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# Compensatory responses of late watergrass (*Echinochloa phyllopogon*) and rice to resource limitations

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The development of optimal weed management strategies that rely, in part, on crop interference will require an understanding of how weeds compensate for limitations in above- and belowground resources. Trade-offs in the leaf morphology and biomass partitioning of rice and late watergrass were investigated under glasshouse conditions in 1999 and 2000. Both species responded to shade with increased height, reduced biomass, greater partitioning of biomass to leaves, and greater leaf area ratios. At the lowest light level (18% sunlight), plants of both species showed little response to nitrogen (N). However, height, tillers, biomass, and leaf area increased for plants grown at 50% and full sunlight as N increased from 0 to 224 kg N ha<sup>-1</sup>. Late watergrass exhibited more plasticity in specific leaf area and root weight ratio than rice in response to shade. This plasticity contributed to the ability of late watergrass to maintain a higher percent of its tillers and total dry weight than rice when sunlight was reduced by 50%. These results support the hypothesis that except at low light levels, limited N further reduces the growth of shaded late watergrass plants. Thus, weed management strategies that limit the plasticity of late watergrass by manipulating light and N availability are likely to be more effective than strategies that rely on manipulating a single resource.

**Nomenclature:** Late watergrass, *Echinochloa phyllopogon* (Stapf) Koss ECHPH; rice, *Oryza sativa* L.

**Key words:** Biomass allocation, nitrogen, phenotypic plasticity, plant morphology, shade.

Late watergrass is one of the most economically important weeds in water-seeded rice (Bayer and Hill 1992; Yamasue et al. 1997). Late watergrass germinates and grows well under flooding and closely mimics crop development (Yamasue 2001). Resistance to four of five herbicides available for use in California rice has developed in late watergrass populations (Fischer et al. 2000a, 2000b). In addition to anaerobic germination, mimicry, and herbicide resistance, late watergrass may have morphological and physiological adaptations that allow the weed to reduce the effects of competition from the crop. Yamasue et al. (1997) reported that late watergrass was able to adjust its height to place leaves above the rice canopy irrespective of crop height. Gibson and Fischer (2001) found that early watergrass [*Echinochloa oryzoides* (Ard.) Fritsch], a morphologically similar species widespread in California rice, reduced the effects of shading by altering biomass partitioning, leaf morphology, and leaf physiology. The use of more competitive cultivars has been proposed as a tool to improve weed control in water-seeded rice (Dingkuhn et al. 1999; Fischer et al. 1997, 2001; Garrity et al. 1992; Gibson et al. 2001). However, Gibson et al. (2002) speculated that even accelerated rates of canopy closure associated with more competitive cultivars might prove insufficient to overcome the growth plasticity demonstrated by watergrass species.

Although shade alone may not provide control of watergrass species, it might be of value if used in combination with other management tools. Gibson and Fischer (2001) reported that early watergrass compensated for shade, in part, by increasing biomass partitioning to leaves at the expense of roots, a response typical of weeds (Patterson 1995).

The authors speculated that at lower N fertility, watergrass species might be constrained from partitioning biomass to leaves, thus limiting the ability of these species to tolerate shade. Researchers have examined the effect of N and light separately but have rarely studied the effect of multiple resource limitations on rice and weeds (Ampong-Nyarko and De Datta 1993a, 1993b; Ampong-Nyarko et al. 1992; Gibson and Fischer 2001; Makino et al. 1997). We are unaware of any research conducted on the response of *Echinochloa* species in temperate water-seeded rice to multiple resource limitations. The primary objective of our experiments was to determine the effect of reduced light and N on the morphological plasticity of late watergrass and rice.

## Materials and Methods

Glasshouse experiments were conducted at the Rice Experiment Station in Biggs, CA, in 1999 and at the University of California, Davis, CA, in 2000 to determine the response of late watergrass and a medium-grain semidwarf rice cultivar (M-202) to shade and N fertilizer. Late watergrass seed for both experiments were collected from mature plants at the Rice Experiment Station in 1998 and 1999.

## Plant Culture

Seed of both species were soaked for 48 h before being hand seeded into 20-cm-diam by 15-cm-deep pots filled with Yolo clay loam soil (fine-silty, mixed, nonacid, thermic Typic Xerorthents, 1.7% organic matter). Pots were placed in basins and flooded, and the water level was maintained

at 5 cm above the soil surface throughout the experiment. N was hand incorporated as ammonium sulfate into pots before flooding at 0, 42, 84, 168, and 224 kg ha<sup>-1</sup> based on the surface area of the pot. The penultimate rate is typical of N fertilizer rates in California rice production. Phosphorus and potassium were incorporated at a rate of 30 kg ha<sup>-1</sup> each. Pots were seeded on August 2, 1999, or on June 22, 2000, and thinned to 1 plant pot<sup>-1</sup> 10 d after seeding (DAS). Average minimum and maximum daily temperatures in the glasshouses were 24 and 35 C in 1999 and 16 and 33 C in 2000, respectively, and were typical of local climatic conditions (Statewide Integrated Pest Management Project, University of California, Davis; <http://www.ipm.ucdavis.edu>). Photosynthetically active photon flux density (PPFD) was measured at the start of each experiment with a linear ceptometer.<sup>1</sup> The glasshouses intercepted approximately 10% of sunlight at noon. Average daily PPFD in the glasshouses, calculated from local weather station records (Statewide Integrated Pest Management Project, University of California, Davis; <http://www.ipm.ucdavis.edu>), was 1,044  $\mu\text{mol m}^{-2} \text{s}^{-1}$  in 1999 and 1,320  $\mu\text{mol m}^{-2} \text{s}^{-1}$  in 2000.

## Experimental Design

The split-split-plot experiment with four replicates was conducted with light treatments as the main plots, species as subplots, and N as sub-subplots. Plants were grown continuously in full sunlight (100%) or started that way and placed under black plastic mesh screens (Gibson and Fischer 2001) 21 DAS, which coincided with the five- to six-leaf stage of rice. The shade screens reduced PPFD to 50 or 18% of full sunlight. Light quality was measured with a Li-Cor 1800 Portable Spectoradiometer; light under the shade screens was not enriched in either red or far-red wavelengths. Plants were randomized biweekly and spaced to avoid shading from neighbors.

