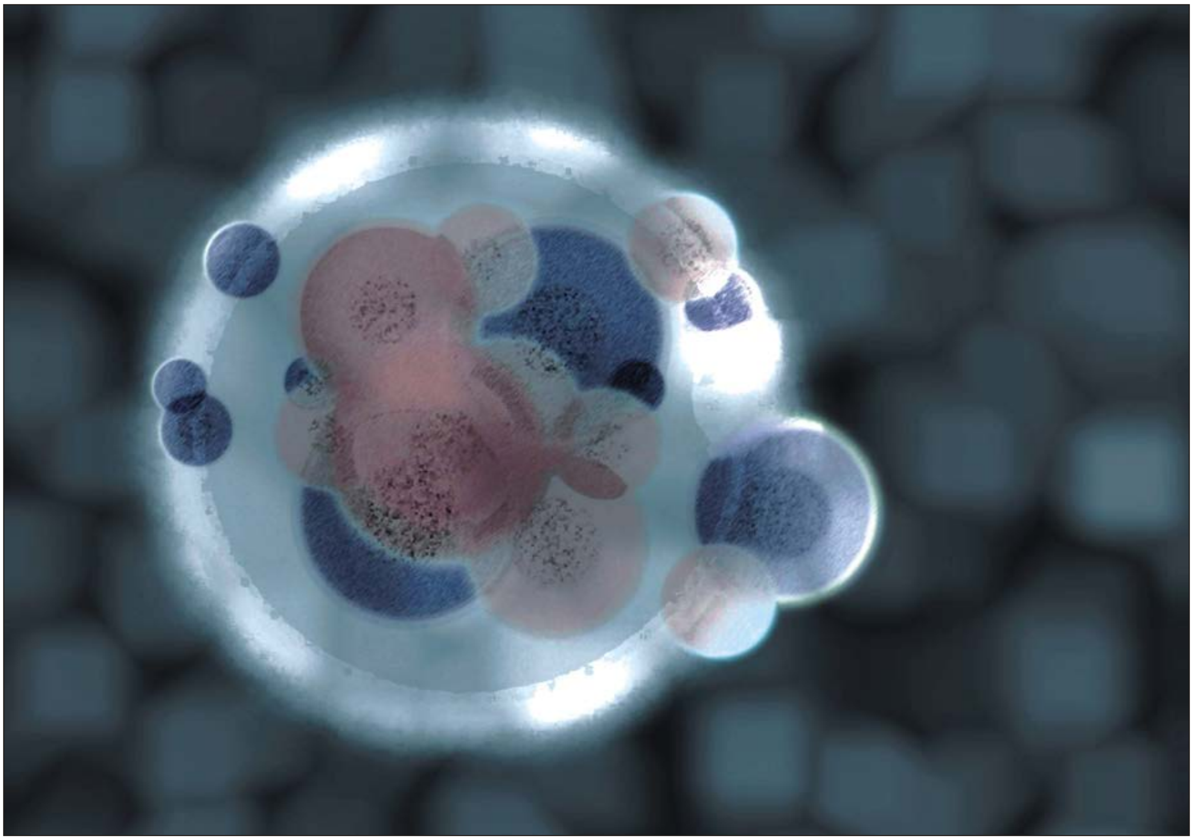

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The Effects of Shading on the Growth, Development and Partitioning of Biomass in Bermudagrass (*Cynodon dactylon* (L.) Pers.)

