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Phenotypic Plasticity of Spiny Amaranth (*Amaranthus spinosus*) and Longfruited Primrose-Willow (*Ludwigia octovalvis*) in Response to Rice Interference

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The growth of spiny amaranth and longfruited primrose-willow was studied by growing them alone and in competition with 4 and 12 rice (cv. RC222) plants. Interference with 12 rice plants reduced the height of spiny amaranth beyond 6 wk after planting. The height of longfruited primrose-willow was significantly reduced by the crop interference starting from 4 wk after planting. Both weed species showed the ability to reduce the effects of rice interference by increasing leaf area, leaf and stem biomass in the upper half of the plant, and specific stem length. At 9 wk after planting, for example, longfruited primrose-willow had 89 and 99% leaf biomass in the upper half of the plant when grown with 4 and 12 rice plants compared with only 34% when grown alone. These values for spiny amaranth were 15, 29, and 72% when grown alone, with 4 rice plants, and 12 rice plants, respectively. Despite such plasticity, spiny amaranth's aboveground biomass at final harvest was reduced by 34 and 70% when grown with 4 and 12 rice plants, respectively, compared with its biomass without crop interference. The corresponding values for longfruited primrose-willow were 92 and 98%, respectively. These results suggest that uniform and high crop density could be an important tool to reduce competition from these weeds in direct-seeded rice.

Nomenclature: Spiny amaranth, *Amaranthus spinosus* L., AMASP; longfruited primrose-willow, *Ludwigia octovalvis* (Jacq.) Raven, LUDOC; rice, *Oryza sativa* L.

Key words: Crop interference, leaf area, biomass, direct-seeded rice.

Rice is a principal source of food for more than half of the world's population, especially in Asia. Recently, due to high labor and production costs, the crop establishment method has been or is being changed from manual transplanting of rice seedlings to direct seeding of rice in many Asian countries (Pandey and Velasco 2005). However, weeds are the major constraint to rice production in direct-seeding systems because of the absence of a seedling size differential between the weed and the crop and the absence of standing water in the early stages of crop establishment. Herbicides are used to manage weeds in these systems, but there is a risk of resistance development in weeds, and there are concerns about the high cost of new chemicals, availability of new herbicide products, and the environment (Chauhan and Johnson 2010a). These concerns, which are related to reliance on herbicides, have led to increased interest in the use of cultural practices in integrated weed management programs. However, the use of these practices in direct-seeded rice has been limited by inadequate knowledge of basic weed biology.

Spiny amaranth, a C_4 species, is widespread in tropical and subtropical regions of the world and has been reported to occur in 28 crops in 44 countries (Holm et al. 1991). It is a principal and troublesome weed of upland rice, corn (*Zea mays* L.), cotton (*Gossypium hirsutum* L.), peanuts (*Arachis hypogaea* L.), soybean [*Glycine max* (L.) Merr.], and vegetables. In recent studies in the Philippines, spiny amaranth was one of the dominant weed species present in aerobic rice systems (Chauhan and Johnson 2011; Chauhan et al. 2011b). A single plant of spiny amaranth can produce 114,000 seeds (Sellers et al. 2003), and seeds can germinate at a high concentration of salt (Chauhan and Johnson 2009a). In addition, the spines present on the plant cause problems during hand weeding and hand harvest.

Longfruited primrose-willow, a C_3 species, is a common weed of transplanted and direct-seeded rice systems in Asia and Africa, and it can be a problematic weed species where the soil is subjected to intermittent flooding in the early stages of the crop (Moody 1989; Chauhan and Johnson 2009b). The plants of longfruited primrose-willow flower all year in the Philippines, and a single plant can produce more than 375,000 seeds (Pancho 1964). In spite of the importance of spiny amaranth and longfruited primrose-willow in rice, relatively little information is available on the effects of rice interference on growth of these weed species under direct-seeded conditions.

