Growth of ryegrass and white clover under canopies with contrasting transmission of ultraviolet-B radiation.

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Abstract

To determine sensitivity to UVB radiation, canopies of an acrylic perspex glass (UVB transmitting) and a polythene plastic (UVB opaque) were placed over an established ryegrass-white clover sward. A third control treatment with no canopy was also included in the experiment. A range of sward measurements were conducted between October 1995 and February 1996, but with a more intensive measurement programme during January 1996. Measurements included point analysis of ryegrass-white clover balance in the canopy, herbage accumulation measured by cutting quadrats to a simulated grazing height, perennial ryegrass leaf tissue turnover and area and petiole length of white clover leaves. A SKYE SKU-430 broad band sensor was used to monitor UVB levels during the experiment, and results of some calibration checks are reported. During mid-summer when ambient UVB levels were highest, herbage accumulation under UVB transmitting canopies was significantly reduced ($P<0.01$) compared with UVB absorbing canopies, with a 5% reduction in leaf extension rate of adult ryegrass tillers ($P<0.10$) and a 25% reduction in leaf extension of young tillers ($P<0.01$). Similarly, there was a reduction in white clover petiole length and area per leaf ($P<0.05$). These differences in growth are considered to be attributable to contrasting UVB levels under the two canopy types, although the possibility of an alternative explanation cannot be ruled out. Canopies of either type reduced seasonal clover dominance of the sward ($P<0.05$) compared with control plots with no canopy.

Additional key words: *leaf elongation rate,* Lolium perenne, Trifolium repens, *ultraviolet-B, young tillers.*

Introduction

Anthropogenic activities in recent decades, especially the use of chlorine-containing compounds such as chlorofluorocarbons (CFCs), are causing a net increase at the earth's surface of ultraviolet-B radiation (UVB; wavelength 280-320 nm) due to depletion of the ozone layer (Kerr and McElroy, 1993). First studies reporting potential depletion of the ozone layer were published in the early seventies (Johnston, 1971; Crutzen, 1972). Since then, a large body of knowledge has developed concerning consequences of increased UVB for plants (e.g., Bornman and Teramura, 1993; Tevini, 1994; Caldwell *et al.*, 1995). More than half of the species and cultivars investigated exhibit damage resulting from UVB. Damaging effects of UVB radiation include morphological and physiological changes (e.g., stunted growth, alteration of leaf characteristics, reduced protein synthesis, damage to DNA, and reduced photosynthesis).

However, most of the extant studies were conducted in glass houses, growth chambers or in the laboratory. Investigations under such controlled conditions provide valuable mechanistic information, but cannot accommodate all the interactions of UVB with other environmental factors (e.g., high light, drought, mineral deficiency). Where field studies have been conducted, numerous modifications of UVB effects have been observed as a result of such interactions (e.g., Murali and Teramura, 1985; Sullivan and Terramura, 1990, Chen and Bornman, 1990). This highlights the need for more studies in the natural field situation where a wide variety of abiotic and biotic factors are interacting with UVB. Such studies are of particular relevance in regard to the temperate pasture species growing under the relatively high UVB levels in New Zealand (Laing, 1991; McKenzie, 1992; McKenzie *et al.*, 1996). Despite recognition of this need for information on UVB effects on New Zealand pastoral species (Laing, 1991), only limited research has been conducted in New Zealand into UVB effects on pasture plants. The present study attempted to investigate response of the most common New Zealand pasture species association, white clover (*Trifolium repens* L.) and perennial ryegrass (*Lolium perenne* L.), to reduced UVB exposure in the field.

Materials and Methods

The experiment was conducted between October 1995 and February 1996 at Massey University, Palmerston North. The site was a ryegrass dominant perennial pasture, with white clover as the main legume species present, and was located on an alluvial terrace adjacent to the Turitea stream. The soil at the site is a Te Arakura silt loam and soil test details for an adjacent paddock of similar fertiliser history are given by Kemp *et al.* (1994).

