

Climate change: a response surface study of the effects of CO₂ and temperature on the growth of beetroot, carrots and onions

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SUMMARY

Ten daylit, controlled-environment cabinets were used to investigate the possible impacts of global rises in atmospheric CO₂ concentration and temperature on beetroot (*Beta vulgaris* L.), carrot (*Daucus carota* L.) and bulb onion (*Allium cepa* L.) plants. Their responses to CO₂ concentrations of 350, 450, 550, 650 and 750 vpm and temperatures of 12, 13.5, 15, 16.5 and 18 °C were examined by using a fractional factorial design for the two treatment factors. Use of the daylit cabinets allowed the plants to be grown in natural light, common atmospheric humidities (vpd 0.7 kPa) and non-limiting supplies of water and mineral nutrients.

Polynomial models were used to summarize the whole plant dry weight and fresh weight yield responses and to indicate the potential impact of climate change. Additionally, the models were used to generate predictions of the percentage change in whole plant dry weight and plant fresh weight yield for the years 2025 and 2050 relative to 1992. Baseline values of 350 vpm for CO₂ and a mean temperature of 13.5 °C for 1992 together with forecast CO₂ values of 407 and 442 vpm and temperature increases of 0.7 and 1.1 °C for 2025 and 2050 respectively were used. For 2025, fresh weight yield changes of +19%, +9% and +13% were obtained for beetroot, carrot and onion crops respectively, while for 2050 the respective changes were +32%, +13% and +21%.

Measurements of the ratio of the maximum diameter of the bulb to the minimum diameter of the neck for onions showed that there was little or no influence of CO₂, whereas the effect of temperature was substantial. Bulbing was accelerated by high temperature and was greatly delayed at low temperature. At temperatures < 15 °C, the delays to bulbing resulted in the development of undesirable, thick-necked onions which tended to remain green with erect leaves. These results suggest, therefore, that a warmer climate will be advantageous for the commercial production of bulb onions in Britain.

INTRODUCTION

A detailed scientific assessment of the 'greenhouse effect' and climate change has been produced for the Intergovernmental Panel on Climate Change (IPCC) by a Working Group of international scientists. It notes (IPCC 1990) that human activities are substantially increasing the emissions of 'greenhouse gases' such as carbon dioxide (CO₂), methane, chlorofluorocarbons and nitrous oxide into the atmosphere. These increases will enhance the natural 'greenhouse effect' and the Earth's atmosphere will, in consequence, be warmer. Six scenarios suggesting

temperature rises ranging from 1.1 to 1.7 °C by the year 2050 have been produced (IPCC 1992); these are less than earlier estimates of 1.5–4.5 °C (DoE 1988). Estimates of the corresponding increase in atmospheric CO₂ concentration vary between 442 and 546 vpm (IPCC 1995).

A review of the potential effects of climate change in the UK (DoE 1996) suggests that, according to one scenario, by the 2020s the climate of the UK will be c. 0.9 °C warmer than the period 1961–90. Although the timing and scale of the climatic change is still uncertain, it is likely that rises in ambient CO₂ and mean temperature will have important effects on the productivity of many horticultural crops. However, according to Monteith (1981) until we can adequately relate crop growth to specific features of our current

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weather we have little hope of predicting the effects of possible future changes in temperature.

The effects of raised temperature and raised CO₂ concentration on the growth of beetroot, carrot and onion plants were examined by using daylit cabinets with a range of controlled CO₂ concentrations and temperatures. The experiments were designed by assuming that a second-order response function model would be adequate for the combined effects of CO₂ and temperature and the results were modelled by fitting either a first or a second-order polynomial model to the data as judged appropriate by goodness-of-fit comparisons.

MATERIALS AND METHODS

Experimental design

The true form of the growth response function of plants grown in different CO₂ and temperature regimes is unknown, but it was assumed here that a second-order polynomial response function would be adequate for the three species tested. Ten growth cabinets were available and these were used to test five concentrations of CO₂ and five temperatures. Not every possible factorial combination of CO₂ concentration and temperature could be tested and it was therefore important to choose the best fractional factorial design for estimating an assumed second-order model.

