is a 7 % increase in water use efficiency at 550 ppm of CO₂ concentrations Hunsaker et al. (1996). Similarly, Allen (1991) found that there is a 10 % reduction in crop canopy water use under doubled CO₂. In contrast, Yoshimoto et al. (2005)

reported that in a FACE experiment, there is a 19 % increase in WUE of rice at 587 ppm of CO₂ concentrations. The response of crop water use to elevated CO₂ depends on crop species and environmental conditions. For example, a doubled CO₂ can lead to a decrease in evapotranspiration (ET) of rice at 26 °C, while it increased in ET at 29.5 °C (Horie et al. 2000).

Drought stress has a great impact on the magnitude of CO₂ fertilization effect of a crop. Some experimental results found that there were higher increases in growth and yield of wheat in response to elevated CO₂ under drought stress conditions than under high soil moisture (Gifford 1979; Chaudhuri et al. 1990; Samarakoon et al. 1995). However, other research on wheat showed that there were greater CO₂ fertilization effects under optimal soil water conditions than in water deficit conditions (Kramer 1981; Kimball 1983; Poorter 1998; Wu and Wang 2000). Similarly, Smith et al. (2000) found that in dry year CO₂, fertilization effect has no beneficial impacts on desert shrub growth under severe water deficit conditions (Acevedo et al. 1991). These results imply that sufficient soil moisture is an important factor in maintaining stomata opening and improving CO₂ conductance (Loomis and Amthor 1996).

10.5 Applications of Crop Models

There have been many studies on investigation of the impact of water on crops using various crop models. For example, Yang et al. (2009) modified the leaf area module of a soil–plant–atmosphere continuum corn simulation model (MaizeSim) to better simulate leaf area of corn crops at different water status and reported that the modified model improved the simulation of leaf area. Katerji et al. (2013) investigated the impacts of water stress on productivity, evapotranspiration, and water use efficiency of corn and tomato crops using the FAO AquaCrop model (a crop water productivity model). They concluded that the model can be a useful tool for research purposes to enhance the water use efficiency and to manage irrigation practices.

Crop models have been widely used to simulate the response of crops to elevated CO₂. Tubiello et al. (2007) compared the simulated response of crop yield to elevated CO₂ from the DSSAT-CERES which is widely used for cereal grains, Environmental Policy Integrated Climate (EPIC), and Agro-Ecological Zones (AEZ) models. The results showed that at 550 ppm of CO₂ concentrations, the yields of C₃ crops increased by 10–19 %, while yields of C₄ crops only increased by 4–8 %. The magnitude of CO₂ fertilization effect is close to the reported value by Long et al. (2006) for FACE experiments. However, the results simulated from CERES (Boote and Pickering 1994) and EPIC/Cropping Systems Simulation Model (CropSyst) (Tubiello et al. 2000) showed a 25 % increase in C₃ crop yield for a doubling of CO₂. The effects of climate change with combined CO₂ fertilization on potential crop yield (e.g., Tubiello and Ewert 2002) and water use (Asseng et al. 2004) have been investigated using crop models. However, the long-term and large-scale CO₂ fertilization effect still remains uncertain. The uncertainties in land use change scenarios under future climate conditions may contribute to this uncertainty (Levy et al. 2004).

The interactions of water and CO₂ not only affect the crop growth and yield, but also crop development. The results from FACE experiments showed that the crop developmental rate can be accelerated by the water and CO₂ interactions; however, many crop models may not be able to accurately capture these interactions due to the ignorance of CO₂-related canopy temperature (Ewert et al. 2002; Tubiello et al. 1999). The effects of water and CO₂ interactions on canopy temperature were included in the DEMETER crop model, and Kartschall et al. (1995) reported that the simulated values of phenology, growth, and yields are in good agreement with the observed values.

Under dryland conditions, grain yield was highly related with evapotranspiration (Sadras and Angus 2006). The different effects of drought stress on crops were reported at each phenological period (Andresen et al. 1989). From emergence to anthesis, leaf area expansion can be greatly affected by water deficit (Acevedo et al. 2002). Eitzinger et al. (2003) found that during the grain filling stage, crop yield was most sensitive to drought stress, whereas Chipanshi et al. (1999) showed the flowering and heading periods were most sensitive stages to drought stress. The difference in environmental conditions and parameterization of drought stress for crop modeling may contribute to this discrepancy.