Plastic canopies, as described below, were used to create contrasting "near ambient" UVB and "reduced" UVB light environments. To assess the effect of canopies themselves, additional control plots were maintained without canopies. For all plots, including control plots, frames (Fig. 1) were constructed from 25 x 100 mm tanalised pine timber. Frames were designed to be oriented with a diagonal axis aligned in a north-south direction. For plots with canopies, the plastic materials were fastened over the top of the frame and the two north-facing sides, leaving the two south-facing sides open to reduce temperature build up under the canopies, but still protecting plots from direct sunlight except for early morning and late afternoon. Canopies were fitted with irrigation nozzles calibrated to deliver 5 mm water per hour over the plot area as a fine spray, and were removable to allow grazing by sheep as required, typically at three to four week intervals.

After testing a variety of plastic materials with a Hitachi U-2000 scanning spectrophotometer, two materials, a perspex glass (trade name Casocryl, used in manufacture of sun-beds) and a UVB absorbing glass house polythene film (Cosio Industries, Polycrop), were selected as having similar transmission of visible light but contrasting transmission in the UVB band (>85% and <5% UVB transmittance, respectively, see Fig. 2). The experiment comprised four replicates of the three different canopy types, laid out in a randomised complete block design.

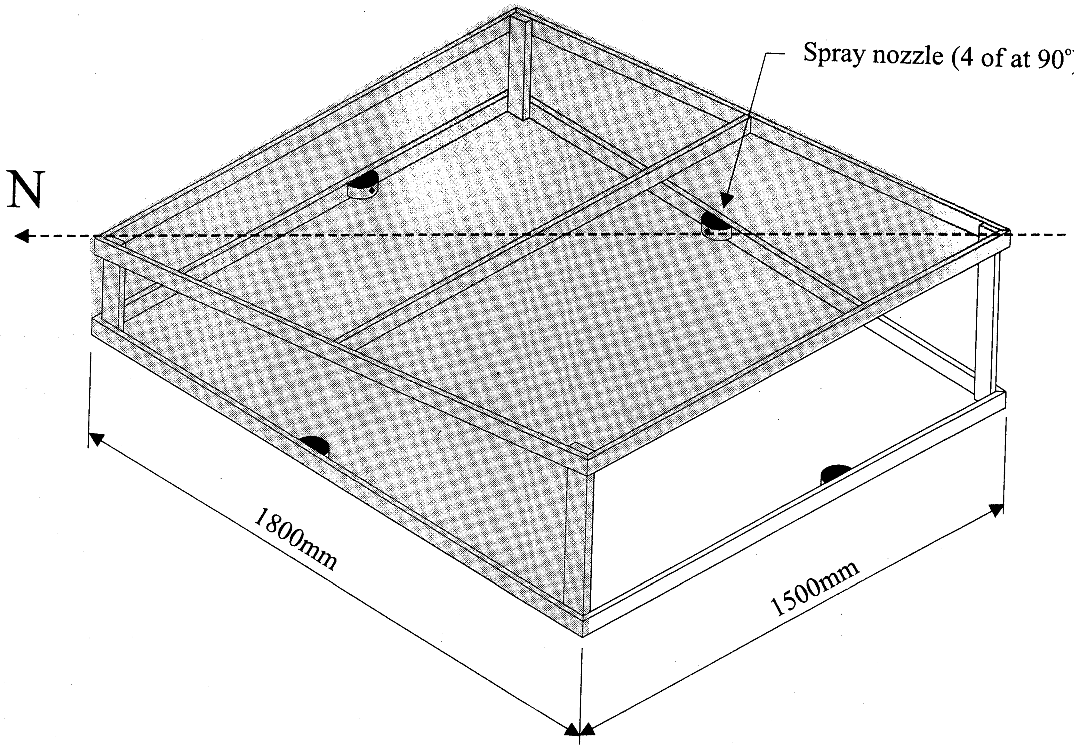

Figure 1. Construction of canopies. Framing material was 25 x 100 mm tanalised pine timber. Semicircles indicate position of 180° microjet irrigation nozzles. Diagonal line indicates north/south axis. Shading indicates presence of plastic or perspex glass canopy. Canopy height was 250 mm at the northeast side and 450 mm at the southwest side.