Bailey (1982) has shown that by proper choice of a set of quantitative treatment factor levels, it is possible to establish a correspondence between the contrasts of a factorial treatment effects model and the orthogonal polynomial contrasts of a polynomial treatment effects model. Her method facilitates the use of standard techniques of fractionation and aliasing for the construction of fractional factorial designs for polynomial models (see Kempthorne (1952) for a discussion of classical fractionation and aliasing techniques). Suppose that A and B represent a pair of five-level factors each with quantitative factor levels chosen according to the equation:

$$l(\theta) = k_1 + k_2 \sin(2\pi\theta/5) \quad (1)$$

where k_1 and k_2 are arbitrary location and scale parameters, possibly different for the two factors, $\theta = 0, \dots, 4$ are coded factor levels and $l(\theta)$ is the actual quantitative factor level corresponding to the coded factor level θ . Edmondson (1994) has shown that by choosing quantitative factor levels according to Eqn (1) the ten-point design obtained by adding together two blocks of five points defined by the principal fractions $AB^2 = 1$ and $AB^3 = 1$ is a fully efficient, orthogonal second-order response function design for the two factors A and B. The actual factor levels given by Eqn (1) are not evenly spaced but, in the five-level case, the spacings can be well approxi-

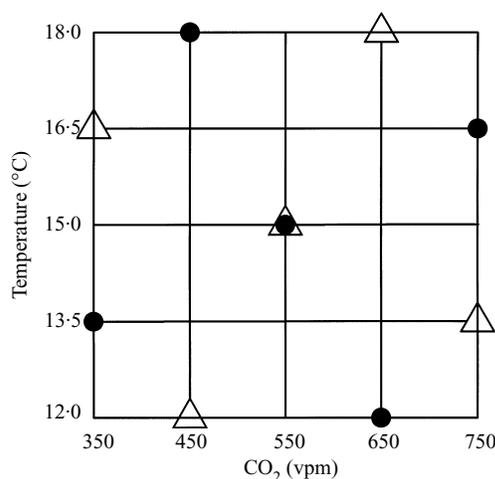


Fig. 1. Design points of a ten-point design for a second-order response function model for two five-level factors, A (temperature) and B (CO₂), where symbol \triangle denotes a principal fraction defined by AB^2 and symbol \bullet denotes a principal fraction defined by AB^3 .

mated by evenly spaced factor levels with little loss of efficiency. In the present series of experiments, evenly spaced factor levels were used with the ordering of the levels chosen according to Eqn (1). The resulting ten-point design in two blocks of five is shown in Fig. 1.

Experimental methods

Ten daylit, controlled-environment cabinets, contained within a glasshouse, were used at HR1 Littlehampton during the spring and early summer of 1992 to examine the responses of beetroot cv. Boltardy, carrots cv. Nandor and onions cv. Hysam to CO₂ concentrations of 350, 450, 550, 650 and 750 vpm and temperatures of 12, 13.5, 15, 16.5 and 18 °C, in the factorial combinations shown in Fig. 1. The basic construction of the cabinets has been summarized by Acock *et al.* (1977). Each cabinet had an effective growing area of 1.22 × 1.14 m and a growing height of 1.2 m. On overcast days the solar radiation flux density inside the cabinets was 50% of that outside but on brighter days this was as high as 60%. The plants were grown in natural light, common atmospheric humidities and non-limiting supplies of water and mineral nutrients. A common vapour pressure deficit of 0.7 ± 0.05 kPa was maintained in all cabinets throughout the experiment and a mineral nutrient solution based on the Hoagland No. 1 formula (Hoagland 1948) and with an electrical conductivity of 1.8 mS cm⁻¹, was supplied to the plants through a 'drip' system of irrigation.

The overall daytime means for the five pairs of cabinets with the five CO₂ concentrations were: (i)

Table 1. Analysis of mean squares of the linear effects and quadratic effects of CO₂ and temperature on the growth of beetroot, carrots and onions

Source	D.F.	Fresh weight (g)			Dry weight (g)			Bulbing ratio
		Root	Root	Bulb	Plant	Plant	Plant	
		Beetroot	Carrots	Onions	Beetroot	Carrots	Onions	Onion
Linear	2	2578.50	78.97	2357.70	61.425	1.828	113.413	2.7173
Quadratic	3	257.08	36.82	140.24	9.330	0.747	4.194	0.1012
Residual	4	85.07	8.57	181.85	1.766	0.240	7.633	0.0454
R^2_{Lin}	(%)	77.2	38.5	74.8	71.5	40.0	79.5	89.5
R^2_{Full}	(%)	87.8	74.5	72.1	89.9	68.6	74.6	93.1

