Growth variability of Italian weedy rice populations grown with or without cultivated rice

André Andres*, Silvia Fogliatto, Aldo Ferrero, and Francesco Vidotto

* A. Andres, Terras Baixas Experimental Station, Embrapa Temperate Agriculture, BR 392 km 78 Cx.P. 403, Pelotas (RS), 96.010-971, Brazil; S. Fogliatto, A. Ferrero and F. Vidotto, Dipartimento di Scienze Agrarie, Forestali e Alimentari, Università di Torino, via Leonardo da Vinci 44, Grugliasco (TO), 10095, Italy. "Received _____________. *Corresponding author (andre.andres@embrapa.br)"

Abbreviations: DAS**,** days after sowing; G_{50}, days required to reach 50% maximum value; SLA, specific leaf area; SSL, specific stem length;

Abstract

Weedy rice (*Oryza sativa* L.) exhibits a great variability of morphological traits. To detect if this variability can affect its growth behaviour, two experiments were carried out on ten Italian weedy rice populations grown as pure stand and in competition with rice. Five awnless and five awned populations were grown in field conditions in 15-L pots. In the pure stand experiment, each pot hosted a single plant of weedy rice, while in the competition experiment the weedy rice plant was surrounded by ten plants of cultivar Sirio CL. Plant height, tiller, and leaf numbers were recorded 6 times during the growing season. In competition, leaf area, culm weight and leaf weight were also assessed. In pure stand, no significant differences between awned and awnless groups were found for all the considered parameters. Differences were found in plant height (from 70.7 to 91.9 cm) and leaf weight (from 5.64 to 9.85 g plant^{-1}) among awned populations only. In competition, weedy rice showed lower and more variable growth indices. The least and most affected growth variables were plant height (16% of average reduction in comparison to pure stand) and leaf weight (70.3% of average reduction), respectively. Awned populations showed higher and more variable values of growth parameters, suggesting a stronger competitiveness and a wider phenotypic plasticity. Knowledge of growth behaviour related to weedy rice variability could improve modelling of infestation dynamics and highlights the need of an integrated weed management approach.

Keywords: *Oryza sativa*, red rice, competition, awnedness, growth indices

Weedy rice (*Oryza sativa* L.) is a troublesome weed in most rice ecosystems. In Europe, Italy first reported its appearance in the beginning of the 19^{th} century (Biroli, 1807). The species became more difficult to manage after 1960, when transplanting was substituted by direct seeding (Ferrero and Vidotto, 1998). Weedy rice can cause serious yield losses in rice production and can also affect rice milling and the seed trade (Delouche et al., 2007). A study conducted in Italy showed losses from weedy rice competition can rise to 50% primarily due to reduced rice panicle density and filled grains per panicle (Vidotto and Ferrero, 2009). In Ariette and Thaibonnet cultivars, infestations caused rice yield losses of 46% and 58%, respectively, when plant density was high (40 weedy rice plants m^{-2}) (Eleftherohorinos et al., 2002). Even though practices have been developed to counter weedy rice infestations, such as stale seedbedding, pre-planting treatment and herbicide application, its control remains difficult due to its high genetic affinity to cultivated rice and its great morphological variability (Vidotto and Ferrero, 2005; IRC, 2006).

Weedy rice displays wide morphological (i.e. plant size, leaf and tiller number, hull coloration, awnedness) and physiological (i.e. seed dormancy, emergence and flowering time) variability in many ecotypes (Noldin et al., 1999; Vidotto, 2001; Sánchez-Olguín et al., 2007). Different weedy rice populations are usually distinguished by hull coloration (Arrieta-Espinoza et al., 2005; Shivrain et al., 2010). In certain areas where strawhulled populations are largely prevailing, populations were grouped on the basis of other traits. This is the case of Italy, where recent studies used awnedness to sort weedy rice populations (Fogliatto et al., 2011; Fogliatto et al., 2012). Regarding hull coloration, strawhull is the most dominant group of weedy rice in all the world. The blackhulls are less widespread, and the brownhulls and greyhulls are minor groups (Gealy et al., 2002; Delouche et al., 2007). In all the rice areas across the world, the most common biotype is strawhull awnless, followed by strawhull awned but brown- and black-awned populations are also found (Gealy et al., 2002; Delouche et al., 2007).

