

Effects of elevated CO₂ concentration on water use efficiency of *Tamarix ramosissima* in an extremely arid region

Zongqiang Chang¹ · Yali Ma¹ · Chenglin Zhou¹

Received: 2 July 2014 / Accepted: 27 June 2015 / Published online: 27 October 2016
© Springer-Verlag Berlin Heidelberg 2016

Abstract The variation of net photosynthetic rate (P_n), transpiration rate (T_r), and intercellular CO₂ concentration (C_i) with changes in light intensity of *Tamarix ramosissima* leaves was studied during the growing seasons of 2012 and 2013 in the extremely arid region of Ejina Oasis, using the LI-6400 portable photosynthesis measurement system. Results indicate that C_i decreased and P_n and T_r increased with light intensity. After reaching the light saturation point, P_n decreased gradually with the enhanced greater light intensity. The apparent maximum photosynthetic rate increased with CO₂ concentration, from 17.69 to 27.05 $\mu\text{mol}/(\text{m}^2 \text{ s})$; apparent quantum efficiency also increased, as did the light saturation point of *T. ramosissima* leaves. Water use efficiency (WUE) increased initially but gradually decreased after maximizing with the enhanced light intensity. T_r and C_i increased with elevated CO₂ concentration. P_n and WUE increased with CO₂ concentration when that concentration was 200–600 $\mu\text{mol}/\text{mol}$. When that concentration increased to 1000 $\mu\text{mol}/\text{mol}$, WUE increased initially but eventually decreased.

Keywords *Tamarix ramosissima* leaves · Transpiration · Water use efficiency · Concentration of CO₂

Introduction

Human activities have caused an increase in atmospheric CO₂ content from approximately 280 $\mu\text{mol}/\text{mol}$ before the industrial revolution to 379 $\mu\text{mol}/\text{mol}$ at present, and the increase continues at an annual rate of 1.4 $\mu\text{mol}/\text{mol}$ (Forster et al. 2007; Zhou et al. 2009). CO₂ is one of the key factors affecting plant growth, development, and function. It is the basis of photosynthesis and the regulator of primary metabolic processes, allocation, and growth of photoassimilates (Kerstiens et al. 1995). Therefore, elevated CO₂ concentrations have far-reaching effects on photosynthesis and yield (Agrell et al. 2000). Such concentrations cause the greenhouse effect, which can gradually warm the climate, influence water balance, alter seasonal precipitation patterns, and vary water resources regionally (Richard et al. 2001; Duan et al. 2013). Moreover, elevated temperature increases potential evaporation, causing the most arid regions on earth to become more arid (Rind et al. 1990). Therefore, water use efficiency (WUE) of plants in response to elevated atmospheric CO₂ concentration has become a worldwide research focus (Berryman 1994; Ellsworth 1999; Duan et al. 2013).

WUE is an important index that reflects the energy conversion efficiency of plant growth, and has been widely used in plant physiology and ecology (Escher et al. 2008). The definition and understanding of WUE in different disciplines and areas are dissimilar (Letts et al. 2008). At the level of leaves, WUE is represented by the ratio of the net photosynthetic rate (P_n) and transpiration rate (T_r) (Leakey et al. 2006). Thus, WUE of plant leaves depends on the coupling processes of photosynthesis and transpiration controlled by stoma (Liu et al. 2005). Photosynthesis is the basis of growth and development of plants and is also

✉ Zongqiang Chang
changzq@lzb.ac.cn

¹ Cold and Arid Regions Environmental and Engineering Research Institute, Chinese Academy of Sciences, Lanzhou 730000, China

a complex biological physical chemistry process influenced by numerous factors (Bernacchi et al. 2005). Under natural conditions, it is important to study photosynthetic characteristics, their relationships with photosynthesis, light radiation, CO₂ concentration, and other factors (Poorter and Nagel 2000). The relationship between the diurnal course of plant photosynthesis and environmental factors has been studied extensively, but most such studies are qualitative or involve simple correlation analysis (Chen et al. 2006). The effect of light intensity on plants is a research focus on plant physiological ecologists. Various light intensity conditions can cause plastic responses and consequently the environmental modification of plants (Christidis et al. 2013). The carbon source required for plant photosynthesis is mainly atmospheric CO₂; therefore, CO₂ concentration has a significant influence on photosynthesis. In recent years, there have been numerous studies regarding elevated CO₂ and adaptation mechanisms for plant photosynthesis (Morse and Bazzaz 1994). Transpiration directly drives water migration in the soil–plant–atmosphere continuum (SPAC) system and is the driving force of the ecosystem water cycle. Thus, simulating plant *WUE* becomes key to assessing the interaction between the water and carbon cycles in the ecosystem (Letts et al. 2008). Based on the principle of gas exchange of leaves, the present study establishes a model of *WUE* response to CO₂. We choose the typical plant *Tamarix ramosissima* in an extremely arid region to verify and analyze *WUE* change. The goal was to provide a theoretical basis to present physiological and ecological mechanisms of the coupling cycle of carbon and water in an extremely arid region and to establish a model of this cycle under global change.

