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Climate change: a response surface study of the effects of CO₂ and temperature on the growth of French beans

D. C. E. WURR*, R. N. EDMONDSON AND J. R. FELLOWS

Horticulture Research International, Wellesbourne, Warwick CV35 9EF, UK

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SUMMARY

The possible impact of global rises in atmospheric CO₂ concentration and temperature on the growth and development of French beans (*Phaseolus vulgaris*) was examined using growth cabinets. Five CO₂ concentrations of 350, 450, 550, 650 and 750 vpm and five temperatures of 14.5, 15.5, 16.5, 17.5 and 18.5 °C were tested using a fractional factorial design comprising nine treatment combinations of the two factors. Plants were grown under constant irradiance, common atmospheric humidities (vpd 0.5 kPa) and non-limiting supplies of water and mineral nutrients. The plant growth response was modelled by fitting polynomial response function curves to the times to first flower opening, first bean set, 50% maturity and the number and yield of beans. The effects of temperature were large and positive for most of the measured variables, whereas the effects of CO₂ were small and negative or non-existent. Increased temperature substantially reduced the time to flowering and the time from bean set to 50% maturity and increased the number and yield of mature beans whereas increased CO₂ concentration had little effect on plant growth except that bean yield was very slightly reduced. There was no significant evidence of interaction between the CO₂ concentration effects and the temperature effects.

The time to maturity and yield of mature beans was simulated for the 2020s (2010 to 2039) and the 2050s (2040 to 2069) using the fitted polynomial models and four climate change scenarios suggested by the UK Climate Impacts Programme. These simulations showed that, depending upon the assumed scenario, the 2020s yields could rise by 39–84% and time to maturity reduce by between 6 and 15 days whereas the 2050s yields could rise by 51–118% and time to maturity reduce by between 9 and 25 days.

INTRODUCTION

Atmospheric concentrations of greenhouse gases have risen by about 50% in less than 200 years and these have been accompanied, during the twentieth century, by a warming of 0.5 °C in UK climate (UKCIP 1998*a*). There is no doubt that the UK climate is changing and there is little likelihood that historical climate records will be adequate to predict future trends.

A report prepared for the UK Climate Impacts Programme (UKCIP 1998*a, b*) describes how the UK climate may change during the next 100 years. It presents a range of future possible climate scenarios for global warming, described as *low*, *medium-low*, *medium-high* and *high*, for the respective warming

rates. These UK-wide scenarios cover future global warming rates from 0.1 to 0.3 °C per decade, and suggest increases of 0.6, 1.0, 1.2 and 1.4 °C, respectively, by the 2020s and 0.9, 1.5, 2.1 and 2.4 °C, respectively, by the 2050s, relative to the 1961–90 average. The corresponding CO₂ concentrations are 415, 398, 447 and 434 vpm, respectively, in the 2020s and 467, 443, 554 and 528 vpm, respectively, in the 2050s, compared with the current concentration of about 360 vpm.

It is already known that increased temperature will improve the growth and extend the season of production of *Phaseolus* beans in the UK (Wurr 1993) but there have been no quantitative estimates of these effects. Information is available on the effects of temperature on bean growth and development (Ferreira *et al.* 1997; Yan & Wallace 1998) but not in combination with high CO₂ concentrations. Nor have there been any reports of the effect of increased CO₂

* To whom all correspondence should be addressed.
Email: david.wurr@hri.ac.uk

concentrations on French beans. In the work reported here, the effects of a range of raised temperatures and raised CO₂ concentrations on the growth, development and yield of French beans were examined using controlled environment cabinets. Temperatures in the range 14.5–18.5 °C and CO₂ concentrations in the range 350–750 vpm were tested and polynomial response function models were fitted to describe the plant response everywhere within the region spanned by the two treatment factors.

