

Shading and the growth and photosynthetic responses of *Ammannia coccinea*

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Summary

The effects of shade on the growth and CO₂ exchange rate (CER) of *Ammannia coccinea* Wild., a noxious weed in water-seeded rice, were determined under glasshouse conditions. Shade substantially reduced *A. coccinea* growth when imposed early and maintained throughout the growing season. However, plants transferred from full light to 18% or 50% sunlight 30 or 45 days after seeding had only slightly less dry weight than unshaded plants. Constant shade reduced growth severely (94%). In contrast, plants that were shaded for 45 days and then placed in full light largely recovered from the effects of shading by final harvest. The ability of *A. coccinea* to reduce the effects of shade appears related to increased partitioning to leaves, increased specific leaf area and decreased dark respiration rates. The ability of the weed to recover from shade appears related to its ability to greatly increase CER in new leaves in response to increased light. Plasticity in *A. coccinea* morphology and physiology appears to explain its persistence in California rice fields and suggests that management strategies that rely on shade alone may not improve control of this weed.

Keywords: *Ammannia coccinea*, light acclimatization, shade, CO₂ exchange rate, dark respiration.

Introduction

Ammannia auriculata Wild. (redstem) and *A. coccinea* Rottb. (purple ammannia) are obligate aquatic annual broad-leaved species found in many California rice (*Oryza sativa* L.) fields (Barrett & Seaman, 1980). *Ammannia* species reduce rice yields by shading the crop, interfering with harvest operations and increasing the lodging of rice (Bayer & Hill, 1992; Caton *et al.*, 1997). *Ammannia* spp. populations resistant to bensulfuron-methyl were detected within 4 years of the herbicide's introduction in California rice (Pappas-Fader *et al.*, 1994). Local rice growers have few herbicide alternatives to bensulfuron-methyl and the difficulty of registering new herbicides makes it likely that they will have even fewer herbicide options in the future (Hill & Hawkins, 1996). Additional tools must be developed if rice yields, which are among the highest

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per hectare in the world, are to be maintained. Improving the ability of the crop to suppress weed growth, either through the development of more competitive cultivars or by manipulating factors such as water management and the timing of herbicide applications, may be possible (Williams *et al.*, 1990; Gibson *et al.*, 2001). The successful implementation of these control practices depends on an improved understanding of how weeds respond to alterations in their environment.

Caton *et al.* (1997) reported a 97% reduction in *Ammannia* spp. dry weight when grown in competition with rice under glasshouse conditions and concluded that the reduction was due primarily to competition for light. While more competitive rice cultivars or management strategies that increase the crop's ability to shade the weed might be developed, Caton *et al.* (1997) noted that plasticity in *Ammannia* spp. growth (i.e. increased height and shoot/root partitioning) might allow the weed to escape shading by the crop. Shade-avoidant species (Lambers *et al.*, 1998) can limit the effects of reduced photosynthetically active photon flux density (PPFD) by increasing leaf area in proportion to total plant tissue (Patterson, 1979), by increasing photosynthetic rate per unit leaf area at low PPFD (Fischer *et al.*, 2000) and by decreasing energy consumption, i.e. dark respiration (Patterson, 1979; Regnier *et al.*, 1988). However, the role of these mechanisms in the response of *Ammannia* spp. to shade remains unknown. Caton *et al.* (1997) measured *Ammannia* spp. height and dry weight (DW) partitioning but did not determine the effect of PPFD on leaf morphology, rates of photosynthesis or dark respiration. Before cultural control methods that rely on shading *Ammannia* spp. can be developed, we need to gain a better understanding of how *Ammannia* spp. respond to shade. Also, knowledge of the responses of *Ammannia* spp. to shade will be useful to evaluate algorithms for ecophysiological modelling where light attenuation is a relevant component of competitive interactions between crops and weeds (Kropff & van Laar, 1993).

