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RESEARCH ARTICLE

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Photosynthetic response to variation in CO_2 concentrations and temperature of four broad-leaved trees in Beijing region

Abstract Responses of the photosynthetic characteristics to variation in CO_2 concentration and temperature of *Ginkgo biloba*, *Eucommia ulmoides*, *Magnolia denudata* and *Tilia japonica* were measured during the peak growing season. The results show that the ambient CO_2 concentration could not meet the requirements for photosynthesis of these four species. The optimal temperatures for photosynthesis were lower than the average daytime air temperature. Hence, the photosynthesis of these four species was restricted by the low CO_2 concentration and high daytime air temperature at the time of measurement. Marked enhancements in the net photosynthetic rate were found in all four species when the CO_2 concentration was doubled. When the dependency on CO_2 and temperature were examined simultaneously, it was seen that for increased CO_2 concentrations there was a shift in the optimum temperature for *M. denudata* and *T. japonica* towards higher temperatures. Due to their independence on CO_2 concentrations, this trend could not be found in the *G. biloba* and *E. ulmoides* data sets. The stomatal conductance (G_s) was sensitive to a vapor pressure deficit (VPD) which in turn was sensitive to temperature. An increase in temperature would cause the VPD to increase and plants might be assumed to react by reducing their stomatal apertures. The effect on stomatal resistance would be most significant at high temperatures. The restriction to stomatal conductance for these four species would increase if CO_2 concentrations were elevated at the same temperature.

Keywords photosynthesis, CO_2 concentration, temperature, vapor pressure deficit, stomatal conductance

1 Introduction

For some time now, the concentration of atmospheric carbon dioxide has been increasing gradually. Experts predict a 200% increase in CO_2 concentrations (Callander et al., 1996) and a 3.5–5.2°C increase in the mean global temperature by the middle of the 21st century (Wetherald, 1991). CO_2 and temperature may have profound effects on plant development, especially on photosynthesis. The effects of their variation on plants have become a field of study of major interest worldwide (Poorter, 1993; Allen, 1994; Gunderson et al., 2000; Rustad et al., 2001). The photosynthetic response to variation in CO_2 concentration and temperature of four broad-leaved trees, *Ginkgo biloba*, *Eucommia ulmoides*, *Magnolia denudata* and *Tilia japonica*, has been investigated in this article which will provide a theoretical basis for research into the ecological responses to the combined variation in CO_2 concentrations and temperatures in trees.

2 Natural general situation

Beijing is located at the north latitude 39°28′–40°05′ and the east longitude 115°25′–117°30′, an area with standard temperate zone mainland monsoon weather. The four seasons are well defined, the winter is chilly but arid, and the summer is warm and moist. The hottest month is July with an average temperature of 26.1°C. The coldest month is

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January, with an average temperature of −4.7°C. The average annual precipitation is 500–650 mm, of which 74% falls in the three months from June to August.

3 Materials and methods

Four well irrigated, young broad-leaved trees, *G. biloba*, *E. ulmoides*, *M. denudata* and *T. japonica*, were selected for our study in the summer at the Beijing Forestry University. The third to the fifth leaves from the apex were examined and measured.

The photosynthetic responses to the variation in CO_2 concentration and temperature were measured with a Li-6400 portable photosynthesis system (Licor Inf, Lincoln, NB, USA). The ratios of A (photosynthetic rate)/C_i (intercellular CO_2 concentration) were measured at leaf temperatures of 28, 30, 32, 34, 36 and 38°C at CO_2 concentrations of 50, 100, 200, 380, 600, 760, 900, 1000, 1300 and 1500 μmol/mol. Curves were plotted for each of the four species. Additionally, the ratios of A/C_i also were measured and plotted at 25, 30, 35 and 40°C with the lower CO_2 concentration of 50, 100, 150, 200, 250 and 300 μmol/mol. At the same time, the optimal temperature for photosynthesis was analyzed at different CO_2 concentrations by the test described. To avoid light inhibition, the photon flux density (*PFD*) was maintained at 1000 μmol/(m^2·s) (Ma et al., 2004). We selected the period from 7:00–10:00 in the morning for making our measurements in order to avoid the higher outside temperatures. During the determination, CO_2 was provided by a liquefied CO_2 steel container of Li-6400-01, the temperature of the leaves was controlled with a Pelteer thermoelectric condenser and *PFD* was provided by the red-blue light source of Li-6400-02B.