MATERIALS AND METHODS

Experimental design

The experiment was one of a series of climate change experiments at Horticulture Research International intended to investigate crop response to changes in temperature and atmospheric CO₂ concentration. The same basic experimental design (Edmondson 1994) of ten growth cabinets was used throughout to investigate five CO₂ concentrations and five temperatures and is fully described in Wurr *et al.* (1998). The planned design had the nine different combinations of CO₂ and temperature shown in Figs 1*a* and 1*b* with double replication of the central design point to give a fractional factorial design with ten design points. It was intended that the experiment would have two blocks of five treatments with one central point and four alternating radial points forming one block and the remaining central and radial points forming the other block. For exact design orthogonality, factor spacings would have been chosen according to a suitable trigonometric sine function (see Wurr *et al.* 1998) but here evenly spaced factor levels were used. Evenly spaced five-level factors give a near-orthogonal

design and the convenience of evenly spaced factor levels far outweigh any slight loss of design orthogonality.

Unlike the experiment discussed in Wurr *et al.* (1998), which used ten identical growth cabinets in a completely randomized design, this experiment used five cabinets in each of two separate runs. The original design plan was to use the design points shown in Fig. 1*a* as a block for the first run and the remaining design points as a block for the second run. Unfortunately, owing to a major failure in CO₂ supply to the 750 vpm CO₂ treatment in the first run, the results from this cabinet were unreliable. The eight radial treatment combinations were on the outer boundary of the experimental factor space and the loss of any one radial treatment was likely to result in a serious loss of treatment information. Therefore for the second run the centre point was omitted and the unreliable radial point was repeated. Fig. 1*b* shows the actual design points used for the second run. Overall, every radial design point was used once, as originally planned, but the centre point was used only once instead of twice as originally planned.

Experimental methods

Plants were grown in five controlled environment Saxcil cabinets for two separate experimental runs. The cabinets were set up with a total irradiance of 120 W/m² supplied by Colour 35 fluorescent tubes, supplemented by twenty 15 W tungsten lamps providing a total irradiance of 40 W/m², and a 16 h photoperiod. Water vapour pressure deficit was 0.5 kPa. The first batch of plants was tested in five cabinets set at 14.5, 15.5, 16.5, 17.5 and 18.5 °C with CO₂ concentrations of 450, 750, 550, 350 and 650 vpm

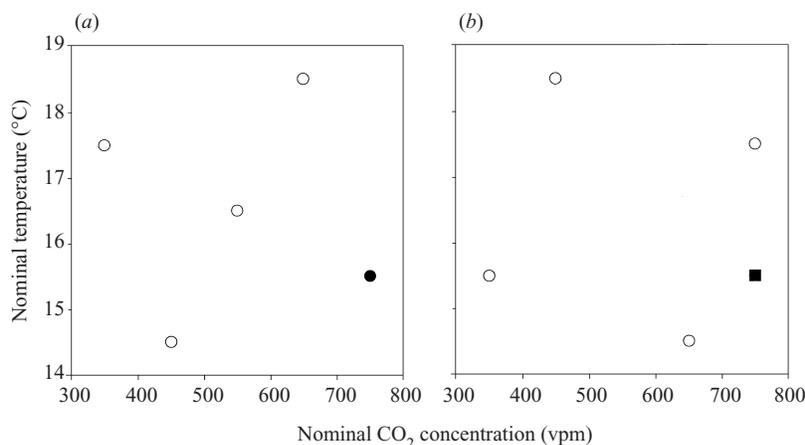


Fig. 1. Experimental design for (a) the first run and (b) the second run. ○, valid treatment combinations; ●, invalid treatment combination omitted from the results of block 1; ■, valid treatment combination replacing centre point in block 2.