Most of the traits that are commonly displayed by weedy rice populations are also those with a strong influence on competitivity towards rice crop: high tillering ability, elevated seed production, heavy shattering, prolonged and deep seed dormancy, protracted emergence, and high vigour until reproduction (Delouche et al., 2007). Tillering ability is generally more indicative of rice competitiveness than plant height or leaf area (Fischer et al., 1997; Mennan et al., 2012); the same is thought to be true for weedy rice because of the similarities between the two plant types. While tillering is associated with leaf area and biomass mostly, it is also positively correlated with leaf number and negatively correlated with plant height (Noldin et al., 1999). In fact, plants with high tillering capacity colonize space faster and have greater plant density, which makes them more competitive (Sánchez-Olguín et al., 2007).

The causes of competitiveness are controversial. One study suggested that early rice leaf area alone predicts crop competitiveness (Lindquist and Kropff, 1996); however other authors indicate several factors influence competitiveness. Noldin et al. (1999) found rice cultivars had more leaf area per plant compared to weedy rice populations in the southern United States while Kwon et al. (1992) found Arkansas weedy rice populations with higher or lower leaf areas than that of particular rice cultivars. Biomass production is yet another indicator of plant competitive ability (Gaudet and Keddy, 1988). Weedy rice growth is in turn affected by competition with other weedy rice and cultivated rice plants. Weedy rice has been shown to produce more tillers and shoot biomass when grown in competition compared to rice cultivars (Kwon et al., 1992), and it can produce more biomass per unit of nitrogen up-take (Burgos et al., 2006).

Also true, is that weedy rice is usually 40% to 57% taller than cultivated rice with a less upright habit (Delouche et al., 2007; Sánchez-Olguín et al., 2007), which gives it an advantage over cultivated rice as it captures light more easily (Kwon et al., 1992). However, short weedy rice plants can escape detection when they match height with cultivated rice (Kwon et al., 1992; Delouche et al., 2007). As a consequence, the entire set on measures available to manage weedy rice may result in a variable rate of success, depending on the variability of morphological and biological traits of the weedy rice populations growing in a certain area. Thus, the knowledge of the range of variability of competition-related traits of weedy rice, both when plants are grown alone and in competition with cultivated rice, can be regarded as crucial information for a correct tuning of the management of this weed. Therefore, we hypothesize that the variability normally found in the morphological traits of weedy rice could also be detected in the growth parameters and the response of the populations to competition could vary accordingly.

Thus, the objectives of this study were: 1) to evaluate growth variability among Italian weedy rice populations as pure stand (experiment 1) and 2) to estimate the effect of competition of cultivated rice on weedy rice (experiment 2). Both experiments were conducted in pots maintained in open fields.

MATERIALS AND METHODS

Ten weedy rice populations (five awned and five awnless) were evaluated for their growth in pure stand and in the presence of cultivated rice in 2011 growing season. The populations included in the study are part of a larger set of 149 weedy rice populations collected in northwest Italian rice fields (Fogliatto et al., 2012). We defined population as a group of weedy rice plants with similar morphological traits collected in a same rice field. An awnedness group is a set of weedy rice populations sharing the same awn trait (awned or awnless).

Weedy rice growth in pure stand (experiment 1)

In this experiment weedy rice plants were grown individually in 15-L plastic pots filled with loam soil. Three seeds were sown at each pot centre, at a depth of 0.5 cm, and thinned to one plant three days after emergence. The pots were irrigated daily. Nitrogen was applied, as urea, in two times, when weedy rice plants had 4 leaves (at a rate equivalent to 30 kg N ha^{-1}) and at 3 tillers (at a rate equivalent to 30 kg N ha^{-1}). No insects or disease problems were observed on weedy rice during the trial period; unwanted weeds were manually removed. A total of 180 pots (ten weedy rice populations by six growth assessments by three replications) were arranged in a completely randomised design and maintained in the field (45° 3.998' N; 7° 35.567' E– WGS84) at the University of Torino, Italy.

Growth was assessed at 30, 40, 50, 60, 70, and 80 days after sowing (DAS) by measuring plant height, culm number, and leaf number. In this interval, plant growing stage spanned from 2 leaves (12 BBCH; 30 DAS) to heading (59 BBCH; 80 DAS). In particular, plant height was measured from the ground to the last fully developed leaf tip stretched along the culm axis. At the 80 DAS sampling, culm and leaf biomass and leaf area were also measured. Culms and leaves were dried in a forced-air oven at 70°C for approximately 72h and weighed. Leaf area was measured with a LI-3100 leaf area meter.