352 and 352 (350 vpm), (ii) 450 and 453 (450 vpm), (iii) 543 and 548 (550 vpm), (iv) 649 and 650 (650 vpm), and (v) 748 and 751 (750 vpm) while the overall 24 h averages for the five pairs of cabinets with the five temperature settings were (i) 12.1 and 12.1 (12.0 °C), (ii) 13.6 and 13.7 (13.5 °C), (iii) 15.1 and 15.1 (15.0 °C), (iv) 16.6 and 16.7 (16.5 °C) and (v) 18.0 and 18.0 (18.0 °C). The control systems maintained the levels of CO₂ and temperature to within ± 30 vpm and ± 0.5 °C respectively. The weather during the 16 weeks of the experimental treatments (9 March to 27 June 1992) was characterized by daily solar radiation integrals which were *c.* 4% above the long-term mean for HRI Littlehampton for this period of the year.

Cultural methods

Seeds of onions and beetroot were sown into a peat-based seed compost in 22 ml plugs on 31 December 1991 and 19 February 1992, respectively. The seedlings were transplanted into 1.5 litre pots, filled with a peat-based compost, on 4 February and 5 March 1992, respectively. On 6 February 1992, pelleted seeds of carrots were sown into each corner of square 1.5 litre plastic pots containing a peat-based compost. A minimum temperature of 13 °C was maintained throughout germination and seedlings were thinned to a single carrot per corner after emergence.

Plants were transferred to the daylight cabinets on 9 March and spaced at 0.14 m on six slats 0.19 m apart. A pair of adjoining slats was allocated to each of the three species. No 'guarding' was possible between the different species, but the sides of the cabinets were screened with green polyethylene netting to the height of the plants to simulate the shading effect of adjacent plants. The overall planting densities, equivalent to 39 plants m⁻² for beetroot and onions and 156 plants m⁻² for carrots, were comparable with those used in field crops. Biological methods of pest control were used to prevent infestations of whitefly, red spider mite, leafminer, thrips, aphids and vine weevil.

Harvests

Plants were harvested on 14 and 21 May for beetroot, 13 and 20 May for carrots, and 30 June for onions. Beetroot and carrots were mature and of marketable size; onions were of marketable size with bulbs > 40 mm in diameter and their tops had started to fall over. Spare plants grown in the glasshouse were used to fill the gaps after sampling to maintain the planting densities. Beetroot and carrot plants were separated into roots and tops while onion plants were separated into bulbs and foliage. Progress in bulb development of the onions was assessed by determining the ratio of the maximum diameter of the bulb to the minimum diameter of the neck (Clark & Heath 1962). Plant parts were weighed after drying at 80–85 °C for 2–3 days.

RESULTS

Choice of model

Table 1 shows an analysis of the mean squares of the polynomial linear and quadratic model effects of CO₂ and temperature on each measured variate for beetroot, carrots and onions. The linear mean squares show the amount of variability explained by the linear effects of CO₂ and temperature, whereas the quadratic mean squares show the additional amount of variability explained by the quadratic effects of CO₂, the quadratic effects of temperature and the CO₂ by temperature interaction effects. The aim of response surface modelling is to explain data from quantitative level factor experiments by fitting concise low-order polynomial function models appropriate to the observations. The models must capture all the useful information in the data but must be simple enough to provide a concise summary of the data. Table 1 compares the fit of a first-order linear model with the fit of a full second-order quadratic model by comparing R² statistics for the two models. The R² statistic for any particular model is 1 minus the ratio of the residual mean square to the overall mean

Table 2. Model coefficients and standard errors for whole plant dry weight and root fresh weight of beetroot and carrot

