

Effect of Water Stress on the Growth and Development of *Amaranthus spinosus*, *Leptochloa chinensis*, and Rice

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ABSTRACT

Drought is the most important abiotic constraint in rainfed rice systems. In these systems, *Amaranthus spinosus* and *Leptochloa chinensis* are the dominant weed species, which may reduce the available water to rice by competition and cause water stress in the crop. Two studies were conducted in a greenhouse to evaluate the growth response of *A. spinosus* and rice and *L. chinensis* and rice to water stress. The water stress treatments were 12.5%, 25%, 50%, 75%, and 100% of field capacity and the plants were grown until weed maturity (*i.e.*, 63 days from seeding). Rice plants did not survive at 12.5% and 25% of field capacity, but both weed species survived in all the treatments. Both weed species produced a significant number of tillers/branches and leaves even at the lowest soil water content. The maximum amount of total shoot biomass produced by weed plants was 2.5 to 3 times more than that of rice plants. The soil water content to achieve 50% of the maximum aboveground biomass was 47% - 50% of field capacity for rice, whereas it was 39% and 31% of field capacity for *A. spinosus* and *L. chinensis*, respectively. *A. spinosus* plants responded to increasing water stress with increased leaf weight ratio, whereas the leaf weight ratio of *L. chinensis* decreased with increases in water stress. The ability of *A. spinosus* and *L. chinensis* to produce shoot biomass under water-stressed conditions suggests that weed management strategies are needed that can minimize weed survival in water-limited environments. These strategies may include the use of weed-competitive and drought-tolerant cultivars, high seeding rates, and optimum timing of fertilizers.

Keywords: Biomass; Soil Moisture; Weed; Rainfed; Drought

1. Introduction

Water stress or drought is one of the most important abiotic constraints in rice, reducing yield on 23 million (M) ha of area in South and Southeast Asia [1,2]. In Asia alone, the average loss in rice production in years of drought can exceed one billion US dollars. In water-limited regions, drought risk reduces yield because growers avoid investing money in inputs when they fear crop loss [2,3]. In irrigated areas, too, water shortage is becoming an increasing problem because of the rising demand for water in urban areas. Water shortage has been historically associated with food shortage, especially in Asia and Africa [3]. By 2025, 13 Mha of irrigated wetland rice in Asia may experience physical water scarcity and 22 Mha of irrigated dry-season rice may suffer from economic water scarcity [4]. Therefore, limited water availability in the future may decrease the capacity of growers to irrigate their fields frequently in irrigated areas, resulting in water stress for crops as well as weeds [5,6]. In

rainfed areas, growers depend on rain and the sporadic rainfall events may result in water stress at any time during the growing season.

Growers in many parts of Asia are shifting their rice production systems from traditional transplanting of seedlings to direct-seeded systems in response to water and labor scarcities. Weeds, however, are the most important biological constraint in direct-seeded rice production systems [7] as weeds and rice emerge simultaneously and there is no standing water at the time of crop emergence. In water-limited fields, weeds may reduce the available water to crops by competition and cause water stress in crops [8]. *Amaranthus spinosus* L. (spiny amaranth, a C₄ broadleaf species) and *Leptochloa chinensis* (L.) Nees (Chinese sprangletop, a C₄ grass species) are amongst the dominant weed species occurring in direct-seeded rice (C₃ species) systems [9-13]. *A. spinosus* was reported to occur in 15 countries in dry-seeded rice systems [14]. It is a prolific seed producer and the spines

present on the plants cause management problems during hand weeding and hand harvest. *L. chinensis* has the ability to grow well in both flooded and upland environments. The widespread introduction of direct-seeded systems, coupled with herbicide use, is thought to be responsible for the increased infestation of this weed in rice. In Malaysia, for example, *L. chinensis* became widespread with the change to direct-seeding of rice from transplanting [15]. Similarly, in Sri Lanka, repeated use of bispyribac-sodium has resulted in a shift in the composition of the weed flora to dominance by *L. chinensis* [16].

Amaranthus spinosus and *L. chinensis* are problematic weed species in rice culture; however, published information is limited concerning the growth and development of these weeds to water stress. In general, C_4 species require less water than C_3 species because of the higher carbon dioxide uptake rates and greater stomatal resistance to water loss [17]. Under drought, plants with the C_4 carbon fixation pathway have a competitive advantage over plants possessing the more common C_3 pathway [18,19]. Therefore, *A. spinosus* and *L. chinensis* are expected to be more tolerant of water stress than the rice crop. The aim of our study was to determine the effect of water stress on the growth and development of *A. spinosus*, *L. chinensis*, and rice.

2. Materials and Methods

Seeds of *A. spinosus* and *L. chinensis* were collected in May 2012 from rice fields in Los Baños, Philippines (14°10'N, 121°13'E). Soil used in the study was collected from upland rice fields, autoclaved, and passed through a 3-mm sieve. Soil (9 kg) was placed in plastic pots (30 cm in diameter and 25 cm in height). Experiments were conducted separately for each weed species. In each pot, two plants of weeds and two plants of rice (cv. Apo in the *A. spinosus* experiment and cv. Rc222 in the *L. chinensis* experiment) were grown together. The distance between the plants was 10 cm and the plants were about 8 cm away from the edge of the pot. For this, two and four seeds of rice and weeds, respectively, were planted in the soil (1 cm deep for rice and 2 mm deep for weeds). Immediately after sowing, the pots were saturated with a sprinkler system. The seedlings emerged 3 to 4 days after sowing and were thinned to two plants of each species per pot immediately after emergence. Nitrogen at 100 kg·ha⁻¹ was applied before irrigation in two equal splits at 14 and 28 days after planting (DAP).