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Abstract: The effect of shade on the growth and development of Bermudagrass (*Cynodon dactylon*) (L.) Pers.) was determined under glasshouse conditions. The plants were grown from shoot propagules in full light, under different layers of green netting (provides 42, 58 and 77% shade) and under plants canopy {maize (65% shade) and soybean (67% shade)} for 42 to 84 days. Results have shown that continuous shading severely reduced the number of tillers, leaf area, leaf dry weight, stem dry weight, root dry weight and total dry weight of *C. dactylon*. After 84 days continuous shading, plants grown in 42, 58 and 77% shade and with maize (65% shade) or soybean (67% shade) yielded only 25, 21, 7, 11 and 15%, respectively as much total dry weight as the plants grown in full light. Shading at later growth stages also reduced growth of *C. dactylon* but early shading followed by full light at later stages had less shade effect. For example at the final harvest, plants that were transferred from 77% shade to full light at day 42 after planting had 45% of the total dry weight of the plants in the continuous full light treatment, but plants transferred from full light to 77% shade at day 42 had only 27% as much. Constant shading reduced Dry Matter Production (DMP), Net Assimilation Rate (NAR), Relative Growth Rate (RGR) and Leaf Area Duration (LAD) but increased Leaf Area Ratio (LAR). Plants shaded after 42 days in full light maintained larger LAD then continuously shaded plants but had similar or lower NAR values to them during the shaded period. Early shaded plants had slightly larger NAR than the plants that were maintained continuously in the full light treatment and increased their LAD compared to the continuously shaded plants.

Key words: Shading, bermudagrass, *Cynodon dactylon*,, maize, soybean

INTRODUCTION

Bermudagrass [*Cynodon dactylon* (L.) Pers.] is a highly competitive perennial grass that has been rank second in the world's worst weeds[1]. World wide *C. dactylon* is perhaps the most serious weed of the grass family. It occurs as a weed in about 40 crops species in 80 countries and is one of the troublesome grass weeds because of it's dynamic, aggressive competitiveness resulting in reduced crop growth and yield[1-3]. In Malaysia, *C. dactylon* is prominent among the 60 weeds species found in plantation areas[4]. Although this species has become important, little is known about environmental effects on the growth and survival of this species.

Light is important to plant growth based on the photosynthesis process and phytochrome reactions[5]. Light is one of the limitation factors of plant growth and the plant productivity will be reduced when the amount of light is decreased[6]. Light energy is the primary environmental resources for which weeds and crop plants compete[7]. Competition for light of shading stress influence the ability of weeds and crops to compete for water and nutrients by reducing photosynthate available to support root growth[8].

The effect of light on growth varies between species. Dall'armellina and Zimdahl[9] found that leaf area, shoot, root and rhizome dry weight of *Convolvulus arvensis* were reduced for every reduction of light. Conversely, *Centaura repens* leaf area was increased as light intensity

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decreased from 520 to 236 umol m^{-1} s^{-1} [9]. The potential of shade for suppressing weed growth has been reported[10-12]. For example, Keeley and Thullen[10] was concluded that rapidly developing crops such as corn or potato would suppress the weed through competition for light.

It is important to study the response of individual species to shade in order to understand its competitive interaction with other species[13]. In consistent results have been reported on the effect of shading on *C. dactylon*. Burton *et al*.[14], Schmidt and Blaser[15] reported that shading reduced both forage and rhizome production of *C. dactylon*. However Monk and Gabrilelson[16] found that shade treatment did not affect *C. dactylon* growth, but Ugyur *et al*.[17] reported that *C. dactylon* showed slightly greater shade tolerance than *Sorghum halpense* but heavier shade reduced growth. In the present study, the responses of *C. dactylon* to shading under greenhouse condition were investigated to determine how the weed might respond to crop canopy shading as part of an understanding of its competitive interactions with crops. Mathematical growth analysis techniques were used to evaluate the responses of *C. dactylon* to shading[18].

MATERIALS AND METHODS

Plant material, growing condition and harvest procedures: The experiment was conducted in a temperature (25°C) controlled glasshouse of Department of Agricultural Botany, Earley Gate, University of Reading. The material used was from one clonal stock originally from Sri Lanka but maintained at Reading for many years. The soil used was John Innes No. 1 commercial potting compost (Keith Singleton's Seaview Nurseries, Cumbria, UK). *C. dactylon* shoot propagules (10-15 cm length) without roots were taken from stock plants in the weed glasshouse and planted in soil in propagation trays. After 8-10 days, similar sized rooted *C. dactylon* propagules were then transplanted into 12.5 cm diameter pots (two shoots per pot). *C. dactylon* plants were then grown for two more weeks when the shading treatments started.