Table 1. Observed temperatures and CO₂ concentrations

Temperature (°C)			CO ₂ concentration (vpm)		
Nominal	Mean daily mean	S.E.M.	Nominal	Mean daily mean	S.E.M.
First run					
14.5	14.5	0.02	450	442	2.8
15.5	15.3	0.02	750	686	13.9
16.5	16.4	0.01	550	531	5.4
17.5	17.4	0.01	350	372	2.4
18.5	18.4	0.01	650	615	8.7
Second run					
14.5	14.5	0.02	650	649	0.1
15.5	15.4	0.01	750	750	0.2
15.5	15.5	0.01	350	371	1.4
17.5	17.5	0.01	750	748	0.2
18.5	18.5	0.01	450	458	0.7

respectively. Temperature values and carbon dioxide concentrations were logged every 5 min throughout the duration of the experiment and the overall daily means are shown in Table 1. The achieved mean CO₂ concentration of 686 for the cabinet set at nominal 750 vpm was caused by a major breakdown in gas supply part way through the experiment. As a result, the experimental design was modified as previously described and the unreliable treatment repeated during the second run. Thus, the second batch of plants was tested in cabinets set at 14.5, 15.5, 15.5, 17.5 and 18.5 °C with CO₂ concentrations of 650, 750, 350, 750 and 450 vpm respectively. All other settings were maintained as previously described and the overall daily means are shown in Table 1.

Cultural methods

On 22 July 1996 and 21 July 1997, seeds of cv. Groffy were sown into 10 cm round pots filled with Levington M2 compost. Pots were put in an unheated polyethylene tunnel for germination and emergence until 5 August 1996 and 4 August 1997 respectively, whereupon they were placed in the Saxcil cabinets. Plants were watered as necessary throughout germination and early growth until they had approximately two unfurled true leaves. The plants were then supplied with modified Hewitt's solution (Austin & Maclean 1972), providing 172 mg/l N, 41 mg/l P and 243 mg/l K via troughs in which the pots stood. The level of nutrient in the troughs was checked daily and replenished as necessary to ensure that nutrition was always adequate to meet the demands of growth. Fifty pots were placed in each of the five environments in each run. Biological methods of pest control were used to prevent infestations of brown thrips and aphids.

Daily observations were made of the times of flower opening and bean set in each cabinet. Individual

beans on all plants were assessed for maturity three times a week, and were picked when mature and weighed fresh and after drying for 48 h at 80 °C. Maturity was defined as firm beans that were at least 10 cm in length.

RESULTS

Analysis of data

Tables 2 and 3 show, respectively, the analysis of mean squares of days to various defined events and the mean squares of yield components. The purpose of the significance tests in these tables was model choice not hypothesis testing. The effects of temperature on growth rates and yield were large and therefore the linear and quadratic effects of temperature were fitted first, followed by the linear and quadratic effects of CO₂, followed by the linear temperature by CO₂ interaction effect. Owing to the non-orthogonality caused by the missing treatment, the analysis of mean squares in Tables 2 and 3 is sequential with each term adjusted for the preceding terms but not for the succeeding terms.

The linear and quadratic effects of temperature were large and significant for most of the measured variables, whereas the effects of CO₂ were small, with only the linear effect of CO₂ showing significant treatment effects and then only on the yield data. The absence of significant quadratic or interaction effects due to CO₂ meant that it was not necessary to fit a full response surface model. Instead, a quadratic temperature model was fitted to the data in Table 2 and a quadratic temperature with additive linear CO₂ model was fitted to the data in Table 3.

Timing

Table 4 shows the model coefficients and standard errors for the days to first flower opening, first bean set and 50% pick of mature beans assuming a

Table 2. *Sequentially fitted mean squares for the effects of CO₂ and temperature on days to defined events, shown in the order in which the terms were fitted*

Polynomial model effects	D.F.	Days to first flower opening	Days to first bean set	Days to 50 % pick of mature beans
Linear runs	1	3.47	4.05	72.20
Linear temperature	1	369.34	425.70	1781.91
Quadratic temperature	1	14.12	0.07	30.94
Linear CO ₂	1	0.69	0.48	10.41
Quadratic CO ₂	1	0.07	1.68	31.62
Linear temperature × Linear CO ₂	1	0.01	0.75	25.01
Residual	2	2.26	3.64	13.95

