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# Radiation use efficiency increases when the diffuse component of incident radiation is enhanced under shade

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*Abstract.* Theoretical analyses have shown the radiation use efficiency of maize, soybean, and peanut to increase with a decrease in the level of incident radiation and an increase in the proportion of diffuse radiation. This study compared the growth and radiation use efficiency of *Panicum maximum* cv. Petrie (green panic) and *Bothriochloa insculpta* cv. Bisset (creeping bluegrass) beneath shading treatments (birdguard and solarweave shadecloths) with that in full sunlight. A level of incident radiation reduced by 25% under birdguard shadecloth decreased final yield and final leaf area index, but increased canopy leaf nitrogen concentration and radiation use efficiency (19–14%) (compared with the full sun treatment). A similar level of reduced incident radiation under solarweave shadecloth (which provided an increased proportion of diffuse radiation), increased final yield and radiation use efficiency (46–50%). An understanding of the effects of composition of incident radiation on radiation use efficiency of tropical grasses enables more accurate estimation of potential pasture growth in shaded environments. It also has impact upon crop production in glasshouses and greenhouses.

## Introduction

Pastures under tree canopies experience more shade and a higher proportion of diffuse radiation than pastures growing without trees (Ludlow 1978). Wilson and Ludlow (1991) proposed that the potential pasture growth rate under a plantation canopy could be estimated using the simplified growth model:

$$G = EJ - V \qquad (1)$$

where $G$ is growth rate of herbage in $\mathrm{g/m^2 \cdot day}$, $E$ is radiation use efficiency in g/MJ photon irradiance (photosynthetically active radiation), $J$ is the average amount of photon irradiance intercepted over any chosen time interval in $\mathrm{MJ/m^2 \cdot day}$, and $V$ is the loss of biomass in $\mathrm{g/m^2 \cdot day}$. For practical purposes, the energy content of photosynthetically active radiation can be taken as half the radiative energy recorded with a solarimeter (Monteith 1973); this proportion will vary beneath a tree canopy because photosynthetically active radiation is absorbed more and reflected less by plant canopies than are longer wavelengths (Ludlow 1978).

Factors that influence the radiation use efficiency of plants include nitrogen status (e.g. Muchow and Davis 1988; Wright *et al.* 1993), temperature (e.g. Squire *et al.* 1984; Ong and Monteith 1985), stage of crop development (Gallagher and Biscoe 1978; Garcia *et al.* 1988), and partial shading.

Wright and Hammer (1994) suggested that discrepancies between measured and derived theoretical values of radiation use efficiency may be caused by the level of incident radiation and/or the proportion of diffuse radiation. Radiation use efficiency of maize, soybean, and peanut has been theoretically calculated to increase with a decrease in the level of incident radiation and an increase in the proportion of diffuse radiation (Sinclair *et al.* 1992; Hammer and Wright 1994). Although differences in radiation use efficiency


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due to changes in the prevailing radiation environment have been reported (Bange 1995), the only work relevant to pasture species appears to be that of Sophanodora (1989). Sophanodora (1989) found that the radiation use efficiency of 2 tropical grasses was higher under black shadecloth with nominal shade factors of 70% and 30% than when grown in full sunlight, but the nature of the radiation environment beneath the shadecloths was not assessed.

The influence of a changed proportion of diffuse radiation to direct radiation under shade materials has not, to our knowledge, been determined in the field. Quantification of the effects of direct and diffuse radiation on radiation use efficiency of tropical grasses would enable more accurate estimation of growth, particularly for pastures grown under plantations (e.g. coconuts) and turfgrasses under many types of shade. It may help explain increases in herbage yield associated with shade that cannot be attributed entirely to enhanced nitrogen availability (e.g. Wong *et al.* 1985; Samarakoon *et al.* 1990). The objective of this study was to investigate the effects of reduced levels of incident radiation, and increased proportions of diffuse radiation, on radiation use efficiency and growth of 2 tropical grass species.

## Methods and materials

*Treatments and design*

A field trial consisting of 3 shade treatments over *Panicum maximum* cv. Petrie (green panic) and *Bothriochloa insculpta* cv. Bisset (creeping bluegrass) was conducted at the University of Queensland Gatton College (152° 17′ E, 27° 33′ S). A split-plot design with 3 replications arranged in blocks was used. Main plot treatments were full sunlight (as control), a double layer of black Rheem Birdguard, and clear Rheem Solarweave. Subplot treatments were the 2 species. The shading materials birdguard and solarweave were selected because birdguard affects both the direct and diffuse components of the radiation similarly, whereas the diffuse component is increased below solarweave (Healey and Rickert 1998).

*The field environment*

The climate of the experimental site is subtropical with a summer-dominant rainfall (784 mm average). Summers (December–February) have a mean maximum temperature of 26·4°C and winters (June–August) have a mean minimum of 13·1°C (Bureau of Meteorology 1988) (Fig. 1). Rainfall during the experimental period (autumn 1995) was below average. Plots were irrigated to enhance establishment, immediately after each fertiliser application, and at other times so that water supply was non-limiting to growth.