## Plant Growth Analysis

Plant height was measured from the base of each plant to the tip of its longest leaf, and plants were clipped at the soil surface 56 DAS in 1999 and 2000. Plants were harvested when rice grown in full light reached panicle initiation, approximately  $R_0$  to  $R_2$ , according to the rice development system proposed by Counce et al. (2000). Shoots were separated into leaves and stems. Roots were separated from the soil by rinsing the contents of each pot over a 1.18-mm screen. Leaf area, number of tillers, and dry weights (DWs) (60 C oven dried) of leaves, stems, and roots were measured. The following ratios were calculated: leaf weight ratio (LWR) or the amount of leaf DW per unit plant DW; root weight ratio (RWR) or the amount of root DW per unit plant DW; specific leaf area (SLA) or the amount of leaf area per unit leaf DW; and leaf area ratio (LAR) or the amount of leaf area per unit plant DW. LAR measures a plant's ability to use dry matter for leaf area development. LWR and RWR are indicators of dry matter allocation to leaves and roots, respectively. The coefficient of variation, calculated as  $100 \times (\text{standard deviation of the treatment means} / \text{grand mean of the treatment means})$  (Schlichting 1986), was used to estimate plasticity in leaf morphology and biomass partitioning exhibited in response to light and N for each species (Ryser and Eek 2000).

## Data Analysis

Data were analyzed in both years with a split-split-plot analysis of variance to test for main effects and interactions. Linear and quadratic regression was used to determine the effect of N fertilizer rate on plant growth variables. DW, leaf area, SLA, and LAR data were  $\log_e$  transformed and partitioning ratios (LWR and RWR) were angular transformed (arcsine square root) when necessary to homogenize variances. Untransformed data were used for presentation.

## Results and Discussion

### Biomass

There were interactions ( $P < 0.05$ ) in both years between species and light treatments and between light and N treatments for most biomass parameters. Therefore, the relationship between N and biomass was examined separately for each species and light treatment. In general, late watergrass and rice plants grown at 18% sunlight had lower leaf, stem, root, and total DW than plants grown at higher light levels and were only slightly affected by N (Figures 1–4). However, late watergrass and rice plants grown at 50 and 100% sunlight had a linear or quadratic response to N in both years (Figures 1–4), with the exception of rice root DW at 50% sunlight in 1999 (Figure 3). Consequently, differences in biomass between plants grown at 18% light and those grown at 50 and 100% sunlight typically increased as N rates increased (Figures 1–4). Both species largely conserved leaf DW in 1999 and 2000 when light was reduced from 100 to 50% (Figure 1). Stem, root, and total DW were lower for plants of both species grown in 50% sunlight than for plants grown in full sunlight (Figures 2–4), and differences were greater in 2000 than in 1999. The total DW of rice plants grown at 50% sunlight and the highest N rate were 56 and 40% of plants grown in full light and the highest N rate in 1999 and 2000, respectively. In contrast, late watergrass total DW for the same treatments were 77 and 58% in 1999 and 2000, respectively. Average daily temperatures were greater in 1999 than in 2000 and may have contributed to greater biomass production in 1999 than in 2000.

### Leaf Morphology

Leaf area increased linearly with N in both years for both species at 50 and 100% sunlight (Figure 5). Leaf area did not decrease in proportion to reductions in light; both species maintained or increased leaf area when sunlight was reduced by 50% (Figure 5). Rice leaf area was lower for plants grown at 18% sunlight than for plants grown at greater levels of light. However, late watergrass plants grown at 18% sunlight produced leaf areas similar to those grown at full sunlight at all but the highest N rate (Figure 5).

There were interactions between light and species treatments for SLA in both years (Table 1). The SLA of late watergrass more than doubled as light decreased from full to 18% sunlight, but differences among light treatments were not detected for rice (Table 1). N did not affect SLA in either year.

