Weed Technology

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Effects of competition from California weedy rice (*Oryza sativa* f. *spontanea*) biotypes on a cultivated rice variety

Elizabeth Karn[1], Teresa De Leon[2], Luis Espino[3], Kassim Al-Khatib[4] and Whitney Brim-DeForest[5]

[1]Staff Research Associate, University of California Division of Agricultural and Natural Resources, Cooperative Extension Sutter-Yuba Counties, Yuba City, CA, USA; [2]Postdoctoral Research Associate, Department of Plant Sciences, University of California, Davis, Davis, CA, USA; [3]Cooperative Extension Advisor, University of California Division of Agricultural and Natural Resources, Cooperative Extension Colusa County, Colusa, CA, USA; [4]Professor and Cooperative Extension Specialist, Department of Plant Sciences, University of California, Davis, Davis, CA, USA and [5]Cooperative Extension Advisor, University of California Division of Agricultural and Natural Resources, Cooperative Extension Sutter-Yuba Counties, Yuba City, CA, USA

Research Article

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Author for correspondence:
Whitney Brim-DeForest, Associate Cooperative Extension Advisor, University of California Division of Agricultural and Natural Resources, Cooperative Extension Sutter-Yuba Counties, 142A Garden Hwy, Yuba City, CA 95991.
(Email: wbrimdeforest@ucdavis.edu)

Abstract

Weedy rice is an emerging problem of cultivated rice in California. Infestations of weedy rice in cultivated rice result in yield loss and reduced grain quality. In this study, we aimed to evaluate growth and yield components of a widely grown cultivated rice variety in California in response to weedy rice competition. Greenhouse competition experiments in an additive design were conducted in 2017 and 2018 to determine the growth and yield components of 'M-206' rice and five weedy rice biotypes found in California at varying weed densities. M-206 rice initially grew at a faster relative growth rate of 0.53 $\mathrm{cm^{-1}\ wk^{-1}}$ under competitive conditions compared with 0.47 $\mathrm{cm^{-1}\ wk^{-1}}$ in the absence of weedy rice, but absolute and relative growth rates declined more rapidly under competitive conditions as plants approached maturity. At harvest, M-206 plant height was reduced 13% under competitive conditions, and M-206 tiller number was reduced 23% to 49%, depending on the weedy rice biotype it was competing with. Except for 100-grain weight, the growth traits and grain yield components of M-206 rice were reduced with increasing density of weedy rice. At the highest weed density measured, 40 plants $\mathrm{m^{-2}}$, M-206 rice had yield losses of 69% grain yield $\mathrm{plant^{-1}}$, 69% panicle weight, 59% fresh and dry biomass, 55% grain yield $\mathrm{panicle^{-1}}$, and 54% panicle number. The five evaluated weedy rice biotypes varied widely in early growth rates, height, biomass production, and grain yield, indicating differing competitive strategies. Most weedy rice biotypes produce plants with greater plant height, tiller number, panicle number, and above- and below-ground biomass compared with cultivated rice. Weedy rice biotypes produced 45% to 57% higher grain yield per plant than M-206 rice under competitive conditions.

Introduction

Rice is one of the most important crops, providing food for billions of people worldwide. Rice is grown in a wide variety of agroecosystems with diverse management strategies and constraints (Global Rice Science Partnership 2013). Weedy rice, also called red rice, is a conspecific relative of cultivated rice that infests cultivated rice fields (Langevin et al. 1990) and has likely been present in rice production since rice was first domesticated in Asia (Wedger and Olsen 2018). It has become more problematic with the modern shift from traditional hand transplanting and hand weeding to direct-seeding cultivation and mechanized farming (Chauhan 2013). Weedy rice is currently a pest in almost every rice-growing region in the world, including in the United States (Londo and Schaal 2007), southern Europe (Fogliato et al. 2011), South America (Merotto et al. 2016), Asia (He et al. 2017; Qiu et al. 2014; Sun et al. 2013), and Africa (Federici et al. 2001). Weedy rice biotypes vary phenotypically in different regions, but are typically characterized by red pericarp, high rates of seed shattering, and high rates of seed dormancy (Gealy 2005; Huang et al. 2017; Noldin et al. 1999).

Weedy rice presents unique challenges to weed management in rice. It is phenotypically similar to cultivated rice during the vegetative stage, making it difficult to identify until late in the growing season. The phenotypic and physiological similarities of weedy rice to cultivated rice make it difficult to control in season with either hand weeding or chemical weed control methods. In some rice-growing systems, cultivated rice varieties bred to be resistant to imidazolinone or quizalofop herbicides allow for the use of these herbicides during the growing season to control weedy rice (Lancaster et al. 2018; Tan et al. 2005). Weedy rice is not naturally resistant to these herbicides, although there are concerns about movement of herbicide-resistance traits

Table 1. Descriptions of the five weedy rice biotypes from California used in this study.

Biotype	Hull color	Awns	Grain size	Counties present, as of 2018
1	Strawhull	Absent	Short	Butte, Glenn, Placer, San Joaquin, Sutter, Yuba
2	Bronzehull	Absent	Medium	Butte, Glenn, Sutter, Yuba
3	Strawhull	Long	Medium	Colusa, Glenn
4	Blackhull	Long	Short	Glenn
5	Strawhull	Partially awned or absent	Medium or long	Butte, Sutter, Yuba

from cultivated rice into the weed (Burgos et al. 2008; Singh et al. 2017b). These herbicide-resistant traits are not available in all rice-growing regions, including California. Rather, weedy rice in these regions must be controlled through cultural practices, such as using a stale seedbed, planting clean seed, hand pulling, or fallowing.