The experimental site was on an alluvial-prairie soil (Stace *et al.* 1968) (USDA Soil Taxonomy: Fluventic Haplustoll), of the Lockyer Series (Schafer *et al.* 1984). The soil was a brownish black light clay, becoming browner at depth. Soil pH(1 : 5 water) was 8·2 in the 0–10 cm layer and the soil was fertile for all nutrients except available nitrogen.

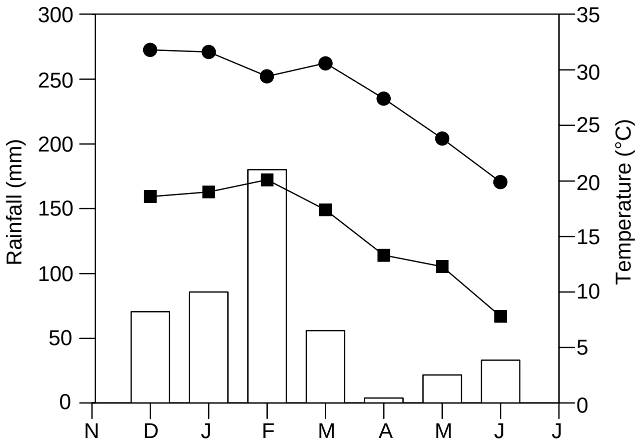


**Fig. 1.** Monthly distribution of rainfall (mm), and maximum (●) and minimum (■) temperatures (°C) during the experimental period.

After preparation of a firm, fine seedbed and a basal application of 30 kg N/ha, 17 kg P/ha, 23 kg K/ha, and 27 kg S/ha, the plots and irrigation furrows were constructed. Each of the main plots (10 m by 8 m) was separated by a 5-m guard area and subplots (10 m by 1 m) had a 0·5-m irrigation furrow between them. Blocks were aligned east–west. Pathways and irrigation furrows were maintained weed-free by regular herbicide application (Roundup) and hand chipping. Nitrogen fertiliser (urea) was broadcast on 21 December 1994 (100 kg N/ha), 15 March 1995 (40 kg N/ha), and 18 April 1995 (80 kg N/ha).

On 16 November 1994, seed of the 2 grass species was broadcast onto the subplots at the rate of 12 kg viable seed/ha for green panic and 8 kg viable seed/ha for bluegrass. The outer subplot on each side of the main plots was a guard plot planted with green panic. Subplots were subsequently raked to enhance seed–soil contact, irrigated as required, and hand-weeded until the sown grasses became established.

The established pastures in each plot were cut to 20 cm on 22 December 1994 and the cut material was removed. Arching shade frames were constructed from lightweight galvanised pipe. They were 10 m long, 7·5 m wide, and 4 m high. The shading material was installed on 22 February 1995 and was attached to the frame so that the sides and ends were open to a height of 1·5 m to allow adequate ventilation. Air temperature and relative humidity were measured at several times on several days during the experimental period. The birdguard had no effect on either air temperature or relative humidity, compared with 'outside' conditions. Under the solarweave, mean air temperature and relative humidity 1·5 m above ground level both increased ($P < 0·05$), but by <1°C and 1·5%, respectively. However, at 0·4 m above ground level neither air temperature nor relative humidity was altered by solarweave. Green panic was mowed at 10 cm and the bluegrass at 5 cm height above ground on 23 February 1995 and cut material removed.

*Measurements*

*Yield*

Harvests were taken 18, 28, 39, 48, 60, 69, 81, 91, and 102 days following an initial cut on 23 February 1995. The sampling area on each occasion was $0 \cdot 5$ m by $0 \cdot 5$ m, randomly positioned within the portion of subplot not previously harvested. Green panic was cut at 10 cm height and bluegrass at 5 cm height. On 12 April and 24 April, green panic was harvested in canopy strata and the bluegrass was harvested in canopy strata on 3 May, 15 May, and 25 May. Strata were 10–30 cm, 30–60 cm, 60–90 cm, and >90 cm above ground for green panic and 5–25 cm, 25–50 cm, 50–75 cm, and >75 cm above ground for bluegrass. Leaf area distribution was assumed to be regular within each stratum.

Fresh subsamples were separated into leaf, stem plus sheath, inflorescence, and dead material. Leaf area of each subsample was measured with an electronic planimeter (Paton, Adelaide, Australia). All plant samples were oven-dried for 3 days at 70°C and subsequently weighed.