Even though lots of crop models have been developed and evaluated as discussed in this section, the models still need to be improved to adequately address phenology with respect to water stress. A stomatal control and transpiration models were incorporated into the photosynthesis model initially proposed by Farquhar et al. (1980) to address stomatal limitations to CO₂ assimilation (Ball et al. 1987). This approach is generally considered as one of the most popular approaches for coupled models of stomatal control and photosynthesis. However, there are still controversies on the use of crop models that resulted from complexity, testability, and parameterization (Timlin et al. 2008). It is suggested that more robust and realistic parameters should be provided to address these controversies.

10.6 Summary and Conclusions

Increasing CO₂ may change precipitation patterns and evapotranspiration, implying increases in the risks of drought in many areas. The impacts of elevated CO₂ and drought stress on growth and development of crops were discussed in the previous sections. The different responses of CO₂ have been reported according to the spatial distribution of pathways of CO₂ fixation within leaf tissues. The response of C₄ plants to elevated atmospheric CO₂ is lower than that of C₃ plants. Elevated CO₂ reduces transpiration for both C₃ and C₄ plants. These results indicate that WUE should be primarily controlled by transpiration in C₄ plants, while both photosynthesis and transpiration are important in C₃ plants. Numerous literatures suggest that crops will use less water under high atmospheric CO₂ in the future than at present.

The use of crop models has been used for assessment of the impacts of elevated CO₂ and drought stress on crop growth and development. However, many crop

models still need to be improved to adequately address phenology with respect to water stress. In addition, there are still controversies on the use of crop models that resulted from complexity, testability, and parameterization, suggesting that more robust and realistic parameters should be provided to address these controversies. It is concluded that crop models can be a useful tool to quantify the impacts of elevated CO₂ and drought stress and to assess agricultural management practices. This review can provide a better understanding of the interactive effects of elevated CO₂ and drought stress on crop growth and development.

References

- Abbate PE, Dardanellib JL, Cantarero MG, Maturano M, Melchiorid RJM, Sueroa EE. Climatic and water availability effects on water-use efficiency in wheat. *Crop Sci.* 2004;44:474–83.
- Acevedo E, Hsiao TC, Henderson DW. Immediate and subsequent growth responses of maize leaves to changes in water status. *Plant Physiol.* 1971;48:631–6.
- Acevedo E, Harris H, Cooper PJM. Crop architecture and water use efficiency in Mediterranean environments. In: Harris H, Cooper PJM, Pala M, editors. *Soil and crop management for improved water use efficiency in rainfed areas*. Ankara: ICARDA; 1991. p. 106–18.
- Acevedo E, Silva P, Silva H. Wheat growth and physiology. In: Curtis BC, Rajaram S, Gómez Macpherson H, editors. *Bread wheat improvement and production*. Rome: FAO plant production and protection series; 2002. p. 567.
- Acock B, Allen Jr LH. Crop responses to elevated carbon dioxide concentrations. In: Strain BR, Cure JD, editors. *Direct effects of increasing carbon dioxide on vegetation*. Washington, DC: DOE/ER-0238, Office of Energy Research, U.S. Dept. of Energy; 1985. p. 317–46.
- Ainsworth EA, Long SP. What have we learned from 15 years of free-air CO₂ enrichment (FACE)? A meta-analysis of the responses of photosynthesis, canopy properties and plant production to rising CO₂. *New Phytol.* 2005;165:351–72.
- Ainsworth EA, Rogers A. The response of photosynthesis and stomatal conductance to rising CO₂: mechanisms and environmental interactions. *Plant Cell Environ.* 2007;30:258–70.
- Allen Jr LH. Effects of increasing carbon dioxide levels and climate change on plant growth, evapotranspiration, and water resources. *Proceedings of a colloquium on managing water resources in the west under conditions of climatic uncertainty*. Washington, DC: National Research Council, National Academy Press; 1991. p. 101–47.
- Allen LH. Carbon dioxide increase: direct impact on crops and indirect effects mediated through anticipated climatic changes. In: Boote KJ, Sinclair TR, Bennett JM, editors. *Physiology and determination of crop yield*. Madison, WI: ASA, CSSA, SSSA; 1994. p. 425–59.
- Allen Jr LH, Valle RR, Mishoe JW, Jones JW. Soybean leaf gas-exchange responses to carbon dioxide and water stress. *Agron J.* 1994;86:625–36.
- Allen Jr LH, Valle RR, Jones JW, Jones PH. Soybean leaf water potential responses to carbon dioxide and drought. *Agron J.* 1998;90:375–83.
- Amthor JS. Terrestrial higher-plant response to increasing atmospheric CO₂ in relation to the global carbon cycle. *Glob Chang Biol.* 1995;1:243–74.
- Amthor JS. Effects of atmospheric CO₂ concentration on wheat yield: review of results from experiments using various approaches to control CO₂ concentration. *Field Crop Res.* 2001;73:1–34.
- Andresen JA, Dale RF, Fletcher JJ, Preckel PV. Prediction of county-level corn yields using an energy-crop growth index. *J Climate.* 1989;2:48–56.
- Arp WJ. Effects of source-sink relations on photosynthetic acclimation to elevated CO₂. *Plant Cell Environ.* 1991;14:869–75.

