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The effect of grasses on the quality of transmitted radiation and its influence on the growth of white clover *Trifolium repens*

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Summary. Plants of white clover *Trifolium repens* were grown under the canopies of three grass species, *Lolium perenne, Agrostis tenuis and Holcus lanatus*, and under simulated canopies of black polythene and controls were exposed to unfiltered natural radiation. The canopies were adjusted so that they transmitted equal intensities of Photosynthetically Active Radiation (P.A.R.). The ratio of red to far red radiation (ζ) was unchanged under the black polythene canopies but was reduced under canopies of *Lolium* and *Agrostis* and even more so under *Holcus*. The effect of canopy filtered radiation on the growth of clover was greatly to reduce internode length, mean number of nodes, the number of branched nodes and the number of rooted nodes and greatly to increase petiole length. The effect of canopies of *Holcus* was greater than that of the other grass species both in its effect on ζ and on the responses of the clover plant to its shade.

Key words: Light quality – Canopy effect on light – Growth – Morphogenesis – *Trifolium repens*

White clover (*Trifolium repens* L.) grows as a plagiotropic shoot system (sometimes wrongly called stoloniferous), rooting at the nodes. The growth habit ensures that the plants continually meander through the patchwork of associated vegetation. White clover is a typical "guerilla" species (*sensu* Clegg 1978; Harper 1985) which is continually growing into and escaping from the neighbourhoods of its own and other species. In its most typical communities in nature and in agriculture it is found associated with grasses which have typical "phalanx" form, with closely packed tillers and little lateral spread. Individual genets of white clover, as they extend and branch in a sward, experience a range of environments from open, well illuminated, gaps to deep shade under the canopies of grass plants. Different parts of the same genet may experience quite different environments. The growth of clover in a grassland sward is promoted by close grazing or mowing and reduced by treatments that favour the growth of grasses. This effect is usually ascribed to competition between the grasses and clover for limiting resources below ground (Snaydon 1971) or to competition in the canopy for light (Stern and Donald 1962; Harvey 1977; Davies and Evans 1983). Solangaarachchi and Harper (1987) grew plants of white clover under simulated canopies of detached clover leaves floating on tanks of water and under canopies of black polythene "leaves" adjusted in density so that the intensity of Photosynthetically Active Radiation (P.A.R.) was the same as under the real leaves. The growth habit of the clover plants, especially their frequency of branching, differed markedly between the two canopies and this was ascribed to the altered ratio of red to far-red radiation (ζ) after transmission through clover leaves. The present paper reports experiments in which clover plants were grown under the canopies of grasses. The grass canopies were of plants that were naturally rooted, but root competition between the grasses and clovers was prevented.

Grass species differ in their ability to suppress clover. Turkington and Harper transplanted clones of white clover into natural and deliberately sown swards of *Lolium perenne, Cynosurus cristatus, Holcus lanatus* and *Agrostis tenuis*. The growth of clover was greatest in the presence of *Agrostis* and most suppressed in the presence of *Holcus*. A similar order of "aggressiveness" of the grasses was found by Solangaarachchi (1985). We therefore compared the effects of canopies of *Agrostis tenuis, Lolium perenne* and *Holcus lanatus* on the quality of radiation transmitted and the growth of associated clover plants. The comparisons also included plants of clover grown under canopies of black polythene strips which did not affect the quality of radiation and clover plants receiving full natural radiation.

Materials and methods

30 trays, 20 cm × 30 cm × 5 cm were filled with John Innes compost No 1. Six of the trays were allocated to each of 5 treatments (i) sown with seed of *Lolium perenne*, (ii) sown with seed of *Agrostis tenuis*, (iii) sown with seed of *Holcus lanatus*, (iv) no grasses were sown but the trays were placed under a neutral canopy of black polythene strips and (v) no grasses were sown and the trays were used as controls. 14 days after sowing the grasses were thinned to the same density per tray (approximately 300 plants m^{-2}). The neutral canopy for treatment (iv) was made from strips (3 cm wide) of black polythene stretched across a frame (30 × 40 cm). Half trays were placed in the centre of each tray to provide a template-preventing grasses from growing into the area to be used for the *T. repens* cuttings. The

