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Carbon dioxide enrichment studies: Current knowledge and trends in plant responses

Taoufik Saleh Ksiksi

Biology Department, P. O. Box 15551, UAEU - Al-Ain, United Arab Emirates.

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Atmospheric CO_2 concentrations are increasing and studies about the impact on plant species' responses are on the rise. Unfortunately the wide range of variations in the published data is a concern when it comes to usefulness and application. Simple descriptive analyses on the published results are needed to make sense of the overall trends in plant responses to CO_2 enrichment. In the present report, 90 articles were the basis of a 395-entry database analyzed for general trends on how terrestrial plant species were reported to have responded to CO_2 fertilization. The CO_2 concentrations that were studied range between 440 ppm and 900 ppm. The results revealed that 238 and 40 entries dealt with C3 and C4 pathways; respectively. A significant regression analysis (P=0.111), between CO_2 levels and average response, was detected for C3 plant species only. This highlights the need for more studies on C4 plants which constitute an important component of primary productivity on terrestrial ecosystems. Of the total entries into the database C4 plants had the highest average magnitude of response (27.1±0.4%). At the functional group level, woody species were reported to have the highest average response (33.5±0.4%). Salinity, nutrient, defoliation and water stresses had average responses of 15.7±0.2, 12.3±0.3, 10.80±0.2 and 7.6±0.2%, respectively. In short, the above simplistic descriptive approach places much of what was studied in relation to plant responses to CO_2 fertilization into a practical perspective. Furthermore, detailed periodic analyses, including meta-analyses, are therefore highly recommended in order to summarize the body of published data, suggest up-to-date interpretations and make it available for practical use.

Key words: Stress, CO_2, floral response.

INTRODUCTION

Atmospheric CO_2 concentrations have increased by more than a third and are expected to rise because of fossil fuel and changes in land usage (Houghton, 2003). Globally as well as locally, this has led to what is currently referred to CO_2 fertilization. The impact of CO_2 enrichment studies has become better understood with the advances in the available technology dealing with field as well as greenhouse experimentations. The

E-mail: tksiksi@uaeu.ac.ae. Fax: +971-3-7671291

variations within the published data are the consequences of differences in experimental protocols adopted, plant species used, ecosystems covered, biotic and abiotic stresses applied and CO_2 concentrations tested. Added to these in-consistencies, are the complexity of scales, both temporal and spatial, and interpretations of research outcomes. Consequently, data comparisons are becoming challenging and may lead to various, and sometimes contradictory, interpretations and uses. The increase in plant production was reported to be negative (Newman et al., 1999), neutral (Ghannoum et al., 1997) or positive (Kinsman et al., 1997). Carbon dioxide enrichment trials also have a range of setups such as Free Air Carbon Dioxide protocol, also known as FACE sys- tem, (Idso and Idso, 1994), open top chambers (Kimball, 1992), controlled growth chambers (Cave et al., 1981) and even locally made chambers erected within greenhouses (Ksiksi and Youssef, 2010).

The variety of studies relating to CO_2 enrichment and plant responses has led to major challenges facing collective interpretation of results from CO_2 trials. Grass species such as *Agrostis curtisii* have been reported to have no response to CO_2 enrichment (Norton et al., 1999), while other grass species (*Lolium perenne*) were reported to have benefited by about 20% from CO_2 enrichment. A forb like *Hemizonia congesta* has been reported to benefit from CO_2 by about 69.6% (Edwards et al., 2001). Different photosynthetic pathways (eg. C3 and C4) have also been assessed with varied responses (Ebersberger et al., 2003; Mateos-Naranjo et al., 2008).

Ecosystem variations are an added complexity when trying to compare results from the variety of the published body of information on CO_2 en-richment. Studies have been reported about temperate (Kammann et al., 2005), humid (Ebersberger et al., 2003), semi-arid (Xu and Zhou, 2008) and Mediterranean (Roumet et al., 2000) ecosystems, with a wide range of re- sponses. The CO_2 concentrations that have been studied were between 440 and 900 ppm.

In this study, we conducted an analysis of 90 articles published between 1994 and 2010. Analyses included simple descriptive information on proportions of responses as well species functional groups in addition to correlation and regression analyses. The focus was on overall morphological responses of each plant species. The overall aim was to make sense of what was found in order to contribute toward future research directions as well as modeling exercises relating to the field of CO_2 enrichment and plant responses.