The objectives of the research reported here were to determine the ability of *A. coccinea*, the dominant *Ammannia* species in California rice (Graham, 1979), to tolerate prolonged shade and to recover from shade if subsequently exposed to greater PPFD. We were also interested in identifying changes in morphology and leaf physiology that might relate to *A. coccinea* growth in low light.

Materials and methods

Plant material and growing conditions

Experiments were conducted under glasshouse conditions at the University of California at Davis, CA in 1998 and 1999 to determine the response of *A. coccinea* to shade. Seed for both experiments was collected in 1997 from mature plants at the Rice Experiment Station near Biggs, CA. Seed was soaked for 48 h before hand-seeding into 20-cm diameter by 15-cm deep pots filled with Capay silty clay (fine, smectic, thermic Typic Haploxererts) soil. Pots were placed in basins, flooded and water level maintained at 5–10 cm above the soil surface throughout the experiment. Nitrogen, phosphorus and potassium were hand-incorporated into pots before flooding at rates of 168, 30 and 30 kg ha⁻¹ respectively. Pots were seeded on 20 June 1998 and 30 June 1999. Seedlings were thinned to one plant per pot 10 days after seeding (DAS). Mean daily temperatures in the glasshouse were typical of local climatic conditions (Statewide Integrated Pest Management Project, University of California, Davis; <http://www.ipm.ucdavis.edu>) and ranged between 16 and 32 °C in 1998 and between 16 and 30 °C in 1999. PPFD was measured

with a Decagon Sunfleck Ceptometer (Decagon Devices, Pullman WA, USA) at noon on 20 June 1998 and 30 June 1999. PPF in the glasshouse was $1300 \mu\text{mol m}^{-2} \text{s}^{-1}$ in 1998 and $1380 \text{ mol m}^{-2} \text{s}^{-1}$ in 1999. There was a 20% reduction in PPF in the glasshouse compared with outside the glasshouse.

Experimental design and sampling

A complete randomized design with one factor (PPF regime) and four replicates was used in 1998. Plants were grown continuously in full light (100%) or started that way and placed under black plastic mesh screens at 30 DAS. The screens reduced PPF to 50% and 18% of full sunlight (100 → 50, 100 → 18) according to measurements taken with the Sunfleck Ceptometer, but had no effect on measured red/far red ratios. In 1999, plants were placed under the screens at 45 DAS. Thirty and 45 DAS correspond to approximate dates of rice canopy closure. The experimental design was expanded in 1999 to include plants grown continuously at 18% or 50% sunlight (18, 50) and plants transferred from shade to full light at 45 DAS (18 → 100, 50 → 100). In both years, pots were randomized bi-weekly within shade treatments and spaced to avoid among-pot shading. Plants were harvested at 120 DAS in 1998 and at 45 and 110 DAS in 1999. Final harvests were conducted when shaded plants produced seed.

Plants were separated into leaves, stems, roots and seed and dried at 60 °C to a constant weight. Dry weight (DW) was measured at each harvest. Live roots were collected by washing the soil contents of each pot through a 0.1-mm² screen. The ratio of leaf DW to total DW (leaf weight ratio, LWR) was calculated at each harvest. Plant height was measured from the base of a plant to the tip of its longest leaf. Leaf area and specific leaf area (leaf area/leaf DW, SLA) were determined at 45 DAS in 1999. At the final harvest in 1999, main stem and branch DW were determined separately.

Data were analysed in both years with a single-factor analysis of variance (ANOVA). Means were separated by orthogonal contrasts at a significance level of 5%. Dry weight and leaf area data from both harvests in 1999 were log_e transformed to homogenize variances. The transformations were not sufficient for the first harvest in 1999; consequently, leaf and stem DW for the 50% light treatment were excluded from analysis. The 50 → 100 treatment for leaf and total DW was excluded from analysis of the final 1999 harvest for the same reason.