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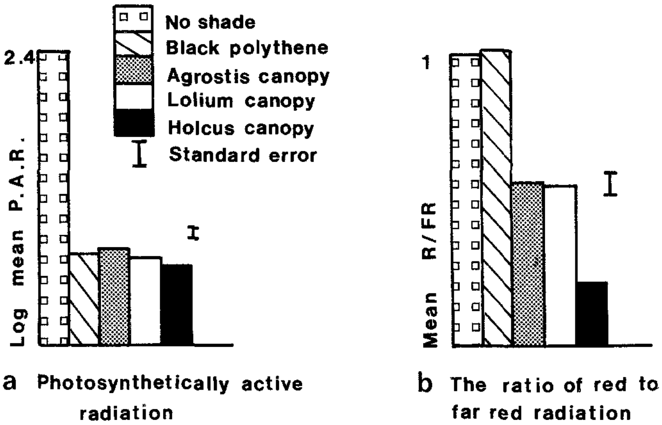

Fig. 1a, b. The influence of grass canopies and a canopy of black polyethene strips on transmitted radiation

trays were arranged in a randomised block design and the position of blocks and of treatments within blocks was rerandomised at three day intervals. After a further 20 days measurements of P.A.R. were made beneath the grass canopies and these were clipped to ensure a maximum difference of 10% in P.A.R. transmitted. The black polythene canopies were adjusted to give transmitted P.A.R. within the same range as the grass canopies. Trays containing clover plants were then placed in the centre of each large treatment tray.

The trays containing clover plants were prepared by taking an excess of single node cuttings from the shoot apices of a single clone of *Trifolium repens* that had been sampled from permanent grassland at Henfaes, Abergwyngregyn, near Bangor, N. Wales. These were then grown in a mist propagator for 7 days, selected for uniformity and transplanted into trays, 20 × 15 × 5 cm of John Innes compost No 1, with two plants per tray. The trays were positioned in the centre of the large trays after removal of the half tray templates. The arrangement ensured that the grass canopies overtopped the clover plants but the root systems did not meet. The grass canopies were held in position by strings to prevent any great fluctuations in the light environment caused by draughts. During the course of the experiment measurements of P.A.R. and ζ were taken as close as possible to the clover plants during rerandomisation and the grasses were clipped when necessary to maintain transmitted P.A.R. as constant as possible. P.A.R. was measured with a "Crump" quantum sensor and ζ with a zetameter constructed from a design by Woodward (1983). The spectral transmission of isolated leaves of *Holcus* and *Lolium* was measured using a scanning spectrophotometer (Pye, Unicam; model SP800). The clover plants remained under the canopies and in the control trays for 28 days and were then harvested. Measurements were made of the dry weight of the clover plants, the length of the main shoot and its lateral branches, the number of branched nodes and rooted nodes, the length of internodes and of petioles.

Results

The effects of the various canopies on P.A.R. and ζ in the environment of the clover plants are shown in Fig. 1a and b. All of the canopies reduced P.A.R. to ca. 32% of the controls and there was no significant difference between the P.A.R. under the three grass species or between the grass and the black polythene canopies. The effect of canopies on ζ was quite different. The values of ζ under the black polythene canopy did not differ significantly from values obtained in the control (unshaded) treatments; this confirmed that the effect of the black polythene canopies was neutral in respect of the quality of radiation transmitted in the relevant wavelengths.

Under canopies of *Lolium* and *Agrostis* values of ζ were very significantly reduced and the effect was yet more pronounced under the canopy of *Holcus* (Fig. 1b). Values of ξ obtained from measurements on isolated leaves with a scanning spectrophotometer confirmed the greater effect of the leaves of *Holcus* than of *Lolium* on the quality of radiation transmitted. Values of ζ were consistently lower under *Holcus* ($P < 0.001$).