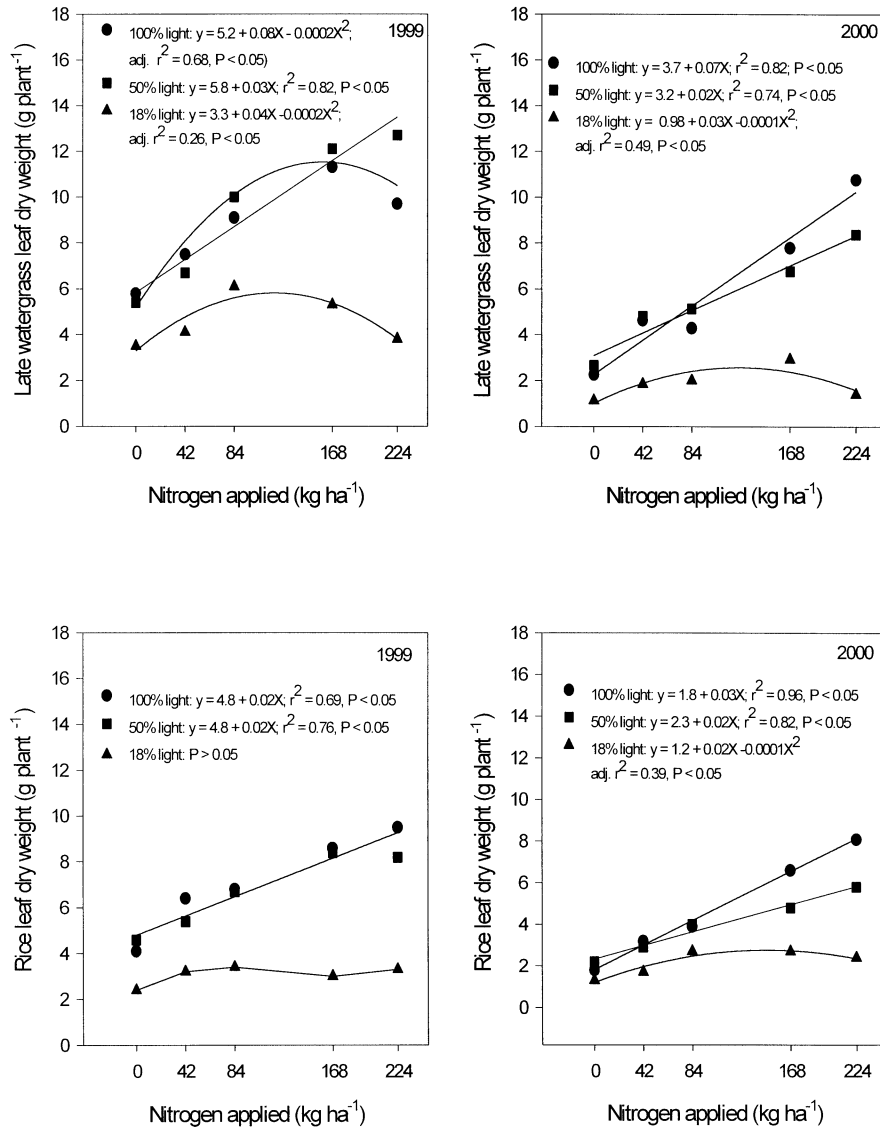


FIGURE 1. Response of rice and late watergrass leaf dry weight to nitrogen fertilizer rates when grown continuously in full sunlight or transferred to 50 or 18% sunlight at 21 d after seeding in 1999 and 2000.

### Biomass Partitioning

LAR increased and RWR decreased for both species as light decreased (Table 1). However, LAR increased fivefold or more for late watergrass compared with a two- to threefold increase for rice (Table 1). Similarly, late watergrass RWR was reduced more by shade than rice RWR (Table 1). Regression analysis revealed no relationship between LAR and N for either species. RWR decreased with increasing N for late watergrass plants grown in full light in 1999 and 2000 ( $Y = 0.48 - 0.007X$ ,  $r^2 = 0.21$ ,  $P < 0.05$ , in 1999; and  $Y = 0.64 - 0.0008X$ ,  $r^2 = 0.36$ ,  $P < 0.01$ , in 2000). RWR also decreased linearly with N for late watergrass plants grown in 18% light in 1999 ( $Y = 0.28 - 0.0005X$ ,  $r^2 = 0.31$ ,  $P < 0.01$ ). No relationship was detected between RWR and N for rice in either year. LWR increased for both species as light decreased (Table 2). There were no detectable species by light interactions, and differences in LWR between species were detected only in 1999 (LWR was  $0.31 \pm 0.014$  and  $0.28 \pm 0.015$  for rice and late watergrass, respectively). There were no detectable ( $P > 0.05$ ) differ-

ences in LWR among N levels in either year. Increased partitioning to late watergrass roots at lower N levels should have been accompanied by reduced partitioning to leaves or stems. Although the relationship was not statistically significant, the proportion of late watergrass biomass partitioned to stems appeared to decrease as RWR increased (data not shown). Additional work is needed to clarify this issue.

### Height and Tillers

Both species increased their height in response to shade (Figure 6). Whereas the height of rice and late watergrass plants grown at 18% light did not increase with N in either year, the height of plants grown at higher light levels was affected by N (Figure 6). Late watergrass plants in both years and rice plants in 2000 increased linearly with N when grown in full sunlight. Rice plants grown at 50% sunlight also increased linearly with N in both years (Figure 6). Consequently, differences in height between plants grown in 18% light and plants grown at higher light levels tended to decrease as the N fertilizer rate increased.