Table 3. *Sequentially fitted mean squares for the effects of CO₂ and temperature on days to maturity characters, shown in the order in which the terms were fitted*

Polynomial model effects	D.F.	Number of mature beans per plant	Yield of mature beans (g/m ²)
Linear runs	1	2.048	26.533
Linear temperature	1	246.883	6184.591
Quadratic temperature	1	19.990	157978
Linear CO ₂	1	8.067	84205
Quadratic CO ₂	1	0.001	10701
Linear temperature × Linear CO ₂	1	0.075	3338
Residual	2	0.558	1061

Table 4. *Polynomial model coefficients and standard errors for days to defined events*

Polynomial model effects	Days to first flower opening			Days to first bean set			Days to 50 % pick of mature beans		
	Estimate	S.E.	D.F.	Estimate	S.E.	D.F.	Estimate	S.E.	D.F.
Linear temperature	-30.7	7.20	5	-6.5	9.98	5	-48.5	30.50	5
Quadratic temperature	0.80	0.218	5	0.05	0.303	5	1.18	0.924	5

quadratic temperature model with no significant CO₂ effects. Figure 2*a-c* shows the effects of temperature on these characters ignoring CO₂ concentration whereas Fig. 2*d-f* shows the effects of CO₂ after fitting a quadratic model for the effects of temperature and adjusting all the data to a common temperature of 16.5 °C using the statistical model. Thus Fig. 2*d-f* shows the effects of CO₂ independently of temperature and visualizes the effects of the CO₂ treatments at a constant temperature of 16.5 °C. The graphical plots in Fig. 2*a-f* visualize the analysis of mean squares shown in Table 2 by showing strong temperature trend effects with no evidence of CO₂ trend effects.

Increased temperature reduced days to defined events and for days to first bean set and days to 50 % pick of mature beans the reduction was approximately linear with temperature. For days to first flower opening, the quadratic temperature effect was significant and the rate of reduction in time to first flower

opening due to a unit increase in temperature was greater at the low temperatures than at the high temperatures. The day of first flower opening was 18 days earlier at 18.5 °C than at 14.5 °C (Fig. 2*a*), and the day of the set of the first beans was advanced by 19 days over the same temperature range (Fig. 2*b*). Harvest of 50 % of mature beans was advanced by 38 days as shown in Fig. 2*c* and there were corresponding linear effects on the timing of 10 and 90 % harvests (data not shown). In addition to the positive effects of temperature on the rate of flowering, there were also positive effects of temperature on the rate of maturation of beans from flower set (Fig. 3).

Characters at maturity

Table 5 shows the individual model coefficients and standard errors for number of mature beans per plant and yield of mature beans assuming a quadratic