Weedy rice growth in competition with cultivated rice (experiment 2)

Two sets of pots were prepared, one with and one without cultivated rice. Three pots per population without rice were prepared as in Experiment 1, and considered as a second run of the previous experiment and would be used for competition comparison.

To evaluate the response of weedy rice to cultivated rice presence, three other pots per population were arranged in the same field which hosted Experiment 1. Three weedy rice seeds were sown at pot centres equidistant from each other, and then surrounded by 10 cultivated rice seeds (cv. Sirio CL) about 7 cm away; the rice density equalled 162 plants m^{-2}. The weedy rice was thinned to one plant and maintained as described in Experiment 1 for the season.

Weedy rice plants were cut at the soil surface at 30, 40, 50, 60, 70, and 80 DAS (corresponding to the same growth stages described for Experiment 1). The dry weight of plants was assessed for each sampling date, using the method described for Experiment 1. Other growth parameters were assessed at each sampling: leaf and culm number and weight, plant height, and leaf area per plant.

At the final sampling (80 DAS), percent reductions in the growth parameters named above were calculated for weedy rice grown in the presence of cultivated rice compared to that grown alone. Finally, specific stem length (SSL), which is the ratio between culm length (cm) and culm biomass (g), and specific leaf area (SLA) which is the ratio between leaf area (cm^2) and leaf biomass (g), were calculated for each sampling date. SSL and SLA were reported as average of awned and awnless groups.

Statistical analyses

Weedy rice growth in pure stand (experiment 1)

ANOVA was performed on plant height, leaf and culm number, leaf and culm weight, and leaf area at the final sampling, using statistical software SPSS[1] (version 16) to find differences between awned and awnless groups and among populations within each awnedness group. Means were separated using the Bonferroni test ($P \leq 0.05$).

Regression analysis was used to determine the relationship between time and growth parameters by considering both a linear and sigmoid model. In the case of plant height, in keeping with Chauhan and Johnson (2010), data expressed as percent of final height achieved by population at the last sampling were better fitted to the following linear model:

$$y = a + bx \quad [1]$$

where x represents DAS, a and b are the constant and angular coefficient, respectively. Culm and leaf number data, expressed as percent of population values achieved at the last sampling were better fitted to a three-parameter sigmoid model (Chauhan and Johnson, 2010):

$$y = \frac{a}{1 + e^{-\left(\frac{x - x_{50}}{b}\right)}} \quad [2]$$

where x represents DAS, x_{50} is days required to reach 50% of the final value, a is the upper asymptote, and b is the slope of the curve at inflection. Regression analysis was performed using software Sigma Plot 2001, version 7. The fitted curve equations were then utilized to calculate the days required to reach 50% maximum leaf and culm numbers and plant height (G_{50}) per population.

Weedy rice growth in competition with cultivated rice (experiment 2)

As for experiment 1, leaf and culm number and weight, and leaf area data for weedy rice populations grown with and without rice presence were fitted using equation [2], while for plant height equation [1] was applied. For each population, the estimated curves of weedy rice grown in competition or not with rice were compared using a lack-of-fit test (Seefeldt et al., 1995) to assess if rice presence affected the overall weedy rice growth curve.

Weedy rice growth data when rice was grown in competition were subjected to *t*-test to detect awnless *versus* awned group differences. Within each awnedness group, growth parameters among populations were compared by using ANOVA and Bonferroni test ($P \leq 0.05$).

For each sampling, ANOVA and the Bonferroni test ($P \leq 0.05$) were performed for SSL and SLA for each awnedness group. A *t*-test for each assessment date was carried out to assess differences between weedy rice grown in pure stand and in rice competition for both SSL and SLA values.

RESULTS

Weedy rice growth in pure stand (experiment 1)

At the final sampling (80 DAS), no significant differences were found between the two awnedness population groups (Table 1). However, significant differences were found among weedy rice populations within awnedness group. At 80 DAS, awnless plant height ranged between 68.9 cm (population 27) and 84.1 cm (population 76). Awned height varied from 70.7 to 91.9 cm (populations 89 and 100, respectively).