*Solar radiation*

Incident solar radiation was recorded with a spot pyranometer (Type LI-200SA, Licor, NE) at a meteorological station 500 m from the experimental site. Incident solar radiation was also measured in the experiment with a similar spot pyranometer and a tube solarimeter (Type TSL, Delta-T Devices, Cambridge; absorption band $0 \cdot 35$–$2 \cdot 5$ $\mu$m) installed in one block of each main plot (shading treatment). These instruments were mounted at a height of $1 \cdot 5$ m. Diffuse radiation incident at the experiment (i.e. in full sun) was measured with a spot pyranometer mounted below a shadow band at $1 \cdot 5$ m height, as described by Horowitz (1969), in each main treatment of one block. Since the shadow band occludes a portion of the sky, there is an inherent error in this method of measuring the diffuse component of the total radiation. This error corresponds to the actual area of the shadow band and was calculated to be <6%. The error is tolerable when diffuse radiation is low and the error is avoided by expressing the diffuse radiation as a proportion (i.e. the ratio of diffuse radiation under the shading material to the diffuse radiation in the open).

In addition, tube solarimeters were placed centrally in each subplot of one block, in a level cradle at ground level, to measure the radiation at the base of the plant canopy. Tube solarimeters were also mounted, in level cradles, in the middle of each stratum prior to making stratified harvests. Light transmission per stratum was not monitored at Day 48 for green panic. All instruments were spaced so that they did not shade each other. The extinction coefficients ($k$) were calculated by adapting Beer's Law:

$$I = I_0 \mathrm{e}^{-k.\mathrm{LAI}} \quad (2)$$

where $I$ is the irradiance at the midpoint of the stratum within the canopy, $I_0$ is the irradiance above the canopy, and LAI is the cumulative leaf area index above the midpoint of the stratum (Milthorpe and Moorby 1988).

All solarimeters were placed in a similar east–west alignment. Solarimeters and pyranometers were scanned at intervals of 5 s and the readings were averaged hourly and recorded by a programmable data-logger (Type DT-100F, Datataker, Melbourne).

*Chemical analyses*

At each harvest, leaf samples from high in the canopy were oven-dried overnight at 70°C, and then ground to pass through a $0 \cdot 5$-mm screen. Nitrogen contents were calculated from Kjeldahl digests by an autoanalytical procedure (Johnson *et al.* 1985).

*Statistical analyses*

The analysis of variance was performed for a split-plot experimental design with 3 replications. The extinction coefficient is a measure of the overall effectiveness of the canopy to intercept light. Instantaneous extinction coefficients were estimated from Eqn 2 by substituting leaf area index and light interception for each harvest.

## Results

*The radiation environment*

Average proportions of incident radiation transmitted by the double layer of birdguard and by solarweave were 75% and 77%, respectively. The double layer of birdguard reduced the diffuse component to a similar extent to the shortwave radiation (Table 1). In contrast, solarweave increased the proportion of diffuse radiation and the magnitude of the increase varied inversely with the proportion of diffuse radiation in the total incident radiation. On cloudy days, when the incident diffuse component was high, the increase in diffuse radiation under the solarweave was minimal. On clear days, when the incident diffuse component was low, the amount of diffuse radiation under the solarweave canopy was up to 5 times that in the incident radiation.

The frequency distribution for the proportion of diffuse radiation in the incident radiation shows that the experimental period consisted of relatively sunny days with diffuse radiation <30% of total:

| Proportion of diffuse radiation | <30% | 30–70% | >70% |
|---|---|---|---|
| Number of days | 69 | 29 | 18 |

Both birdguard and solarweave may be considered to be neutral filters. Yates (1989) recorded similar proportional decreases of total shortwave radiation and photosynthetically active radiation under several black shademeshes (made of similar fabric to the birdguard). Further, Bange (1995) reported spectral transmittance for solarweave over the 400–800 nm wavelength range and found solarweave to be spectrally neutral.

*Effects of radiation environment on grass yield*

The radiation environment had little influence on the yield during the first 50 days of regrowth of both bluegrass and green panic (Fig. 2). Thereafter, both species produced significantly more dry matter under the solarweave than in full sun and there was no difference between species. Maximum dry matter yield occurred at Day 91 in full sun and at Day 102 under both shading treatments, so final yield was taken as the average of the yields on Day 91 and Day 102 (Table 2).