Materials and methods

Study site

The test was conducted in the Er Dao Qiao *T. ramosissima* forest to the southeast of Ejina Qi town in Inner Mongolia, from May to October during 2012–2013. Geographic coordinates in this inland area are 41°58'N, 101°06'E, and altitude is 920.46 m. The climate is extremely arid, with annual average temperature of 8.2 °C, annual average precipitation of 37.9 mm, and amount of evaporation over 3700 mm. The region is one of the most arid regions in China.

Study materials

We selected the natural *T. ramosissima* forest as pastoral land fenced in 1988. The vegetation coverage exceeds

70%, 1300 plexus/hm². Average plant height is ~2 m, and tree age is >20 a. Soil parent material is river alluvium, and soil type is *T. ramosissima* forest soil. Sulfate salt spots are present locally. The level of underground water is approximately 2–3.5 m.

Test method

Using the LI-6400-05 conifer chamber of portable photosynthesis measurement system (Li-COR Inc., Lincoln, NE, USA) during the growing seasons of 2012 and 2013, we selected reciprocal third and fourth mature leaves from *T. ramosissima* treetops. We took measurements hourly from 8:00 to 21:00 local time. In each measurement, we randomly selected six to eight branches to determine diurnal variation of the photosynthetic rate and corresponding ecological environment elements. We set the flow of the photosynthesis system to 500 μmol s⁻¹ to determine the response of photosynthetic rate to light intensity and CO₂ concentration. Leaf chamber temperature was 30 °C. Photosynthetic photon flux density (*PPFD*) was set at nine levels: 2000, 1500, 1000, 500, 200, 100, 50, 20, and 0 μmol/(m² s). CO₂ concentrations were set at eight levels in a reference room: 0, 20, 50, 100, 200, 400, 600, and 1000 μmol/mol.

Data analysis and calculation

Plant *WUE* was analyzed at the leaf scale. *WUE* was defined as the ratio of P_n and T_r (type 1), calculated via

$$WUE = P_n/T_r \quad (1)$$

P_n and T_r are given by subsequent equations.

As early as 1913, Michaelis–Menten proposed a relationship of biochemical reaction rate and source concentration. Although light is not the source of photosynthesis, it is its energy source and so can be considered a source. P_n response to light intensity follows the Michaelis–Menten equation. Farquhar (1980) improved the model (Eq. 2). As the classic relationship, this equation is widely used as the characteristic description of P_n response to light intensity.

$$P_n = \frac{PPED * \Theta + P_{max} - \sqrt{(PPED * \Theta + P_{max})^2 - 4 * PPED * \Theta * P_{max} * k}}{2k} - R_{day} \quad (2)$$

where P_n is net photosynthetic rate; P_{max} is under a certain CO₂ concentration the maximum net P_n in response to light intensity; Θ is the apparent quantum efficiency characterizing maximum photosynthetic light energy conversion rate; k is the angle of light response curves; R_{day} is the dark respiration rate.

Results

Intercellular CO₂ concentration and stomatal conductance under varying CO₂ concentrations with change in light intensity