Weedy rice is highly competitive with cultivated rice. Weedy rice seedlings from a population in China had a higher photosynthetic rate than did cultivated rice, allowing for vigorous early growth (Dai et al. 2016). Weedy rice from the southern United States grows taller than cultivated rice varieties and produces more tillers and biomass (Estorninos et al. 2005). It has higher nitrogen use efficiency when in competition with cultivated rice (Chauhan and Johnson 2011), absorbing up to 60% of applied nitrogen and reducing the amount of nitrogen available to the crop (Burgos et al. 2006). The higher nitrogen use efficiency of weedy rice is possibly related to more root growth and a stress-adaptive mechanism related to nitrogen and sucrose availability (Sales et al. 2011).

Studies of yield loss due to weedy rice competition indicate maximum yield losses from 49% to 90% (Estorninos et al. 2005; Marambe and Amarasinghe 2000; Shivrain et al. 2009), depending on experimental conditions, cultivar, and weed biotype. Yield loss increases with later rice planting dates and higher weed density in the southern United States (Shivrain et al. 2009). The impact of weedy rice on cultivated rice yield also depends on the rice variety. Cultivated varieties that are taller, produce more tillers, and have greater leaf area generally are more competitive against weedy rice (Estorninos et al. 2002; Kwon et al. 1992). Cultivated rice in China is more competitive against weedy rice when direct seeded rather than transplanted (Cao et al. 2007). The competitive ability of weedy rice can also vary greatly between weedy biotypes (Dai et al. 2013; Estorninos et al. 2005), with variation in seed size, timing of seedling emergence, plant height, shoot biomass, time to flowering, and time to maturation affecting competition with cultivated rice (Chauhan and Johnson 2011; Gealy et al. 2000; Shivrain et al. 2010; Zhao et al. 2018). In addition to rice yield loss, weedy rice infestations can reduce the value of harvested rice, due to reduced grain quality and contamination with red-bran rice (Shivrain et al. 2010; Singh et al. 2017a).

In California, weedy rice was reported in the 1930s, shortly after the beginning of commercial rice production in the region, and was hypothesized to have originated from contaminated seed transported from the southern United States (Bellue 1932). In the 1950s, weedy rice was thought to be eradicated (Miller and Brandon 1979) as a result of adopting a continuously flooded system and the use of certified seed. In 2003, however, a single biotype of weedy rice was reported in a dry-seeded rice field (Kanapeckas et al. 2016). Since then, weedy rice has been identified infesting more than 130 fields and 5,600 ha in California as of 2018 (Luis Espino, personal communication, August 4, 2019), consisting of several distinct biotypes. These biotypes are distinguishable from each other by phenotypic differences, including presence and length of awns, hull color, and grain size (Table 1). They are also genetically distinct and have separate origins from diverse rice ancestors (De Leon et al. 2019). Although the effects of weedy rice competition on cultivated rice yield has been studied for other locations and weedy rice biotypes, the effects of competition on growth and yield of California rice cultivars due to local weedy rice biotypes have not been previously investigated, to our knowledge.

To understand and quantify the effects of weedy rice infestation on cultivated rice, plant competition between cultivated rice and weedy rice in California was investigated in this study. The objectives of this study were to (1) measure the impact of weedy rice competition on cultivated rice growth and yield components using an additive design competition experiment, (2) examine how growth rates of cultivated and weedy rice are altered under competitive conditions, and (3) characterize the differing competitive strategies of weedy rice biotypes in California.

Materials and Methods

Weed Competition Experiment

The most widely grown rice variety in California (California Cooperative Rice Research Foundation 2019), ‘M-206’, a medium-grain, temperate japonica variety, was selected for this study, as were five weedy rice biotypes from California (Table 1). Weedy rice biotypes were obtained from rice fields in the northern Sacramento valley of California.

Competition growth experiments were conducted in a greenhouse because of a lack of field sites where weedy rice could be grown uncontrolled. An additive design competition experiment was conducted in a randomized complete block design. Blocks were planting time, and treatments were weedy rice density and weedy rice biotype. Each block consisted of 25 pots(18.9-L), each containing four M-206 rice plants, representing a density of 32 plants m^{-2}. Each pot also contained one of five weedy rice biotypes at a density of 0, 1, 2, 3, or 5 weedy rice plants pot^{-1}, representing a planting density of 0, 8, 16, 24, or 40 plants m^{-2}. Pregerminated rice was direct seeded into the pots. The experiment was repeated in time, with four successive plantings 2 wk apart in August and September 2017, in a greenhouse set at 33/17 C day/night temperature, 33%/84% relative humidity, and ambient light at the Rice Experiment Station in Biggs, CA. Pots were fertilized with 10 g pot^{-1} 15-15-15 NPK fertilizer 2 wk after planting and then kept at water saturation for the duration of the experiment. Beginning 1 wk after planting, the height and tiller number of each M-206 and weedy rice plant were measured weekly for 12 wk. At maturity 40 d after M-206 flowered, M-206 yield-component measurements were taken for plant height, tiller number, panicle number, panicle weight, seed weight adjusted to 14% moisture content, fresh biomass, and dry biomass. Panicle weight and fresh biomass were measured immediately after harvesting before seeds were removed and were not adjusted for moisture content.