One group of plants received full available light, while three other groups of plants were kept under different layers of green netting to provide three shade treatments; 42, 58 and 77% shade (shade relative to full available light measured at solar noon on a clear day). Another group of similar plants were placed between parallel rows of 2 weeks old maize and soybean plants to provide a maize and soybean canopy. After 4 weeks growth these canopies provided 65 and 67% shade at the level of the *C. dactylon* pots. These levels of shading were chosen to encompass/represent a range of severe shade occurring under the canopy of many row crops species.

The glasshouse was maintained at a minimum temperature of 25°C day and night, 40-80% of relative humidity and received natural sunlight, supplemented by sodium lamps for 2 h in the morning and evening to increase the light intensity over a photoperiod of 13 h. The average light intensity was 738 um $M^{-2}s^{-1}$. Pot were watered daily and fertilised with 100 mL/pot of a 1% complete range liquid fertiliser nutrient solution every 2 weeks. Pesticides for insect control were also sprayed on the plants when necessary.

At 42 days after planting, 4 replicate plants from each of the six treatment groups were harvested. At this time an additional group of 4 replicate plants were transferred from the full light treatment to each of the five shade treatments. At the same time groups of plants from each of the five shade treatments were also transferred to the full light treatment. Thus, from 42 days after planting until the final harvest at 84 days after planting, there were 16 separate treatment groups consisting of plants maintained continuously in the six original treatments [0 (unshaded), 42, 58, 77, 65 (maize) and 67 (soybean)% shade]; plants transferred from full light to each of the five shade treatment and plants transferred from each of the shade treatments back to full light. At both the 42 and 84 day harvests, leaf area and total plant dry weight (80°C, oven-dried) were determined. At the 84 day harvest, separate dry weight of the leaves, stems, roots and rhizomes also were determined. All data were subjected to separate analysis of variance and LSD Test used to separate the differences among treatments at the $p<0.05$ probability level.

RESULTS

Vegetative growth and biomass partitioning: Generally all levels of continuous shading or shading from 0 to 42 or 42 to 84 DAP (days after planting) severely reduced the number of tillers, leaf area, leaf dry weight, stem dry weight, root dry weight and total dry weight of *C. dactylon* (Table 1 and 2). After 84 days, plants grown in 42, 58, 77% shade and with maize (65% shade) or soybean (67% shade) yielded only 25, 21, 7, 11 and 15%, respectively as much total dry weight as the plants grown in full light. Effect on leaf area and the number of tillers were equally dramatic.

When plants were transferred from shade to full light at 42 DAP their growth increased very considerably when compared to that of plants which remained in shade. Conversely, transferring plants from full light to shade at

Table 1: Effect of shade on the growth and development of *C. dactylon*, at 42 days after planting (DAP)[x]

Shade (%)	Tillers No. pot^{-1}	Leaf area dm^2/pot	Leaf dry weight	Stem dry weight	Root dry weight	Total dry weight
			g pot^{-1}			
0	25	259.0a	2.14a	2.75a	0.75a	5.64a
42	14	107.2bc	0.65b	0.59bc	0.17b	1.4b-d
58	10	44.7c	0.50b	0.56bc	0.16b	1.22cd
77	5	39.0c	0.41c	0.39c	0.12b	0.92d
65 (maize)	7	144.7b	0.73b	0.8b	0.21b	1.74bc
67 (soybean)	7	90.1bc	0.79b	0.88b	0.22b	1.89b
LSD (p<0.05)		80.1	0.36	0.34	0.13	0.62

[x]Within each column, values sharing the same letter(s) are not significantly different at the p<0.05 according to LSD test

Table 2: Effect of shade on the growth and development of *C. dactylon*, at 84 days after planting (DAP)[x]