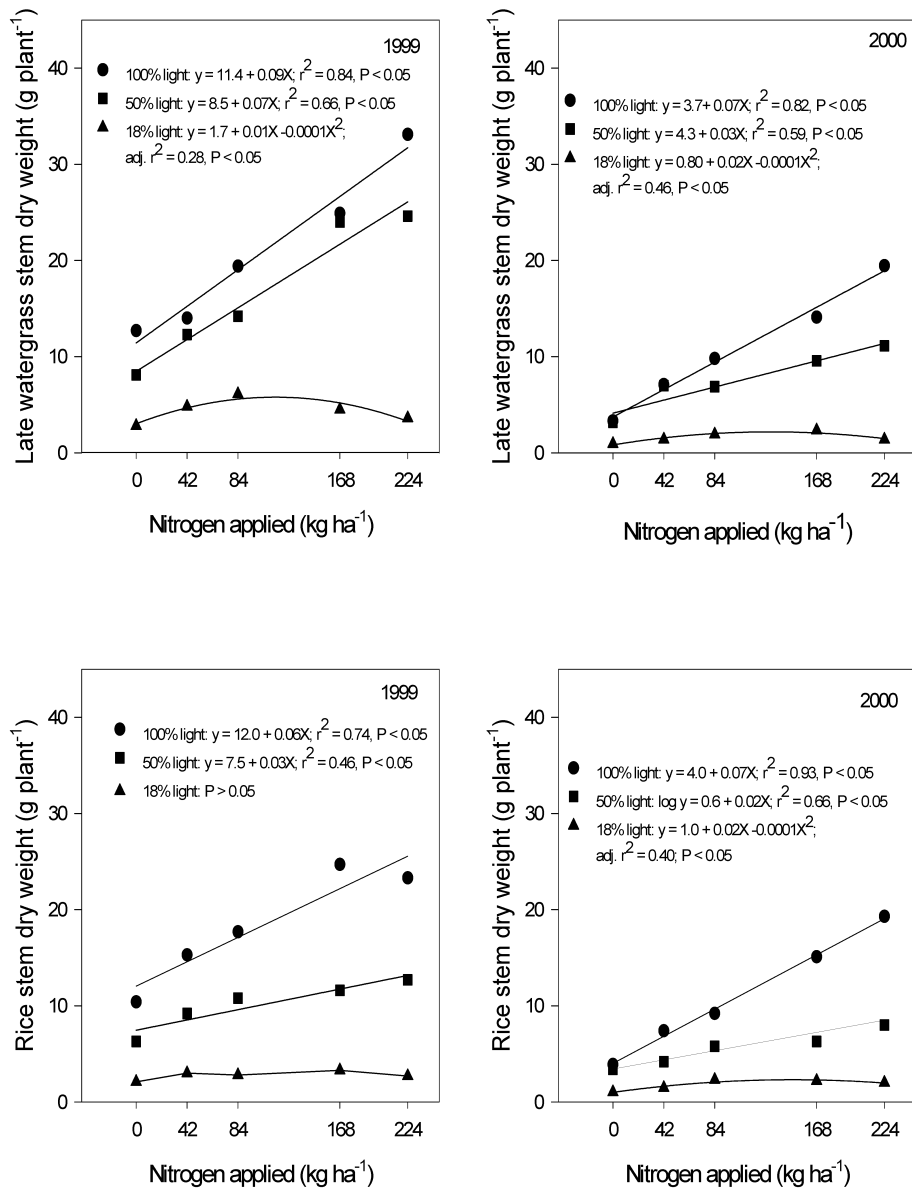


FIGURE 2. Response of rice and late watergrass stem dry weight to nitrogen fertilizer rates when grown continuously in full sunlight or transferred to 50 or 18% sunlight at 21 d after seeding in 1999 and 2000.

At full and intermediate light levels, the number of tillers per plant increased linearly with N for both species (Figure 7). Response to N at the lowest light level was minimal for both species, although a quadratic relationship between N and tiller production was detected at the lowest light level for rice (Figure 7). The number of tillers for late watergrass grown at the intermediate light level and high N were 78 and 91% of plants grown in full light in 1999 and 2000, respectively. The number of tillers for rice grown at the intermediate light level and the highest N level were 46 and 82% of plants grown in full light in 1999 and 2000, respectively. However, the smaller reduction in rice tillers in 2000 may not accurately represent the effect of a 50% reduction in sunlight on rice growth. Rice plants grown in 2000 at 50% sunlight and the highest N rate produced only 42% of the stem DW of plants grown in full light and the highest N rate (Figure 2), indicating that shading had a strong negative effect on rice tiller weight in 2000.

## Plasticity

Late watergrass exhibited more plasticity in SLA, LAR, and RWR in response to light treatments than rice (Table 3). Interactions between species and light treatments were not detected for LWR, indicating that rice and late watergrass exhibited similar levels of plasticity in partitioning biomass to leaves in response to shade. There were no species by N interactions for SLA, LAR, LWR, or RWR in either year. However, late watergrass RWR decreased with increasing N at 100 and 18% sunlight in 1999 and at 18% sunlight in 2000. At each of these light levels, late watergrass had greater plasticity in RWR than rice (data not shown).

Plants are phenotypically plastic and can alter their morphology and physiology to improve the acquisition of a resource when that resource limits growth (Gibson and Fischer 2001; Holt 1995; Patterson 1995; Ryser and Eek 2000). Increased partitioning of biomass to leaves at the expense of

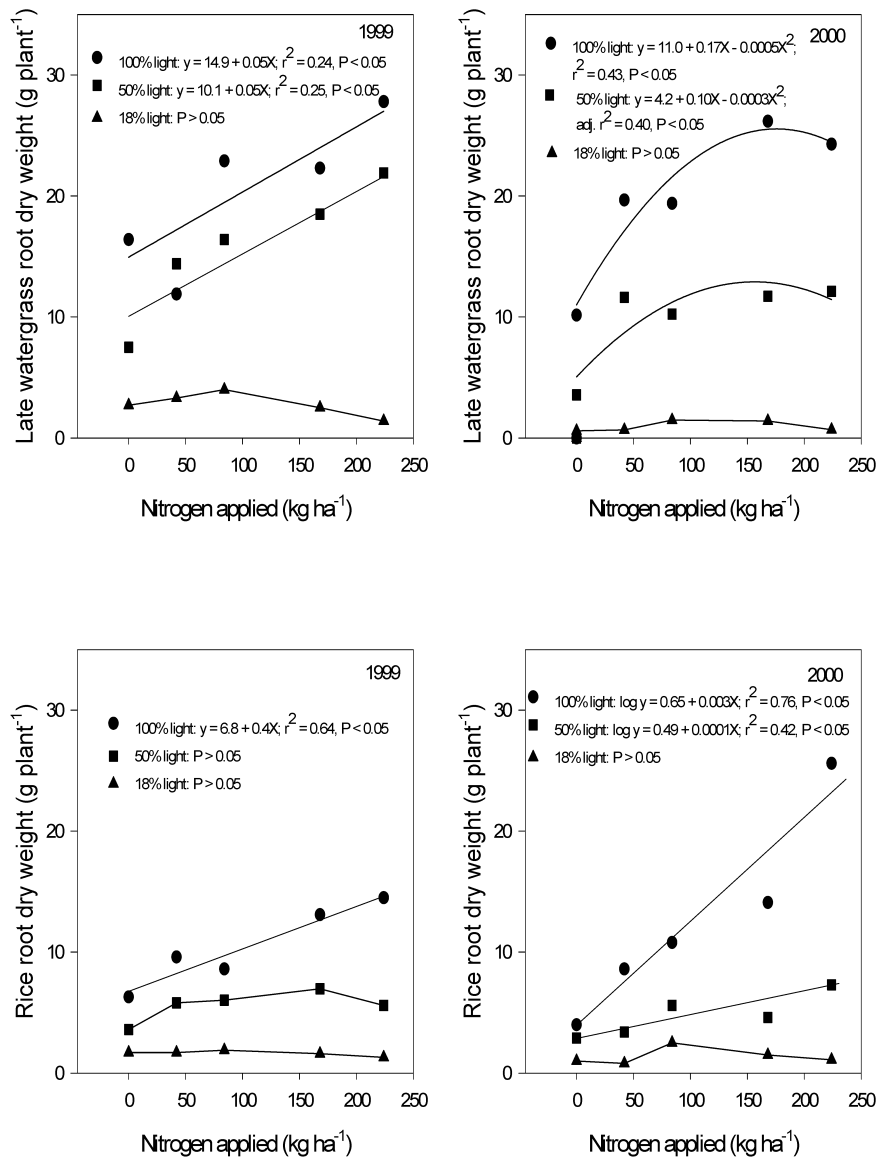


FIGURE 3. Response of rice and late watergrass root dry weight to nitrogen fertilizer rates when grown continuously in full sunlight or transferred to 50 or 18% sunlight at 21 d after seeding in 1999 and 2000.

