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Growth, water and nitrogen relations in grassland model ecosystems of the semi-arid Negev of Israel exposed to elevated CO_2

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Abstract Are ecosystems in dry regions particularly responsive to atmospheric CO_2 enrichment? We studied responses of semi-arid grassland assemblages from the northern Negev (Israel) to CO_2 concentrations representative of the pre-industrial era, and early and mid to late 21st century (280, 440, and 600 µl l^{-1}, respectively). Communities of 32 mostly annual species were grown for a full season in large containers (ca 400 kg each) on native soil and under a simulated winter climate of the northern Negev. Ecosystem water relations were monitored weekly by wheeling containers onto a large electronic freight balance. Evapotranspiration was lower and soil water content was higher at elevated atmospheric CO_2. Deep soil drainage was increased, thus reducing the amount of applied rainwater that was effectively captured by the model ecosystems at elevated CO_2. At peak season, midday net ecosystem CO_2 exchange increased with rising CO_2 concentration, whereas night-time exchange was not significantly affected. Above-ground biomass was 7% greater at 440 µl l^{-1} and 17% greater at 600 µl l^{-1} compared to 280 µl l^{-1} CO_2. Reproductive output at the end of the season was increased by 10% and 24% at the two elevated CO_2 concentrations. Shoot nitrogen concentration was slightly reduced (significantly for grasses), but the total plant nitrogen pool reflected the biomass gain and was increased. While some responses, such as water savings and plant nitrogen pool, were more pronounced across the higher (440–600 µl l^{-1}) than across the lower CO_2 (280–440 µl l^{-1}) interval, total plant biomass (above- plus belowground) was already CO_2 saturated at 440 µl l^{-1} (14% increase over biomass at 280 µl l^{-1}). Surprisingly, the biomass, reproduction, and nitrogen responses at the community level were largely caused by a single legume species (*Onobrychis crista-galli*), with the other five legume species contributing less, and most grasses, non-leguminous forbs, and geophytes hardly responding to elevated CO_2. Overall, responses were relatively small, despite the fact that we compared elevated to pre-industrial concentrations of CO_2. This contrasts with our original assumption that ecosystems in seasonally dry regions will be particularly responsive to elevated CO_2. Impacts of CO_2 enrichment on soil moisture depletion and biomass production in semi-arid ecosystems will largely depend on the net effect of reduced water use (evapotranspiration) versus increased water loss (deep drainage and runoff), and on the presence of certain species. In this case, 1 out of 32 species was responsible for most of the effects at the community level.

Keywords Gas exchange · Evapotranspiration · Legumes · Reproduction · Soil moisture

Introduction

The arid and semi-arid regions of the world account for about one-third of the total land area of the globe, and have a significant impact on global climate and biogeochemistry (Schlesinger et al. 1990). Desertification in part results from overgrazing, intensification of agriculture, and other consequences of rapid population growth, and is especially grave in semi-arid regions (Warren et al. 1996). These processes lead to a decrease in plant cover and pasture value (Schlesinger et al. 1990). Based on current knowledge, elevated CO_2 might mitigate desertification in these dry regions.

Responses to elevated CO_2 have been studied for a variety of grasslands, ranging from alpine to Mediterranean climates (Navas et al. 1995; Chiariello and Field 1996; Drake et al. 1996; Field et al. 1996; Körner et al. 1997; Potvin and Vasseur 1997; Stöcklin et al. 1998; Warwick et al. 1998; Leadly et al. 1999; Owensby et al. 1999). These studies include field experiments using

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open-top chambers on undisturbed communities as well as container experiments with reconstructed or model communities in the field, greenhouse, or growth chamber. Aboveground plant biomass in these grasslands was typically increased by 0–30%, although negative, statistically insignificant responses of down to –30% were also found (Drake et al. 1996). Exceptionally large growth increases of up to 40% were reported in a tallgrass prairie in dry years (Owensby et al. 1999).

Plant productivity in desert or semi-desert ecosystems is expected to be particularly stimulated by elevated CO_2 (Mooney et al. 1991). Photosynthetic down-regulation was observed for well-watered, but not for drought-affected desert plants, suggesting that CO_2 enrichment offsets drought-induced stress to the photosynthetic apparatus (Huxman et al. 1998). Leaf diffusive conductance is often lower at elevated CO_2, thus decreasing transpiration and reducing soil moisture depletion (Bremer et al. 1996; Field et al. 1997; Niklaus et al. 1998b). As conditions become drier, these effects are expected to increase, thereby stimulating plant growth and ecosystem productivity to a relatively larger extent (Lockwood 1999).

In the ideal case, experiments with CO_2-enriched air should be conducted in situ. This is a difficult task in the Middle East where the common open-top chambers are not applicable because of the risk of overheating, and free-air CO_2 enrichment is not affordable. Besides many advantages, a drawback of all field techniques is that evapotranspiration (ET) cannot be assessed accurately and continuously. For the present study, we decided to use large model ecosystems (ca 400 kg each) of a semi-arid grassland from the Negev of Israel, built on original soil shipped to Switzerland. In addition, we simulated a diurnally and seasonally variable climate according to local meteorological data. Model ecosystems have been shown to produce valuable information at the ecosystem level over the course of a growing season (e.g., Körner and Arnone 1992; Naeem et al. 1994; Navas et al. 1995; Field et al. 1997), and results of such systems have often been confirmed by field studies (Luo et al. 1996; Field et al. 1997; Fredeen et al. 1997; Niklaus et al. 1998a). A particular advantage of studying CO_2 responses in a controlled environment is the possibility to apply subambient as well as future CO_2 concentrations. We used pre-industrial as well as two elevated CO_2 concentrations, in order to quantify the potential influence of atmospheric CO_2 enrichment close to the current situation, as compared to the much longer-term pre-industrial situation. The three levels also enabled us to account for non-linearity of responses (Körner 1995). We studied ecosystem water relationships, plant biomass production, reproductive output, and nitrogen relationships in species-rich plant communities resembling the structure of natural ‘winter’ vegetation over the full life cycle from seed to seed. Based on the above theory and published data, we expected elevated CO_2 to induce larger water savings and biomass increase than in most other ecosystems.

