Decreased ultraviolet-B radiation alters the vertical biomass distribution in cocksfoot

E. CAYENBERGHS, G. DECKMYN* and R. CEULEMANS

Research Group of Plant and Vegetation Ecology, Department of Biology, University of Antwerp UIA, Universiteitsplein 1, B-2610 Wilrijk, Belgium

Abstract

A greenhouse experiment was conducted to investigate whether small differences in UV-B irradiance would lead to changes in competition between cocksfoot (*Dactylis glomerata* L. cv. Athos) and white clover (*Trifolium repens* L. cv. Mervi). Plants were grown in greenhouses covered with different thicknesses of UV-transmittant plexi (3 and 5 mm) resulting in 82 % and 88 % of ambient UV-B radiation. Aboveground biomass was harvested at 4-week intervals and the vertical distribution of biomass, leaf thickness and specific leaf area were determined. Tillering, stubble and root biomass and crop height were also measured. There was only one significant effect: at 88 % of ambient UV-B radiation a larger fraction of the biomass was present in the lower layers and a smaller fraction was present in the upper layers.

Additional key words: *Dactylis glomerata*, growth parameters, *Trifolium repens*.

Introduction

Since it was shown that the depletion of the stratospheric ozone layer would lead to an increased irradiance of UV-B radiation at the earth's surface, numerous studies have been performed to investigate the consequences of this global change for life on earth. A large number of plant species have been screened for their UV-B sensitivity and a wide variety of possible effects have been described (see Björn 1996 and Caldwell *et al.* 1998 for recent reviews). It is now clear that plant responses to UV-B differ not only between species and even between cultivars (Barnes *et al.* 1993), but they are also highly dependent on other environmental conditions, especially irradiance (Deckmyn *et al.* 1994, Deckmyn and Impens 1997).

There is a growing consensus that real UV-B damage (*e.g.* breakdown of DNA, disruption of thylakoids and impairment of photosynthesis) is unlikely for most species under realistic experimental conditions (Allen *et al.* 1998). Most plant species are able to defend themselves against UV-B radiation by accumulating UV-B absorbing pigments in the epidermal cell layer (Adamse and Britz 1992, 1996, Ambasht and Agrawal 1997, Landry *et al.* 1995) and it is questionable if any UV-B radiation at all is able to penetrate into the photosynthetic tissue (Bornman and Vogelmann 1991, Day *et al.* 1992). UV-B induced changes in normal growth patterns, mediated by a putative UV-B photoreceptor or caused by effects on plant hormones (Greenberg *et al.* 1996, Jenkins 1997), seem to occur more frequently and therefore deserve our particular interest especially in relation to the interactions of plants with their biotic and abiotic environment (Caldwell *et al.* 1998). Subtle photomorphogenic effects like changes in leaf angles or a reduction in leaf insertion height and leaf blade length can have an effect on the light-competition between species in a mixture (Barnes *et al.* 1996).

It is also suggested that the canopy architecture of a crop is an important factor in determining the sensitivity of a plant species to UV-B. Both UV-B and PAR behave differently in planophile and erectrophile vegetations: UV-B penetrates much deeper into erectophile vegetations than it does in planophile vegetations (Deckmyn and Impens 1998). If the meristematic zone of grasses, which is located at the bottom of the crop, is an important

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*Corresponding author, fax: (+32) 3 8202271, e-mail: gaby.deckmyn@ua.ac.be

target for UV-B effects (both harmful and photomorphogenic) then one could expect these effects to be less pronounced in mixtures of grasses with more planophile species.

The purpose of this study was to obtain some preliminary information about the effect of UV-B on the growth, crop architecture and light-competiton of cocksfoot (*Dactylis glomerata* L. cv. Athos) and white clover (*Trifolium repens* L. cv. Mervi). Both species are common competitors in cold-temperate pastures. Cocksfoot was chosen because it has a highly erectophile architecture and appeared to be very UV-B sensitive in previous experiments (Deckmyn and Impens 1999). No data were found on the sensitivity of white clover.

Materials and methods

Plants and growth conditions: Plants were sown in April 1999 in large trays containing a 3:1 mixture of normal potting soil and sand. After two weeks, seedlings were transplanted in 20 × 30 cm plastic boxes at even intervals and with a total of 40 plants per box. In mixtures, both species were alternated to maximize the effect of competition.