roots is a common response of plants to shade and, in addition to changes in leaf morphology and physiology, can reduce the effects of shade on plant growth (Meziane and Shipley 1999; Patterson 1995; Regnier et al. 1988). Similarly, increased partitioning to roots is a common compensatory response of plants to low N availability (Meziane and Shipley 1999; Reynolds and D'Antonio 1996). Although many plant species have the ability to adjust their biomass partitioning in response to shade, plants cannot simultaneously increase the proportion of biomass allocated to above- and belowground organs, and researchers have speculated that nutrient availability may place constraints on the ability of plants to respond to shade (Bazzaz and Grace 1997; Bloom et al. 1985). In our study, both species responded to shade with increased partitioning of biomass to leaves at the expense of roots. Increased partitioning to leaves allowed both species to maintain or even increase their leaf areas when light was reduced by 50%. Late watergrass but not rice also increased SLA in response to shade and produced as much leaf area when grown at 18% light as at

100% light at all but the highest N rate. However, N had a relatively small effect on biomass partitioning. The RWR of late watergrass was affected by N, but no relationship was detected between N and LWR. Leaf area increased with N at full and 50% sunlight for both species, but this can be attributed to changes in total DW because SLA was not affected by N. LWR remained constant across N rates but leaf DW, which is highly correlated with leaf area, increased because more total DW was available for allocation to leaves as N increased. However, it should be noted that specific root length was not measured in this study. Researchers have suggested that plants may compensate for lower nutrient availability by increasing the specific root length rather than altering the RWR (Ryser and Eek 2000). Increased specific root length might have allowed plants in our study to compensate for lower N without altering biomass partitioning patterns.

Plants were harvested when rice grown in full light reached panicle initiation. However, rice plants grown in 50 and 18% sunlight were at early- to mid-tillering stages when

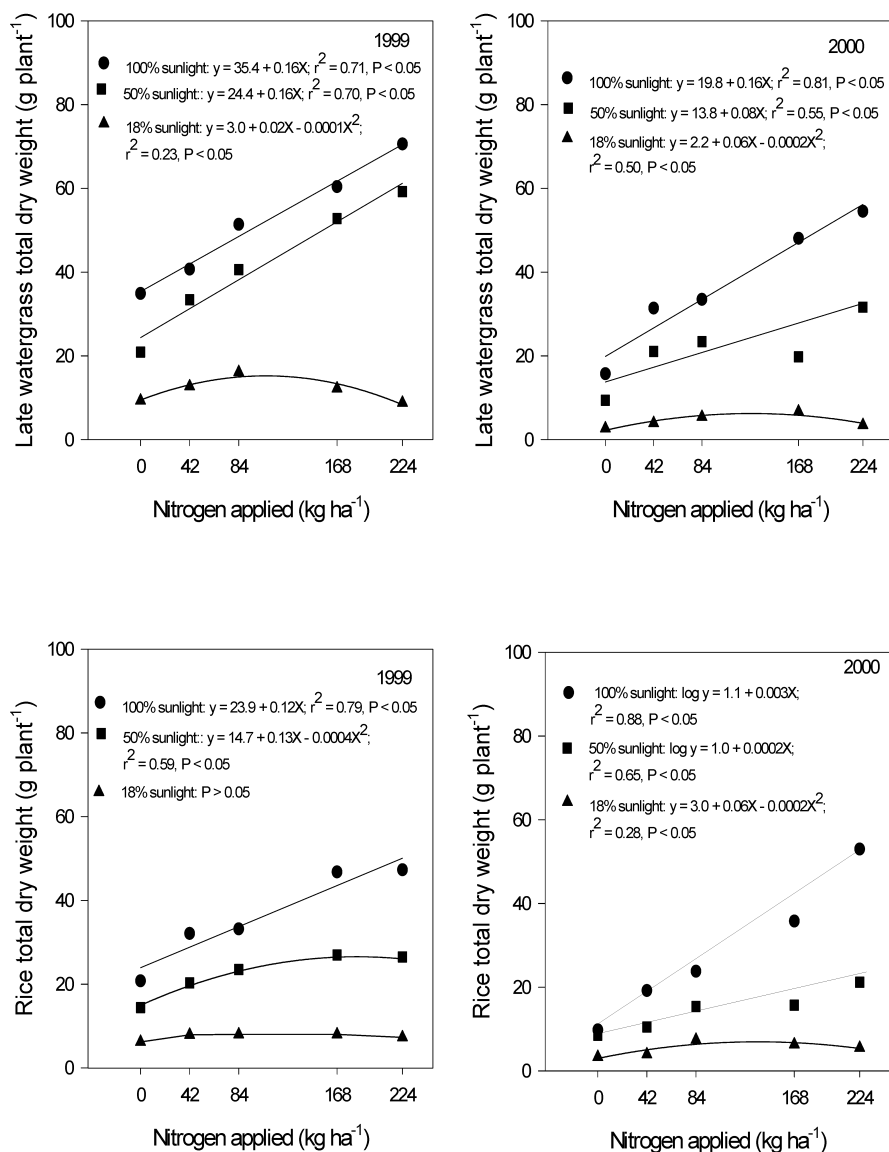


FIGURE 4. Response of rice and late watergrass total dry weight to nitrogen fertilizer rates when grown continuously in full sunlight or transferred to 50 or 18% sunlight at 21 d after seeding in 1999 and 2000.

harvested. Therefore, it is possible that rather than reflecting a plastic response to resource availability, differences in biomass partitioning among treatments should be attributed to differences in developmental stage (McConnaughay and Coleman 1999). Because partitioning to roots typically decreases as plants grow and develop (Klepper 1991), one would expect a younger plant to have greater RWR than an older plant. However, rice and late watergrass plants grown at 18 and 50% sunlight had lower RWR and greater LWR than plants grown at 100% sunlight. Thus, it seems likely that reduced partitioning to roots observed in shaded plants should be attributed to a compensatory response to shade and not to differences in developmental stages. On the other hand, the developmental stage of late watergrass was not determined in this study, and it is possible that late watergrass plants grown at low N rates were at an earlier developmental stage than plants grown at higher N rates. The inverse relationship observed between late watergrass RWR and N may therefore reflect differences in developmental stages rather than a plastic response to N availability. Given

the inconsistent response of late watergrass RWR to N across light and year, it seems likely that biomass partitioning in this species is more affected by limitations in light than in N availability.