Measurements made on the main stolon

The effects of the reduced P.A.R. on the growth of clover under canopies are shown by differences between control plants and those grown under black polythene canopies (Fig. 2a–e). Under the polythene canopies the mean length of the main shoot was reduced by more than half and the numbers of nodes, branches and the length of internodes were all significantly reduced. The number of rooted nodes

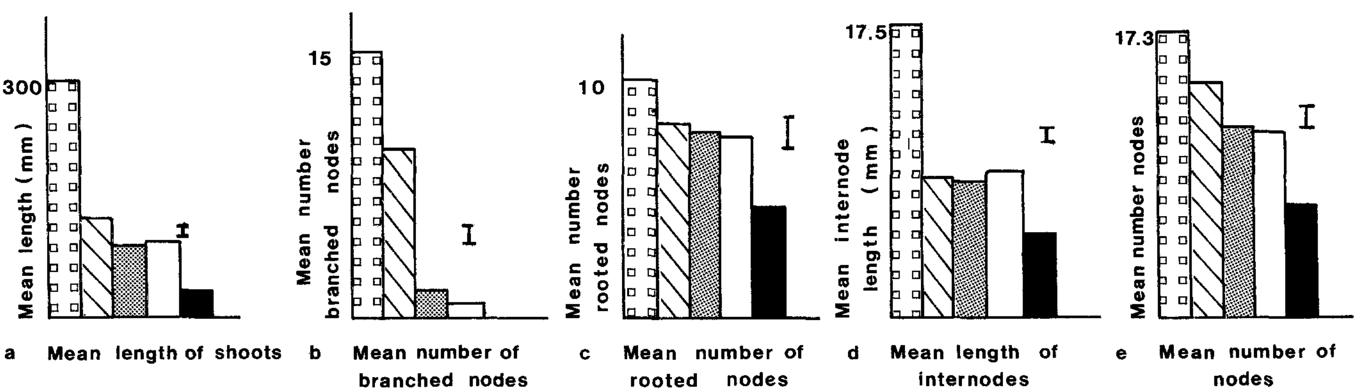

Fig. 2a–e. The influence of grass canopies and a canopy of black polythene on the growth of main shoots of white clover (*Trifolium repens*)

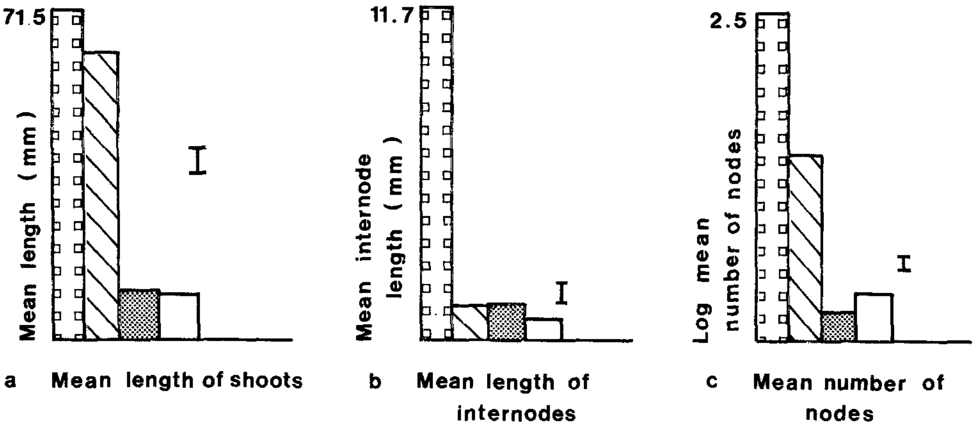

Fig. 3a–c. The influence of grass canopies and neutral shade on the growth of primary branches of white clover

was also reduced though the effect was not significant at $P<0.05$.

The effects of the quality of radiation transmitted by the various canopies are shown by the differences between the behaviour of clover under the black polythene canopy and under the grasses. The most conspicuous effect was on the number of first order branches formed on the main shoot; their formation was very greatly reduced under canopies of *Lolium* and *Agrostis* and completely inhibited under *Holcus* (Fig. 2b). The length of internodes on the main shoot and the number of rooted nodes did not differ significantly between plants under black polythene canopies and under *Lolium* or *Agrostis* but both were significantly reduced under *Holcus* (Fig. 2c, d). The canopies of both *Lolium* and *Agrostis* significantly reduced the number of nodes formed on the main shoot of clover below the number formed under the neutral shade and again the effect of the *Holcus* canopy was much more pronounced (Fig. 2e).

