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Effect of Nitrogen Application, Rice Planting Density, and Water Regime on the Morphological Plasticity and Biomass Partitioning of Chinese Sprangletop (*Leptochloa chinensis*)

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Due to the looming water and labor crisis, farmers are adopting dry-seeded rice establishment, in which Chinese sprangletop is becoming a major weed. Concerns about the excessive use of herbicides in controlling Chinese sprangletop highlight the need for cultural weed management strategies. Such strategies require an adequate understanding of Chinese sprangletop response to rice plant density, nutrition, and water regime. Therefore, a greenhouse study was conducted to determine the effect of water regime (aerobic and saturated), nitrogen (N) fertilization (50 and 150 kg ha^{-1}), and rice density (0, 160, and 640 plants m^{-2}) on the growth and reproduction of Chinese sprangletop. Chinese sprangletop plants were taller than rice in aerobic conditions than in saturated conditions. All growth parameters (shoot, root, and inflorescence biomass and leaf area, leaf weight, and inflorescence weight ratio) of Chinese sprangletop were higher in aerobic conditions than in saturated conditions when grown without rice. However, no difference was observed for these parameters between water regimes when Chinese sprangletop was grown with rice. Chinese sprangletop growth and seed production was not affected, but rice growth was affected by N rates. Irrespective of N rate and water regime, Chinese sprangletop height (34 to 59%), tiller number (87 to 92%), leaf number (83 to 89%), shoot biomass (93 to 99%), and inflorescence biomass (95 to 99%) decreased as rice density increased from 0 to 640 plants m^{-2}. The ability of Chinese sprangletop to grow taller and produce more plant biomass (107%) and inflorescence biomass (183%) under aerobic than saturated conditions suggests the need for integrated weed management strategies for controlling weeds under water-limited environments. Such strategies might include the use of weed-competitive and drought-tolerant rice cultivars, high seeding rates, and optimum rate of fertilizer application.

Nomenclature: Chinese sprangletop, *Leptochloa chinensis* (L.) Nees LEFCH; rice, *Oryza sativa* L.

Key words: Aerobic, cultural weed management, dry-seeded rice, phenotypic plasticity, rice–Chinese sprangletop competition, saturated soil.

Among the abiotic constraints in rice production, drought is very critical because it results in yield reduction in 23 million (M) ha of area in south and southeast Asia (Kumar et al. 2009). Drought can cause a loss of more than US$1 billion in water-limited rice production areas in Asia. The threat of drought decreases rice production because farmers do not invest their money for fear of crop loss (Kumar et al. 2009; Pandey et al. 2007). In irrigated areas, water scarcity is also becoming a problem due to the increasing demand for fresh water, brought about by increasing urbanization and industrial usage. Historically, water scarcity has been coupled with famine, especially in Asia and Africa (Pandey et al. 2007). By 2025, 13 M ha of irrigated wetland rice and 22 M ha of irrigated dry season rice could experience economic water shortage in Asia (Tuong and Bouman 2003). Because of this looming water shortage, future rice production could experience water stress even in irrigated areas (Chauhan 2013; Webster and Grey 2008).

In response to water and labor scarcities, rice establishment methods have been changing from transplanting of seedlings to dry seeding in many Asian countries for the last two decades. In dry-seeded rice (DSR) systems, weeds are the main biological constraint because weeds and rice emerge simultaneously, and there is no standing water at the time of rice emergence to suppress weeds (Chauhan 2013). Under water-limited conditions, weeds can consume more water than the crop, thus reducing the amount of water available to the crop (Chauhan and Abugho 2013a; Patterson 1995).

Chinese sprangletop, a C_4 grass species, is one of the dominant weed species occurring in direct-seeded

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rice (C_3 species) systems (Azmi et al. 2005; Chauhan and Johnson 2008; Marambi 2002). It is an invasive, noxious, and troublesome weed in rice fields in many countries and is widely spread in south and southeast Asian counties and Australia (Galinato et al. 1999; Holm et al. 1991). It can grow from 0 to 1,400 m above the sea level (Mannetje 2014). Moist conditions, such as in DSR, favor its germination, thus making it a problematic weed in DSR systems (Azmi et al. 2005), replacing broadleaf and sedge weeds (Ho and Zuki 1988). After germination, Chinese sprangletop has the ability to endure water logging as well as drought conditions. Chinese sprangletop survival is attributed to its quick seedling development to keep pace with the rising level of floodwater (Mannetje 2014). The dissemination of Chinese sprangletop is enhanced by the use of contaminated rice seeds (Holm et al. 1991).

Chinese sprangletop is an alternate host of many insects and nematodes (Barrion and Litsinger 1987; Khan et al. 1996). In Philippines, for example, it was reported as an alternate host of blast, sheath blight, and Udbatta diseases, which are caused by *Pyricularia oryzae* Cavara, *Rhizoctonia solani* Kuhn, and *Ephelis oryzae* Sydow, respectively (Mackill and Bonman 1986). Leafhoppers, which transmit rice tungro spherical virus (RTSV) and rice tungro bacilliform badnavirus (RTBV), feed on Chinese sprangletop, signifying its potential role in the dispersal of rice viruses (Khan et al. 1996). Chinese sprangletop densities at 2, 3, 4, 5, and 6 plants m^{-2} resulted in mean yield reductions of rice by 14, 23, 25, 39, and 44%, respectively (Prusty et al. 1992). Labor is scarce and expensive to use for manual weeding, and therefore farmers have to rely on herbicides to manage weeds. In some countries, including Pakistan (TH Awan, personal observations) and Sri Lanka (Marambe 2002), the repeated use of bispyribac-sodium resulted in the shift of the weed flora dominated by Chinese sprangletop, because this herbicide is weak on some grasses, including Chinese sprangletop (Chauhan 2013; Mahajan et al. 2009). Moreover, the repeated use of herbicides with a single mode of action can develop resistance in weeds, shifts in weed flora composition, and harmful impacts on living organisms and the environment (Buhler et al. 2002; Johnson and Mortimer 2008). Sprangletop with resistance to fenoxaprop-p-ethyl is confirmed in Thailand (Pornprom et al. 2006).