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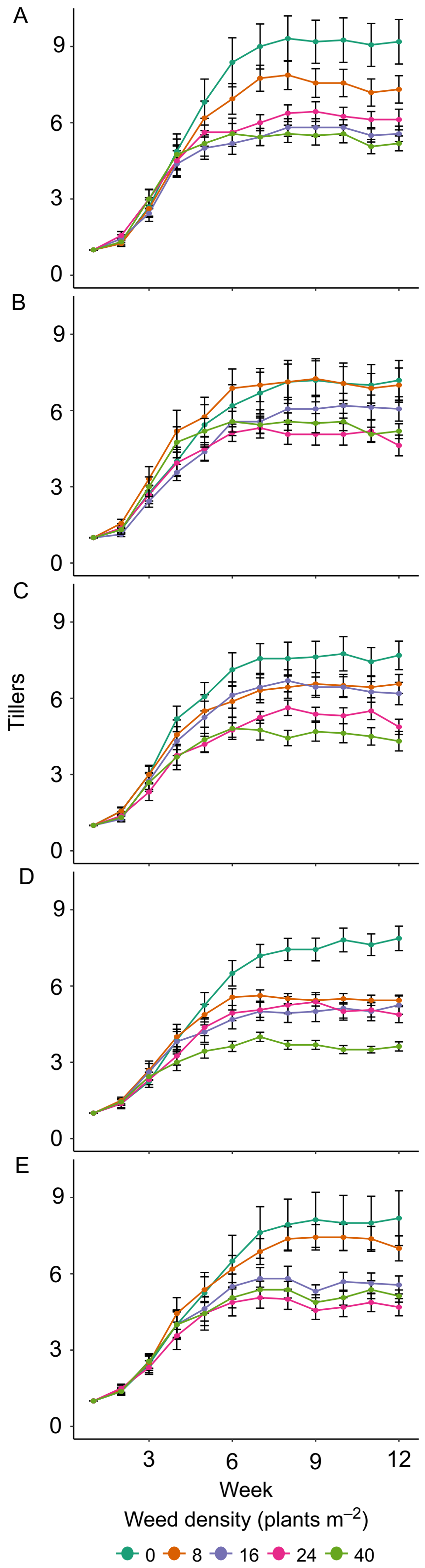

Figure 1. Weekly early growth measurements of M-206 rice tillers plant^{-1} when grown in competition with types (A) 1, (B) 2, (C) 3, (D) 4, (E) 5 weedy rice at varying weed density.

For 100-seed weight, weight was measured for pooled M-206 plants from each pot, because individual plants at high weed densities produced small quantities of seeds. Yield-component measurements for the high-density treatment of weedy rice biotypes were collected for plant height, tiller number, panicle number, panicle weight, fresh weight, and dry weight.

Data Analysis

Two-way ANOVA was conducted for weekly M-206 rice plant height and tiller number data with repeated measures to determine significance of block, weed biotype, and weed density at each week. R software, version 3.5.1 was used (R Foundation for Statistical Computing, Vienna, Austria). Differences among biotypes were tested by a Tukey honest significant difference (HSD) test. Harvest yield-component measurements were analyzed by ANOVA, and differences among biotypes were tested by a Tukey HSD test. Logarithmic transformation was applied when data did not meet normality or homogeneity of variance. For data that were transformed, detransformed means are reported with detransformed SEs. Weekly growth and harvest yield-component data for weedy rice were analyzed in the same manner for only the highest weed density treatment, because at lower weed densities, the weedy rice sample sizes were very small.

To more closely examine differences in M-206 growth at varying weed density treatments and between M-206 and weedy rice, relative growth rate analysis was conducted using the weekly plant height measurements. For comparison of M-206 growth with and without competition, data for competition from all weedy rice biotypes were combined because all biotypes affected M-206 height growth similarly, with no significant differences among weedy rice biotypes. Three-parameter logistic curves were fitted to M-206 weekly height data for the 0 and 40 plants m^{-2} treatments and to weedy rice measurements for 40 plants m^{-2} using the self-starting logistic model function SSlogis in R, using the following model:

$$\frac{dM}{dt} = rM\left(1 - \frac{M}{K}\right)$$

where M is plant height, r is growth rate, and K is the upper asymptote (Paine et al. 2012). Absolute growth rate and relative growth rate per unit time were calculated from the logistic function, following the method of Paine et al. (2012).

Results and Discussion

Effect of Competition on Rice

When grown in the absence of competition, M-206 rice plants initially grew rapidly before leveling off at 99.6-cm tall with 8.2 tillers at 12 wk as plants approached maturity (Figures 1 and 2). In the presence of weedy rice competition, M-206 tiller production during early growth was reduced by varying amounts by different weedy rice biotypes (Figure 1A–1E). For type 4, the lowest weed density tested of 8 plants m^{-2}, or 1 weedy rice plant pot^{-1}, resulted in a substantial reduction in tiller number from 7.9 tillers plant^{-1} to 5.4 tillers plant^{-1} by week 12 (Figure 1D). In contrast, the same density of type 2 or type 5 weedy rice resulted in a small and not significant decrease in tiller number at most time points (Figure 1B and 1E). At higher weed densities, competition from all five weedy rice biotypes resulted in a significant decrease in M-206 tiller production, with tiller numbers ranging from 4.3 tillers when competing with type 2 to 5.2 tillers when competing with type 5 at 12 wk after planting (Figure 1). Differences in tiller