MATERIALS AND METHODS

Data sources

A total of 90 published papers was included in this database. The years of publications ranged between 1994 and 2010. Each of the articles included in the database has more than one entry because of different species, functional groups and/or photosynthetic pathways reported. Therefore, a total of 395 entries was analyzed in the present attempt to understand the practical implications of (CO_2 enrichment studies. Data analyzed in this report were extracted from the published data (tables and graphs) within each of the database articles. Each data entry contained the following variables: photosynthetic pathway (C3, C4 and unknown), plant functional groups (forbs, grasses, legumes, mixed and woody), biotic/abiotic stress (CO_2 (defoliation, nutrient, salinity, temperature and water) and the studied ecosystem (alpine, dry, humid, Mediterranean, spring, temperate and semi-arid). Studies dealing with Cadmium stress were not included in the summary. The magnitude of response was another important variable which was entered as an average plant species response for a specific database entry. Consequently, an average response was calculated for each functional group and photosynthetic pathway based on specific species magnitude of responses. Specific ecosystem differences were not included as the sample data covering many of the ecosystems are not enough to run a robust analysis.

Standard deviations of each group is also included in the graphs (vertical bars). Some low SD values are an indication of the limited number of articles within the studied category, in addition to low variations among the different entries. Magnitude of response above 200% were not included in the analysis. Simply because of the high variability and most of these data points were identified as outliers using Statistical Package for the Social Sciences or SPSS (Norusis, 2010). It is also worth noting that the listed article published by (Wand et al., 1999) is not included in the analysis. It was an article dealing with meta-analysis of published data.

Descriptive and analytical approach

SPSS was also used to perform a correlation analysis using Pearson correlation coefficient between the magnitude of responses and the level of CO_2 under which the study was conducted. Linear regression analyses were performed between CO_2 fertilizing levels and average magnitude of responses within each photosynthetic pathway (that is, C3, C4 and unknown). It was decided to report the exact P values to allow the reader to make their own judgment on the relevance of the statistical significance of the regression tests. The hypothesis was meant to address the question if the increase in the CO_2 content was correlated with the magnitude of plant growth, within each photosynthetic pathway (C3, C4 and unknown). The analyses did not show any significant correlation for all 3 pathways at $P \geq 0.05$.

RESULTS

The database included 90 references with a total of 395 entries. As each article has multiple entries for different species, functional groups and/or photosynthetic path- ways. Averages are reported in this section, including standard deviations. Please refer to the experimental section below for more details on the articles and resulting database included in this analysis.

Out of the total entries, the results revealed 238 and 40 entries for C3 and C4 pathways; respectively (Figure 1). All unidentified photosynthetic pathways were grouped into a class of unknowns with a total of 117 entries grouped under this rubrique. Figure 2 summarizes the magnitude of response of the different photo- synthetic pathways. Of the total entries into the database. C4 plants

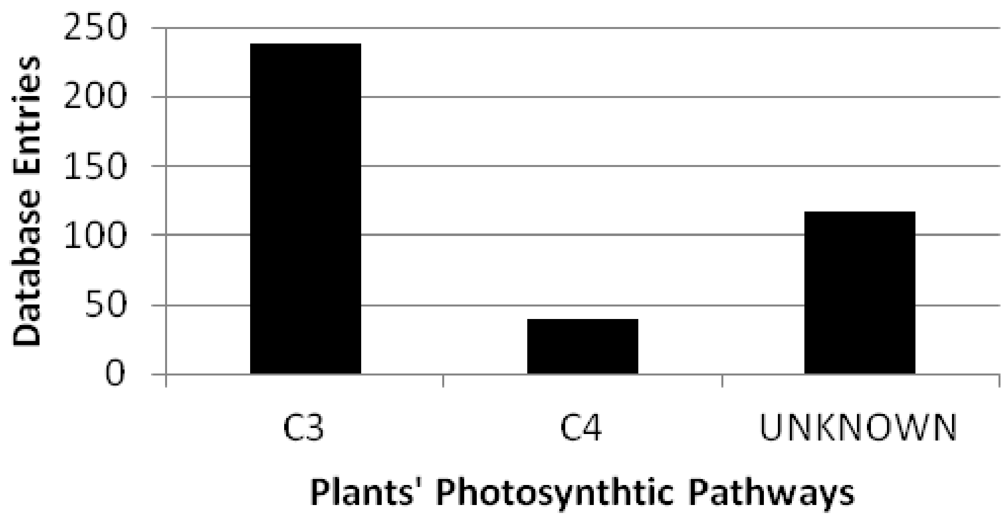

Figure 1. Variations of the different database entries from 90 publications relating to plant responses to $_{CO2}$ fertilization for C3, C4 and unknown photosynthetic pathways.