Experiments were modified from studies by Chauhan and Johnson [20] and water stress treatments started at 7 DAP. Water treatments were 12.5%, 25%, 50%, 75%, and 100% of soil field capacity (FC). To determine FC [21], four pots were filled with 9 kg of soil. The weight of the pots containing the dry soil was measured. Pots were watered, allowed to drain for 24 hours, and re-

weighed to determine the field (pot) capacity. The amount of 100% of FC was 1.0 L water, and the volume of water was applied at 3-day intervals. The pots were arranged in a greenhouse as a completely randomized design with four replications. Experiments with each weed species were conducted two times (planting time of *A. spinosus* experiment: first week of July 2012 and second week of September 2012, and planting time of *L. chinensis* experiment: second week of July 2012 and third week of September 2012). Minimum and maximum temperatures recorded in the greenhouse were 24°C and 40°C, respectively, and photosynthetically active photon density was 1300 mol·m⁻²·s⁻¹. Experiments were conducted in natural light.

In all experiments, plant height and number of tillers (or branches for *A. spinosus*) and leaves per plant were determined at 14, 21, 28, 35, 42, 49, 56, and 63 DAP. Plant height was measured from the soil surface to the tip of the uppermost leaf. At weed maturity (63 DAP for both weed species), all plants were removed from the pots and separated into different parts: stems, leaves, and inflorescence (for weeds only). These plant parts were placed in separate paper bags and dried in an oven at 70°C for 72 hours. In addition, leaf weight ratio was estimated by dividing the amount of leaf biomass by total shoot biomass (g·g⁻¹). In *L. chinensis*, we also estimated inflorescence weight ratio by dividing the amount of inflorescence biomass by total shoot biomass (g·g⁻¹).

Data were subjected to analysis of variance (ANOVA). Due to a lack of interactions between treatment and experimental run [22], the data were pooled over the experimental runs (therefore, a total of eight replications). Plant height, leaf number, and tiller/branch number data were analyzed using a three-parameter sigmoid model:

$$y = a \left\{ 1 + e^{\left[-(x-x_{50})/b \right]} \right\},$$

where a is the maximum height, leaf number, or tiller/branch number; x_{50} is the time (DAP) to reach 50% of the final height, leaf number, or tiller/branch number; and b is the slope at time x . The same model was fitted to the leaf, stem, and total shoot biomass of all species and leaf weight ratio of *L. chinensis*, where a is the maximum biomass or leaf weight ratio, x_{50} is the soil water content (SWC) to reach 50% of the maximum biomass or leaf weight ratio, and b is the slope at SWC x . Leaf weight ratio data of *A. spinosus* were analyzed using an exponential model, $y = axe^{-bx}$, where a is the intercept and b is the slope at SWC x .

3. Results

3.1. *Amaranthus spinosus*

Soil moisture content (percent of FC) greatly affected plant height and growth of rice and *A. spinosus*. The plant height of both species at different SWC increased

in a sigmoid manner over the experimental period (**Figures 1(a) and (d)**). Rice plants had a maximum height of 79 cm at 100% of FC, whereas this was 68 cm at 50% of FC (**Figure 1(a) and Table 1**). Although rice plants achieved the maximum height of 59 and 56 cm at 25 and 12.5% of FC, respectively, these plants could not survive until 63 DAP and they died before the final harvest. The slope (b) value was maximum at 100% of FC and it decreased with decreases in SWC (**Table 1**).

Amaranthus spinosus plants had a maximum height of 137 cm at 100% of FC (**Figure 1(d); Table 1**). Decreases in SWC decreased plant height of the weed, but, unlike rice, the weed plants survived at all levels of SWC until the harvest period (63 DAP). At 25% and 12.5% of FC, *A. spinosus* still produced plants with a height of 30 and 25 cm, respectively. The slope (b) was similar at 50% or greater FC and it decreased drastically at 25% and 12.5% of FC (**Figure 1(d); Table 1**).

Rice plants produced a maximum number of 19 - 20 leaves plant⁻¹ at 75% and 100% of FC (**Figure 1(b); Table 1**). The leaf production of rice declined with decreases in FC below 75%. At 25% and 12.5% of FC, rice plants produced a maximum of 13 and 10 leaves plant⁻¹; however, these plants died by 63 DAP. The slope (b) of leaf production was similar at 50% or higher FC and it decreased below 50% of FC (**Table 1**). At 50% or higher FC, rice plants took a similar time (22 to 24 days) to produce 50% of the maximum leaves. At 12.5% and 25% of FC, rice plants produced 50% of the maximum leaves in only 16 to 17 days (**Table 1**).

Amaranthus spinosus plants produced the maximum

number of leaves (147 plant⁻¹) when grown at 100% of FC; however, the number of leaves produced by the weed at 75 and 100% of FC was statistically similar (**Figure 1(e); Table 1**). The weed also produced a similar number of leaves (46 to 51 plant⁻¹) at 12.5% and 25% of FC. The slope of leaf production was similar at 50% or higher FC and it decreased below 25% of FC. The weed plants took a similar time (31 to 32 days) at 75 and 100% of FC to produce 50% of the maximum number of leaves (x_{50}). Below 75% of FC, the weed took less time to produce 50% of the maximum number of leaves (**Table 1**).

As estimated from the fitted model, rice plants produced an average of 4 tillers plant⁻¹ at 100% of FC, which was similar to the tillers produced at 75% of FC (**Figure 1(c); Table 1**). Although rice plants produced an average of 3 tillers plant⁻¹ at 12.5% and 25% of FC, these plants did not survive until 63 DAP. The slope of tiller production was similar at different SWC (**Table 1**). Similarly, the time (x_{50}) taken to produce 50% of the maximum number of tillers was similar at different SWC (**Figure 1(c); Table 1**).