- Asseng S, Jamieson PD, Kimball BA, Pinter Jr PJ, Sayred K, Bowden JW, Howden SM. Simulated wheat growth affected by rising temperature, increased water deficit and elevated atmospheric CO₂. *Field Crop Res.* 2004;85:85–102.
- Baker JY, Allen Jr LH, Boote KJ. Growth and yield responses of rice to carbon dioxide concentration. *J Agric Sci.* 1990;115:313–20.
- Ball JT, Woodrow IE, Berry JA. A model predicting stomatal conductance and its contribution to the control of photosynthesis under different environmental conditions. In: Biggens J, editor. *Progress in photosynthesis research.* Dordrecht: Martinus-Nijhoff; 1987. p. 221–4.
- Bates BC, Kundzewicz ZW, Wu S, Palutikof JP, editors. *Climate change and water.* Technical paper of the intergovernmental panel on climate change. Geneva: IPCC Secretariat; 2008.
- Batts GR, Morison JIL, Ellis RH, Hadley P, Wheeler TR. Effects of CO₂ and temperature on growth and yield of crops of winter wheat over several seasons. *Eur J Agron.* 1997;7:43–52.
- Bazzaz FA. The response of natural ecosystems to the rising global CO₂ levels. *Annu Rev Ecol Syst.* 1990;21:167–96.
- Boote KJ, Pickering NB. Modeling photosynthesis of row crop canopies. *Hort. Science* 1994;29:1423–1434.
- Cen Y-P, Sage RF. The regulation of rubisco activity in response to variation in temperature and atmospheric CO₂ partial pressure in sweet potato. *Plant Physiol.* 2005;139:979–90.
- Chaudhuri UN, Burnett RB, Kirkham MB, Kanemasu ET. Effect of carbon dioxide on sorghum yield, root growth, and water use. *Agr For Meteorol.* 1986;37:109–22.
- Chaudhuri UN, Kirkham MB, Kanemasu ET. Carbon dioxide and wheat level effects on yield and water use of winter wheat. *Agron J.* 1990;82:637–41.
- Chaves MM, Flexas J, Pinheiro C. Photosynthesis under drought and salt stress: regulation mechanisms from whole plant to cell. *Ann Bot.* 2009;103:551–60.
- Chiotti QP, Johnston T. Extending the boundaries of climate change research: a discussion on agriculture. *J Rural Stud.* 1995;11:335–50.
- Chipanshi AC, Ripley EA, Lawford RG. Large-scale simulation of wheat yield in semi-arid environments using a crop-growth model. *Agric Syst.* 1999;59:57–66.
- Chun JA, Wang Q, Timlin D, Fleisher D, Reddy VR. Effect of elevated carbon dioxide and water stress on Gas exchange and water Use efficiency in corn. *Agric For Meteorol.* 2011;151:378–84.
- DeLucia EH, Heckathorn SA. The effect of soil drought on water-use efficiency in a contrasting Great Basin desert and Sierran montane species. *Plant Cell Environ.* 1989;12:935–40.
- Dugas WA, Prior SA, Rogers HH. Transpiration from sorghum and soybean growing under ambient and elevated CO₂ conditions. *Agric For Meteorol.* 1997;83:37–48.
- Egilla JN, Davies Jr FT, Boutton TW. Drought stress influences leaf water content, photosynthesis, and water-use efficiency of *Hibiscus rosa-sinensis* at three potassium concentrations. *Photosynthetica.* 2005;43:135–40.
- Eitzinger J, Štastná M, Žalud Z, Dubrovský M. A simulation study of the effect of soil water balance and water stress on winter wheat production under different climate change scenarios. *Agric Water Manage.* 2003;61:195–217.
- Ellsworth DS. CO₂ enrichment in a maturing pine forest: are CO₂ exchange and water status in the canopy affected? *Plant Cell Environ.* 1999;22:461–72.
- Evans TE. The effects of changes in the world hydrological cycle on availability of water resources. In: Bazzaz F, Sombroek W, editors. *Global climate change and agricultural production.* Chichester: Wiley; 1996. p. 248.
- Ewert F, Rodríguez D, Jamieson P, Semenov MA, Mitchell RAC, Goudriaan J, Porter JR, Kimball BA, Pinter Jr PJ, Manderscheid R, Weigel HJ, Fangmeier A, Fereres E, Villalobos F. Effects of elevated CO₂ and drought on wheat: testing crop simulation models for different experimental and climatic conditions. *Agric Ecosyst Environ.* 2002;93:249–66.
- Farquhar GD, von Caemmerer S, Berry JA. A biochemical model of photosynthetic CO₂ assimilation in leaves of C3 species. *Planta.* 1980;149:78–90.
- Fischer RA. Influence of water stress on crop yield in semi arid regions. In: Turner NC, Kramer P, editors. *Adaptation of plants to water and high temperature stress.* New York: Wiley; 1980. p. 323–40.