Rice and watergrass species have coexisted and coevolved for hundreds of years (Yabuno 1984). By examining the responses of rice and late watergrass to resource limitations, we can identify differences in adaptive traits that may have been lost from rice in the process of domestication and breeding for high yields (De Wet 1975). Late watergrass exhibited more plasticity in leaf morphology (SLA) and biomass partitioning in its response to light than rice. This plasticity contributed to the superior tolerance of late watergrass to shade relative to rice. In particular, late watergrass had much greater plasticity in SLA, which allowed the weed to conserve its leaf area even when grown at the lowest light level. This supports research conducted by Gibson and Fischer (2001), who suggested that the ability of early watergrass to increase SLA in response to shading contributed to its superior tolerance of shade relative to

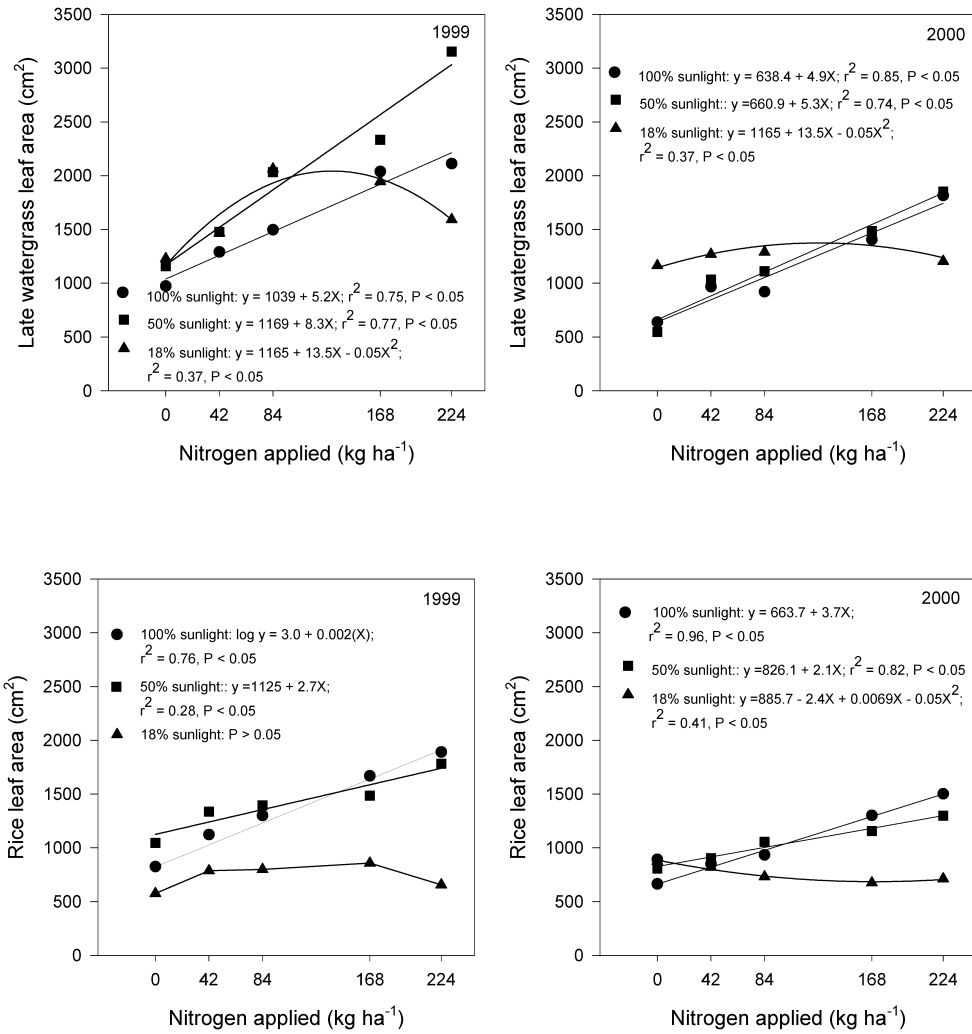


FIGURE 5. Response of rice and late watergrass leaf area to nitrogen fertilizer rates when grown continuously in full sunlight or transferred to 50 or 18% sunlight at 21 d after seeding in 1999 and 2000.

TABLE 1. Rice and late watergrass leaf morphology and biomass partitioning 56 d after seeding in 1999 and 2000.<sup>a</sup>

Light regime <sup>b</sup>	1999		2000	
	Rice	Late watergrass	Rice	Late watergrass
Specific leaf area (cm <sup>2</sup> leaf area g <sup>-1</sup> leaf DW) <sup>c</sup>				
18	243 (21.5) a <sup>d</sup>	392 (30.9) a	120 (4.5) a	185 (11.3) a
50	217 (12.1) a	217 (8.5) b	138 (11.1) a	95 (6.2) b
100	199 (10.8) a	172 (10.1) c	126 (11.1) a	76 (4.6) c
Leaf area ratio (cm <sup>2</sup> leaf area g <sup>-1</sup> total DW)				
18	105 (11.3) a	155 (12.2) a	49.4 (2.4) a	79 (4.5) a
50	66 (4.7) b	48 (2.3) b	37.6 (2.8) b	24 (1.6) b
100	38 (1.5) c	29 (2.0) c	22.4 (2.5) c	12 (1.2) c
Root weight ratio (g root DW g <sup>-1</sup> total DW)				
18	0.20 (0.016) b	0.22 (0.017) b	0.24 (0.019) c	0.19 (0.009) c
50	0.25 (0.016) ab	0.36 (0.022) a	0.33 (0.012) b	0.41 (0.017) b
100	0.29 (0.013) a	0.40 (0.027) a	0.43 (0.015) a	0.56 (0.025) a

<sup>a</sup> Abbreviation: DW, dry weight.

<sup>b</sup> Plants were grown in full light continuously (100%) or transferred to 50 or 18% sunlight 21 d after seeding.