Amaranthus spinosus plants produced a similar number of branches (24 to 25 plant⁻¹) at 50% or higher FC (**Figure 1(f); Table 1**). With decreases in FC below 50%, however, the number of branches also declined. At 12.5 and 25% of FC, *A. spinosus* produced 11 branches plant⁻¹. A similar response was observed for the slope (b) and time (x_{50}) taken to produce 50% of the maximum number of branches (**Figure 1(f); Table 1**). The x_{50} , for example, was 33 to 36 days at 50% and higher FC and it was only 21 to 22 days at 12.5% and 25% of FC.

Table 1. Parameter estimates of a three-parameter sigmoid model ($y = a / \{1 + e^{[-(x - x_{50}) / b]}\}$), where a is the maximum height, leaf number, or tiller/branch number; x_{50} is the time (days after planting) to reach 50% of the final height, leaf number, or tiller/branch number; and b is the slope at time x) fitted to plant height, leaf number, and tiller or branch number of rice and *Amaranthus spinosus* when grown at different soil water contents.

Field capacity (%)	a	b	x_{50}	R^2	a	b	x_{50}	R^2	a	b	x_{50}	R^2
	Plant height (cm plant ⁻¹)				Leaves (number plant ⁻¹)				Tillers/branches (number plant ⁻¹)			
Rice												
100	79 (2.1) ^a	8.4 (0.9)	21.7 (0.9)	0.99	19.7 (1.8)	7.6 (3.1)	22.0 (3.2)	0.90	4.0 (0.2)	5.6 (1.5)	19.3 (1.6)	0.96
75	75 (1.6)	7.6 (0.7)	21.0 (0.7)	0.99	19.0 (1.6)	8.9 (2.9)	23.6 (3.0)	0.93	3.7 (0.1)	5.5 (1.3)	19.0 (1.4)	0.97
50	68 (0.7)	6.2 (0.4)	19.2 (0.4)	0.99	16.4 (0.7)	7.5 (1.4)	21.7 (1.5)	0.98	3.5 (0.1)	4.6 (0.9)	18.8 (0.9)	0.98
25	59 (1.0)	5.4 (0.5)	17.3 (0.5)	0.99	13.3 (0.8)	4.8 (1.9)	17.3 (1.8)	0.94	3.3 (0.1)	4.0 (0.7)	17.4 (0.7)	0.99
12.5	56 (1.0)	5.2 (0.5)	16.6 (0.5)	0.99	10.4 (1.1)	3.8 (2.7)	16.1 (2.6)	0.94	3.0 (0.2)	5.0 (1.4)	18.6 (1.4)	0.97
<i>Amaranthus spinosus</i>												
100	137 (13.1)	12.7 (1.2)	49.2 (2.9)	0.99	147 (11.7)	7.9 (1.9)	32.4 (2.4)	0.97	25.4 (2.1)	9.9 (1.9)	35.5 (2.6)	0.98
75	128 (15.7)	14.0 (1.6)	48.8 (4.0)	0.99	134 (7.7)	8.4 (1.5)	30.8 (1.8)	0.98	23.7 (1.6)	9.4 (1.6)	33.0 (2.1)	0.98
50	73 (6.4)	12.5 (1.9)	36.5 (3.0)	0.99	104 (5.4)	7.2 (1.6)	25.7 (1.7)	0.97	23.9 (2.7)	10.5 (2.7)	33.5 (3.6)	0.96
25	30 (1.2)	4.7 (1.2)	19.9 (1.2)	0.97	51 (2.5)	2.7 (1.2)	19.4 (1.3)	0.94	11.2 (0.7)	4.1 (1.6)	21.9 (1.7)	0.94
12.5	25 (1.6)	3.4 (1.7)	17.9 (1.9)	0.90	46 (3.8)	2.5 (1.7)	18.3 (2.3)	0.84	10.5 (0.6)	3.1 (1.5)	20.9 (1.5)	0.93

^aValues in parentheses are standard error of mean.