Intercellular CO₂ concentration (*C_i*) of *T. ramosissima* leaves gradually decreased under variable CO₂ concentrations with enhanced light intensity. *C_i* rapidly declined when light intensity was increased from 0 to 400 μmol/(m² s). *C_i* slowdown eventually decreased and tended to be constant with enhanced light intensity (Fig. 1a). Early days of enhanced light intensity are precisely the rapidly growing period for *P_n* of *T. ramosissima* leaves. Increasing *P_n* raised CO₂ consumption, which led to rapid *C_i* decline. When light intensity exceeded a certain value, the increasing *P_n* amplitude slowed and even reached light saturation. Photosynthesis consumption of CO₂ and outside CO₂ diffusion reached a balance, such that *C_i* tended to stabilize. For different light intensities, *C_i* of *T. ramosissima* leaves increased with CO₂ concentration. This phenomenon may be caused by an increase in environmental CO₂, accelerating the latter's diffusion into leaf cells. The diffusion amount far exceeded that required by increasing *P_n*, which caused elevated *C_i* of leaves with increasing environmental CO₂ concentration. There was a certain difference in variation of the stomatal conductance (*G_s*) of *T. ramosissima* leaves with varying CO₂ concentration and increasing light intensity. *G_s* represented a regular change in initial increase and subsequent decrease with increasing light intensity. The demarcation point of increase and decrease was at the light saturation point (Fig. 1b).

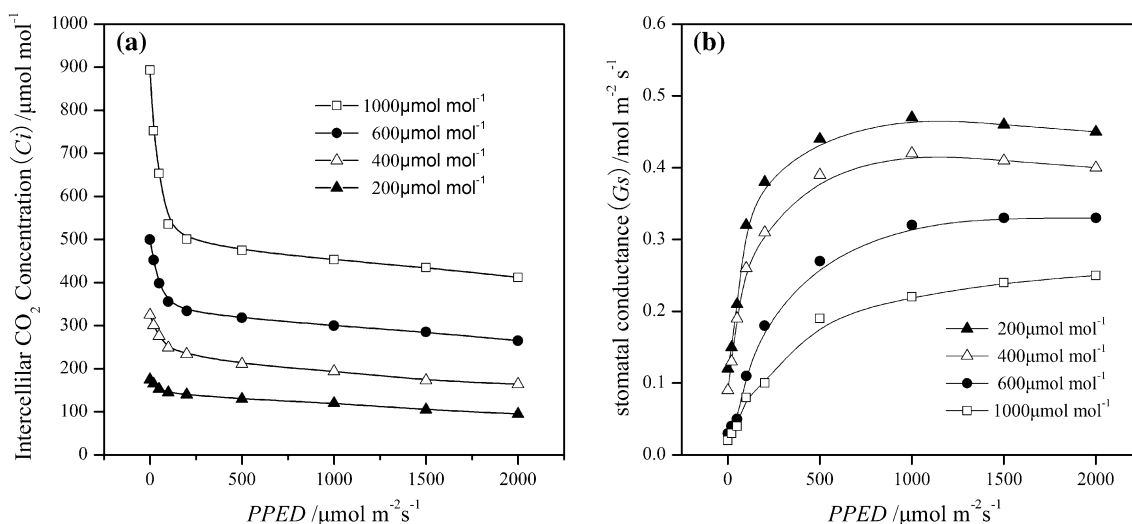


Fig. 1 Changes of intercellular CO₂ concentration (*C_i*) and stomatal conductance (*G_s*) to photosynthetic photon flux density (*PPED*) in *Tamarix ramosissima* leaves under different CO₂ concentrations

Change in photosynthetic rate at different CO₂ concentrations with variable light intensity

Figure 2 shows *P_n* of *T. ramosissima* leaves under different CO₂ concentrations with variable light intensity. For each CO₂ concentration, this *P_n* had a certain difference from the variable light intensity. With increasing light intensity, *P_n* increased and eventually reached saturation. When the concentration of environmental CO₂ was varied, light intensity upon appearance of the light saturation point was different. This point of the blade was 1200 μmol/(m² s) when CO₂ concentration was 200 μmol/mol and was 1700 μmol/(m² s) for CO₂ concentrations 400 and 600 μmol/mol. The point was 2000 μmol/(m² s) for CO₂ concentration 1000 μmol/mol. Within a certain range, the increasing CO₂ concentration augmented photosynthesis to a certain extent. After exceeding the CO₂ saturation point, continued increase in CO₂ concentration had a minimal effect on photosynthesis.

Table 1 shows that the fit for various treatments reached an extremely significant level. The apparent maximum photosynthetic rate increased with CO₂ concentration, from 17.69 to 27.05 μmol/(m² s); apparent quantum efficiency also increased, as did the light saturation point of *T. ramosissima* leaves. The latter varied from 1458.3 ± 2.4 to 2316.4 ± 2.1 μmol/(m² s). The light compensation point of the leaves decreased with increasing CO₂ concentration.