Materials and methods

Plant and soil material

The grassland that served as the source for plants and soil is located in the uplands of the northern Negev, Israel, near the village of Lehavim (400 m, 31°21′ N, 34°51′ E). The site is part of the Bedouin Demonstration Farm of the Agricultural Research Organization, Ministry of Agriculture and Rural Development, and has a long history of grazing by domestic animals. Seeds (bulbils in the case of *Poa bulbosa*) of the following species were collected in late spring of 1996 and 1997: *Aegilops kotschyi*, *A. peregrina*, *Brachypodium distachyon*, *Bromus alopecuros*, *Bromus fasciculatus*, *Bromus lanceolatus*, *Crithopsis delileana*, *Hordeum spontaneum*, *Stipa capensis* (nine annual grasses); *Dactylis glomerata*, *P. bulbosa* (two perennial grasses); *Hippocrepis unisiliquosa*, *Hymenocarpos circinnatus*, *Medicago minima*, *M. truncatula*, *Onobrychis crista-galli*, *Trifolium campestre* (six annual legumes); *Biscutella didyma*, *Carrichtera annua*, *Daucus subsessilis*, *Hedypnois cretica*, *Plantago coronopus*, *Plantago cretica*, *Pterocephalus plumosus*, *Reboudia pinnata*, *Rhagadiolus stellatus*, *Scabiosa porphyroneura* (ten annual non-leguminous forbs). In summer 1997, soil (light lithosol on calcareous bedrock, pH 7.9; 7.5, 3.0 and 4.7 μg g^{-1} mineral N, available P, and water-extractable K, respectively) was collected to a depth of 30 cm (soil depth was nowhere deeper than 40 cm). A number of plant species, such as *Parentucellia flaviflora* (annual non-leguminous forb), and *Ranunculus asiaticus*, *Gagea* spp., *Gynandriris sisyrinchium*, and *Ornitogallum* sp. (four geophytes), emerged spontaneously from the diaspore bank in the soil during the experiment. Plant material and soil were shipped to the University of Basel, Switzerland, where model ecosystems were constructed.

Model ecosystems and experimental design

Polyethylene containers (100×70 cm, 35 cm deep) were mounted on wheeled trolleys and were split by a vertical separator into two equal compartments to permit two consecutive harvests. Each container was filled with a bottom layer (13–35 cm) of 270 kg marl (particle diameter 0–8 mm, bulk density 1.45 g cm^{-3}, bare of any organic components and organic-matter-derived nutrients) from the Swiss Jura Mountains similar to the underlying substrate in the Negev, a middle layer (8–13 cm, bulk density 1.54 g cm^{-3}) of 50 kg of a marl/soil mixture (4/1), and a top layer (0–8 cm, bulk density 1.04 g cm^{-3}) of 60 kg pure native Negev soil. Seeds were sown into a few-millimeter surface layer of a 1:1 soil/sand mixture.

Prior to sowing on 24 November, the seed coat of legumes was slightly abraded to guarantee rapid and homogenous germination. Seeds were dispersed uniformly over the container according to the natural species densities in ungrazed plots on north- and south-facing slopes (Y. Osem, M. Sternberg, and J. Kigel, personal communication). All seeds were stratified in the moist soil of the model ecosystems at 10°C in the dark for 3 days immediately after sowing (this is known to improve germination from earlier experiments). Plant communities (2,600 individuals m^{-2}) were dominated by grasses (55% of the total number of individuals), with legumes amounting to 11%, forbs to 17%, and geophytes to 17% of all individuals.

Model ecosystems were exposed during day and night to one of the following CO_2 concentrations: 280 (pre-industrial level), 440 (expected by early 21st century) or 600 μl l^{-1} (expected by mid to late 21st century; Houghton et al. 1995). One CO_2 concentration was applied to three model ecosystems within a growth chamber (total of three growth chambers). We randomized CO_2 treatments between growth chambers and positions of the wheeled containers within growth chambers every week throughout the 5-month growing period. This procedure occurred 23 times, and was intended to minimize possible chamber effects.

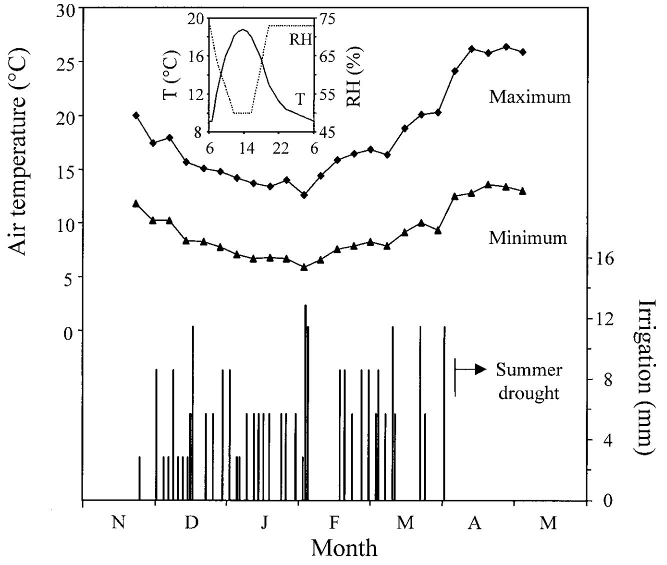

Fig. 1 Climate simulation of the growing season in the northern Negev. Mean weekly minimum and maximum air temperatures and irrigation as imposed on the model ecosystems. *Insert* temperature (*T*) and relative humidity (*RH*) course on a day in mid March. Forty-nine millimeters of water were applied prior to sowing

Climate simulation

Climatic data (daily minimum and maximum air temperatures, relative air humidity for 0600, 1200 and 1800 hours GMT, and daily amounts of rain) were obtained from the Lahav Meteorological Station, located a few kilometers from the sampling site (Baram 1996). Rain data were also available from a rain gauge in the nearby Lehavim settlement. These data were used to simulate a typical Negev climate in the fully controlled growth chambers, as follows: daily minimum and maximum temperatures (each averaged over the years 1987–1995) were used to compute diurnal temperature courses (Ephrath et al. 1996; Fig. 1, insert). Diurnal relative air humidity regimes were created by stepping between the values for 0600, 1200, and 1800 hours GMT (each averaged over the years 1987–1995), with the associated vapor pressure deficit smoothly driven by the diurnal course of temperature. Temperature (Fig. 1) and humidity regimes were adjusted weekly in the course of the growing season. Relative humidity ranged between 55% at midday and 80% at night in the winter and between 35 and 65% in spring. In late February and again in early March, typical hot spells of 2 days each were simulated, as they naturally occur in late winter and spring.

The photoperiod was adjusted weekly to the natural situation in Israel, i.e., 10.04 h of light in late December and 13.24 h in early May (end of the growing season). Light was applied by all or part of the 30 lamps per growth chamber (10 lamps m^{-2}; metal halide lamps, Eye MF 400 LE/BUH; Iwasaki Electric, Tokyo, Japan). Days started and ended with 1 or 2 h of the lowest light intensity (mean photosynthetical photon flux density, PPFD, of 190 µmol m^{-2} s^{-1}) and had 4–5 h of the highest PPFD around midday (810 µmol m^{-2} s^{-1}) with medium PPFD (400 µmol m^{-2} s^{-1}) in intermediate periods. Light intensity between December and February, the three critical months for plant development, averaged 19.1 mol m^{-2} day^{-1}. Global radiation in the northern Negev during that period averages 12.5 MJ m^{-2} day^{-1} (Bitan and Rubin 1991). Assuming 45% photosynthetically active radiation and 0.22 MJ mol^{-1} radiation at 550 nm (Larcher 1995), PPFD in real field conditions was estimated at 25.6 mol m^{-2} day^{-1}. Hence, light intensity in our growth chambers amounted to 75% of Negev winter levels. Due to the wide spacing of plants, mutual shading in the canopy played a minor role.