Declining availability of irrigation water and concerns related to the herbicide use have aroused the interest for including cultural practices in integrated weed management (IWM) programs (Azmi et al. 2005). However, the application of these practices in rice to obtain full benefits has been limited because of insufficient information on biology and ecology of major weeds, including Chinese sprangletop. A better understanding of the response of weeds to changes in cultural practices (e.g., crop competitiveness, density, N, and water) can contribute to the development of an IWM program. Competition for light can be an important factor influencing plasticity in weeds (Caton et al. 1997; Gibson et al. 2001). However, such published information is limited regarding the plasticity in Chinese sprangletop in response to cropping density, N rates, and water stress.

Crop–weed competition can be influenced by N rate, water availability, and seeding rates. Several researchers have suggested the usage of high rice planting density to control weeds and achieve high grain yield in DSR crops (Ahmed et al. 2014; Chauhan et al. 2011). The crop at high planting densities, however, might need more nutrients to produce high yield. Although N fertilization is one of the fundamental components for crop–weed competitive interactions (Liebman and Janke 1990), some weeds consume greater quantities of N than the rice crop, resulting in reduced N uptake, growth, biomass accumulation, and yield of rice (Awan et al. 2014a; Ampong-Nyarko and De Datta 1993). Other researchers found that high doses of N fertilizer benefited rice more than weeds, and, under shaded conditions, weeds were less responsive to added N (Awan et al. 2014b; Evans et al. 2003; Mishra and Kurchania 2001). The competitive ability of high N-responsive weed species increases with increasing N rates (Awan et al. 2014a), whereas low N-responsive weed species are not influenced by N rate (Awan et al. 2014b; Blackshaw and Brandt 2008). The effects of crop seeding rate on weed suppression could be modified by N rates and water availability. The effect of a high crop-seeding rate appears to be more prominent at low N levels because weeds grow slowly at low N levels (Awan et al. 2014a; Blackshaw et al. 2003). On the other hand, high N rates and high moisture levels can increase crop growth and the suppressive effect of high seeding rates on weeds (Awan et al. 2014b; Chauhan and Abugo 2013b). Thus, it is necessary to understand the response of weeds to increasing N rates to improve the strategies that decrease N availability to weeds, and also to determine the moisture levels at which rice becomes more competitive than weeds.

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In general, plants with a C_4 pathway of carbon dioxide (CO_2) fixation require less water than species with a C_3 pathway, because of higher CO_2 uptake rates and greater stomatal resistance to water loss (Ehleringer et al. 1997). Under water stress conditions, C_4 plants have a competitive advantage over C_3 plants (Fuhrer 2003; Yin and Struik 2008). Therefore, Chinese sprangletop, being a C_4 plant, is expected to be more tolerant of drought than a C_3 rice plant.

Weed control practices that increase the competitive ability of crops over weeds should be a fundamental component of an IWM strategy. Before cultural methods that rely on crop interference and optimum nutrient and water management can be developed, an adequate understanding is needed on how Chinese sprangletop evades or reduces the negative effect of resource competition with rice. At present, relatively limited information is available on the biology and ecology of Chinese sprangletop in response to the combined effect of rice planting density, N application rates, and water availability. We hypothesized that (a) high rice planting density can be used to suppress Chinese sprangletop growth, (b) rice competitiveness against Chinese sprangletop can be improved by increasing N rates, and (c) water regime can affect N availability to the crop and Chinese sprangletop plants. To test these hypotheses, this study was conducted to evaluate the physiological and morphological responses of Chinese sprangletop to multiple resource limitations (water, N, and light), and examine how this weed responds to rice competition.

Materials and Methods

Seeds of Chinese sprangletop were collected in May 2012 from rice fields in Los Baños, Laguna, Philippines (14.18°N, 121.25°E). Soil was collected from upland rice fields of the International Rice Research Institute (IRRI), Los Baños, Philippines, sieved through a 3-mm sieve, and sterilized before being used in this study. The soil (9.7 kg) was placed in plastic pots (25 cm diam and 25 cm height). The soil had 6.4 pH, 0.94% organic carbon, 0.093% Kjeldahl N, 55 mg kg^{-1} available phosphorus (P_2O_5), and 0.948 meq 100^{-1} g soil potassium (K). In this study, 12 treatment combinations (having three factors: two water regimes [saturated and aerobic], three rice planting densities [0, 8, and 32 plants pot^{-1}], and two N rates [50 and 150 kg ha^{-1}]) were studied under natural light conditions in a greenhouse. Phosphorus and potassium fertilizers were applied as basal at 40 kg P_2O_5 and 40 kg potassium oxide (K_2O) ha^{-1}. N was applied in two equal splits at 20 and 40 d after sowing (DAS).

Rice variety NSIC Rc222 and Chinese sprangletop were grown together. For eight rice plants per pot (i.e., 160 plants m^{-2}), 16 rice seeds were planted 1 cm deep in a single circle at a distance of 5 cm from the Chinese sprangletop seeds. For 32 rice plants per pot (i.e., 640 plants m^{-2}), 64 rice seeds were planted in two circles. The placement of the first circle was the same as previously described and the distance of the second circle was 2.5 cm away from the first circle. In each circle, the rice seeds were planted at an equal distance from each other. Immediately after sowing, pots were saturated with a sprinkler irrigation system, and three to five Chinese sprangletop seeds were placed at the center of each pot and gently pressed into soil. By 7 DAS, thinning was done to maintain the required density of rice and Chinese sprangletop plants per pot. Only one plant of Chinese sprangletop was maintained at the center of each pot, which was about 8 cm away from the periphery of the pots.

Irrigation started on the day of sowing (November 18, 2012) and continued up to 12 DAS (December 1, 2012), and then irrigation was withheld for 8 d to create water stress conditions. Water stress treatments began at 21 DAS. The water treatments used were 50% (aerobic) and 100% (saturated) of the soil field capacity. The water regimes in this study were chosen from earlier studies (Chauhan 2013; Webster and Grey 2008). The field capacity of pots was determined in the manner described by Chauhan and Johnson (2010b) and Steadman et al. (2004), and a measured quantity of water was applied at 5-d intervals. The experiment was repeated in February 2013 in the greenhouse to preclude the effect of rainfall on the experimental treatments. Pots were arranged in a completely randomized split-plot design with four replications. Minimum and maximum temperatures of 22 to 25 C and 35 to 45 C, respectively, and the photosynthetically active photon flux density of 1,200 to 1,300 mol m^{-2} s^{-1} were recorded during the experiments.