- Flexas J, Bota J, Loreto F, Cornic G, Sharkey TD. Diffusive and metabolic limitations to photosynthesis under drought and salinity in C3 plants. *Plant Biol.* 2004;6:269–79.
- Flexas J, Diaz-Espejo A, Galmés J, Kaldenhoff R, Medrano H, Ribas-Carbo M. Rapid variations of mesophyll conductance in response to changes in CO₂ concentration around leaves. *Plant Cell Environ.* 2007;30:1284–98.
- Freschi L, Mercier H. Connecting environmental stimuli and crassulacean acid metabolism expression: phytohormones and other signaling molecules. *Prog Bot.* 2012;73:231–55.
- Gamo M. Classification of arid regions by climate and vegetation. *J Arid Land Stud.* 1999;1:9–17.
- García del Moral LF, Rharrabti Y, Villegas D, Royo C. Evaluation of grain yield and its components in durum wheat under Mediterranean conditions: an ontogenic approach. *Agron J.* 2003;95:266–74.
- Ghannoum O, von Caemmerer S, Ziska LH, Conroy JP. The growth response of C4 plants to rising atmospheric CO₂ partial pressure: a reassessment. *Plant Cell Environ.* 2000;23:931–42.
- Gifford RM. Growth and yield of CO₂ enriched wheat under water-limited conditions. *Aust J Plant Physiol.* 1979;6:367–78.
- Gunasekera D, Berkowitz GA. Use of transgenic plants with ribulose-1,5-bisphosphate carboxylase/oxygenase antisense DNA to evaluate the rate limitation of photosynthesis under water stress. *Plant Physiol.* 1993;103:629–35.
- Herrick JD, Maherali H, Thomas RB. Reduced stomatal conductance in sweetgum (*Liquidambar styraciflua*) sustained over long-term CO₂ enrichment. *New Phytol.* 2004;162:387–96.
- Hochman ZVI. Effect of water stress with phasic development on yield of wheat grown in a semi-arid environment. *Field Crop Res.* 1982;5:55–67.
- Horie T, Baker JT, Nakagawa H, Matsui T, Kim HY. Crop ecosystem responses to climatic change: rice. In: Reddy KR, Hodges HF, editors. *Climate change and global crop productivity*. New York: CAB International; 2000. p. 81–106.
- Hu Q, Buyanovsky G. Climate effects on corn yield in Missouri. *J Appl Meteorol.* 2003;42:1626–35.
- Hunsaker DJ, Kimball BA, Pinter Jr PJ, LaMorte RL, Wall GW. Effects of CO₂ enrichment and irrigation on soil water balance evapotranspiration of wheat grown under open-air field conditions. *Trans ASAE.* 1996;4:1345–55.
- Hunsaker DJ, Kimball BA, Pinter PJ, Wall GW, LaMorte RL, Adamsen FJ, Leavitt SW, Thompson TL, Matthias AD, Brooks TJ. CO₂ enrichment and soil nitrogen effects on wheat evapotranspiration and water use efficiency. *Agric For Meteorol.* 2000;104:85–105.
- Jones P, Allen Jr LH, Jones JW, Valle R. Photosynthesis and transpiration responses of soybean canopies to short- and long-term CO₂ treatments. *Agron J.* 1985;77:119–26.
- Kartschall T, Grossman S, Pinter Jr PJ, Garcia RL, Kimball BA, Wall GW, Hunsaker DJ, LaMorte RL. A simulation of phenology, growth, carbon dioxide exchange and yields under ambient atmosphere and free-air carbon dioxide enrichment (FACE) Maricopa, Arizona, for wheat. *J Biogeogr.* 1995;22:2467–77.
- Katerji N, Campi P, Mastrorilli M. Productivity, evapotranspiration, and water use efficiency of corn and tomato crops simulated by AquaCrop under contrasting water stress conditions in the Mediterranean region. *Agric Water Manage.* 2013;130:14–26.
- Keeling CD, Whorf TP. Trends: A compendium of data on global change, Atmospheric CO₂ records from sites in the SIO air sampling network. Oak Ridge, TN: Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, U.S. Dept. Energy; 2001. p. 14–21.
- Kimball BA. Carbon dioxide and agricultural yield: an assemblage and analysis of 430 prior observations. *Agron J.* 1983;75:779–88.
- Kimball BA. The effects of free-air CO₂ enrichment of cotton, wheat and sorghum. In: Nösberger J, Long SP, Norby RJ, Stitt M, Hendrey GR, Blum H, editors. *Managed ecosystems and CO₂, Case studies, processes and perspectives*. Heidelberg: Springer; 2006. p. 47–70.