**Table 1. Composition of radiation incident on grasses beneath the shading treatments during the regrowth period**

| Treatment | Days (24 February–5 June) | | | | | | Mean |
|---|---|---|---|---|---|---|---|
| | <20 | 21–40 | 41–60 | 61–80 | 81–100 | >100 | |
| *Av. daily total shortwave (MJ/day)* | | | | | | | |
| Sun | 21·1 | 21·8 | 19·2 | 13·6 | 12·5 | 11·2 | 16·7 |
| Birdguard | 15·4 | 16·3 | 14·4 | 9·9 | 9·3 | 8·6 | 12·5 |
| Solarweave | 15·8 | 16·3 | 14·4 | 10·6 | 10·1 | 9·1 | 12·8 |
| *Av. daily diffuse (MJ/day)* | | | | | | | |
| Sun | 6·0 | 2·2 | 3·8 | 5·2 | 3·4 | 3·3 | 4·0 |
| Birdguard | 5·0 | 1·4 | 3·0 | 4·0 | 2·6 | 2·5 | 3·1 |
| Solarweave | 8·8 | 7·5 | 6·9 | 6·9 | 5·8 | 5·2 | 6·9 |
| *Mean diffuse proportion (%)* | | | | | | | |
| Sun | 33·1 | 10·2 | 26·3 | 44·9 | 36·0 | 43·6 | 32·0 |
| Birdguard | 37·1 | 8·5 | 27·3 | 47·5 | 36·3 | 42·4 | 32·9 |
| Solarweave | 60·3 | 48·4 | 53·2 | 69·8 | 63·2 | 69·1 | 60·4 |
| *Total under shade material : total in open* | | | | | | | |
| Birdguard | 0·73 | 0·75 | 0·75 | 0·73 | 0·74 | 0·77 | 0·75 |
| Solarweave | 0·75 | 0·75 | 0·75 | 0·78 | 0·81 | 0·81 | 0·77 |
| *Diffuse under shade material : diffuse in open* | | | | | | | |
| Birdguard | 0·84 | 0·65 | 0·78 | 0·78 | 0·77 | 0·78 | 0·78 |
| Solarweave | 1·47 | 3·45 | 1·81 | 1·32 | 1·67 | 1·56 | 1·72 |

**Table 2. Effect of shading treatment on final dry matter yield (DMY kg/ha), leaf area index (LAI), accumulated intercepted radiation (AIR MJ), and radiation use efficiency (RUE g/MJ)**

Data presented are means across species, since species were not significantly different. Within a row, means followed by the same letter are not significantly different at $P = 0{\cdot}05$

| Measurement | Sun | Birdguard | Solarweave |
|---|---|---|---|
| DMY | 13574b | 12160c | 16019a |
| DMY of stem | 8447b | 7582b | 10051a |
| DMY of leaf | 3802a | 3097b | 4135a |
| LAI | 8·42a | 6·61b | 9·31a |
| AIR | 1133a | 836b | 893b |
| RUE | 1·28c | 1·49b | 1·89a |

*Proportion of plant parts*

Stem dry matter yield, at the time of final dry matter yield, was higher under solarweave than in the other 2 treatments and leaf dry matter yield was lowest under birdguard (Table 2). There was no difference between species in final dry matter yield of leaf or stem, nor were the proportions of leaf, stem, inflorescence, and dead material within each species affected by the shading treatments. Bluegrass contained a higher proportion of leaf than the green panic, whereas green panic produced more stem and inflorescence, and less dead material, than bluegrass.

*Leaf area*

Both species showed similar trends in leaf area development (data not shown). Final leaf area index was taken as an average of the last 2 harvests and was highest in full sun, and lowest under birdguard (Table 2). There was no significant difference between species for final leaf area index.

*Light interception*

Interception of incident radiation was similar across treatments throughout the regrowth period and maximum light interception was attained by about Day 40 (data not shown).

Leaf area index profiles after full light interception may be combined since no strong difference between species was evident (Table 3). Leaf area index was generally higher under the solarweave and lower under the birdguard, compared with the sun treatment. Overall increases in leaf area index beneath solarweave were associated with an increased leaf area index in the uppermost stratum but the proportion of leaf area index above 50 cm was similar across shade treatments. Extinction coefficients for the whole canopy were similar across treatments for bluegrass, but significantly decreased for 60-day regrowth of green panic under solarweave compared with the birdguard and full sun treatments.

There were developmental differences between light treatments in terms of light interception down the canopy. Developing bluegrass and green panic grown under solarweave had increased leaf area index high in the canopy, so that leaf area under solarweave was more evenly distributed, compared with other treatments (data not presented). For the sun treatment, the effectiveness of light interception at the top of the canopy was very different from that of the strata below; the difference was not as extreme under birdguard and solarweave. Bluegrass and green panic canopies developed differently according to the light environment. Thus, the light extinction coefficient down the profile was influenced by the light environment both directly and through the effect of the light environment on canopy development. An increased proportion of diffuse radiation relative to total incident radiation resulted in an increase in radiation transmission and penetration within the canopy and, hence, a more uniform light distribution over the leaf surface. This was especially evident in the uppermost strata (lower values for the light extinction coefficient under solarweave, compared with the other treatments) (Table 3).