Transpiration rate under different CO₂ concentrations with change in light intensity

Figure 3 shows *T_r* of *T. ramosissima* leaves under variable CO₂ concentrations with change in light intensity. Under

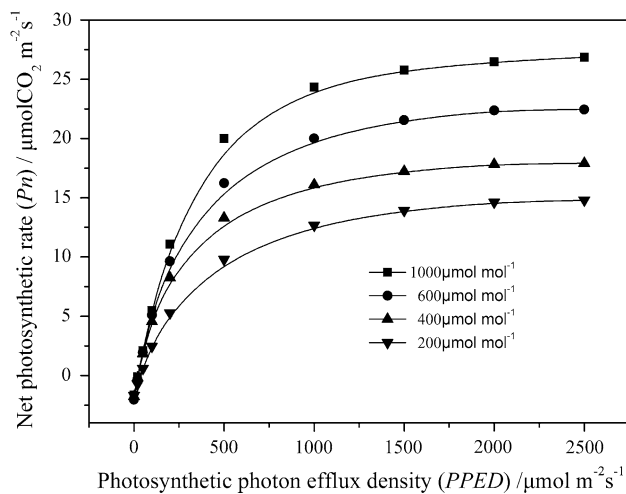


Fig. 2 Response of net photosynthetic rate (P_n) to $PPED$ in *T. ramosissima* leaves under different CO_2 concentrations

variable CO_2 concentrations, T_r increased with enhanced light intensity, as did P_n . The emission of CO_2 of leaves increased, as did stomatal conductance. Leaf temperature gradually increased, promoting the *T. ramosissima* transpiration. For different light intensities and increasing CO_2 concentration, T_r variations of *T. ramosissima* were similar, with a downward trend. The extent of stomatal opening influenced leaf water loss, with a significant positive correlation between them. Therefore, leaf T_r declined with elevated CO_2 concentration, which may have been the result of increased environmental CO_2 . The stoma gradually closed, gradually reducing G_s of *T. ramosissima*. Leaf T_r decreased accordingly.

Water use efficiency at different CO_2 concentrations with change in light intensity

Figure 4 shows WUE variation of *T. ramosissima* leaves under different CO_2 concentrations and light intensities. Under variable CO_2 concentrations, WUE of the leaves increased with enhanced light intensity in the early stage of that enhancement. After maximum WUE increase, its value increased and then gradually decreased with enhanced light intensity, although the decline was minimal. For different

CO_2 concentrations, light intensity varied when leaf WUE maximized. CO_2 concentrations were 200, 400, 600, and 1000 $\mu\text{mol}/\text{mol}$. Respective light intensities were 1500, 2000, 2100, and 2100 $\mu\text{mol}/(\text{m}^2 \text{s})$ when leaf WUE maximized. Under different light intensities, WUE initially rose and then decreased with increasing CO_2 concentration. When CO_2 concentration was 200–600 $\mu\text{mol}/\text{mol}$, WUE increased with CO_2 concentration. When CO_2 concentration rose to 1000 $\mu\text{mol}/\text{mol}$, WUE declined after light intensity exceeded 1200 $\mu\text{mol}/(\text{m}^2 \text{s})$. This result is attributable to P_n increase when CO_2 concentration increased to 200–600 $\mu\text{mol}/\text{mol}$. Thus, T_r decreased with increasing CO_2 concentration, while WUE increased. When CO_2 concentration was 1000 $\mu\text{mol}/\text{mol}$, leaf P_n decreased significantly and T_r decreased slightly (Fig. 4). This caused WUE to decline rapidly.

Discussion and conclusions

Discussion

The effects of increasing CO_2 concentration are important in enriching G_s (Liu et al. 2005). According to the measurement results, G_s of *T. ramosissima* leaves gradually declined with increasing CO_2 concentration. Several scholars argue that reduced stomatal density is the reason that elevated CO_2 concentration can reduce G_s (Berryman 1994). A number of researchers believe that the main reason is not reduced stomatal density but partial stomatal closure, directly caused by internal CO_2 increase in leaves (Morison and Gifford 1983). The present study gives results of short-term high CO_2 concentration. Thus, the partial closure of stoma was the main cause of G_s decrease. With the increasing outside CO_2 concentration, it was easier for plant leaves to acquire CO_2 . CO_2 consumption for photosynthesis did not increase significantly, which reduced C_i . Plants reduced C_i through stomatal closure regulation to continuously maintain intercellular CO_2 partial pressure less than atmospheric pressure (Morse and Bazzaz 1994). Thus, G_s of *T. ramosissima* leaves gradually decreased with increasing environmental CO_2 concentration.

