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## Water relations in grassland and desert ecosystems exposed to elevated atmospheric CO<sub>2</sub>

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**Abstract** Atmospheric CO<sub>2</sub> enrichment may stimulate plant growth directly through (1) enhanced photosynthesis or indirectly, through (2) reduced plant water consumption and hence slower soil moisture depletion, or the combination of both. Herein we describe gas exchange, plant biomass and species responses of five native or semi-native temperate and Mediterranean grasslands and three semi-arid systems to CO<sub>2</sub> enrichment, with an emphasis on water relations. Increasing CO<sub>2</sub> led to decreased leaf conductance for water vapor, improved plant water status, altered seasonal evapotranspiration dynamics, and in most cases, periodic increases in soil water content. The extent, timing and duration of these responses varied among

ecosystems, species and years. Across the grasslands of the Kansas tallgrass prairie, Colorado shortgrass steppe and Swiss calcareous grassland, increases in aboveground biomass from CO<sub>2</sub> enrichment were relatively greater in dry years. In contrast, CO<sub>2</sub>-induced aboveground biomass increases in the Texas C<sub>3</sub>/C<sub>4</sub> grassland and the New Zealand pasture seemed little or only marginally influenced by yearly variation in soil water, while plant growth in the Mojave Desert was stimulated by CO<sub>2</sub> in a relatively wet year. Mediterranean grasslands sometimes failed to respond to CO<sub>2</sub>-related increased late-season water, whereas semiarid Negev grassland assemblages profited. Vegetative and reproductive responses to CO<sub>2</sub> were highly

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varied among species and ecosystems, and did not generally follow any predictable pattern in regard to functional groups. Results suggest that the indirect effects of CO<sub>2</sub> on plant and soil water relations may contribute substantially to experimentally induced CO<sub>2</sub>-effects, and also reflect local humidity conditions. For landscape scale predictions, this analysis calls for a clear distinction between biomass responses due to direct CO<sub>2</sub> effects on photosynthesis and those indirect CO<sub>2</sub> effects via soil moisture as documented here.

**Keywords** Biomass · Carbon dioxide enrichment · Landscape predictions · Soil water · Stomata

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## Introduction

Atmospheric CO<sub>2</sub> concentrations have risen from 280 μl l<sup>-1</sup> at the beginning of the industrial revolution to ca. 370 μl l<sup>-1</sup> today, and are projected to exceed 600 μl l<sup>-1</sup> by the end of the present century (IPCC 2001). Increases in CO<sub>2</sub> and other trace gases are implicated in global warming that occurred in the past century and are predicted to cause further increases in temperature and alter precipitation patterns in the twentieth century. However, the effect of CO<sub>2</sub> on plant and soil responses may be just as important, and in some cases, more important than projected climatic change. Thus an understanding of how ecosystems respond to rising CO<sub>2</sub> concentrations is key to predicting their future functioning and impacts in a CO<sub>2</sub> enriched world.

Research into the mechanisms underlying CO<sub>2</sub>-induced growth responses of plants has focused primarily on photosynthesis and water relations. Since C<sub>3</sub> photosynthesis is CO<sub>2</sub>-limited at present atmospheric concentrations of CO<sub>2</sub>, while C<sub>4</sub> photosynthesis is saturated or nearly saturated (Bowes 1993), early predictions were that rising atmospheric CO<sub>2</sub> concentrations would enhance photosynthesis and growth more in C<sub>3</sub> than C<sub>4</sub> species (Percy and Ehleringer 1984; Bazzaz 1990). However, even though photosynthetic and growth responses tended to be greater in C<sub>3</sub> plants, the differences were often not as large as predicted by photosynthetic pathway (Poorter 1993; Wand et al. 1999). Further, regardless of photosynthetic type, photosynthetic responses to elevated CO<sub>2</sub> were often unreliable predictors of plant growth responses.

There are several reasons why photosynthetic attributes have failed to predict intermediate- or long-term plant and community productivity responses to elevated CO<sub>2</sub>, especially when determined from short-term experiments. Photosynthetic “down-regulation”, or acclimation to high CO<sub>2</sub> (Sage 1994), soil nutrient limitations (Newbery et al. 1995; Niklaus 1998; Niklaus et al. 1998a; Stöcklin et al. 1998; Stitt and Krapp 1999; Lee et al. 2001; Morgan et al. 2001a; Grünzweig and Körner 2003), and species differences in carbon allocation (Poorter 1993) have all been shown to influence plant growth responses to elevated CO<sub>2</sub>, and have often confounded CO<sub>2</sub>-productivity predictions based on photosynthetic type. But perhaps

the most important reason why photosynthetic attributes have failed in predicting plant species growth response to elevated CO<sub>2</sub> involves the second important area of plant CO<sub>2</sub> enrichment research, water relations (Körner 2000).

Increasing CO<sub>2</sub> induces stomatal closure in most herbaceous species, regardless of photosynthetic pathway (Kimball and Idso 1983; Morrison and Gifford 1983; Wand et al. 1999). This can result in reduced transpiration per unit leaf area, and under many circumstances, particularly in canopies that are aerodynamically rough or have low leaf areas, lead to reduced canopy evapotranspiration (ET) and higher soil water content compared to non CO<sub>2</sub>-enriched plant communities (Field et al. 1995). At the stand level, stomatal responses to CO<sub>2</sub> often lead to higher plant biomass and water use efficiency in CO<sub>2</sub> enriched environments (Knapp et al. 1993; Drake et al. 1997; Owensby et al. 1997; Stocker et al. 1997; Niklaus et al. 1998a; Sindhøj et al. 2000; Morgan et al. 2001a; Grünzweig and Körner 2001a; Wullschleger et al. 2002; Ferretti et al. 2003). In this paper, such water relations effects of CO<sub>2</sub> will be referred to as indirect effects or responses; as compared to the more direct photosynthetic responses of plants to CO<sub>2</sub>. These indirect effects of CO<sub>2</sub> on plant biomass production through improved water use efficiency may be especially important in drier ecosystems or at times when soil water is limiting growth. Although some limited evidence within single experimental sites indicates that soil water availability can significantly affect the CO<sub>2</sub> production response (Owensby et al. 1999; Körner 2000; Volk et al. 2000), comparisons need to be made across experimental sites and ecosystems to determine whether this response is consistent and substantial enough to account for much of the variability in CO<sub>2</sub> responses among studies and ecosystems.

A number of field and microcosm CO<sub>2</sub> enrichment studies have been completed in grassland ecosystems, and a survey of the pertinent literature reveals a wide range of responses to increases in CO<sub>2</sub>, from no biomass responses in alpine grasslands (Körner et al. 1997) and for wet years in the sub-humid tallgrass prairie (Owensby et al. 1999), to consistent and substantial production responses in the semi-arid shortgrass steppe (Morgan et al. 2001a, 2004). What could explain such variable responses to CO<sub>2</sub> in various grassland ecosystems, and how can we use such data to predict grassland responses to CO<sub>2</sub> and other aspects of global change around the world? Much of the variation in grassland production responses to CO<sub>2</sub> may be due to variability in precipitation and soil/plant water dynamics, with production in drier systems being enhanced relatively more by increased CO<sub>2</sub> than in wet systems. Native grasslands are defined in large part by water limitation (Stephenson 1990; Campbell et al. 1997). While semi-natural, human-made grasslands may be more mesic, they still generally include periods of considerable water stress. Thus, the vast majority of grasslands have the capability to respond to CO<sub>2</sub> through alterations in water relations.