<sup>c</sup> Means within a variable and columns having a common letter are not significantly different at the 5% significance level, according to Fisher's Protected LSD.

<sup>d</sup> Parentheses enclose standard error of the mean.



TABLE 2. Leaf weight ratio 56 d after seeding in 1999 and 2000. Data were pooled across species and N treatments.

Light regime <sup>a</sup>	1999 <sup>b</sup>	2000
18	0.43 (0.01) a <sup>c</sup>	0.42 (0.01) a
50	0.28 (0.01) b	0.27 (0.01) b
100	0.18 (0.01) c	0.17 (0.01) c

<sup>a</sup> Plants were grown in full light continuously (100%) or transferred to 50 or 18% sunlight 21 d after seeding.

<sup>b</sup> Means within each year having a common letter are not significantly different at the 5% significance level, according to Fisher's Protected LSD.

<sup>c</sup> Parentheses enclose standard error of the mean.

rice. Differences in physiology between rice (a C<sub>3</sub> species) and late watergrass (a C<sub>4</sub> species) also may explain the differences in their tolerance of intermediate shade. Bouhache and Bayer (1993) reported greater photosynthetic rates in full and low light for late watergrass than for rice. Gibson and Fischer (2001) reported greater maximum photosynthetic rates for early watergrass than for rice and attributed the superior ability of early watergrass to tolerate shading in part to its ability to maintain high photosynthetic rates even under shade. Additional research on differences be-

tween these species in their physiological response to light and N is needed.

The large reductions in late watergrass growth observed when light or N were reduced suggest that the potential exists to limit late watergrass growth by manipulating either resource. Substantial reductions in late watergrass growth can be achieved through shading alone if shading is imposed early, maintained throughout the growing season, and severe enough to limit the response of the shaded plant to N. This might be achieved by delaying the emergence of late watergrass relative to rice or by the use of more competitive cultivars (Gibson et al. 2002, 2003). Gibson et al. (2002) reported that relatively short delays (15 d) in the emergence of watergrass species relative to rice greatly reduced the growth of the weed. When watergrass emergence was delayed to rice canopy closure, the crop alone was able to completely suppress the weed. The integration of early herbicide application timing and crop development may enable farmers to confer a substantial growth advantage on the crop. However, late watergrass is resistant to the few herbicides available for early-season use in water-seeded rice. Therefore, it may not be possible to confer a large growth advantage on the crop, and growers also may need to ma-

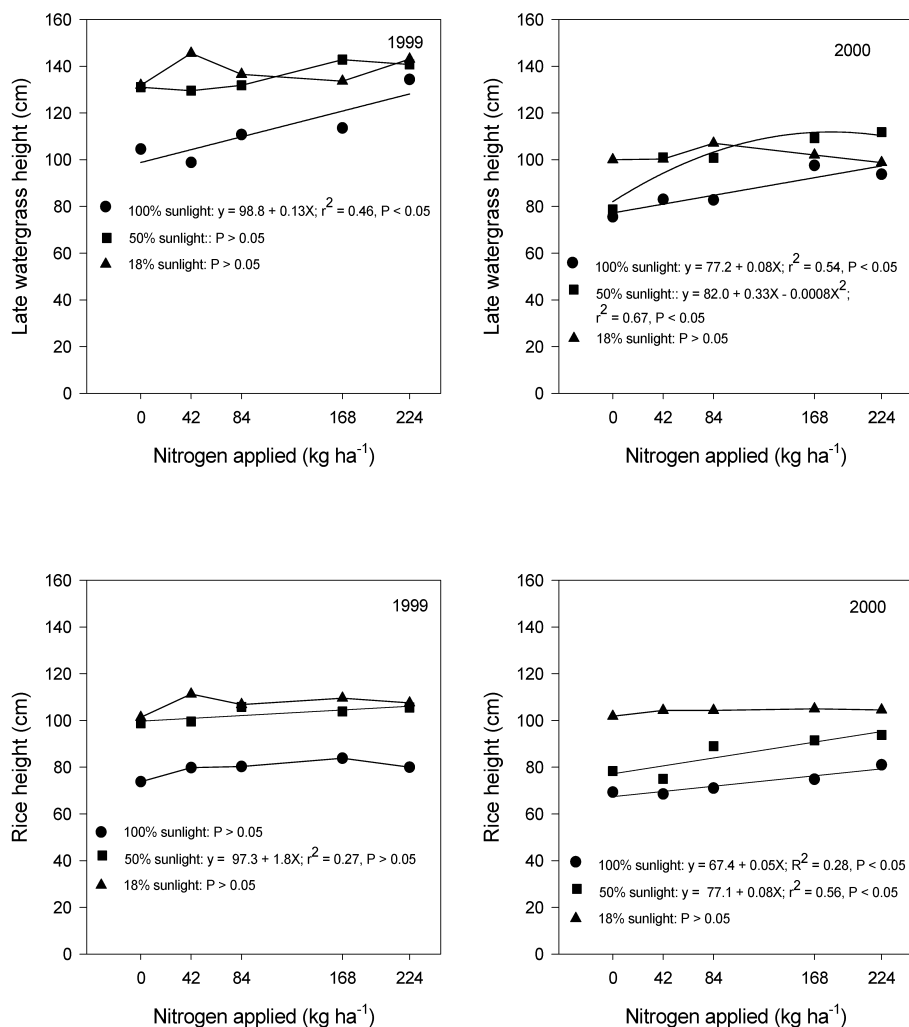


FIGURE 6. Response of rice and late watergrass height to nitrogen fertilizer rates when grown continuously in full sunlight or transferred to 50 or 18% sunlight at 21 d after seeding in 1999 and 2000.