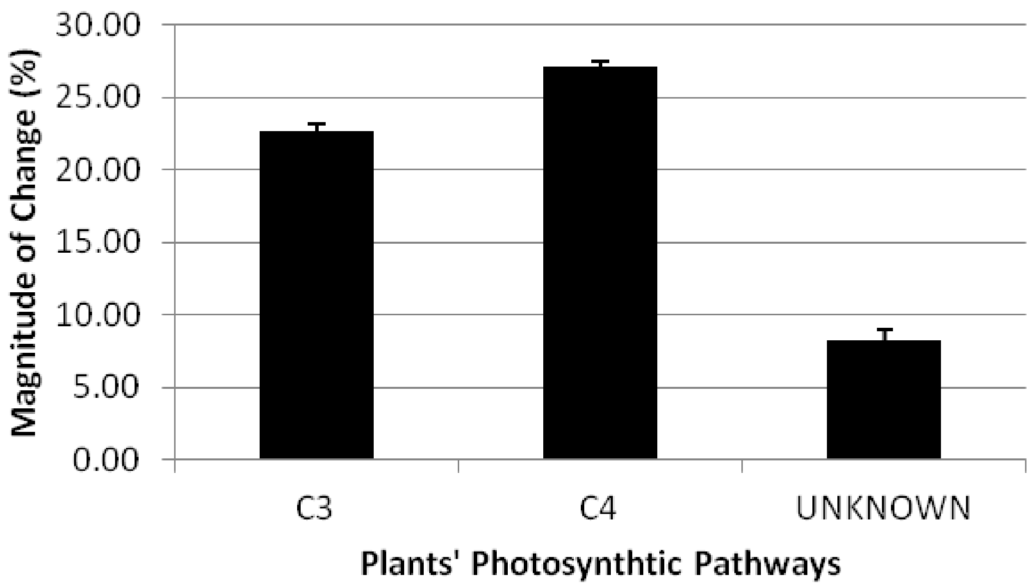

Figure 2. Magnitude of change in in published studies relating to plant responses to CO_2 fertilization for C3, C4 and unknown photosynthetic pathways. Vertical bars show Standard Deviation.

had an average magnitude of response of 27.1±0.4%. C3 plant species had an average growth response of 22.7 ±0.4% while 8.2±0.8% was the response attributed to unknown pathways of the species included in the database. For comparison purposes, the average response across pathways was 19.3 ±0.5%.

Figure 3 presents the average response for each of the studied plant functional groups. Studies with woody species reported the highest magnitude of plant responses (33.5±0.4%). Legumes were reported to have had an average magnitude of plant response of 31.4±0.5%. Forb and grass species were reported to have a growth response of 23.8±0.7% and 16.9±0.5%; respectively. Mixed species functional group had the lowest reported response of -1.25±0.3%.

Figure 4 shows the summary of the plant species responses to CO_2 enrichment for various stress factors. Among the experimental factors or stresses studied in the reviewed articles, CO_2 alone was reported to have the highest magnitude of response of about 20.4±0.6%. Temperature stress, coupled with CO_2 enrichment, had the lowest response of about 5.2 ± 0.1%. Salinity,