**Table 1** Experimental site descriptions and key references

Experimental site	Vegetation and soils	Growing season	Temperature (C)	Precipitation (mm)	Key references
Nenzlingen, near Basel, Switzerland Lat 47°26'N, Lon 7°34'E	Humid calcareous grassland in a Swiss lowland, nutrient poor, dominated by <i>Bromus erectus</i> Rendzina soil. Top soil (10–15 cm A horizon) is a neutral to slightly basic (pH ca. 7.8) silty clay loam with 3.9% Corg and 0.33% Norg.	Apr–Oct	Mean Ann. 9.5 Sum 17.2 Win 2.3	Annual 1100 GS 700	Stocker et al. 1997; Niklaus et al. 1998b, 2001, 2003; Leadley et al. 1999; Volk et al. 2000; Niklaus and Körner 2004
North Island, New Zealand Lat 40°14'S, Lon 175°16'E	Humid grassland with mixture of legumes, C <sub>3</sub> and C <sub>4</sub> grasses and forbs, 20–25 plant species Pukepuke black sand (Mollic Psammaquent)	All year	Mean Ann. 12.9 Sum 16.8 Win 8.6	Annual 870 GS 870	Von Caemmerer et al. 2001; Edwards et al. 2001; Newton et al. 2001
Manhattan, Kan., USA 39°12'N, 96°35'W	Humid tallgrass prairie with perennial warm-season C <sub>4</sub> grasses dominated by <i>Andropogon gerardii</i> and <i>Sorghastrum nutans</i> . Species-rich C <sub>3</sub> forbs also abundant Fine Tully series soils (Ustolls to Udolls) with a 5% slope	Apr–Oct	Mean Ann. 13 Sum. 27 Win –3.0	Annual 840 GS 630	Knapp et al. 1993, 1994b; Owensby et al. 1993, 1999; Ham et al. 1995
Grassland Laboratory, Temple Tex., USA Lat 31°05'N, Lon 97°20'W	Humid C <sub>3</sub> /C <sub>4</sub> restored grassland, dominated by perennial C <sub>4</sub> grasses and C <sub>3</sub> forbs, many common to the tallgrass prairie Fine-silty carbonatic, thermal Udothentic Haplustolls	Mar–Nov	Mean Ann. 20.5 Sum. 30.9 Win 10.3	Annual 878 GS 688	Johnson et al. 2000; Anderson et al. 2001; Gill et al. 2002; Polley et al. 2002, 2003
Jasper Ridge Biol. Preserve, Calif., USA Lat 37°24'N, Lon 122°14'W	Mediterranean annual grassland on two soils: 1. C <sub>3</sub> Eurasian annual grasses, with some native perennial bunchgrasses and late annual forbs on productive sandstone soil (Dibble Series, Lithic Xerochrepts) 2. C <sub>3</sub> native annual grasses and forbs, perennial bunch-grasses and forbs on nutrient poor serpentine soils (Montara clay loam and Obispo clay)	Oct–May	Annual 582 GS ~582		Jackson et al. 1994; Field et al. 1997; Fredeen et al. 1997; Lund 2002; Shaw et al. 2002
LTFR Site Lehavim, Israel Lat 31°21'N, Lon 34°51'E	Semi-arid seasonal grassland of the Negev Desert, a species-rich C <sub>3</sub> grassland dominated by annual grasses, with many annual legume, annual forb and geophytic species Light Lithosol on calcareous bedrock	Nov–Apr	Mean Ann. 18.6 Sum 23.3 Win 14.0	Annual 304 GS 294	Grünzweig and Kömer 2000, 2001a, 2001b
Central Plains Experimental Range, Nunn, Co., USA Lat 40°50'N, Lon 104°43'W	Semi-arid shortgrass steppe, a continental grassland, with perennial C <sub>3</sub> and C <sub>4</sub> grasses, site dominated by C <sub>4</sub> <i>Bouteloua gracilis</i> , and C <sub>3</sub> <i>Pascopyrum smithii</i> and <i>Stipa comata</i> ; some annuals and forbs Remmit fine sandy loam (Ustollic camborthids)	Apr–Sep	Mean Ann. 9.0 Sum 15.6 Win 0.6	Annual 320 GS 256	Hunt et al. 1996; Morgan et al. 2001a, 2004; LeCain et al. 2003; Nelson et al. 2004
Nevada Desert FACE Facility, near Las Vegas, Nevada, USA Lat 36°49'N, Lon 115°55'W	Arid Mojave Desert, a hot, dry ecosystem containing annual and perennial grasses, forbs, and shrubs Loamy sand near surface to coarse or gravelly sands at depth (Aridosols)	March–June; additional growth at times of year depending on precipitation and temperature	Mean Ann. 17.9 Sum 28.4 Win 7.6	Annual 130 GS 93	Huxman et al. 1998a; Jordan et al. 1999; Smith et al. 2000; Hamerlynck et al. 2002; Nowak et al. 2004

To evaluate the notion that CO<sub>2</sub> biomass responses may be understood and even predicted by considering soil/plant water relations, experimental results from several CO<sub>2</sub>-enrichment studies from contrasting grasslands and one desert ecosystem were compared. We focused on responses of leaf gas exchange, soil and plant water relations, biomass and productivity, and species and plant community attributes. This presentation will be limited mostly to natural or semi-natural grasslands and semi-arid systems where available essential nutrients are not always abundant and primary production depends on natural precipitation. Such systems may be closer to a steady-state with the current environment than recently planted, fertilized or irrigated plant communities.

## Materials and methods

### Experiments and site descriptions

#### Site descriptions

The results reported in this paper are taken from several CO<sub>2</sub> enrichment studies, all of which have had some results reported elsewhere. Thus, our descriptions of the experiments will be brief, sufficient to provide a general description of the experiment and the environmental characteristics of the particular grassland. A summary of the site descriptions for the major experiments presented, including supporting references with more detailed information, can be found in Table 1. The experiments are grouped into the three major types, humid temperate grasslands, Mediterranean grasslands, and semi-arid systems.

#### Humid temperate grasslands

Two cool, humid temperate grasslands were evaluated, a calcareous, nutrient poor grassland near Basel, Switzerland and a second grassland on the North Island of New Zealand. The Swiss work was conducted in semi-natural grassland exposed for 6 years to 600  $\mu\text{l l}^{-1}$  CO<sub>2</sub> (Niklaus and Körner 2004) using screen-aided CO<sub>2</sub> control techniques (Leadley et al. 1997). The semi-natural grassland ecosystem is representative of many in Europe that were created in the Middle Ages and are sustained by humans by biomass removal. It is very rich in vascular plant species (close to 100 species per 100 m<sup>2</sup>), and is dominated by *Bromus erectus*. Livestock grazing or mowing is essential in preventing dominance of rank grass and scrub. The study pasture had been previously grazed, and management was converted to mowing for the studies, a frequent practice in these grasslands.

The New Zealand study was established on a pasture in the west of the North Island. The pasture had not been sown for at least 40 years and during that period had been managed with infrequent application of phosphate based fertilizer and grazing by a mixture of sheep, goats and cattle. Between 20 and 25 plant species are present depending on the season and these include C<sub>3</sub> grasses, C<sub>4</sub> grasses, legumes and forbs. The study began in 1997, and continues today, with continuous, year-round CO<sub>2</sub> enrichment to 475  $\mu\text{l l}^{-1}$  CO<sub>2</sub> concentration in three 12-m diameter Free Air CO<sub>2</sub> Enrichment (FACE) rings. Three same-sized ambient rings serve as controls. Sheep graze the experiment, and excrete back onto the plots. Biomass cuts are taken pre- and post-grazing. Fertilizer, typically 30 g m<sup>-2</sup> superphosphate and 5 g m<sup>-2</sup> potassium, is applied during spring each year.

Two warm, humid temperate grasslands were studied, a tallgrass prairie in Kansas and a restored C<sub>3</sub>/C<sub>4</sub> grassland in Texas. The Kansas study was conducted over 8 years (1989–1996) in native

tallgrass prairie in Manhattan, Kan. (USA), evaluating the effect of twice-ambient CO<sub>2</sub> (imposed via six 4.5-m diameter Open Top Chambers or OTCs; three maintained at present ambient CO<sub>2</sub>, the other three at twice-ambient CO<sub>2</sub>) on intact tallgrass prairie (Knapp et al. 1993; Owensby et al. 1993). Plots remained unclipped during the growing season, but the entire site was mowed in the dormant season. Half of the chamber area was regularly harvested in 0.2×0.5 m subplots for aboveground net primary productivity (ANPP). Species composition and basal cover were measured over the duration of the study.

A 4-year study (1997–2000) was conducted in a restored pasture near Temple, Texas (USA) that had been managed for at least 50 years as an intensively grazed pasture. The plant community was exposed in elongated chambers to a continuous gradient in atmospheric CO<sub>2</sub> spanning pre-historical to predicted future concentrations (200–560  $\mu\text{l l}^{-1}$ ) (Johnson et al. 2000). Cattle grazing was replaced by simulated annual mowing during the experiment. All vegetation was clipped to 5 cm height at the end of the growing season to measure aboveground biomass and to simulate late-season mowing.

