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# Crop traits related to weed suppression in water-seeded rice (*Oryza sativa* L.)

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Resistance to herbicides and the lack of viable control options have led to an interest in increasing the role of crop competition as a weed management tool in water-seeded rice production. Weed-suppressive rice cultivars have been suggested as a tool that could improve weed control and reduce the reliance of growers on herbicides. Field studies were conducted at Biggs, CA, in 1999 and 2000 with six to eight semidwarf rice cultivars to identify water-seeded rice traits related to the suppression of watergrass growth. Cultivars S-201 and M-302 were the most suppressive in both years. The dry weight (DW) of watergrass grown with the most suppressive cultivar was only 16% in 1999 and 57% in 2000 of the DW of watergrass grown with the least suppressive cultivar. Rice leaf area and root DW in weed-free plots were linearly related to watergrass DW in both years. Weed-suppressive traits were not inversely correlated with rice yields in monoculture; competitive cultivars also had high yields. This study suggests that an indirect selection program, based on traits that can be identified early in the season under weed-free conditions, has great potential for developing more competitive cultivars for water-seeded rice.

**Nomenclature:** Early watergrass, *Echinochloa oryzoides* (Ard.) Fritsch ECHOR; late watergrass, *Echinochloa phyllopogon* (Stapf) Koss. ECHPH; rice, *Oryza sativa* L.

**Key words:** Competition, weed-suppressive ability, crop interference, competitive traits, indirect selection.

Early watergrass and late watergrass, referred to collectively as watergrass, are the most economically important weeds in California rice production (Bayer and Hill 1992). Both watergrass species have been controlled in California rice primarily with herbicides; however, biotypes resistant to four (molinate, thiobencarb, bispyribac-sodium, and fenoxaprop-ethyl) of the five herbicides available for grass control have been detected in California rice (Fischer et al. 2000). Alternative tools to maintain control of these species, reduce the reliance of growers on herbicides, and reduce selection pressure toward further resistance are needed to insure the sustainability of water-seeded rice production. Several authors have reported that differential weed-suppressive ability (WSA) among crops and cultivars can affect the herbicide rates necessary to achieve weed control (Christensen 1994; Lemerle et al. 1996; Salonen 1992). Gibson et al. (2001) compared the WSA of two water-seeded rice cultivars at several herbicide rates. Cultivars differed significantly in their ability to suppress watergrass, and to achieve equivalent levels of weed suppression, higher rates of herbicides were required with the less competitive cultivar than with the more competitive cultivar. If competitive cultivars were developed for California rice, growers might be able to reduce their herbicide rates and lessen their near-exclusive reliance on herbicides for weed control.

Variation among cultivars in their ability to compete with weeds has been documented for many crops, including rice (Callaway 1992; Gibson and Fischer 2002; Pester et al. 1999). Growth parameters associated with the competitive ability of rice grown in the tropics include seedling growth rate, leaf area, specific leaf area (SLA), plant height, tillering, leaf angle, and root growth (Gibson and Fischer 2002). Although some researchers have argued that competitive ability in rice is inversely correlated with yield potential (Jennings and Aquino 1968, Jennings and De Jesus 1968; Jennings and Herrera 1968; Kawano et al. 1974), more recent work in tropical rice has suggested that competitive cultivars could be developed without substantially lowering yields (Fischer et al. 1995, 1997, 2001; Fofana and Rauber 2000; Garrity et al. 1992; Johnson et al. 1998; Ni et al. 2000). The belief that competitive rice genotypes have lower yields, in addition to the effectiveness and availability of herbicides, has limited research on competitive rice cultivars in the United States. If competitive cultivars are to be developed for water-seeded rice, researchers must both identify the rice traits that contribute to competitive ability and determine whether rice yields under weed-free conditions are inversely related to competitive ability.

The selection of more competitive genotypes can be conducted under two screening procedures: direct and indirect. In direct selection, crop genotypes are evaluated under weedy conditions, and more competitive lines are selected for breeding. Direct selection of crop genotypes based on performance under weedy conditions can be costly and labor-intensive, and can be conducted only in the later stages of a breeding program when sufficient seed for each genotype is available (Wall 1983). Indirect selection is a screening procedure in which selection is based not on differential performance among cultivars under weedy conditions but on attributes associated with competitive ability, such as plant height (Lemerle et al. 1996). In this approach, traits associated with competitive ability are identified in competition studies, and genotypes are subsequently selected in a breeding program on the basis of these traits. The advantage of indirect selection is that genotype selection can occur early in the breeding process and in the absence of weeds.

A requirement of indirect selection is that competitive traits can be identified under weed-free conditions. But Fischer et al. (1995, 1997) reported that tropical rice traits measured in monoculture did not correlate well with reductions in weed growth. The authors suggested that selection should be conducted in competition rather than in monoculture. If cultivar growth in water-seeded rice monoculture is not well correlated with competitive ability, then a breeding program based on indirect selection would be counterproductive.