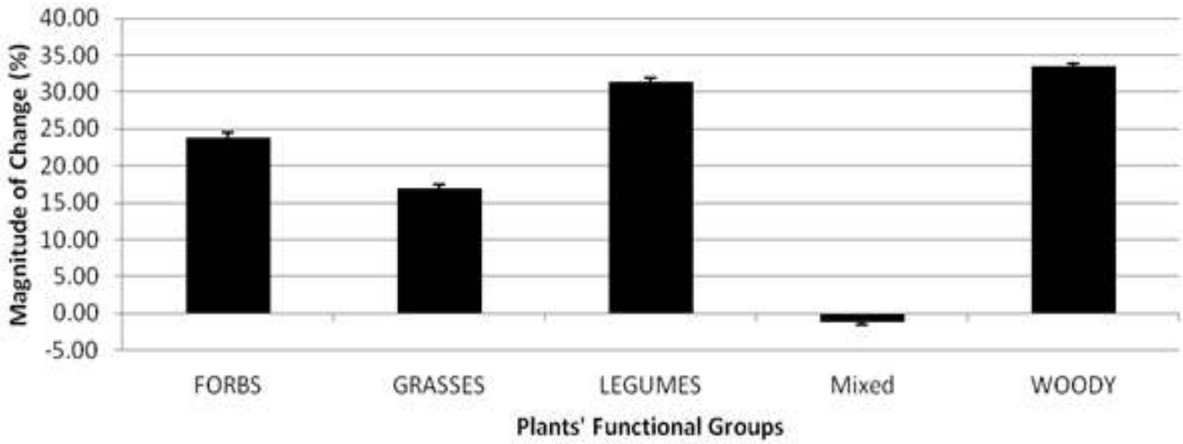

Figure 3. Magnitude of change in published studies relating to plant responses to CO_2 fertilization for different plant functional groups. Vertical bars show Standard Deviation.

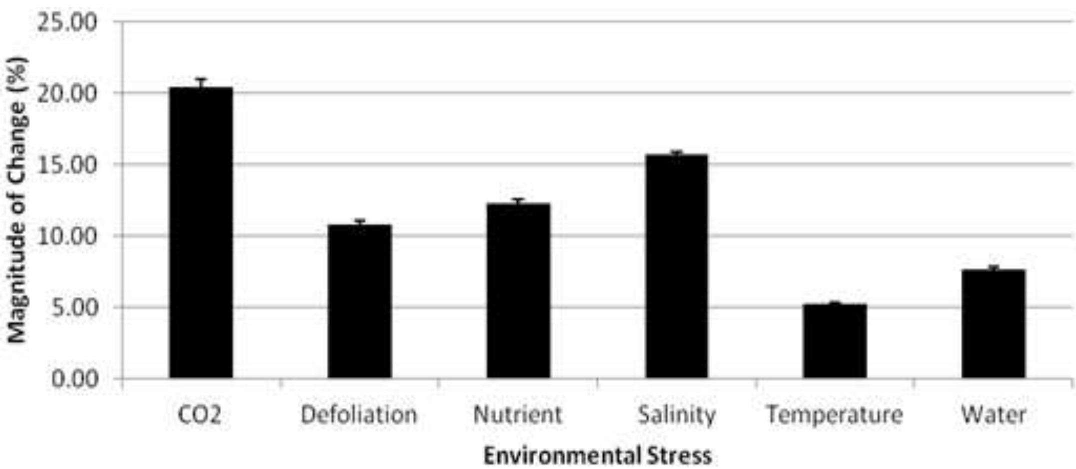

Figure 4. Magnitude of change in published studies relating to plant responses to CO_2 fertilization for C3, C4 and unknown photosynthetic pathways. Vertical bars show Standard Deviation.

nutrient, defoliation and water stresses had average responses of 15.7±0.2%, 12.3±0.3%, 10.80 ±0.2% and 7.6±0.2%; respectively.

Figure 5 presents the average plant responses within the various terrestrial ecosystems for studies dealing with CO_2 fertilization. The highest average response was reported for alpine ecosystems (187 ± 0.2%) while the second highest response was for dry ecosystems (126.3 ± 0.2%). The average magnitude of plant responses within humid and mediterranean ecosystems was 93±0.04% and 71.5±0.1%; respectively. Negative reponses, however, were reported for semi-arid and temperate ecosystems as -32.2 ±0.02% and -141.2 ±1.6%; respectively. Article number 38 (THÜRIG et al., 2003) was not included in the report as it was discovered that it dealt with a spring ecosystem, not considered a terrestrial ecosystem, in Switzerland.