Leaf number did not vary significantly neither among awned nor awnless populations. Leaf weight varied significantly only among awned populations, with populations 100 and 106 being the lightest and heaviest, respectively. Awnless and awned population culm weights showed no statistical differences; culm number differed only in awnless ones. The average number of culms per plant was greater in populations 27 (26.5) and 110 (23.7) and lower in 76 (20.2) and 116 (20.7). Leaf area was similar in both awnless and awned, with values ranging from 880 to 1325.2 cm^2 per plant.

Generally, weedy rice growth parameters were more variable among awned populations than among awnless ones. In both groups, the greatest variability was found in leaf weight, which varied 43% and 24% between the heaviest and lightest awned and awnless populations, respectively (Table 1).

The pattern of leaf and culm production over time was similar among populations, even though moderate variability existed within each awnedness group. The calculated G_{50} values referred to leaf and culm number varied from 43 to 50 days and from 38 to 45 days, respectively (Table 2). The G_{50} values for plant height varied by about 10% within each awnedness group.

In general, the final values of growth variables were directly related to their G_{50}. In particular, considering the awnless group, population 27 showed the highest leaf and culm number final values (Table 1) and the higher G_{50} for both leaf (50.4 days) and culm numbers (44.8 days). The same population showed the smaller G_{50} for plant height (38.9 days) and it was the shortest population at final sampling. The same behaviour was displayed by awned population 89, which needed 49.5 and 44.0 days to reach 50% of its maximum number of leaves and culms, yet was the fastest (35.8 days) in reaching half its height as the shortest among the awned populations (Table 2).

The direct relation between a growth variable final value and its G_{50} was observed also in population 76, which displayed a nearly opposite behaviour of previous populations, as it was the fastest in the awnless group to emit 50% of its total leaves (43.9 days) and culms (38.1 days), even though it had the lowest culm number at final sampling; this population was tallest within the awnless group, and the slowest to reach 50% maximum height (42.9 days).

Weedy rice growth in competition with cultivated rice (experiment 2)

In general, weedy rice growth was affected by competition with cultivated rice. As indicated by the lack-of-fit test (Table 3), the variation over time of plant height, leaf and culm number, leaf and culm weight and leaf area was significantly different when weedy rice populations grew alone or in competition with rice. The sole exceptions were represented by plant height in populations 27 and 72. The competition effect exerted by rice on weedy rice resulted in a reduction of final values of growth variables (Table 4). In particular, the least and most affected growth variables of weedy rice were plant height (16% of average reduction in comparison to weedy rice grown alone) and leaf weight (70.3% of average reduction), respectively.

Differences between awnless and awned weedy rice groups on the values measured at the last sampling were detected for leaf number and weight, culm number and leaf area, with awned group showing the highest values (Table 4). It should be noted that the two groups exhibited no significant differences in all the considered growth variables when grown without competition (Table 1). By comparing populations within each awnedness group, no differences were found among awnless populations, while among awned ones significant differences were found for three growth variables out of six: plant height, leaf number, and culm weight.

In the awned group, plant height was significantly different only between populations 83 (being the shortest one) and 106 (the tallest). Population 106 exhibited also the highest number of leaves and the heaviest culm weight, as already observed in Experiment 1 when the population grew alone. The lowest number of leaves and culm weight were recorded in population 89.

Overall, weedy rice showed the tendency to reach faster the final values of growth variables when grown in competition with rice. The different time taken by the weed to reach the maximum value in competition compared to non competition varied according to the studied population and the considered growth variable, being modest in culm weight and more evident in leaf area (data not shown).

Rice presence had limited influence on weedy rice SSL (Table 5). This parameter followed a decreasing pattern, which indicated weedy rice plants first concentrate their resources for height growth and second for biomass. Significant differences between plants grown in competitive conditions or as pure stand were found only at 50 DAS and 80 DAS for awned and awnless populations, respectively.

Weedy rice SLA decreased until the last sampling (Table 5), and displayed a tendency to decrease biomass *versus* leaf area. Absent competition, weedy rice SLA decreased 54.7% between the first and last samplings; in rice presence, SLA of weedy rice declined 47.2% in the same period. At 70 and 80 DAS, populations grown with rice had higher specific leaf areas than when grown alone, which demonstrated a tendency to a larger leaf area per biomass unit.