The data were analyzed with EXCEL software (Microsoft Corporation, USA) with three replications.

4 Results and analysis

The photosynthetic rates under CO_2-elevated conditions were greater than those observed in the control (Fig. 1). The concentration of CO_2 was higher than that of ambient CO_2 (about 380 μmol/mol) when the net photosynthetic rates (P_n) of the four trees attained their highest value, although they were at different states of growth. Our results show that enriched CO_2 concentrations benefit photosynthesis of the four trees.

The response curves of P_n-C_i have similar trends although the temperature of the leaves was different (Fig. 1). P_n gradually increased with an increase in C_i. After it reached its highest value, P_n gradually decreased with a further increase in C_i. The elevated levels of CO_2 increased its competition for the same Rubisco active site (Wong, 1979) which resulted in an increase of P_n with an increase in the CO_2 concentration at the optimal condition. It has been speculated that utilization of triose phosphate and the regeneration of phosphate ions (Pi) are the limiting factors of CO_2 incorporation during the synthesis of starch and fructose if CO_2 concentration were above 700 μmol/mol (von Caemmerer and Farquhar, 1981; Farquhar and Sharkey, 1982). However, the CO_2 saturation point could increase further with an increase in temperature (Fig. 1). Taking *G. biloba* as an example, its CO_2 saturation point is 760 μmol/mol at a temperature of 28 and 30°C, 900 μmol/mol at 34°C and 1000 μmol/mol at 38°C. The results demonstrate that a higher CO_2 concentration is favorable to photosynthesis. The other three trees show similar phenomena, as shown in Fig. 1.

The optimal temperatures for photosynthesis in the four trees were lower than 32.4°C, the average temperature in the daytime during the determination (Table 1). The results suggest that a high temperature is the limiting factor of photosynthesis of the four trees during the summer. A doubling of the CO_2 concentration significantly increased P_n of the four trees, but their optimal temperature for photosynthesis varied. The optimal temperature of photosynthesis of *M. denudata* increased to 30°C from 28°C, while that of *T. japonica* was to 34°C from 30°C. The optimal temperatures of *G. biloba* and *E. ulmoides* clearly did not change at the increased level of CO_2. High temperatures would slow down photosynthesis of *G. biloba* and *E. ulmoide* and increase that of *M. denudata* and *T. japonica* if an increase of 3.5–5.2°C in atmospheric temperature were to occur at elevated CO_2 concentrations in the future (Wetherald, 1991).

Carboxylation efficiency is referred as the slope of the correlation curve between P_n and C_i (Lawlor, 1993). The rates of the carboxylation efficiency (i.e., the slopes of the linear equations) of the four trees were lower than those of the determination at 30°C when designated temperatures were above or below 30°C (Table 2). The results indicate that the optimal temperature for photosynthesis is about 30°C for these four trees in the summer, which is consistent with the results shown in Table 1. A previous study shows that a decline in Rubisco activity led to a decrease of carboxylation efficiency due to the regulation of Rubisco (Sheu and Lin, 1999).

The vapor pressure deficit (*VPD*) changed significantly with the increase in temperature under the same CO_2 concentration. However, the *VPD* did not change significantly with an increased CO_2 concentration under the same temperature (Fig. 2). This result explains that the *VPD* is sensitive to changes in temperature but not to changes in the CO_2 concentration. Additionally, the stoma is sensitive to changes in the *VPD*, which agrees with the findings of other studies (Joon and Shashi, 1991; Franks and Farquhar, 1999; Medlyn et al., 2002). The decrease of stomatal conductance (G_s) induced by