Plant height, number of leaves per plant, and number of tillers per plant were measured at 14, 28, 42, 56, and 70 DAS. The height of Chinese sprangletop and rice plants were measured from the ground level to the tip of the longest leaf. At Chinese sprangletop maturity (70 DAS), rice plants

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were harvested from the soil surface, and pots, along with the Chinese sprangletop plants were brought to the laboratory for leaf area measurement. After detaching the leaves, shoots were separated into stems and inflorescence. Leaf area was measured using a leaf area meter (model #LI-3100, LI-COR). After measuring the leaf area, the stems, leaves, and inflorescence were placed in paper bags separately and dried in an oven at 70 C to achieve constant dry biomass. From each pot, roots were removed along with soil and then the soil was washed off through a steel strainer. Chinese sprangletop and rice roots were separated and placed in separate paper bags for oven drying and biomass measurements.

The following ratios were calculated: root to shoot weight ratio (RSWR), leaf area ratio (LAR), leaf weight ratio (LWR), specific leaf area (SLA), and specific stem length (SSL).

$$\text{RSWR} = [\text{Root biomass (g)}]/[\text{Shoot biomass (g)}] \quad [1]$$

$$\text{LAR} = \left[\text{Leaf area } \left(\text{cm}^2\right)\right]/[\text{Total plant biomass(g)}]. \quad [2]$$

$$\text{LWR} = [\text{Leaf biomass(g)}]/[\text{Total plant biomass(g)}] \quad [3]$$

$$\text{SLA} = \left[\text{Leaf area} \left(\text{cm}^2\right)\right]/[\text{Total leaf biomass(g)}] \quad [4]$$

$$\text{SSL} = [\text{Stem length(cm)}]/[\text{Stem weight(g)}] \quad [5]$$

Data from both experiments were subjected to analysis of variance (ANOVA). Data variance was visually inspected by plotting residuals to confirm homogeneity of variance before statistical analysis. The results of the ANOVA indicated that there was no significant interaction between two experimental runs and treatments; therefore, the data were pooled over experimental runs for further analysis (GenStat 8.0 2005). A regression analysis was performed to study the functional relationship between two or more variables. A regression of the Chinese sprangletop height data was performed using a three-parameter sigmoid model as described by Brown and Mayer (1988):

$$y = a \Big/ \left\{1 + e^{[-(x - d50)/b]}\right\} \quad [6]$$

where y is the estimated plant height as a function of rice planting density or DAS at time x, a is the maximum plant height, $d50$ is the time to reach 50% of the final plant height, and b is the slope around $d50$.

A linear model of the form Draper and Smith (1998)

$$y = a + bx \quad [7]$$

was fitted to leaf and tiller numbers per plant and SSL of Chinese sprangletop, where y is the estimated variable of Chinese sprangletop as a function of DAS or rice planting density at time x; a is the estimate of the regression constant, the value of y when x = 0; and b (slope of the regression curve) is the estimate of the regression coefficient, measure the change in y per unit change in x. Direction of the line is determined by the sign of the regression coefficient. If $b > 0$, the line goes upward and there is a direct relationship (positive correlation) between y and x. If $b < 0$, the line goes downward and there is an inverse relationship (negative correlation) between y and x. When $b = 0$, the line is horizontal and there is no relationship.

An exponential model of the form (Awan et al. 2014a; Ritz and Streibig 2008):

$$y = a \times e^{-bx} \quad [8]$$

was fitted to the data of leaf, stem, inflorescence, shoot (total aboveground biomass), root, and whole plant biomass, and leaf area.

An exponential model of the form (Schabenberger et al. 1999; Awan et al. 2014a):

$$y = y0 + \left(a \times e^{-bx}\right) \quad [9]$$

was fitted to leaf weight ratio, where y is the estimated parameter at different rice densities (plants pot^{-1}) x, a is the intercept, and b is the slope.

Adequacy of the model can be measured by coefficient of determination (R^2). The R^2 gives the proportion of the total variation in y that is accounted for by x. R^2 ranges from 0 to 100%; the nearer it is to 100%, the better is the fit of the model on the data. Parameter estimates were compared using their standard errors.

Results and Discussion

A sigmoid growth response curve was observed for the height of rice and Chinese sprangletop when grown under different water regimes, N rates, and rice planting densities (Figures 1a and 1b; Table 1).

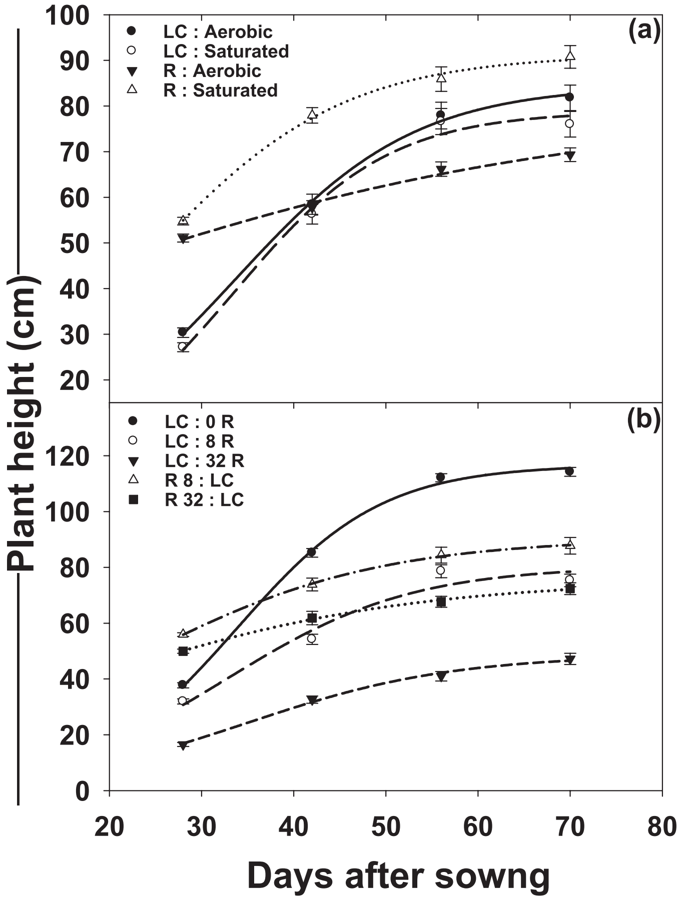

Figure 1. Plant height of Chinese sprangletop (LC) and rice (R) affected by (a) water regime (aerobic and saturated conditions), (b) rice density (when grown without rice [LC:0R] or in competition with different densities of rice plants [LC:8R and LC:32R]). Rice plant height is shown from the competition treatment having eight rice plants (R8:LC) and 32 rice plants (R32:LC). The lines represent a three-parameter sigmoid model, $y = a/\{1 + e^{[-(x - d0)/b]}\}$, fitted to the plant height. The vertical bars represent standard error of means. Parameter estimates of the model are shown in Table 1.