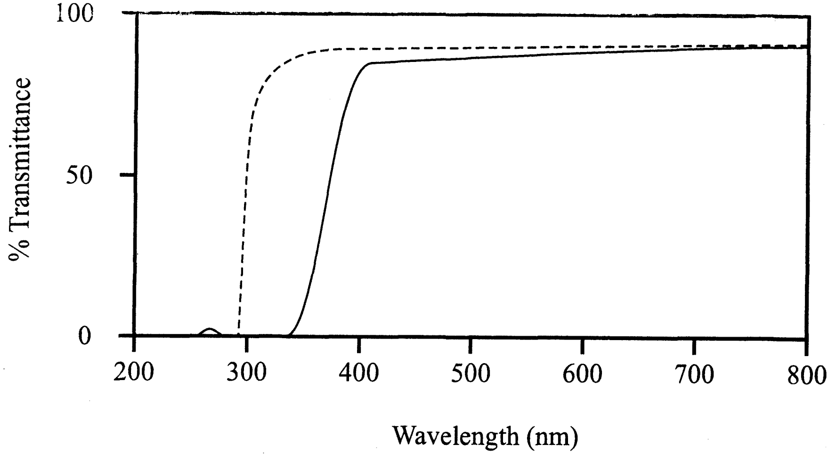

Figure 2. Spectral transmittance of casocryl perspex glass film (dotted line, reduced UVB canopies) and Cosio Polycrop glasshouse film (solid line, near ambient UVB canopies) as determined by a Hitachi U-2000 scanning spectrophotometer.

Conditions under the canopies possibly affecting plant growth were monitored using a SKYE Instruments five channel data logger, configured with one SKU430 UVB sensor, two SKP201/I PAR sensors, and two SKTS200/1 air temperature sensors. This instrument allowed monitoring of UVB levels above and below canopies and at different positions beneath canopies, but it must be recognised that a broad band sensor such as the SKU430 is subject to some calibration uncertainties and that results obtained must be interpreted with care. The additional sensors allowed simultaneous pairwise comparisons between two canopy types for temperature and PAR levels. To check performance of the SKU-430 UVB sensor, its output was calibrated against simultaneous readings from a second identical sensor loaned by SKYE Instruments Ltd., and also against a purpose-built UV spectroradiometer operated at Lauder, Central Otago, by the National Institute of Water and Atmospheric Research. The Lauder instrument is designed to measure the spectral distribution of solar UV radiation at the land surface and is based on a Bentham DM300 double monochromator. It has a spectral resolution of approximately 0.9 nm and is programmed to automatically log data from 290 to 450 nm at 5 degree steps of solar zenith angle throughout the day, and also to make several scans around noon. Systems such as this have been operated at Lauder since December 1989 (McKenzie *et al.*, 1992), and have been intercompared with similar systems in use in Australia, Germany, USA and Antarctica (McKenzie *et al.*, 1993).

Canopies were placed in the field in September 1995. Since Caldwell plant weighted UVB levels (UVB_{BE}, Caldwell, 1971) increase between winter and summer by a factor of 20 or more, and between September and mid summer by a factor in excess of 4 at this latitude, UVB effects on sward growth were not expected to emerge until later in the season at this site. Initially, prior to each grazing, herbage height was measured with a rising plate meter. In December 1995, when these measurements showed increased sward height on reduced UVB plots compared with near ambient UVB plots, more detailed sward measurements were commenced. These included use of a point quadrat apparatus to determine grass:clover balance in the sward, measurement of herbage mass and herbage accumulation by cutting quadrats to a simulated grazing height of 50 mm, and measurement of ryegrass leaf and clover stolon development. Following defoliation on 6 January 1996, twelve randomly selected adult ryegrass tillers and twelve young daughter tillers under each canopy were marked and monitored to determine rate of perennial ryegrass leaf elongation and senescence. These tissue turnover measurements were carried out over a time period spanning the second week of regrowth and were repeated for a second time period in the third and fourth weeks of regrowth. For white clover, 12 advancing stolons under each canopy were marked at the beginning of the first ryegrass observation period. At the end of the second observation interval, marked stolons were destructively harvested, and leaf area and petiole length of leaves at each nodal position recorded. Percentage of marked tillers and stolons lost between measurements was normally less than 20%, but for one canopy was as high as 66%. Plot mean values were obtained for each canopy by averaging data for all tillers or stolons relocated under that canopy. Since not all canopies could be measured on the same day (although all canopies within a replicate were normally measured on the same day or at most within 24 hours), leaf extension measurements were expressed as mean values (mm/tiller/day) over the actual measurement interval for each plot, then subjected to analysis of variance, as a randomised complete block design (4 replicates of 3 canopy types).

