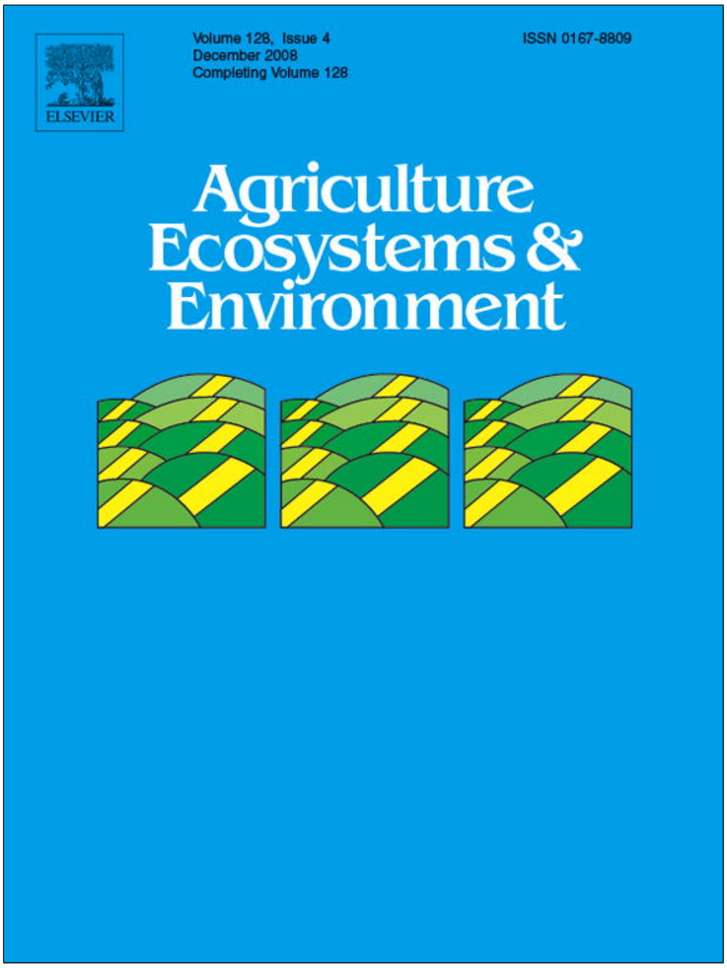
Volume 128, Issue 4
December 2008
Completing Volume 128
ISSN 0167-8809
ELSEVIER
Agriculture
Ecosystems &
Environment

Agriculture, Ecosystems and Environment 128 (2008) 219–224

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

journal homepage: www.elsevier.com/locate/agee

Contrasting responses of seed yield to elevated carbon dioxide under field conditions within *Phaseolus vulgaris*

James A. Bunce *

USDA-ARS Crop Systems and Global Change Laboratory, B-001, BARC-West, 10300 Baltimore Avenue, Beltsville, MD 20705-2350, USA

ARTICLE INFO

Article history:
Received 4 March 2008
Received in revised form 3 June 2008
Accepted 5 June 2008
Available online 10 July 2008

Keywords:
Phaseolus vulgaris
Common bean
CO_2
Yield
Photosynthesis
Seed number
Pod number

ABSTRACT

The rising concentration of carbon dioxide [CO_2] in the atmosphere represents an increase in a growth-limiting resource for C_3 crop species. Identification of lines or characteristics of lines which have superior yield at elevated [CO_2] could aid in adaptation to this global change. While intraspecific variation in responses to elevated [CO_2] has been found in several species, intraspecific differences in crop yield responses to elevated [CO_2] under field conditions have seldom been documented. In this 4-year study, the responses of photosynthesis, growth, pod number, seed number and size, and seed yield to the elevation of [CO_2] to 180 μmol mol^{-1} above the current ambient concentration were examined in four varieties of *Phaseolus vulgaris* in the field, using open-top chambers. There was a significant variety by [CO_2] interaction for seed yield, with seed yield at elevated [CO_2] ranging from 0.89 to 1.39 times that at ambient [CO_2] (mean 1.17×) in the different varieties, when averaged over 4 years. The highest yielding variety at elevated [CO_2] was not the highest yielding variety at ambient [CO_2]. The varieties with the largest and smallest yield responses both had an indeterminate growth habit. Down-regulation of photosynthesis at elevated [CO_2] only occurred in the two indeterminate varieties, and there was no significant correlation between the response of single leaf photosynthetic rate and the response of seed yield to elevated [CO_2] among varieties, nor between the responses of stem mass and seed yield. The change in the number of pods at elevated [CO_2] was the primary determinant of the response of seed yield. These results indicate that significant variation in the response of seed yield to elevated [CO_2] under field conditions does exist among varieties of *P. vulgaris*, and that variation in the response of pod and seed number may be more important than variation in photosynthetic response.

Published by Elsevier B.V.