Chinese sprangletop initially grew more slowly than rice. Rice plants were taller (51 to 56 cm) than Chinese sprangletop (27 to 30 cm) at 28 DAS, regardless of the water regime, N rate, and rice planting density. Beyond 42 DAS, however, Chinese sprangletop plants were taller than rice plants under aerobic conditions, whereas the opposite was true under saturated conditions (Figure 1a). The height of Chinese sprangletop was affected by rice density, and the Chinese sprangletop plants grown without rice were taller than those grown with rice. At a rice density of 32 plants pot^{-1}, however, Chinese sprangletop height was significantly suppressed and rice plants were 55% taller (76 cm) than Chinese sprangletop plants (49 cm) (Figure 1b). Compared with the plants grown without rice, Chinese sprangletop height decreased by 34 and 59% when the Chinese sprangletop plants were grown with rice at densities of 8 and 32 plants pot^{-1}, respectively.

The height of Chinese sprangletop decreased with increasing rice density under saturated conditions, but not under aerobic conditions. Similar results were reported in an earlier study, in which Chinese sprangletop height was not suppressed by increasing rice density up to 169 rice plants m^{-2} under an aerobic water regime (Chauhan and Abugho 2013a). In barnyardgrass [*Echinochloa crus-galli* (L.) Beauv.] and itchgrass [*Rottboellia cochinchinensis* (Lour.) W. D. Clayton], however, the height decreased with increasing rice seeding rates, regardless of N rate and water regime (Chauhan 2013; Chauhan and Abugho 2013b; Chauhan and Johnson 2010a). In our study, N application did not affect Chinese sprangletop height but had a distinct effect on rice height. Water regime had a pronounced effect on the height

Table 1. Regression parameters for plant height of Chinese sprangletop and rice as affected by water regime, nitrogen rate, and rice density when grown without rice or in competition with different densities of rice plants.

Species	Treatments	Parameter estimates (± standard error)			
		a	*b*	*d*50	R^2
Rice	Saturated	91 (1.8)	11 (1.5)	24 (0.9)	0.99
	Aerobic	79 (11.7)	29 (15.9)	11 (4.5)	0.99
Chinese sprangletop	Aerobic	85 (2.0)	10 (0.9)	34 (0.8)	0.99
	Saturated	79 (3.9)	8 (1.8)	34 (1.7)	0.99
Chinese sprangletop	0 plants pot^{-1}	117 (2.6)	8 (0.7)	34 (0.8)	0.99
	8 plants pot^{-1}	80 (9.3)	10 (4.7)	33 (4.0)	0.96
	32 plants pot^{-1}	49 (2.7)	11 (2.1)	35 (1.9)	0.99
Rice	8 plants pot^{-1}	90 (1.1)	14 (1.0)	22 (0.6)	0.99
	32 plants pot^{-1}	76 (2.3)	18 (3.2)	16 (1.7)	0.99

[a] Abbreviations: *a*, maximum plant height; *b*, slope at time x; *d*50, time (days after sowing) to reach 50% of the final height.