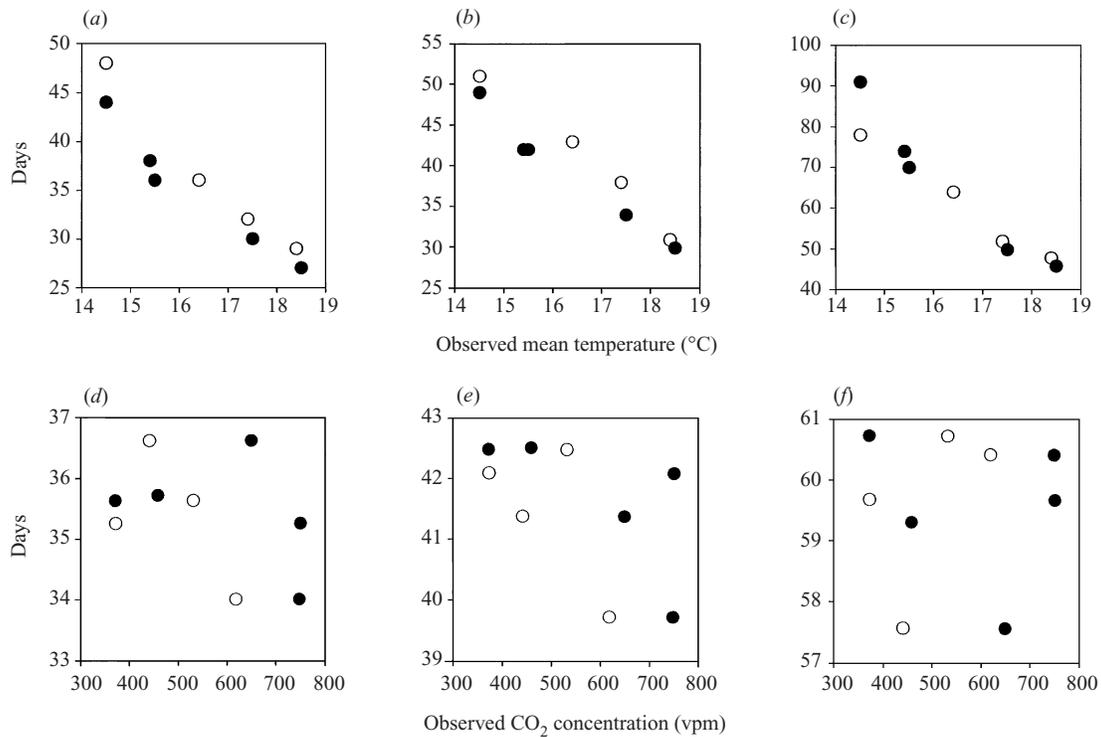


Fig. 2. Days from transfer to the Saxcil cabinets plotted against temperatures for three defined events. (a) Days to first flower opening, (b) days to first bean set, (c) days to 50% pick of mature beans, and against CO₂ concentrations after standardizing to a common temperature of 16.5 °C, (d) days to first flower opening, (e) days to first bean set, (f) days to 50% pick of mature beans. ○, first run; ●, second run.

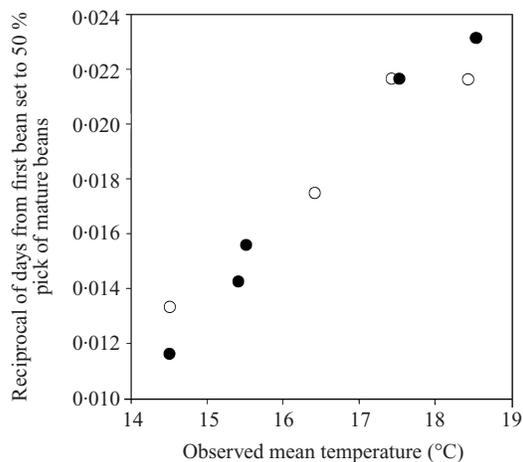


Fig. 3. Rate of bean maturation expressed as the reciprocal of days from first bean set to 50% pick of mature beans. ○, first run; ●, second run.

temperature model with significant additive linear CO₂ effects. Figure 4a–b shows the effects of temperature on these characters ignoring CO₂ con-

centration whereas Fig. 4c–d shows the effects of CO₂ after fitting a quadratic model for the effects of temperature and adjusting all data to a common temperature of 16.5 °C using the statistical model. Thus Fig. 4a–d visualizes the analysis of mean squares shown in Table 3 by showing the temperature trend effects ignoring the CO₂ concentration and the CO₂ trend effects after adjusting for the temperature effects.

Increased temperature increased yields, with some evidence that the rate of increase in yield was highest at the lowest temperature. The yield of mature beans increased from 125 g/m² at 14.5 °C to 2352 g/m² at 18.5 °C as shown in Fig. 4b. Number of mature beans per plant increased with increasing temperature from one bean at 14.5 °C to 15 beans at 18.5 °C (Fig. 4a). Bean quality also improved with increasing temperature. Many of the beans on plants at lower temperatures were curled, did not fill out and matured slowly with skins that were rough and leathery in texture. The dry matter percentage of mature beans was constant over all treatments, so the effects on fresh and dry weight were similar.