Shade treatments (%)	Tillers No. pot^{-1}	Leaf area dm^2 pot^{-1}	Leaf dry weight	Stem dry weight	Root dry weight	Rhizome dry weight	Total dry weight
			g pot^{-1}				
0	52.5a	61.51a	11.12a	15.16a	3.81a	0.25a	30.03a
42	26.0de	28.27e-g	3.30f	3.22ef	0.99fg	0.00c	7.5e-g
58	15.0fg	20.82g-I	3.03fg	2.56e-g	0.75g-I	0.00c	6.33f-h
77	8.0g	9.84j	1.10h	0.78g	0.26j	0.00c	2.14I
65 (maize)	11.0g	16.30ij	1.81gh	1.12fg	0.40ij	0.00c	3.34hi
67 (soybean)	11.5g	17.72h-j	2.65fg	1.23fg	0.53h-j	0.00c	4.41g-I
0→42[y]	29.0de	44.06bc	7.68b	5.81d	2.13bc	0.00c	15.51bc
0→58[y]	29.8c-e	39.62cd	5.23cd	3.59c	1.34ef	0.00c	10.16de
0→77[y]	24.8de	30.44d-f	4.09d-f	3.02ef	1.09e-g	0.00c	8.19ef
0→65 (maize)[y]	23.3ef	27.75e-g	3.37f	2.41e-g	0.97f-h	0.00c	6.77e-h
0→67 (soybean)[y]	15.5fg	27.13f-h	3.65ef	2.57e-g	0.90f-h	0.00c	7.12e-g
42→0[z]	44.0ab	44.19bc	5.93c	10.23b	2.08bc	0.08bc	18.29b
58→0[z]	41.8b	52.07ab	6.01c	9.83b	2.26bc	0.15ab	18.25b
77→0[z]	32.8bc	38.32cd	5.02c-e	6.99cd	1.49de	0.08bc	13.57cd
65 (maize)→0[z]	37.8bc	36.84c-e	5.91c	9.18b	2.41b	0.02c	17.52b
67 (soybean)→0[z]	46.0ab	42.33c	5.42cd	8.53bc	1.86cd	0.06bc	15.86bc
LSD (p<0.05)	8.7	9.62	1.49	2.18	0.45	0.12	3.63

Table 3: Effect of shade on the partitioning of biomass in *C. dactylon*, at 84 days after planting (DAP)[x]

Shade treatments ratio (%)	Leaf area (LAR)	Specific Leaf Area (SLA)	Leaf Weight Ratio (LWR)	Stem Weight Ratio (SWR)	Root Weight Ratio (RWR)
	(dm^2 g^{-1})		(g g^{-1})		
0	2.04g	5.54d	0.37de	0.50a	0.13a
42	3.83b-d	9.01a	0.43cd	0.43b	0.13a
58	3.35c-f	6.99a-d	0.48bc	0.40bc	0.12a
77	4.58ab	8.94a	0.51b	0.37b-d	0.12a
65 (maize)	4.97a	9.07a	0.55ab	0.33de	0.12a
67 (soybean)	4.05a-c	7.27a-d	0.58a	0.29e	0.13a
0→42y	2.84d-g	5.82cd	0.49bc	0.37b-d	0.14a
0→58 y	3.91a-d	7.78a-d	0.51ab	0.36cd	0.13a
0→77 y	3.65b-e	7.29a-d	0.50bc	0.37b-d	0.13a
0→65 (maize) y	4.03a-c	8.11a-c	0.50bc	0.36cd	0.12a
0→67 (soybean) y	3.74b-e	7.53a-d	0.51ab	0.36cd	0.14a
42→0 z	2.49fg	8.10a-c	0.32e	0.55a	0.12a
58→0 z	2.85d-g	8.66ab	0.33e	0.54a	0.13a
77→0 z	3.03c-g	8.08a-c	0.37de	0.51a	0.12a
65 (maize)→0 z	2.13g	6.30b-d	0.34e	0.52a	0.14a
67 (soybean)→0 z	2.68e-g	7.86a-d	0.34e	0.54a	0.12a
LSD (p<0.05)	0.99	2.50	0.07	0.07	0.04

[x]Within each column, values sharing the same letter(s) are not significantly difference at the p<0.05 according to LSD test
[y]Transferred from full light to 42, 58, 77, 65 (Maize) or 67% (Soybean) shade at 42 DAP
[z]Transferred from 42, 58, 77, 65 (Maize) or 67% (Soybean) shade to full light at 42 DAP

42 DAP significantly (p<0.05) decreased their growth when compared to that of plants that remained in full light for the full 84 days. There was little rhizome growth evident in the plants of any treatment. The only small amounts present being on plants starting in shade and transferring to full available light at 42 days or in full light for 84 days.