	Plant dry weight (g)				Root fresh weight (g)			
	Beetroot		Carrot		Beetroot		Carrot	
	Estimate	S.E.	Estimate	S.E.	Estimate	S.E.	Estimate	S.E.
Linear CO ₂	0.019	0.0373	0.022	0.0137	-0.123	0.2590	0.051	0.0822
Linear temperature	-0.47	3.604	3.09	1.328	6.71	25.020	26.51	7.939
Quadratic CO ₂	-0.000066	0.0000262	-0.000021	0.000010	-0.000212	0.0001819	-0.000073	0.0000577
Quadratic temperature	-0.033	0.1165	-0.111	0.0429	-0.485	0.8085	-0.889	0.2566
Linear CO ₂ × Linear temperature	0.0048	0.00157	0.0004	0.00058	0.0300	0.01087	0.0031	0.00345

S.E.S based on 4 D.F.

square for that model. The closer R^2 is to unity, the better the fit of the model. In Table 1, R_{Lin}^2 and R_{Full}^2 measure the goodness of fit of the first-order and the second-order response surface models respectively for each measured variate and the relative magnitude of R_{Full}^2 to R_{Lin}^2 can be used to measure the improvement in fit of a second-order model compared with a first-order model. Table 1 shows that a first-order model is adequate for the onion data but that a second-order model is necessary for both the beetroot and the carrot data.

Table 2 shows the individual model coefficients and standard errors for the beetroot and carrot data assuming a second-order model; Table 3 shows the individual model coefficients and standard errors for the onion data assuming a first-order model. Examination of the coefficients in Tables 2 and 3 shows that certain of the coefficients are small compared with their standard errors. For example, the linear CO₂ × linear temperature interaction coefficients for carrot are small compared to their standard errors. Sometimes it can be appropriate to omit small coefficients from response surface models of given order to simplify the interpretation of the model. For example, if one factor axis is special, say a quantitative nuisance factor effect that needs to be eliminated from an analysis, interactions between the treatment factor effects and the nuisance factor effects are undesirable and, if small, can be eliminated. For climate change work, however, the CO₂ and the temperature axes are not special. This is because there is no reason to assume that climate change will be special to the CO₂ axis or special to the temperature axis. Indeed, if a simple linear relationship is assumed between CO₂ and temperature over time, that linear relationship could well provide the most natural axis for climate change research. The line orthogonal to that linear relationship would then represent deviations from the climate change model and would provide a second natural axis for climate change research. Provided that a full set of second-order model parameters is fitted, a model fitted to any one set of model axes is fully equivalent to a model fitted to any other set of axes apart from an orthogonal transformation of parameters. If, however, model terms that appear small relative to any one special pair of axes are omitted, all general predictions from that model and all comparisons with other models will be biased by that special choice of axes. For this reason, Table 2 shows a full set of second-order model coefficients for each analysed variate with no special assumptions about the directions of the model axes. The second-order response surfaces fitted by these coefficients are the best unbiased estimates of the second-order Taylor series expansions for the unknown response surfaces. Standard texts on response surface modelling include Draper & Smith (1966) Chapter 5, Box & Draper (1987) and Myers & Montgomery (1995).

Table 3. Model coefficients and standard errors for whole plant dry weight and bulb fresh weight and bulbing ratio of onion

	Fresh weight (g)		Dry weight (g)		Bulbing ratio	
	Estimate	S.E.	Estimate	S.E.	Estimate	S.E.
Linear CO ₂	0.140	0.028 6	0.0264	0.005 55	0.00043	0.000 589
Linear temperature	4.24	1.910	-1.39	0.370	0.346	0.039 2

S.E.S based on 7 D.F.