- Kimball BA, Idso SB. Increasing atmospheric CO₂: effects on crop yield, water use, and climate. *Agric Water Manage.* 1983;7:55–72.
- Kohler B, Blatt MR. Protein phosphorylation activates the guard cell Ca²⁺ channel and is a prerequisite for gating by abscisic acid. *Plant J.* 2002;32:185–94.
- Kramer PJ. Carbon dioxide concentration, photosynthesis and dry matter production. *BioScience.* 1981;31:29–33.
- Kruijt B, Witte J-PM, Jacos CMJ, Kroon T. Effects of rising atmospheric CO₂ on evapotranspiration and soil moisture: a practical approach for the Netherlands. *J Hydrol.* 2008;349:257–67.
- Lawlor DW, Cornic G. Photosynthetic carbon assimilation and associated metabolism in relation to water deficits in higher plants. *Plant Cell Environ.* 2002;25:275–94.
- Lazaridou M, Kirilov A, Noitsakis B, Todorov N, Katerov I. The effect of water deficit on yield and water use efficiency of lucerne. Optimal forage systems for animal production and the environment. Proceedings of the 12th Symposium of the European Grassland Federation, Pleven, Bulgaria; 2003. 26–28 May 2003.
- Lazaridou M, Koutroubas SD. Drought effect on water use efficiency of berseem clover at various growth stages. New directions for a diverse planet. Proceedings of the 4th International Crop Science Congress Brisbane, Australia; 2004. 26 Sept–1 Oct 2004.
- Leakey ADB, Bernacchi CJ, Dohleman FG, Ort DR, Long SP. Will photosynthesis of maize (*Zea mays*) in the US Corn Belt increase in future CO₂ rich atmospheres? An analysis of diurnal courses of CO₂ uptake under free-air concentration enrichment (FACE). *Glob Chang Biol.* 2004;10:951–62.
- Leakey ADB, Bernacchi CJ, Ort DR, Long SP. Long-term growth of soybean at elevated CO₂ does not cause acclimation of stomatal conductance under fully open-air conditions. *Plant Cell Environ.* 2006a;29:1794–800.
- Leakey ADB, Uribebarrea M, Ainsworth EA, Naide SL, Rogers A, Ort DR, Long SP. Photosynthesis, productivity, and yield of maize are not affected by open-air elevation of CO₂ concentration in the absence of drought. *Plant Physiol.* 2006b;55:591–628.
- Levy PE, Cannel MGR, Friend AD. Modelling the impact of future changes in climate, CO₂ concentration and land use on natural ecosystems and the terrestrial carbon sink. *Glob Environ Change.* 2004;14:21–30.
- Long SP, Ainsworth EA, Rogers A, Ort DR. Rising atmospheric carbon dioxide: plants FACE the future. *Annu Rev Plant Biol.* 2004;55:591–628.
- Long SP, Ainsworth EA, Leakey ADB, Nosberger J, Ort DR. Food for thought: lower-than-expected crop yield stimulation with rising CO₂ concentrations. *Science.* 2006;312:1918–21.
- Loomis RS, Amthor JS. Limits of yield revisited. In: Reynolds MP, Rajaram S, McNab A, editors. Increasing yield potential in wheat: breaking the barriers DF. Mexico: CIMMYT; 1996. p. 76–89.
- Loomis RS, Lafitte HR. The carbon economy of a maize crop exposed to elevated CO₂ concentrations and water stress, as determined from elemental analyses. *Field Crop Res.* 1987;17:63–74.
- Makino A, Mae T. Photosynthesis and plant growth at elevated levels of CO₂. *Plant Cell Physiol.* 1999;40:999–1006.
- Maroco JP, Edwards GE, Ku MSB. Photosynthetic acclimation of maize to growth under elevated levels of carbon dioxide. *Planta.* 1999;210:115–25.
- Marques da Silva J, Arrabica MC. Effect of water stress on Rubisco activity of *Setaria sphacelota*. In: Mathis P, editor. Photosynthesis: from light to biosphere, vol. 4. Dordrecht: Kluwer; 1995. p. 545–8.
- Medici LO, Azevedo RA, Canellas LP, et al. Stomatal conductance of maize under water and nitrogen deficits. *Pesq Agrop Brasileira.* 2007;42:599–601.
- Medlyn BE, Barton CVM, Broadmeadow MSJ, et al. Stomatal conductance of forest species after long-term exposure to elevated CO₂ concentration: a synthesis. *New Phytol.* 2001;149:247–64.