The daily rain data from the village of Lehavim and the Lahav Meteorological Station were averaged at a total of 314 mm per year (years 1987–1995). This amount was provided (in the form of deionized water) in a winter rain scheme at 3- to 4-day intervals (average natural rain event every 4.5 days between late November and the end of the rain season; Fig. 1). Deep drainage of soil water was collected through a bottom hole in each container. In early February, a soil-saturating irrigation and thereafter a rainless period of 14 days, typical for dry regions, was applied. In mid March, a second drought period of 10 days was imposed. Water input was terminated at the beginning of April when natural rain in the Negev becomes insignificantly low, and ecosystems were subsequently allowed to slowly dehydrate.

Water balance

The ecosystem water balance was monitored weekly by wheeling containers onto a large electronic freight balance (±10 g). Daily ecosystem ET was calculated as follows:

$$ET=(\Delta W+P-D)/\Delta t$$

where ΔW is the change in the weight of the system over the calculation period, P is the water input and D the loss of soil water by deep drainage over the same period, and Δt is the length of that period in days. Cumulative ET was calculated as the sum of ET from sowing until the specific date. Actual soil moisture was calculated by subtracting the known dry soil and container weights from the actual model ecosystem weight.

To separate water loss into soil evaporation and plant transpiration components, intact soil cores 3 cm in diameter and 10 cm deep (two per container, 18 in total) were removed from canopy gaps at peak season. Cores were inserted in plastic cylinders and returned to the holes, serving as in situ evaporimeters that were reweighed over short intervals.

Pan evaporation was monitored to insure comparable evaporative forcing in each growth cabinet, close to conditions in the northern Negev (2.35 mm day^{-1}; Baram 1996). Beakers (100 ml, surface area 17 cm^2, six beakers per growth chamber, 18 in total) filled with water served as evaporation pans at canopy level. Evaporation was measured for 12 weeks between sowing and peak season harvest. In a preliminary experiment, evaporation from these beakers was found to be similar to that from larger, 220-cm^2 pans.

CO_2 exchange

CO_2 fluxes were measured shortly before the peak season harvest at growth CO_2 concentrations. Net ecosystem CO_2 uptake was determined at midday, and nighttime CO_2 losses were measured at least 3 h after termination of daylight. We used a closed-system method, consisting of an infrared gas analyzer (Li-6200; Li-Cor, Lincoln, Neb.) and a 50-cm-high transparent chamber sealed to the containers for the measuring period of a few minutes. The rate of increase or depletion of CO_2 in this known volume was recorded and expressed per unit ground area.

Harvests and plant measurements

Canopy development and leaf area index (LAI, total area of live leaves per unit ground area) were monitored 4 (late December) and 10 weeks (early February) after sowing. At both dates, two narrow strips (1 cm wide, 70 cm long) were harvested in all compartments (two per container). Above- and belowground dry matter was determined at peak season (maximal vegetative development at the onset of anthesis in grasses) by destructively harvesting one of the two compartments of each container (mid March, 16 weeks after sowing). The reproductive output was determined as total fruit dry matter (capsules, ears, dry inflorescences, etc.) at the final harvest of the remaining compartment after ‘natural’ desiccation of all plants (early May, 23 weeks after sowing). Aboveground plant material was divided into functional groups (grasses, legumes, non-legume forbs, geophytes). Perennial grasses amounted to only 2% of aboveground grass phytomass, and were lumped with annual grasses. Belowground biomass was harvested in two layers, the top 13 cm and the marl subsoil (13–35 cm). We report 80°C oven-dry weights for all plant material. Water use efficiency (WUE) was calculated for the peak season harvest in the classical way as the ratio of total phytomass to cumulative ET or as the ratio of total phytomass to total water loss (cumulative ET+deep drainage). Leaf diffusive conductance was measured with a diffusion porometer (AP4; Delta-T Devices, Cambridge, UK) 14 and 19 weeks after sowing on a few species with relatively large leaves (lower side of leaves measured). Leaf area was measured by a photoplanimeter (Li-3100; Li-Cor), carbon and nitrogen concentrations were determined by a CHN analyzer (CHN-900; Leco, St. Joseph, Mich.), and ^{15}N was measured by isotope-ratio mass spectrometry (Finnigan MAT, Bremen, Germany).

Statistical analysis

Entire model ecosystems were replicated three times for each of the three CO_2 treatments. Variables were tested for CO_2 effects with one-way ANOVA. Ratios were log-transformed prior to analysis. ET and soil water content were tested over the entire season or part of it using repeated-measures ANOVA. Where applicable, multiple comparisons were made with the Tukey-Kramer honestly significant difference (HSD) post hoc test. The same test was used for contrasts comparing two levels of CO_2.

Results

Evapotranspiration and water drainage

Pan evaporation did not differ among treatments, and averaged 2.31 mm day^{-1} between sowing and peak season harvest. Thus, evaporation was essentially identical to real field conditions (2.35 mm day^{-1}) during the same period. ET was lower at 600 µl l^{-1} than at 280 µl l^{-1} CO_2 for most of the season (significant during 7 weeks until peak season harvest in mid March), with intermediate values for 440 µl l^{-1} CO_2 (Fig. 2a). During the 16-week period from the beginning of the experiment until peak season, model ecosystems at 440 and 600 µl l^{-1} lost 2% (6 mm, $P=0.023$) and 11% (26 mm, $P<0.001$) less water by ET than those at 280 µl l^{-1} CO_2 (Fig. 3a). This amount of moisture corresponds to the water consumption during 3 and 13 days, respectively, at the given mean ET. Toward the end of the season, soils were considerably drier at the lowest CO_2 concentration, and the ecosystems in 440 and 600 µl l^{-1} lost more water by ET than those at 280 µl l^{-1}, causing the differences in cumulative ET to diminish.

Evaporation from bare soil (weighing soil evaporimeters) amounted to circa 20% of ET at peak season and was not affected by CO_2 enrichment (Fig. 4). Thus, the reduction in ET at elevated CO_2 was solely due to reduced plant transpiration, which accounted for circa 80% at the time of maximal vegetative development.

At peak season, leaf diffusive conductance of two grasses, one legume, and one forb was reduced at elevated CO_2 by 5–75% (Table 1). Five weeks later, toward the end of the season, leaf conductance was quite low, averaging 56 mmol m^{-2} s^{-1} for *B. distachyon* and 38 mmol m^{-2} s^{-1} for *S. phorphyroneura*, with no differences between treatments (not measurable for the other two species).