Shading which occurred early in the growth period had a less suppression effect on growth than later shading. For example at the final harvest, plants that were transferred from 58% shade to full light at day 42 after planting had 60% of the total dry weight of the plants in the continuous full light treatment, but plants transferred from full light to 58% shade at day 42 had only 33.5% as much. In addition to reducing growth, shading affected the partitioning of plant biomass (Table 3). The plants which received continuous shade or were given shade later in the growth period partitioned proportionally less

Table 4: Effect of shade on dry matter production, net assimilation rate and leaf area duration of *C. dactylon* from 42 to 84 days after planting (DAP)[x]

Shade treatments (%)	Dry Matter Production (DMP) (g)	Net Assimilation Rate (NAR) (mg dm^{-2} day^{-1})	Relative Growth Rate (RGR)(mg g^{-1} day^{-1})	Leaf Area Duration (LAD) (dm^2 days)
0	24.69a	14.2a	41d	1666.3a
42	6.10e	8.5b	40d	694.7e-g
58	5.11ef	9.8b	39d	515.1gh
77	1.06g	3.3c	16fg	311.1h
65 (maize)	1.59fg	3.9c	15fg	562.1f-h
67 (soybean)	2.52e-g	0.4c	20ef	540.2gh
0→42y	9.97d	7.3b	24e	1371.4ab
0→58y	4.57e-g	3.8c	14fg	1306.2bc
0→77y	2.56e-g	2.4c	9gh	1128.4b-d
0→65 (maize) y	1.12g	1.0c	4h	1075.9b-d
0→67 (soybean) y	1.45g	1.6c	6h	1050.7cd
42→0z	16.89b	17.3a	60ab	884.5ed
58→0z	17.03b	17.0a	65a	917.9de
77→0z	12.51cd	16.9a	60ab	691.9e-g
65 (maize)→0z	15.77bc	16.5a	54bc	866.4d-f
67 (soybean)→0z	13.98bc	14.8a	51c	881.4de
LSD ($p<0.05$)	3.63	3.0	8	304.7

[x]Within each column, values sharing the same letter(s) are not significantly difference at the $p<0.05$ according to LSD test
[y]Transferred from full light to 42, 58, 77, 65 (Maize) or 67% (Soybean) shade at 42 DAP
[z]Transferred from 42, 58, 77, 65 (Maize) or 67% (Soybean) shade to full light at 42 DAP

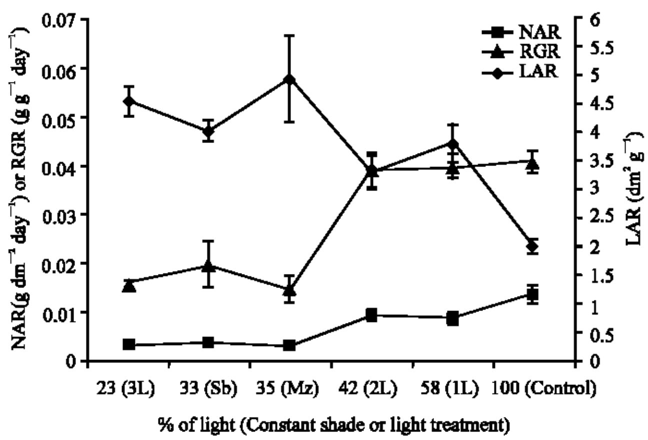

Fig. 1: Effect of continuous shading on RGR (g g^{-1} day^{-1}), NAR (g dm^2 day^{-1}) and LAR in dm^2 g^{-1} of *C. dactylon* 42 to 84 days after planting (± SE)

biomass into stems (SWR), but increased the partitioning of biomass into leaf (LWR). However there were no significant differences in partitioning of biomass into roots between shaded and full light plants. When plants were transferred from shade to full light they increased their SWR and decreased their LWR to values comparable to plants maintained continuously in the original full light treatment.