Table 1 Parameters of photosynthetic rate in response to light intensity of *Tamarix ramosissima* under different CO_2 concentrations

CO_2 concentrations ($\mu\text{mol}\cdot\text{mol}^{-1}$)	Light saturation ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	Light compensation ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	Apparent quantum efficiency ($\mu\text{molCO}_2\cdot\mu\text{mol}^{-1}\text{photons}$)	P_{\max} ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	R_{day} ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	R^2 ($n = 9$)
1000	2316.4 ± 2.1	7.12 ± 0.26	0.084 ± 0.0016	27.05	1.78 ± 0.04	0.9826**
600	2262.1 ± 2.3	11.58 ± 0.31	0.076 ± 0.0014	25.32	1.89 ± 0.05	0.9817**
400	1836.5 ± 2.2	21.31 ± 0.37	0.068 ± 0.0015	20.57	1.76 ± 0.06	0.9854**
200	1458.3 ± 2.4	36.52 ± 0.49	0.065 ± 0.0019	17.69	1.63 ± 0.04	0.9876**

** represent the values that have passed the significance level at 0.05

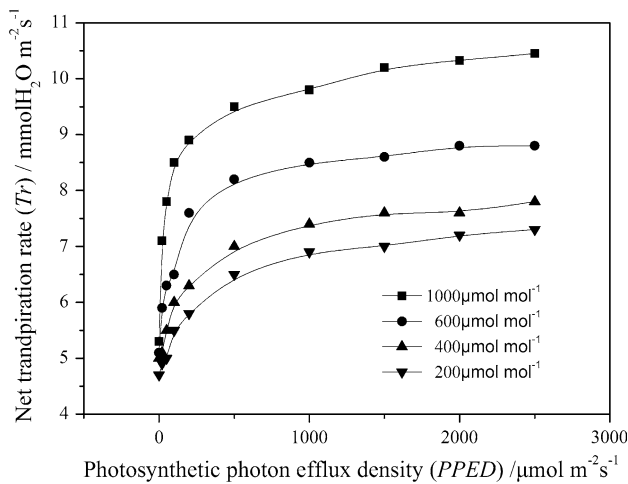


Fig. 3 Response of net transpiration rate (T_r) to $PPED$ in *T. ramosissima* leaves under different CO_2 concentrations

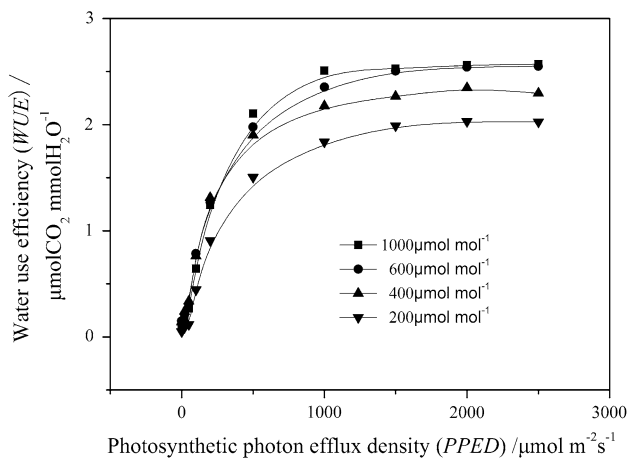


Fig. 4 Water use efficiency (WUE) of *T. ramosissima* under different CO_2 concentrations

The photoinhibition phenomenon is relatively common in photosynthesis of higher plants. Strong light is the major cause of photoinhibition, whereas temperature, moisture, nutrient deficiency, and salt stress tend to reduce it (Demming and Adams 1992). *T. ramosissima* leaves photoinhibited in variable degrees with increasing light intensity under different CO_2 concentrations. The reflection of solar radiation by shallow and immature leaves is generally strong, because different colors and developments weaken solar radiation variably. The color of *T. ramosissima* leaves is shallow, which makes their light reflectance strong, and we determined significant temperature variation. The reason for this phenomenon may be that intense light generated significantly high leaf temperature and excessive transpiration. The plant closes its stoma to reduce water loss via transpiration. Stomatal closure caused C_i decline, thereby reducing the photosynthetic rate (Wang