1. Introduction

The increasing concentration of carbon dioxide [CO_2] in the atmosphere represents an increase in a growth-limiting resource for C_3 crop species, because C_3 photosynthesis is seldom saturated with carbon dioxide at the current ambient concentration. Elevated [CO_2] generally increases photosynthesis, growth and yield of C_3 crop plants, but with large differences among species in the magnitude of the yield stimulation (e.g. Kimball et al., 2002). Not surprisingly, significant intraspecific variation in responses to elevated [CO_2] has been found in several non-crop species (reviewed in Ward and Kelly, 2004), and intraspecific variation in yield response to elevated [CO_2] has been found in rice (Ziska et al., 1996; Moya et al., 1998; Baker, 2003), cowpea (Ahmed et al., 1993), wheat (Manderscheid and Weigel, 1997; Ziska et al., 2004), and soybean (Ziska and Bunce, 2000; Ziska et al., 2001). However, much of the work on intraspecific variation in crops has been done in controlled environment chambers, in glasshouses or with plants in pots, and it is uncertain how those results may extrapolate to field conditions. Identification of lines or the characteristics of lines which have superior yield at elevated [CO_2] in the field could aid in adaptation of crops to this global change by facilitating the development of varieties better able to exploit the increase in atmospheric [CO_2].

Phaseolus vulgaris L. (Fabaceae) is an annual species with C_3 photosynthetic metabolism. The cultivated varieties of the species are presumed to be derived from the wild species which is widely distributed from northern Mexico to northern Argentina (Singh et al., 1991). The cultivated varieties have been classified into two major groups, Middle American and Andean South American, each group having three distinct races (Singh et al., 1991). With limited chamber space available, and no information about what ecological or agronomic adaptations might affect the responsiveness of seed yield to elevated [CO_2], it was decided to compare varieties from different races as well as with different agronomic uses in order to increase the chance of finding different responses

* Tel.: +1 301 504 7629; fax: +1 301 504 5823.
E-mail address: James.Bunce@ars.usda.gov.

0167-8809/$ – see front matter. Published by Elsevier B.V.
doi:10.1016/j.agee.2008.06.003

to elevated [CO_2]. Two varieties were chosen from each of the two major groups, and for the Middle American group, from two different races, Durango and Mesoamerica. Within the Andean South American group, we used two varieties with contrasting agronomic uses (a kidney bean and a snap bean) both from the Nueva Granada race. The Nueva Granada race is the only race within the Andean South American group substantially represented in germplasm used in agriculture in the United States. Within these classes, we arbitrarily selected varieties known to grow well in Maryland. Most of the work with this species at elevated [CO_2] has been conducted in controlled environments and has focused primarily on photosynthetic response and acclimation, changes in leaf nitrogen, and leaf and plant morphology (Radoglou and Jarvis, 1992; Socias et al., 1993; Mjwara et al., 1996; Jifon and Wolfe, 2002; Joutei et al., 2003). Here, we compared responses of seed yield to elevated [CO_2] in four varieties grown for 4 years in field plots in open top chambers.

2. Materials and methods

2.1. Materials

The four varieties of *P. vulgaris* L. used were Matterhorn, a great northern variety of the Durango race of the Middle American group, Jaguar, a black bean of the Mesoamerica race of the Middle American group, Red Hawk, a kidney bean of the Nueva Granada race of the Andean South American group, and Brown Beauty, a snap bean of the Nueva Granada race of the Andean South American group. Jaguar and Matterhorn are upright, indeterminate, short-vine types, and Red Hawk and Brown Beauty are determinate, bush types. None of the varieties had apparent disease problems when grown at Beltsville, MD, and all had seed yields under ambient conditions of about 200–300 g dry mass m^{-2}.

2.2. Plant culture

Plants were grown in six square chambers 2.75 m on a side and 1.22 m tall at the outer edge. The chambers were made of clear acrylic plastic, and had sloping partial roofs which restricted the opening at the top to about one-third of the basal area. The sloping partial roofs reduced wind penetration and the fluctuation of the [CO_2]. About 60 m^3 min^{-1} of air was continuously blown into the chambers through perforated pipe on the ground. Three of the chambers had pure CO_2 constantly introduced into the inlets of the blowers at flow rates sufficient to increase the [CO_2] in the chambers to 180 ± 20 μmol mol^{-1} above that of the ambient air. Samples of air of the three elevated [CO_2] chambers and one ambient [CO_2] chamber were pumped into an adjacent building for sequential measurement of their [CO_2] using an absolute infrared analyzer (LI-6252, Li-Cor, Inc., Lincoln, NE). The [CO_2] and temperatures of air inside and outside the chambers were recorded every 5 min. Shaded air temperatures within the chambers averaged 2.3 °C above that of outside air. The [CO_2] of ambient air averaged 385 μmol mol^{-1} during the day (368 at midday) and 493 μmol mol^{-1} during the night during the experiments. An automated weather station about 100 m from the chambers recorded photosynthetically active radiation and standard meteorological variables. Chambers were irrigated to prevent significant soil water deficits from developing at any time.

All four varieties were grown simultaneously in each chamber. Chambers were divided into four-square equal-sized sections, and each section was randomly assigned to a variety. Within each section, seeds were planted directly into recently tilled soil in three 1.37 m rows on day of year 134 in 2003, 153 in 2004 and 2005, and 203 in 2006. The planting date was determined by when soil moisture conditions were suitable for tilling. All varieties had completed their growth cycle and had fully mature, dried pods before cold weather would have limited growth. The rows were over-seeded, then thinned during early vegetative growth to a final density of 14 plants m^{-2}. The soil was a silt loam, with a pH of 6.5, a bulk density of 1.3 g cm^{-3}, with about 2% organic matter. Plots were fertilized with 8 g N m^{-2}, based on soil tests and recommendations of the State of Maryland Nutrient Management System.