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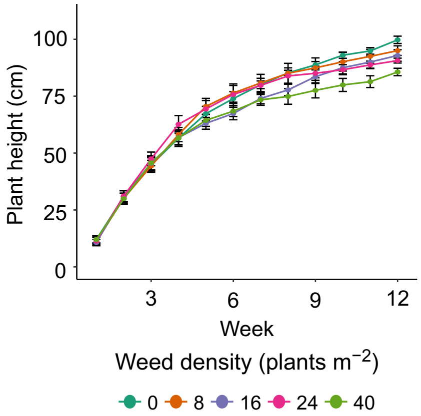

Figure 2. Weekly early growth measurements of M-206 rice height plant^{-1} when grown in competition with weedy rice biotypes at varying weed density. Effects of competition on rice height was not significant between biotypes.

number among weed density treatments became significant by week 3 for all five weedy rice biotypes (Figure 1A–1E).

Competition from all weedy rice biotypes resulted in similar trends of reduction in M-206 rice height with increasing density, with a maximum height reduction of 13% (Figure 2). Differences in height between weed density treatments became significant by week 2 and resulted in diverging plant height over time between weed density treatments.

To examine further the effects of weedy rice competition on M-206 growth, relative growth analysis was conducted for weekly plant height measurements in the absence of competition and at high weed density competition. Three-parameter logistic curves were fitted to plant height data (Figure 3A and 3D; Table 2). Absolute growth rate, calculated as change in plant height wk^{-1}, increased initially in the early weeks of growth (Figure 3), reaching a maximum rate of 13.6 cm wk^{-1} at 3.6 wk after planting in the absence of competition (Figure 3B; Table 2). M-206 growth peaked earlier under high competition conditions, at a growth rate of 13.8 cm wk^{-1} at 2.9 wk after planting (Figure 3E; Table 2). In both cases, absolute growth rate declined to approach 0 as plants approached mature size. The relative growth rate, calculated as change in plant height relative to the already accumulated height of the plant wk^{-1}, showed that rice grew fastest relative to its size initially and slowed over time (Figure 3C and 3F). M-206 growth was already affected by competition at the earliest measured growth stages, with an initial relative growth rate of 0.47 cm^{-1} wk^{-1} without competition (Figure 3C) versus 0.53 cm^{-1} wk^{-1} with competition (Figure 3F). Competition then resulted in a steeper decline in relative growth rate over time. This indicates that M-206 rice detects and responds to competition very early on, initially growing rapidly to compete with the weed. But this competition slows growth earlier and results in a shorter mature size than rice grown in the absence of competition.

Yield-component measurements at harvest of M-206 rice showed a negative impact of weedy rice competition on most yield components (Table 3). Some yield components were not very sensitive to weedy rice competition and decreased less than 30% with increasing weedy rice density. For example, competition reduced M-206 plant height by 14.4 cm averaged across all biotypes (Table 3). Competition from type 5 weedy rice reduced M-206 tiller number by 1.7 tillers plant^{-1}, and competition from type 1 weedy rice reduced M-206 yield panicle^{-1} by 0.9 g. In contrast, panicle number, total panicle weight, yield per plant, and aboveground biomass of M-206 rice were highly sensitive to weedy rice competition, with yield reduction of more than 50% for each yield component at 40 plants m^{-2} (Table 3). The greatest losses were observed for total panicle weight and yield plant^{-1}, with 69% yield reduction for each component. The exception to the trend of decreasing yield with increasing weed density was 100-seed weight, which did not decrease significantly (Table 3). Because M-206 rice has been bred to be a medium-grain variety, the size and weight of grains would not be expected to vary much. This result contrasts with that of a previous study of Asian weedy rice competition, in which seed weight declined with increasing weed density (Dai et al. 2013), but this may be attributable to differences in the rice cultivar.

Even at low weedy rice densities, competition resulted in large reductions in M-206 rice yield for some yield components. Yield plant^{-1} was reduced from 19.5 g at 0 plants m^{-2} to 11.8 g at 8 plants m^{-2} averaged across all biotypes, and panicle weight was reduced from 21.4 g to 12.9 g at the same densities (Table 3). These results agree with findings of a study of Asian weedy rice competition on cultivated rice yield using a replacement series experimental design in which weedy rice infestations of less than 20% relative density reduced the relative cultivated rice yield by more than 50% (Dai et al. 2013). Unlike in the southern United States, where significant numbers of severely infested fields have been reported (Burgos et al. 2008), California does not currently have any known fields with high-density weedy rice infestations. In a recent survey, California rice growers and pest control advisors reported only one or sparse patches of weedy rice per infested field (unpublished data). It is likely that such localized weedy rice infestations would have limited yield effects at the scale of a rice field. But these results do suggest that small infestations should be taken seriously by growers because they could locally affect rice yield in addition to contributing to future weedy rice infestations if not controlled.