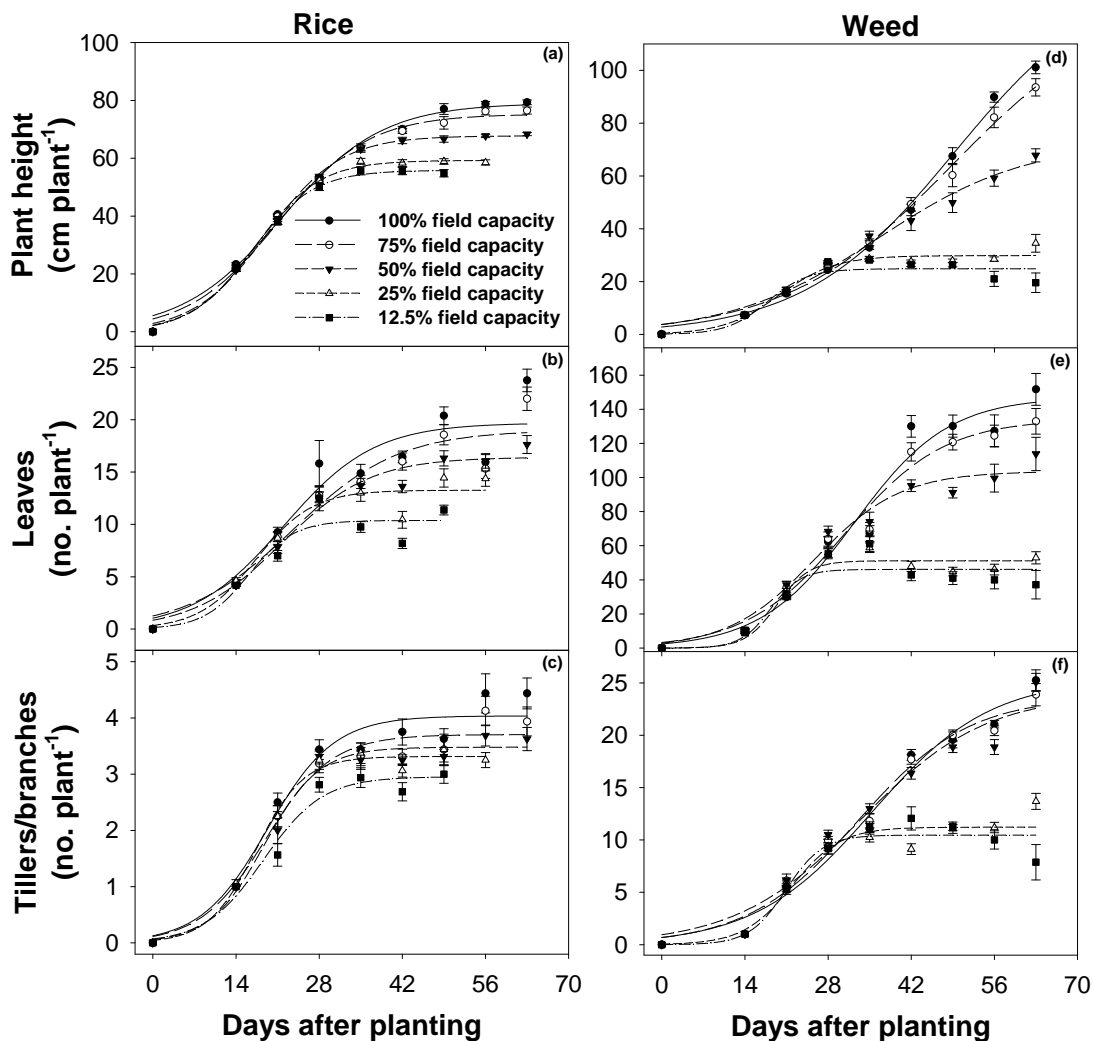


Figure 1. Height (a and d), number of leaves (b and e), and number of tillers or branches (c and f) of rice and *Amaranthus spinosus* plants grown over 63 d after planting in different field capacity regimes. Water stress treatments were imposed at 7 days after planting and vertical bars represent standard error of mean ($n = 8$). The lines represent a three-parameter sigmoid model ($y = a / \{1 + e^{[-(x-x_{50})/b]}\}$) fitted to the data. Parameter estimates are shown in Table 1.

Leaf, stem, and total shoot biomass of rice and *A. spinosus* increased with increases in SWC (**Figures 2(a)-(c)**). Rice plants did not survive at 25 and 12.5% of FC and, therefore, there was no biomass at these SWC. The maximum leaf, stem, and total shoot biomass (a) of rice was 1.5, 2.1, and 3.6 $\text{g} \cdot \text{plant}^{-1}$, respectively (**Table 2**). The estimated model predicted that the FC to achieve 50% of the maximum leaf, stem, and total shoot biomass of rice was 48%, 53%, and 50%, respectively. In *A. spinosus*, however, the corresponding SWC was 25%, 42%, and 39% of FC, respectively (**Table 2**). The weed plants had a maximum total shoot biomass (a) of 10.6 $\text{g} \cdot \text{plant}^{-1}$, which was around 3 times more than that of rice biomass.

As rice plants did not survive at 25% and 12.5% of FC, there were only three data points of leaf weight ratio and the models did not fit the leaf weight ratio of rice. Leaf weight ratio was higher at 50% of FC than at 100% of FC.

Leaf weight ratio values (\pm standard error of mean) were 0.42 ± 0.01 , 0.44 ± 0.01 , and 0.47 ± 0.01 at 100%, 75%, and 50% of FC, respectively. The leaf weight ratio of *A. spinosus* decreased with increases in SWC (**Figure 2(d); Table 2**).

3.2. *Leptochloa chinensis*

Rice plants had a maximum height of 77 cm at 100% of FC and height decreased with decreases in SWC (**Figure 3(a); Table 3**). As observed in the *A. spinosus* experiment, rice did not survive until 63 DAS in the *L. chinensis* experiment, too, at 25% and 12.5% of FC. *Leptochloa chinensis* plants had the maximum height (147 cm) at 100% of FC (**Figure 3(d); Table 3**). Plant height decreased with decreases in FC. At 12.5% to 25% of FC, the weed plants were still 63 to 67 cm tall. The slope (b) was similar

Table 2. Parameter estimates of a three-parameter sigmoid model ($y = a/[1 + e^{-(x-x_{50})/b}]$), where a is the maximum biomass; x_{50} is the field capacity (%) to reach 50% of the final biomass; and b is the slope at field capacity x) fitted to leaf, stem, and total shoot biomass and an exponential model ($y = a \times e^{-bx}$) fitted to the leaf weight ratio of rice and *Amaranthus spinosus* when grown at different soil water contents.

Parameter estimates	Rice	Weed
Leaf biomass (g·plant ⁻¹)		
a	1.53 (0.08) ^a	2.26 (0.26)
b	6.8 (3.4)	18.3 (9.0)
x_{50}	48.1 (2.0)	24.6 (7.5)
R^2	0.99	0.93
Stem biomass (g·plant ⁻¹)		
a	2.14 (0.20)	6.88 (0.28)
b	10.8 (3.9)	12.7 (1.8)
x_{50}	52.9 (4.4)	42.0 (2.4)
R^2	0.98	0.99
Total shoot biomass (g·plant ⁻¹)		
a	3.63 (0.27)	10.56 (0.47)
b	9.0 (3.7)	13.4 (2.0)
x_{50}	50.1 (3.2)	39.1 (2.8)
R^2	0.99	0.99
Leaf weight ratio (g·g ⁻¹)		
a	-	0.593 (0.058)
b	-	0.013 (0.003)
R^2	-	0.92

^a Values in parentheses are standard error of mean. - Models did not fit.