2.3. Plant sampling

Rates of photosynthesis of mature upper canopy leaves were measured twice each year, late in vegetative development, and during pod filling. Steady-state rates of CO_2 assimilation, stomatal conductance and substomatal [CO_2] were determined near midday on clear days using a portable photosynthesis system (Ciras-1, PP Systems, Amesbury, MA). Gas exchange was measured under the ambient conditions of light, air temperature and water vapor pressure. Leaves of plants grown at elevated [CO_2] were measured at their daytime growth [CO_2] of about 550 μmol mol^{-1}. Leaves of plants grown at ambient [CO_2] were measured both at their daytime growth [CO_2] of about 370 μmol mol^{-1} and also at 550 μmol mol^{-1}, for direct comparison with data from the plants grown at elevated [CO_2]. Leaf gas exchange was measured on two leaves of each variety in each chamber on each measurement date, but statistical analysis was conducted on chamber means for each variety.

Plants were harvested only from the center, bordered row of each variety. A harvest was conducted during early vegetative growth, when plants had leaf areas of about 300 cm^2 per plant. Three plants of each variety in each chamber were cut at ground level for determination of total leaf area, and leaf and stem dry mass of the three plants combined. The percentage N in the dried material of the three plants and leaf N per unit leaf area was determined using a PerkinElmer 2400 Series II CHNS/O analyzer. At seed maturity, the center approximately 80 cm of the bordered row of each cultivar was cut at ground level, and bulked material was separated into stems, pods and seeds for determination of pod and seed number, dry mass, and percentage N of seeds. Seed yield was expressed as oven-dry mass per unit of ground area.

2.4. Statistics

The experiment was analyzed as a split-plot design, using the restricted maximum likelihood method implemented in JMP v.5 (SAS Institute, Cary, NC). There were three replicate chambers of both [CO_2] levels, for each of 4 years, with each chamber containing all four varieties. Chamber was used as a random variable, and growth [CO_2], variety and year were fixed variables. Effects of variety, growth [CO_2], year, and their interactions were tested, using a probability level of 5%. The vegetative and final harvests were analyzed separately, as were the gas exchange measurements during the vegetative and reproductive periods. For the leaf gas exchange measurements, these comparisons were made of assimilation rates, stomatal conductances and substomatal [CO_2] measured at 550 μmol mol^{-1} external [CO_2]. Where significant effects of variety were found, means were compared using Tukey's Honestly Significant Difference Test.

3. Results

3.1. Vegetative growth

At the harvest during early vegetative growth, elevated [CO_2] significantly increased shoot dry mass of all four varieties, but not

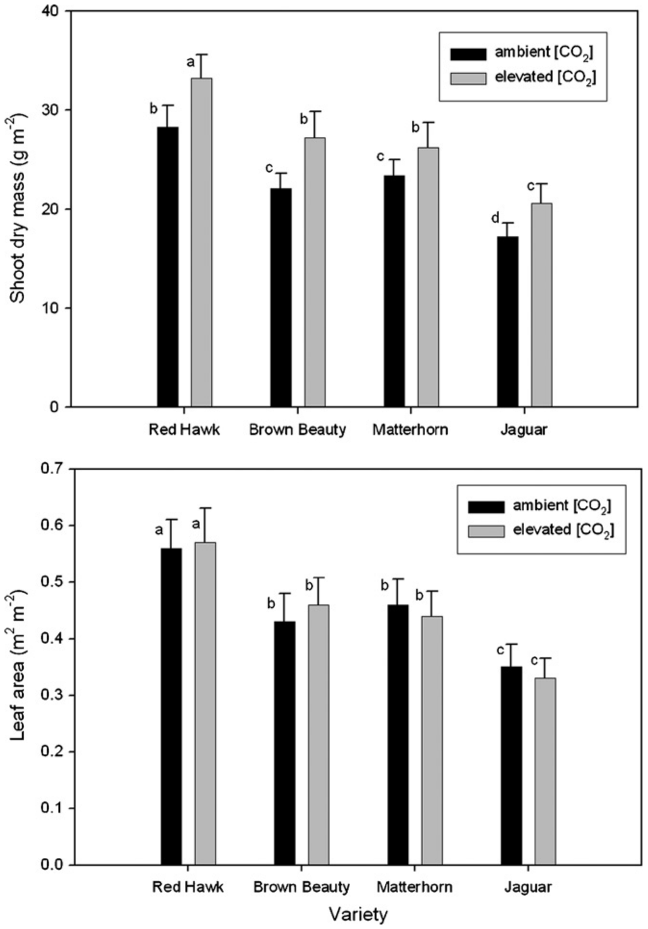

Fig. 1. Mean values of shoot dry mass and leaf area during early vegetative growth expressed per unit of ground area for four varieties of beans grown at ambient and elevated [CO_2] for 4 years in open top chambers. Vertical bars indicate S.E. For each variable, different letters indicate values which are significantly different at the 5% level of probability.