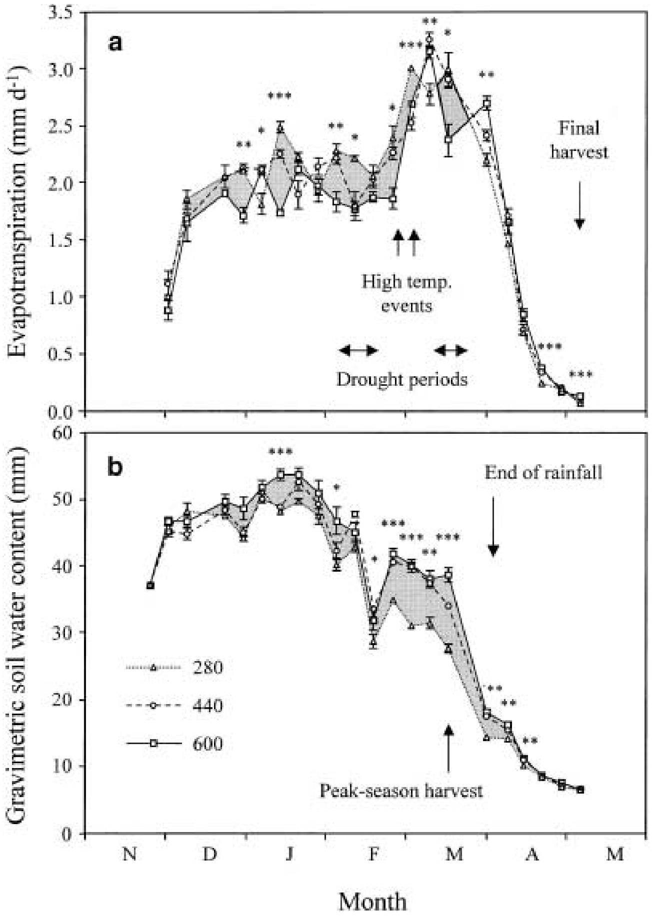

Fig. 2 Daily evapotranspiration (ET) (**a**) and total ecosystem soil water content (**b**) during the growing season for the three CO_2 treatments. Values are means±SE for $n=3$ model ecosystems. *Gray areas* represent lower ET (**a**) and higher soil moisture (**b**) at 600 than at 280 µl l^{-1} CO_2. $P<0.001$ for ET and $P=0.009$ for soil water content over the entire season (analyzed by repeated-measures ANOVA) (*$P\leq0.05$, **$P\leq0.01$, ***$P\leq0.001$ per date)

During the earlier, wetter part of the season, water occasionally percolated out of the soil profile. Deep drainage was considerably higher from model ecosystems at 600 µl l^{-1} than from those at 280 and 440 µl l^{-1} ($P<0.001$) and made up 8% of total water loss (ET and drainage) in the former systems (Fig. 3b). No deep drainage of water was observed during the later, drier part of the season.

Soil moisture

As a result of reduced ET, soil moisture was less depleted in elevated compared to pre-industrial CO_2 (Fig. 2b). A significant CO_2 effect was first observed in mid January. Until mid February, model ecosystems at 440 and 600 µl l^{-1} CO_2 had, on average, a 5 and 10% higher water

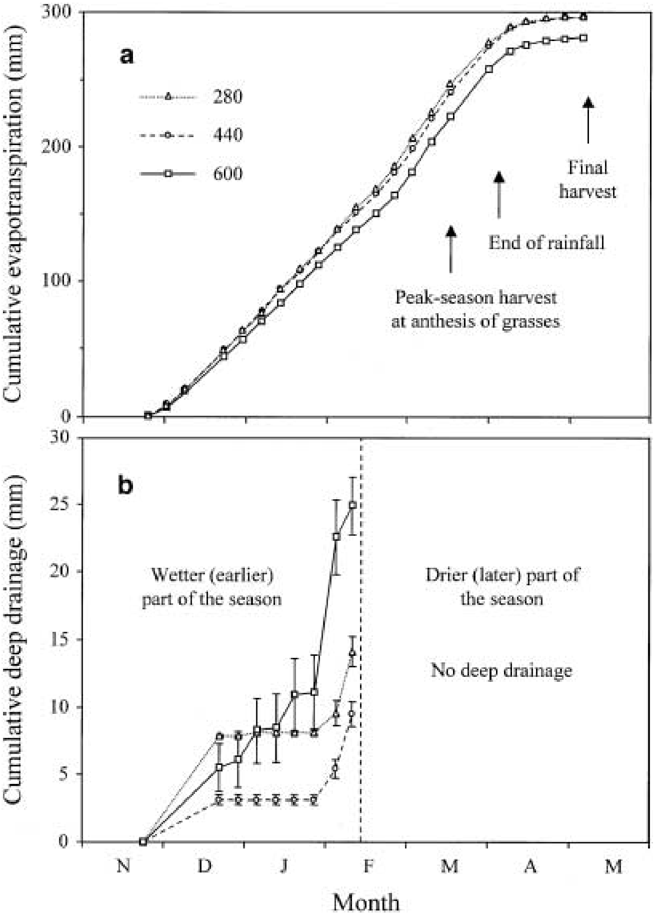

Fig. 3 Cumulative evapotranspiration (**a**) and deep soil drainage (**b**) from model ecosystems at the three CO_2 concentrations during the growing season. Values are means±SE for n=3 model ecosystems. *Error bars* are obscured by symbols for cumulative evapotranspiration

content than those at 280 µl l^{-1} CO_2 (P=0.051 across all three CO_2 treatments). Between the time of the first and the second imposed drought (mid February–mid March), soil moisture was 22 and 27% higher at 440 and 600 µl l^{-1}, respectively, than at 280 µl l^{-1} (P<0.001). Between early January and mid February, soil moisture at 440 µl l^{-1} was intermediate between the other two treatments, but was similar to 600 µl l^{-1} and considerably higher than 280 µl l^{-1} CO_2 between late February and early April. At the end of the season in early May, all model ecosystems reached the same low soil water content of circa 6.5 mm (2% of soil volume).

CO_2 exchange

Net ecosystem CO_2 uptake at peak season increased (marginally significant) with increasing CO_2 concentration, and was 21% higher at 440 and 31% higher at 600 compared to 280 µl l^{-1} CO_2 (Fig. 5). At the same time, nighttime CO_2 exchange was not significantly affected by the CO_2 treatments.

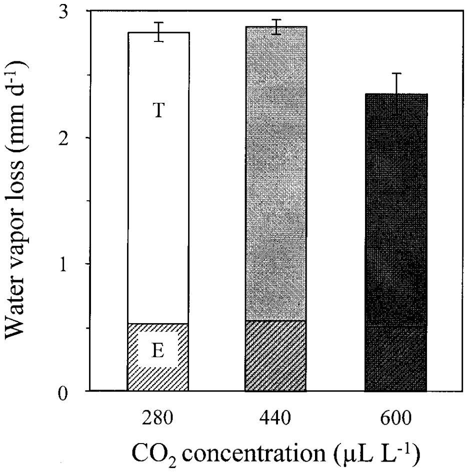

Fig. 4 Separation of evapotranspiration (ET) into transpiration (T) and evaporation (E) at peak season. Transpiration was calculated as T=ET-E for each model ecosystem. Values are means±SE for n=3 model ecosystems. P=0.024, 0.028, and 0.893 for ET, T, and E, respectively (ANOVA across the three CO_2 concentrations)

Phytomass and LAI

Seedling emergence of grasses, legumes, and non-legume forbs was similar among CO_2 treatments, and seedling mortality was negligible. Therefore, no difference was observed in abundance of functional groups of species between treatments (data not shown).