Figure 4c–d shows the effects of CO₂ on yield data standardized to a common temperature of 16.5 °C. Table 3 shows significant evidence of linear CO₂ trend

Table 5. Polynomial model coefficients and standard errors for characters at maturity

Polynomial model effects	Number of mature beans per plant			Yield of mature beans (g/m ²)		
	Estimate	S.E.	D.F.	Estimate	S.E.	D.F.
Linear temperature	35.4	3.82	4	3401	445.0	4
Quadratic temperature	-0.96	0.116	4	-86	13.5	4
Linear CO ₂	-0.0073	0.00139	4	-0.74	0.162	4

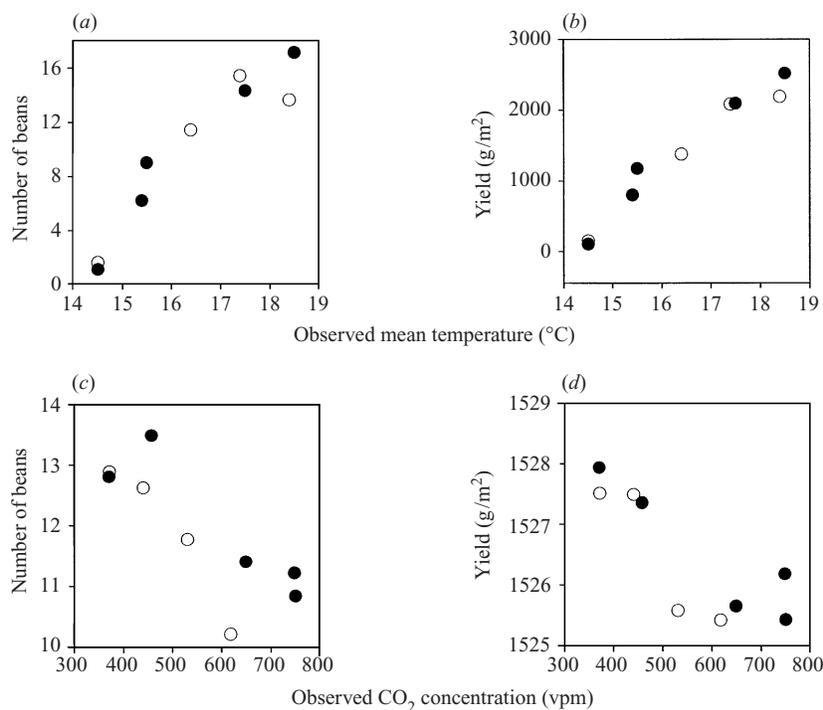


Fig. 4. Maturity characters plotted against temperatures, (a) number of mature beans per plant, (b) yield of mature beans, and against CO₂ concentrations after standardizing to a common temperature of 16.5 °C, (c) number of mature beans per plant, (d) yield of mature beans. ○, first run; ●, second run.

effects on the bean yield data and Fig. 4c–d shows that the CO₂ effects caused a very small reduction in the number and yield of mature beans as the CO₂ concentration increased.

Effects of climate scenarios

The importance of polynomial response function models for climate change research is that quantitative yield predictions can be made with a known level of precision over a range of possible future conditions. Polynomial response function models are, therefore, well suited to the problem of predicting the effects of future possible changes in climate. The utility of the models can be exemplified by predicting the effects for

a range of future possible scenarios. The model regression equations were used to predict the timing of maturity and the yield of mature beans using the climatic conditions predicted by the UKCIP98 climate scenarios. The uncertainties of future global warming rates mean that no single scenario is adequate for all possible outcomes and the UKCIP98 scenarios give spatial and temporal changes in UK climate for four possible global warming outcomes. The temperature data used here were downscaled for a 10 km land grid cell containing HRI Wellesbourne (UKCIP 1998b) and were taken as an average over June, July and August to represent the growing season for French beans. The four scenarios predict increases in mean temperature of 0.7, 1.1, 1.4 and 1.5 °C for the 2020s