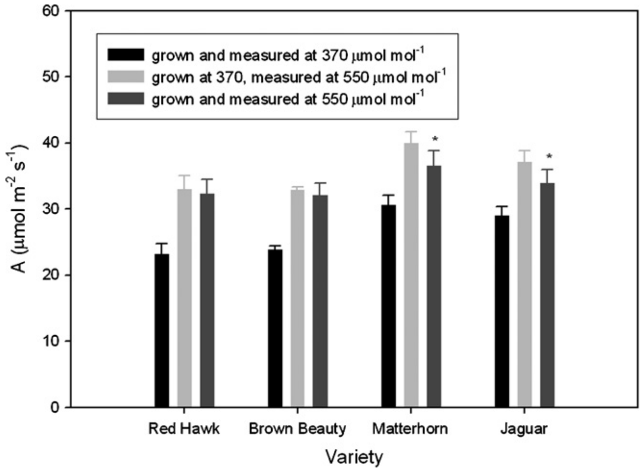

Fig. 2. Mean values of leaf photosynthetic net CO_2 assimilation rates (A) of four varieties of bean grown at ambient and elevated [CO_2], measured at either ambient or elevated [CO_2]. Measurements were made near midday in full sunlight at the ambient conditions of air temperature and water vapor pressure. Values are means over 4 years of measurements made during the pod-filling stage. Vertical bars indicate S.E. (*) Indicates a significant difference (at the 5% level of probability) between rates measured at the higher [CO_2] for plants grown at ambient and at elevated [CO_2].

leaf area (Fig. 1). At that stage, Red Hawk had the greatest shoot dry mass, and Jaguar the least. There were no interactions between varieties or years in the effect of [CO_2] on shoot dry mass or leaf area (not shown).

The percentage of nitrogen in the stem mass at the harvest during vegetative growth was never significantly reduced at elevated [CO_2] in any variety in any year, with mean values of 2.2% at ambient [CO_2], and 2.1% at elevated [CO_2]. In leaves, the percentage of N was significantly reduced at elevated [CO_2] in all varieties and in all years, with mean values of 4.3% at ambient [CO_2] and 3.3% at elevated [CO_2]. However, leaf N m^{-2} leaf area never differed between [CO_2] treatments, averaging 1.75 g m^{-2} at ambient [CO_2] and 1.78 g m^{-2} at elevated [CO_2]. There were no significant differences among varieties in stem or leaf percent nitrogen or in leaf nitrogen per unit of leaf area, and no interactions among [CO_2], variety or years (not shown).

3.2. Leaf gas exchange

Leaf gas exchange rates were measured at leaf temperatures of 28–33 °C on the different measurement dates, and leaf to air water vapor pressure differences ranged from 1.8 to 2.6 kPa. Leaf gas exchange characteristics measured near midday did not differ substantially for the two growth stages used, nor did the mean leaf temperatures and water vapor pressure differences, and only the data for the measurements during reproductive growth are presented. Elevated [CO_2] stimulated photosynthesis in all varieties, both in the short term, and in the long term (Fig. 2). Long-term growth at elevated [CO_2] decreased photosynthesis measured at the elevated [CO_2] in the varieties Matterhorn and Jaguar, but not Red Hawk or Brown Beauty (Fig. 2). The absolute stimulation in photosynthesis in the short term was very similar in all varieties (Fig. 2), but the relative short-term stimulation in Red Hawk and Brown Beauty averaged 40% compared with 30% in Matterhorn and Jaguar, because of the higher rates at ambient [CO_2] in the latter two varieties. This difference, combined with the down-regulation of photosynthesis at elevated [CO_2] in Matterhorn and Jaguar, resulted in the net long-term stimulation of midday photosynthesis in Matterhorn and Jaguar averaging only 18%, compared with an average of 36% in both Red Hawk and Brown Beauty.

No significant differences among varieties or growth [CO_2] conditions occurred for substomatal [CO_2] during the photosynthetic measurements. At 370 μmol mol^{-1} external [CO_2], the substomatal [CO_2] averaged 296 μmol mol^{-1}, and at 550 μmol mol^{-1} external [CO_2], the substomatal [CO_2] averaged 430 μmol mol^{-1}. Corresponding with the differences among varieties in the net long-term stimulation of midday photosynthesis presented earlier, stomatal conductance measured at the midday growth [CO_2] conditions was reduced to a larger extent in Matterhorn and Jaguar (a mean reduction of 32%) than in Red Hawk and Brown Beauty (a mean reduction of 5%).

3.3. Final harvest

Seed yield averaged over the 4 years was significantly increased by elevated [CO_2] in Matterhorn, slightly increased in Red Hawk and Brown Beauty, and slightly decreased in Jaguar (Fig. 3). The [CO_2] by variety interaction was highly significant, and there was no significant effect of year on the [CO_2] by variety interaction (Table 1). Jaguar had significantly higher yield than the other varieties at ambient [CO_2], but at elevated [CO_2], Matterhorn had significantly higher yield than all other varieties (Fig. 3). The seed yield averaged over varieties varied substantially among years, with higher yields in 2004 and 2006 than in 2003 and 2005 (Fig. 4).