Table 3. Parameter estimates of a three-parameter sigmoid model ($y = a/[1 + e^{-(x-x_{50})/b}]$), where a is the maximum height, leaf number, or tiller number; x_{50} is the time (days after planting) to reach 50% of the final height, leaf number, or tiller number; and b is the slope at time x) fitted to plant height, leaf number, and tiller number of rice and *Leptochloa chinensis* when grown at different soil water contents.

Field capacity (%)	a	b	x_{50}	R^2	a	b	x_{50}	R^2	a	b	x_{50}	R^2
	Plant height (cm·plant ⁻¹)				Leaves (number·plant ⁻¹)				Tillers (number·plant ⁻¹)			
Rice												
100	77 (2.5)	8.5 (1.1)	23.8 (1.1)	0.99	27.7 (1.4)	6.2 (1.3)	30.3 (1.5)	0.98	7.5 (0.7)	10.0 (2.2)	34.9 (3.0)	0.97
75	71 (1.1)	7.1 (0.5)	21.4 (0.5)	0.99	26.5 (1.6)	6.2 (1.5)	29.3 (1.8)	0.97	6.9 (0.4)	8.2 (1.5)	31.6 (1.8)	0.98
50	69 (1.5)	6.7 (0.7)	21.3 (0.7)	0.99	24.5 (1.0)	4.6 (1.0)	26.9 (1.1)	0.98	6.0 (0.2)	6.1 (1.0)	27.1 (1.1)	0.99
25	63 (0.8)	6.0 (0.4)	20.0 (0.4)	0.99	22.1 (0.6)	5.2 (0.6)	26.1 (0.7)	0.99	4.8 (0.3)	6.1 (1.6)	25.1 (1.8)	0.97
12.5	55 (0.7)	5.0 (0.4)	18.1 (0.4)	0.99	18.4 (0.5)	4.1 (0.7)	23.4 (0.8)	0.99	4.0 (0.2)	4.2 (1.3)	22.4 (1.5)	0.96
<i>Leptochloa chinensis</i>												
100	147 (7.7)	10.8 (1.1)	37.7 (1.6)	0.99	34.1 (2.7)	4.8 (1.9)	29.1 (2.2)	0.93	9.6 (1.1)	9.4 (2.2)	37.7 (3.2)	0.97
75	120 (4.6)	9.1 (0.9)	33.5 (1.2)	0.99	35.2 (2.9)	5.7 (2.1)	29.7 (2.4)	0.93	10.2 (1.0)	10.0 (1.8)	39.7 (2.8)	0.98
50	86 (0.8)	5.8 (0.3)	27.2 (0.3)	0.99	37.4 (2.6)	5.4 (1.7)	29.9 (2.0)	0.95	9.5 (0.7)	8.9 (1.7)	36.0 (2.2)	0.98
25	67 (0.6)	4.2 (0.2)	24.6 (0.3)	0.99	33.5 (1.1)	6.4 (0.9)	29.1 (1.0)	0.99	8.8 (0.8)	11.3 (1.9)	38.2 (3.0)	0.98
12.5	63 (0.9)	3.7 (0.3)	24.0 (0.4)	0.99	22.8 (0.9)	3.9 (0.9)	24.0 (1.1)	0.97	4.7 (0.3)	6.2 (2.0)	25.2 (2.2)	0.94

^a Values in parentheses are standard error of mean.

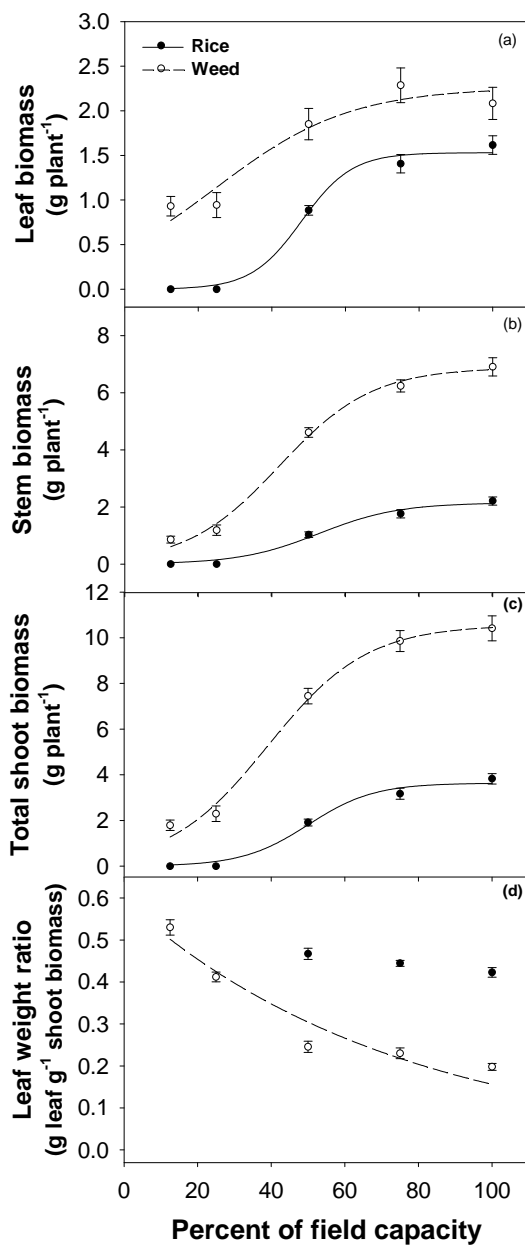


Figure 2. Leaf (a) stem; (b) total shoot; (c) biomass and leaf weight ratio; (d) of rice and *Amaranthus spinosus* plants (at 63 days after planting) grown in different field capacity regimes. Vertical bars represent standard error of mean ($n = 8$). The lines represent a three-parameter sigmoid model ($y = a / \{1 + e^{[-(x-x_{50})/b]}\}$) fitted to the leaf, stem, and total shoot biomass of rice and *A. spinosus* and an exponential model ($y = a \times e^{-bx}$) fitted to the leaf weight ratio of *A. spinosus* when grown at different soil water contents. Parameter estimates are shown in Table 2.

at 75% and 100% of FC, but then it decreased at a lower SWC.