*Leaf nitrogen concentration and specific leaf nitrogen*

Canopy leaf nitrogen concentration varied during the experiment and was highest after nitrogen was applied on Days 20 and 54. Sequential analyses of variance (data not shown) showed that canopy leaf nitrogen concentration was higher in material grown

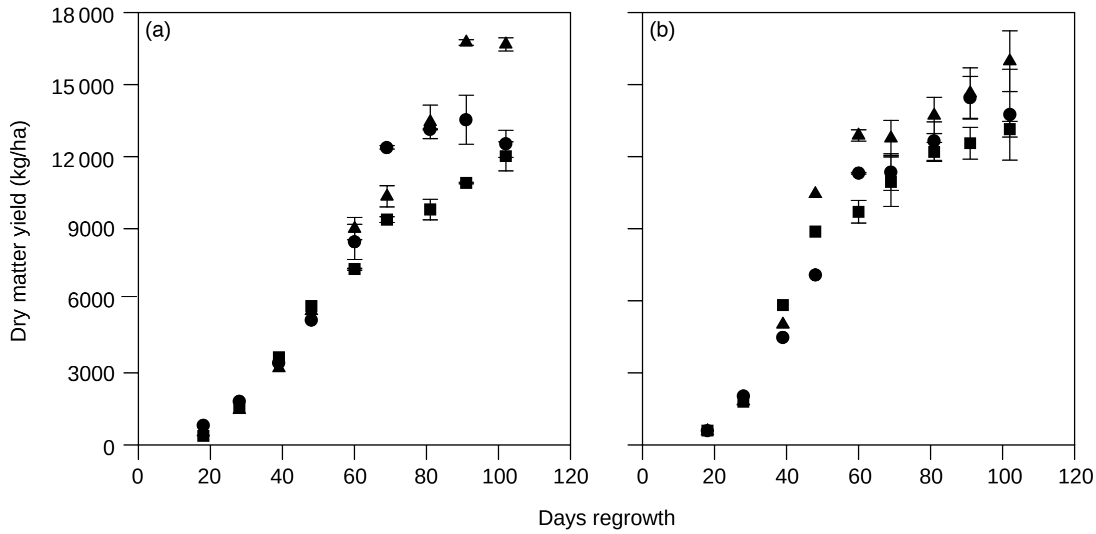


**Fig. 2.** Dry matter yields of (*a*) bluegrass and (*b*) green panic grown in full sun (●) and beneath birdguard (■) and solarweave (▲).

under birdguard, but similar for material grown in the sun and under solarweave.

Specific leaf nitrogen has been related more directly to radiation use efficiency than leaf nitrogen concentration (Sinclair and Horie 1989). The specific leaf nitrogen [the amount of nitrogen (g) per unit area of green leaf ($m^2$)] was calculated as the product of leaf nitrogen content and specific leaf area ($g/m^2$). As with canopy leaf nitrogen concentration, specific leaf nitrogen also varied in response to the fertiliser regime. Analyses of variance showed that specific leaf nitrogen was similar across treatments, except at Day 48 of regrowth, when leaf from plants grown under birdguard contained more nitrogen ($7\cdot4$ $g/m^2$) than leaf from plants grown in the other 2 treatments ($5\cdot2$ and $6\cdot0$ $g/m^2$ for sun and solarweave treatments, respectively).

**Table 3. Leaf area index (LAI) profiles from after full light interception**

Times refer to days of regrowth. Within a column, means followed by the same letter are not significantly different at $P = 0\cdot05$

| Item | Green panic 48 days | Green panic 60 days | Bluegrass 81 days | Bluegrass 91 days | Mean |
|---|---|---|---|---|---|
| | | *Full sun* | | | |
| LAI | 4·92 | 8·25 | 7·37 | 7·74 | 7·07 |
| | | *Fractional* | | | |
| LAI >50 cm | 2·10 | 4·30 | 4·17b | 4·00b | 3·64 |
| %LAI >50 cm | 43 | 52 | 57 | 52 | 51 |
| *k* at 63/75 cm | n.a. | 0·48a | 0·41 | 0·46 | 0·45 |
| | | *Birdguard* | | | |
| LAI | 7·92 | 6·28 | 7·17 | 6·24 | 6·90 |
| | | *Fractional* | | | |
| LAI >50 cm | 3·21 | 3·44 | 3·15c | 3·26c | 3·27 |
| %LAI >50 cm | 41 | 55 | 44 | 52 | 48 |
| *k* at 63/75 cm | n.a. | 0·51a | 0·44 | 0·30 | 0·42 |
| | | *Solarweave* | | | |
| LAI | 8·59 | 8·44 | 8·44 | 9·06 | 8·63 |
| | | *Fractional* | | | |
| LAI >50 cm | 3·49 | 4·61 | 4·55a | 5·00a | 4·41 |
| %LAI >50 cm | 41 | 55 | 54 | 55 | 51 |
| *k* at 63/75 cm | n.a. | 0·31b | 0·38 | 0·24 | 0·31 |

### *Effect of radiation environment on radiation use efficiency*

Radiation use efficiency is a function of both the dry matter yield and accumulated intercepted radiation. Overall radiation use efficiency was taken as the slope of the linear regression of mean dry matter yield versus accumulated intercepted shortwave radiation using data from all harvests (Fig. 3). Radiation use efficiency was lowest in full sun and highest under solarweave (Table 2). Within each treatment, radiation use efficiencies of the two species were similar.