#### Mediterranean grasslands

Most of the research on Mediterranean grasslands comes from research conducted at Stanford University's Jasper Ridge Biological Preserve, in San Mateo County, Calif. (USA). Two annual grassland ecosystems are featured, one on sandstone derived soils, the other on infertile serpentine soils. Results come from experiments conducted with both OTCs and FACE systems on native/semi-native grasslands and also in re-constituted grassland microcosms. Supporting research conducted on French and Italian Mediterranean grasslands is also mentioned.

#### Semi-arid systems

Experiments were carried out in three semi-arid systems: a semi-arid temperate grassland (shortgrass steppe, Colo., USA); semi-arid scrub vegetation (Mojave Desert, Nev., USA); and semi-arid seasonal grassland (Negev Desert, Israel). Two different studies were conducted in Colorado. A controlled environment study was initially conducted to evaluate responses of important shortgrass steppe species to CO<sub>2</sub>. The study was performed in deep soil columns, with dominant (*Bouteloua gracilis*, C<sub>4</sub>) and sub-dominant (*Pascopyrum smithii*, C<sub>3</sub>) grasses and soils extracted in monoculture directly from the Colorado shortgrass steppe (Morgan et al. 1994a; Hunt et al. 1996). A 5-year CO<sub>2</sub> enrichment field experiment (1997–2001) was conducted in north-eastern Colorado, near the northern limit of the shortgrass steppe, a semi-arid continental grassland on the western edge of the North American Great Plains (Lauenroth and Milchunas 1991). The experimental site had been previously grazed by cattle at a moderate rate for over 50 years. CO<sub>2</sub> enrichment to 720  $\mu\text{l l}^{-1}$  was achieved in three 4.5 m diameter OTCs each year from late March until October, and findings were contrasted to results obtained in three ambient air OTCs. Grazing was simulated by clipping half of the standing aboveground forage at mid-summer, an amount of forage removal for the recommended stocking rate.

The Nevada Desert FACE Experiment began in April 1997 and continues today in the Mojave Desert, which is the hottest, driest ecosystem in North America. The design consists of an array of three elevated CO<sub>2</sub> plots maintained at ~550  $\mu\text{l l}^{-1}$  CO<sub>2</sub> 24 h per day, 365 days per year, plus six ambient CO<sub>2</sub> plots to assess both CO<sub>2</sub> and FACE apparatus effects (Jordan et al. 1999). Since initiation of the experiment, precipitation has varied greatly, from very wet at ~240% of the long-term average during the 1998 El Niño to below average for 1999, 2000, 2001, and 2002 (83%, 76%, 79%, and 37% of long-term average, respectively). Unlike the grassland studies, there are no management practices, nor are the plants destructively sampled.



One study investigated responses of semi-arid seasonal grassland assemblages from the Long Term Ecological Research Lehavim in the northern Negev (Israel) to three CO<sub>2</sub> concentrations (280, 440 and 600 µl l<sup>-1</sup>). Communities consisted of 32 mostly annual species (all C<sub>3</sub>), including grasses, legumes, non-leguminous forbs and geophytes, grown from seeds on native soil (Grünzweig and Körner 2001b). The experimental period covered a full growing season, and ended with mature seeds at the terminal dehydration of the systems (Grünzweig and Körner 2000). Communities were grown in fully controlled high light-intensity growth chambers under dynamic simulation of climatic conditions. Systems were in large mobile containers (ca. 400 kg each), which were weighed weekly. We included this particular controlled environment study because its intensive measurements of water-related variables and drainage water collections enabled a full water budget on the ecosystem scale (Grünzweig and Körner 2001a).

#### Attributes measured

Leaf gas exchange measurements were conducted in most of the studies to evaluate photosynthetic, transpiration and leaf conductance responses of individual species. Plant and soil water status were determined using a variety of techniques, including primarily pressure chambers for water potentials, plus neutron probes, time-domain reflectometry and gravimetric measurements for soil water status. Aboveground biomass was determined in all grassland studies on a species basis, so plant community information could be evaluated along with production responses. All biomass data reported here refer to the oven-dry (55–60°C) mass of the live plant material.

#### Modeling soil water content

The DAYCENT ecosystem model (Parton et al. 1998; Del Grosso et al. 2001) was used to simulate the effects of elevated CO<sub>2</sub> on soil water content for three of the grassland sites discussed in this paper. Climate, soils, vegetation, and land management data from elevated CO<sub>2</sub> experiments conducted at the tallgrass prairie, shortgrass steppe, and California annual grassland were used to drive the simulations. DAYCENT simulates the effects of enhanced CO<sub>2</sub> by increasing maximum photosynthesis rates, decreasing transpiration demand, and increasing C/N of biomass. The parameters controlling

the magnitudes of these CO<sub>2</sub> induced responses were adjusted for each grassland based on measurements.

## Results

### Leaf gas exchange

Elevated CO<sub>2</sub> caused reductions in leaf conductance in most grassland and semi-arid species studied (Table 2; Knapp et al. 1993, 1994b; Owensby et al. 1993; Jackson et al. 1994; Morgan et al. 1994a; Lauber and Körner 1997; Bettarini et al. 1998; Hamerlynck et al. 2000, 2002; Roumet et al. 2000; Nowak et al. 2001; Grünzweig and Körner 2001a; Maherali et al. 2002; Lund 2002; LeCain et al. 2003). Occasional increases in stomatal conductance as a result of water savings during preceding dry periods under elevated CO<sub>2</sub> were observed in the Swiss calcareous grassland (Lauber and Körner 1997), the Mojave Desert (Pataki et al. 2000), and in shortgrass steppe (LeCain et al. 2003). Thus, stomatal responses to CO<sub>2</sub> involved both direct responses resulting in stomatal closure as well as more indirect responses via longer-term changes in soil water availability that sometimes resulted in a reversal of the closure response.

CO<sub>2</sub>-induced stomatal closure was generally associated with reduced leaf-level transpiration, increased leaf and stand water use efficiency (Table 2; Jackson et al. 1994; Morgan et al. 1994a, 2001a; Ham et al. 1995; Bremer et al. 1996; Stocker et al. 1997; Anderson et al. 2001; Grünzweig and Körner 2001a; Von Caemmerer et al. 2001; Polley et al. 2002; Lund 2002; LeCain et al. 2003; Ferretti et al. 2003; Nelson et al. 2004), and increased photosynthetic rates (Knapp et al. 1993, Owensby et al. 1993, Jackson et al. 1994; Knapp et al. 1994a; Huxman et al. 1998b; Hamerlynck et al. 2000; Anderson et al. 2001; Huxman and Smith 2001; Housman 2002). In some

**Table 2** Responses of plant and system attributes in eight ecosystems to CO<sub>2</sub> enrichment. Symbols indicate that responses were generally affected negatively (–), positively (+) or were unaffected (=) by growth at elevated CO<sub>2</sub>. In experiments in which more than one response was observed, the predominate response is listed first, followed by the less frequent response(s). Changes in species composition (Species shift) during the course of the

experiment due to growth at elevated CO<sub>2</sub> are indicated as either *yes* or *no*. No species shift response is given for the Negev grassland since the study ran for just one growing season. Parenthetical descriptors indicate observations of: (1) leaf photosynthetic acclimation (*ac*), resulting in lowered photosynthetic capacity, (2) leaf water use efficiency (*lf*), and (3) standwater use efficiency (*st*)