Weedy Rice Competitive Strategies

Differences in the impact of weedy rice biotypes on M-206 yield components may be due to differences in the competitive abilities of biotypes to take up available resources required for M-206 growth. Overall growth patterns are similar between weedy rice biotypes and M-206 rice (Figures 1, 2, and 4), but weedy rice biotypes vary in their early growth and final yield components. Only the highest-density weedy rice treatment of 40 plants m^{-2} is considered here, because lower-density treatments had correspondingly smaller sample sizes. When grown in competition with M-206 rice, differences in height and tiller growth among weedy rice biotypes became significant by week 2 (Figure 4). By week 8, type 3 weedy rice produced 9.9 tillers plant^{-1}, whereas type 1 and type 5 produced only 6.3 and 6.6 tillers plant^{-1}, respectively (Figure 4B). Type 2 and type 4 weedy rice initially had high absolute height growth rates of 12.2 cm wk^{-1} and 12.5 cm wk^{-1}, respectively (Figure 5E and 5K). Although type 2 maintained its relatively tall plant height, type 4 weedy rice growth was decreased sharply due to competition (Figure 5L). Type 4 weedy rice reached its maximum growth rate earlier than other biotypes, at 2.7 wk after planting (Table 4).

Measurements of yield components of weedy rice at harvest showed significant phenotypic diversity among biotypes when grown in competition with M-206 rice. Most weedy rice biotypes were tall relative to M-206 rice, with an average final height of

Table 2. Calculated relative growth rate parameters for three-parameter logistic curves of M-206 plant height with no weedy rice competition and with high competition.

Weed density	Y_{max}[a]	SE	X_{mid}	SE	Scal	SE	R^2	AIC	RMSE
plants m^{-2}	cm		wk		wk				
0	98.5	0.9	3.6	0.07	1.89	0.08	0.7821	8451.45	453.652
40	83.4	0.7	2.9	0.06	1.63	0.07	0.7434	8140.05	405.055

[a] Abbreviations: AIC, Akaike information criterion of model; RMSE, root mean square error of model; Scal, scalar factor of the model equivalent to the inverse of growth rate at time X_{mid}; X_{mid}, time at which plants reach maximum absolute growth rate; Y_{max}, maximum plant height at maturity.

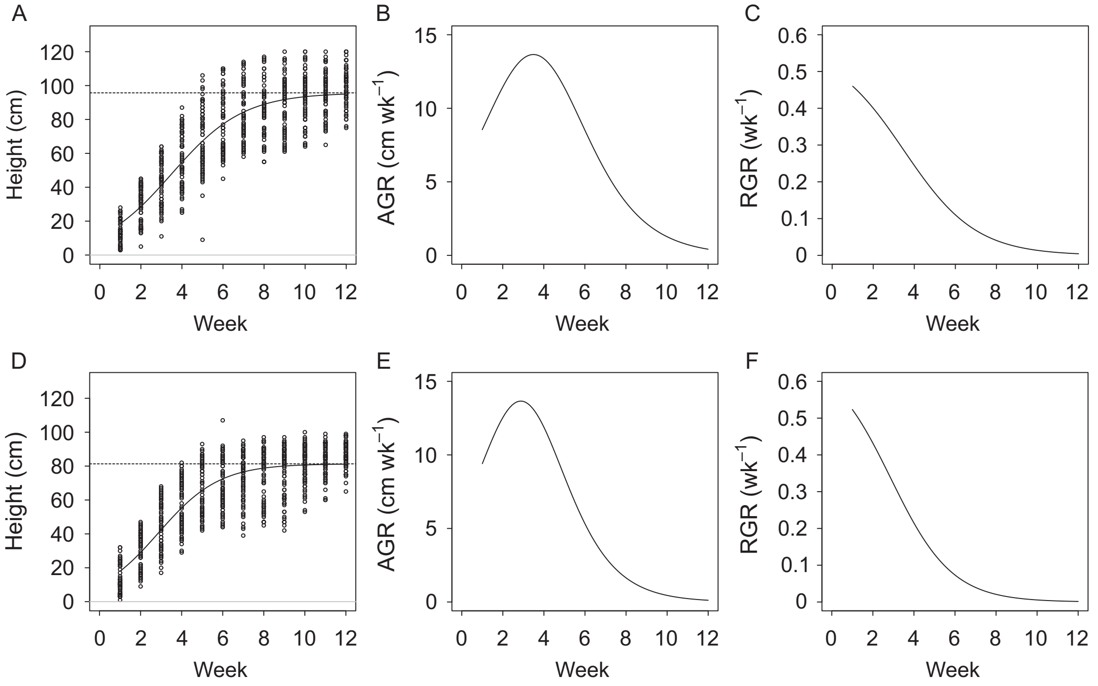

Figure 3. Growth rates of M-206 rice over time grown with (A–C) no weedy rice competition and with (D–F) high-density weedy rice competition, with logistic curves fitted to (A, E) plant height data; (B, E) absolute growth rate (AGR) over time; and (C, F) relative growth rate (RGR) per unit time.

109.4 cm across all biotypes versus 89.9 cm in M-206 under competitive conditions, although type 4 weedy rice was short, with a final height of only 78.9 cm (Tables 3 and 5). Weedy rice biotypes had correspondingly high or low biomass accumulation relative to plant height. Type 4 weedy rice produced the most tillers (11.6 tillers plant^{-1}) (Table 5) compared with 4.2 tillers in M-206 rice when competing with each other (Table 3). All weedy rice biotypes had higher yield plant^{-1} under high competition than did M-206 rice (Tables 3 and 5), indicating these biotypes are highly successful competitors. The wide variation in growth and yield components between weedy rice biotypes suggests multiple strategies for success as a weed with differing allocation of resources to height, tillering, or seed production. Tall plant height and tiller production, like that seen in many biotypes, may contribute to competitive ability in the current growing season, whereas the high allocation to seed production seen in type 3 could lead to a larger weedy-rice seed bank and more severe infestations in future growing seasons if not controlled effectively. Significant diversity in plant height, tiller and panicle production, and other yield and seed characteristics has been reported in previous studies of weedy rice from other regions, and these affect the competitive abilities of biotypes (Chauhan and Johnson 2011; Shivrain et al. 2010).