et al. 1998). At the same time, the increasing CO_2 concentration raised the light saturation point and delayed photoinhibition. This result is consistent with the findings of Lu (2012). However, the specific reason for this phenomenon remains to be investigated. Nonetheless, the raising of the light saturation point enhanced the photosynthetic ability of *T. ramosissima* leaves under bright light conditions, thereby increasing the assimilated amount. Studies have shown that a short-term increase in CO_2 concentration can promote plant photosynthesis to a certain extent (Morse and Bazzaz 1994). This photosynthesis declines to the original level, demonstrating photosynthetic acclimation to long-term high CO_2 concentrations (Gunderson 1993; Ottman et al. 2001). However, other studies have also indicated that plant photosynthetic capacity does not demonstrate such acclimation (Zhou et al. 2011). The present experiment was conducted under short-term increase in CO_2 concentration. Whether *T. ramosissima* leaves can maintain a high photosynthetic rate under long-term high CO_2 concentrations needs further study.

Several studies have shown that elevated CO_2 concentration that increased plant WUE was caused by such concentration substantially increasing P_n and reducing T_r (Letts et al. 2008). A number of works have indicated that WUE increases only because of T_r decrease and not because of P_n increase (Rogers et al. 1984). Other studies determined that WUE increase was attributable to P_n increase alone (Gunderson 1993).

Conclusions

This paper described the variation of net photosynthetic rate (P_n), transpiration rate (T_r), and intercellular CO_2 concentration (C_i) with changes in light intensity of *Tamarix ramosissima* leaves during the growing seasons of 2012 and 2013 in the extremely arid region of Ejina Oasis of Northwest China. We conclude that the G_s of *T. ramosissima* leaves gradually decreased with increasing environmental CO_2 concentration. There was a certain difference in variation of the G_s with varying CO_2 concentration and increasing light intensity. G_s represented a regular change in initial increase and subsequent decrease with increasing light intensity. The demarcation point of increase and decrease was at the light saturation point. The apparent maximum photosynthetic rate increased with CO_2 concentration, from 17.69 to 27.05 $\mu\text{mol}/(\text{m}^2 \text{ s})$; apparent quantum efficiency also increased, as did the light saturation point of *T. ramosissima* leaves. Leaf T_r declined with elevated CO_2 concentration, which may have been the result of increased environmental CO_2 . The stoma gradually closed, gradually reducing G_s of *T. ramosissima*. Leaf T_r decreased accordingly. Therefore, that C_i decreased and P_n and T_r increased with light intensity. After reaching the

light saturation point, P_n decreased gradually with the enhanced greater light intensity. Water use efficiency (WUE) increased initially but gradually decreased after maximizing with the enhanced light intensity. T_r and C_i increased with elevated CO_2 concentration. The results of the study determined that for CO_2 concentrations 200–600 $\mu\text{mol/mol}$, WUE of *T. ramosissima* increased with CO_2 concentration. This finding is attributed to the combined results of substantial P_n increase and T_r decrease. When CO_2 concentration rose to 1000 $\mu\text{mol/mol}$, despite T_r decrease, P_n was reduced significantly, leading to the WUE decrease.

Acknowledgements This work was funded by the Natural Science Foundation of Gansu Province (145RJZA052) and the National Key Technology R & D Program (2012BAC08B05). The authors would like to express their deep gratitude to the anonymous reviewers for their valuable suggestions that greatly improved the manuscript.