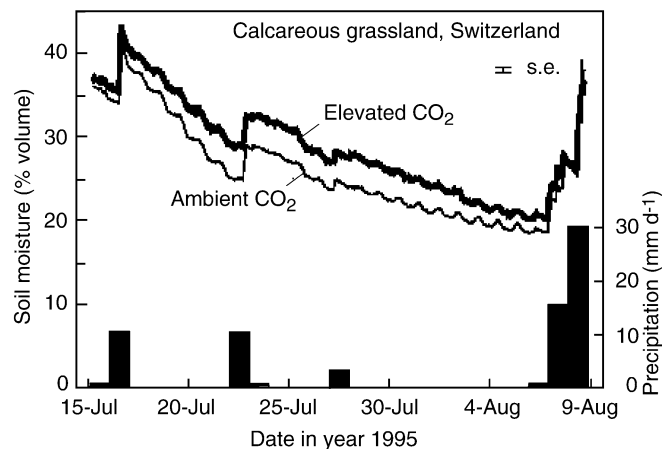
System type	Humid temperate grasslands				Mediterranean	Semi-arid systems		
	Swiss calcareous grassland	Texas C <sub>3</sub> /C <sub>4</sub> grassland	New Zealand pasture	Kansas tallgrass prairie	California annual grassland	Colorado shortgrass steppe	Nevada Mojave desert	Negev Desert simulated grassland
Responses								
Leaf conductance	–/+	–	–	–	–	–/+	–/=/+	–
Leaf photosynthesis	+(ac)*	+	+(ac)	+	+	+/(ac)	+/(ac)	
Plant water potential		+		+	+	+	+/=	
Soil water content	+	=/+	=/+	+	+	+	=	+
Biomass/production	+	+	=/+	+/=	+/=–	+	=/+	+
Water use efficiency	+(sd)	+(lf,st)	+(lf)	+(lf,st)	+/=–(st)	+(lf,st)	+/(lf,st)	+(st)
Species shift detected	yes	yes	yes	no	yes	yes	no	

experiments, increases in photosynthesis could be attributed to increased soil moisture and improved plant water relations rather than the direct CO<sub>2</sub> effect (Jackson et al. 1994; Morgan et al. 1994a, 2001; LeCain and Morgan 1998; LeCain et al. 2003), particularly for C<sub>4</sub> species (Hamerlynck et al. 1997; Owensby et al. 1997; Adam et al. 2000). However, evidence for direct photosynthetic enhancements due to CO<sub>2</sub> were also observed, generally in C<sub>3</sub> species (Jackson et al. 1994; Stocker et al. 1997; Niklaus and Körner 2004), but occasionally in C<sub>4</sub> species as well (Anderson et al. 2001; Morgan et al. 2001a). Further, photosynthetic acclimation was determined to occur commonly in C<sub>3</sub> species of the shortgrass steppe (Morgan et al. 2001a; LeCain et al. 2003), the Mojave Desert (Huxman et al. 1998b; Hamerlynck et al. 2002), and in the New Zealand (Von Caemmerer et al. 2001) and Swiss (Stocker et al. 1997; Niklaus and Körner 2004) pastures, such that photosynthetic capacity was often reduced in C<sub>3</sub> plants grown under CO<sub>2</sub>-enriched atmospheres. Photosynthetic acclimation under elevated CO<sub>2</sub> was linked to a reduction in foliage N concentration (Morgan et al. 2001a; LeCain et al. 2003; King et al. 2004; Niklaus and Körner 2004).

#### Plant/soil water relations and evapotranspiration

The reduced leaf conductance and transpiration occurring under elevated CO<sub>2</sub> often led to increased leaf or stem xylem water potential (Table 2; Morgan et al. 1994b, 1998, 2001a; Jackson et al. 1994; Roy et al. 1996; Field et al. 1997; Huxman et al. 1998b; Lund 2002; Housman 2002; Hamerlynck et al. 2002, Nelson et al. 2004). However, while leaf-level conductance under elevated CO<sub>2</sub> was often 20–50% of ambient, ecosystem-scale effects on ET and soil moisture rarely exceeded 20% (Knapp et al. 1996, 1999; Field et al. 1997; Fredeen et al. 1997; Owensby et al. 1997; Hamerlynck et al. 1997; Stocker et al. 1997; Niklaus et al. 1998a; Zavaleta 2001; Grünzweig and Körner 2001a; Lund 2002; Polley et al. 2002; Nelson et al. 2004; Nowak et al. 2004).

For example, in the calcareous grassland, leaf conductance was approximately halved in most species, including the dominant grass *Bromus erectus* (Lauber and Körner 1997). Due to aerodynamic constraints this led to only a ca. 6% reduction in ET (Stocker et al. 1997), but resulted in generally higher soil moisture content under elevated CO<sub>2</sub> during rainless periods (Fig. 1; Niklaus 1998b; Niklaus et al. 2003). During drying cycles, ambient soils dried out faster due to higher rates of ET; after prolonged drought, ET in ambient CO<sub>2</sub> was therefore lower than in elevated CO<sub>2</sub>, and the soil moisture difference between treatments became smaller as the soil became dry (Fig. 1). However, the CO<sub>2</sub>-effect on soil moisture never disappeared, except after heavy rainfall when soils in both treatments became saturated (Niklaus et al. 1998b). Elevated CO<sub>2</sub> soils therefore were always wetter when water might have been limiting.



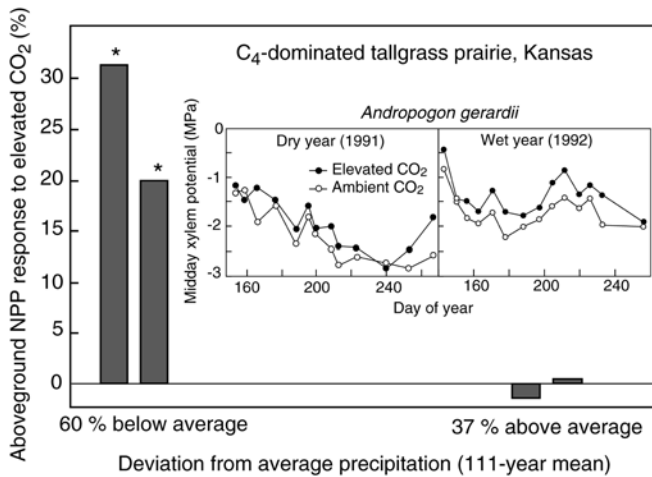
**Fig. 1** Despite increases in biomass and LAI, reductions in leaf conductance resulted in reduced evapotranspiration at elevated CO<sub>2</sub> (–6% averaged across all measurements; Stocker et al. 1997) and soil moisture increased at elevated CO<sub>2</sub>. The figure shows a representative drying cycle during summer of the 2nd year of treatment (Niklaus et al. 1998b)

In the New Zealand pasture, soil moisture content had a strong seasonal pattern with very low levels at the start of each year (summer in the Southern hemisphere) (Newton et al. 2003). Despite greater leaf water use efficiency (1.28 times) at elevated CO<sub>2</sub> (Von Caemmerer et al. 2001), average soil moisture content for the four years 1998–2002 was not different between CO<sub>2</sub> treatments (mean 21.1%).

In warm, mesic grasslands of Kansas and Texas, CO<sub>2</sub> enrichment decreased stomatal conductance (Knapp et al. 1993, 1994b; Owensby et al. 1993; Maherali et al. 2002), and improved plant (Fig. 2, see inset panel) and soil water status (Knapp et al. 1996, 1999; Owensby et al. 1997; Hamerlynck et al. 1997; Polley et al. 2002). Ham et al. (1995) reported fairly substantial impacts on water balance in the tallgrass prairie, with 22% reductions in daily ET under elevated CO<sub>2</sub>.

In Mediterranean grassland, community ET was significantly reduced at elevated CO<sub>2</sub> (Field et al. 1997; Fredeen et al. 1997; Lund 2002), and leaf and xylem water potential were increased in a majority of species (Jackson et al. 1994; Roy et al. 1996; Field et al. 1997; Lund 2002). The reduction in plant water-use resulted in a marked increase in soil water content, extension of the growing season into the dry summer, and enhanced drainage of water below the rooting zone (Field et al. 1997; Fredeen et al. 1997; Zavaleta 2001; Lund 2002).