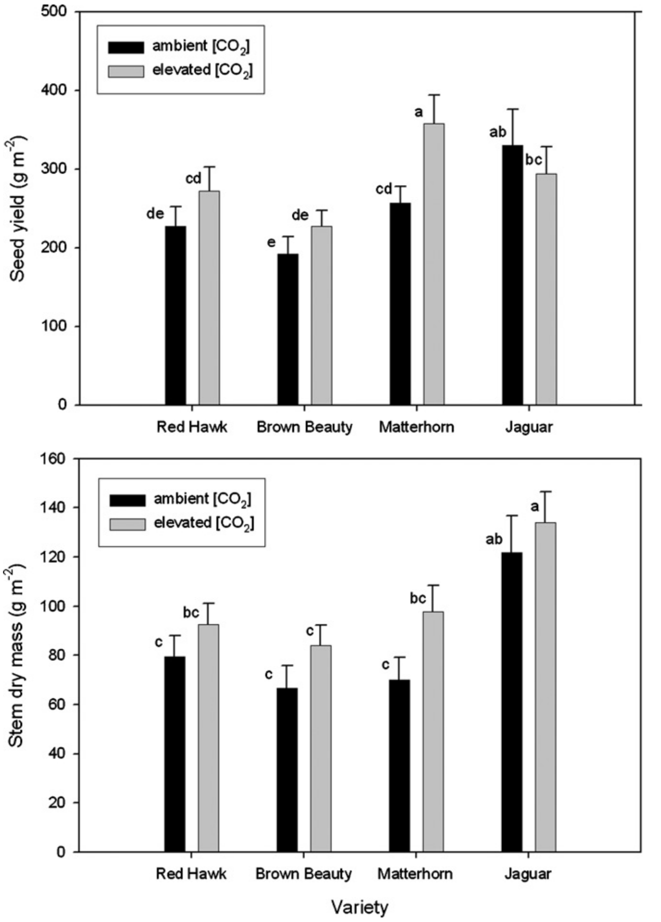

Fig. 3. Mean values of seed and stem dry mass at maturity expressed per unit of ground area of four varieties of beans grown at ambient and elevated [CO_2] for 4 years in open top chambers. Vertical bars indicate S.E. For each variable, different letters indicate values which are significantly different at the 5% level of probability.

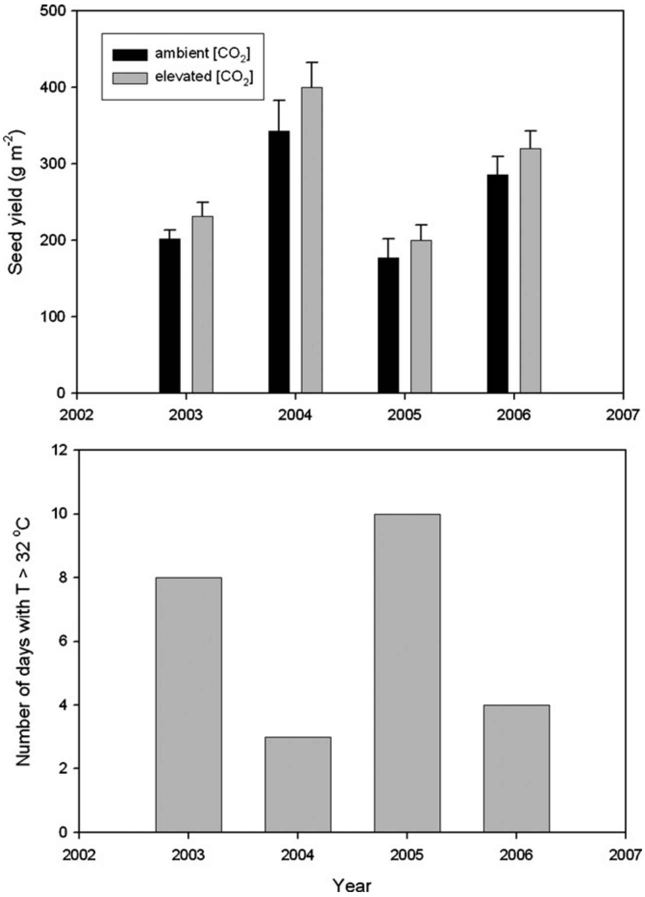

Fig. 4. Mean values of seed dry mass at maturity of four varieties of beans grown at ambient and elevated [CO_2] for 4 years, and the number of days during the last 30 days before maturity for which maximum air temperature exceeded 32 °C. Vertical bars indicate S.E. The results of statistical tests of effects of year and [CO_2] on seed mass are given in Table 1.

Average yield was inversely related to the number of days in the last 30 days before maturity when the maximum air temperature exceeded 32 °C (Fig. 4). Relationships with other weather variables were less clear, but were not fully investigated. There was no apparent relationship between average yield and planting date. From the year with the lowest mean yield to that with the highest, the yield of Jaguar increased by a factor of 2.3, compared with a mean increase of about 1.9 in the three other varieties, but the year by variety interaction term was not significant at $P = 0.05$ (Table 1). The percentage of N in the seeds did not differ significantly between the [CO_2] treatments, averaging 3.9% at ambient and 3.7% at elevated [CO_2].