Final dry matter yield was higher under solarweave and lower under birdguard, compared with full sun. Final accumulated intercepted radiation was taken as the average of the accumulated intercepted radiation on Days 91 and 102 of the regrowth period (Table 2). Final accumulated intercepted radiation by bluegrass and green panic was similar under solarweave and birdguard, but higher under full sun.

## Discussion

### *Growth and development*

In comparison with full sun, the shade treatments in this experiment were selected to reduce incident radiation by 25%, in one case without changing the

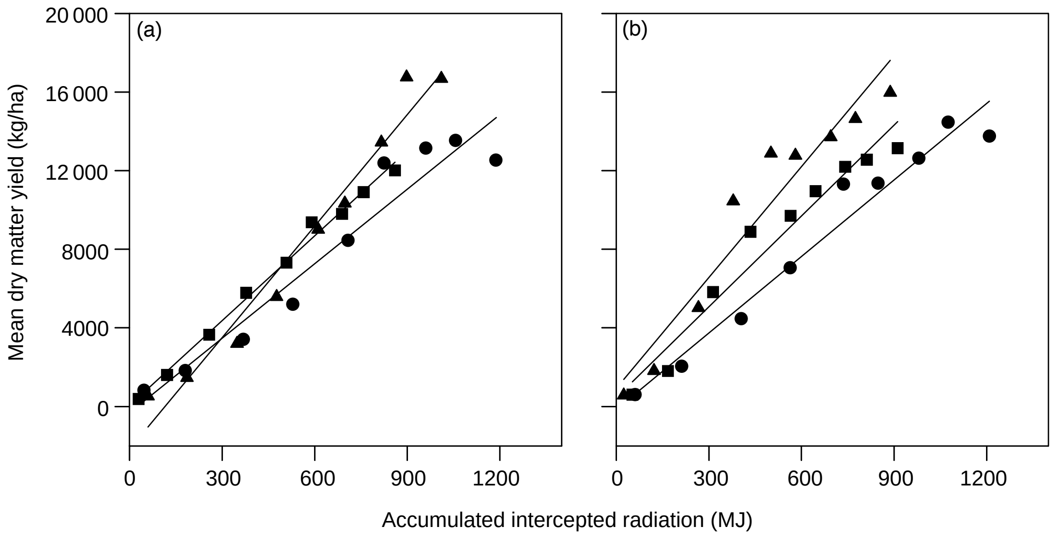


**Fig. 3.** Relationship between accumulated dry matter yield and accumulated intercepted shortwave radiation during the regrowth period for (*a*) bluegrass and (*b*) green panic grown in full sun [●, (*a*) $r^2 = 0{\cdot}93$, (*b*) $r^2 = 0{\cdot}96$] and beneath birdguard [■, (*a*) $r^2 = 0{\cdot}99$, (*b*) $r^2 = 0{\cdot}96$] and solarweave [▲, (*a*) $r^2 = 0{\cdot}97$, (*b*) $r^2 = 0{\cdot}93$].

proportion of diffuse radiation (birdguard), and in the other substantially increasing the proportion of diffuse radiation (solarweave). Since there was a high proportion of sunny days during the experimental period, and the shade structures did not alter either the air temperature or the humidity at the sward level, the difference in grass growth under the shades is believed to be a direct response to the differences in proportion of direct to diffuse radiation. Final yield of both bluegrass and green panic was lower under birdguard than in full sun, but in contrast was higher under solarweave where the lower level of incident radiation was combined with an increased proportion of diffuse radiation. This increased yield under solarweave was a consequence of higher yields of both leaf and stem dry matter. Shading is known to stimulate etiolation (Eriksen and Whitney 1981), but this response was not evident in either bluegrass or green panic, as the proportions of dry matter in plant parts were not affected.

Final leaf area index of both grasses was similar under both solarweave and full sun, but was reduced for grasses grown under birdguard. Since the amount of irradiance incident on the grasses was reduced by birdguard and solarweave, the average amount of irradiance intercepted by the grasses was also reduced. The growth rate of herbage is a function of both the average amount of irradiance intercepted and radiation use efficiency (Eqn 1).

*Radiation use efficiency and radiation environment*

Lower levels of incident radiation under birdguard increased canopy leaf nitrogen concentration and radiation use efficiency, compared with the sun treatment; radiation use efficiencies of green panic and bluegrass increased by 19% and 14%, respectively. This is consistent with the findings of Sophanodora (1989), who measured an increase in radiation use efficiency of up to 44% for guinea grass (*Panicum maximum*) and 12% for signal grass (*Brachiaria decumbens*) when incident radiation was reduced by 30%. However, the increase in radiation use efficiency reported by Sophanodora (1989) was also confounded by a significantly increased leaf nitrogen content under low radiation levels; Sophanodora (1989) made this measurement only once (Day 28) during the 51-day regrowth period.

