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Response of barley and pea crops to supplementary UV-B radiation

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SUMMARY

Four cultivars of winter barley (*Hordeum vulgare* L.) and two cultivars of combining pea (*Pisum sativum* L.) were grown in the field in the UK (52° N) and irradiated under banks of UV-B lamps in 1994/95 (barley) and 1996 (pea). Supplementary UV-B radiation was applied to treated plots as a proportional addition to the UV-B dose received under a control plot. Treated plants received a UV-B enhancement simulating the consequence of a 15% reduction in the amount of stratospheric ozone. No significant effect on yield and few significant effects on growth, pigment composition or chlorophyll fluorescence variables were detected. However, interplot variability was such that yield differences of $< 8{\cdot}5\%$ (pea) and $< 21{\cdot}6\%$ (barley) had less than a 95% probability of being detected as significant at the 5% level. The results indicate that yields of pea, and probably barley, would not be markedly affected by the increase in UV-B associated with a 15% reduction in stratospheric ozone. However, given uncertainties, such as the possible interactions between the effects of UV-B and those of other environmental factors, the possibility of significant crop responses to stratospheric ozone depletion cannot be excluded.

INTRODUCTION

The amount of ozone in the stratosphere over middle latitudes in the northern hemisphere has declined since 1978 (Stolarski *et al*. 1992). Assuming full compliance with the 1987 Montreal Protocol on Substances that Deplete the Ozone Layer and its 1992 amendments, it is predicted that ozone depletion at northern mid-latitudes will peak at the turn of the century and be 12–13% less in winter/spring and 6–7% less in summer/autumn relative to 1960 (Madronich *et al*. 1994). Stratospheric ozone will return to pre-depletion concentrations by the end of the 21st century (Madronich *et al*. 1994). However, continued implementation of the Montreal Protocol remains uncertain (Greene 1995; Jordan 1995) and factors other than the concentration of ozone depleting substances may place the ozone layer at risk. For example, spring-time ozone destruction in the arctic stratosphere, which has significantly reduced ozone concentration in north temperate latitudes in several recent years, is predicted to increase by global warming models (Austin *et al*. 1992). Other factors remaining constant, ozone reductions are accompanied by predictable increases in surface ultraviolet-B radiation (UV-B, 280–315 nm). In recent springs, episodic ozone losses have been associated with significant increases in ground-level UV-B in a number of European countries, including the United Kingdom (UK) (DoE 1996).

Many experiments have shown that plants can be damaged or otherwise affected by UV-B radiation (Tevini 1993). However, 80% of the studies of plant responses to UV-B published up to 1994 were conducted in controlled environment (CE) chambers or glasshouses (Caldwell & Flint 1994). In these experiments, plants usually received daily integrated doses of photosynthetically active radiation (PAR: 400–700 nm) and UV-A (315–400 nm) much less than summer sunlight: conditions which tend to exaggerate plant responses to UV-B (Caldwell & Flint 1994; Teramura & Sullivan 1994; Fiscus & Booker 1995). Of the 20% of studies conducted in the field, many involved pot-grown plants, $> 90\%$ were of < 4 months duration during a single growing season and,

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in the two which considered crop responses over a number of growing seasons, the magnitude of responses varied from year to year (Teramura *et al.* (1990) with soyabeans; Barnes *et al.* (1988), with a wheat/wild oat mixture). In field experiments, ambient solar UV-B was either reduced using wavelength-selective filters or supplemented by radiation from UV-B-emitting lamps. When artificial UV-B sources were used, incident solar UV-B was supplemented either by a fixed dose-rate ('square-wave') addition or a variable ('modulated') addition that was a constant proportion of the ambient dose (or of the dose incident on a control plot). A typical square-wave system provides supplementary UV-B radiation at one or two fixed dose-rates for a certain number of hours centred around solar noon. It takes no account of variation in cloud cover and provides an addition based on the modelled consequences of ozone depletion under clear sky conditions. Square-wave systems thus tend to provide UV-B additions greater than those expected from any realistic prediction of future ozone losses, and so are likely to over-estimate the effects of stratospheric ozone loss on crop production. Fiscus & Booker (1995) pointed out that a proper understanding of crop responses could only be obtained from field experiments that simulate the consequences of likely ozone loss and, in particular, from those using 'modulated' lamp systems, which provide a more realistic increased UV-B environment. Unfortunately, modulated systems are technically more complex and expensive than square-wave systems and have not been widely used (Caldwell & Flint 1994).