Strip harvests revealed similar aboveground phytomass in late December (4 weeks after sowing), but indicated that phytomass was increased with rising CO_2 concentration as early as the beginning of February (10 weeks after sowing; n.s.; Fig. 6). At the peak season harvest (16 weeks after sowing), aboveground phytomass was 7% greater (P=0.097 for the contrast) at 440 µl l^{-1} and 17% greater (P=0.003) at 600 µl l^{-1} compared to 280 µl l^{-1} CO_2 (Table 2, Fig. 6). This growth stimulation was almost exclusively due to 12 and 34% larger aboveground dry matter of legumes at 440 and 600 µl l^{-1} (Table 2). The largest species in size, the legume *O. crista-galli*, which contributed between 9–15% of the total aboveground phytomass, was especially responsive. This species was responsible for two-thirds (440 µl l^{-1}) and half (600 µl l^{-1}) of the total aboveground phytomass increase. To illustrate the magnitude of the contribution of this species to the overall phytomass increase at elevated CO_2, we calculated CO_2 effects without *O. crista-galli*, a valid procedure in view of its relatively small contribution to total aboveground phytomass (see above). Without *O. crista-galli*, the overall growth stimulation would have been reduced to only 3% (P=0.727) at 440 µl l^{-1} and 9% (P=0.077) at 600 µl l^{-1}, and hence would be statistically non-significant. This remaining CO_2 effect on phytomass was contributed mainly by three other legumes (*H. circinnatus*, *M. minima*, and *M. truncatula*), and by the dominant grass (*Aegilops* spp., *C. delileana*) and forb (*P. flaviflora*) species. None of them were significantly affected by CO_2 when tested individually

Table 1 Leaf diffusive conductance (mmol m^{-2} s^{-1}) 2 weeks prior to peak season. *Aegilops* species were indistinguishable at the vegetative stage. Values are means±SE for n=3 model ecosystems (measurements of two leaves per model ecosystem were pooled). Values within rows followed by different letters are significantly different at $P \leq 0.05$ (summary of two-way ANOVA for factors CO_2 and Species: CO_2, F_2=6.56, P=0.005; Species, F_3=35.93, P<0.001; CO_2×Species, F_6=0.72, P=0.640)

Species	280 µl l^{-1} CO_2	440 µl l^{-1} CO_2	600 µl l^{-1} CO_2
Aegilops spp. (grasses)	212±73 ^{a}	104±5 ^{a}	63±5 ^{a}
Brachypodium distachyon (grass)	331±26 ^{a}	171±41 ^{b}	76±3 ^{b}
Hymenocarpos circinnatus (legume)	553±68 ^{a}	313±51 ^{b}	288±39 ^{b}
Scabiosa porphyroneura (forb)	1,120±268 ^{a}	1,067±230 ^{a}	676±10 ^{a}

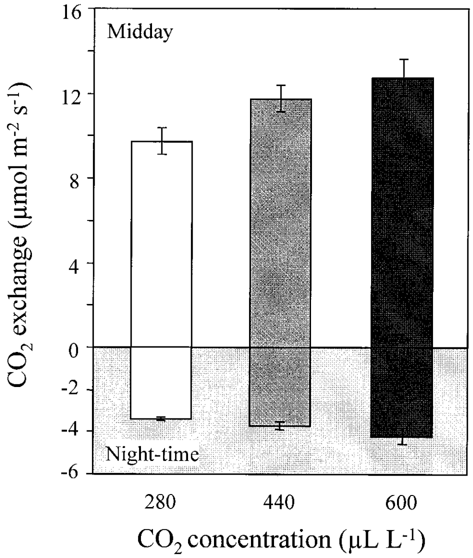

Fig. 5 Net midday and nighttime ecosystem CO_2 exchange at peak season. Values are means±SE for n=3 model ecosystems. P=0.055 for midday values, P=0.123 for nighttime values (ANOVA over all three CO_2 concentrations)

Table 2 Effect of CO_2 concentration on phytomass (g m^{-2}) and water use efficiency (*WUE*, g total phytomass kg^{-1} H_2O lost by evapotranspiration since the beginning of the experiment) at peak season. Values are means±SE for n=3 model ecosystems. Values within rows followed by different letters are significantly different at $P \leq 0.05$

	280 µl l^{-1} CO_2	440 µl l^{-1} CO_2	600 µl l^{-1} CO_2
Aboveground			
Grasses	133±4 ^{a}	138±2 ^{a}	142±3 ^{a}
Legumes	89±4 ^{b}	100±4 ^{b}	119±3 ^{a}
Forbs	26±3 ^{a}	27±3 ^{a}	29±3 ^{a}
Geophytes	7.5±0.4 ^{a}	8.7±0.5 ^{a}	7.9±0.8 ^{a}
Total	255±4 ^{b}	273±8 ^{b}	298±2 ^{a}
Belowground	185±1 ^{b}	226±12 ^{a}	207±10 ^{ab}
Total	439±4 ^{b}	499±5 ^{a}	505±9 ^{a}
WUE	1.79±0.02 ^{c}	2.08±0.02 ^{b}	2.29±0.04 ^{a}

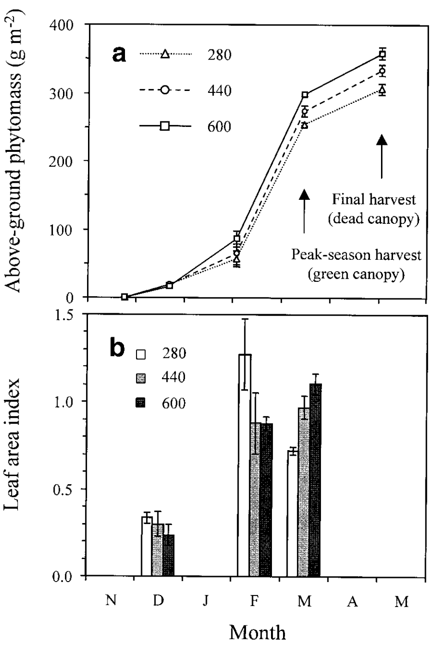

Fig. 6 Accumulation of aboveground phytomass (**a**) and development of leaf area index (LAI) (**b**) during the growing season for the three CO_2 treatments. Values are means±SE for n=3 model ecosystems. P=0.497 (December), P=0.204 (February), and P=0.007 (March, peak season) for CO_2 effect on LAI

(data not shown). At the end of the season, aboveground phytomass (largely necromass) was increased by 20% compared to peak season mass, and differences between treatments remained as observed at peak season (Fig. 6).

At the two strip harvests, LAI tended to be lower in model ecosystems at elevated than in those at pre-industrial CO_2 (n.s.; Fig. 6). In contrast, at peak season, LAI was significantly higher by 35% at 440 µl l^{-1} and by 53% at 600 µl l^{-1} compared to 280 µl l^{-1} CO_2. This increase was mainly caused by legumes (by *O. crista-galli* in particular), but to a smaller extent also by the other functional groups.

Belowground biomass (not separated into functional groups) was larger at 440 than at 280 µl l^{-1} with an intermediate value for 600 µl l^{-1} CO_2 (Table 2). Total plant mass (above- plus belowground, live plus dead) at peak season was increased by 14% at 440 and 15% at 600 µl l^{-1} relative to 280 µl l^{-1} CO_2 (P<0.001). The carbon concentration in dry matter did not differ significantly among treatments (data not shown). Total plant dry matter and carbon concentrations were used to calculate total plant C pools which amounted to 170, 181, and 193 g C m^{-2} at 280, 440, and 600 µl l^{-1}, respectively. Thus, the total plant C pool was only 7% (P=0.096) larger at 440 µl l^{-1}, but 14% (P=0.005) larger at 600 µl l^{-1} compared to 280 µl l^{-1}.