Boxes were placed in 1.5 m^3 ventilated greenhouses covered with UV-transmittant plexiglas with a thickness of either 3 or 5 mm, resulting in two treatments with an 8 % difference in weighted UV-B ($UV\text{-}B_{BE}$, biologically effective UV-B dose, weighted with the general plant action spectrum, Caldwell 1971). Although both treatments have lower than ambient UV-B levels, they will be referred to as lower (82 % of ambient) and higher (88 % of ambient) UV-B in the text to facilitate reading. Two greenhouses of each treatment were used to avoid pseudoreplication. PAR was reduced by 10 % inside the greenhouses and there was no difference in PAR between treatments.

All plants were cut back to a height of 5 cm in May. Afterwards, biomass above 5 cm was harvested every 4 weeks, from June to October. After each cutting, fertiliser (N-P-K) was added. Plants were watered daily during the experiment.

Growth parameters: Aboveground biomass was harvested, dried and weighed separately for each box. Prior to drying, the leaf area of small subsamples was measured. These subsamples were dried and weighed separately to calculate the leaf specific area (leaf area/ mass ratio). For each box, the cumulative aboveground biomass was calculated to assess the total aboveground biomass produced throughout the growing season. For mixtures, biomass of each species was dried and weighed separately and the percentage of biomass occupied by each species in the mixture was calculated.

In June, July and August, two aspects of the crop architecture were determined: the vertical distribution of biomass and the vertical variation of the specific leaf area. The biomass above 5 cm height was arbitrarily divided into layers of 10 cm and the biomass of each layer was harvested, dried and weighed separately. Subsamples of each layer were taken to calculate the specific leaf area. These measurements were not repeated in September and October because the crops were no longer as heigh and dense as in the summer months.

At the final harvest in October, also the number of tillers per plant was counted, the stubble (0 - 5 cm) and root biomass of each box were harvested and dried and the root/shoot ratio was calculated. Since it was practically impossible to separate the roots of both species in a mixture, only roots of monocultures were harvested.

Statistical analysis: Each box with 40 plants was treated as a unit. Since there were no differences between greenhouses of the same treatment, these data were pooled. Data of succesive harvests were analysed with a repeated measures analysis of variance (*MANOVA*) using SAS. The following factors were tested: treatment and time for aboveground biomass and cumulative biomass, treatment, layer and time for the vertical distribution of biomass and variaton of specific leaf area. Interactions between all of these factors were also tested. Student's *t*-tests were used to compare the means of the additional parameters that were obtained from the final harvest in October.

Results

Growth and competition: Although at first sight the growth of cocksfoot seems to be reduced and the growth of white clover stimulated by the higher UV-B treatment (Fig. 1), there are no significant differences between treaments ($P > 0.05$). The highest biomass-production occurred in the monocultures of white clover and the lowest in the monocultures of cocksfoot.

Cocksfoot occupied about 80 % of the biomass in mixtures at the beginning of the experiment and about 60 % at the end (Fig. 2). Although the fraction of biomass occupied by cocksfoot tends to be higher in the higher UV-B treatment (and the reverse for white clover) there is no significant difference between treatments ($P > 0.05$).

No differences are found between treatments in the biomass between 0 and 5 cm (the stubble), the total aboveground biomass, the root mass and the root/shoot ratio (Table 1).

Canopy architecture: The vertical biomass-distribution of white clover was not different between treatments, neither in monocultures nor in mixtures with cocksfoot