It is possible in some areas that multiple weedy rice biotypes could be present in the same field, and it is unclear whether the combined action of different weedy rice biotypes may result in greater yield loss, similar levels of yield loss as observed for each biotype alone, or if their competitive strategies may interfere with each other, resulting in lower M-206 yield loss. It is also unclear from this study how competitive California weedy rice biotypes would be against other cultivars of rice, because cultivars can differ in their competitive abilities (Estorninos et al. 2002). M-206 rice accounted for 46% of California rice acreage in 2018 (California Cooperative Rice Research Foundation 2019).

Additional study would be needed to determine whether the results of this greenhouse study translate into similarly high rice yield losses under field conditions. Field studies of weedy rice competition in other areas have shown yield losses ranging from 22% to 90% (Estorninos et al. 2005; Marambe and Amarasinghe 2000; Shivrain et al. 2009; Vidotto and Ferrero et al. 2005), putting the results of this greenhouse study in the top half of that range. Additional weedy rice experiments have recently begun in research fields. To limit the spread of weedy rice, weedy rice cannot be grown uncontrolled for yield-loss studies in grower fields. However, it is clear from the results of this study that California

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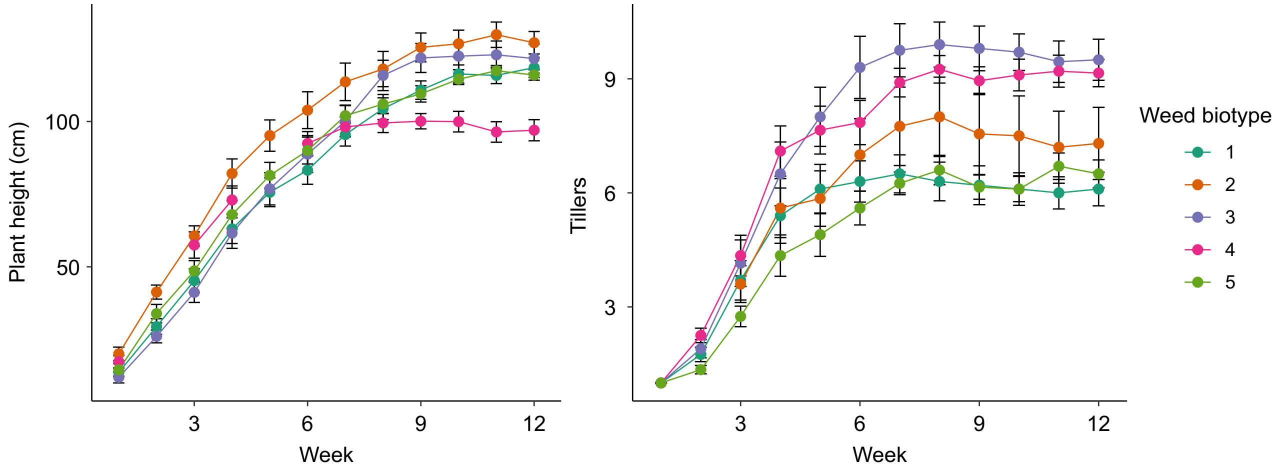

Figure 4. Weekly early growth measurements of plant (A) height and (B) number of tillers for weedy rice biotypes during the vegetative growth stage.

Table 3. Final measurements of yield components of M-206 rice at varying densities of competition from five weedy rice biotypes.