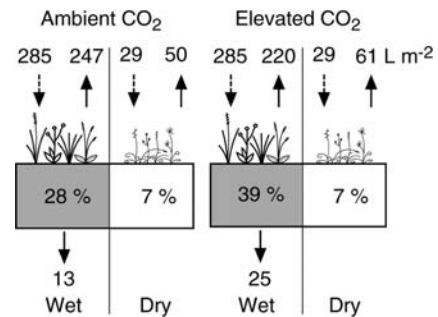
CO<sub>2</sub>-related reductions in leaf conductance of shortgrass steppe species (Morgan et al. 2001b; LeCain et al. 2003) led to 24–30% increases in leaf water potential (Nelson et al. 2004), regardless of soil water content (Fig. 3c, d). Over the 5-year period, soil water content was enhanced an average 13% over the ambient treatment (LeCain et al. 2003; Nelson et al. 2004). Conditions that led to similar soil water contents among treatments were large precipitation events, which re-charged the soil profile, and long dry periods, which caused a convergence in soil water to 1 m depth (Fig. 3d). Water conservation



**Fig. 2** Responsiveness of aboveground net primary production (NPP) to elevated CO<sub>2</sub> concentrations (double ambient) relative to ambient levels in Kansas tallgrass prairie (data from Owensby et al. 1999). Data shown are for the two wettest (1992, 1993) and the two driest (1991, 1994) years during an 8-year study. Asterisks indicate significant differences between elevated and ambient treatments. Insets show the seasonal course of midday xylem potential for *Andropogon gerardii*, the dominant C<sub>4</sub> grass in this grassland, at elevated and ambient CO<sub>2</sub> concentrations for both a dry year (1991) and a wet year (1992; from Knapp et al. 1993)

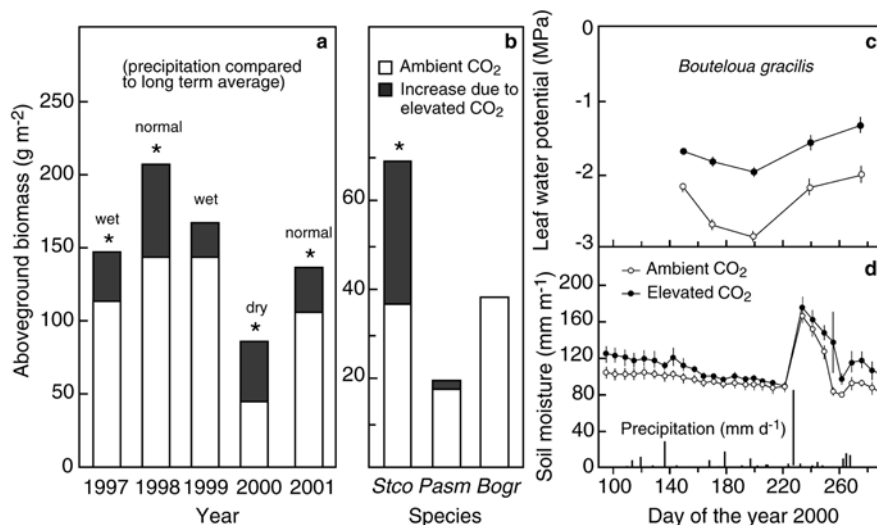
due to elevated CO<sub>2</sub> did not translate into less seasonal ET, but instead resulted in water being withdrawn more slowly from the soil, with subsequent increases in biomass, and in leaf (Ferretti et al. 2003) and stand (Nelson et al. 2004) water use efficiencies.

In semi-arid seasonal grassland assemblages of Israel, a complete water balance showed a 10% decrease in ET and consequently almost doubling of deep drainage at elevated



**Fig. 4** Water balance (in L m<sup>-2</sup>) of model ecosystems at low (280 µl l<sup>-1</sup>) and high CO<sub>2</sub> (600 µl l<sup>-1</sup>). Cumulative precipitation (dotted arrows), evapotranspiration (full upward arrows) and drainage (full downward arrows) were separated for the wet (112 days; 'wet') and the dry period of the growing season (49 days; 'dry', ending with dehydration of vegetation and soil). Soil water content (shown in boxes; profile depth 0.35 m) was measured at the end of the respective periods. Note that evapotranspiration was higher at high CO<sub>2</sub> during the dry period because more moisture was left over from the wet period. For growth conditions, see Grünzweig and Körner (2001a)

compared to pre-industrial CO<sub>2</sub> during the wet part of the growing season, i.e. the main growth period (Fig. 4). Reduced depletion of soil water at elevated CO<sub>2</sub> throughout most of the rainy period resulted in 40% higher soil moisture at the beginning of the drier, later part of the growing season. Thus, more moisture was left in the soil towards the end of the season, allowing for an extended period of water extraction by plants into the dry summer (Grünzweig and Körner 2001a). This explains both the increased ET at elevated CO<sub>2</sub> during the dry part of the growing season and the identical soil moisture content under both CO<sub>2</sub> treatments at the end of the season (Fig. 4).



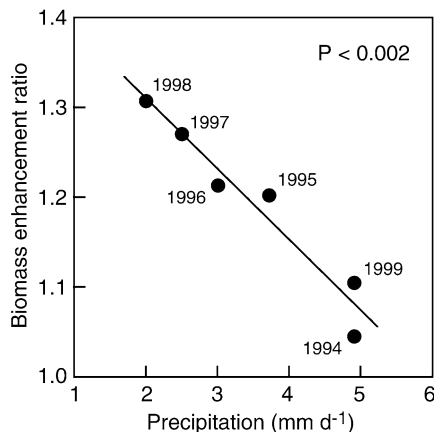
**Fig. 3** Yearly aboveground total plant biomass (panel a), species aboveground biomass averaged across 5 years (panel b: species are *Sto* *Stipa comata*; *Pasm* *Pascopyrum smithii*, and *Bogr* *Bouteloua gracilis*), leaf water potentials for the dominant C<sub>4</sub> grass, *Bouteolua gracilis* (panel c: year 2000), and soil water content (panel d: year 2000) in Colorado shortgrass steppe under present ambient and elevated (720 µl l<sup>-1</sup>) CO<sub>2</sub> concentrations. In panels a and b, \*

indicates significant CO<sub>2</sub> treatment effect for years and species, respectively, at  $P < 0.05$  as determined by Tukey's means comparisons test. Standard error bars are given with means in panels c and d. Water relations data for 2000 are typical of what occurred in other study years (Morgan et al. 2001a; Nelson et al. 2004)

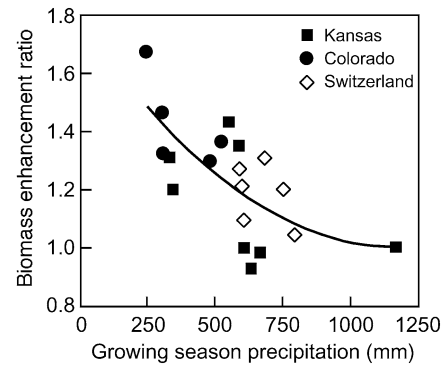
## Productivity and biomass

Elevated CO<sub>2</sub> increased plant biomass in many, but not all, studies (Table 2). In some studies, biomass responses to CO<sub>2</sub> were related to interannual variability in soil/plant water availability. Increased productivity in Kansas occurred primarily during years with considerable water limitation (Fig. 2). In the Swiss calcareous grassland, the ratio of biomass at elevated CO<sub>2</sub> to biomass at ambient CO<sub>2</sub> (the Biomass Enhancement Ratio; BER, Poorter and Navas 2003) was strongly correlated with precipitation in the 6 weeks prior to biomass harvest in June and October of each year, explaining over 95% of the observed variance (Fig. 5; Niklaus and Körner 2004); precipitation during other periods was not related to the observed CO<sub>2</sub> response. In the shortgrass steppe, doubling CO<sub>2</sub> concentration enhanced aboveground biomass throughout the study (Morgan et al. 2001a, 2004), with relative biomass responses ranging from as little as 16% (ns) in a wet year (1999) to 93% in a dry year (2000) (Fig. 3a). To evaluate the overall effects of CO<sub>2</sub> on plant biomass in these water-sensitive grasslands, BER was calculated for the tallgrass prairie, shortgrass steppe, and calcareous grassland sites and related to growing season precipitation. The resulting relationship (Fig. 6;  $r^2=0.48$ ,  $P=0.005$ ) suggests higher BER in drier site-years, and little to no CO<sub>2</sub>-induced plant biomass enhancements in these native or semi-native grasslands when growing season precipitation exceeds 750 mm.