Results and Discussion

Performance of the SKU-430 UVB sensor

Usefulness of broad band sensors has often been discounted by those working in this field, due to

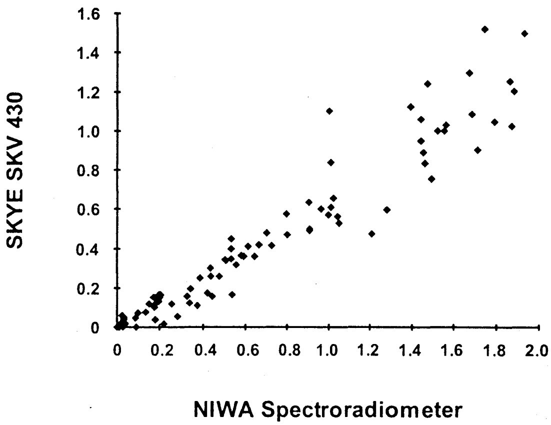

Figure 3. Intercomparison between NIWA spectroradiometer readings and SKYE SKU430 broad band sensor. Data are for 10 degree intervals of solar zenith angle, recorded over a 9 day period in February 1996. Outliers can be explained by differences in scanning time for the two instruments. The NIWA instrument has a scan time of approximately 3 minutes. The SKYE instrument was set to integrate data over 10 minute intervals. On days with intermittent cloud cover this discrepancy can lead to large differences in reading.

ambiguity as to which wavelengths within the sensor band contribute to a particular reading. This reaction is perhaps excessive. UVB incidence is highly correlated with total PAR, ozone fluctuations accounting for only a small part of the variation in total UVB insolation.

Due to the correlation between UVB and total radiation, a broad band sensor such as the SKU-430 would measure day to day variation in UVB incidence due to variation in total sunlight reasonably accurately. For contrasting conditions of high and low atmospheric ozone, a preliminary calculation performed by weighting typical solar UVB spectra (McKenzie, 1990) against the spectral response curve for the SKU-430 UVB sensor, predicted the response from the SKU-430 sensor should shift from 1.27 to 1.79 W/m^2 (40% change), given actual variation in UVB insolation from 0.89 to 1.34 W/m^2 (51% change). Thus it would be possible to use a broad band sensor to obtain approximate comparative information, such as: day-to-day variation in total UVB incidence, the extent of penetration of diffuse UVB radiation under canopies with open south-facing sides, and canopy transmittance properties under field conditions of varying sun angle. A broad band sensor would be contra-indicated, however, for applications such as comparing UVB output of artificial lamps with different emission spectra in the UVA.

The values 1.79 and 1.34 in the above calculation indicate that the contribution from the UVA band to SKU430 output is approximately 30-40%. As we did not know if the manufacturer corrects for this by incorporating a scaling factor into the meter calibration, or whether such a scaling factor for a British-built instrument would be applicable to New Zealand conditions, an intercomparison was carried out between the SKYE SKU-430 sensor and the NIWA instrument at Lauder (W/m^2 over the 280 - 315 nm UVB band).