Irrespective of UV-B delivery system, most agricultural UV-B field experiments have been performed under conditions unlike those in the UK. An exception is the study of four cultivars of pea (*Pisum sativum* L.) in which increases in UV-B equivalent to a 15% ozone depletion reduced yield by an average of *c.* 10% (Mepsted *et al.* 1996). However, the experiment of Mepsted *et al.* (1996) was limited to one season and results may have been influenced by particular conditions during that season, for example late sowing, the unusually dry conditions and pathogen attack. The present study aimed to extend the observations of Mepsted *et al.* (1996) to a second year and to consider barley (*Hordeum vulgare* L.), a crop of greater economic significance in the UK (cultivated areas in 1994: pea 124000 ha, barley 1106000 ha; FAO 1996). An assessment of the statistical power of the experiments is also presented.

MATERIALS AND METHODS

Winter barley (1994/95) and pea (1996) were grown at Horticulture Research International, Wellesbourne, Warwickshire, UK (52° N). The crops were irradiated with supplementary UV-B, simulating seasonally variable ozone depletion equivalent to a year-round average of 15%, using the modulated system and sensor calibration procedure described in detail by Mepsted *et al.* (1996). Plants were grown under frames (4 × 1·3 m ground dimensions) which each held eight UV-B emitting fluorescent tubes (Philips TL40/RS12). Control plots were beneath frames in which the fluorescent tubes were unpowered. There were ten control arrays and ten providing increased UV-B. The UV-B proportional addition was defined in terms of a generalized plant action spectrum normalized to 300 m (PAS300; Caldwell 1971). The limitations of PAS300 are recognized (Fiscus & Booker 1995) but it has been the standard used in most studies of plant responses to UV-B and was adopted in this study for comparability with previous studies.

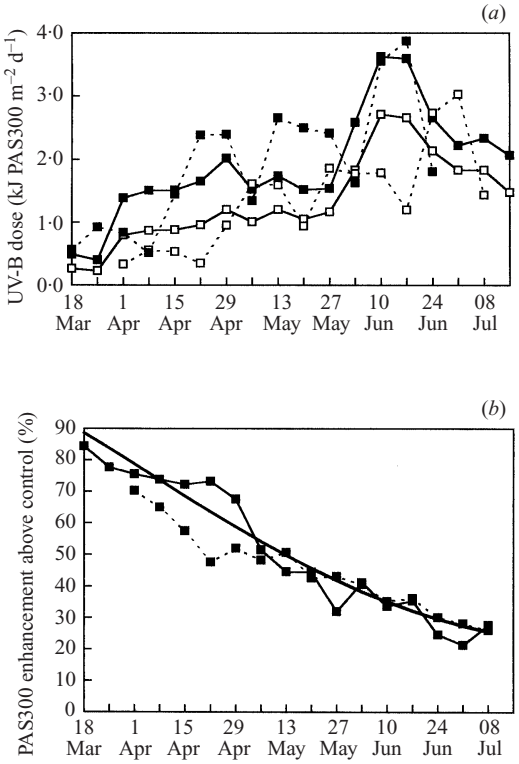

Fig. 1. (*a*) Weekly mean UV-B (PAS300) dose in control plots (□) and plots with supplementary UV-B (■) during the pea (——) and barley (– – –) experiments. Overall means for the entire duration of the experiments, for control and elevated UV-B plots respectively, were 1·38 and 1·92 kJ m^{-2} d^{-1} in the barley experiment and 1·34 and 1·91 kJ m^{-2} d^{-1} in the pea experiment. (*b*) Weekly mean UV-B (PAS300) enhancement as percentage of control dose received by plants during the pea (——) and barley (– – –) experiments. The heavy line represents the mean weekly target enhancement.

Barley experiment

Four winter barley cultivars were used: Halcyon, Pastoral and Target are 2-row cultivars, Manitou is 6-row. Seed was sown by precision drill (row spacing 13 cm) on 23 September 1994 in parallel beds (each 30 m long, 1·83 m wide, running north–south). The 20 experimental beds were divided into five replicate blocks, and each cultivar was assigned randomly to one of the four beds in each block. Frames were positioned so that each one treated two subplots containing different cultivars. Within each block, there was one control and one UV-B-treatment subplot for each cultivar, giving five subplots per cultivar per treatment (40 subplots in total).