In Mediterranean grasslands, total community biomass (aboveground + belowground) increased significantly at elevated CO<sub>2</sub> in California (Field et al. 1997; Joel et al. 2001), but was not affected in a French (Navas et al. 1995), an additional Californian (Shaw et al. 2002) or in an Italian ecosystem (Körner and Miglietta 1994). The 2–4 week extension of the growing season by elevated CO<sub>2</sub> in these systems was correlated with several plant responses to CO<sub>2</sub> enrichment: late-season canopy photosynthesis was increased, which translated into a small



**Fig. 5** The ratio of elevated to ambient CO<sub>2</sub> aboveground plant biomass (Biomass Enhancement Ratio, BER) in Swiss calcareous grassland as a function of precipitation 6 weeks prior to biomass harvests in June and October each year. Reproduced with permission from Niklaus and Körner 2004



**Fig. 6** The ratio of elevated to ambient CO<sub>2</sub> aboveground plant biomass (Biomass Enhancement Ratio, BER) in Kansas tallgrass prairie, Colorado shortgrass steppe and Swiss calcareous grasslands as a function of yearly precipitation. The fitted line has an  $r^2$  of 0.48,  $P=0.005$

increase in net annual ecosystem production (Lund 2002); plant senescence was delayed (Zavaleta 2001); CO<sub>2</sub> effects on biomass of some early- and mid-flowering species did not appear until late in the growing season (Joel et al. 2001).

In the semi-arid seasonal grassland assemblages of the Negev, community biomass was increased by 15% at elevated compared to pre-industrial CO<sub>2</sub> (Grünzweig and Körner 2001a). This response was in large part due to the moisture-related extension of the growing season, which extended the flowering period of a late-flowering legume that dominated the biomass response (Grünzweig and Körner 2001b), and resulted in greater reproductive than vegetative responses to elevated CO<sub>2</sub> at the community and the species level (Grünzweig and Körner 2001a, 2001b).

The water relations aspect of the CO<sub>2</sub> production response discussed previously was either not evident in other investigations, or the response was reversed. CO<sub>2</sub> enrichment increased aboveground biomass in Texas, even in years with above-average precipitation (Polley et al. 2003). In the Mojave Desert, large increases in new shoot biomass for shrubs were found at elevated CO<sub>2</sub> in the wet year 1998 (Smith et al. 2000; Hamerlynck et al. 2002; Housman 2002). In dry years, the CO<sub>2</sub>-induced increase in shoot production typically was small, except for the winter-deciduous shrub *Krameria* that had similar CO<sub>2</sub>-induced increases in wet and dry years. In the New Zealand temperate pasture, average annual standing biomass (harvests being accrued with each year) for the period 1998–2002 was 733 g m<sup>-2</sup> at ambient and 786 g m<sup>-2</sup> at elevated CO<sub>2</sub>. Annual aboveground growth was not different between treatments but differences were apparent at some times of the year. In particular, the stimulation due to elevated CO<sub>2</sub> was strongest during the moist spring period (Morgan et al. 2001b).



## Community composition and species responses

Although shifts in plant species composition to elevated CO<sub>2</sub> were common (Table 2), no consistent pattern of CO<sub>2</sub>-sensitive functional groups was observed. In the Swiss calcareous grassland, no significant CO<sub>2</sub> response in biomass of the matrix-forming species *Bromus erectus* (50% of community biomass) was detected, despite relatively high statistical power. The subdominant sedge *Carex flacca*, however, increased biomass several times under elevated CO<sub>2</sub>. All other subdominants did not respond significantly to CO<sub>2</sub> enrichment, nor were effects detected for the other ca. 30 species present. More aggregate measures of community structure showed increases in evenness, primarily due to an increase in low-abundance species (Leadley et al. 1999; cf. Niklaus et al. 2001; Niklaus and Körner 2004). The likely dominant mechanism for this increase is an increase in seed production (Thürig et al. 2003) and increased seedling survival due to higher soil moisture (cf. Niklaus et al. 2001). The effect of soil moisture on species competition was also investigated in experimental swards consisting of *Bromus erectus* and *Carex flacca*. These species exhibited differential responses to CO<sub>2</sub> as water supply was changed. *B. erectus* had little response to CO<sub>2</sub> at intermediate soil moisture, whereas *C. flacca* was most responsive under these conditions. On a per tiller basis, the CO<sub>2</sub> enrichment effect on *B. erectus* was solely indirect, due to moister soils, whereas *C. flacca* also showed direct photosynthetic effects of elevated CO<sub>2</sub> (Volk et al. 2000).

A greater abundance of legumes and forbs (Edwards et al. 2001; Newton et al. 2001) was observed in the elevated CO<sub>2</sub> New Zealand Pasture. These changes could not be simply ascribed to increased rates of photosynthesis as after 1 and 2 years of enrichment there was strong acclimation of photosynthesis among the more abundant legumes (*Trifolium repens* and *T. subterraneum*; Von Caemmerer et al. 2001). In addition, individual plants (seedlings or adults) of the more abundant legumes (*Trifolium repens* and *T. subterraneum*) or forbs (*Hypochaeris radicata*, *Leontodon saxatilis*) were not larger at elevated CO<sub>2</sub> (Edwards et al. 2001). Increased seed dispersal of these species at elevated CO<sub>2</sub> and the positive relationship between the amount of seed dispersed and seedling recruitment (Edwards et al. 2001) suggest a possible mechanism for the increased abundance of legumes and forbs.

In Kansas, increases in aboveground production that occurred in dry years was attributed to responses of the dominant C<sub>4</sub> grasses (Owensby et al. 1993, 1999). Few of the predicted shifts to greater C<sub>3</sub> plant abundance were noted in this long-term study with relative abundance of the dominant C<sub>4</sub> grasses changing little after long-term exposure to elevated CO<sub>2</sub>. Indeed, relative cover of C<sub>3</sub> grasses declined and that of C<sub>3</sub> forbs increased only slightly at elevated CO<sub>2</sub> (Owensby et al. 1999). This pattern reflects the primary mechanism by which elevated CO<sub>2</sub> impacted this grassland: through improved water relations in mid- to late season when many cool season C<sub>3</sub>

species are past peak growth but C<sub>4</sub> species are still active (Knapp et al. 1993; Owensby et al. 1993). However, in Texas both the dominant grasses and perennial forbs had strong production response to elevated CO<sub>2</sub>, depending on the year (Polley et al. 2003). Increasing CO<sub>2</sub> accelerated a successional shift initiated by release from grazing in which C<sub>3</sub> forbs increased at the expense of the dominant C<sub>4</sub> grass.

In Mediterranean grasslands, a majority of the numerous species tested for biomass and reproductive output were not significantly affected by CO<sub>2</sub> enrichment (Körner and Miglietta 1994; Navas et al. 1995; Chiariello and Field 1996; Körner 2000; Joel et al. 2001; Zavaleta et al. 2003). A few species gained and others lost at high CO<sub>2</sub>, with several legumes among the winners. Legumes might have taken advantage of the extension of the growing season (indeterminate growth type enabling continued growth after the onset of flowering) or were released from N limitation under elevated CO<sub>2</sub> (Verville 2000), with higher moisture enhancing phosphate availability. In a recent California grassland experiment, elevated CO<sub>2</sub> reduced diversity, with substantial losses of two annual forbs, *Epilobium brachycarpum* and *Erodium botrys* and one annual grass, *Bromus diandrus* (Zavaleta et al. 2003). Elevated CO<sub>2</sub> increased soil moisture as much as a precipitation treatment in 2 of 3 years, but CO<sub>2</sub> effects on the community could not be explained by water relations responses, as in a previous report (Chiariello and Field 1996). Delayed growth and senescence of grasses (E.E. Cleland, unpublished data) under elevated CO<sub>2</sub> remain as possible factors underlying the dominant effects of elevated CO<sub>2</sub>.

In Colorado, photosynthesis, water relations and growth of *Pascopyrum smithii* (C<sub>3</sub>) and *Bouteloua gracilis* (C<sub>4</sub>) had initially been shown to respond positively to increased CO<sub>2</sub> in controlled environment studies utilizing deep soil/plant columns comprised of single species and native soils of the shortgrass steppe (Morgan et al. 1994a, 1994b, 1998; Hunt et al. 1996). In the plant community selected for the OTC study, these two important site co-dominants were present in substantial proportions with another important C<sub>3</sub> grass of the shortgrass steppe, *Stipa comata*. Yet CO<sub>2</sub>-induced production responses were observed only for *S. comata*, (Morgan et al. 2004), despite the fact that water relations in all three species were enhanced under elevated CO<sub>2</sub>, and higher soil and plant water status sometimes increased photosynthesis of both *P. smithii* and *B. gracilis* (LeCain et al. 2003; Nelson et al. 2004). Increased seed recruitment of *S. comata* appeared to be an important factor in its exclusive production response in the shortgrass steppe OTC experiment (Morgan et al. 2004).