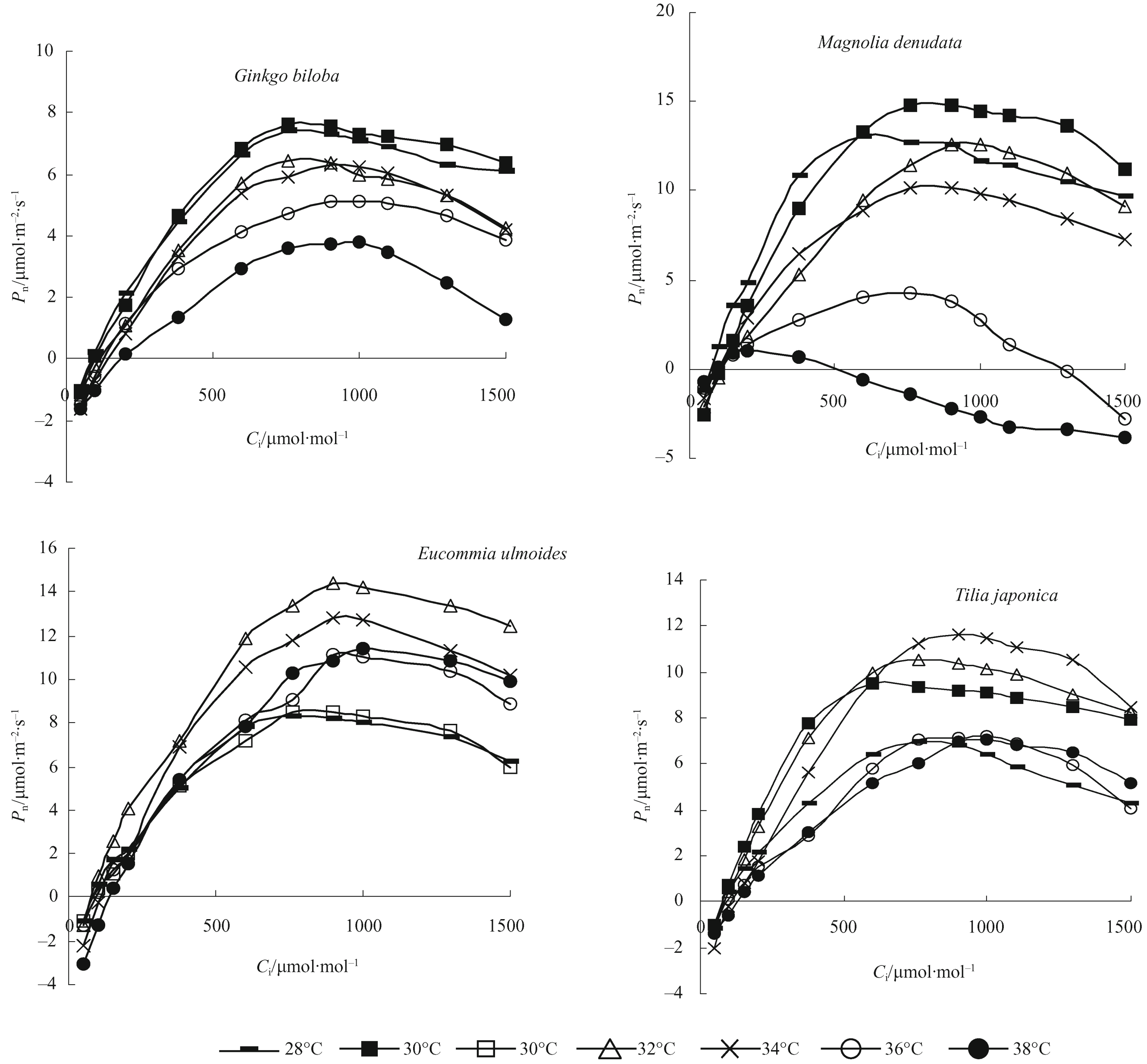

Fig. 1 Variations of net photosynthetic rates (P_n) with CO_2 concentrations at different leaf temperatures in four broad-leaved trees
Note: P_n was calculated according to the CO_2-flux passed in and out the leaf-chamber.

the increase of *VPD* could limit the assimilation of environmental CO_2, which might be one of factors why high temperatures depress photosynthesis of plants.