		M-206								
Weed density	Weedy rice biotype	Plant height	Tiller	Panicle	Total panicle weight	Yield panicle^{-1}	Yield plant^{-1}	Fresh biomass	Dry biomass	100-Seed weight
plants m^{-2}		cm	no.	no.	g					
0	1	103.7 ab	8.8	7.5	21.9	3.0	19.9	51.5	22.8	3.00
	SE	2.3	0.7	1.4	0.5	0.1	1.4	3.9	2.3	0.07
	2	102.8 a	7.7	6.4	22.0	3.4	19.7	43.8	18.0	2.98
	SE	1.1	0.8	1.9	0.5	0.2	1.7	4.0	1.5	0.10
	3	102.4 a	8.3	6.6	20.6	3.1	18.6	41.7	21.3	3.01
	SE	2.0	0.6	2.4	0.4	0.2	2.1	3.9	2.0	0.12
	4	110.8 b	8.3	6.3	20.4	3.3	19.0	44.2	23.4	3.02
	SE	1.6	0.6	1.6	0.3	0.2	1.6	3.5	2.4	0.19
	5	103.8 ab	8.0	7.1	24.3	3.5	22.1	46.3	22.2	3.04
	SE	2.1	1.0	2.9	0.9	0.3	2.7	5.1	3.1	0.14
8	1	99.0 ab	8.3 b	5.2	11.6	2.4	10.1	35.0	15.9	3.07
	SE	1.6	0.8	1.1	0.5	0.2	1.0	2.7	1.2	0.14
	2	95.2 a	6.5 ab	4.9	11.1	2.2	10.2	28.5	14.2	2.97
	SE	2.0	0.7	1.6	0.5	0.2	1.5	2.9	1.3	0.16
	3	100.0 ab	7.4 ab	5.6	14.9	2.7	13.7	33.3	16.9	3.00
	SE	1.0	0.5	1.1	0.3	0.2	1.1	3.1	1.6	0.15
	4	103.3 b	5.7 a	4.6	13.0	2.8	12.4	28.8	14.3	2.97
	SE	1.5	0.4	0.8	0.2	0.2	0.8	1.9	0.8	0.11
	5	99.3 ab	8.1 ab	4.8	13.7	2.8	12.5	34.0	16.8	3.05
	SE	2.1	0.7	1.6	0.3	0.2	1.5	1.8	2.0	0.10
16	1	96.2	5.8	4.4	11.0	2.5	9.9	27.9 ab	10.8	3.03 b
	SE	2.0	0.4	1.1	0.3	0.2	1.0	2.6	0.7	0.14
	2	101.4	6.6	3.9	9.7	2.4	8.9	27.2 ab	13.7	2.95 ab
	SE	2.5	0.6	0.8	0.4	0.2	0.7	2.8	1.3	0.19
	3	94.7	7.0	4.6	9.1	1.9	8.4	19.8 a	12.3	2.64 a
	SE	1.2	0.4	1.3	0.3	0.2	1.1	2.2	0.5	0.21
	4	95.9	6.3	3.7	8.9	2.5	8.0	30.4 b	14.7	3.10 b
	SE	2.7	0.6	1.1	0.3	0.2	0.9	2.7	1.7	0.12
	5	93.7	7.7	4.4	9.4	2.2	8.4	25.6 ab	11.7	3.01 b
	SE	2.9	0.9	0.8	0.3	0.1	0.7	1.8	1.1	0.15
24	1	94.4	6.4	4.3	9.3	2.2 ab	8.2	26.8	12.6	3.00
	SE	1.0	0.4	0.9	0.4	0.1	0.8	1.8	0.9	0.21
	2	91.3	4.5	3.8	7.5	1.9 a	6.8	20.0	8.9	3.08
	SE	1.5	0.3	0.8	0.2	0.2	0.8	2.3	0.7	0.14
	3	93.4	5.5	3.9	9.0	2.3 ab	8.2	20.7	10.8	3.08
	SE	1.5	0.4	0.5	0.1	0.1	0.5	2.4	0.9	0.16
	4	95.9	6.4	3.7	9.9	2.7 b	9.1	23.5	11.5	3.11
	SE	1.4	0.6	0.9	0.3	0.1	0.9	1.6	1.1	0.13
	5	94.1	6.6	3.4	7.8	2.3 ab	7.0	25.6	12.3	3.14
	SE	1.6	0.8	1.0	0.3	0.2	0.9	2.5	1.1	0.12
40	1	89.8	5.2 ab	3.0 ab	6.1 a	2.1	5.4 a	18.3 ab	8.5 ab	3.00
	SE	1.2	0.3	0.5	0.2	0.2	0.4	1.8	0.5	0.19
	2	90.1	5.1 ab	2.9 ab	5.7 a	2.0	5.1 a	16.3 a	7.1 a	3.03
	SE	1.6	0.4	0.4	0.2	0.1	0.4	1.3	0.3	0.19
	3	89.2	4.1 a	3.4 bc	6.6 ab	1.9	6.1 ab	14.1 a	7.8 a	3.13
	SE	1.5	0.3	0.5	0.2	0.1	0.5	1.2	0.7	0.14
	4	91.7	4.2 a	2.3 a	6.2 ab	2.2	5.6 ab	16.5 a	7.2 a	3.13
	SE	2.2	0.3	0.7	0.2	0.3	0.6	1.7	0.8	0.17
	5	88.8	6.3 b	4.0 c	8.7 b	2.2	7.9 b	24.1	10.8	3.09
	SE	1.1	0.5	0.8	0.3	0.2	0.8	1.8	0.6	0.17

[a]For measurements at weed densities where differences among biotypes were significant, letters indicate significant differences among biotypes at that weed density, determined by Tukey test (α = 0.05).