Several factors have been put forward to explain increased radiation use efficiency under lower levels of incident radiation: more dry matter is partitioned to above-ground herbage (shoot to root ratio increases); leaf to stem ratio may increase, thereby reducing light interception by less efficient stem tissue; leaf nitrogen concentration may increase; and the leaves are less carbon dioxide limited for photosynthesis (Wilson and Ludlow 1991). Leaf to stem ratio did not increase in response to reduced incident radiation in this study. An increase in shoot to root ratio has been reported as an adaptive response to decreasing incident radiation, with variation between species and shade levels in the extent of the response (e.g. Wong *et al*. 1985; Samarakoon *et al*. 1990). Decreased respiration rates of whole plants have been measured under decreased levels of incident radiation (Ludlow *et al*. 1974). Reduction of the respiration rate allows for a decrease in the light compensation point at which the rate of carbon dioxide fixation equals the rate of carbon dioxide respired (Wilson and Ludlow 1991). It is possible that either or both an increased shoot to root ratio or a decreased respiration rate contributed to the increase in radiation use efficiency found under the birdguard canopy. Increases in radiation use efficiency, as a result of lower levels of incident radiation, could also be a result of slight increases in radiation flux on the lower shaded leaves and slight decreases in the flux on the higher exposed leaves, thus increasing canopy efficiency (Hammer and Wright 1994). An increase in leaf nitrogen content has been shown to increase radiation use efficiency, with linear relationships measured for maize and sorghum (Muchow and Davis 1988) and peanut (Wright *et al*. 1993). According to the linear relationship derived by Muchow and Davis (1988) for maize and sorghum, an increase in specific leaf nitrogen of $0 \cdot 25$ g/m$^2$ could account for the change in radiation use efficiency recorded under birdguard in this study.

Under solarweave, the increased proportion of diffuse radiation further increased the radiation use efficiency of the grasses over that of the other treatments; with an increase of 46% and 50% for green panic and bluegrass, respectively (compared with the sun treatment). Nitrogen can be excluded as a factor causing this extra increase in radiation use efficiency of the grasses under solarweave, since leaf nitrogen concentration and specific leaf nitrogen were similar for the solarweave and full sun treatments. Wright and Hammer (1994), with peanut, and Bange (1995), with sunflower, demonstrated 'theoretically' that an increase in diffuse proportion can increase radiation use efficiency. They attributed the theoretical increase in radiation use efficiency to more light being spread over sunlit and shaded leaves. In this study, better canopy penetration by diffuse light was evident beneath the solarweave, as increased leaf area index in upper strata did not proportionately reduce light transmission to the strata below. This response was also supported by the light extinction coefficent ($k$) at 63 cm for bluegrass and 75 cm for green panic (75% of canopy height). The coefficient was significantly less under solarweave (compared with the other treatments), indicating a deeper light penetration down the profile and, hence, a more uniform light distribution over the total leaf surface. Consequently, a higher optimum leaf area index was supported and greater crop growth rate was attained under solarweave.

In conclusion, this is the first work, of which we are aware, showing a clear, experimentally demonstrated increase in radiation use efficiency in response to a changed light environment to support previously presented theoretical calculations. Increased radiation use efficiency in response to a decrease in the level of incident radiation and an increase in the proportion of diffuse radiation is the most likely explanation for discrepancies between expected and measured pasture yields under shade. The response is relevant to grass growth under any shaded environment where the diffuse component is altered, including shading by tree canopies such as plantation crops or natural woodlands, as well as shading by manufactured materials, such as in a glasshouse or shadehouse situation. The response may potentially be used to manipulate plant production under filtered covers in glasshouse and shadehouse situations. Also, the response may have implications for crop modelling since current crop models do not take account of this effect which could be significant under cloudy or overcast conditions.

## References


Bange, M. P. (1995). Environmental control of potential yield of sunflower in a sub-tropical environment. PhD Thesis, University of Queensland, Australia.

Bureau of Meteorology (1988). 'Climatic Averages Australia.' (Australian Government Printing Services: Canberra.)

Eriksen, F. I., and Whitney, A. S. (1981). Effects of light intensity on growth of some tropical forage species. 1. Interaction of light intensity and nitrogen fertilisation on six forage grasses. *Agronomy Journal* **73**, 427–33.

Gallagher, J. N., and Biscoe, P. V. (1978). Radiation absorption, growth and yield of cereals. *Journal of Agricultural Science, Cambridge* **91**, 47–60.

Garcia, R., Kanemasu, E. T., Blad, B. L., Bauer, A., Hatfield, J. L., Major, D. J., Reginato, R. J., and Hubbert, K. G. (1988). Interception and use efficiency of light in winter wheat under different nitrogen regimes. *Agricultural and Forest Meteorology* **44**, 175–86.