The allocation of leaf or stem biomass of a plant may be different when it is grown with or without crop interference (Håkansson 2003). In a recent study, for example, ludwigia [*Ludwigia hyssopifolia* (G. Don) Exell], a closely related species to longfruited primrose-willow, showed the ability to reduce the effects of rice interference by increasing stem and leaf biomass in the upper half of the plant and increasing specific stem length (Chauhan et al. 2011a). Although such information on weeds is widely assumed, it has not been studied in spiny amaranth and longfruited primrose-willow. A better understanding of spiny amaranth and longfruited primrose-willow response to competition is required to improve the cultural methods that rely on crop interference. The major objective of this study was to determine the effects of rice interference on the growth of spiny amaranth and longfruited primrose-willow.

Materials and Methods

Plant Material and Culture. Seeds of spiny amaranth and longfruited primrose-willow were collected in June 2007 and January 2010, respectively, from several rice fields in Los Baños, Philippines. The experiments were begun on March 8 and May 17, 2011 (for spiny amaranth), and April 15 and June 24, 2011 (for longfruited primrose-willow), in a screenhouse. The experiments were conducted by growing

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plants in 25-cm-diam pots filled with 9 kg of soil. The soil (silt loam) used in the experiments had a pH of 6.6; organic carbon of 2.7%; and sand, silt, and clay contents of 24, 52, and 24%, respectively. Nitrogen (urea) was applied at 80 kg ha^{-1} in three split applications as 30, 30, and 40% at 2, 4, and 8 wk after planting (WAP), respectively (Chauhan et al. 2011a). Insect or disease problems were not observed during the experimental period, and no control measures were undertaken.

Sampling. Individual plants of each weed species were grown alone and with 4 and 12 rice (cv. RC222) plants in the pots. The selected rice densities represent different levels of shading caused by crop competition after canopy closure and were equivalent to 20 and 60 kg rice seed ha^{-1}. These seeding rates are used for direct-seeded rice. Four to five weed seeds were sown at the center of each pot. Rice seeds were sown equidistantly from each other at a distance of 5 cm from the weed seeds. Rice and weed plants took 3 to 5 d to emerge. Plants were subsequently thinned to the desired number of plants (one plant for weed species, and 4 or 12 plants for rice) immediately after emergence. The pots were irrigated daily such that water was not limiting.

Rice and each weed species were harvested weekly starting from 4 to 9 WAP. Weed and rice height was measured from the soil surface to the tip of the uppermost leaf. Weed plants were removed from the pots and the main stem was divided into two parts, lower and upper halves (Chauhan et al. 2011a). The leaf area of each part was measured with a leaf area meter (LI-3100 C Area Meter, LI-COR Inc., Lincoln, NE). Lamina and petiole parts were considered as a leaf. The dry biomass of leaf and stem in the upper and lower halves of the weed plants was measured separately by oven-drying samples at 70 C for 72 h. In addition, specific stem length (SSL, plant height per unit of stem biomass, cm g^{-1}) was calculated at each harvest.

Statistical Analysis. The treatments were arranged in a randomized complete block design with four replications. The experiment with each weed species was repeated. ANOVA indicated no significant interactions between treatments and experimental trials; therefore, the data were pooled over the two trials (a total of eight replications) for further analysis (GenStat 8.0 2005). Data variance was visually inspected by plotting residuals to confirm homogeneity of variance before statistical analysis. After ANOVA, means at each harvest time were separated using Fischer's protected LSD at $P = 0.05$.

Results and Discussion

Plant Height. Plant height of spiny amaranth was significantly reduced by rice interference beyond 6 WAP (Figure 1A). Plants grown alone were taller than plants grown with 12 rice plants, but there was no difference between weed plants grown alone and plants grown with four rice plants. The results suggest that the height of spiny amaranth can be suppressed by planting rice at high crop density (60 kg ha^{-1} in this study). Use of low seeding rate with no other weed management practice may not suppress the height of spiny amaranth.