DISCUSSION

Multiple factors interact under CO_2 enrichment, or fertilization, and simple predictions are to be adopted to foresee future projections at regional and global scales. Sophisticated modeling and experimentation techniques have come a long way in studying CO_2 fertilization (Norby and Luo, 2004). Moreover, interactions between CO_2 and biotic/abiotic stresses are to be simplified in order to predict possible outcomes at the species, population and ecosystem levels. Especially that extreme variations in the published data are a concern during application and modeling. Plant species groups responded differently to CO_2 enrichment (Reich et al., 2001). C4 plant species have been reported to benefit from CO_2 fertilization (Ghannoum et al., 1997). While other reports stated reduction in biomass production for C4 plants (Reich et

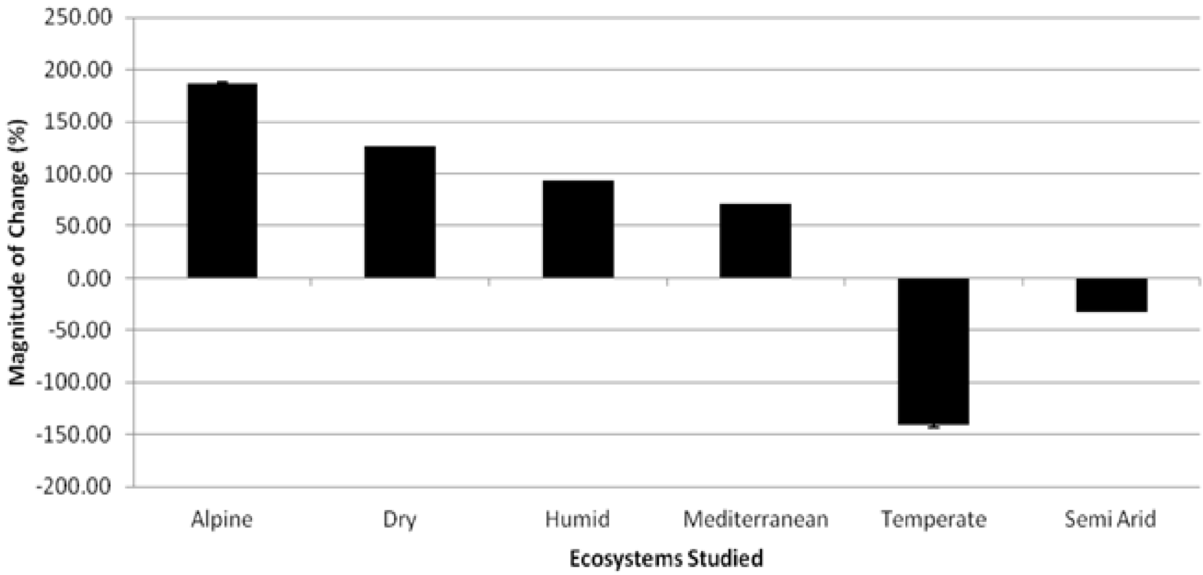

Figure 5. Magnitude of change in published studies relating to plant responses to CO_2 fertilization for various terrestrial ecosystems. Vertical bars show Standard Deviation.

al., 2001). Classifications based on functional groups may be useful but not enough to assess plant and ecosystem responses to CO_2 enrichment (Reich et al., 2001). The present 90-article assessment revealed a high bias for C3 plant species, against those with C4 photosynthetic pathways. This high-lights the need for more studies on C4 plants which constitute an important majority of primary production within terrestrial ecosystems. On average, C4 plants were reported to have growth responses of about 27.1 ±0.4%. At the functional group level, woody species had the highest magnitude of plant responses (33.5 ±0.4%), while salinity as a stress tested under CO_2 enrichment conditions – led to an average response of 15.7±0.2%. The regression analyses revealed a negative predictive power (P=0.111) between CO_2 levels and magnitude of C3 plant responses. The regression results were not significant for C4 plants and for all other plant species grouped as unknown. The above attempt places much of what was studied in relation to plant responses to CO_2 enrichment (1994 to 2010) into an understandable level which can contribute in directing future research endeavours in the field of CO_2 enrichment and plant responses. It is also believed that much of what has been reported here could be incorporated into simplistic predictive modeling of CO_2 enrichment impact on terrestrial ecosystems, functional plant groups and floral species. This does not lessen the importance of deeper and more sophisticated analyses, such as those using meta analyses, to summarize the body of published data and make it useful and practical. But whichever analysis we adopt, periodic assessments, every 12 to 15 years, are to be conducted in order to keep up with the body of research into CO_2 fertilization and terrestrial plant responses.

In short, there are unbalances in the published data on CO_2 responses of C3 vs C4 species. Stresses such as salinity, nutrient, defoliation and water have not been appropriately studied too.

Conflict of Interests

The authors have not declared any conflict of interests.

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Conflict of interests

The author has not declared any conflict of interest.