Hammer, G. L., and Wright, G. C. (1994). A theoretical analysis of nitrogen and radiation effects on radiation use efficiency in peanut. *Australian Journal of Agricultural Research* **45**, 575–89.

Healey, K. D., and Rickert, K. G. (1998). Shading material changes the proportion of diffuse radiation in transmitted radiation. *Australian Journal of Experimental Agriculture* **38** (in press).

Horowitz, J. L. (1969). An easily constructed shadow-band for separating direct and diffuse solar radiation. *Solar Energy* **12**, 543–5.

Johnson, A. D., Simons, J. G., Hansen, R. W., and Daniel, R. A. (1985). Chemical procedures for the analysis of plant material: multielement, oil, sugars, and gum. Division of Tropical Crops and Pastures, CSIRO Australia, Tropical Agronomy Technical Memorandum No. 40.

Ludlow, M. M. (1978). Light relations of pasture plants. *In* 'Plant Relations in Pastures'. (Ed. J. R. Wilson.) pp. 35–49. (CSIRO: East Melbourne.)

Ludlow, M. M., Wilson, G. L., and Heslehurst, M. R. (1974). Studies on the productivity of tropical pasture plants. V. Effect of shading on growth, photosynthesis, and respiration in two grasses and two legumes. *Australian Journal of Agricultural Research* **25**, 425–33.

Milthorpe, F. L., and Moorby, J. (1988). 'An Introduction to Crop Physiology.' 2nd Edn. (Cambridge University Press: Sydney.)

Monteith, J. L. (1973). 'Principles of Environmental Physics.' (Edward Arnold Limited: London.)

Muchow, R. C., and Davis, R. (1988). Effect of nitrogen supply on the comparative productivity of maize and sorghum in a semi-arid tropical environment. II. Radiation interception and biomass accumulation. *Field Crops Research* **18**, 17–30.

Ong, C. K., and Monteith, J. L. (1985). Response of pearl millet to light and temperature. *Field Crops Research* **11**, 141–60.

Samarakoon, S. P., Wilson, J. R., and Shelton, H. M. (1990). Growth, morphology, and nutritive value of shaded *Stenotaphrum secundatum*, *Axonopus compressus*, and *Pennisetum clandestinum*. *Journal of Agricultural Science, Cambridge* **114**, 161–9.

Schafer, B. M., Powell, B., Smith, K. J., and Hughes, K. K. (1984). Lockyer Valley. *In* 'Proceedings of the Pre-Conference Tour, 13 May 1984, Gatton, Australia'. (Australian Society of Soil Science: Brisbane.)

Sinclair, T. R., and Horie, T. (1989). Leaf nitrogen, photosynthesis, and crop radiation use efficiency: a review. *Crop Science* **29**, 90–8.

Sinclair, T. R., Shiraiwa, T., and Hammer, G. L. (1992). Variation in crop radiation use efficiency in response to increased proportion of diffuse radiation. *Crop Science* **32**, 1281–4.

Sophanodora, P. (1989). Productivity and nitrogen nutrition of some tropical pasture species under low radiation environments. PhD Thesis, University of Queensland, Australia.

Squire, G. R., Marshall, B., Terry, A. C., and Monteith, J. L. (1984). Response to temperature in a stand of pearl millet. VI. Light interception and dry matter production. *Journal of Experimental Botany* **153**, 599–610.

Stace, H. C. T., Hubble, G. D., Brewer, R., Northcote, K. H., Sleeman, J. R., Mulcahy, M. J., and Hollsworth, E. G. (1968). 'A Handbook of Australian Soils.' (Rellim Technical Publishers: Glendside, S. Aust.)

Wilson, J. R., and Ludlow, M. M. (1991). The environment and potential growth of herbage under plantations. *In* 'Forages for Plantation Crops'. (Eds H. M. Shelton and W. W. Stur.) Proceedings of a Workshop, Sanur Beach, Bali, Indonesia, 27–29 June 1990. ACIAR Proceedings No. 32, pp. 10–24. (ACIAR: Canberra.)

Wong, C. C., Mohd. Sharudin, M. A., and Rahim, H. (1985). Shade tolerance potential of some tropical forages for integration with plantations. 1. Grasses. *MARDI Research Bulletin* **13**, 225–47.

Wright, G. C., Bell, M. J., and Hammer, G. L. (1993). Leaf nitrogen content and minimum temperature interactions affect radiation use efficiency in peanut. *Crop Science* **33**, 476–81.

Wright, G. C., and Hammer, G. L. (1994). Distribution of nitrogen and radiation use efficiency in peanut canopies. *Australian Journal of Agricultural Research* **45**, 565–74.

Yates, D. J. (1989). Shade factors of a range of shadecloth materials. *Acta Horticulturae* **257**, 201–17.

Zaffaroni, E., and Schneiter, A. A. (1989). Water-use efficiency and light interception of semidwarf and standard-height sunflower hybrids grown in different row arrangements. *Agronomy Journal* **81**, 831–6.

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