Plant height of longfruited primrose-willow was significantly reduced by rice interference, and plants grown alone were always taller than plants grown with 12 rice plants (Figure 1B). The height of weed plants grown with four rice plants was reduced only beyond 6 WAP. At 9 WAP, interference with 4 and 12 rice plants reduced longfruited primrose-willow height by 25 and 41%, respectively, compared with longfruited primrose-willow grown alone.

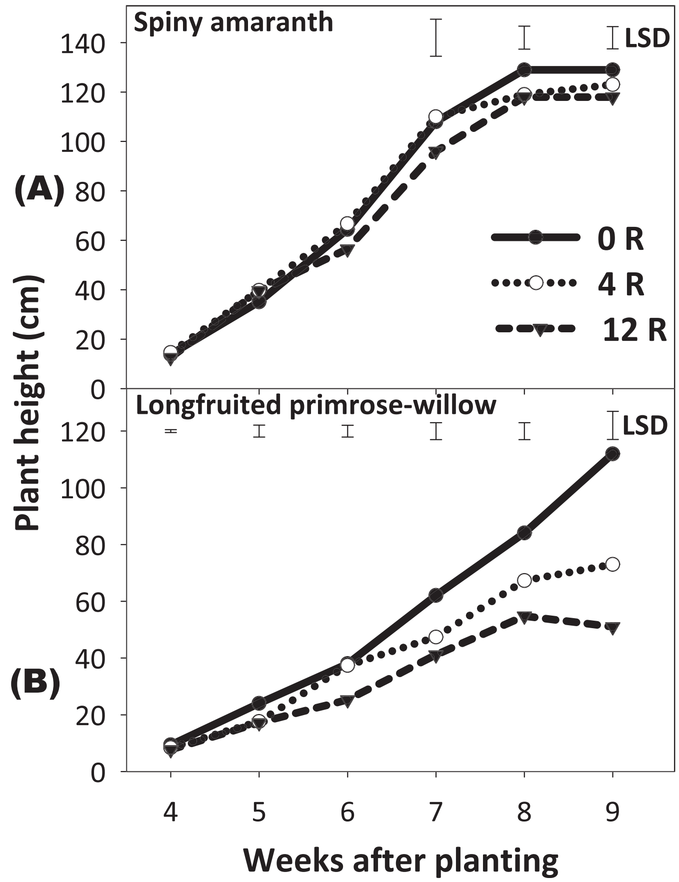

Figure 1. Plant height of spiny amaranth (A) and longfruited primrose-willow (B) when grown alone (0 R) or in competition with 4 (4 R) and 12 (12 R) rice plants.

Leaf Area and Biomass. Rice interference greatly influenced the leaf area of both species (Figures 2A and 2D). At 9 WAP, when grown with 4 and 12 rice plants, leaf area of longfruited primrose-willow was reduced by 89 and 97%, respectively, as compared with plants grown alone (Figure 2D). Spiny amaranth leaf area declined by 43 and 75% at these levels of crop interference (Figure 2A). As in the response of weed leaf area to crop interference, total shoot biomass was greatly reduced by rice interference. At 9 WAP, shoot biomass of spiny amaranth was reduced by 34 and 70% when grown in competition with 4 and 12 rice plants compared with the weed plants grown alone (Figure 2B). Longfruited primrose-willow shoot biomass was reduced by 92 and 98% when grown in competition with 4 and 12 rice plants, respectively (Figure 2E). These results show that longfruited primrose-willow biomass can be suppressed effectively by using low seeding rates (e.g., 20 kg ha^{-1}). However, to reduce the biomass of spiny amaranth, high seeding rates need to be used.