- Medrano H, Parry MAJ, Socias X, Lawlor DW. Longterm water stress inactivates rubisco in subterranean clover. *Ann Appl Biol.* 1997;131:491–501.
- Meyer WS, Green GC. Water use by wheat and plant indicators of available soil water. *Agron J.* 1980;72:253–7.
- Meyer WS, Green GC. Plant indicators of wheat and soybean crop water stress. *Irrig Sci.* 1981;2:167–76.
- Morgan JA, Pataki DE, Körner C, et al. Water relations in grassland and desert ecosystems exposed to elevated atmospheric CO₂. *Oecologia.* 2004;140:11–25.
- Morison JIL. Response of plants to CO₂ under water limited conditions. *Vegetatio.* 1993;104(105):193–209.
- Mumm P, Wolf T, Fromm J, et al. Cell type-specific regulation of ion channels within the maize stomatal complex. *Plant Cell Physiol.* 2011;52:1365–75.
- Nerd A, Nobel PS. Effects of drought on water relations and nonstructural carbohydrates in cladodes of *Opuntia ficus-indica*. *Physiol Plant.* 1991;81:495–500.
- Nesmith DS, Ritchie JT. Effects of soil water deficits during tassel emergence on development and yield component of maize (*Zea mays* L.). *Field Crop Res.* 1992;28:251–6.
- Nikinmaa E, Hölttä T, Hari P, Kolari P, Mäkelä A, Sevanto S, Vesala T. Assimilate transport in phloem sets conditions for leaf gas exchange. *Plant Cell Environ.* 2013;36:655–69.
- Norby RJ, Wullschlegel SD, Gunderson CA, Johnson DW, Ceulemans R. Tree responses to rising CO₂ in field experiments: implications for the future forest. *Plant Cell Environ.* 1999;22:683–714.
- Pan Y, Birdsey RA, Fang J, Houghton R, Kauppi PE, Kurz WA, Phillips OL, Shvidenko A, Lewis SL, Canadell JG, et al. A large and persistent carbon sink in the world's forests. *Science.* 2011;333:988–93.
- Penning de Vries FWT, Keulen van H, Rabbinge R. Natural resources and the limits of food production. In: Bouma J et al., editors. *Ecoregional approaches for sustainable land use and food production.* Dordrecht: Kluwer Academic Press; 1995.
- Poorter H. Do slow-growing species and nutrient-stressed plants respond relatively strongly to elevated CO₂? *Glob Chang Biol.* 1998;4:693–7.
- Prior SA, Rogers HH, Sionit N, Patterson RP. Effects of elevated atmospheric CO₂ on water relations of soya bean. *Agr Ecosyst Environ.* 1991;35:13–25.
- Prior SA, Runion GB, Rogers HH, Arriaga FJ. Elevated atmospheric carbon dioxide effects on soybean and sorghum gas exchange in conventional and no-tillage systems. *J Environ Qual.* 2010;39:596–608.
- Radmer R, Kok B. Photosynthesis: limited yields, unlimited dreams. *BioScience.* 1977;27:599–605.
- Reddy KR, Hodeges HF, Kimball BA. Crop ecosystem response to climatic change: cotton. In: Reddy KR, Hodges HF, editors. *Climate change and global crop productivity.* New York: CABI; 2000. p. 161–87.
- Riedo M, Gyalistras D, Fuhrer J. Pasture responses to elevated temperature and doubled CO₂ concentration: assessing the spatial pattern across an alpine landscape. *Clim Res.* 2001;17:19–31.
- Rogers HH, Runion GB, Krupa SV, Prior SA. In: Allen Jr LH, Kirkham MB, Olszyk DM, Whitman CE, editors. *Advances in carbon dioxide effects research, Plant responses to atmospheric CO₂ enrichment: Implications in root-soil-microbe interactions.* Madison, WI: ASA Special Publication No. 61. ASA, CSSA, and SSSA; 1997. p. 1–34.
- Rosenzweig C, Hillel D. *Climate change and the global harvest.* New York: Oxford University Press; 1998. p. 324.
- Sadras VO, Angus JF. Benchmarking water use efficiency of rainfed wheat in dry environments. *Aust J Agr Res.* 2006;57:847–56.
- Sage RF, Monson RK. *C4 plant biology.* San Diego: Academic; 1999.
- Samarakoon AB, Müller WJ, Gifford RM. Transpiration and leaf area under elevated CO₂: effects of soil water status and genotype in wheat. *Aust J Plant Physiol.* 1995;22:33–44.