Figure 3 compares the output of the two instruments at ten degree intervals of solar zenith angle and at solar noon over an eight day period in February 1996. Regression analysis of data in Figure 3 confirmed that the SKU-430 sensor reading was strongly related to total PAR ($F_{1,93} = 1161$, $P < 0.0001$), and that Dobson Ozone reading as a second predictor was also statistically significant ($F_{1,67} = 10.3$, $P = 0.002$). The output of the two instruments shows a linear relationship (Fig. 3, r = 0.96) and a fitted quadratic term was not significant. From this, we deduce that diurnal variation in solar angle is not a major factor affecting the calibration. Many of the outliers on Figure 3 occurred during periods of intermittent cloud cover, and are explained by the fact that the SKYE instrument had a 10 minute integration cycle, whereas the Lauder instrument integrated data over a scanning cycle of approximately 3 minutes. Variation in cloud cover during a scanning cycle therefore affected the two instruments differently. During the test period there were few observations with clear sky conditions, so it was not possible to omit observations made in cloudy conditions.

Since Figure 3 has variation on both *X* and *Y* axes, slope was calculated by principal components analysis (PCA, Mohler *et al.*, 1978) rather than by ordinary least squares regression, and was 0.68, indicating that the manufacturer's scaling factor needs to be adjusted for New Zealand conditions. Similarly, a linear relationship (PCA slope = 3.60 $\pm$ 0.10, r = 0.95), was seen when the SKU-430 data was plotted against UVB_{BE}, as calculated from the Lauder instrument output.

Assuming the above calibrations of the SKU-430 are applicable to the experimental site at Palmerston North, the daily UVB dose received by control plots at the experimental site on a sunny day in December/January 1995/1996 was approximately 35 kJ/m^2, and for UVB_{BE}, approximately 7.2 kJ/m^2. For comparison, Tosserams and Rozema (1995) considered daily doses of 6.7, 10 and 14.9 kJ/m^2 UVB_{BE} to be equivalent to atmospheric ozone reductions of 10%, 28% and 44%, respectively, for the Netherlands, while Barnes *et al.* (1990) equated 9.6 kJ/m^2/day UVB_{BE} at Logan, Utah (latitude 41.5 N) with a 20% depletion of the ozone column.

A test of spatial variation in UVB incidence under canopies, to gauge extent of penetration of diffuse UVB from the open southern sides of canopies was made by taking sequential readings with a SKU-430 meter above and below the canopy on a 150 mm x 300 mm grid pattern, under clear sky conditions. For reduced UVB canopies, readings varied approximately linearly from 9.6% of ambient 150 mm from the closed northern ends of the canopies to 17.1% of ambient 150 mm from the open southern ends*. Comparable figures for UVB incidence under transmitting canopies were 71.2% ambient near closed northern ends and 79.6% ambient near open southern ends of canopies. The conclusion from this limited quantification of UVB regimes under canopies, therefore, is that even though near ambient UVB plots were subjected to exposures perhaps 25% less than full sunlight, and there were appreciable amounts of UVB reaching swards beneath UVB absorbing canopies, there was at least a sharp contrast in UVB level between the two canopy types, and minimal variation in UVB over the sampled plot area (>150 mm from open edges). Comparisons of PAR and temperature for the two canopy types showed that PAR levels were 3 - 4% higher and temperatures about 0.4_C higher under UVB transmitting canopies than under reduced UVB canopies.

Sward height and herbage mass

At the first grazing after placing canopies on plots, on 4 October 1995, sward height was significantly increased for both canopy types compared with control plots (Table 1). This result is attributable to increased temperatures under canopies at a time of year when growth is temperature-limited (Butler *et al.*, 1990). Comparison of temperatures in plots with and without canopies showed that night temperatures under canopies were typically 0.5 to 1.0 °C higher and daytime temperatures in strong sunlight up to 4 °C higher under canopies than on control plots in December 1995. Statistically significant, pre-grazing sward height differences between near

Table 1. Sward height (mm) and herbage mass (kg DM/ha above a simulated grazing height of 40 mm), for selected dates in the 1995/96 growing season, for control plots (no canopy), near ambient UVB canopies and reduced UVB canopies.