Stem biomass at the final harvest averaged over the 4 years was increased by elevated [CO_2] in all varieties, including Jaguar (Fig. 3). The [CO_2] effect was significant overall, but not for any individual variety, and the [CO_2] by variety interaction was not significant (Table 1). Mass per seed and seeds per pod differed among varieties, but the [CO_2] treatment had no significant effect and there were no significant [CO_2] by variety interactions (Table 1). Jaguar averaged about five seeds per pod, with each seed weighing about 0.17 g, while the other varieties all averaged about three seeds per pod, each seed weighing about 0.35 g.

The relative stimulation of seed yield by elevated [CO_2] among the four varieties was highly correlated with the relative

Table 1
Degrees of freedom (d.f.), *F* ratios and probabilities (*P*) for some plant parameters at the final harvest

Effect	d.f.	Seed mass (g m^{-2})		Stem mass (g m^{-2})		Pod number (pods m^{-2})		Mass per seed (g seed^{-1})		Seeds per pod	
		F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
CO_2	1	2.59	0.183	10.57	**0.031**	3.34	0.142	0.59	0.484	0.02	0.896
Variety	3	12.72	**0.001**	23.32	**0.001**	82.7	**0.001**	45.3	**0.001**	38.45	**0.001**
Year	3	36.78	**0.001**	30.53	**0.001**	5.28	**0.003**	11.02	**0.001**	5.32	**0.003**
CO_2 × variety	3	4.20	**0.009**	0.53	0.662	3.13	**0.032**	0.90	0.446	2.41	0.075
CO_2 × year	3	0.28	0.842	0.80	0.497	0.56	0.642	1.46	0.233	3.77	**0.015**
Variety × year	9	1.86	0.075	1.14	0.352	4.29	**0.001**	2.73	**0.010**	2.52	**0.016**
CO_2 × variety × year	9	1.37	0.221	0.89	0.537	1.55	0.151	1.02	0.439	1.20	0.361

Values of $P < 0.05$ are in bold.

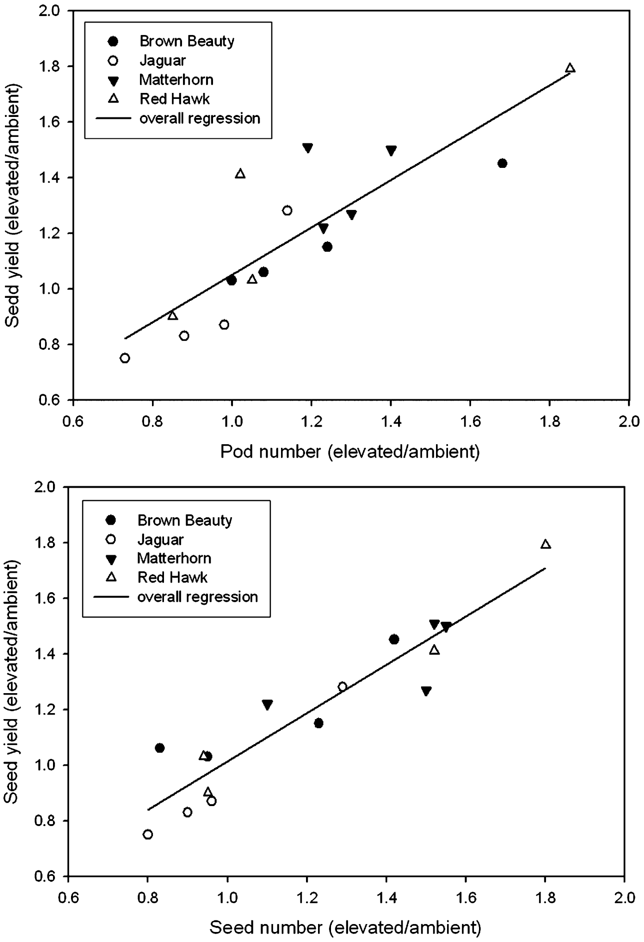

Fig. 5. Relationships between the ratio of seed yield at elevated to that at ambient $[CO_2]$ and the ratio of pod and seed numbers for four varieties of beans grown at ambient and elevated $[CO_2]$ for 4 years. Each point represents the mean for a year for a variety. The r^2 values for the overall linear regressions were 0.740 for pod number and 0.787 for seed number. These r^2 values are both significant at the 5% level of probability.

stimulation of both pod number and seed number. This is shown in Fig. 5 for all years. When ratios of elevated to ambient yields were averaged over years within each variety, the r^2 value with the relative stimulation of pod number was 0.943 and with seed number was 0.962 (not shown). Correlations between the relative stimulation of average seed yield by elevated $[CO_2]$ among the four varieties and the relative stimulation of stem mass at the final harvest or leaf photosynthetic rates under the midday growth conditions were not significant at the $P = 0.05$ level (not shown), nor were correlations between the absolute stimulation of seed mass and the absolute stimulation of stem mass or leaf photosynthesis at elevated $[CO_2]$.