Within each subplot, surrounded by at least two guard rows, was a destructive harvest area (DHA, 0·3 m^2) and a final harvest area (FHA, 0·3 m^2). Destructive measurements involved plants from the DHA; other measurements were from the FHA. Harvest areas were thinned to 84 plants (278 plants m^{-2}) shortly after germination. Fertilizer and pesticides were applied following normal commercial practice. UV-B-treatments were imposed from 181 days after sowing (DAS), when ambient UV-B reached doses that could be measured accurately by the sensing equipment, and continued until harvest at 291 DAS when all plants in each FHA were removed. Ambient UV-B, measured in a control plot, increased from *c*. 0·3 kJ m^{-2} d^{-1} PAS300 in March to a maximum of 2·5–3·0 kJ m^{-2} d^{-1} in mid-June (Fig. 1*a*). The UV-B supplementation that was achieved was consistently close to target from May until the end of the experiment, but tended to be lower than the target during spring. Overall, the mean enhancement over ambient was 45% compared with the target of 48% (Fig. 1*b*).

Pre-harvest growth measurements were made on 12 plants per plot. Harvest measurements (inflorescence dry weight, grain dry weight, number of stems, stem-plus-leaf dry weight) were of all material in the FHA. Growth characters measured (number of times in brackets) were: height (11), relative growth rate of youngest emerged leaf (2), height to flag leaf ligule (2), interligule lengths (1), stem dry weight (1), total green leaf dry weight (1), total senescent leaf dry weight (1), inflorescence dry weight (1), green leaf area (1), green leaf lengths (2), root dry weight from cores (1), grain dry weight (1), above-ground dry weight (1), stem number (1), and inflorescence number (1).

On three occasions (200, 209 and 234 DAS), the tip (1 cm) was removed from the youngest mature leaf blade of 12 stems growing in each DHA. Six tips per plot (totalling 0·1 $\pm$ 0·02 g) were bulked together for chlorophyll and carotenoid determination and six for determination of UV-B-absorbing compounds and anthocyanins. Tips were stored in liquid nitrogen until analysis. To determine the concentration of chlorophyll and carotenoids, tip tissue was ground to powder with liquid nitrogen and added to methanol (10 cm^3), shaken by hand in darkness for 1 min and then centrifuged for 5 min at 3000 ***g***. Absorbance of the supernatant was measured at 665·2, 652·4 and 470 nm in a dual beam spectrophotometer (Uvikon 930; Kontron Instruments Ltd, Watford, UK) with methanol as reference. Chlorophyll and carotenoid concentration (g^{-1} fresh weight (FW)) were calculated from these absorbance measurements according to Lichtenthaler (1987). To determine concentrations of UV-B-absorbing compounds and anthocyanins, tip tissue was ground to powder with liquid nitrogen and added to acidified methanol (concentrated aqueous HCl (specific gravity 1·18):methanol, 1:99 v/v, 10 cm^3), shaken and centrifuged as for chlorophyll. In the spectrophotometer, using matched quartz cuvettes (pathlength 5 mm) and with acidified methanol as reference, absorbance of the supernatant was measured at 300 and 530 nm. This method combines elements of those of Stapleton & Walbot (1994), Tevini *et al*. (1991) and Dillenburg *et al*. (1995). The results were expressed as absorbance g^{-1} FW at 300 and 530 nm (A300 and A530: measures of UV-B-absorbing compounds and anthocyanins respectively).

Chlorophyll fluorescence variables (F_v/F_m, $t_{\frac{1}{2}}$, F_m, F_o; as defined by Bolhàr-Nordenkampf & Öquist (1993)) were measured morning and afternoon over several days starting 230 DAS, using an induction fluorimeter (Plant Stress Meter; Biomonitor, Sweden). Five flag leaves per plot were dark-adapted for 30 min prior to measurement.

Harvested grain from each plot was dried (2 days, 80 °C) and milled to flour prior to analysis for UV-B-absorbing compounds and total organic nitrogen. Four flour samples from each plot were analysed. Each sample (*c*. 1 g) was weighed and put in a centrifugation tube with acidified methanol (10 cm^3). The tube was shaken for 5 min prior to centrifugation, otherwise the procedure was as described above. Total organic nitrogen content of harvested grain was determined by continuous flow analysis after Kjeldahl digestion. One flour sample per plot was analysed.