	Canopy type				
	None	Near ambient	Reduced UVB	S.E.	Significance[1]
Sward height, 4 Oct	88	115	116	6	*
Sward height, 13 Dec	131	156	168	14	ns
Sward height, 6 Jan	117	133	154	4	**
Herbage mass, 6 Jan	1040	1200	1490	88	*

[1] For tables 1 to 3, + denotes P < 0.10, * denotes P < 0.05, ** denotes P < 0.01.

* Since the maufacturers advise that the SKU-430 has negligible response above 350 nm wavelength, and UV-A transmittance by absorbing canopies falls to zero below 350 nm (Fig. 2) these readings should not be inflated by UVA response of the broad band sensor, although we did not specifically test the spectral response of the SKU430 to confirm the manufacturer's advice.

ambient and reduced UVB canopies were first evident on 6 January 1996 (Table 1). At this harvest reduced UVB swards had greater height, compared with near ambient UVB swards (Table 1), although trends consistent with the differences observed in early January were present at the previous harvest made on 13 December 1995. Herbage mass measurement on 6 January confirmed treatment differences consistent with the sward height differences (Table 1). Despite the difference in total herbage mass, separate analysis of ryegrass and clover components in the sward did not yield statistically significant treatment differences, due to increased variance arising from sub-sampling.

Clover stolon growth

Detailed measurements on white clover stolons showed a 27% increase in petiole length in reduced UVB swards, compared with near ambient UVB swards (Table 2). Clover mean leaf area in reduced UVB plots was 14% greater than in control plots and 17% greater than in near ambient UVB plots, but these differences were statistically significant only at the 10% probability level, and then only when analysed as an orthogonal contrast design (reduced UVB versus near ambient and control). No treatment differences in rate of stolon elongation were detected (Table 2). Since legumes are generally regarded as exhibiting UVB sensitivity (Krupa and Kickert, 1989; Hodgson *et al.*, 1992) it is perhaps surprising that the sward height and herbage mass responses to reduced UVB were not more strongly reflected in the white clover component of the sward.

Ryegrass tissue turnover

Ryegrass leaf tissue turnover measurements carried out during January 1996 showed that both canopy types reduced leaf senescence compared with control plots and that leaf elongation rate was higher on reduced UVB plots, compared with near ambient UVB plots, especially for young tillers (Table 3). In general these effects were present as non-significant trends in the first measurement period (i.e., the second week after grazing), but were more pronounced and assumed statistical significance in the second measurement period (i.e., the third and fourth weeks after grazing, Table 3).

Grass/clover balance

Herbage mass data for December 13, together with data from point quadrat analysis of ryegrass and white clover cover percentage for the December 13 harvest, indicate that both canopy types increased the ratio of ryegrass to white clover in the sward. Since this shift in grass:clover balance in favour of ryegrass appears to apply in both near ambient and reduced UVB environments, it is not a light quality effect. There is a possibility that this effect could be linked with decreased rates of ryegrass leaf senescence, also observed to differ between control plots and both canopy types (Table 2). Reduced ryegrass leaf senescence (Table 3) and increased grass:clover ratio (Table 2) would be consistent with increased N mineralisation, possibly due to higher soil temperatures under canopies. However, in view of the lack of measurement of herbage or soil N levels, it would be of interest to carry out a follow up study to confirm this.

General

Examining responses of plant species to near ambient and reduced UVB light environments under canopies of contrasting transmittance has limitations. Canopies increase temperature and humidity, compared with control plots. The effect of supra-ambient UVB doses cannot be evaluated, and the possibility that canopy differences other than UVB transmission could have contributed to differences in plant growth cannot be ruled

Table 2. Measures of white clover development and sward grass:clover ratio.