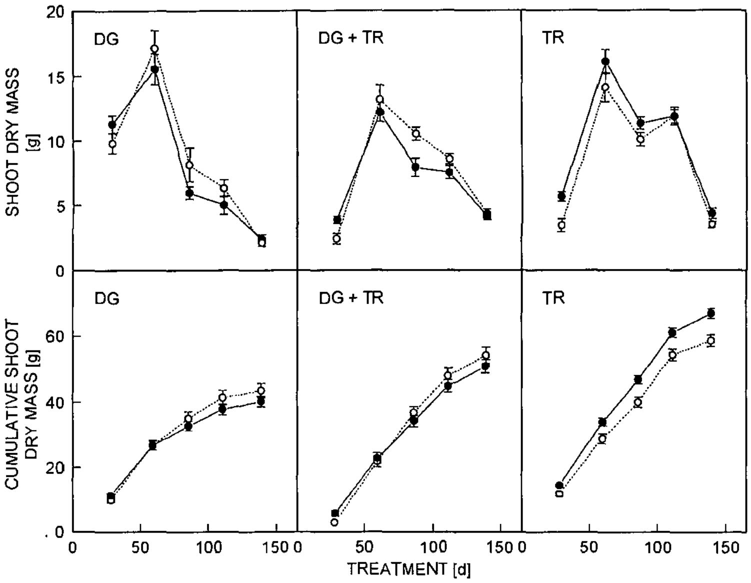

Fig. 1. Shoot dry mass and cumulative shoot dry mass of *Dactylis glomerata* and *Trifolium repens* and mixtures of both species. *Closed symbols* and *solid lines*: UV-B 88 % of ambient, *open symbols* and *dotted lines* UV-B 82 % of ambient. Means of 12 replicates ± SE.

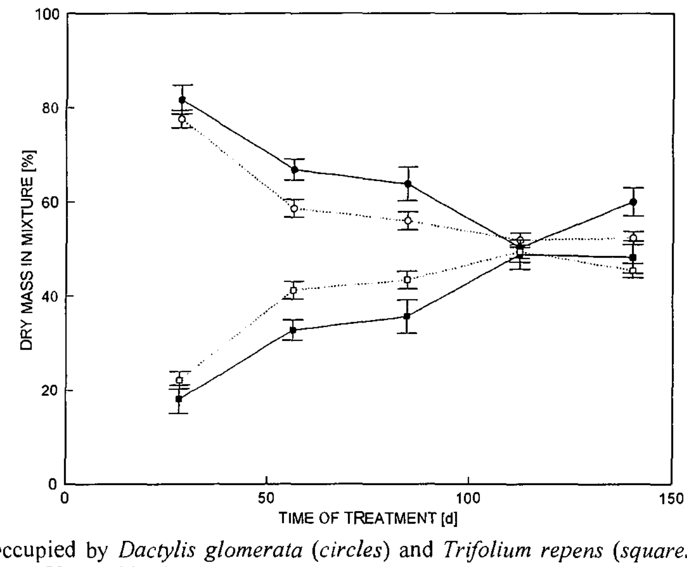

Fig. 2. Fraction of biomass occupied by *Dactylis glomerata* (*circles*) and *Trifolium repens* (*squares*) in mixtures of both species. *Closed symbols* and *solid lines*: UV-B 88 % of ambient, *open symbols* and *dotted lines*: UV-B 82 % of ambient. Means of 12 replicates ± SE.

($P > 0.05$). These data are not shown. However, there was a significant difference for cocksfoot, both in monocultures and in mixtures. The vertical distribution of aboveground biomass for monocultures of cocksfoot, determined in June, July and August (Table 2). The same trend is apparent each month: in the higher UV-B treatment a larger fraction of biomass is present in the lower layers of the crop and a smaller fraction is present in the upper layers. This is confirmed by an *ANOVA* with treatment, time and layer as independent variables: there is no interaction between all three variables, nor between treatment and time ($P > 0.05$) indicating that the same trend is present at every harvest. Treatment has a significant effect ($P < 0.01$) and there is a significant interaction between treatment and layer ($P < 0.01$) indicating that the vertical distribution of biomass is indeed different for the lower and higher UV-B treatments.

Table 1. Growth parameters of *Dactylis glomerata*, *Trifolium repens* and mixtures of both species after five months of growth at 82 % and 88 % of ambient UV-B (d.m. 0-5 = dry mass of the stubble, tot d.m. = dry mass of stubble + dry mass of shoot, r/s = root/shoot dry mass ratio. Means ± SE, n = 12, all differences were not significant at $P < 0.05$.