Many studies have indicated that elevated CO_2 concentrations induced a decrease of G_s in C_3 and C_4 herbal plants, where the effect is larger than woody plants (Farquhar and Sharkey, 1982; Cure and Acock, 1986). The levels of G_s in elevated CO_2 concentrations are close to or less than those at environmental CO_2 concentrations under the same temperature (Fig. 2).

Table 1 Optimum temperatures for net photosynthetic rate (P_n) and the P_n at optimum temperature (T_{leaf}) at ambient and doubled CO_2 concentration

CO_2 concentration	*Ginkgo biloba*		*Eucommia ulmoides*		*Magnolia denudata*		*Tilia japonica*	
	P_n	T_{leaf}	P_n	T_{leaf}	P_n	T_{leaf}	P_n	T_{leaf}
380	4.7	30	7.2	32	10.9	28	7.7	30
760	7.6	30	13.4	32	14.8	30	11.2	34

Units: CO_2 concentration, μmol/mol; P_n, μmol/(m^2·s); T_{leaf}, °C.

Table 2 Regression equations of net photosynthetic rates (P_n) against lower intercellular CO_2 concentrations (C_i) at different leaf temperatures (T_{leaf})

T_{leaf}/°C	*Ginkgo biloba*	*Eucommia ulmoides*	*Magnolia denudata*	*Tilia japonica*
25	$y = 0.0091x–0.5192$ $R^2 = 0.8921$	$y = 0.0131x–0.9109$ $R^2 = 0.968$	$y = 0.0196x–0.1820$ $R^2 = 0.8663$	$y = 0.0113x–0.6394$ $R^2 = 0.9571$
30	$y = 0.0124x–1.0144$ $R^2 = 0.9635$	$y = 0.0125x–1.3271$ $R^2 = 0.9457$	$y = 0.0246x–2.2485$ $R^2 = 0.962$	$y = 0.0147x–0.0526$ $R^2 = 0.8802$
35	$y = 0.0111x–1.6105$ $R^2 = 0.9591$	$y = 0.0179x–2.7226$ $R^2 = 0.9689$	$y = 0.0164x–1.2499$ $R^2 = 0.956$	$y = 0.0110x–1.1246$ $R^2 = 0.9853$
40	$y = 0.0076x–1.7071$ $R^2 = 0.9768$	$y = 0.0146x–1.1219$ $R^2 = 0.9715$	$y = 0.0111x–1.0599$ $R^2 = 0.9948$	$y = 0.0084x–1.7662$ $R^2 = 0.9642$

Note: y: P_n (μmol/(m²·s)), x: C_i (μmol/mol).