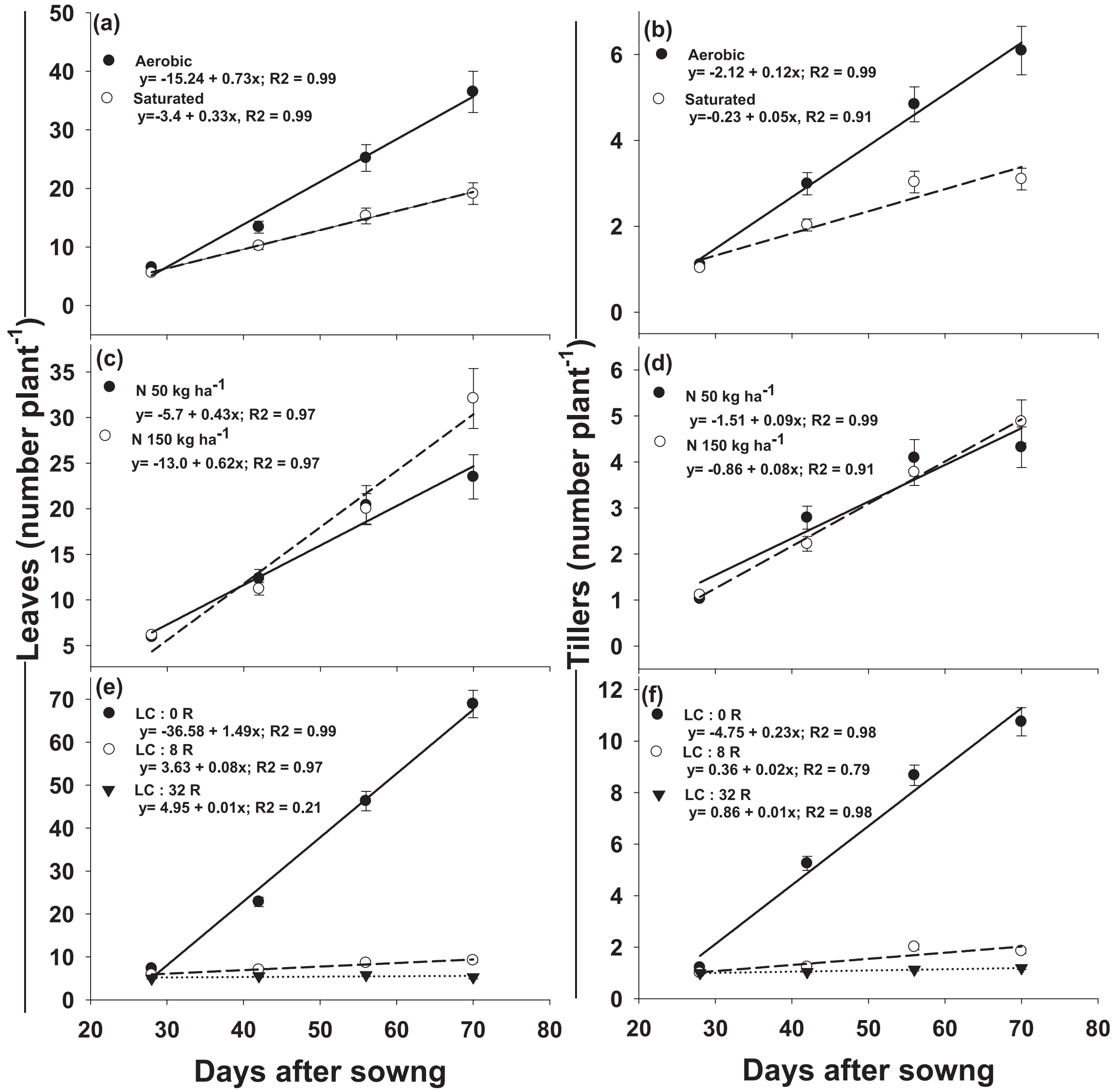

Figure 2. Number of leaves (a, c, e) and tillers (b, d, f) of Chinese sprangletop (LC) when grown at different water regimes (a, b), nitrogen rates (c, d), and rice (R) planting densities (e, f). Chinese sprangletop plants were grown without rice (LC:0R) or in competition with different densities of rice plants (LC:8R and LC:32R). The lines represent a linear model ($y = a + bx$) fitted to the data. The vertical bars represent standard error of means.

of both rice and Chinese sprangletop. Irrespective of N rate, rice plants were taller than Chinese sprangletop plants under saturated conditions, whereas under aerobic conditions, the Chinese sprangletop was always taller than the rice plants. These results suggest that Chinese sprangletop can grow taller than rice in DSR fields and take advantage of its developed height in intercepting solar radiation (Caton et al. 1997).

The number of leaves and tillers of Chinese sprangletop increased linearly with time (DAS) at different water conditions, N rates, and rice planting densities (Figure 2). Water regimes had significant effects on both number of leaves and tillers plant^{-1}. More leaves and tillers plant^{-1} were noted under aerobic than saturated conditions from 42 DAS onwards (Figures 2a and 2b). By 70 DAS, Chinese sprangletop plants grown in aerobic conditions produced 97% more tillers and 91% more leaves than plants grown in saturated conditions. N rate did not affect the production of tillers, but significantly increased (by 37%) the number of leaves plant^{-1} when N rate increased from 50 to 150 kg ha^{-1} (Figures 2c and 2d). The number of tillers and leaves produced by Chinese sprangletop were reduced when grown with rice. Chinese sprangletop produced a maximum of 11 tillers plant^{-1} without competition, whereas, when in competition with 8 and 32 rice plants pot^{-1}, the Chinese sprangletop produced only 2.0 and 1.2 tillers plant^{-1}, respectively (Figure 2f). Similarly, by 70 DAS, Chinese sprangletop produced 9.2 and 5.3