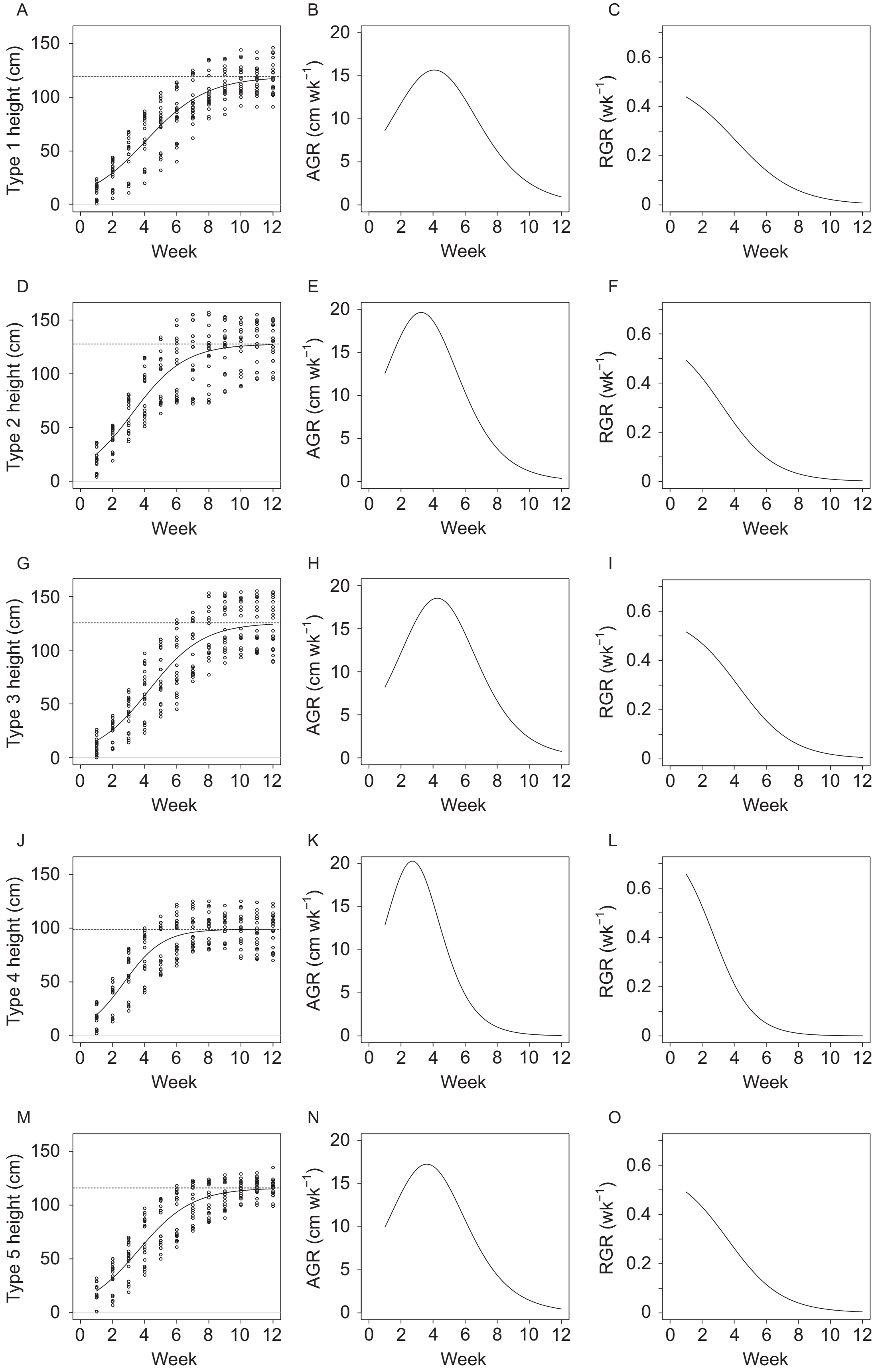

Figure 5. Growth rates of weedy rice over time under high competition conditions (n = 40) weedy rice plants m^{-2} for types (A–C) 1, (D–F) 2, (G–I) 3, (J–L) 4, and (M–O) 5, with logistic curves fitted to plant (A, D, G, J, M) height data, (B, E, H, K, N) absolute growth rate (AGR) over time, and (C, F, I, L, O) relative growth rate (RGR) per unit time.

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Table 4. Calculated relative growth rate parameters and error estimates for three-parameter logistic curves of plant height for weedy rice biotypes at 40 plants m^{-2} weed density.

Weedy rice biotype	Y_{max}[a]	SE	X_{mid}	SE	Scal	SE	R^2	AIC	RMSE
	cm		wk		wk				
1	119.1	2.7	4.1	0.2	1.89	0.15	0.8079	2,036.54	256.59
2	127.7	2.6	3.3	0.2	1.63	0.15	0.7309	2,152.87	326.97
3	125.4	3.1	4.3	0.2	1.69	0.15	0.7725	2,146.71	322.79
4	98.9	1.6	2.7	0.1	1.22	0.12	0.7271	1,999.76	248.92
5	116.0	2.0	3.6	0.1	1.68	0.12	0.8326	1,981.01	228.56

[a] Abbreviations: AIC, Akaike information criterion of model; RMSE, root mean square error of model; Scal, scalar factor of the model equivalent to the inverse of growth rate at time X_{mid}; X_{mid}, time at which plants reach maximum absolute growth rate; Y_{max}, maximum plant height at maturity.

Table 5. Final measurements of yield components of weedy rice biotypes when grown at a density of 40 plants m^{-2} in competition with M-206 rice.

Biotype	Plant height[a]	Tiller	Panicle	Yield plant^{-1}	Fresh weight	Dry weight
	cm	no.	no.	g		
1	121.0 c	6.7 a	6.1 ab	11.1 a	27.4 bc	10.8 b
SE	4.3	0.5	0.4	1.0	4.2	0.7
2	120.5 c	7.9 a	6.6 b	12.8 bc	31.0 c	10.2 b
SE	3.7	0.8	0.5	0.8	2.9	0.4
3	115.2 bc	10.0 ab	9.0 c	14.1 c	28.3 c	10.9 b
SE	3.2	0.6	0.8	1.3	3.2	1.0
4	78.9 a	11.6 b	8.0 c	12.7 ab	18.3 a	5.4 a
SE	2.3	0.6	0.6	0.9	1.7	0.3
5	111.8 b	6.8 a	5.7 a	12.4 ab	24.8 b	10.3 b
SE	2.3	0.4	0.3	0.6	3.0	1.0

[a] Letters indicate significant differences between weed biotypes arranged vertically, determined by Tukey test ($\alpha = 0.05$).

weedy rice biotypes are highly competitive and have the potential to cause high yield losses in rice.

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