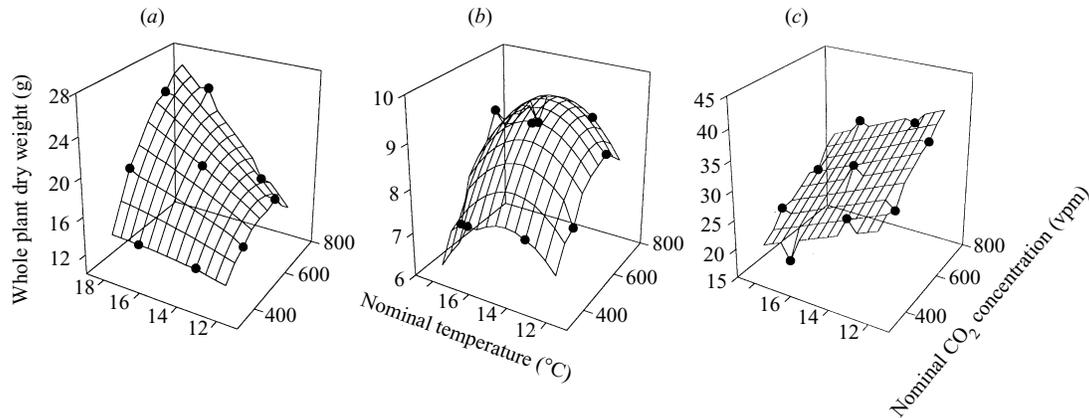


Fig. 2. 3-Dimensional plots showing the response of whole plant dry weight to temperature and CO₂ concentration represented by second-order response function models for (a) beetroot, (b) carrot and by a first-order response function model for (c) onion. ● indicates the observed values.

Graphical representation

Figures 2 and 3 show 3-dimensional representations of the observed data and the fitted models for the dry weights and fresh weights, respectively, of the beetroot, carrot and onion data. The representations show the actual observations superimposed on a 3-dimensional mesh of fitted values calculated from the assumed polynomial models. In the locality of each observed value the fitted mesh has been distorted to accommodate the observed value. Thus the lack of model fit can be assessed by the magnitude of the distortion needed to accommodate each observed value. The viewpoint for the 3-dimensional representations has been chosen to ensure that all observed points are viewed separately and to give a good overall impression of the shape of each surface but the same viewpoint has been used for every representation to ensure strict comparability of the representations. It should be noted that the four corner regions of each representation lie outside the region enclosed by the experimental data points. The corner regions are therefore extrapolations and may not be fully reliable.

Figure 4 is a 3-dimensional representation of the bulbing ratio of onion.

Whole plant dry weight

The 3-dimensional plots of whole plant dry weight response to temperature and CO₂ concentration (Fig. 2) show that each species responded in a different way. Over the ranges of temperature and CO₂ used, the maximum of the interpolated surface for beetroot was at 18 °C and 650 vpm CO₂, whereas in carrots the maximum was at *c.* 15 °C and 650 vpm CO₂. In onions the maximum of the interpolated surface was at 13.5 °C and 750 vpm CO₂. At current ambient CO₂ concentration, increased temperature had little effect on the dry weight of beetroot but caused a decrease in the dry weight of onions. With carrots, dry weight increased up to *c.* 15 °C but then at higher temperatures it decreased. The general effect of increasing CO₂ concentration was to increase whole plant dry weight, although the pattern of change varied with species. In beetroot the effect of increasing CO₂ was greatest at 18.0 °C, whereas in carrots it was greatest

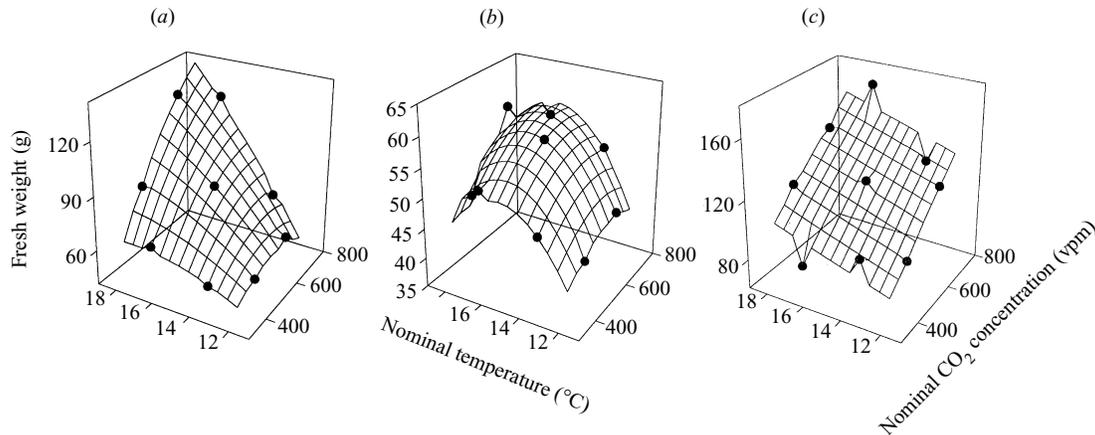


Fig. 3. 3-Dimensional plots showing the response of fresh weight per plant to temperature and CO₂ concentration represented by second-order response function models for (a) beetroot roots, (b) carrot roots and by a first-order response function model for (c) onion bulbs. ● indicates the observed values.