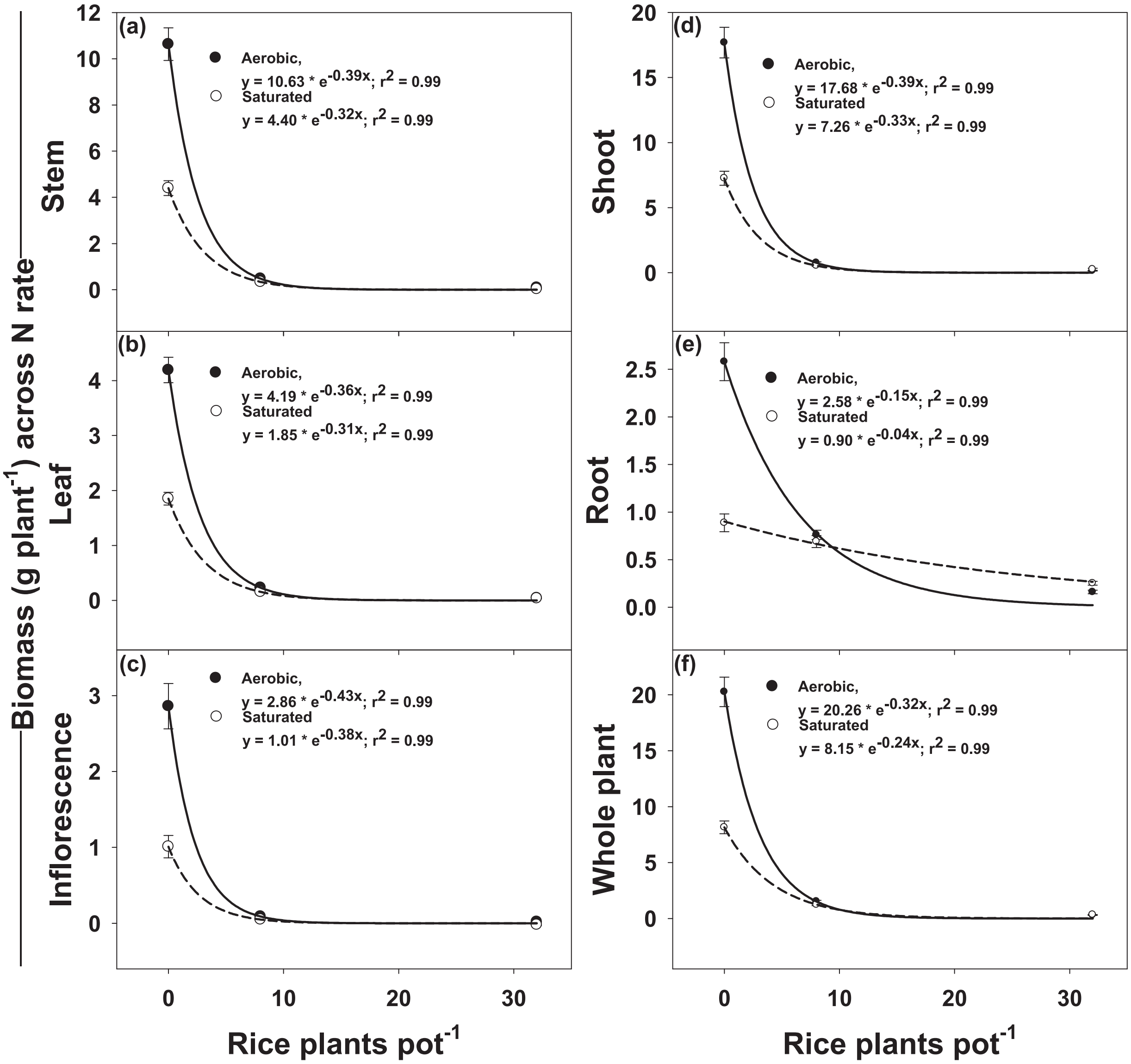

Figure 3. (a) Stem, (b) leaf, (c) inflorescence, (d) shoot, (e) root, and (f) whole plant biomass of Chinese sprangletop as affected by the interaction of water regime and rice planting density. The vertical bars represent standard error of means. The lines represent an exponential model, $y = a \times e^{-bx}$, fitted to the biomass data.

leaves plant^{-1} in competition with 8 and 32 rice plants, respectively, compared with 69 leaves plant^{-1} when grown without competition (Figure 2 e). The number of tillers plant^{-1} in Chinese sprangletop decreased by 87 and 92% when grown with rice densities of 8 and 32 plants pot^{-1}, respectively, and the corresponding values for the number of leaves plant^{-1} were 83 and 89%, respectively (Figures 2e and 2f).

The interaction effect of water regime and rice planting density was pronounced on the production of stem, leaf, shoot, inflorescence, root, and whole-plant biomass of the Chinese sprangletop (Figure 3), whereas for rice plants, the interaction among all three factors was evident for tiller number and shoot, root, and whole plant biomass (Table 2). The biomass for all plant parts of Chinese sprangletop decreased with increasing rice planting density in both aerobic and saturated conditions (Figure 3). By 70 DAS, compared to Chinese sprangletop plants grown without rice, Chinese sprangletop shoot biomass under saturated conditions decreased by 93 and 96% when grown with rice densities of 8 and 32 plants pot^{-1}, respectively; whereas, under aerobic conditions, the corresponding values were 96 and 99%, respectively (Figure 3d).

Averaged over N rates, the root biomass of Chinese sprangletop was higher (2.58 g plant^{-1}) when grown under aerobic conditions than that under saturated conditions (0.9 g plant^{-1}) (Figure 3e). Increased rice planting density resulted in lower Chinese sprangletop root biomass plant^{-1}

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Table 2. Interaction effect of water regime (WR), nitrogen (N) rates, and rice planting densities (PD) on tiller numbers pot^{-1}, aboveground shoot, root, and whole plant biomass of rice (R) at 70 d after sowing.[a]

Water regime	Nitrogen rates	Tillers		Biomass: Shoot		Biomass: Root		Biomass: Whole plant	
		8 R	32 R	8 R	32 R	8 R	32 R	8 R	32 R
	(kg ha^{-1})	(no. pot^{-1})		(g pot^{-1})					
Aerobic	50	35.0	64.8	38.5	36.2	8.2	7.7	46.7	43.9
	150	61.3	98.0	43.0	39.9	9.7	10.3	51.0	50.2
Saturated	50	28.3	45.5	51.9	55.4	12.6	13.2	64.5	68.7
	150	50.3	95.3	89.3	61.0	16.93	17.47	106.3	78.5
$LSD_{0.05}$ for WR by N by R		8.42		9.57				10.73	
$LSD_{0.05}$ for WR						2.125			
$LSD_{0.05}$ for N						2.125			
P values									
WR		<0.001		<0.001		<0.001		<0.001	
N		<0.001		<0.001		0.005		<0.001	
PD		<0.001		0.003		0.748		0.014	
WR by N		0.146		<0.001		0.28		<0.001	
WR by PD		0.605		0.048		0.798		0.068	
N by PD		<0.001		0.001		0.827		0.007	
WR by N by PD		<0.001		0.002		0.777		0.003	

[a] Abbreviations: $LSD_{0.05}$, least significant difference at 5% level of significance; 8 R, 8 rice plants pot^{-1}; 32 R, 32 rice plants pot^{-1}.

compared with the Chinese sprangletop plants grown without rice. Under aerobic conditions, 8 and 32 rice plants pot^{-1} reduced Chinese sprangletop root biomass by 71 and 94%, respectively, whereas under saturated conditions, the corresponding values were 22 and 72%, respectively (Figure 3e).

The inflorescence biomass of Chinese sprangletop was greatly influenced by moisture availability and rice planting density. When Chinese sprangletop was grown without rice , it produced the highest inflorescence biomass (2.86 g plant^{-1}) under aerobic conditions, which was 183% higher than for plants grown under saturated conditions (1.01 g plant^{-1}) (Figure 3c). The inflorescence biomass of the Chinese sprangletop in competition with rice decreased by 95 to 96% and 98 to 99% at densities of 8 and 32 plants pot^{-1}, respectively, compared with those grown without rice. The number of tillers and leaves, leaf area, aboveground shoot biomass, root biomass, and seed production of Chinese sprangletop were affected by water regime. A study conducted on bearded sprangletop [*Leptochloa fusca* (L.) Kunth) var. uninervia (J. Presl.) N. Snow] revealed that this species exhibits high rates of N fixation. It was observed that 60 to 80% of the plant N was derived from atmospheric fixation (Malik et al. 1987). It could be because of this reason that the effect of N rates, even at 150 kg N ha^{-1}, was not significant on several growth parameters of Chinese sprangletop.