Rice plants produced a similar number of leaves (27 to 28 plant⁻¹) at 75% and 100% of FC (**Figure 3(b); Table 3**). Although rice produced a maximum of 18 to 22 leaves

plant⁻¹ at 12.5% to 25% of FC, these plants could not survive until 63 DAP. The x_{50} was similar (29 to 30 days) at 75% and 100% of FC. At 12.5% of FC, rice produced 50% of the maximum leaves at 23 DAP.

Leptochloa chinensis produced a similar number of leaves (34 to 37 plant⁻¹) at FC from 25 to 100% (**Figure 3(e); Table 3**). At 12.5% of FC, the weed still produced 23 leaves plant⁻¹. There was no consistent response of the slope (b) of leaf production to SWC. Similar to the results observed for the number of leaves, the time taken to produce 50% of the maximum leaves was similar (29 to 30 days) at FC ranging from 25% to 100%. At 12.5% of FC, *L. chinensis* produced 50% of the maximum number of leaves at 24 DAP.

Rice produced a similar number of tillers (7 to 8 plant⁻¹) at 75% and 100% of FC and the number of tillers decreased below 75% of FC (**Figure 3(e); Table 3**). The time taken to achieve 50% of the total tillers was similar (32 to 35 days) at 75% and 100% of FC, but decreased below 75% of FC.

Leptochloa chinensis produced an average of 9 to 10 tillers plant⁻¹ at 25% to 100% of FC (**Figure 3(f); Table 3**). At 12.5% of FC, the weed produced an average of 5 tillers plant⁻¹. Similarly, the slope (b) was similar at FC ranging from 25% to 100%. Based on estimates from the sigmoid model, 50% of the maximum tillers were reached within 36 to 40 days (x_{50}) at 25 to 100% of FC and these values were statistically similar. At 12.5% of FC, *L. chinensis* plants took an average of 25 days to reach 50% of the maximum tiller production at this moisture content.

Rice and *L. chinensis* biomass increased with increases in SWC. Rice produced the maximum leaf, stem, and total shoot biomass of 1.9, 3.1, and 4.9 g plant⁻¹, respectively, whereas *L. chinensis* produced the maximum leaf, stem, and total shoot biomass of 4.5, 3.6, and 11.8 g plant⁻¹, respectively (**Figures 4(a)-(c); Table 4**). Rice plants did not survive until 63 DAP at 25% and 12.5% of FC. The 50% of the maximum total shoot biomass was achieved at 47% of FC in rice, whereas this value for *L. chinensis* was only 31% of FC.

As rice did not survive at 12.5% and 25% of FC, leaf weight ratio data of rice could not fit any model. However, the leaf weight ratio decreased with increases in FC above 25%. The leaf weight ratio (\pm standard error of mean) at 50%, 75%, and 100% of FC was 0.44 ± 0.01 , 0.40 ± 0.01 , and 0.37 ± 0.01 , respectively. The leaf weight ratio of *L. chinensis*, on the other hand, increased with increases in SWC (**Figure 4(d); Table 4**). As estimated from the sigmoid model, the maximum leaf weight ratio of *L. chinensis* was 0.39. The inflorescence weight ratio of *L. chinensis* increased with increases in water stress. The inflorescence weight ratio (\pm standard error of mean) at 12.5%, 25%, 50%, 75%, and 100% of FC was 0.70 ± 0.05 , 0.57 ± 0.04 , 0.40 ± 0.04 , 0.33 ± 0.03 , and 0.29 ± 0.04 , respectively.