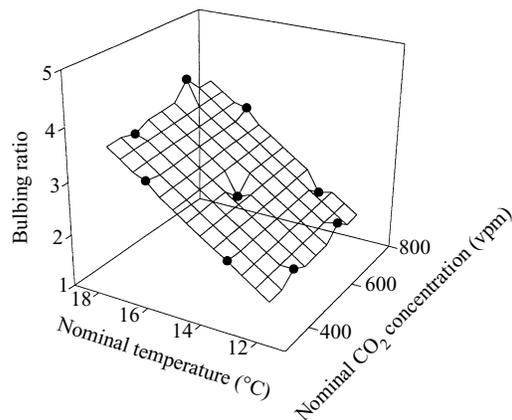


Fig. 4. 3-Dimensional plots showing the response of onion bulbing ratio to temperature and CO₂ concentration represented by a first-order response function model. ● indicates the observed values.

at 15 °C. In onions the effects of CO₂ and temperature were independent and additive.

Plant fresh weight and quality

The plots of root fresh weight for beetroot and carrots and bulb fresh weight for onions (Fig. 3) again show that each species responded to CO₂ and temperature change in different ways. Beetroot fresh weight was at a maximum at 18.0 °C and 650 vpm CO₂ within the interpolated region whereas bulb fresh weight of onion was at a maximum at 16.5 °C and 750 vpm CO₂ within the interpolated region. Carrot root fresh weight was at a maximum at *c.* 16.5 °C and 700 vpm CO₂. Increasing temperature caused an

increase in onion bulb fresh weight. At ambient CO₂ concentration, beetroot fresh weight was slightly increased by temperature, whereas carrot root fresh weight increased with temperature to an optimum at *c.* 15.5 °C before decreasing at higher temperatures. Increasing CO₂ concentration increased bulb fresh weight at all temperatures in onion, whereas in carrot increasing CO₂ concentration increased root fresh weight mainly at temperatures within a range of *c.* ±2–3 C of the optimum at *c.* 16 °C. In beetroot the effect of increasing CO₂ concentration on root fresh weight increased with temperature.

The onion bulbing ratio, the ratio of the maximum diameter of the bulb to the minimum diameter of the neck, gives an indication of crop quality. Since thick-necked bulbs are undesirable, a high ratio means bulbs of good quality, whereas a low ratio means 'bull-necked', and therefore unacceptable, bulbs. There was little or no effect of CO₂ concentration on the bulbing ratio, whereas the effect of temperature was considerable (Fig. 4). Bulbing was accelerated at high temperatures and delayed at low temperatures to such an extent that below *c.* 15 °C, undesirable thick-necked onions were produced. Thus increased temperatures are likely to increase the quality of bulb onions as already suggested by Wurr (1993).

DISCUSSION

During the past 25 years the protected crops industries of Europe and North America have greatly benefited from the use of supplementary CO₂ (Hand 1982; Bauerle & Kimball 1984; Stanev & Tsonev 1986) with improvements in the output, quality and value of vegetables, cut flowers and ornamental plants

Table 4. Estimated percentage changes in whole plant dry weight and fresh weight yield of roots or bulbs of beetroot, carrot and onion crops for the years 2025 and 2050 relative to 1992, assuming the IS92c scenario

	Year	Crop		
		Beetroot	Carrots	Onions
Whole plant dry weight	2025	+17	+10	+2
	2050	+27	+15	+3
Fresh weight yield	2025	+19	+9	+13
	2050	+32	+13	+21

(Mortensen 1987). Since climate change involves increases in both CO₂ concentration and temperature, there is obvious potential for increased field vegetable crop productivity and the work described here has explored some possible effects. The results for biomass (whole plant dry weight) are generally similar to those of Idso (1990), Wheeler *et al.* (1993) and Daymond *et al.* (1997) who showed positive effects of elevated temperature on carrots, a negative effect of temperature on onions at current ambient CO₂ concentration and a positive effect of elevated CO₂ on carrots and onions. Nevertheless, there are some minor differences in detail. For example, Idso (1990) showed that in carrots at elevated CO₂ there was a positive effect on growth of increasing temperature up to 30 °C, whereas we found an optimum temperature. The negative effect of temperature on onions is evident because onions can be regarded as a determinate crop (Daymond *et al.* 1997) and Parry (1990) has indicated that temperature increase is likely to decrease leaf canopy duration of determinate species.