Results showed that inflorescence biomass production of Chinese sprangletop was greatly reduced (99%) with increasing rice density up to 32 plants pot^{-1}, but even then, plants produced 0.02 g inflorescence biomass plant^{-1}. After leaf, inflorescence was the second plant part to which Chinese sprangletop allocated more biomass under water stress conditions. Under aerobic conditions, the inflorescence weight ratio of Chinese sprangletop was around two times more than that under saturated conditions when grown with 32 rice plants pot^{-1}. Although we did not estimate the seed production of Chinese sprangletop in different water regime treatments because of its very small seed size, the inflorescence biomass data suggest that Chinese sprangletop can produce a considerable amount of seeds, even at severe rice–Chinese sprangletop competition under aerobic conditions. Our results are in line with a previous study on barnyardgrass, in which seed production was reduced by 82 to 87% when grown with rice at a density of 16 rice plants pot^{-1} (approximately 80 kg seed ha^{-1}), and the weed still produced 420 to 500 seeds plant^{-1}(Chauhan and Abugho 2013b). Our findings are supported by previous studies, where itchgrass and junglerice [*Echinochloa colona* (L.) Link] produced a small amount of seeds even at 12.5% of the field capacity, and the authors suggested that a small amount of seeds per plant might be enough to cause heavy infestation in the

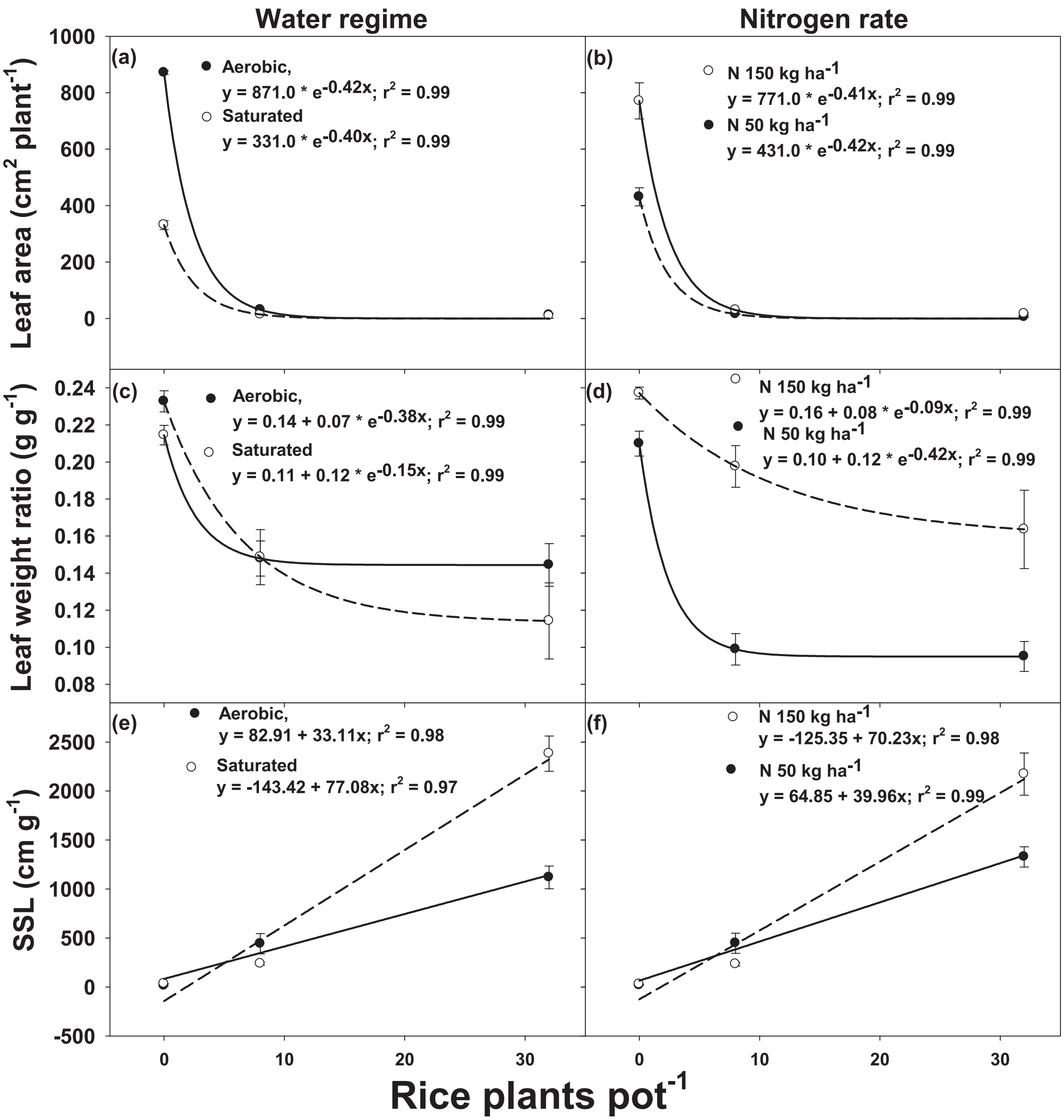

Figure 4. Leaf area (a, b), leaf weight ratio (c, d), and specific stem length (SSL) (e, f) of Chinese sprangletop as affected by the interaction of water regime and rice planting density (a, c, e) and nitrogen rate and rice planting density (b, d, f). The vertical bars represent standard error of means. The lines represent exponential models [($y = a \times e^{-bx}$ for leaf area, $y = y0 + (a \times e^{-bx})$ for leaf weight ratio)] and a linear model ($y = a + bx$ for SSL) fitted to all data.

next growing seasons (Chauhan 2013; Chauhan and Johnson 2010b; Chauhan and Abugho 2013a). This capability of the weed to produce seeds under water-limited and severe rice–weed competition would enable Chinese sprangletop to survive in unpredictable environments.

Maximum leaf area (871 cm^2 $plant^{-1}$) was observed in Chinese sprangletop grown under aerobic conditions, which was 163% higher than Chinese sprangletop grown under saturated conditions (331 cm^2 $plant^{-1}$) (Figure 4a). The application of 150 kg N ha^{-1} produced a higher leaf area (771 cm^2 $plant^{-1}$) compared with the application of 50 kg N ha^{-1} (431 cm^2 $plant^{-1}$). Increased rice planting density reduced leaf area $plant^{-1}$, irrespective of N rate and water regime. Averaged over N rates and rice planting densities, the leaf area decreased by 96% and 98% when grown with rice densities of 8 and 32 plants pot^{-1}, respectively (Figure 4b).

Chinese sprangletop produced higher LWR, LAR, and inflorescence weight ratio (IWR) (data not shown) under aerobic than under saturated conditions. The Chinese sprangletop responded with increased LWR to a decrease in soil water

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content (or increase in water stress) (Figure 4c). Our results suggest that, because of phenotypic plasticity, Chinese sprangletop under aerobic conditions allocated more biomass to the leaf than to other shoot parts. Our results are in line with an earlier study on itchgrass, in which LWR at 12.5% of the field capacity was 2.5 times greater than at 100% of the field capacity (Chauhan 2013). In another study, spiny amaranth (*Amaranthus spinosus* L.) increased LWR as a response to a decrease in soil water content (Chauhan and Abugho 2013a).