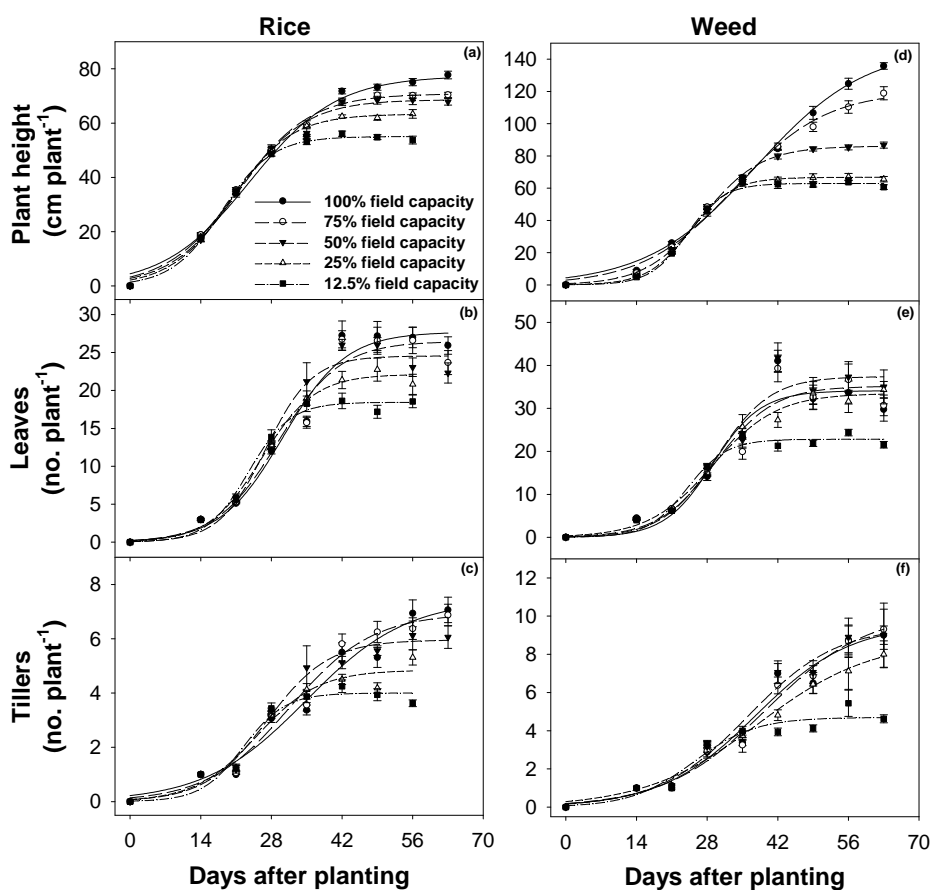


Figure 3. Height (a and d), number of leaves (b and e), and number of tillers (c and f) of rice and *Leptochloa chinensis* plants grown over 63 d after planting at different soil water contents. Water stress treatments were imposed at 7 days after planting and vertical bars represent standard error of mean ($n = 8$). The lines represent a three-parameter sigmoid model ($y = a / \{1 + e^{[-(x - x_{50})/b]}\}$) fitted to the data. Parameter estimates are shown in Table 3.

Table 4. Parameter estimates of a three-parameter sigmoid model ($y = a / \{1 + e^{[-(x - x_{50})/b]}\}$), where a is the maximum biomass or leaf weight ratio; x_{50} is the field capacity (%) to reach 50% of the final biomass or leaf weight ratio; and b is the slope at field capacity (x) fitted to leaf, stem, and total shoot biomass and leaf weight ratio of rice and *Leptochloa chinensis* when grown at different soil water contents.

Parameter estimates	Rice	Weed
Leaf biomass (g plant^{-1})		
a	1.88 (0.01) ^a	4.51 (0.07)
b	1.2 (0.1)	15.4 (0.8)
x_{50}	48.6 (0.1)	39.3 (1.0)
R^2	0.99	0.99
Stem biomass (g plant^{-1})		
a	3.06 (0.13)	3.56 (0.04)
b	6.1 (3.3)	15.0 (0.5)
x_{50}	47.6 (1.8)	47.0 (0.7)
R^2	0.99	0.99
Total shoot biomass (g plant^{-1})		
a	4.92 (0.12)	11.83 (0.20)
b	4.6 (3.4)	20.9 (1.1)
x_{50}	46.8 (2.4)	31.4 (1.1)
R^2	0.99	0.99
Leaf weight ratio (g g^{-1})		
a	-	0.39 (0.01)
b	-	12.72 (1.38)
x_{50}	-	12.01 (0.90)
R^2	-	0.99

^aValues in parentheses are standard error of mean. -Models did not fit.

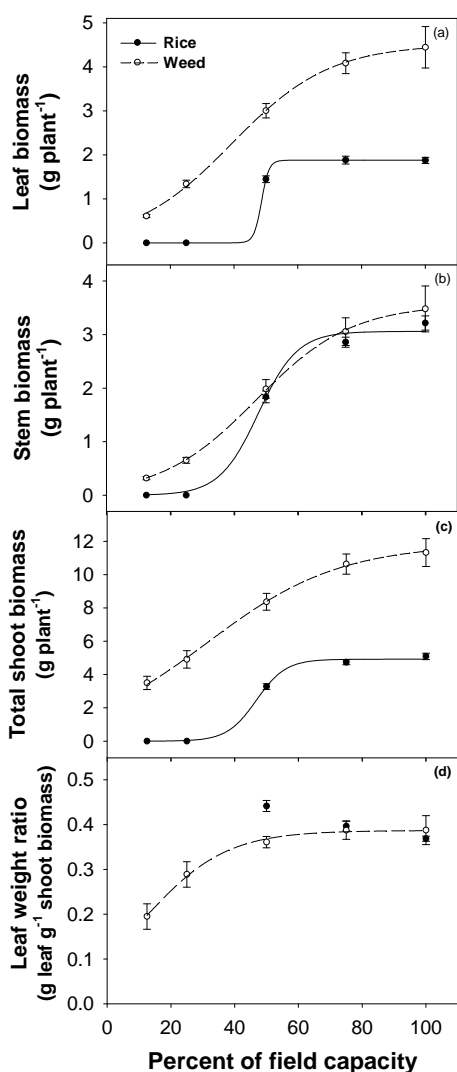


Figure 4. Leaf (a), stem (b), and total shoot (c) biomass and leaf weight ratio (d) of rice and *Leptochloa chinensis* plants (at 63 days after planting) grown in different field capacity regimes. Vertical bars represent standard error of mean ($n = 8$). The lines represent a three-parameter sigmoid model ($y = a / \{1 + e^{[-(x-x_{50})/b]}\}$) fitted to the leaf, stem, and total shoot biomass and leaf weight ratio of rice and *L. chinensis* when grown at different soil water contents. Parameter estimates are shown in Table 4.

4. Discussion

We studied the growth of *A. spinosus* and *L. chinensis* in two experiments, in which these weeds were grown with rice plants at different moisture content. Rice plants in both experiments could not survive at 25% and 12.5% of FC; however, both weeds survived at these field capacities. The plants in our study were irrigated at an interval of 3 days. In field conditions in the rainfed environment, rain may be sporadic and a longer dry spell, coupled with high temperatures, may cause rice plants to die even earlier than observed in our greenhouse study. Compared

with the rice plants, the weeds in both experiments survived until their maturity. Such information suggests that, compared with both weed species, the rice cultivars (Apo and Rc222) used in our study were less tolerant of high water stress. The number of rice tillers and leaves was lower in the *A. spinosus* experiment than in the *L. chinensis* experiment. This response could be due to different rice cultivars used in our study.

In previous studies, rice grew best at 120% to 160% of FC and rice was more competitive than weeds with sufficient moisture, but weeds were more competitive than rice with water stress [23,24]. In water-limited environments, weeds may have higher leaf water potential than rice, suggesting that a limited amount of water in soil would benefit weeds more than rice [25]. In another study, too, *A. spinosus* had higher water potential values than the rice in both well-watered and water-stress treatments [13]. Such information, however, was not found for *L. chinensis*.