Kimball & Idso (1983) analysed the results of 81 experiments with controlled concentrations of CO₂ and concluded that a doubling of atmospheric CO₂ concentration will probably increase agricultural yields by about a third. Information on the effects of increased temperature on crop yield and quality is not so readily available, although Wurr (1993) has reviewed the possible effects on field vegetable crops of changes in mean temperature associated with global warming and found them to be generally beneficial. Enrichment studies at Littlehampton with lettuce, cucumber and tomato, respectively (Hand 1980; Slack & Hand 1985; Slack *et al.* 1988), suggest a figure similar to that of Kimball & Idso (1983). As an example, consider the effects of the IS92c scenario (IPCC 1992, 1995) for the years 2025 and 2050 together with a baseline CO₂ concentration of 350 vpm in 1992 and an assumed mean temperature of 13.5 °C. This temperature was chosen to represent the average temperature in the major vegetable

production area of south Lincolnshire, during May, June and July, which is the main growth period for these crops. The scenario increases CO₂ concentration to 407 and 442 vpm in association with temperature increases of 0.7 and 1.1 °C in 2025 and 2050 respectively. The predicted percentage changes in whole plant dry weight and fresh weight yield in 2025 and 2050, based on the models discussed in Tables 2 and 3 are shown in Table 4. Effects on yield are greatest for beetroot and least for carrots, although increases in whole plant dry weight are least for onions. Effects on yield of beetroot and onions are greater than on whole plant dry weight, although the reverse is true with carrots. Over the range of temperatures examined in this paper, CO₂ effects on beetroot will be greatest at the higher end of the range (see Fig. 3), whereas in carrots increases in mean temperature beyond *c.* 15.8 °C will be detrimental. Wheeler *et al.* (1994) also found that increased CO₂ concentration and temperature increased carrot root yield but found no interaction between temperature and CO₂. Daymond *et al.* (1997) reported that in onion additional CO₂ increased bulb weight, while increased temperature reduced bulb weight because of earlier bulbing and more rapid maturity. Nevertheless, as with our work, a scenario involving increases in temperature and CO₂ had a net beneficial effect.

A key feature of this work is that it is possible to estimate the effect of any temperature × CO₂ combination on measured characters. Sometimes the effects of temperature or CO₂ are examined in isolation, but the reality of climate change is that both factors will change together. There is uncertainty over the magnitude of future CO₂ and temperature changes but the strength of our modelling approach is that the effect of any climate change scenario can be estimated for a wide range of CO₂ concentrations and mean temperatures in the UK. Furthermore, any future alteration in the IPCC climate change scenarios can easily be dealt with by the model. The general pattern of response is similar, although the details differ slightly from other published evidence (Idso & Kimball 1989; Wheeler *et al.* 1994; Daymond *et al.* 1997) because the scenarios also differ.

Now that a pattern for the impact of increased temperature and CO₂ on at least some field vegetable crops is emerging, it is pertinent to consider what adaptation strategies may be necessary. The concentration of atmospheric CO₂ will continue to change at a similar rate throughout the UK. Growers are unlikely to supplement or artificially deplete CO₂ in field crops and, since yields will rise with increased CO₂, there is scope for improvements in the efficiency of photosynthesis and water use (Idso 1990). Selection during variety trials can capitalize upon this opportunity. The situation with temperature is not so simple. If increased temperature is beneficial for a crop then there could be an extension of the crop

area. There are substantial imports of carrots and for this crop there would be a net national benefit. With onions, however, increased temperature alone will not increase yields substantially, although the full scenario, taking into account CO₂ and temperature, looks likely to increase yields. Because quality will also be improved, there will be an opportunity to extend production further north.

This work helps to predict how three field vegetable crop species are likely to respond to predicted changes in CO₂ and temperature in the near future. However,

any practical adaptation strategy will also be determined by the availability of water and future work on climate change should also include studies of the interaction between temperature and water supply.

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