Pea experiment

Seed of two combining pea cultivars was sown by hand on 6 March 1996, in rows 10 cm apart, at a density of 100 seeds m^{-2}. Guido is a normal leaved, marrowfat cultivar grown for human consumption; Montana is a semi-leafless, white cultivar grown for animal feed (NIAB 1996). In a previous comparison of four cultivars (Mepsted *et al*. 1996), cv. Montana responded most (with four significant effects of UV-B treatment) and cv. Guido responded least to UV-B treatment (no significant effects of UV-B treatment). The present study used only two cultivars in order to

increase the statistical power over the Mepsted *et al.* (1996) study.

The experiment was arranged in a split-plot design of ten replicate blocks of two treatments (increased UV-B and control), with frames as main plots. Under each frame were two subplots, one of each cultivar, giving a total of ten subplots per cultivar per treatment. Each 2·6 m^2 subplot (2 m × 1·3 m) contained a 0·9 m^2 (1·5 m × 0·6 m) final harvest area (FHA) which was left undisturbed until the final harvest. The irradiation system was operational from 2 DAS. Seedlings emerged 31 DAS. Ambient UV-B, measured in a control plot, increased from *c.* 0·25 kJ m^{-2} d^{-1} PAS300 in March to a maximum of 2·5–3·0 kJ m^{-2} d^{-1} in mid-June (Fig. 1 *a*). The UV-B supplementation achieved was consistently close to target. Overall, the mean enhancement over ambient was 51% compared with the target of 48% (Fig. 1 *b*).

Height was measured on three occasions during vegetative growth (both cultivars 70 and 78 DAS, cv. Guido 83 DAS), until tendril growth made such measurements unfeasible. In each subplot, the height of the tallest stem of 15 plants each in the rows to the immediate north and south of the FHA were measured. External to the measured plants were two guard rows. At harvest, all above-ground tissue of all plants rooted within the HA was removed for analysis.

To determine the concentration of UV-B-absorbing compounds in plants in each subplot, discs (44 mm^2 each, one per plant) were taken 86 DAS from fully expanded stipules at canopy height for eight plants in each of the rows to the immediate north and south of the FHA. At 111 DAS, in each subplot, five discs (44 mm^2 each, one per plant) and five pieces (*c.* 50 mm^2, 1 per plant) were taken from fully expanded stipules at canopy height of plants in the row 10 cm to the immediate south of the HA. Stipule material was stored in the field in liquid nitrogen and later in the laboratory at −80 °C prior to analysis as described for barley.

Chlorophyll fluorescence variables (F_v/F_m, $t_{\frac{1}{2}}$, F_m, F_o) were measured as for barley, but using stipules rather than leaves. Measurements were made either in the morning (09.00–10.00 h) or afternoon (14.00–15.00 h) on sunny days when pods were filling. During any particular measurement period, plants of only one cultivar were examined (cv. Guido 99 DAS (morning), 103 DAS (morning), 104 DAS (afternoon) and 118 DAS (morning and afternoon); cv. Montana 100 DAS (morning and afternoon)).

Statistics

In the barley experiment, not all cultivars were represented under all arrays, resulting in an incomplete blocking structure that was not suitable for analysis of variance (ANOVA). Therefore, results were analysed statistically using the method of residual maximum likelihood (REML), available within the software package Genstat 5 (Payne *et al.* 1989). Data from three waterlogged plots, in which growth was poor, were excluded from the analysis. In the pea experiment, both cultivars were presented under all arrays and results were analysed statistically by analysis of variance (ANOVA). All analyses were performed using the software package Genstat 5 (Payne *et al.* 1989).

Treatment effects for individual varieties were declared significant ($P \leqslant 0{\cdot}05$) only where the overall treatment × variety effect was significant. An indication of the statistical power of the experiments was obtained from the detectable difference (DD) defined as the smallest difference between the population values under the different treatments that would have had a 95% probability of being detected as significant. For convenience DD was expressed as a percentage of the experiment grand mean. It should be noted that a less stringent requirement for detecting significance (lower power) gives a smaller DD, e.g. if we accept a probability of 0·5, rather than 0·95, of detecting difference as being significant, the differences required are smaller by a factor of *c.* 0·54.