Our study observed that, regardless of FC, weed plants were taller than the rice plants. These observations are supported by field observations of *A. spinosus* and *L. chinensis* often visible above the rice canopy in commercial fields, especially where there is a gap between rice plants (*i.e.*, poor plant population). In the crop, these weeds may grow taller than rice to take advantage of the higher light intensity as C_4 plants and, at the same time, shading rice [13,26,27]. Both weeds produced a considerable number of leaves and tillers/branches, even at 50% or less FC. Usually, the time taken to reach 50% of the maximum leaves and tillers/branches was less at 25% and 12.5% of FC compared with 50% or higher FC. These responses were not due to early leaf or tiller/branch production at 12.5% or 25% of FC but rather to the lack of an increase in leaf and tiller/branch number beyond 35 DAP. Similar results were reported in a similar study on *Rottboellia cochinchinensis* (Lour.) W. D. Clayton (itchgrass) [5].

Compared with that of rice, total shoot biomass was higher in weeds at all the levels of FC. At 100% of FC, for example, weed biomass was 2.5 to 3 times more than rice biomass. Both weeds produced a significant amount of biomass at 12.5% and 25% of FC; however, rice did not survive at these moisture contents. These results again suggest that *A. spinosus* and *L. chinensis* are more tolerant of water stress than rice. These observations were also supported by the parameter estimates fitted to the biomass data. In the *A. spinosus* experiment, the FC to achieve 50% of the maximum biomass (x_{50}) was 50% for rice, whereas this value for *A. spinosus* was only 39% of FC. Similarly, in the *L. chinensis* experiment, the x_{50} values were 47% for rice and 31% for *L. chinensis*. An earlier study [5] reported *R. cochinchinensis* to be more tolerant than the weeds included in our study. Compared

with 100% of FC, the aboveground biomass of *R. cochinchinensis* declined by only 54% at 25% of FC. However, the weed plants were grown without rice and there was only one plant per pot. High plant density may deplete moisture content much faster than with low plant density.

As rice did not survive at the lowest two levels of SWC, its leaf weight ratio could not be analyzed using regression analysis. However, the leaf weight ratio data in both experiments at other FC (50%, 75%, and 100%) indicated that rice plants responded with increased leaf weight ratio to increases in water stress. Both weed species responded differently to water stress. Similar to rice, *A. spinosus* plants responded with increased leaf weight ratio to a decrease in SWC (or increase in water stress). These results suggest that *A. spinosus* under water stress conditions allocated more biomass to the leaf than to other shoot parts, and this could be a survival strategy in water-limited environments. Similar results were reported for *R. cochinchinensis*, in which leaf weight ratio at 12.5% of FC was 2.5 times greater than at 100% of FC [5]. In contrast to *R. cochinchinensis* and *A. spinosus*, *L. chinensis* responded with decreased leaf weight ratio to an increase in water stress or decrease in SWC. These results suggest that *L. chinensis* under water stress conditions allocated more biomass to other shoot parts than to the leaf. Inflorescence weight ratio data suggest that *L. chinensis* allocated more biomass to the inflorescence than to leaf and stem parts. The inflorescence weight ratio was around two times more at 25% of FC than at 100% of FC. Although we did not determine the seed production of these weed species in different water stress treatments (the seed size was very small), the inflorescence data suggest that *L. chinensis* can produce a considerable amount of seeds, even at high water stress. In earlier studies, *R. cochinchinensis* and *Echinochloa colona* produced a small amount of seeds even at 12.5% of FC and the authors suggested that the amount of seeds per plant may be enough to cause heavy infestations in the next growing seasons [5,20]. The ability of the weeds to produce seeds in water-limited conditions would help *L. chinensis* to survive in an unpredictable environment.

The results of our study demonstrated that *A. spinosus* and *L. chinensis* are more tolerant of water stress than the rice crop. As mentioned earlier, both weed species utilize a C₄ photosynthetic pathway and rice belongs to the C₃ group. The C₄ photosynthetic pathway overcomes the limitation of the photorespiration, improves photosynthetic efficiency, and minimize the water loss in hot, dry environments [28,29]. In a previous study, Ozturk and colleagues [30] studied the effect of water availability on competition between C₃ and C₄ species and concluded that C₃ species were least productive under dry conditions. If weeds utilize water more efficiently than rice, then a limited amount of water in soil would benefit the

weeds more than the crop [23]. There is a need to breed improved rice cultivars tolerant of water stress. Weed infestation in water-limited environments may decrease rice yield in addition to the effect of water stress on the rice crop. Therefore, it is important to control weeds in the early stages of crop growth and preserve moisture for the crops. Post-emergence herbicide efficacy may be less in water-stressed conditions, mainly because of less herbicide absorption. An earlier study showed that the doses of herbicides to effectively control *Commelina benghalensis* L. (Bengal dayflower) increased upto 250 times at 25% of FC compared with herbicide application at 100% of FC [31]. Weed plants may develop a thicker leaf cuticle in water-stressed conditions, and the thick cuticle may reduce herbicide entry into the leaf [8,32]. Therefore, any weed plants escaping after herbicide application in water-stressed fields should be removed to prevent future infestation.

Asia has a significant amount of water-limited area and this is likely to increase in the future. In rainfed and drought-prone rice areas, not much attention has been given to managing weeds. There is a need to focus research in such areas on understanding the effects of water stress on weed-rice competition and on improving herbicide efficacy in rice weeds. Such research becomes more important in the changing climates scenario. There is a need to exploit weed management strategies, including the use of weed-competitive and drought-tolerant cultivars, high seeding rates, and optimum timing of fertilizers, to minimize weed survival in water-limited environments.

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