In the semi-arid assemblages of Israel, vegetative biomass and particularly reproductive output of most legumes increased and those of Brassicaceae tended to decrease at elevated CO<sub>2</sub> (Grünzweig and Körner 2001b). The increased seed yield of legumes and a hemiparasite (Grünzweig and Körner 2001b) and the reduced seed quality and germination success of several grasses (Grünzweig and Körner 2000) suggested a future shift in

species composition. The massive stimulation of the late-flowering legume *Onobrychis crista-galli* determined the CO<sub>2</sub> response of the entire community (Grünzweig and Körner 2001a). As a relatively mesic legume species, *O. crista-galli* profited from higher soil moisture under elevated CO<sub>2</sub> at the end of the growing season, thus suggesting increased water availability as the main mechanism for the community response to CO<sub>2</sub> enrichment.

In the Mojave Desert, elevated CO<sub>2</sub> increased the density, size, and seed production of an exotic annual grass, *Bromus madritensis* ssp. *rubens*, in the wet year 1998, and this CO<sub>2</sub> effect was further enhanced in nutrient-rich microhabitats (Smith et al. 2000). Native annuals responded to elevated CO<sub>2</sub> with fewer but larger plants with little change in seed production. Despite much higher seed production at elevated CO<sub>2</sub>, results from both controlled-environment and field FACE conditions indicate that *Bromus* produces smaller seeds of lower quality (Huxman et al. 1998a; 1999), which in turn produce seedlings with reduced initial growth rates (Huxman et al. 1998a, 2001). Results from native annuals, such as the grass *Vulpia octoflora*, do not show lower seed quality. During dry years (1999–2002), either no annuals germinated or the effects of CO<sub>2</sub> on annual productivity were not significant. No significant species shift has yet been observed in the Mojave due to elevated CO<sub>2</sub>, although the duration of the experiment has probably not been sufficiently long to detect such a change in this desert ecosystem.

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## Discussion

Examination of plant responses to CO<sub>2</sub> enrichment in experiments mostly conducted in the field at several different sites in humid temperate grasslands, Mediterranean type grasslands and in native semi-arid vegetation confirmed that the indirect responses of these systems through CO<sub>2</sub>-induced alterations in soil/plant water relations are important. Increasing CO<sub>2</sub> led to decreased leaf conductance, improved plant water status, altered stand ET dynamics, and in most cases, periodic increases in soil water content (Table 2). The extent, timing and duration of these responses varied among ecosystems, species and years, but much of the CO<sub>2</sub> effects could be attributed to moisture effects. The indirect effect of CO<sub>2</sub> on soil/plant water relations may even dominate the biomass and plant community responses of drier ecosystems, and thus may be more important than the direct photosynthetic responses to CO<sub>2</sub> enrichment.

### Native and semi-natural systems

The presence and nature of native grasslands are largely determined by seasonal water dynamics (Stephenson 1990; Campbell 1997). Thus, the functioning of such ecosystems should be especially sensitive to perturbations

in soil/plant water dynamics. Two such grasslands were evaluated herein: the tallgrass prairie in Kansas, and the shortgrass steppe in Colorado. The Swiss calcareous grassland, although maintained by human activities, has low fertility and a plant community that has evolved over the centuries, and also appears driven strongly by water relations (Volk et al. 2000). The negative correlation between biomass enhancement ratio (BER) and annual precipitation determined from 19 site-years of experiments conducted in these three grasslands (Fig. 6) confirms that improved water relations are a key feature in the CO<sub>2</sub> biomass responses in these ecosystems. The annual precipitation/BER relationship is admittedly a simple one that does not account for seasonal variations or other important aspects of climate that co-affect plant growth, like temperature, nor does it explicitly document soil water content. However, an approximately 50% contribution to the variation in BER of seasonal precipitation suggests a major soil moisture influence on CO<sub>2</sub>-induced biomass responses.

In the Kansas tallgrass prairie, dominant C<sub>4</sub> grasses control in large part the water relations and biomass responses to CO<sub>2</sub> enrichment (Hamerlynck et al. 1997; Owensby et al. 1997; Adam et al. 2000), and the effect of CO<sub>2</sub> enrichment was more important in relatively dry years. In the shortgrass steppe, low soil and plant N resulted in consistent photosynthetic acclimation that precluded direct photosynthetic responses of C<sub>3</sub> grasses to CO<sub>2</sub> enrichment (Morgan et al. 2001a; LeCain et al. 2003). This type of nutrient limitation likely applies to many native and semi-natural grasslands, and may explain why plant biomass responses of such ecosystems to CO<sub>2</sub> are driven so strongly by water relations.

One of the main mechanisms by which CO<sub>2</sub> enrichment can enhance production increases as systems become progressively drier is extension of the growing season (Polley et al. 2000). Increases in growing season length have typically been discussed in terms of the final days of the growing season (Chiariello and Field 1996; Field et al. 1997; Fredeen et al. 1997; Grünzweig and Körner 2001a; Lund 2002), but extensions may also occur by decreasing the number of periodic drought days throughout the growing season, thereby extending the effective growing season. These effects are illustrated by results from the model DAYCENT for a Mediterranean-type annual grassland in California and two Great Plains grasslands (tallgrass prairie and shortgrass steppe; Fig. 7). While precipitation in Great Plains grasslands tends to be concentrated in spring, substantial rainfall occurs throughout the growing season, accompanied by periodic dry spells. In contrast, Mediterranean climates like the California annual grassland are characterized by a several month-long rainy season that culminates in a single season-end dry period. Such a rainfall pattern yields a CO<sub>2</sub> water relations benefit mostly near the end of the growing season only, whereas multiple in-season wet/dry cycles are possible in the Great Plains grasslands (Fig. 7). This may partly explain the more consistent and substantial CO<sub>2</sub>-induced production increases seen in Great Plains grass-

lands, especially the semi-arid shortgrass steppe, compared to Mediterranean grasslands.

In the Mojave Desert, CO<sub>2</sub>-induced biomass and plant recruitment responses were significantly greater in a wet year. Further, despite reductions in leaf conductance of some species under elevated CO<sub>2</sub>, effects of CO<sub>2</sub> on soil water dynamics were generally not detected in this desert ecosystem (Nowak et al. 2004). This implies that a certain base level of water availability is necessary to detect substantial CO<sub>2</sub>-induced soil water and plant production responses. Under conditions of the Mojave Desert, that critical amount of precipitation was between 150 and 250 mm year<sup>-1</sup>.

In addition to its more direct effect on plant performance, percolation of water saved under CO<sub>2</sub> enrichment to lower soil depths is certain to have important consequences on plant community dynamics. This percolation was demonstrated in the semi-arid seasonal grassland assemblages from the northern Negev (Fig. 4), as well as in the shortgrass steppe (Nelson et al. 2004), and was predicted in a modeling exercise using the DAYCENT model (W.J. Parton et al, personal communication) in which a doubling of atmospheric CO<sub>2</sub> increased deep drainage by 100–200% in the shortgrass steppe of Colorado and the tallgrass prairie of Kansas. CO<sub>2</sub>-induced increases in deep drainage were predicted only during wet years, and the Kansas site had substantially more drainage below the rooting depth (rainfall is more than two times