- Sau F, Mínguez MI. Adaptation of indeterminate faba beans to weather and management under a Mediterranean climate. *Field Crop Res.* 2000;66:81–99.
- Schneider SH. What is 'dangerous' climate change. *Nature.* 2001;411:17–9.
- Shpiler L, Blum A. Heat tolerance to yield and its components in different wheat cultivars. *Euphytica.* 1991;51:257–263.
- Siddique MRB, Hamid A, Islam MS. Drought stress effects on water relations of wheat. *Bot Bull Acad Sin.* 2001;41:35–9.
- Simane B, Peacock JM, Struik PC. Differences in development and growth rate among drought-resistant and susceptible cultivars of durum wheat (*Triticum turgidum L. var. durum*). *Plant Soil.* 1993;157:155–166.
- Sionit N, Strain BR, Hellmers H, Kramer PJ. Effects of atmospheric CO₂ concentrations and water stress on water relations of wheat. *Bot Gaz.* 1981;142:191–6.
- Sionit N, Rogers HH, Bingham GE, Strain BR. Photosynthesis and stomatal conductance with CO₂-enrichment of container- and field-grown soybeans. *Agron J.* 1984;76:447–51.
- Smith SD, Huxman TE, Zitzer SF, Charlet TN, Housman DC, Coleman JS, Fenstermaker LK, Seemann JR. Nowak RS. Elevated CO₂ increases productivity and invasive species success in an arid ecosystem. *Nature.* 2000;408:79–81.
- Somerville C, Briscoe J. Genetic engineering and water. *Science.* 2001;292:2217.
- Surano KA, Shinn JH. CO₂ and water stress effects on yield, water-use efficiency and photosynthate partitioning in field grown corn. UCRL-90771. Livermore: Lawrence Livermore National Laboratory; 1984.
- Timlin D, Bunce J, Fleisher D, et al. Simulation of the effects of limited water on photosynthesis and transpiration in field crops: can we advance our modeling approaches? In: Ahuja L et al., editors. Response of crops to limited water: understanding and modeling water stress effects on plant growth processes. Madison, WI: Advances in Agricultural Systems Modeling Ser. 1. ASA, CSSA, SSSA; 2008.
- Tubiello FN, Ewert F. Simulating the effects of elevated CO₂ on crops: approaches and applications for climate change. *Eur J Agron.* 2002;18:57–74.
- Tubiello FN, Rosenzweig C, Kimball BA, Pinter Jr PJ, Wall GW, Hunsaker DJ, Lamorte RL, Garcia RL. Testing CERES-wheat with FACE data: CO₂ and water interactions. *Agron J.* 1999;91:1856–65.