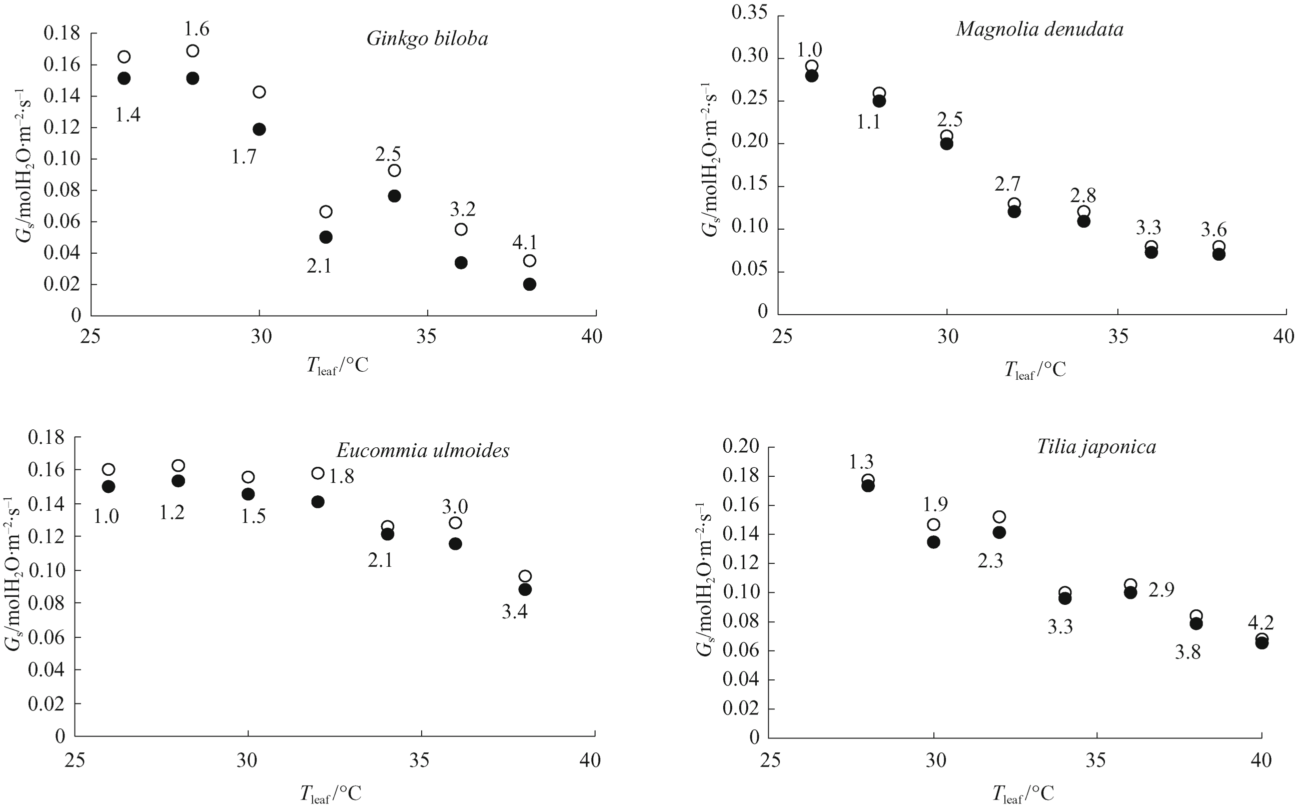

Fig. 2 Relationship between T_{leaf} and stomatal conductance G_s as affected by *VPD* at doubled CO_2 (●) and at ambient CO_2 (○) concentrations

Note: the number near the points represent levels of *VPD*.

5 Conclusions and discussion

During the sunny summer days, the atmospheric temperature in the day is beyond 30°C, which is the optimal temperature for photosynthesis in our four trees. Therefore, higher temperatures inhibit photosynthesis of these four trees. Elevated CO_2 concentrations increased P_n, while the optimal temperature for photosynthesis also changed. Clearly, the rate of photosynthesis in *G. biloba* and *E. ulmoides* did not change, while that of *M. denudata* increased to 30°C from 28°C and that of *T. japonica* to 34°C from 30°C. It is predicted that high temperatures will decrease the rate of photosynthesis of *G. biloba* and *E. ulmoide* and slow down that of *M. denudata* and *T. japonica* with elevated CO_2 concentrations in the future.

VPD is sensitive to variations in temperature but not to CO_2 concentrations; the increase of *VPD* resulted in a decrease of G_s and then limited absorbance of ambient CO_2, which might be one of reasons why high temperatures depressed the photosynthesis of the four trees. The values of G_s exhibited a decreasing trend with elevated-CO_2 concentrations at the same temperature in the four trees.

It has been long considered that the interaction between CO_2 and temperature prompts the increase of optimal temperature with elevated levels of CO_2 under light saturation (Long, 1991). The report of Idso et al. (1993) about lime trees, showing that a 300 μmol/mol increase of CO_2 concentration over ambient CO_2 levels, could lead to an increase of 75% in P_n at 31°C at the average temperature of leaves, an increase of 100% at 35°C and an increase of 200% at 42°C. These results indicate that the range of optimal temperatures for photosynthesis would be smaller given the extent of variation in atmospheric temperatures with an increase of 3.5–5.2°C by the middle of the 21st century (Wetherald, 1991; Callander et al., 1996). As a result, an increase in atmospheric temperature will counteract the advantage for photosynthesis that elevated CO_2 concentrations bring.