Table 3 Phytomass fractionation at peak season (g m^{-2}). Values are means±SE for *n*=3 model ecosystems. Values within rows followed by different letters are significantly different at $P \leq 0.05$

	280 µl l^{-1} CO$_2$	440 µl l^{-1} CO$_2$	600 µl l^{-1} CO$_2$
Aboveground			
Live leaves	42±2 ^{b}	55±3 ^{ab}	67±5 ^{a}
Dead leaves	38±1 ^{a}	35±1 ^{a}	36±2 ^{a}
Stems	110±1 ^{c}	119±2 ^{b}	129±2 ^{a}
Flowers/fruits	65±5 ^{a}	64±5 ^{a}	65±3 ^{a}
Dead leaf dry matter/total leaf dry matter	0.47±0.01 ^{a}	0.39±0.01 ^{b}	0.35±0.03 ^{b}
Belowground			
Storage structures[a]	48±2 ^{a}	55±3 ^{a}	48±5 ^{a}
Roots	136±1 ^{a}	171±14 ^{a}	159±5 ^{a}
Above-/belowground ratio	1.38±0.03 ^{a}	1.22±0.10 ^{a}	1.45±0.07 ^{a}

[a] Bulbils of *Poa bulbosa* and geophytes

Table 4 Fruit dry matter (g m^{-2}) and relative investment into reproductive plant mass (fruit dry matter/total aboveground dry matter) at the end of the growing season. Fruit dry matter for geophytes was only 0.1 g m^{-2} with no treatment effect. Values are means±SE for *n*=3 model ecosystems. Values within rows followed by different letters are significantly different at $P \leq 0.05$

	280 µl l^{-1} CO$_2$	440 µl l^{-1} CO$_2$	600 µl l^{-1} CO$_2$
Grasses	67±6 ^{a}	72±7 ^{a}	66±3 ^{a}
Legumes	61±1 ^{c}	68±1 ^{b}	89±1 ^{a}
Forbs	11±2 ^{a}	13±3 ^{a}	18±1 ^{a}
Total	139±4 ^{b}	153±5 ^{b}	173±1 ^{a}
Fruit dry matter/total aboveground dry matter	0.46±0.01 ^{a}	0.46±0.01 ^{a}	0.49±0.01 ^{a}

Table 5 Effect of atmospheric CO$_2$ concentration on nitrogen concentration and plant nitrogen pools (all above- and belowground plant parts) at peak season. Values are means±SE at *n*=3 model ecosystems. Values within rows followed by different letters are significantly different at $P \leq 0.05$

	Nitrogen concentration (% of dry matter)			Plant nitrogen pool (g m^{-2})		
	280 µl l^{-1} CO$_2$	440 µl l^{-1} CO$_2$	600 µl l^{-1} CO$_2$	280 µl l^{-1} CO$_2$	440 µl l^{-1} CO$_2$	600 µl l^{-1} CO$_2$
Aboveground						
Grasses	0.86±0.01 ^{a}	0.71±0.01 ^{b}	0.72±0.02 ^{b}	1.13±0.03 ^{a}	0.99±0.02 ^{b}	1.02±0.02 ^{b}
Legumes	2.52±0.12 ^{a}	2.39±0.08 ^{a}	2.34±0.04 ^{a}	2.24±0.03 ^{b}	2.38±0.03 ^{b}	2.80±0.12 ^{a}
Forbs+geophytes	1.51±0.05 ^{a}	1.37±0.06 ^{a}	1.38±0.09 ^{a}	0.50±0.06 ^{a}	0.49±0.05 ^{a}	0.51±0.07 ^{a}
Total				3.87±0.05 ^{b}	3.85±0.07 ^{b}	4.32±0.16 ^{a}
Belowground	0.82±0.03 ^{a}	0.71±0.06 ^{a}	0.77±0.01 ^{a}	1.52±0.05 ^{a}	1.59±0.09 ^{a}	1.60±0.09 ^{a}
Total				5.39±0.10 ^{b}	5.44±0.10 ^{b}	5.92±0.07 ^{a}

WUE, calculated as the ratio of total accumulated phytomass (above- plus belowground) and cumulative ET at peak season, was 17% higher at 440 µl l^{-1} and 28% higher at 600 µl l^{-1} compared to 280 µl l^{-1} CO$_2$ ($P<0.001$; Table 2). If calculated per total water loss (ET and deep drainage), WUE at 440 µl l^{-1} remained 17% higher, but at 600 µl l^{-1} was only 22% higher than at 280 µl l^{-1}.

Phytomass fractionation and leaf senescence

At the community level, plants invested more in leaf and stem dry matter when growing at elevated CO$_2$ (Table 3). This includes greater total leaf production (live+dead leaves; $P=0.003$, across all three CO$_2$ treatments), but dead-leaf mass alone was similar among treatments. Consequently, the fraction of dead leaves (dead mass/live+dead mass) was significantly smaller at 440 and 600 µl l^{-1} than at 280 µl l^{-1} CO$_2$, indicating delayed leaf senescence in the CO$_2$-enriched ecosystems. The enhanced total community leaf production resulted from increased leaf mass of grasses and legumes ($P=0.038$ and <0.001); the enhanced stem production resulted from a larger stem mass of legumes alone ($P<0.001$). Delayed leaf senescence at elevated CO$_2$ was observed in legumes and forbs ($P=0.004$ and 0.017), but not in grasses and geophytes ($P=0.353$ and 0.664).

CO$_2$ had no significant effect on the aboveground/belowground biomass ratio or on bulbil (perennial grasses and geophytes) mass (Table 3). Root dry matter was slightly larger at 440 µl l^{-1} than at 280 µl l^{-1} CO$_2$ ($P=0.061$ for the contrast), thus being the main contributor to the significantly greater belowground biomass at elevated CO$_2$ (Table 2). Root biomass at 600 µl l^{-1} was intermediate between 280 and 440 µl l^{-1} (Table 3). Eighty-six percent of root biomass was harvested from the top soil layer (0–13 cm), and the relative distribution of roots between soil layers was similar among CO_2 treatments (data not shown).

Reproductive output

CO_2 had no effect on the flower and fruit mass at the peak season harvest (Table 3). At the end of the season, reproductive output (measured as fruit dry matter) increased with rising CO_2 concentration, reaching 10% (*P*=0.095 for the contrast) higher values at 440 µl l^{-1} and 24% (*P*=0.002) higher values at 600 µl l^{-1} compared to 280 µl l^{-1} CO_2 (Table 4). Most of this increase was contributed by the 12 and 45% greater fruit production of legumes at 440 and 660 µl l^{-1}, respectively. Reproductive output in four out of the six legume species was significantly increased by elevated CO_2 (unpublished data). Without *O. crista-galli*, fruit dry matter would be increased by only 7% (*P*=0.369) at 440 µl l^{-1} and 16% (*P*=0.039) at 600 µl l^{-1}. Other species contributing to this increase were the legumes *H. circinnatus* and *M. truncatula*, the dominant grasses *A. kotschyi* and *A. peregrina*, and the dominant forb *P. flaviflora* (statistically significant only for the pooled legume fraction at 600 µl l^{-1} compared to 280 and 440 µl l^{-1} CO_2, *P*=0.017 across all three concentrations). Legume reproductive output (including *O. crista-galli*) exceeded that of grasses at 600 µl l^{-1}, whereas the opposite was true at 280 µl l^{-1}. However, the ratio of fruit dry matter to total aboveground dry matter was not affected by CO_2, hence there was no change in relative investment into reproduction (Table 4).