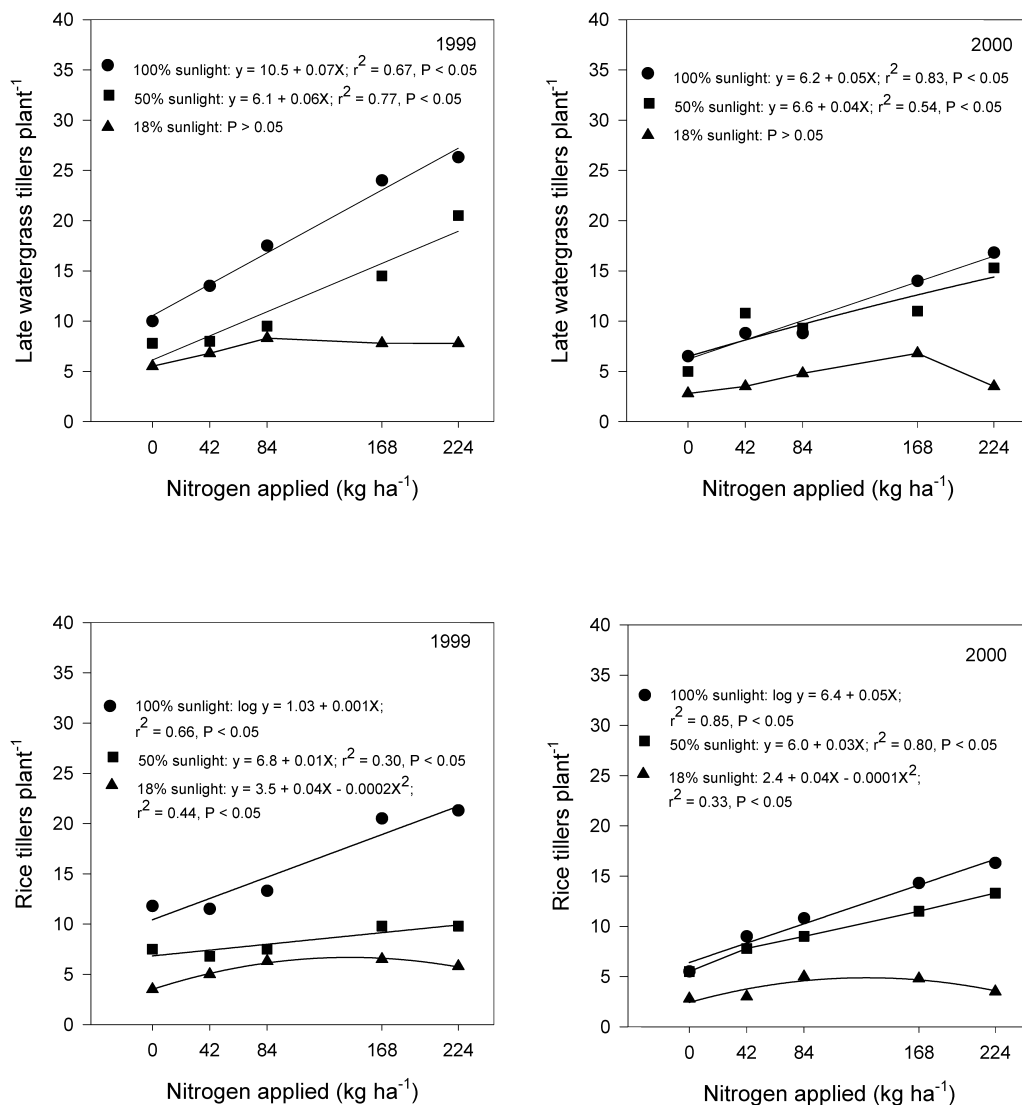


FIGURE 7. Response of rice and late watergrass tillers to nitrogen fertilizer rates when grown continuously in full sunlight or transferred to 50 or 18% sunlight at 21 d after seeding in 1999 and 2000.

nipulate N availability to improve control of late watergrass. N availability can strongly affect rice–weed interactions (Ampong-Nyarko and De Datta 1993a; Assemat et al. 1981; Kim and Moody 1980; Perera et al. 1992), and reducing N uptake by late watergrass has the potential to both directly

reduce the growth of the weed and limit the ability of late watergrass to interfere with rice growth. Approaches to favor crop uptake of N at the expense of weeds include the timing and placement of N fertilizer (Ampong-Nyarko and De Datta 1993a; DiTomaso 1995) and the use of rice cultivars

TABLE 3. Coefficient of variation (plasticity) exhibited in response to light regimen and nitrogen in 1999 and 2000 for rice and late watergrass.

Year	Coefficient of variation							
	Specific leaf area		Leaf area ratio		Leaf weight ratio		Root weight ratio	
	Rice	Late watergrass	Rice	Late watergrass	Rice	Late watergrass	Rice	Late watergrass
<b>Light treatments<sup>a</sup></b>								
1999	10.2	44.6* <sup>b</sup>	48.0	87.4*	37.8	43.5	18.3	28.9*
2000	7.0	49.2*	37.1	92.5*	41.4	49.1	28.2	47.7*
<b>Nitrogen treatments</b>								
1999	6.1	12.1	10.9	7.0	3.4	7.0	4.7	11.5
2000	13.9	4.6	12.2	4.6	5.2	7.8	10.0	8.7

<sup>a</sup> The coefficient of variation, calculated as  $100 \times (\text{standard deviation of the treatment means}/\text{grand mean of the treatment means})$ .

<sup>b</sup> Asterisks indicate that a significant ( $P < 0.10$ ) interaction between species and light regimen or nitrogen was detected by analysis of variance.

that compete more strongly with weeds for N (Gibson and Fischer 2003). However, research on the effectiveness of such approaches under field conditions has not been conducted for water-seeded rice.

Although this study should not be extrapolated directly to management practices or to predict the outcome of competitive interactions, our results can be used to aid in the conceptualization of weed management strategies for water-seeded rice. The interactions between resource availability and late watergrass growth suggest that weed management strategies that limit the growth of late watergrass by imposing multiple resource limitations may be more effective than strategies that rely on limiting a single resource. Such strategies will require the integration of several tools (water and fertility management, competitive rice cultivars, tillage and seedbed preparation, and herbicide use) that favor resource acquisition by the crop at the expense of the weed (Gibson and Fischer 2003; Liebman and Gallandt 1993).

### Sources of Materials

<sup>1</sup> Linear AccuPAR ceptometer, Decagon Devices, Inc., P.O. Box 835, Pullman, WA 99163.

### Acknowledgments

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