At 5 WAP and during later harvests, spiny amaranth grown alone had lower SSL than those grown with 4 and 12 rice plants and, by the last harvest (9 WAP), SSL of spiny

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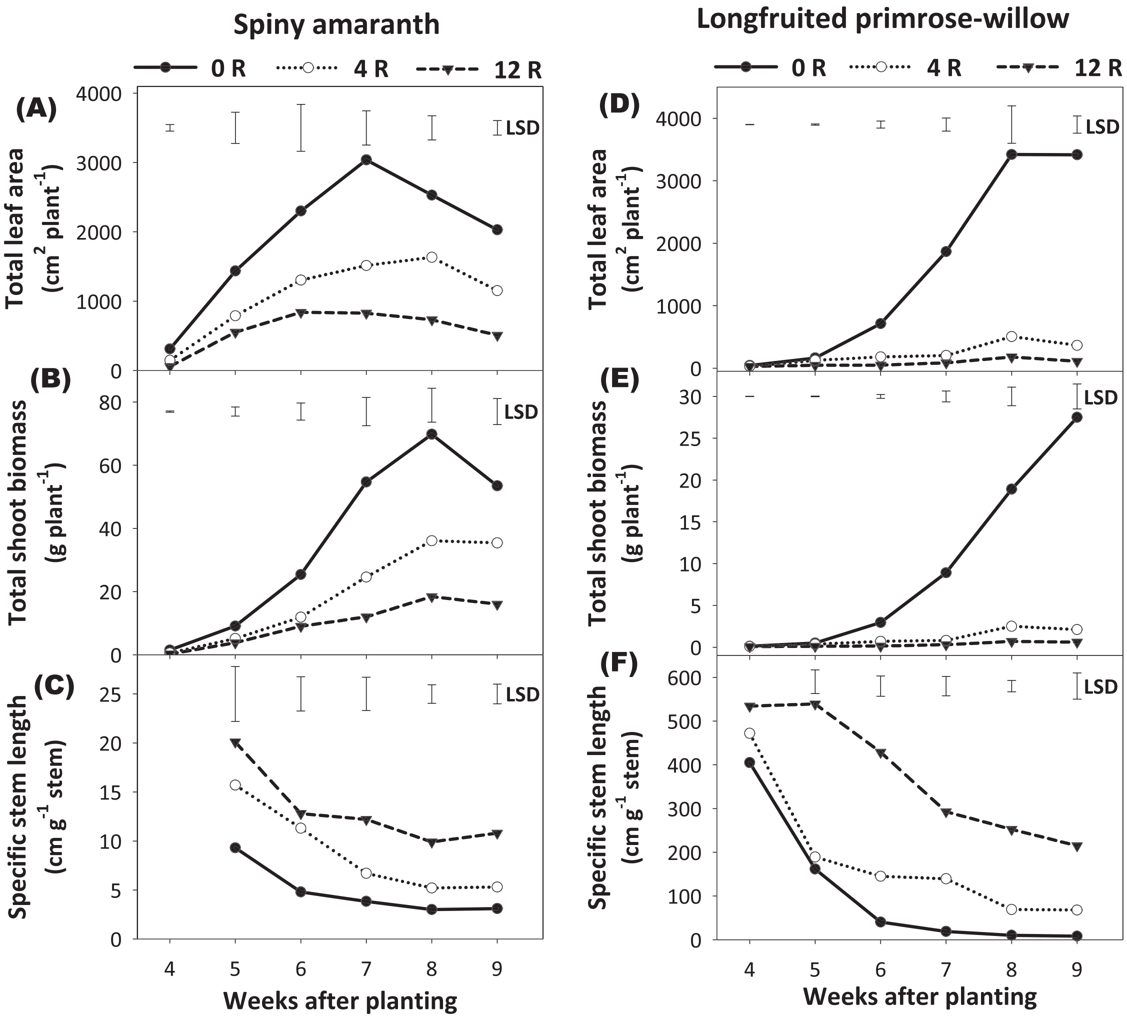

Figure 2. Total leaf area (A, D), total aboveground shoot biomass (B, E), and specific stem length (C, F) of spiny amaranth and longfruited primrose-willow when grown alone (0 R) or in competition with 4 (4 R) and 12 (12 R) rice plants.

amaranth grown alone was 58 and 29% of the plants grown with 4 and 12 rice plants, respectively (Figure 2C). A similar response was observed for longfruited primrose-willow (Figure 2F). At the last harvest, for example, SSL of longfruited primrose-willow grown alone was 12 and 4% of the plants grown with 4 and 12 rice plants, respectively.