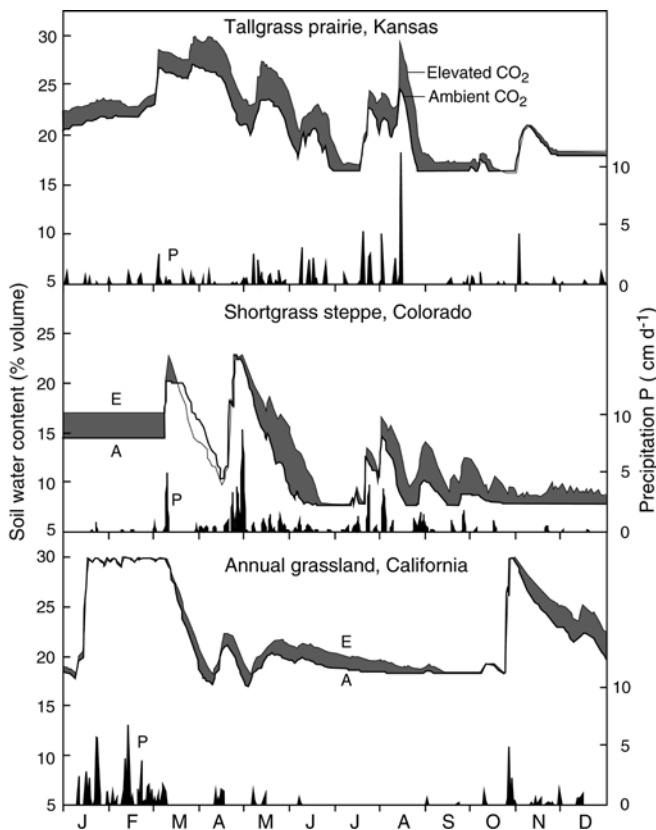
greater at the Kansas site). Movement of water into deeper soils may open niches for deeper-rooted species (Polley et al. 1997; Nelson et al. 2004), and is certain to alter competitive interactions for soil water among plant species. However, CO<sub>2</sub>-induced deep-water drainage beyond the plant community rooting zone represents a loss of available plant water to the local community with important implications for larger scale groundwater recharge hydrology.

### Mesic grasslands

Biomass production of the New Zealand pasture to CO<sub>2</sub> enrichment was on average stimulated less by CO<sub>2</sub> compared to the other systems, and was greater during the moist spring period. The magnitude of the elevated CO<sub>2</sub> treatment was lowest in this study, at slightly more than 100 µl l<sup>-1</sup> over present ambient concentrations, which was likely an important factor in the relatively small aboveground biomass responses observed. The apparent reversal of the expected water relations/biomass response appears to have been due to the seasonality of productivity in this plant community, with the species with the largest responses (legumes and forbs) having their period of maximum growth during the moist spring period (Newton et al. 1994). The New Zealand pasture was fertilized with superphosphate, which makes legumes responsive to CO<sub>2</sub> enrichment (Stöcklin et al. 1998; Grünzweig and Körner 2003). Further, in some systems, forbs have been found to be one of the more CO<sub>2</sub>-sensitive plant functional types (Reich et al. 2001). If root growth and turnover are considered, then there was a stimulation in plant biomass at elevated CO<sub>2</sub> that appeared to be strongest under conditions of low soil moisture in New Zealand (Newton et al. 1996; Allard et al. 2004).

In the Texas pasture, plant biomass was stimulated more under elevated CO<sub>2</sub> compared to the tallgrass prairie of Kansas, and was unresponsive to the annual variation in precipitation. The CO<sub>2</sub> treatments in Texas were between sub-ambient and super-ambient concentrations, so on average, contrasts were made in a steeper and therefore more sensitive portion of the CO<sub>2</sub> response curve of photosynthesis, which would tend to enhance the possibility of a direct photosynthetic response.

In more mesic ecosystems like the humid grasslands of North America or cool, mesic grasslands of Europe or New Zealand, biomass responses to CO<sub>2</sub> enrichment are likely to result from a combination of direct photosynthetic and indirect water relations responses, including recruitment. The more direct photosynthetic response may become important when sufficient soil nutrients (nitrogen, phosphate) and the appropriate plant species (C<sub>3</sub> plants, forbs, legumes) are an important plant community component (Texas and New Zealand). But when soil water content is limiting and available soil nutrients, especially N and P, are in low supply (Switzerland), CO<sub>2</sub>-induced improvements in water relations will likely be featured in mesic systems as well, and at times may dominate the



**Fig. 7** Model of soil water responses to CO<sub>2</sub> enrichment and measured precipitation in Kansas tallgrass prairie, Colorado shortgrass steppe, and California annual grassland



grassland biomass responses to CO<sub>2</sub>. It is worth mentioning, however, that soil moisture and nutrient mineralization rates are often correlated; the availability of nutrients to plants could increase as soil moisture increases, allowing for photosynthetic responses to manifest. This apparent nutrient/photosynthesis-effect in reality is a soil moisture effect in disguise via increased rates of decomposition and N mineralization in wetter soils.

### Species responses

In all systems investigated, the nature and degree to which species responded to CO<sub>2</sub> differed. Some appeared unrelated to water relations. Forbs were important in the plant biomass responses of New Zealand and Texas pastures (Polley et al. 2003), and their increased biomass under elevated CO<sub>2</sub> did not appear due to altered plant/soil water relations. Greater production of legumes in the New Zealand pasture occurred at times of abundant soil water, and may have been due, in part, to their capability to fix atmospheric N (given the ample P-supply) rather than to improved water relations. Greater seed dispersal of legumes and forbs appears to have been a major mechanism behind the production responses of these two functional groups under elevated CO<sub>2</sub>. In the Swiss calcareous grassland, increased biomass of the mesic *C. flacca* under elevated CO<sub>2</sub> was attributed to a combination of direct photosynthetic stimulation and the facilitative effect of soil water savings by its dominant neighbor species.

Conversely, improved water relations appeared to be the dominant factor in the tallgrass prairie underlying greater biomass of CO<sub>2</sub>-enriched C<sub>4</sub> grasses in dry years. Increased recruitment of *S. comata* in the shortgrass steppe under elevated CO<sub>2</sub> likely resulted from one or more aspects of improved soil/plant water relations over the duration of the experiment (Morgan et al. 2004). Finally, the ability of some Mediterranean species to respond positively to CO<sub>2</sub> was due to several factors, including additional N in the case of legumes and increased reproductive output of late-flowering species that were able to take advantage of the prolonged growing season under elevated CO<sub>2</sub>.

Collectively, these results indicate that the ability of particular species and plant communities to respond and change as a result of CO<sub>2</sub> enrichment depends on a variety of unique plant traits and environmental circumstances. While it seems likely that species water relations traits will figure importantly in these changes, especially in drier ecosystems, other adaptations, especially traits related to nutrient acquisition, will likely be key to understanding plant community changes as well.

### Conclusions

This report underscores the importance of water relations in driving critical plant responses to rising atmospheric

CO<sub>2</sub> concentrations. It is important to note that the duration of the field experiments was only 3–8 years, which is short in relation to the time-constants of important longer-term processes, such as plant community species changes and shifts in soil C and organic matter pools, which may result in system feedbacks that will likely modulate or alter the plant responses reported herein. Thus, in many cases, the absolute responses of these systems to CO<sub>2</sub> will likely change over time. However, these studies are long-term compared to most published experiments and allowed for some adjustment of ecosystem processes.

The results presented here indicate that increasing atmospheric CO<sub>2</sub> induces water relations responses which in many situations dominate the system biomass and species responses to CO<sub>2</sub>, and could possibly be induced by moisture treatments alone. It is therefore a central question as to the degree to which CO<sub>2</sub> enrichment experiments produce direct CO<sub>2</sub> (photosynthesis-driven) responses vs. indirect, water-driven responses, which are tightly coupled to climatic co-variables like temperature and humidity. In considering whole landscape responses (rather than small experimental plots), rising atmospheric CO<sub>2</sub> may alter atmospheric humidity, through widespread stomatal and transpirational responses, resulting in atmospheric feedbacks that will tend to lessen responses presently observed in our experimental CO<sub>2</sub>-enriched islands. Such landscape-wide feedback would more likely materialize downwind from large landmasses, whereas ecosystems downwind from the coastal edges of landmasses would see responses more similar to what experiments (which lack atmospheric feedback) reveal. Because of the uncertainty of such feedback, it is crucial that CO<sub>2</sub> experiments separate direct and indirect (water-driven) CO<sub>2</sub> effects. The latter may bear little scaling potential to the real world in regions prone to climatic feedback by altered vegetation vapor loss. These experimental results can be a starting point to examine the role of ecosystem responses to elevated CO<sub>2</sub> in larger scale climatic and hydrological process in coupled land-atmosphere models.

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