4. Discussion

Because stimulation of photosynthesis is considered to be a primary mechanism by which elevated $[CO_2]$ stimulates plant growth (Gifford, 1994; Long et al., 2005), it seemed reasonable to hypothesize that greater stimulation of yield would occur in varieties with greater stimulation of leaf photosynthesis. The data presented here clearly do not support this hypothesis, because the two varieties with the largest and smallest increases in seed yield both had relatively little stimulation in photosynthesis, and the two varieties with the largest increases in photosynthesis had intermediate yield responses (Figs. 1 and 2). In a field study of the yield response of two cultivars of soybean to elevated $[CO_2]$, no differences in leaf photosynthetic response to elevated $[CO_2]$ occurred, while seed yield responses differed (Ziska and Bunce, 2000). Another field study with soybean identified intraspecific differences in photosynthetic response to elevated $[CO_2]$, but did not report seed yields (Ainsworth et al., 2004). A field comparison of rice responses to elevated $[CO_2]$ documented intraspecific differences in yield response (Moya et al., 1998), but did not report photosynthetic rates. In spring wheat grown in pots in the field, Manderscheid and Weigel (1997) found no differences in photosynthetic characteristics of flag leaves among varieties which differed in biomass response to elevated $[CO_2]$. The data reported here for beans may be the first field study to report significant intraspecific differences in both photosynthetic and yield responses to elevated $[CO_2]$. There is often a poor correlation between leaf photosynthesis and yield within crop species (e.g. Elmore, 1980; Evans, 1993), so it is perhaps not surprising that photosynthetic and yield responses to elevated $[CO_2]$ were poorly correlated in this intraspecific comparison. Poor correlations between leaf photosynthesis and yield have been attributed to overriding variations in leaf size, display, and duration, the partitioning of photosynthate among organs, and especially reproductive features (e.g. Bunce, 1986; Evans, 1993).

The fundamental cause of down-regulation of photosynthesis after long-term exposure to elevated $[CO_2]$ is thought to be inability to utilize the extra products of photosynthesis (Stitt, 1991). This hypothesis does have predictive capability in some species (Bunce and Sicher, 2003). Ainsworth et al. (2004) hypothesized that in soybean, plants with an indeterminate growth habit would have larger "sink strength" and less down-regulation of photosynthesis at elevated $[CO_2]$. In two paired comparisons of soybean isolines differing only in the degree of determinacy, the hypothesis was supported in one comparison, but not in the other. While the varieties of beans compared here differed in many characteristics in addition to determinacy, the data for beans do not support the hypothesis, because only the two indeterminate varieties had significant down-regulation of photosynthesis (Fig. 2). The cause of the down-regulation was not identified in this study, but down-regulation occurred at both the vegetative and reproductive stages.

It might be thought that an indeterminate growth habit would provide more flexibility in node number, flowering sites and pod number, and hence in the stimulation of seed yield at elevated $[CO_2]$. This did not consistently occur in the bean varieties studied here, because, of the two indeterminate varieties, one had the largest increase in pod number and yield at elevated $[CO_2]$, but the other had a decrease in pod number and yield. In soybean the increase in pod numbers at elevated $[CO_2]$ did not differ between an indeterminate and a determinate cultivar (Ziska and Bunce, 2000). Clearly, under field conditions determinate versus indeterminate growth habit is not a good predictor of changes in pod number at elevated $[CO_2]$ in either soybeans or beans. Among these bean varieties, the effect of elevated $[CO_2]$ on pod and seed numbers were good predictors of the response of seed yield (Fig. 5). This occurred because seeds per pod and mass per seed were nearly unaffected by the $[CO_2]$ treatment in any variety. By what means elevated $[CO_2]$ affected pod and seed number is unknown, but was not obviously related to the amount of stimulation in leaf photosynthesis or in stem mass in this study, and warrants further investigation. Increases in pod number at elevated $[CO_2]$ were also the primary cause of increased seed yield in soybean (Ziska and Bunce, 2000).

Whether traits which lead to high yields at elevated $[CO_2]$ are manifest at lower $[CO_2]$ is an open question of some importance for the development of plant breeding strategies for global environmental changes (Newton and Edwards, 2007). In the present study of beans, the highest yielding variety at ambient [CO_2] was outyielded by a different variety at elevated [CO_2]. This was not specifically examined in field studies of cultivar differences in yield response to elevated [CO_2] in rice (Moya et al., 1998) and soybean (Ziska and Bunce, 2000), but the results for bean suggest that varieties best adapted to the current environment may not have the characteristics best adapted to future [CO_2]. If this were true generally, it might imply that elite modern genetic lines may provide too narrow a genetic base to fully exploit the potential of rising atmospheric [CO_2] to increase crop yields. Only testing of other varieties will reveal whether more closely related varieties than those used here also have significant variation in response to elevated [CO_2] and what ecological or agronomic adaptations affect responsiveness.

In conclusion, these results indicate that consistent and significant variation in the response of seed yield to elevated [CO_2] under field conditions does exist among varieties of *P. vulgaris*, and that variation in the response of pod and seed number may be more important than variation in the response of photosynthesis or stem biomass.

Acknowledgements

I thank Dr. James Kelly and Dr. Marcial Pastor Corrales for advice on selecting the varieties and for providing seeds, and Martha Tomecek for expert technical assistance.

References

Ainsworth, E.A., Rogers, A., Nelson, R., Long, S.P., 2004. Testing the "source-sink" hypothesis of down-regulation of photosynthesis in elevated [CO_2] in the field with single gene substitutions in *Glycine max*. Agric. For. Meteorol. 122, 85–94.