References

Allen L H (1994). Carbon dioxide increase: Direct impacts on crops and indirect effects mediated through anticipated climatic changes. In: Boote K J, Bennett J M, Sinclair T R, Paulsen G M eds. Physiology and Determination of Crop Yield. Madison, Wisconsin: American Society of Agronomy, Crop Science Society of America, and soil Science Society of America, 425–459

Callander B A, Harris N, Maskell K (1996). Climate Change 1995: The Science of Climate Change. Cambridge: Cambridge University Press. 151–160

Cure J D, Acock B (1986). Crop response to carbon dioxide doubling: a literature survey. Agric For Meterorol, 38:127–145

Farquhar G D, Sharkey T D (1982). Stomatal conductance and photosynthesis. Ann Rev Plant Physiol, 33: 317–345

Franks P J, Farquhar G D (1999). A relationship between humidity response, growth form and photosynthetic operating point in C_3 plants. Plant Cell Environ, 22(11): 1337–1349

Gunderson C A, Norby R J, Wullschleger S D (2000). Acclimation of photosynthesis and respiration to stimulated climatic warming in northern and southern populations of *Acer saccharum*: laboratory and field evidence. Tree Physiol, 20: 87–95

Idso S B, Kimball B A, Hendrix D L (1993). Air temperature modifies the size-enhancing effects of atmospheric CO_2 enrichment on sour orange tree leaves. Environ Exp Bot, 33(2): 293–299

Joon K, Shashi B V (1991). Modeling canopy stomatal conductance in a temperature grassland ecosystem. Agric For Meteorol, 55: 149–166

Lawlor D W (1993). Photosynthesis Molecular Physiological and Environmental Processes. Hong Kong: Longman Scientific and Technical, 260–268

Long S P (1991). Modification of response of photosynthetic productivity to rising temperature by atmospheric CO_2 concentration: Has its importance been underestimated? Plant Cell Environ, 14: 729–739

Ma Z B, Ma Q Y, Han H R, Chen X L (2004). Photosynthetic characteristics of six broad-leaved deciduous trees in Beijing. J Beijing For Univ, 26(3): 13–18 (in Chinese)

Medlyn B E, Loustau D, Delzon S (2002). Temperature response of parameters of a biochemically based model of photosynthesis. I. Seasonal changes in mature maritime pine (*Pinus pinaster* Ait.). Plant Cell Environ, 25(9): 1155–1165

Poorter H (1993). Interspecific variation in the growth response of plants to an elevated ambient CO_2 concentration. Vegetation, 104–105

Rustad L, Campbell J, Marion G, Norby R, Mitchell M, Hartley A, Cornelissen J, Gurevitch J (2001). A meta-analysis of the response of soil respiration of respiration, net N mineralization, and aboveground plant growth to experimental ecosystem warming. Oecologia, 126(4): 543–562

Sheu B H, Lin C K (1999). Photosynthetic response of seedling of the sub-tropical tree *Schima superba* with exposure to elevated carbon dioxide and temperature. Environ Exp Bot, 41(1): 57–65

von Caemmerer S, Farquhar G D (1981). Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. Planta, 153(4): 376–387

Wand S J E, Midgley G F, Jones M H, Curtis P S (1999). Responses of wild C_4 and C_3 grasses (Poaceae) species to elevated atmospheric CO_2 concentration: a meta-analytic test of current theories and perceptions. Global Change Biol, 5(6): 723–741

Wetherald R T (1991). Changes of temperature and hydrology caused by an increase of atmospheric carbon dioxide as predicted by General Circulation Models. In: Wyman R L ed. Global Climate Change and Life on Earth, Routledge. New York, London: Chapman and Hall. 1–17

Wong S C (1979). Elevated atmospheric partial pressure of CO_2 and plant growth. I. Interactions of nitrogen nutrition and photosynthetic capacity in C_3 and C_4 plants. Oecologia, 44(1): 68–74