The shaded plants expanded larger amounts of leaf area per unit of leaf biomass as indicated by higher SLA values giving them larger LAR also. Transferring plants from full light to shade also slightly increased SLA and LAR in comparison to plants maintained at full light. While transferring plants from shade to full light slightly (not significantly) decreased LAR in comparison to plants maintained continuously in the original shade treatments to give them values which did not differ from plants maintained at full light. Leaf growth was clearly dynamically responsive to changes in shading.

Growth analysis: Generally all levels of continuous shading significantly ($p<0.05$) reduced DMP, NAR and LAD (Table 4). While the 77% shading resulted in 95% less DMP, this was caused by 80% less LAD and 75% smaller NAR. Plants transferred from shading treatments to full light at 42 days showed NAR's which were generally slightly larger (by 4 to 20%) than plants continuously in full light and increased their LAD compared to the continuously shaded plants so their final DMP was increased compared to the fully shaded treatments but not to as much (51 to 68%) as full light treatments. Plants shaded after 42 days in full light maintained larger LAD then continuously shaded plants but had similar or lower NAR values to them during

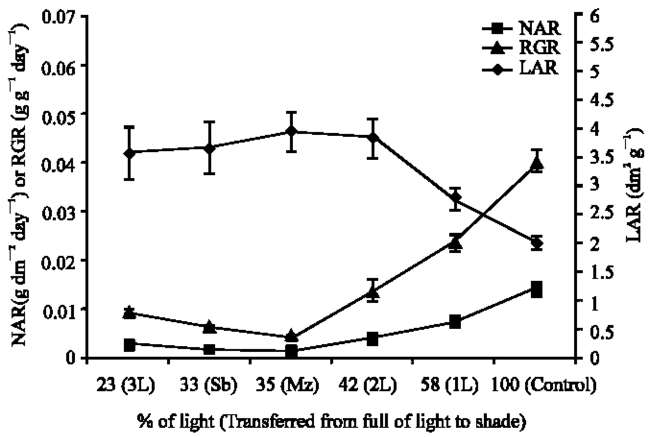

Fig. 2: Effect of shading at later growing stage of plants on RGR (g g^{-1} day^{-1}), NAR(g dm^{-2} day^{-1}) and LAR (dm^2 g^{-1}) of *C. dactylon* 42 to 84 days after planting (± SE)

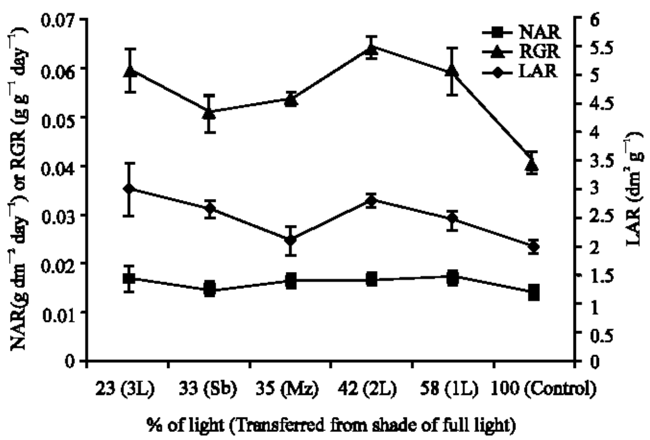

Fig. 3: Effect of shading at early growing stage of plants on RGR (g g^{-1} day^{-1}), NAR (g dm^{-2} day^{-1}) and LAR (dm^2 g^{-1}) of *C. dactylon* 42 to 84 days after planting (± SE)

the shaded period so they did not show better DMP than continuously shaded plants. The changes in Leaf Area Ratio (LAR) observed in response to shading are important because LAR is one of the two components of Relative Growth Rate (RGR) which is the product of Net Assimilation Rate (NAR) and LAR[11] and provides a useful measure of the capacity for light adaptation and shade tolerance at the whole plant level. The responses of RGR, NAR and LAR to shading in *C. dactylon* are shown in Fig. 1-3.