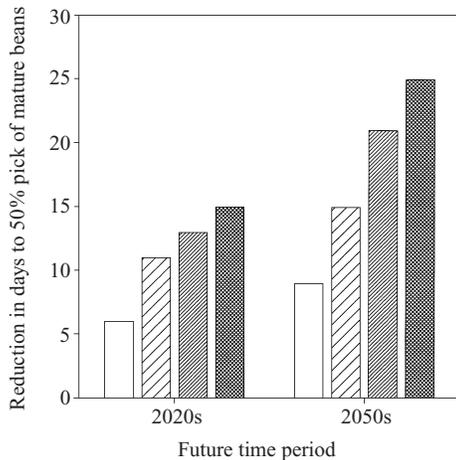


Fig. 5. Prediction of effects on timing of maturity for UKCIP98 climate scenarios. □, low; ▨, medium-low; ▩, medium-high; ■, high.

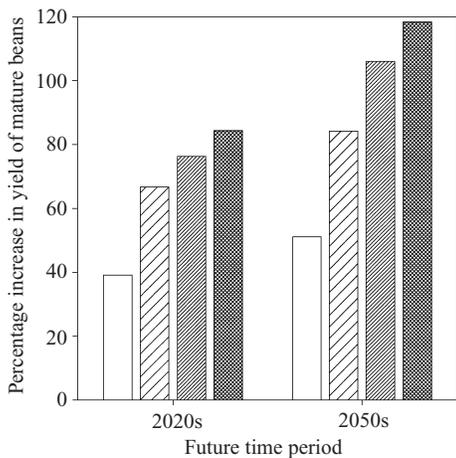


Fig. 6. Prediction of effects on yield for UKCIP98 climate scenarios. □, low; ▨, medium-low; ▩, medium-high; ■, high.

and 0.9, 1.5, 2.2 and 2.6 °C for the 2050s, relative to the mean for June, July and August for 1961–1990 of 15.5 °C. For CO₂, the scenarios predict concentrations of respectively 415, 398, 447 and 434 vpm in the 2020s and 467, 443, 554 and 528 vpm in the 2050s, relative to the baseline value for 1961–1990 of 334 vpm.

For days to 50% maturity, a simple linear regression model with temperature was used and Fig. 5 shows the reduction in days relative to a baseline value of 73 days for the 1961–1990 data. Depending upon the scenario, by the 2020s time to maturity can be reduced by between 6 and 15 days and by the 2050s by between 9 and 25 days. For the yield of mature beans, a model with linear and quadratic terms for

temperature and a linear term for CO₂ concentration was used to account for changes in both temperature and CO₂. Figure 6 presents the resulting predictions, expressed as percentages of the yield predicted using the baseline values for 1961–1990, and shows that by the 2020s yield may be increased by 39–84% and by the 2050s yield may be increased by 51–118%, depending upon the scenario.