Gas exchange rates

The CO₂ exchange rate (CER) was determined in 1999 using an open, portable, infrared gas analyser for H₂O and CO₂ (LiCor LI-6400, LiCor, Lincoln, Nebraska, USA). A portion of leaf located at the third node from the tip of the plant was enclosed in a steady-state gas-exchange cuvette. Leaf temperature was maintained at 32 °C, the maximum glasshouse temperature in 1999. CO₂ partial pressure was maintained at a constant 400 $\mu\text{mol mol}^{-1}$ level within the cuvette. No supplementary lighting was provided; plants were exposed to approximately 15 h of sunlight per day. A red + blue LED light source (LiCor 6400-02B) provided 0, 50, 100, 200, 400, 800 and 1600 $\text{m}^{-2} \text{s}^{-1}$ PPF for measurements of CER. CER was measured at 76 DAS on plants in the 100, 50, 18, 18 → 100 and 50 → 100 treatments. This date was selected to give plants transferred from shade to sunlight adequate time to acclimatize. Leaves measured in the 18 → 100 and 50 → 100 treatments were formed after plants were placed in full light. Leaves received each light treatment for a minimum of 3 min and a maximum of 5 min. Readings were

logged when the coefficient of variation for CER was 1%. Plants remained in full or reduced light while CER was measured and PPFD was increased in a step-wise fashion starting at PPFD = 0 to avoid reductions in quantum yield due to inhibition or damage from higher PPFD (Lambers *et al.*, 1998). The following rectangular hyperbolic regression model was fitted to CER data:

$$Y = a + (bX)/(1 + (bX/c)), \quad (1)$$

where Y is the net photosynthetic rate, X is PPFD, a is the dark respiration rate (PPFD = 0), b is the slope corresponding to the quantum yield and c is the photosynthetic rate at maximum saturating light flux (Loomis & Connor, 1992; Fischer *et al.*, 2000).

Results

Growth response

Reducing sunlight to 50% at 30 DAS in 1998 had relatively little effect on final DW production (Table 1). There were no differences ($P > 0.05$) in total DW or seed DW between plants in the 100 → 50 treatment and those grown continuously at 100% sunlight. Plants in the 100 → 18 treatment produced significantly less seed and total DW than plants in the 100 → 50 or full light treatments. However, seed DW in the 100 → 18 treatment was still appreciable, amounting to 54% of that from plants grown continuously at 100% sunlight. Shaded plants increased their leaf DW, LWR and plant height in response to shade (Table 1).

At 45 DAS in 1999, both shade treatments produced significantly less root and total DW than plants in the 100% sunlight treatment (Table 2). Plants grown at 18% sunlight had much lower leaf and combined branch and stem DW than plants grown in full sunlight (Table 2). Shaded plants were shorter at 45 DAS, although not at maturity (Table 3), and produced less leaf area than plants in the 100% sunlight treatment. Specific leaf area increased as PPFD decreased.

At the final harvest in 1999 (110 DAS), the only treatments that resulted in large reductions in seed and total DW relative to non-shaded plants were the continuous shade treatments (Table 3). Plants grown continuously in shade had significantly ($P < 0.05$) less leaf, stem, branch, seed and total DW than plants grown in the other treatments. Plants grown at 18% and 50% sunlight produced only 6% and 54% of the seed DW of plants grown at 100% sunlight respectively. Plants shaded for 45 days and then placed in full sunlight showed relatively small reductions in seed and total DW compared with plants grown continually in full sunlight. Plants in the

Table 1 Response of *A. coccinea* to shade regime at 120 days after seeding in 1998

Shade regime ¹	Leaf DW (g)	Branch and stem DW (g)	Root DW (g)	Seed DW (g)	Total DW (g)	Leaf weight ratio ²	Height (cm)
100	10.4	18.8	13.8	42.3	98.7	0.11	92.5
100 → 50	17.7	22.2	10.8	37.3	100.6	0.17	122.5
100 → 18	14.9	20.0	7.8	22.7	65.4	0.23	126.8
Pooled SE	0.77	1.81	0.93	2.31	1.64	0.007	2.56

¹ Plants were grown in 100% sunlight continuously or transferred to 50% or 18% sunlight at 30 days after seeding.