The results from Fig. 1 and 2 show that the relative changes in LAR and NAR in response to shading are such that the RGR of *C. dactylon* reaches a maximum at full light. So, *C. dactylon* would be classified as a shade intolerant plant. When plants were transferred from shade to full light they increased their SWR and decreased their LWR compared to plants maintained continuously in the original shade treatments. However result from Fig. 3 has shown that the relative changes in LAR and NAR in response to shading are different in plants of *C. dactylon* after plants have received shade treatments at an early stage. When this is followed by improved light exposure the growth of *C. dactylon* plants recovered quite well after being transferred to full light with an immediate increase in NAR and a relatively small values in LAR.

DISCUSSION

The result of this study demonstrate the considerably decreased growth of *C. dactylon* at all levels of shade treatment. This confirms the result reported by Schmidt and Blaser[15]. In their experiment, they found that total nitrogen content in *C. dactylon* stolons was increased in low light intensity. They believed this was because of nitrate reduction was limited and nitrogen utilisation inhibited which resulted in poor production of forage and underground parts of *C. dactylon*. Burton *et al.*[14] also reported that shade decreased forage yields, stand, root and rhizome yields, underground reserves and available carbohydrates of *C. dactylon*. Plants which received early shading grew fast after being transferred to full light 42 days after planting compared to continuous shading or later shading, but still did not catch up to the growth of plants under continuous full light. Patterson[19,20] found the same results with *Cyperus rotundus, Cyperus esculentus* and *Crotalaria spectabilis*.

Shading also partitioned proportionally less biomass into stems (SWR) but increased the partition of biomass into leaf (LWR). Leaf area per unit of leaf biomass also increased for shaded plants as indicated by higher SLA values which also increased the LAR. This is characteristic of the thinner, less dense leaves generally produced under shade condition[19], but have less palisade and sponge mesophyll volume per unit leaf area[21]. The increase in LAR under shading is an adaptation to low light intensity at the whole plant level because it reflects a greater allocation of plant biomass to photosynthetic tissue and a greater distribution of this tissue as light intercepting structure in the form of leaf area.

Leaf area production was less severely reduced by shading than was total biomass production. The SLA values in the experiment indicate that leaves of *C. dactylon* produced in continuous shade or shade later in the growth stage were thinner and less dense than those grown in full light and early shaded plants. The partitioning of the plant biomass into the leaf (LWR) was also increased from full light to shaded plants. The combination of an increase of SLA and LWR in response to shade also resulted in a great increase in LAR. This represents an adaptation of *C. dactylon* to shading at the whole plant level. Similar results have been previously documented[11,19] on itchgrass (*Rottboellia exaltata*) and *Cyperus* species, respectively. This characteristic could be an adaptation by *C. dactylon* to maintain its potential for high photosynthetic activity even in low light condition and can help to explain how this species is still able to compete effectively with tall and dense crops.

Results from the growth analysis showed that generally shading reduced DMP, NAR LAD and RGR but increased LAR. Semba[22] also found that reduced irradiance resulted in lower DMP, net photosynthetic rate, relative growth rate, NAR and larger LAR when spring barley (*Hordeum vulgare* L.) and five weed species were grown in a growth chamber at three light levels over a four-week period.

The overall responses of *C. dactylon* to shading indicates that the canopy shading typical of many row crops will reduce vegetative growth significantly[10].

However, limited reproductive development would still occur under canopy shade levels if the shading treatment is preceded by 42 days of full light. This type of shading sequence might be expected to occur in a row crop in which the weed usually emerges soon after the emergence of the crop.

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