Spiny amaranth plants grown with rice had greater leaf area and leaf and stem biomass in the upper half of the plants than weed plants grown without rice interference (Figures 3–C). At 9 WAP, for example, spiny amaranth plants grown with 12 rice plants had 70 and 72% of their leaf area and leaf biomass in the upper half of the plant, whereas the weed plants grown alone had only 14 and 15% of leaf area and leaf biomass, respectively, in the upper half of the plant (Figures 3A and 3B). The stem biomass in the upper half of the spiny amaranth plants when grown alone decreased with the progress in weed growth (Figure 3C). At 9 WAP, the spiny amaranth plants had only 12% of stem biomass in the upper half of the plant, whereas the weed plants grown with 4 and 12 rice plants had 19 and 32% stem biomass, respectively, in the upper half of the plant (Figure 3C). At this harvest time, spiny amaranth plants grown with four rice plants had 27 and 29% of its leaf area and leaf biomass in the upper half of the plant.

Similar to results observed for spiny amaranth, longfruited primrose-willow plants grown with rice also had greater leaf area and leaf and stem biomass in the upper half of the plants than weed plants grown without rice interference (Figures 3–C). At 9 WAP, longfruited primrose-willow plants grown alone had only 27% of leaf area in the upper half of the plants, whereas weed plants grown with 4 and 12 rice plants had 86 and 99% of leaf area in the upper half (Figure 3A). Similarly, longfruited primrose-willow plants grown with crop interference had greater leaf and stem biomass in the upper half of the plant than those grown without crop interference (Figures 3E and 3F). Similar results were reported for ludwigia: at 11 WAP, plants grown with 12 rice plants had 82% of its leaf biomass in the upper half of the plants, whereas plants grown alone had only 25% (Chauhan et al. 2011a).

Implications for Weed Management. Spiny amaranth and longfruited primrose-willow showed phenotypic plasticity response to crop interference. Both weeds responded with increased leaf area and leaf and stem biomass in the upper half of the plant and increased SSL when grown with rice interference. This kind of plasticity has been described as a common response of plants to shade (Patterson 1979), and such a strategy may help spiny amaranth and longfruited primrose-willow compete with other species for light. Both weeds in the current study also increased their SSL (plant