² Leaf weight ratio = leaf DW/total DW.

Table 2 Response of *A. coccinea* to shade regime in 1999

Shade regime ¹	Leaf DW ² (g)	Branch and stem DW ² (g)	Root DW ² (g)	Total DW ² (g)	Leaf weight ratio ³	Height (cm)	Leaf area ² (mm ²)	Specific leaf area (mm ² g ⁻¹)
100	3.8 (1.3)	3.3 (1.1)	5.6 (1.7)	12.7 (2.5)	0.31	61	1244 (7.1)	339
50	0.7 ⁴	0.4 ⁴	0.7 (-0.5)	1.8 (0.5)	0.39	41	321 (5.8)	479
18	0.2 (-1.6)	0.2 (-1.6)	0.2 (-1.6)	0.7 (0.5)	0.33	28	123 (4.8)	632
Pooled SE	(0.13)	(0.19)	(0.13)	(0.11)	0.016	0.09	(0.08)	26.8

¹ Plants were grown in 100% sunlight continuously or transferred to 50% or 18% sunlight at 30 days after seeding.

² Data were log_e transformed to homogenize variances. Parentheses enclose the transformed means and pooled SE.

³ Leaf weight ratio = leaf DW/total DW.

⁴ Data not included in analysis of variance. See text for explanation.

Table 3 Response of *A. coccinea* to shade regime at 110 days after seeding in 1999

Shade regime ¹	Leaf DW ² (g)	Stem DW ² (g)	Branch DW ² (g)	Root DW ² (g)	Seed DW (g)	Total DW ² (g)	Height (cm)	Leaf weight ratio ³
100	16.4 (2.8)	9.9 (2.3)	26.0 (3.2)	18.0 (2.9)	32.0	102.3 (4.6)	119	0.16
50	10.8 (2.4)	6.3 (1.8)	8.8 (2.1)	10.3 (2.3)	17.3	53.5 (4.0)	130	0.20
18	6.5 (1.9)	3.9 (1.4)	2.7 (1.0)	3.1 (1.1)	1.9	18.0 (2.9)	125	0.36
100 → 50	18.6 (2.9)	8.3 (2.1)	22.2 (3.1)	12.7 (2.5)	25.1	86.8 (4.5)	133	0.21
100 → 18	17.6 (2.9)	8.9 (2.2)	18.5 (2.9)	9.6 (2.3)	23.1	77.6 (4.4)	133	0.23
50 → 100	20.0 ⁴	8.5 (2.0)	25.2 (3.1)	16.4 (2.8)	30.4	100.4 ⁴	116	0.20
18 → 100	14.7 (2.7)	7.5 (2.1)	16.3 (2.8)	11.1 (2.4)	24.7	74.3 (4.3)	109	0.20
Pooled SE	(0.03)	(0.03)	(0.05)	(0.08)	0.64	(0.03)	0.80	0.004

¹ Plants were grown continuously in full or reduced light. Reciprocal transplants were conducted at 45 days after seeding.

² Data were log_e transformed to homogenize variances. Parentheses enclose the transformed means and pooled SE.

³ Leaf weight ratio = leaf DW/total DW.

⁴ Data not included in analysis of variance. See text for explanation.

18 → 100 treatment produced 77% of the seed DW of plants grown continuously at 100% sunlight and there was no difference in seed DW between the 50 → 100 and 100% sunlight treatments. Plants shaded at 45 DAS also had relatively small reductions in dry weight relative to unshaded plants.

In 1999, plants had a similar response to shade as plants in 1998. Leaf weight ratio increased in all shade treatments compared with plants grown continuously in full sunlight (Table 3). Plants grown continuously at 18% sunlight allocated more than twice as much dry weight to leaves as plants grown in full sunlight (36% vs. 16%). Plants shaded at 45 DAS were taller than plants grown continuously in full light whereas plants transferred from shade to full light were no taller than plants grown continuously in full light.