	Canopy type				
	None	Near ambient	Reduced UVB	S.E.	Significance
Clover petiole length (mm)	131	124	158	8	*
Clover leaf area (mm^2)	430	420	490	26	ns
Clover stolon advance (mm/day)	1.8	1.7	1.8	0.4	ns
[1]Sward % clover, 13 Dec.	41	26	29	4	*
[2]Sward % clover, 6 Jan.	40	16	27	8	ns
[2]Sward % clover, 6 Feb.	12.3	5.9	9.0	1.5	+
[2]Log grass:clover ratio, 6 Feb.	0.14	0.65	0.41	0.11	*

[1] Percentage of 100 cover hits per plot with a point quadrat apparatus.
[2] Determined by dissection of herbage mass samples.

Table 3. Ryegrass leaf elongation and senescence (mm per tiller per day) for adult tillers and daughter tillers in January 1996. Period 1 denotes measurements made during the second week of regrowth following defoliation and Period 2 denotes measurements made during weeks 3 and 4.

	Canopy type				
	None	Near ambient	Reduced UVB	S.E.	Significance
Adult tillers					
Senescence, period 1	3.2	2.2	2.0	0.3	+
Senescence, period 2	6.1	2.8	4.8	0.7	**
Elongation, period 1	18.1	17.4	16.7	0.9	ns
Elongation , period 2	18.7	19.7	22.2	0.82	+
Elongation, mean p1 & p2	18.5	18.4	19.9	0.4	+
Daughter tillers					
Senescence, period 1	1.0	0.4	1.1	0.5	ns
Senescence, period 2	6.3	3.2	3.9	1.0	ns
Elongation, period 1	13.9	14.5	17.7	1.0	ns
Elongation, period 2	14.5	16.4	20.1	1.0	*
Elongation, mean p1 & p2	14.1	15.7	18.0	0.6	**

out. Even so, the method has been used by a number of workers overseas to gain an early indication of sensitive and tolerant species. Tosserams *et al.* (1996) examined responses of four plant species of coastal grassland in the Netherlands. They found no effect on biomass production, morphology or photosynthesis of the species tested, but did report reduced UVB altered patterns of biomass allocation in some species. By contrast, for tropical species in Panama, Searles *et al.* (1995) found a number of responses in several species tested.

Few of the many previous studies have investigated UVB sensitivity in monocot species, although Barnes *et al.* (1995) reported a UVB-induced (dose 9.6 kJ/m^2/day UVB_{BE}) reduction in biomass of oats (*Avena sativa* L.) and a general tendency for reduction in leaf blade and internode lengths and increased axillary shoot production in many of the twelve species tested, six of which were monocots. These authors calculated that such morphological changes are sufficient to affect growth rate and competitive balance between species through changed distribution of canopy leaf area, even where photosynthesis is unaffected. Paradoxically other species such as fathen (*Chenopodium album* L.) had significantly increased biomass with UVB exposure. The picture that emerges, then, is one of ample precedent for the responses observed here, but qualified by a growing awareness that responses to UVB vary with other factors such as plant nutrient status and water supply (Runeckles and Krupa, 1994). Thus, responses observed in one growing season or locality are not necessarily readily repeatable at another time or site. Further investigation of the particular responses observed here would be very helpful.

Conclusions

Since conditions under canopies are different from those in field swards, and since we cannot completely exclude the possibility that differences other than those in UVB incidence contributed to the above results, further research is needed before categorical assumptions can be made about UVB effects in field swards. With this qualification, our results indicate the following:

Canopies which reduced PAR to around 87% to 90% of ambient but reduced UVB incidence to around 10% of ambient, increased leaf elongation rate of ryegrass tillers, compared with similar UVB transmitting canopies. The effect was most evident in young tillers at later stages in the regrowth cycle. Increased sward height and herbage mass was observed on reduced UVB plots, consistent with increases in ryegrass leaf elongation rate.

There was evidence that UVB reduction increased petiole length and leaflet size in white clover, and also increased the ratio of white clover:ryegrass in the sward, but the growth responses in white clover were less conclusive than those in ryegrass.

Both canopy types reduced white clover content of the sward in summer, relative to control plots. Possibly this was due to increased nitrogen mineralisation, as a result of increased temperatures under canopies.

Acknowledgments

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