DISCUSSION

The present study, taking as assumption the fact that weedy rice can cause severe crop yield losses, aimed at investigating the growth behaviour of the weed and in particular its variability when grown in pure stand or with cultivated rice. The effect of weedy rice competition on rice was already proven by numbers of previous studies (Eleftherohorinos et al., 2002; Burgos et al., 2006; Vidotto and Ferrero, 2009), in which rice growth parameters were measured over time. In the literature only very few studies (Chauhan and Johnson, 2010; Caton et al., 1997) had the objective of considering the effects of competition towards the weed; however, knowledge of the weed growth behaviour is essential for the tuning of the most appropriate control strategies. Moreover, for some weeds, such as weedy rice, in which several different populations are often present, even in the same area of rice cultivation, the knowledge of the degree of morphological and physiological variability is even more important. Previous studies involving Italian weedy rice populations (Fogliatto et al., 2011; Fogliatto et al., 2012) pointed out a great differentiation in plant morphology and dormancy between awned and awnless populations. Thus, we selected some populations pertaining to these groups to test if this variability can also be present in the growth behaviour.

In general, each experiment highlighted slightly different behaviours in weedy rice populations grouped by awnedness; the differentiation was clearer when weedy rice grew in competition with rice. While only a few significant differences were observed between awned and awnless groups at the final sampling, awned populations showed more variable growth than did awnless. The higher variability of awned populations was already observed for other morphological characteristics of the larger set of populations from which those included in this study were selected (Fogliatto et al., 2012).

Weedy rice is generally taller than cultivated rice and its height varies considerably among populations (Estorninos et al., 2005a; Delouche et al., 2007; Sánchez-Olguín et al., 2007), as confirmed in this study. Weedy rice plant height may influence competitive ability; it is commonly associated with other growth traits (Kwon et al., 1992). Estorninos et al. (2005a) commented that short weedy rice populations were less competitive against rice, and thus less able to produce seeds compared to tall ones. Though, taller plants can have a certain selective disadvantage, as they can be more easily distinguished and controlled in post-emergence with wiping or cutting bars (Vidotto and Ferrero, 2005) or by hand weeding. A fast increase in plant height, combined with tallness, could indicate early light access, as taller plants shade shorter ones (Kwon et al., 1992; Falster and Westoby, 2003).

When grown in competition with cultivated rice, weedy rice plant height was affected even though less than other traits. Later in the season, the plants shifted to increasing their biomass, as indicated by the lower SSL values. This behaviour may result from competition for light, known as “shade avoidance” strategy, in which height growth is prevalent compared to the accumulation of biomass or to the leaf area growth (Caton et al., 1997).

In non-competitive conditions, culm number and weight did not significantly depend on awnedness. However, weedy rice culm number varied significantly among awnless populations. Moreover, the variability of culm number (between about 20 and 28) was lower than that found in other studies, which reported a range between 24 and 54 culms per plant (Lago, 1982; Estorninos et al., 2005b; Chauhan and Johnson, 2010; Shivrain et al., 2010).

Culm number and weight were among the parameters most sensitive to competitive conditions, as they were affected by more than about 60% when weedy rice was grown with rice. Under competitive conditions, awned populations produced a significantly higher number of culms than awnless ones. Besides, significant differences of culm weight were found among awned populations only. As tillering is reported as one of the most important traits giving competitive advantage to weedy rice (Delouche et al., 2007), these results suggest that awned populations could be less affected by interference with cultivated rice.

Populations 27 and 89, both characterised by shortness, reached high culm numbers. Population 76 had an exactly opposite behaviour. This finding suggests a negative correlation between plant height and culm number as found by Nuruzzaman et al. (2000) in several rice varieties. It should be noted that this relationship was not observed under competitive conditions, mainly because plant height and culm number responded differently to competition. Similarly, also Noldin et al. (1999) did not find a correlation between these to growth parameters in a set of 16 weedy rice populations grown in field under intra-specific competition conditions. This behaviour might again be the consequence of the "shade avoidance" strategy, which causes the plant to invest in stem elongation, while reducing the number of culms produced.