Gas exchange

The rectangular hyperbolic model provided an excellent fit for the data (Table 4). CER at low PPFD was greater for plants grown continuously in full light than for continuously shaded plants, as indicated by the slopes (*b*) of the regression models in Table 4. As PPFD increased,

Table 4 Parameters of the rectangular hyperbolic model¹ fitted to CER data of *A. coccinea* grown at various levels of sunlight under greenhouse conditions and exposed to six levels of PPFD at 60 DAS in 1999

Parameter	Shade regime				
	100	50	18	50 → 100	18 → 100
<i>a</i>	-3.60 (0.40)	-2.45 (0.34)	-1.59 (0.19)	-2.86 (0.61)	-3.93 (0.33)
<i>b</i>	0.17 (0.01)	0.12 (0.01)	0.11 (0.01)	0.11 (0.02)	0.13 (0.01)
<i>c</i>	19.59 (0.51)	15.77 (0.44)	10.85 (0.24)	22.03 (0.89)	27.79 (0.50)
Residual mean square	0.53	0.37	0.12	1.34	0.40

¹ $Y = a + (bX)/(1 + (bX/c))$, where *Y* is the net photosynthetic rate, *X* is PPFD, *a* is the dark respiration rate (PPFD = 0), *b* is the slope corresponding to the quantum yield and *c* is the photosynthetic rate at maximum saturating light flux.

Plants were grown continuously in full or reduced light. Reciprocal transplants were conducted at 45 days after seeding.

Figures in parentheses are standard errors of parameter values.

CER was higher for plants grown in full light or transferred from shade to full light than for plants grown in continuous shade. Plants in the 18 → 100 treatment had greater CER at saturating PPFD (*c*) than unshaded plants or plants that remained shaded throughout the experiment (Table 4). CER at saturating PPFD for plants grown at 18% sunlight was only 39% of plants in the 18 → 100 treatment.

Plants grown in constant shade had lower dark respiration rates (*a*) per unit leaf area than plants grown continuously in full sunlight or transferred into full light at 45 DAS (Table 4). At 18% sunlight, the dark respiration rate was only 44% of plants grown at 100% sunlight. Plants in the 18 → 100 treatment had dark respiration rates as high as plants grown continuously in full light.

Discussion

Our results support work by Caton *et al.* (1997) which indicated that plasticity in the growth response of *Ammannia* spp. to light might explain the persistence of the weeds in California rice fields. *Ammannia coccinea* lessens the effects of shade by partitioning more DW to leaves, decreasing partitioning to branch DW and/or by increasing its specific leaf area. Reduced leaf respiration rates also appear to be part of the weed's acclimatization to shade. This strategy helps *A. coccinea* to survive shading and produce enough carbohydrate to increase height (Caton *et al.*, 1997) until the weed can overtop rice. Also, the ability of *A. coccinea* to increase CER and DW production when subsequently exposed to higher rates of PPFD allows the weed to recover from shading. The ability to withstand shading and recover from it makes control of *A. coccinea* through light manipulation alone seem unlikely.

Holt (1995) also concluded that plasticity in the response of weeds to shade might allow growth and seed production even under very low PPFD, thus making control by light manipulation difficult. *Ammannia coccinea* responded to shading stress with a combination of morphological and physiological changes that are typical of many weeds and crops, i.e. with increased allocation to leaves, greater SLA and lower respiration rates (Patterson, 1995). For example, *Abutilon theophrasti* Medic (velvetleaf) responded to shading by decreasing dark respiration, increasing chlorophyll content per unit leaf volume and by increasing leaf area ratio (Patterson *et al.*, 1978). *Rottboellia cochinchinensis* (Lour.) W. D. Clayton (itchgrass) decreased

its CER and growth rate substantially in response to shade, but those effects were lessened by an increase in leaf area ratio (Patterson, 1979). The same author also suggested that increased plant height at the intermediate light level might allow *R. cochinchinensis* to escape shading by the crop. Stoller & Myers (1989) reported that *A. theophrasti*, *Chenopodium album* L. (common lambsquarters), *Solanum ptycanthum* Dun. (eastern black nightshade) and *Amaranthus albus* L. (tumble pigweed) responded to shade with decreased leaf respiration rates and increased leaf area ratios. The authors suggested that *S. ptycanthum* was the most shade-tolerant of the weeds studied because it had the lowest respiration rate and greatest leaf area ratio.