Ahmed, F.E., Hall, A.E., Madore, M.A., 1993. Interactive effects of high temperature and elevated carbon dioxide concentration on cowpea (*Vigna unguiculata* (L.) Walp.). Plant Cell Environ. 16, 835–842.

Baker, J.T., 2003. Yield responses of southern U.S. rice cultivars to CO_2 and temperature. Agric. For. Meteorol. 122, 129–137.

Bunce, J.A., Sicher, R.C., 2003. Daily irradiance and feedback inhibition of photosynthesis at elevated carbon dioxide concentration in *Brassica oleracea*. Photosynthetica 41, 481–488.

Bunce, J.A., 1986. Measurements and modeling of photosynthesis in field crops. Crit. Rev. Plant Sci. 4, 47–77.

Elmore, C.D., 1980. The paradox of no correlation between leaf photosynthetic rates and crop yields. In: Hesketh, J.D., Jones, J.W. (Eds.), Predicting Photosynthesis for Ecosystem Models, vol. 2. CRC Press, Boca Raton, FL (Chapter 9).

Evans, L.T., 1993. Crop Evolution Adaptation and Yield. Cambridge University Press, UK.

Gifford, R.M., 1994. The global carbon cycle: a viewpoint on the missing sink. Aust. J. Plant. Physiol. 21, 1–15.

Jifon, J.L., Wolfe, D.W., 2002. Photosynthetic acclimation to elevated CO_2 in *Phaseolus vulgaris* L. is altered by growth response to nitrogen supply. Global Change Biol. 8, 1018–1027.

Joutei, A.B., Salager, J.-L., Sonie, L., Van Empe, G., Lebrun, P., 2003. Effects of elevated CO_2 on the physiology and yield parameters of bean. Agrochemie 23, 327–334.

Kimball, B.A., Kobayashi, K., Bindi, M., 2002. Responses of agricultural crops to free-air CO_2 enrichment. Adv. Agron. 77, 293–368.

Long, S.P., Ainsworth, E.A., Leakey, A.D.B., Morgan, P.B., 2005. Global food insecurity. Treatment of major food crops with elevated carbon dioxide or ozone under large-scale fully open-air conditions suggests recent models may have over-estimated future yields. Philos. Trans. R. Soc. B 360, 2011–2020.

Manderscheid, R., Weigel, H.J., 1997. Photosynthetic and growth responses of old and modern spring wheat cultivars to atmospheric CO_2 enrichment. Agric. Ecosys. Environ. 64, 65–73.

Mjwara, J.M., Botha, C.E.J., Radloff, S.E., 1996. Photosynthesis, growth and nutrient changes in non-nodulated *Phaseolus vulgaris* growth under atmospheric and elevated carbon dioxide conditions. Physiol. Plantar. 97, 754–763.

Moya, T.B., Ziska, L.H., Namuco, O.S., Olszyk, D., 1998. Growth dynamics and genotypic variation in tropical, field grown paddy rice (*Oryza sativa* L.) in response to increasing carbon dioxide and temperature. Global Change Biol. 4, 645–656.

Newton, P.C.D., Edwards, G.R., 2007. Plant breeding for a changing environment. In: Newton, P.C.D., Carran, R.A., Edwards, G.R., Niklaus, P.A. (Eds.), Agroecosystems in a Changing Climate. Taylor and Francis, Pubs., London, pp. 309–319.

Radoglou, K.M., Jarvis, P.G., 1992. The effects of CO_2 enrichment and nutrient supply on growth morphology and anatomy of *Phaseolus vulgaris* L. seedlings. Ann. Bot. 70, 245–256.

Singh, S.P., Gepts, P., Debouck, D.G., 1991. Races of common bean (*Phaseolus vulgaris* Fabaceae). Econ. Bot. 45, 379–396.

Socias, F.X., Medrano, H., Sharkey, T.D., 1993. Feedback limitation of photosynthesis of *Phaseolus vulgaris* L. grown in elevated CO_2. Plant Cell Environ. 16, 81–86.

Stitt, M., 1991. Rising CO_2 levels and their potential significance for carbon flow in photosynthetic cells. Plant Cell Environ. 14, 741–762.

Ward, J.K., Kelly, J.K., 2004. Scaling up evolutionary responses to elevated CO_2: lessons from *Arabidopsis*. Ecol. Lett. 7, 427–440.

Ziska, L.H., Manalo, P.A., Ordonez, R.A., 1996. Intraspecific variation in the response of rice (*Oryza sativa* L) to increased CO_2 and temperature: growth and yield response of 17 cultivars. J. Exp. Bot. 47, 1353–1359.

Ziska, L.H., Bunce, J.A., 2000. Sensitivity of field-grown soybean to future atmospheric CO_2: selection from improved productivity in the 21st century. Aust. J. Plant Physiol. 27, 979–984.

Ziska, L.H., Bunce, J.A., Caulfield, F.A., 2001. Rising atmospheric carbon dioxide and seed yield of soybean genotypes. Crop Sci. 41, 385–391.

Ziska, L.H., Morris, C.F., Goins, E.W., 2004. Quantitative and qualitative evaluation of selected wheat varieties released since 1903 to increasing atmospheric carbon dioxide: can yield sensitivity to carbon dioxide be a factor in wheat performance. Global Change Biol. 10, 1810–1819.