In this study, some populations grew earlier than others. The high rate of culm and leaf emission in early growth stages can result in fast canopy closure, which could indicate greater initial competitiveness against rice (Kwon et al., 1992; Caton et al., 2003).

Under competitive condition, values of parameters related to leaves (leaf number, leaf weight, and leaf area) were significantly higher in awned populations than in awnless ones. As leaf area is positively correlated with competitiveness (Ni et al., 2009), these results suggest a different competitive ability between the two awnedness groups.

The evolution of SLA over time followed a similar pattern for both awnedness groups and in both competitive conditions. Generally, SLA values remained stable during the first 40 days after sowing, and then roughly halved already at 10 days later onwards. Later in the season, SLA of plants grown under competitive conditions was significantly higher than that of plants grown in pure stand. In particular, significant differences between the two competitive conditions were found starting from 60 and 70 days after sowing, in awnless and awned populations, respectively. Thus, weedy rice exhibited the effect of competition from rice late in the season. This behaviour mirrors what occurs normally in the field, where weedy rice became a strong competitor of rice in the latter half of the season (Smith, 1968; Delouche et al., 2007). In this respect, weedy rice is different from other important weeds, such as *Echinochloa crus-galli* (Smith, 1968) and *E. phyllopogon* (Gibson et al., 2002), which are strong early-season competitors. Late control of weedy rice plants (e.g. with wiping bars) could then potentially limit yield losses due to competition only if performed before 60-70 days after sowing.

Study results contribute to better estimate the weedy rice intra-specific growth variability and the response to competition. Knowledge of growth trait variability could improve predictive models of infestation dynamics. As pointed out by Neve et al. (2009), most of the weed dynamics models are parameterized by considering data deriving from a single population and for this reason the model predictions are somehow limited.

The results of this study confirmed the initial hypothesis that morphological diversity is related to the variability of growth parameters and response of the populations to competition. The tested populations were grouped on the basis of awnedness. In a previous study (Grimm et al., 2013) on 40 Italian weedy rice populations, in which those considered in the present study were included, awned and awnless groups corresponded to different genetic clusters. Though, the differentiation between the two clusters was not overwhelming. The moderate genetic variability could explain the quite similar growth behaviour found between the two awnedness groups under non-competitive conditions. However, more differences were found when weedy rice grew in competition. This could be due to the phenotypic plasticity of the species, meaning that different phenotypes could arise from the same genotype in response to the environmental and growing conditions. In particular, awned populations showed more variable reactions to competition. The higher plasticity makes this group probably more adaptable to grow in different conditions. In species able to produce phenotypes suitable to different environmental conditions, locally specialized ecotypes have low chances to be selected (Sultan, 2000). The lack of prevalence of one or few particular weedy rice populations in the Italian rice fields (Fogliatto et al., 2012) supports this hypothesis, especially considering that the agronomic practices adopted are quite stable over the years and across the rice cultivation area (Grimm et al., 2013).

The great plasticity of this species can also be one of the reasons for its success as a weed. In spite of the several efforts implemented to get rid of it, weedy rice is still one of the most problematic weeds in most rice areas. In Europe, for example, weedy rice control over last decades has relied upon several methods, including stale seedbed, pre-planting herbicide application, use of certified seed, hand weeding, use of wiping and cutting bars, adoption of imazamox-tolerant rice varieties (Clearfield® varieties). However, weedy rice in Europe is still estimated to infest at least 70% of rice fields (Català et al., 2002), with peaks of 90% in Italy (Jiang et al., 2011). As no one of the above-mentioned methods proved to be able alone to solve the problem, the phenotypic plasticity of weedy rice suggests the need of an IWM (Integrated Weed Management) approach for its control.

Source of material

[1] SPSS version 16.0 for Windows, SPSS Inc., 233 South Wacker Drive, Chicago, IL, 350 60606

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Table 1. Weedy rice growth parameter values at final assessment (80 DAS) (Experiment 1).