References

- Agrell J, McDonald EP, Lindroth RL (2000) Effects of CO_2 and light on tree phytochemistry and insect performance. *Oikos* 88:259–272
- Bernacchi CJ, Morgan PB, Ort DR et al (2005) The growth of soybean under free air $[CO_2]$ enrichment (FACE) stimulates photosynthesis while decreasing in vivo Rubisco capacity. *Planta* 220:434–446
- Berryman CA (1994) Stomatal responses to a range of variables in two tropical tree species grown with CO_2 enrichment. *J Exp Bot* 45:539–546
- Chen YP, Chen YN, Li WH et al (2006) Characterization of photosynthesis of *Populus euphratica* grown in the arid region. *Photosynthetica* 44(4):622–627
- Christidis N, Stott PA, Hegerl GC et al (2013) The role of land use change in the recent warming of daily extreme temperatures. *Geophys Res Lett* 40:589–594
- Demming-Adams B, Adams WW III (1992) Photoprotection and other response of plants to high light stress. *Annu Rev Plant Physiol Plant Mol Biol* 43:599–626
- Duan B, Zhang X, Li Y et al (2013) Plastic responses of *Populus yunnanensis* and *Abies faxoniana* to elevated atmospheric CO_2 and warming. *For Ecol Manag* 296:33–40
- Ellsworth DS (1999) CO_2 enrichment in a maturing pine forest: are CO_2 exchange and water status in the canopy affected. *Plant, Cell Environ* 22(5):461–472
- Escher P, Andreas DP, Bannister P et al (2008) Transpiration, CO_2 assimilation, WUE , and stomatal aperture in leaves of *Viscum album* (L.): effect of abscisic acid (ABA) in the xylem sap of its host (*Populus euamericana*). *Plant Physiol Biochem* 46:64–70
- Farquhar GD, von Caemmerer S, Berry JA (1980) A biochemical model of photosynthetic CO_2 assimilation in leaves of C_3 species. *Planta* 149:78–90
- Forster P, Ramaswamy V, Artaxo P et al (2007) Changes in atmospheric constituents and in radiative forcing. In: Solomon S et al (eds) *Climate change 2007: the physical science basis. Contribution of working group 1 to the fourth assessment report of the intergovernmental panel on climate change*. Cambridge University Press, Cambridge, pp 131–234
- Gunderson CA (1993) Foliar gas exchange responses of two deciduous hardwoods during 3 years of growth in elevated CO_2 : no loss of photosynthetic enhancement. *Plant, Cell Environ* 16:797–807
- Kerstiens G, Townend J, Heath J et al (1995) Effects of water and nutrient availability on physiological responses of woody species to elevated CO_2 . *Forestry* 68:303–315
- Leakey ADB, Uribealarea M, Ainsworth EA et al (2006) Photosynthesis, productivity, and yield of maize are not affected by open-air elevation of CO_2 concentration in the absence of drought. *Plant Physiol* 140:779–790
- Letts MG, Phelan CA, Johnson DR et al (2008) Seasonal photosynthetic gas exchange and leaf reflectance characteristics of male and female cottonwoods in a riparian woodland. *Tree Physiol* 28(7):1037–1048
- Liu F, Andersen MN, Jacobsen SE et al (2005) Stomatal control and water use efficiency of soybean (*Glycine max* L. Merr.) during progressive soil drying. *Environ Exp Bot* 54:33–40
- Lu S, Zhang J, Meng P et al (2012) Soil respiration and its temperature sensitivity for walnut intercropping, walnut orchard and cropland systems in North China. *Food, Agri Environ* 10:1204–1208
- Morison JLL, Gifford RM (1983) Stomatal sensitivity to carbon dioxide and humidity. *Plant Physiol* 71:789–796
- Morse SR, Bazzaz FA (1994) Elevated CO_2 and temperature alter recruitment and size hierarchies in C_3 and C_4 annuals. *Ecology* 75:966–975
- Ottman MJ, Kimball BA, Pinter PJ et al (2001) Elevated CO_2 increases sorghum biomass under drought conditions. *New Phytol* 150:261–273
- Poorter H, Nagel O (2000) The role of biomass allocation in the growth response of plants to different levels of light, CO_2 , nutrients and water: a quantitative review. *Aust J Plant Physiol* 27:595–607
- Richard LL, Brian JK, William FJ et al (2001) Consequences of elevated carbon dioxide and ozone for foliar chemical composition and dynamics in trembling aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*). *Environ Pollut* 115:395–404
- Rind D, Goldberg R, Hansen J (1990) Potential evapo-transpiration and the likelihood of future drought. *J Geophys Res* 95:9983–10004
- Rogers HH, Sionit N, Cure JD et al (1984) Influence of elevated carbon dioxide on water relations of soybeans. *Plant Physiol* 74:233–238
- Wang HL, Yang SD, Zhang CL (1998) The photosynthetic characteristics of differently shaped leaves in *Populus euphratica* Olivier. *Photosynthetica* 34(4):545–553
- Zhou H, Chen Y, Li W et al (2009) Photosynthesis of *Populus euphratica* and its response to elevated CO_2 concentration in an arid environment. *Prog Nat Sci* 19:443–451
- Zhou Y, Tang J, Melillo J et al (2011) Root mass, carbon compounds and nitrogen content after six years of soil warming in a temperate forest. *Tree Physiol* 31:707–717