- Tubiello FN, Donatelli M, Rosenzweig C, Stockle CO. Effects of climate change and elevated CO₂ on cropping systems: model predictions at two Italian locations. *Eur J Agron.* 2000;13:179–89.
- Tubiello FN, Amthor JA, Boote K, Donatelli M, Easterling WE, Fisher G, Gifford R, Howden M, Reilly J, Rosenzweig C. Crop response to elevated CO₂ and world food supply. *Eur J Agron.* 2007;26:215–23.
- van Herwaarden AF, Farquhar GD, Angus JF, Richards RA, Howe GN. 'Haying-off', the negative grain yield response of dryland wheat to nitrogen fertilizer. I. Biomass, grain yield, and water use. *Aust. J. Agr. Res.* 1998;49:1067–1082.
- von Caemmerer S, Quick PW. Rubisco, physiology in vivo. In: Leegood RC, Sharkey TD, von Caemmerer S, editors. In photosynthesis: physiology and metabolism. Dordrecht: Kluwer Academic; 2000. p. 85–113.
- Wang W-H, Yi X-Q, Han A-D, et al. Calcium-sensing receptor regulates stomatal closure through hydrogen peroxide and nitric oxide in response to extracellular calcium in Arabidopsis. *J Exp Bot.* 2012;63:177–90.
- Warren CR. Soil water deficits decrease the internal conductance to CO₂ transfer but atmospheric water deficits do not. *J Exp Bot.* 2008;59:327–34.
- Watson RT, Zinyowera MC, Moss RH. Climate Change 1995: Impacts, Adaptation and Mitigation of Climate Change. Cambridge University Press, Cambridge; 1996.
- Witter SH. Future technological advances in agriculture and their impact on the regulatory environment. *BioScience.* 1979;29:603–10.

- Wu DX, Wang GX. Interaction of CO₂ enrichment and drought on growth, water use, and yield of broad bean (*Vicia faba*). *Environ. Exp. Bot.* 2000;43:131–139.
- Wu DX, Wang GX, Bai YF, Liao JX. Effects of elevated CO₂ concentration on growth, water use, yield and grain quality of wheat under two soil water levels. *Agr. Ecosyst. Environ.* 2004;104:493–507.
- Yang Y, Timlin DJ, Fleisher DH, Kim S-H, Quebedeaux B, Reddy VR. Simulating leaf area of corn plants at contrasting water status. *Agric For Meteorol.* 2009;149:1161–7.
- Yoshimoto M, Oue H, Kobayashi K. Energy balance and water use efficiency of rice canopies under free-air CO₂ enrichment. *Agric. Forest Meteorol.* 2005;133:226–246.