Plant nitrogen

The nitrogen concentration in shoots was reduced by 20% in grasses at elevated relative to pre-industrial CO_2, whereas it was not significantly affected in legumes and forbs+geophytes, or in belowground organs (Table 5). C/N ratios followed similar patterns (data not shown). In desiccated plant remains at peak season, the N concentration was marginally significantly reduced in the forb+geophyte fraction only (an average reduction of 28%, *P*=0.053), but was unaffected in the other functional groups which comprise 90% of total end season debris.

At peak season, the total amount of N per unit ground area in grass shoots decreased in elevated relative to preindustrial CO_2 (Table 5). In contrast, the larger legume aboveground dry matter at 600 µl l^{-1} resulted in a significantly larger N pool in legumes at 600 µl l^{-1} compared to 400 and 280 µl l^{-1} CO_2. Because of the high N concentration in legumes, the above changes added up to a significant increase in the total plant N pool (above- plus belowground) with rising CO_2 concentration, reaching a 10% higher value at 600 µl l^{-1} compared to 280 µl l^{-1}. The amount of N in the soil at the end of the season was not measurably affected by elevated CO_2, and averaged 142 g m^{-2} or 1.3 mg g^{-1} top soil (0–13 cm). Mass spectrometer data for $\delta^{15}N$ in shoots did not permit a strong enough differentiation of functional groups to estimate the contribution of N_2 fixation via legumes ($\delta^{15}N$ averaged 0.37, –1.91, and 0.57 for grasses, legumes, and forbs, respectively, across all treatments).

Discussion

Productivity and possible long-term consequences

Peak season aboveground phytomass of the grassland communities from the semi-arid northern Negev was 7% larger when comparing 440 to 280 µl l^{-1}, and 17% larger when comparing 600 to 280 µl l^{-1} CO_2. In most other studies, natural or semi-natural grasslands were exposed to either enriched (600–700 µl l^{-1}) or ambient CO_2 (350–360 µl l^{-1}), and aboveground biomass was increased by 0–30% at the elevated concentration (Navas et al. 1995; Chiariello and Field 1996; Drake et al. 1996; Field et al. 1996; Körner et al. 1997; Potvin and Vasseur 1997; Stöcklin et al. 1998; Warwick et al. 1998; Leadly et al. 1999; Owensby et al. 1999). No trend toward higher responsiveness was obvious in the studies using 700 µl l^{-1} compared to those using 600 µl l^{-1} CO_2. Considering the fact that we used pre-industrial instead of current ambient CO_2 concentration as the common reference, our results are at the lower end of the biomass response to elevated CO_2 in grasslands. We had expected larger differences among our CO_2 treatments because of the relatively dry conditions associated with the semi-arid climate that we simulated. The assumption that semi-arid ecosystems are particularly responsive in terms of biomass to CO_2 enrichment could, therefore, not be verified in this experiment.

In addition to peak season aboveground phytomass, CO_2 enrichment increased peak season belowground and total phytomass, final aboveground phytomass, reproductive output, and the plant N pool at the community level. Most of these changes were caused by legumes, and largely by one species, *O. crista-galli*. Most of the remaining CO_2 effects were caused by two to three other legume species, while grasses hardly responded at all (Grünzweig and Körner 2000).

A positive effect of CO_2 enrichment on legumes has been suggested earlier (Körner 1993), because of the larger amount of carbohydrates that plants could supply to N_2-fixing bacteria (Bazzaz and Fajer 1992). In agricultural grasslands, legumes were indeed found to respond strongly to elevated CO_2 (Lüscher et al. 1996; Hebeisen et al. 1997), whereas in a semi-natural grassland, legume biomass was stimulated only after P addition (Stöcklin et al. 1998) or when fertile potting compost was mixed into the substrate (Warwick et al. 1998). Our grassland communities grew on a nutrient-poor substrate, but the legume response must have been based on sufficient P availability, perhaps enhanced as a consequence of soil processing for the establishment of our model ecosystems. If maintained in the long run, such a CO_2-

induced stimulation of legumes would have important consequences for ecosystem functioning. A larger legume biomass and the greater seed production associated with it in one season may translate into an increase in legume abundance in following seasons. Thus, while the composition of the plant community could be expected to change, its productivity would further increase. This might be enforced be the legume-induced increase in the community N pool, provided it could be recycled. However, the bottleneck will almost always be P supply, which is typically low in dry regions (Schlesinger et al. 1990).

Some factors, especially under natural conditions, might diminish the CO_2 effect found here (see also below). (1) The aboveground dry mass at pre-industrial CO_2 was twice as large as biomass reported for the site in the northern Negev during a year with slighly (13%) below average rainfall (Osem et al. 1999). The values measured in situ by Osem et al. (1999) included rocks and bare spots, hence the discrepancy between model ecosystems and the field are actually smaller. Furthermore, the site was located in hilly terrain, which can produce considerable runoff and reduce the amount of rainwater effectively infiltrating the soil. If the biomass in our model ecosystems is still larger than in the vegetated areas in the field, this would probably result from enhanced nutrient availability (soil disturbance effect) relative to the original site. Since the biomass response to CO_2 enrichment is typically greater under high as opposed to low nutrient supply (Körner 1996; Poorter 1998), the CO_2 effect might then turn out to be smaller under natural conditions. In contrast to other studies under controlled conditions, where foliar N concentrations were largely increased compared to field levels (e.g., Johnson et al. 1995), no excessive nutrient availability was observed in our study. N concentrations in shoots and roots at peak season (Table 5) and in leaves during vegetative growth (unpublished data) were well within the range commonly observed in Mediterranean or semi-arid grasslands (Körner and Miglietta 1994; Jackson et al. 1995; Pugnaire and Haase 1996). (2) The addition of legume-derived N to the ecosystem may lead to increased competitiveness of grasses. In the long term, and given the lower P dependency of grasses versus legumes, the abundance of legumes might gradually decline. (3) Legumes transpire twice as much per unit leaf area as grasses (Table 1) and, thus, an increasing legume fraction in the plant community will eventually counteract the water-saving effect of elevated CO_2. Legumes are generally more susceptible than grasses to the extreme drought events that occur in semi-arid areas. A more legume-rich plant community in a CO_2-enriched atmosphere may face a higher risk of total system failure. (4) Ruminant productivity is negatively affected by lowered forage quality (N concentration) at elevated CO_2, as these animals cannot compensate for a low-protein diet by consuming more forage (Owensby et al. 1996). Different grazing scenarios of domestic ruminants, which are abundant in the semi-arid rangelands (Harrington 1981), could be expected in a CO_2-enriched atmosphere. Because of reduced grass quality, these animals may select the increasingly abundant legumes for their high N concentration. This would reduce the CO_2-induced stimulation of legumes. On the other hand, elevated CO_2 was found to lower digestibility and nutritive value of a legume (Carter et al. 1999), thus making predictions difficult.