		82 % UV-B	88 % UV-B
Dactylis glomerata	d.m. 0-5 [g]	12.50 ± 0.6	13.20 ± 0.4
	tot d.m. [g]	14.70 ± 0.8	15.60 ± 0.6
	root d.m. [g]	35.70 ± 4.6	32.10 ± 3.3
	r/s	2.40 ± 0.2	2.00 ± 0.2
	tillers[plant^{-1}]	5.40 ± 0.3	5.30 ± 0.3
Trifolium repens	d.m. 0-5 [g]	15.20 ± 0.8	17.30 ± 1.2
	tot d.m. [g]	20.70 ± 0.9	23.90 ± 1.4
	root d.m. [g]	12.70 ± 1.9	12.90 ± 1.6
	r/s	0.61 ± 0.08	0.56 ± 0.07
Mixtures	d.m. 0-5 [g]	15.70 ± 0.8	15.10 ± 0.9
	tot d.m. [g]	22.10 ± 1.0	21.40 ± 1.3

A repeated measures analysis of variance with treatment, layer and culture as factors, showed no difference between monocultures and mixtures ($P > 0.05$ for the interaction between treatment and culture), indicating that the nature and the size of the effect are identical for cocksfoot in monocultures and in mixtures. The effect seems to be related to a reduction in plant height in the high UV-B treatment (data not shown).

Table 2. Vertical distribution of biomass of *Dactylis glomerata* at succesive harvests under 88 % and 82 % of ambient UV-B. Fractions of total shoot mass in 10 cm layers are given. Means ± SE, n = 12, * significant differences at $P < 0.05$.

	layers [cm]	82 % UV-B	88 % UV-B
June	0 - 10	0.583 ± 0.005	0.608 ± 0.039*
	10 - 20	0.289 ± 0.005	0.269 ± 0.009*
	20 - 30	0.111 ± 0.002	0.099 ± 0.015
	30 - 40	0.019 ± 0.007	0.019 ± 0.003
	40 - 50	0	0
July	0 - 10	0.419 ± 0.024	0.489 ± 0.036*
	10 - 20	0.298 ± 0.004	0.298 ± 0.013
	20 - 30	0.168 ± 0.005	0.115 ± 0.014*
	30 - 40	0.080 ± 0.006	0.049 ± 0.015*
	40 - 50	0.030 ± 0.010	0.019 ± 0.005
August	0 - 10	0.560 ± 0.025	0.685 ± 0.038*
	10 - 20	0.318 ± 0.010	0.273 ± 0.020*
	20 - 30	0.099 ± 0.045	0.048 ± 0.015*
	30 - 40	0.016 ± 0.006	0.005 ± 0.002
	40 - 50	0	0

The vertical variation of the specific leaf area was not different between treatments for any of the species, neither in monocultures nor in mixtures ($P > 0.05$) (data not shown).

Discussion

Since there was no significant reduction of growth in any way, it can be concluded that neither cocksfoot nor white clover are sensitive to small changes in near-ambient UV-B radiation. For cocksfoot, this is in contrast with previous results (Deckmyn and Impens 1999).

The shift in the vertical distribution of biomass of cocksfoot is not caused by reduced growth so it should be thought of as a photomorphogenic effect rather than a harmful effect. At low UV-B doses, as in this experiment, such effects are more likely than harmful effects (Jenkins 1997). The precise nature of the observed shift in biomass distribution remains uncertain. It can not be attributed to increased tillering or changes in leaf thickness. None of these effects which are common for grasses (Rozema *et al.* 1997, Deckmyn and Impens 1999) where observed here and this is consistent with previous results for cocksfoot (Deckmyn and Impens 1999). If the meristematic zone of the grass were an important target for UV-B, mediating this effect, then one would expect the effect to be less pronounced in mixtures with white clover since this planophile species effectively blocks UV-B radiation at a higher level in the canopy (unpublished data). Clearly, this is not the case here, questioning the involvement of the meristematic zone in the observed effect. On the other hand, since crops were cut every four weeks, there have been brief periods with an increased exposure to UV-B and it can not be ruled out that this was sufficient to cause the observed effect in mixtures. Also, since nothing is known about critical levels of UV-B for photomorphogenic effects, it can not be ruled out that even in dense mixtures enough UV-B penetrates to the bottom of the canopy to cause these effects. These questions could be addressed by repeating the experiment with different cutting regimes and different densities. Further research on and modeling of the light climate in mixed canopies is needed as well.

Although not significant, the dominance of cocksfoot tends to be more pronounced in the higher UV-B treatment. Such a trend could be related to the downward shift of biomass production of this species, interfering with the horizontal growth of white clover. Further research is needed to elucidate the nature of the observed effect on the growth of cocksfoot and to assess its importance for light-competition.