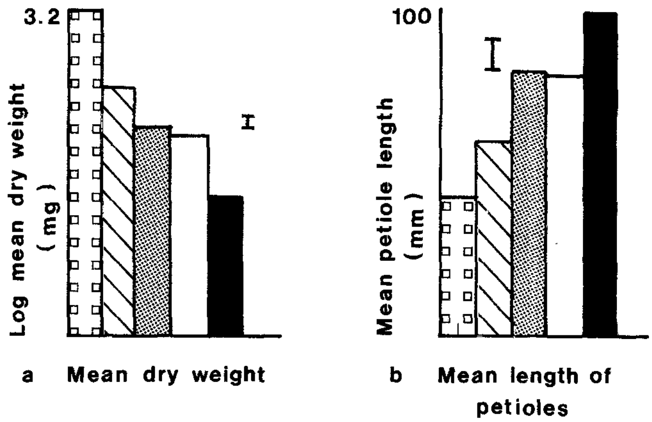

Fig. 4a, b. The influence of grass canopies on the dry weight and petiole length of plants of white clover

Measurements made on first order branches

As no first order branches were developed by clover plants grown under the *Holcus* canopies the measurements illustrated in Fig. 3a–c relate only to the performance of control plants and those grown under the neutral, *Lolium* and *Agrostis* canopies. The length of branches was reduced, but not significantly, by the neutral canopy, Fig. 3a (cf the effect on the main shoot, Fig. 2a) but the branches were very much shorter under the grass canopies. The length of internodes was reduced by about the same amount under the neutral and the grass canopies but to a much greater extent than on the main shoot (Fig. 3b). The number of nodes formed on first order branches was reduced by the neutral shade but much more by the grass canopies; again the effect of treatments on the branches was even more pronounced than on the main shoot.

Measurements made on whole plants

The dry weight per plant of clover was reduced by all the treatments. The neutral (black polythene) canopy reduced dry weight to 76%, the *Lolium* and *Agrostis* canopies to 64–67% and the *Holcus* canopy to 43% of control plants (Fig. 4a). The effect on petiole length was an almost perfect converse response. Exceptionally long petioles were developed under *Holcus* and the shortest petioles were formed by the unshaded and neutral shaded plants (Fig. 4b). The canopies of the grass species did not differ significantly in height so the response of petiole length was not simply a response to the height of the grass leaves. The effects of shading regimes on internode length and petiole length were in opposite directions and profoundly altered the morphology of the plants (Table 1).

Discussion

When clover plants are allowed to grow from an open exposed environment into the neighbourhood of grasses they cease to branch actively and growth becomes largely confined to the linear extension of the main axes (Solangaarachchi 1985). As a result the plants tend to grow through local clumps of grass and branch profusely only when they encounter gaps in the sward. The behaviour of clover in a sward is therefore largely determined by the patchwork distribution of the grasses and the gaps between them. Within this patchwork the growth of clover is largely the opportunistic exploitation of gaps. The experiments reported in this paper show that the quality of incident radiation received by the clover plants plays a part in determining how clover plants react to the presence of neighbouring grasses or to gaps.

Shading with a neutral filter reduced P.A.R. incident on the plants and this was in itself sufficient to change their growth form. The most significant effects were that fewer lateral branches developed and there was less extension growth, because fewer leaves (and so nodes) were

Table 1. The effect of three different shade treatments on the ratio of petiole length of internode length in *T. repens*

Treatment	Mean petiole length mm	Mean internode length mm	Mean petiole l. / Mean internode l.
No shade	34.09	17.47	2.34
Black polyethene	48.57	8.03	4.49
Agrostis canopy	65.94	8.00	12.21
Lolium canopy	66.00	8.47	13.11
Holcus canopy	80.97	4.81	16.83

formed and the internodes were shorter (especially on first order branches). The petioles of plants under neutral shade were longer than on the control plants.