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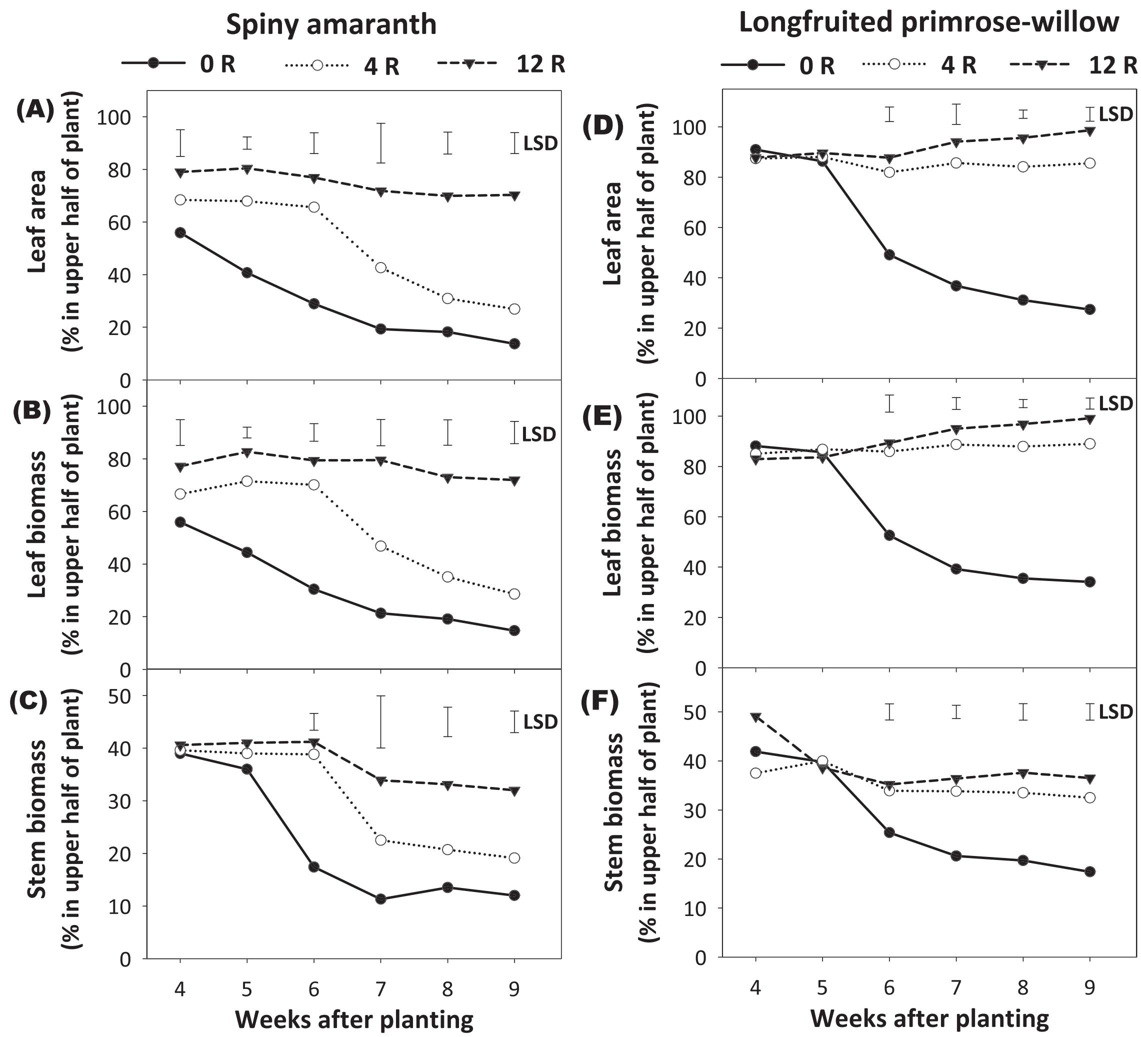

Figure 3. Proportion (%) of leaf area (A, D), leaf biomass (B, E), and stem biomass (C, F) in upper half of spiny amaranth and longfruited primrose-willow plants when grown alone (0 R) or in competition with 4 (4 R) and 12 (12 R) rice plants.

height per unit stem biomass) under crop interference, mainly due to decreased stem biomass. The increased SSL under crop interference may be a strategy to enable weeds to compete more effectively for light under such situations.

The aboveground shoot biomass of spiny amaranth and longfruited primrose-willow at final harvest was reduced by 34 and 92% when grown with four rice plants, and 70 and 98% when grown with 12 rice plants compared with those grown without crop interference. These results suggest that uniform and high crop density could be an important tool to reduce competition from these weeds, especially longfruited primrose-willow. The results also support the recommendations for high crop density and agronomic practices that encourage rapid canopy cover to suppress weeds (Chauhan and Johnson 2010a,b, 2011; Chauhan et al. 2011b). Previous studies with rice, wheat (*Triticum aestivum* L.), and barley (*Hordeum vulgare* L.) have also shown that increased seeding rates improve the ability of crops to suppress weeds and reduce yield loss under weedy conditions (Chauhan et al. 2011b; Ni et al. 2004; O'Donovan et al. 2001; Olsen et al. 2005).

This study illustrates the growth strategy of spiny amaranth and longfruited primrose-willow and their ability to survive at high levels of crop interference. However, the results also suggest that high levels of rice interference can effectively suppress the growth of these weeds, especially that of longfruited primrose-willow. Management practices should consider growth of weeds in response to competition and adjust inputs and management to achieve rapid canopy closure of rice.

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