Weedy rice populations	Plant height (cm)	Leaf number	Leaf weight (g)	Culm number	Culm weight (g)	Leaf area (cm^2)
	Per plant					
Awnless[†]	78.4 NS[‡]	79.1 NS	7.1 NS	22.8 NS	22.8 NS	978.6 NS
Awned [†]	78.3	85.2	7.8	24.6	22.7	1061.5
Awnless						
27	68.9 b[§]	84.7 NS	6.35 NS	26.5 a	21.0 NS	1061.9 NS
52	81.0 a	79.0	7.25	22.8 ab	23.1	1059.6
76	84.1 a	75.7	5.85	20.2 b	24.1	880.0
110	76.7 ab	87.0	7.73	23.7 a	23.3	962.9
116	81.1 a	69.3	6.98	20.7 b	22.1	928.6
Awned						
72	74.3 bc	85.8 NS	8.45 ab	24.5 NS	22.4 NS	1105.4 NS
83	71.4 bc	96.0	8.02 ab	25.7	24.3	1067.4
89	70.7 c	81.0	7.15 bc	23.0	19.1	901.8
100	91.9 a	77.7	5.64 c	22.0	23.2	907.4
106	83.3 ab	85.5	9.85 a	28.0	25.3	1325.2

† average values of all the awnless of awned populations.

[‡] NS indicated no significant differences at the 0.05 probability level.

[§] Values within each column sharing the same letter are not significantly different according to Bonferroni test ($P \leq 0.05$). Comparisons were made between awnless and awned groups and among the populations within each awnedness group.

Table 2. Parameter estimates of the model and calculated G_{50} values for leaf and culm number, and plant height data (Experiment 1).

Weedy rice populations	Parameter estimates								
	Leaf number†			Culm number†			Plant height‡		
	a	*b*	G_{50}§	*a*	*b*	G_{50}	*a*	*b*	G_{50}
Awnless									
27	108.5	10.4	50.4	88.5	7.8	44.8	5.8	1.1	38.9
52	102.2	7.8	47.6	89.3	6.0	42.7	-7.6	1.4	42.0
76	104.6	7.5	43.9	92.8	3.4	38.1	-6.3	1.3	42.9
110	103.6	7.0	46.5	88.1	4.1	41.0	-5.2	1.3	41.2
116	105.8	6.9	44.1	89.9	4.2	39.0	-6.9	1.4	41.5
Awned									
72	107.3	6.8	44.8	93.9	2.4	38.6	-3.7	1.3	40.1
83	104.5	6.8	45.1	96.1	2.6	39.0	1.0	1.2	39.6
89	107.8	9.2	49.5	90.7	7.6	44.0	5.2	1.2	35.8
100	105.0	8.6	47.6	85.5	4.3	39.9	-15.3	1.4	46.4
106	106.7	6.4	43.3	89.2	4.1	40.2	-9.1	1.4	43.0

†parameters refer to a three-parameter sigmoid model (Equation [2]).
‡parameters refer to a linear model (Equation [1]).
§time (days) required to reach 50% of the maximum leaf number, culm number or plant height value.

Table 3. Curve comparison (lack-of-fit) of weedy rice grown without and with rice (Experiment 2).

Weedy rice population	Height		Leaf number		Culm number		Leaf weight		Culm weight		Leaf area	
	F value											
Awnless												
27	0.98	NS	27.39	***	17.24	***	48.94	***	34.69	***	30.88	***
52	9.32	***	37.76	***	26.95	***	272.53	***	64.01	***	31.10	***
76	9.25	***	69.14	***	18.47	***	80.45	***	47.35	***	44.18	***
110	3.51	*	33.88	***	15.33	***	14.49	***	7.827	***	20.89	***
116	5.79	**	39.65	***	23.98	***	56.21	***	32.79	***	34.83	***
Awned												
72	1.39	NS	49.96	***	33.03	***	34.46	***	31.70	***	22.73	***
83	5.60	**	45.88	***	33.21	***	-	-	37.30	***	23.36	***
89	6.34	**	29.33	***	24.37	***	24.37	***	45.78	***	26.79	***
100	19.02	***	30.52	***	-	-	192.66	***	35.89	***	34.78	***
106	5.97	**	34.76	***	21.26	***	57.43	***	47.51	***	40.07	***

*Significant at the 0.05 probability level.

**Significant at the 0.01 probability level.

***Significant at the 0.001 probability level.

Table 4. Weedy rice growth parameters at final assessment of awnless and awned weedy rice populations grown in competition with cultivated rice (cv. Sirio CL) at final assessment (Experiment 2). Values between brackets are reduction percentages in comparison to weedy rice plants grown alone.