RESULTS AND DISCUSSION

UV-B-absorbing pigments

No significant effect of UV-B treatment on the concentration of UV-B-absorbing compounds in barley leaf tissue was detected (for absorbance at 300 nm 209 DAS, the DD was 4·9%). In pea, a small (6%) but significant increase in the concentration of UV-B-absorbing compounds was noted in pea cv. Guido 111 DAS (Table 1). Under CE and glasshouse conditions, enhanced UV-B-treatment typically induces an increase in UV-B-absorbing compounds in leaf tissues (Tevini 1993; Caldwell & Flint 1994). However, high background PAR can also induce pigment production and the concentration of PAR-induced pigments can be high enough to make any UV-B-induced component undetectable (Cen & Bornman 1990). Differences in PAR:UV-B ratio between field and CE experiments may explain the less consistent detection of UV-B-induced pigment increases in field experiments (Caldwell *et al.* 1994; Sullivan *et al.* 1994; Dillenburg *et al.* 1995). Equally, since concentrations of UV-B absorbing compounds can change rather rapidly in response to changing UV-B (González *et al.* 1998), variation in response in the field may simply reflect the variability of natural UV-B. It is notable that the one occasion when we found significant UV-B effects on pigments in the field coincided with a period of rather high PAS300 (approaching 3 kJ m^{-2} d^{-1}), whereas our non-significant comparisons occurred during periods of lower doses (*c.* 2 kJ m^{-2} d^{-1} in the pea experiments and $< 1{\cdot}5$ kJ m^{-2} d^{-1} in the barley experiment).

Table 1. *Effects of enhanced UV-B on the pea cultivar Guido during 1996. All significant ($P \leqslant 0{\cdot}05$) treatment differences are shown (there were no significant effects of UV-B in cv. Montana). Where marked by an asterisk, degrees of freedom have been reduced to take account of a missing value*

Character	DAS	Control	+UV-B	S.E.	D.F.	Replicates
F_v/F_m	103	0·75	0·76	0·003	7	8
$t_{\frac{1}{2}}$	118	239	260	5·3	6*	8
A300 (cm^{-2})	111	0·34	0·36	0·007	17*	10
Leaf mass ($g\ m^{-2}$)	111	213	238	5·9	17*	10

Table 2. *Effects of enhanced UV-B on two winter barley cultivars in 1995/96. All significant ($P \leqslant 0{\cdot}05$) treatment differences shown*

Cultivar	Character	DAS	Control	+UV-B	D.F. (effective)
Target	Height (cm)	141	19·8 ± 0·61	21·4 ± 0·56	6
	Chlorophyll *a* ($mg\ g^{-1}$)	209	2·26 ± 0·068	2·04 ± 0·053	9
	Chlorophyll *b* ($mg\ g^{-1}$)	209	0·65 ± 0·015	0·56 ± 0·013	17
	Total chlorophyll ($mg\ g^{-1}$)	209	2·90 ± 0·083	2·60 ± 0·064	10
	Height above flag (cm)	242	12·1 ± 1·34	8·0 ± 1·21	6
Manitou	Height of 4th last leaf (cm)	242	22·4 ± 1·50	16·5 ± 1·51	—

Data are means of five replicate plots ± one standard error. The lack of balance in the design resulted in different treatment means being estimated with different standard errors. Consequently separate standard errors are given for each mean. Treatment effects are estimated at several strata. The number of degrees of freedom of the standard error depends on the variance components of these strata, and so differs for different characteristics.

Flavonoids are amongst the UV-B-absorbing compounds produced by barley (Liu *et al.* 1995). Flavonoids are involved in the formation of hazes in beer and also affect its colour and taste (McMurrough & Guinness 1980). There were no effects of UV-B treatment on the absorbance of barley flour at 300 and 530 nm, wavelengths at which flavonoids absorb strongly (for absorbance at 300 and 530 nm, the DDs were 1·1 and 19·7% respectively, data not shown). Thus, there is no evidence that increased UV-B would substantially alter this aspect of crop quality in winter barley, although small changes cannot be excluded.