Specific stem length (SSL) increased linearly with increasing rice planting density across water regimes and N rates (Figures 4e and 4f). The SSL of Chinese sprangletop was highest when grown with 32 rice plants pot^{-1} regardless of the N rate and water condition. Averaged over N rates, when Chinese sprangletop was grown with 32 rice plants pot^{-1}, SSL was 113% higher under saturated than under aerobic conditions. Averaged over water regimes, when Chinese sprangletop was grown with 32 rice plants pot^{-1} and fertilized with 150 kg N ha^{-1}, the SSL of Chinese sprangletop was 64% higher than those fertilized with only 50 kg N ha^{-1}. Under aerobic conditions, SSL increased by 33 and 86 times when Chinese sprangletop plants were grown with rice at densities of 8 and 32 plants pot^{-1}, respectively, relative to the Chinese sprangletop plants grown without competition. The corresponding values under saturated conditions were 7 and 72 times, respectively (Figure 4e). At 50 kg N ha^{-1}, rice densities of 8 and 32 plants pot^{-1} increased the SSL of the Chinese sprangletop plant by 25 and 74 times more than the SSL of the plants grown without rice; the corresponding values at 150 N kg ha^{-1} were 8 and 78 times, respectively (Figures 4e and f).

The SSL of Chinese sprangletop increased several times with increasing rice density, regardless of the water regime and N rate. Similar findings were reported in an earlier study on rice flatsedge (*Cyperus iria* L.) and barnyardgrass, in which SSLs increased with increases in rice planting density (Chauhan and Johnson 2010a). Our study showed that under rice–Chinese sprangletop competition, Chinese sprangletop exhibits a phenotypic plasticity. Due to increased SSL, the leaves of Chinese sprangletop were not exposed to low light stress, and therefore, its SLA and LAR were not affected by increasing rice density. Plants with shade-avoiding syndrome, such as Chinese sprangletop, show phenotypic plasticity. Such plants increase SSL as their coping mechanism when there is a reduction in solar radiation within the canopy because of high crop density. Higher SSL under shaded and nonstressed conditions means that Chinese sprangletop has the ability to increase shoot length per allocated biomass and put its leaves at the top of the rice canopy to intercept light for photosynthesis. Such a phenotypic plasticity in plants enables them to alter their morphology to increase the use of most growth-limiting resources (Chauhan and Johnson 2010a; Gibson et al. 2001). As a shade-avoidance syndrome, this might be a survival strategy of this Chinese sprangletop in water-limited environments. This strategy could help Chinese sprangletop to survive, avoid shading (imposed by crop interference), and produce enough photosynthates to boost its height and put its leaves on the rice canopy (Caton et al. 1997). The ability of Chinese sprangletop plants to alter their morphology by modifying LWR, SSL, and RSWR makes them more competitive with the crop (Gibson and Fischer 2001; Gibson et al. 2001), even when weeds germinate later than rice in the field (Marenco and Reis 1998; Vourlitis and Kroon 2013).

When grown without rice, Chinese sprangletop growth parameters were higher in aerobic than in saturated conditions. In competition with rice, all growth parameters were similar between two water regimes, but they decreased with increasing rice planting density. The results of this study do not conform to earlier findings on barnyardgrass, in which different growth parameters were higher under flooded conditions than under the aerobic regime (Chauhan and Abugho 2013b). The reason might be that barnyardgrass is a lowland weed and grows well under flooded conditions (Diop and Moody 1984). In another study, regardless of N rate, growth parameters of barnyardgrass did not vary between water regimes when it was grown in competition with rice; however, biomass declined by 38 to 68% and 83 to 85% when the weed was grown with 4 and 16 rice plants pot^{-1}, respectively (Chauhan and Abugho 2013b). Our results are consistent with earlier studies on other weed species, in which total shoot biomass decreased with increased rice seeding rate and reduced light (Caton et al. 1997; Chauhan 2013; Chauhan and Johnson 2010a).

Results showed that Chinese sprangletop has the capability to produce more biomass under aerobic (water stress) than under saturated conditions, whereas the opposite was found true for rice plants. Chinese sprangletop uses the C_4 photosynthetic

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pathway, whereas rice uses the C_3 pathway. Compared to C_3 plants, C_4 plants have higher water productivity and they minimize water loss in dry and hot weather, improve photosynthetic efficiency, and overcome the limitation of photorespiration (Edwards and Walker 1983). Ozturk et al. (1981) studied the effect of water availability on competition between C_3 and C_4 plant species, and concluded that C_4 plant species were more productive than C_3 species under dry conditions. If weeds are more efficient water-users than rice, a limited amount of water in the soil would benefit weeds more than the crop (Janiya and Moody 1991). In water-limited environments, weed infestation not only decreases rice yield but also causes water stress in rice, in turn causing a need for higher doses of herbicides to control weeds (Steptoe et al. 2006). The reason might be that in water-limited conditions, weed plants can develop a thicker and stiffer leaf cuticle that can lessen herbicide entry into the leaves (Patterson 1995).

Results of this study clearly demonstrated that N fertilization will not increase the growth of Chinese sprangletop when grown in competition with rice, and rice will have a chance to get maximum benefits from applied N fertilizer. Irrespective of the water regime and N rate, increasing the crop seeding rate can greatly reduce the growth and reproduction of Chinese sprangletop. Such results suggest that increasing seeding rates can suppress Chinese sprangletop growth in both low- and high-water and N-input farming systems. Our findings also support the recommendation that weed-competitive rice cultivars should be planted densely and in narrow rows to suppress weed biomass accumulation (Chauhan and Johnson 2010a; Zhao et al. 2007). Although crop interference alone cannot provide the complete control of Chinese sprangletop, it can suppress and reduce weed biomass considerably, which can then be easily eradicated through manual weeding or controlled using other weed management practices.

An understanding of the effects of water stress on rice–weed competition and on improving herbicide efficacy in rice weeds can help in formulating economical and effective weed management tactics. Such research becomes more important, particularly in the scenario of climate change. Direct-seeded rice growers should exploit weed management strategies, including the use of weed-competitive and drought-tolerant cultivars, high seeding rates, and optimum application timing and doses of fertilizer, to minimize weed interference in water-limited environments.

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