Water relations and productivity

The extent of ET from our model ecosystems was similar to ET from other semi-arid grass communities (Amir et al. 1991; Lapitan and Parton 1996), but greater than from a drier ecosystem (Malek et al. 1999), and less than from Mediterranean-type grasslands (Field et al. 1997; Fredeen et al. 1997). Our communities clearly lost less water through ET and experienced less soil moisture depletion when grown in a CO_2-enriched atmosphere. The reduction of ET at elevated CO_2 was due to lower transpiration caused by reduced leaf diffusive conductance, at least in some important species. Interestingly, LAI tended to be lower in elevated than in pre-industrial CO_2 during the first part of the season. This trend started to change only toward peak season when less depleted soil moisture at elevated CO_2 caused delayed leaf dieback (Table 3). Hence, during most of the growing season there was no compensation of reduced leaf-level water loss by increased LAI. A trend for reduced LAI at elevated CO_2 has been noted in several experiments (Körner and Arnone 1992; Hättenschwiler and Körner 1996b; Körner et al. 1997; Thomas et al. 1999; Van Oijen et al. 1999), and no net change of LAI in response to CO_2 enrichment was found across 12 studies analyzed by Drake et al. (1997).

The reduction in soil moisture depletion in the two elevated CO_2 treatments permitted a slightly extended period of water extraction by plants toward the end of the season. Unlike grasses, which have a determinate growth type, legumes took particular advantage of the higher soil moisture at elevated CO_2, and produced additional fruits. Consequently, the CO_2 effect on legumes, and the whole community, was greater for reproduction at the final harvest than for total aboveground phytomass at the peak season harvest. In two Californian grasslands, late-spring soil moisture was also higher at elevated CO_2 (Field et al. 1997; Fredeen et al. 1997), resulting in positive CO_2 effects on plant biomass in late-season annuals (Chiariello and Field 1996; Field et al. 1996). In a tallgrass prairie, photosynthesis and a more favorable plant water status were sustained during dry periods at elevated CO_2 (Ham et al. 1995), and significant growth stimulation was observed only in years with a comparatively dry growing season (Owensby et al. 1999).

CO_2-induced water savings and associated lower soil water depletion were related to larger drainage of water below the rooting zone during the earlier, more humid part of the growing season. Consequently, the amount of rainwater that was effectively captured by model ecosystems and made available for plant growth was reduced at 600 µl l^{-1}. Later in the season, soils were drier and no further deep seepage occurred. Deep drainage is an important factor in these simulated shallow soils, as shown by the following comparison with ET: until early February, model ecosystems at 600 µl l^{-1} saved 17 mm water through reduced ET, but lost 11 mm more water through drainage compared to those at 280 µl l^{-1}. Thus, loss of water by deep seepage exerts a considerable influence on the overall CO_2 effect on seasonal water use in these shallow soils. A rise in deep drainage in grasslands was obvious from microcosm studies (Field et al. 1997) and model analyses (Coughenour and Parton 1996), and was predicted to be more pronounced in grasslands with high transpiration and large water savings at elevated CO_2 (Jackson et al. 1998). Moreover, on slopes, runoff after heavy rain may also increase at elevated CO_2 (Lockwood 1999). Greater deep drainage and/or runoff may be an important negative feedback to elevated CO_2 under natural conditions. The ecological significance of these processes is difficult to estimate, and will depend on rainfall patterns, topography, soil properties, profile depth, and associated nutrient leaching. For example, model outputs for Californian grasslands in years with similar annual precipitation showed that deep drainage was increased but CO_2-induced changes in deep drainage were decreased when rain was concentrated in a few large events compared to being more evenly distributed (Jackson et al. 1998). Therefore, the relatively even rain applications in our model ecosystems should have promoted CO_2 effects on deep drainage. Whether less depleted soil moisture and greater biomass of semi-arid vegetation will occur in a CO_2-enriched future atmosphere will largely depend on the net effect of greater deep drainage and runoff versus reduced ET.

Plant nitrogen

Nitrogen concentration has been found to decrease in most plants studied at elevated CO_2, with symbiotic N_2 fixers often being less affected than other C_3 plants (Cotrufo et al. 1998). With the exception of the small forb+geophyte fraction, our results are in agreement with this notion. The decreased N concentration but unchanged phytomass in the largest biomass fraction (grasses) resulted in a reduction in total N uptake by this community component. In contrast, total N uptake by legume shoots was increased at elevated CO_2, a fact that we attribute to enhanced N_2 fixation. Symbiotic N_2 fixation increased at elevated CO_2 under agricultural conditions (Zanetti et al. 1996), though not in a semi-natural, P-limited calcareous grassland (Niklaus et al. 1998a). Because of the relatively large proportion of legumes in our communities, the aboveground community N pool increased at elevated CO_2, as was found in some (Hungate et al. 1997), but not all (Schäppi and Körner 1997; Niklaus et al. 1998a) grasslands. Nitrogen limitation of the CO_2 response was found in a tallgrass prairie, particularly in dry years (Owensby et al. 1994). In alpine grassland, neither fertilized nor unfertilized communities were affected by elevated CO_2 (Schäppi and Körner 1996).

Non-linear responses

Some non-linear responses detected through the use of three CO_2 concentrations suggest the possibility for enhanced responses at a future higher level of CO_2 enrichment. For example, a reduction in transpirational water loss and increase in plant N pools were more pronounced across the higher (440–600 µl l^{-1}) than across the lower (280–440 µl l^{-1}) CO_2 interval. Other traits seemed to saturate at 440 µl l^{-1} CO_2, similar to findings by Hättenschwiler and Körner (1996a, 1996b). In particular, total above- and belowground phytomass at peak season was increased at 440 compared to 280 µl l^{-1} CO_2, with no further increase at 600 µl l^{-1}. A similar trend for total community production was found by Zangerl and Bazzaz (1984). This indicates that much of the stimulating effect occurs at a relatively low CO_2 concentration.

Conclusions

The biomass effect of elevated CO_2 on seasonal grassland communities of the northern Negev was significant, albeit rather moderate, and depended on a few legumes, and one species in particular. It is remarkable that the community response was largely taxon specific, hence species identity seem to play an important role. Perpetuation of this response in the field could lead to changes in biodiversity as well as to increases in productivity of grasslands in the Negev. On the other hand, a legume dominance could increase drought sensitivity and competition by grasses and, thus, seems unlikely to be successful in the long run. If water savings and biomass increase will indeed be small in a future CO_2-rich world, the chances for CO_2 enrichment to mitigate desertification in this dry region are small.

Reduced soil moisture depletion under elevated CO_2 enhanced the deep-drainage fraction of the water balance, and reduced the overall utilization of scarce rainfall. This generally underestimated phenomenon has the potential to outweigh benefits from increased WUE of growth under field conditions. A hydrologic model based on the current and additional studies in dry regions needs to be developed to account for these counteracting CO_2 enrichment effects.

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