Chlorophyll

In the barley experiment there was no consistent effect of enhanced UV-B radiation on chlorophyll concentration, the only significant change being a transient decrease in chlorophyll concentration in cv. Target 209 DAS (Table 2). The DDs 200 DAS were 6·2% for chlorophyll *a* concentration and 8·0% for chlorophyll *b* concentration (data not shown). CE experiments have shown that UV-B radiation can reduce chlorophyll content (Deckmyn *et al.* 1994; Day & Vogelmann 1995), probably by mechanisms involving both increased degradation of chlorophylls *a* and *b* (Strid & Porra 1992) and lower rates of chlorophyll synthesis (Jordan *et al.* 1994). The few examples in which total chlorophyll content or chlorophyll *a*:*b* ratio have been measured in UV-B field studies have found, variously, no effect of enhanced UV-B (Ziska *et al.* 1993; Nikolopoulos *et al.* 1995), decreased total chlorophyll when enhanced UV-B coincided with drought (Nikolopoulos *et al.* 1995) and increased total chlorophyll (Dillenburg *et al.* 1995). Dillenburg *et al.* (1995) considered whether an increase in chlorophyll under UV-B treatments could be a photomorphogenetic response to UV-A/blue light emitted by the UV-B lamps, but rejected this possibility since their lamps would have produced only a small percentage addition to ambient UV-A/blue light. Given the small addition of UV-A from lamps in our experiments (we calculate that a 25% PAS300 enhancement in summer daylight adds only 0·2–0·3% to ambient UV-A; Mepsted *et al.* 1996) we also consider increased UV-B the most likely cause of the UV-treatment difference, although recent data indicate that a small quantity of additional UV-A may have some biological effect (Newsham *et al.* 1996).

Photosynthetic efficiency

Since photosystem II (PSII) has been perceived as being especially vulnerable to UV-B damage (Bornman 1989), and has thus been considered a key target in determining the possible effects of ozone depletion on crop production, its integrity was studied using chlorophyll fluorescence. The efficiency of open

Table 3. *Barley 1995. Yield of dry grain and vegetative above-ground biomass (dry weight) at final harvest. Data are means of five replicate plots ± one standard error*

Character	Cultivar	Control	+ UV-B	D.F. (effective)	Detectable difference ($P = 0{\cdot}95$) Absolute	Grand mean (%)
Grain yield (t ha^{-1})	Halcyon	6·80 ± 0·389	6·47 ± 0·358	7	2·58	35·4
	Manitou	8·40 ± 0·389	7·73 ± 0·358			
	Pastoral	7·18 ± 0·393	7·17 ± 0·358			
	Target	7·06 ± 0·393	7·30 ± 0·358			
	Overall	7·40 ± 0·257	7·17 ± 0·240		1·57	21·6
Vegetative tissue (t ha^{-1})	Halcyon	8·94 ± 0·490	8·35 ± 0·437	6	3·13	38·0
	Manitou	8·01 ± 0·490	7·88 ± 0·437			
	Pastoral	7·79 ± 0·490	7·62 ± 0·437			
	Target	8·57 ± 0·489	8·83 ± 0·437			
	Overall	8·33 ± 0·262	8·17 ± 0·234		1·79	21·6

No significant ($P \leqslant 0{\cdot}05$) UV-B-treatment effect on yield was detected. The lack of balance in the design resulted in different treatment means being estimated with different standard errors. Consequently separate standard errors are given for each mean. Treatment effects are estimated at several strata. The number of degrees of freedom of the standard error depends on the variance components of these strata, and so differs for different characteristics.

reaction centres of PSII was estimated by F_v/F_m, while the other variables are indicators of the state of the electron transport system (Bolhàr-Nordenkampf & Öquist 1993). No significant UV-B treatment effect on any chlorophyll fluorescence variable was found in the barley experiment. DDs were 2·0% (F_v/F_m), 9·9% ($t_{\frac{1}{2}}$), 7·7% (F_m) and 5·8% (F_o) in the morning series and similar in the afternoon (data not shown). While significant UV-B effects on chlorophyll fluorescence variables (F_v/F_m and $t_{\frac{1}{2}}$) were observed in pea cv. Guido, they were transient (confined to two dates) and small in magnitude (*c.* 5%: Table 1). DDs 99 DAS were 4·7% (F_v/F_m), 9·7% ($t_{\frac{1}{2}}$), 13·8% (F_m) and 4·3% (F_o). The lack of consistent effects of enhanced UV-B on fluorescence characteristics corroborates previous data for pea obtained in the field (Mepsted *et al.* 1996) and under high PAR in CE conditions (González *et al.* 1996, 1998). A similar absence of detected UV-B effects on chlorophyll fluorescence is reported from other crops in the field, e.g. soyabean (Caldwell *et al.* 1994; Fiscus & Booker 1995) and in CE conditions where a high PAR irradiance was provided (Cen & Bornman 1990). Overall, these results suggest that, at least for the 15% ozone depletion assumed in the present study and for crops grown in the UK, any impairment of PSII efficiency due to damage caused by additional UV-B would be small.