References

Adamse, P., Britz, S.J.: Amelioration of UV-B damage under high irradiance. I: Role of photosynthesis. - Photochem. Photobiol. **56**: 645-650, 1992.

Adamse, P., Britz, S.J.: Rapid fluence-dependent responses to ultraviolet-B radiation in cucumber leaves: the role of UV-absorbing pigments in damage protection. - J. Plant Physiol. **148**: 57-62, 1996.

Allen, D.J., Nogués, S., Baker, N.R.: Ozone depletion and increased UV-B radiation: is there a real threat to photosynthesis? - J. exp. Bot. **49**: 1775-178,1998.

Ambasht, N.K., Agrawal, M.: Influence of supplemental UV-B radiation on photosynthetic characteristics of rice plants. - Photosynthetica **34**: 401-408, 1997.

Barnes, P.W., Ballaré, C.L., Caldwell, M.M.: Photomorphogenic effects of UV-B radiation on plants: consequences for light competition. - J. Plant Physiol. **148**: 15-20, 1996.

Barnes, P.W., Maggard, S., Holman, S.R., Vergara, B.S.: Intraspecific variation in sensitivity to UV-B radiation in rice. - Crop Sci. **33**: 1041-1046, 1993.

Björn, L.O.: Effects of ozone depletion and increased UV-B on terrestrial ecosystems. - Int. J. environ. Stud. **51**: 217-243, 1996.

Bornmann, J.F., Vogelmann, T.C.: Effect of UV-B radiation on leaf optical properties measured with fibre optics. - J. exp. Bot. **42**: 547-554, 1991.

Caldwell, M.M.: Solar ultraviolet radiation and the growth and development of higher plants - In: Giese, A.C. (ed.): Photophysiology. Pp. 131-177. Academic Press, New York 1971.

Caldwell, M.M., Bjorn, L.O., Bornman, J.F., Flint, S.D., Kulandaivelu, G., Teramura, A.H., Tevini, M.: Effects of increased solar ultraviolet radiation on terrestrial ecosystems. - J. Photochem. Photobiol. **46**: 40-52, 1998.

Day, T.A., Vogelmann, T.C., De Lucia, E.H.: Are some plant life forms more effective than others in screening out ultraviolet-B radiation? - Oecologia **92**: 513-519, 1992.

Deckmyn, G., Impens, I.: The ratio UV-B/photosyntetically active radiation (PAR) determines the sensitivity of rye to increased UV-B radiation. - Environ. exp. Bot. **37**: 3-12, 1997.

Deckmyn, G., Impens, I.: UV-B and PAR in a grass (*Lolium perenne* L.) canopy. - Plant Ecol. **41**: 95-99, 1998.

Deckmyn, G., Impens, I.: Seasonal responses of six Poaceae to differential levels of solar UV-B radiation. - Environ. exp. Bot. **41**: 177-184, 1999.

Deckmyn, G., Martens, C., Impens, I.: The importance of the ratio UV-B/photosynthetic active radiation (PAR) during leaf development as determining factor of plant sensitivity to increased UV-B irradiance: effects on growth, gas exchange and pigmentation of bean plants (*Phaseolus vulgaris* cv. Label). - Plant Cell Environ. **17**: 295-301, 1994.

Greenberg, B.M., Wilson, M.I., Gerhardt, K.E., Wilson, K.E.: Morphological and Physiological responses of *Brassica napus* to ultraviolet-B radiation: photomodification of ribulose-1,5-biphosphate carboxylase/oxygenase and potential acclimation processes. - J. Plant Physiol. **148**: 78-85, 1996.

Jenkins, G.I.: UV and blue light signal transduction in *Arabidopsis*. - Plant Cell Environ. **20**: 773-778, 1997.

Landry, L.G., Chapple, C.C. S., Last, R.L.: *Arabidopsis* mutants lacking phenolic sunscreens exhibit enhanced ultraviolet-B injury and oxidative damage. - J. Plant Physiol. **109**: 1159-1166, 1995.

Rozema, J., Van de Staaij, J., Björn, L.O., Caldwell, M.M.: UV-B as an environmental factor in plant life: stress and regulation. - Trees **12**: 22-28, 1997.