DISCUSSION

There is no doubt that the climate of the UK is changing (UKCIP 1998*a*) with both temperature and CO₂ concentration increasing. However, there is still uncertainty over the rate of change of each character so that many future scenarios of the levels of temperature and CO₂ that plant species will experience are possible. In recent years there have been many studies of temperature × CO₂ interactions and good published information is available for arable crops. Morison & Lawlor (1999) concluded that there was little hard evidence for large differences in response to CO₂ concentration at different temperatures and found that responses differed between species. However, there appears to be no information on temperature × CO₂ interactions for *Phaseolus* beans although effects of temperature on bean growth and development have been described recently (Ferreira *et al.* 1997; Yan & Wallace 1998). Yan & Wallace reported optimum temperatures between 27 and 32 °C while Ferreira *et al.* (1997) found optima between 21 and 25 °C depending on growth phase and type of temperature records. In both cases, the optima exceeded the maximum temperature used in our experiments but our temperature yield response curves show evidence of flattening at the higher temperatures and are consistent with optima in the mid to high 20s. These results also help to confirm earlier work by Hardwick & Ballantine (1973) who found that yields were reduced at lower temperatures because of fewer pods on axillary branches. They concluded that low temperatures reduce bean yields by directly affecting the growth of axillary buds. Our data for temperature are compatible with those of Hardwick & Ballantine (1973) and Ferreira *et al.* (1997) in showing that higher temperatures increased the rates of flowering and bean maturity from pod set and that both numbers and yields of mature beans were increased by higher temperatures. Indeed, at a mean temperature of 14.5 °C, yields were very low but increased to about 24 t/ha at 18.5 °C.

Work on other crops examining temperature × CO₂ interactions has used a variety of experimental approaches (Morison & Lawlor 1999). Here we adopted an empirical approach using controlled environment cabinets to generate a range of CO₂ concentrations and temperatures. Modelling techniques were then used to determine the response to

temperature and CO₂ so that important crop characters could be predicted under any future climate scenario. There were no significant effects of CO₂ concentration on the timing of any growth phase but there were significant linear effects on numbers and yields of mature beans, with increased CO₂ concentration causing a very small decline in number and yield of beans. It appears likely that the reduction in yield was due to a reduction in bean numbers, possibly due to flower set effects, rather than to any direct effects on assimilation. This is in contrast to cereals where the primary effect of increased CO₂ concentration is to increase numbers of tillers and therefore the numbers of ears per unit area and biomass (Morison & Lawlor 1999). Certainly positive effects of increasing CO₂ concentration on yield of vegetables have been previously reported for onions (Daymond *et al.* 1997), for lettuce, cucumber and tomato, respectively (Hand 1980; Slack & Hand 1985; Slack *et al.* 1988) and by Wurr *et al.* (1998) for beetroot, carrots and onions. While increases in CO₂ concentration are more usually associated with increases in yield, Morison & Lawlor (1999) nevertheless showed clearly that there were reports of zero increase in biomass from increasing CO₂ concentration.

A null response to temperature or CO₂ change was not expected and therefore there was no reason to assume a null response model. The negative effect of CO₂ on bean number and yield in our experiment was very small but the term was included because the effect was statistically significant. For practical purposes, however, it can be assumed that the response of French beans to CO₂ over the tested range of concentrations was almost flat. The true significance of our results is that there was no evidence of any positive effects of added CO₂ on the growth or yield of French beans.

Scarbrick & Daniels (1981) in studies of French bean production indicated that yields of up to 18 t/ha of edible pods could be achieved. This suggests that our yields in controlled environment are realistic and that the results are commercially relevant. The size of the cabinets used (1.37 m × 1.37 m) meant that in order to get good estimates of numbers of beans and yield at maturity it was not possible to carry out any growth analysis sampling to provide additional information on plant development or plant processes. The impact of temperature changes predicted from global warming on navy bean (also *Phaseolus vulgaris*) production in the UK has been studied by Holloway *et al.* (1995). They suggested that parts of southern England would become suitable for production due to the thermal receipt requirement of the crop being met more consistently, but made no specific estimate of effects on yield and crop timing. The models we have developed enable these effects to be estimated for any climate scenario. Indeed, when applied to the four UKCIP98 scenarios for 2020s and 2050s at Wellesbourne, our models predicted reductions of up to 15 days to 50% pick (2020s) and up to 25 days (2050s), together with yield increases of up to 84% (2020s) and up to 118% (2050s). These effects are much larger than those reported by Wurr *et al.* (1998) for beetroot, carrots and onions and indicate that temperature rises due to climate change will be particularly beneficial to the production of French beans in the UK.

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