Growth and yield

In CE experiments, UV-B treatment typically reduces growth (Caldwell & Flint 1994; Teramura & Sullivan 1994). Such reductions in growth can occur even in the absence of significant inhibition of photosynthesis (e.g. González *et al.* 1996, 1998), as was also the case in the field in our previous study of pea cultivars (Mepsted *et al.* 1996). However, field experiments have shown less consistent responses to UV-B in terms of final yield than in terms of vegetative characteristics (Corlett *et al.* 1997), and even vegetative responses have differed markedly, for example plant height has been reported to be unaffected by increased UV-B in cassava (Ziska *et al.* 1993), rice (Kim *et al.* 1996), pea (Day *et al.* 1996) and soyabean (Sullivan & Teramura 1990).

In the current field experiments, there was no consistent or persistent UV-B effect on the vegetative growth or yield of either barley or pea (Tables 3 and 4). Over all cultivars, yield from control and UV-B treatments differed by < 5% in both pea and barley, far smaller than the DDs for yield (8·5% for pea, 21·6% for barley). DDs for individual cultivars were larger (Tables 3 and 4). We have also calculated that in other studies in which no significant UV-B effects were apparent, the DDs for individual cultivars were similar to those in the present study: 33·3% in soyabean (Sinclair *et al.* 1990) and 13·3% in rice (Olszyk *et al.* 1996). The lack of any significant UV-B effects in the 1996 pea experiment contrasts with the results of the 1994 study (Mepsted *et al.* 1996), but this is not exceptional as plant responses to enhanced UV-B have also been reported to differ from season to season in other crops (Barnes *et al.* 1988; Teramura *et al.* 1990). Thus, the UV-B response of UK pea crops might be affected by a number of environmental variables, including water supply and pathogens, that differed between the 1994 and 1996 seasons at Wellesbourne.

The results of this study suggest that pea yield would not be markedly affected by a 15% reduction in the concentration of stratospheric ozone. However,

Table 4. *Pea 1996. Yield of grain and vegetative above-ground biomass (dry weight) at final harvest*

Character	Cultivar	Control	+UV-B	S.E.	D.F.	Detectable difference ($P = 0{\cdot}95$) Absolute	Grand mean (%)
Yield (t ha^{-1})	Guido	1·70	1·70	0·483	18	0·261	12·1
	Montana	2·66	2·54				
	Overall	2·18	2·12	0·338		0·182	8·5
Vegetative tissue (t ha^{-1})	Guido	4·871	4·96	0·1305	18	0·704	14·6
	Montana	4·663	4·82				
	Overall	4·771	4·89	0·993		0·536	11·1

Data are means of ten replicate plots. No significant ($P \leqslant 0{\cdot}05$) UV-B-treatment effects on yield were detected.

the contrast between the response of pea in 1994 (Mepsted *et al*. 1996) and 1996, and the lack of data on the range of UV-B responses possible in UK field conditions, highlights the need for caution in interpreting data from only one or two field seasons. UV-B field experiments continued over several years, and conducted on a larger scale (using larger plots and/or greater replication) are clearly very desirable, and a prerequisite for a more precise quantification of the response of barley to realistic increases in UV-B. Unfortunately, both the technical complexity and cost of UV-B field facilities, especially those using modulated supplements that most accurately simulate future UV-B climates, are significant constraints on such larger experiments which seem unlikely to be overcome in future.

Despite these constraints, it is notable that we observed only limited UV-B responses in pea and barley, even though treatments simulated an ozone depletion that is large compared with those currently predicted if the Montreal Protocol is implemented world-wide. Given such implementation, it seems unlikely that ozone depletion poses a major threat to UK pea or barley crops. However, given uncertainties over possible interactions between UV-B and other environmental factors, we cannot exclude more substantial responses, especially if there is any failure in implementing limits on the release of ozone-depleting substances.

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