REFERENCES

Cave G, Tolley L, Strain B (1981). Effect of carbon dioxide enrichment

Ebersberger D, Niklaus P, Kandeler E (2003). Long term co2 enrichment stimulates n-mineralisation and enzyme activities in calcareous grassland. Soil Biol. Biochem. 35:965-972.

Edwards G, Clark H, Newton P (2001). The effects of elevated co 2 on seed production and seedling recruitment in a sheep-grazed pasture. Oecologia 127:383-394.

Ghannoum O, Von Caemmerer S, Barlow EW, Conroy JP (1997). The effect of CO2 enrichment and irradiance on the growth, morphology and gas exchange of a C3 (*Panicum laxum*) and a C4 (*Panicum antidotale*) grass. Funct. Plant Biol. 24(3):407-407.

Houghton R (2003). Revised estimates of the annual net flux of carbon to the atmosphere from changes in land use and land management 1850–2000. Tellus B. 55:378-90.

Idso KE, Idso SB (1994). Plant responses to atmospheric CO2 enrichment in the face of environmental constraints: a review of the past 10 years' research. Agric. For. Meteorol. 69:153-203.

Kammann C, Grünhage L, Grüters U, Janze S, Jäger H (2005). Response of aboveground grassland biomass and soil moisture to moderate long-term co2 enrichment. Basic Appl. Ecol. 6:351-65.

Kimball B (1992). Cost comparisons among free-air co2 enrichment, open- top chamber, and sunlit controlled-environment chamber methods of co2 exposure. Crit. Rev. Plant Sci. 11:265-270.

Kinsman E, Lewis C, Davies M, Young J, Francis D, Vilhar B, Ougham H (1997). Elevated co2 stimulates cells to divide in grass meris- tems: a differential effect in two natural populations of *dactylis glomerata*. Plant Cell Environ. 20:1309-1316.

Ksiksi T, Youssef T (2010). Effects of CO2 enrichment on growth parti- tioning of chloris gayana in the arid environment of the UAE. Grassland Sci. 56:183-187.

Mateos-Naranjo E, Redondo-Gómez S, Cambrollé J, Luque T, Figueroa M (2008). Growth and photosynthetic responses to zinc stress of an invasive cordgrass, spartina densiflora. Plant Biol. 10:754-62.

Newman J, Gibson D, Hickam E, Lorenz M, Adams E, Bybee L, Thompson R (1999). Elevated carbon dioxide results in smaller populations of the bird cherry–oat aphid *Rhopalosiphum* padi. Ecol. Entomol. 24(4):486-489.

Norby R, Luo Y (2004). Evaluating ecosystem responses to rising atmo- spheric co2 and global warming in a multi-factor world. New Phytol. 162:281-293.

Norton L, Firbank L, GrayA, Watkinson A (1999). Responses to elevated temperature and co2 in the perennial grass agrostis curtisii in relation to population origin. Funct. Ecol. 13:29-37.

Norusis MJ (2010). PASW statistics 18 guide to data analysis. Prentice Hall Press.

on chlorophyll content, starch content and starch grain structure in *trifolium subterraneum* leaves. Physiol. Plant. 51:171-174.

Reich P, Jean K, David T, Joseph C, David E, Mark T, Tali L, David W, Shahid N, Dan B, George H, Shibu J, Keith W, Jenny G, Wendy B (2001). Do species and functional groups differ in acquisition and use of c, n and water under varying atmospheric co2 and n availability regimes? a field test with 16 grassland species. New Phytol. 150:435-448.

Roumet C, Garnier E, Suzor H, Salager JL, Roy J (2000). Short and long-term responses of whole-plant gas exchange to elevated CO2 in four herbaceous species. Environ. Exp. Bot. 43(2):155-169.

THÜRIG B, Körner C, Stöcklin J (2003). Seed production and seed quality in a calcareous grassland in elevated CO2. Glob. Change Biol. 9(6):873-884.

Wand SJ, Midgley GY, Jones MH, Curtis PS (1999). Responses of wild c4 and c3 grass (Poaceae) species to elevated atmospheric CO2 con- centration: a meta-analytic test of current theories and perceptions. Glob. Change Biol. 5:723-741.

Xu Z, Zhou G (2008). Responses of leaf stomatal density to water sta- tus and its relationship with photosynthesis in a grass. J. Exp. Bot. 59:3317-3325.