There were large differences between the behaviour of plants under neutral shade and under grass canopies at the same level of transmitted P.A.R.. It is these differences that appear to reflect the influence of the quality of radiation on clover growth. In particular, the plants grown under grass canopies developed far fewer branches than those under the neutral canopy and there were no lateral banches at all under *Holcus*. In many respects (the length of shoots, number of nodes, number of rooted nodes and internode length) the effect of grass canopies was to exaggerate the effects produced by neutral shade. However there were some major differences, which were especially apparent on the primary branches. The *Lolium* and *Agrostis* canopies and the neutral shade had very similar effects on mean internode length (Figs. 2d and 3b) but the plants under the grass canopies produced far fewer nodes (Figs. 2e and 3c), especially branched nodes (Fig. 2b).

Neutral shade and the shade of grass canopies produced very different effects on petiole extension (Table 1); petioles under the grass canopies were much longer than under neutral shade or on control plants. The greater elongation of petioles under grass canopies contrasts with the shortening of internodes under all shading regimes. The result is that the ratio of petiole length to internode length was increased dramatically under the grass canopies (Table 1). The plants under grass swards bore long petioled leaves that were closely packed along sparsely branched shoots – those under neutral shade bore short petioled leaves more loosely packed along more branched shoots – the control plants bore short petioled leaves, even more loosely packed, along richly branched shoots.

It has been suggested (Holmes and Smith 1977) that one influence of the ratio of red to far-red radiation may be to alter the allocation of limiting resources within the growing plant. In the case of plants with orthotropic shoots a common effect of radiation with a low ζ value is to increase internode length (Smith 1982) and so raise developing shoots above a surrounding canopy. In a plant with plagiotropic growth such as *Trifolium repens* there would be no such advantage in an increased length of internodes: the development of longer petioles is the only way by which laminae may be carried to the top of a sward. Even in ungrazed and unmown grassland, clover petioles commonly extend to the top of the grass canopy. It may be that, in clover, the diversion of resources to petiole extension (stimulated by low values of ζ) is made possible by a sacrifice of resources to branching and the elongation of internodes.

A wholly unexpected finding from these experiments is the contrast between the effects of *Holcus* canopies and those of *Agrostis* and *Lolium*. In every respect in which clover growing under a grass canopy differed from the growth of the controls or of plants under neutral shade, the *Holcus* canopies had much greater effects than those of *Agrostis* or *Lolium*. This contrast gives extra weight to the conclusion that radiation quality has a profound effect on the development of clover because it was the *Holcus* canopies that most reduced ζ. The results confirm the findings of Turkington and Harper (1979) and Solangaarachchi (1985) that *Holcus* is particularly vigorous in suppressing the growth of clover and also suggest why this species is more aggressive than other grasses. Deregibus et al. (1985) showed that the development of grass tillers is inhibited by low values of ζ within a sward and it may be that the invasion of *Holcus* into sown pastures is made possible by its effect on the quality of transmitted radiation and so on the tillering of its asociated grasses. It would be surprising if the ability of *Holcus* so greatly to influence the quality of transmitted radiation had its effects only on clover among its associated species.

It is not clear how a canopy, or a single leaf of *Holcus* changes the quality of transmitted radiation so much more than the other grasses studied. The effects of a *Holcus* canopy on ζ and on clover growth beneath it were much greater than, but not qualitatively different from the effects of the other grasses. We have been unable to detect differences between *Holcus* and the other species in the spectrum of light transmitted through leaf extracts and there is no reason to suppose that *Holcus* leaves contain special pigments. The main differences between the leaves of *Holcus* and the other grasses is that *Holcus* leaves are densely hairy. Gates (1981) has shown with some leaves of *Magnolia virginiana* that more red than far-red radiation is reflected from hairy than from glabrous leaves and it seems likely that it is differential reflection from, rather than differential absorption within, the leaves of *Holcus* that accounts for their rather peculiar effects on the spectrum of radiation received beneath its canopy.

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