Weedy rice population	**Plant height**	**Leaf**		**Culm**		**Leaf area**
	(cm)	**Number**	**Weight (g)**	**Number**	**Weight (g)**	**cm²**
Awnless	66.3 (17.3)	28.1 (64.4)	1.8 (72.8)	7.5 (66.8)	7.0 (68.7)	282.3 (70.2)
Awned	64.3 (14.7)	35.9 (56.3)	2.4 (67.9)	9.7 (61.1)	7.5 (66.7)	410.9 (59.9)
Differences	NS	**	**	**	NS	**
Awnless						
27	68.5(7.3)	22.0(74.1)	1.4(83.0)	6.7 (74.7)	5.8 (75.4)	235.7 (78.5)
52	61.8 (26.5)	30.0(61.2)	2.1(69.8)	7.0 (68.7)	7.2 (73.7)	314.7 (72.4)
76	76.5 (15.6)	31.0(61.3)	1.6(66.4)	7.3 (65.6)	7.8 (61.6)	265.1 (66.5)
110	56.6 (25.4)	32.7(61.8)	2.2(71.4)	8.5 (63.6)	7.4 (65.8)	346.0 (60.5)
116	68.0 (11.4)	26.3(62.6)	1.9(72.8)	8.3 (60.3)	7.1 (66.0)	271.2 (69.8)
Differences	NS	NS	NS	NS	NS	NS
Awned						
72	63.4(4.8)ab[†]	41.0(51.4)ab	2.8 (60.4)	10.0 (59.5)	8.1(59.6)ab	492.7 (46.9)
83	55.1(15.6)b	36.3(62.2)ab	2.4 (67.5)	9.7 (60.3)	6.3(73.1)ab	433.0 (58.4)
89	62.4(8.9)ab	26.3 (61.1)b	2.0 (71.8)	7.0 (69.1)	6.1 (62.6)b	278.5 (62.4)
100	66.2(31.2)ab	32.7(58.6)ab	2.1 (67.9)	10.0 (61.0)	6.8(77.1)ab	345.4 (66.4)
106	74.3(13.2)a	43.0 (48.4)a	2.9 (71.8)	12.3 (55.6)	10.1 (60.9)a	504.8 (65.0)
Differences	*	*	NS	NS	*	NS

*Significant at the 0.05 probability level.

**Significant at the 0.01 probability level.

[†] Values within each column sharing the same letter are not significantly different according to Bonferroni test (P≤0.05). Comparisons were made among the populations within each awnedness group.

Table 5. Development in time of specific stem length (SSL) and specific leaf area (SLA) of weedy rice populations (Experiment 2).

Assessment (days after sowing)	Specific Stem Length (SSL)†			Specific Leaf Area (SLA)‡		
		ps§	rc¶		ps	rc¶
		cm g^{-1}			m^2 g^{-1}	
Awnless						
30	NS	642.0 a#	552.9 a	NS	295.4 a	320.5 a
40	NS	465.9 b	549.9 a	NS	314.9 a	335.1 a
50	NS	449.3 c	514.9 a	NS	154.8 b	157.0 c
60	NS	154.9 c	149.2 b	*	163.0 b	188.6 b
70	NS	93.7 c	91.1 b	*	140.6 b	165.2 bc
80	*	80.8 c	72.7 b	*	141.2 b	155.0 c
Awned						
30	NS	821.3 a	775.6 a	NS	306.0 a	288.7 b
40	NS	514.4 b	510.6 b	NS	297.5 a	317.3 a
50	*	488.4 b	576.3 b	NS	155.7 b	165.8 d
60	NS	189.6 c	189.9 c	NS	175.6 b	193.2 c
70	NS	101.5 c	112.3 c	*	144.8 c	173.3 d
80	NS	83.1 c	84.7 c	*	135.3 c	166.7 d

† Specific stem length (SSL) which is the ratio between culm length (cm) and culm biomass (g).

‡ Specific leaf area (SLA) which is the ratio between leaf area (cm^2) and leaf biomass (g).

§ ps: weedy rice grown in pure stand.

¶ rc: weedy rice grown in rice competition.

means within column (SSL or SLA), for each awnedness between assessments, having the same letter are not significantly different at Bonferroni test (P≤0.05);

* means within rows, between ps and rc, followed by asterisk are significantly different at *t*-test (0.05 probability level).