Ammannia coccinea also followed a pattern reported for several weeds by resuming high rates of photosynthesis and growth when initially shaded and then exposed to higher light levels (Patterson, 1979; Stoller & Myers, 1989; Ampong-Nyarko *et al.*, 1992; Holt, 1995). Plants grown continuously in full light had greater CER at low PPFD. Other studies have reported higher CER at low PPFD for shaded plants than for unshaded plants (Regnier *et al.*, 1988; Stoller & Myers, 1989; Fischer *et al.*, 2000). However, this response is not always detectable on a per unit leaf area basis. Regnier *et al.* (1988) found similar CER at low PPFD between shaded and unshaded plants when CER was measured on a per unit leaf area basis, but rates were significantly different between treatments when CER was measured on a per unit leaf volume basis. The authors suggested that, in thinner leaves associated with shaded plants, chloroplasts were distributed to reduce mutual shading. Shaded *A. coccinea* leaves in our study were thinner than non-shaded plants, so it is possible that we would have reached similar conclusions had we calculated CER on a per unit leaf volume basis.

Our results indicate that, while the growth and seed production of *A. coccinea* can be greatly reduced by shade, reductions in light must occur early in the season and be of sufficient magnitude to prevent *A. coccinea* from overtopping the crop. In our experiments, shade imposed at 30 or 45 DAS, which coincides with crop canopy closure in the field, had relatively little effect (reductions of 34% or less) on seed and total DW. Reductions in seed and total DW were much greater (94% and 82% respectively) when *A. coccinea* was grown continually at 18% sunlight. However, *A. coccinea* plants that germinated with the crop would be tall enough by canopy closure to avoid such a large reduction in PPFD (K D Gibson, unpubl. obs.). Furthermore, plants that were initially shaded and subsequently exposed to higher PPFD responded with photosynthetic rates and DW production similar to plants grown continuously in full light. When grown at 18% sunlight in our experiment, the weed (125 cm in height) would easily have overtopped M-202, the rice cultivar most commonly grown in California, which typically achieves a maximum height of 95–100 cm. This indicates that, under field conditions, the weed would not remain shaded by the crop throughout the season.

In our study, although PPFD was reduced by the shade canopies, the ratio of red to far-red light was unaffected. Changes in light quality can affect the development of shaded plants through phytochrome mediated processes (Ballare *et al.*, 1990) and some plants can alter growth to avoid shading in response to changes in the ratio of far-red to red light (Casal & Smith, 1989; Holt, 1995). *Ammannia coccinea* typically emerges from the water as the crop canopy is closing and may have morphological responses to light quality that increase its ability to escape shading. However, the major morphological and physiological responses discussed in this paper (SLA, leaf weight ratio, and CER) are more influenced by total PPFD than by light quality (Smith *et al.*, 1993; Lambers *et al.*, 1998). The effect of changes in the ratio of far-red to red light on the growth of *A. coccinea* may play a role in its response to shade under field conditions, but they are not sufficient alone to explain the ability of the species to persist in rice canopies.

Our study indicates that plasticity in morphological and physiological traits allows *A. coccinea* to acclimatize to and recover from reduced PPFD. Its growth can be substantially reduced by shade alone but only if the reduction is large, occurs early in the season and is constant. Multiple stresses such as reduced fertility, competition by the crop for both light and nutrients, delayed emergence relative to the crop and deep water (Williams *et al.*, 1990) may be necessary to achieve a cumulative improvement in control of *A. coccinea*.

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