Two factors contribute to crop competitiveness with weeds: weed tolerance (WT), the ability to maintain high yields despite the presence of weeds, and WSA, the ability of the crop to reduce weed growth through competition (Goldberg and Landa 1991; Jannink et al. 2000). Assessing WT can be problematic because researchers must determine first that varietal yield differences reflect weed interference and not genotypic differences in yield potential and second that differences among cultivars in yield do not arise from differences in WSA (Jordan 1993). In addition to problems in quantifying the role of WT, researchers have argued that WSA rather than WT should be emphasized in breeding programs because weed-suppressive cultivars have the potential to reduce within-season weed pressure, thereby limiting yield losses, and to lower weed seed production and recruitment into the soil seedbank, thus potentially reducing weed control costs and yield losses in subsequent years (Gibson and Fischer 2002; Jordan 1993). In contrast, the sustainable use of WT cultivars depends on the availability of other management options that prevent the buildup of weed populations above levels at which even WT cultivars would sustain substantial yield losses (Callaway and Forcella 1993). The lack of such management options in California rice production, particularly as watergrass populations with resistance to multiple herbicides become more widespread, suggests that improving the WSA of cultivars is the most appropriate strategy for this crop production system.

Our three main objectives were to determine whether (1) semidwarf rice cultivars adapted to the water-seeded system of California differed in their ability to interfere with watergrass growth, (2) rice traits measured in weed-free conditions could be related to watergrass growth, and (3) rice yields were inversely correlated with competitive traits.

## Materials and Methods

### Experimental Conditions, Design, and Plant Material

Field experiments were conducted in 1999 and 2000 at the Rice Experiment Station at Biggs, CA. The experimental design was a split–split plot in a randomized complete block with environment (weedy and weed free) as the main plot factor, cultivar as the subplot, and harvest dates (H1, H2, H3) as the sub-subplots. Subplots were 3 by 1.8 m in 1999 and 1.8 by 1 m in 2000. Subplot size was reduced in 2000 to facilitate seed application and sample collection. A 1-m sampling buffer was maintained between cultivars in both years. Main plots were separated by 2-m levees to prevent herbicide movement from weed-free to weedy plots. The soil was a Stockton Clay Adobe (fine, montmorillonite, thermic, Typic Pelloxerts). Nitrogen and phosphorus fertilizers were applied from an airplane at rates of 110 kg N ha$^{-1}$ and 28 kg P ha$^{-1}$ in both years and were incorporated by harrow before flooding. Presoaked rice was sown at 120 kg ha$^{-1}$ on May 12, 1999 and June 2, 2000 into disked, rolled, and flooded fields. Weed-free plots were established by applying molinate (4 kg ai ha$^{-1}$) on May 22, 1999 and June 9, 2000 to control grass species. The experiments were located in fields known to have large populations of early and late watergrass, and naturally occurring populations were used in both years. Watergrass species are difficult to distinguish before the reproductive stage, and we did not attempt to determine the relative proportions of the two species. Carfentrazone was applied at 0.2 kg ai ha$^{-1}$ on June 25, 1999 and July 17, 2000 to control nongrass weeds in all plots. Three replications and six cultivars were used in 1999. Three of the cultivars ('M-302', 'M-101', and 'S-201') were commercially available, short-stature (80 to 100 cm tall) japonica plant types (Brandon et al. 1981). The remaining cultivars ('96Y', '1460', and '2470') were experimental, medium-grain, short-stature, japonica lines chosen for their high seedling vigor. In 2000, two additional cultivars and one additional replication were added to the experiment to improve the precision of our tests. 'Italica livornia' is a cold-tolerant European cultivar believed to be highly competitive with weeds, and 'M-202' is a modern, short-stature cultivar (Johnson et al. 1986) currently used on extensive rice acreage in California.

### Sampling

Subplots were harvested with 0.5-m$^{-2}$ quadrats at the three to four tiller stage of rice (H1), at early booting (H2), and at rice maturity (H3). Rice plants growing in monoculture were uprooted at H1 and H2, washed gently in tubs to remove large chunks of soil, placed on ice, and transported to the laboratory where roots were washed over a 0.1-mm screen. At H1, plants were easily uprooted, and the roots appeared largely intact. At H2, however, rice plants had extensive root masses, and complete extraction of the root system was not possible with this technique. At H1 and H2, rice height and the number of tillers per plant were determined for 10 plants per quadrat before the plants were separated into shoots, roots, and leaves. Leaf area was measured for the 10-plant subsample with a leaf area meter[1] and extrapolated to the whole quadrat using the leaf area–weight ratio (SLA). At each harvest, rice plants were dried for 4 d at 60 C and weighed. Rice total dry weight (DW) per quadrat was determined by adding the weight of the subsample plants to the weight of the whole sample. Rice leaf, shoot, and root DWs were determined for the 10-plant subsample and extrapolated to the entire quadrat. Watergrass plants were uprooted and plant density determined at H1 in weedy plots. Rice and watergrass plants were harvested at rice maturity (H3) by cutting the stems near the soil surface; height was not measured. Rice grain DW and watergrass total aboveground DW were determined at H3. Photosynthetically active photon flux density (PPFD) was measured in weed-free plots with a linear ceptometer[2] 1 wk before the H1 harvests in both years. The average of 10 randomly placed subsamples per main plot was used to calculate percent light interception by the canopy (PPFD at the surface of the water/PPFD above the canopy minus light reflected by the canopy). Reflectance was estimated by inverting the ceptometer approximately 1 m above the top of the crop.

Table 1. Dry weight of a mixed infestation of watergrass (*Echinochloa* spp.) harvested at rice (*Oviza sativa* L.) maturity in 1999 and 2000 as affected by rice cultivar.

| Cultivar | Dry weight | |
|---|---|---|
| | 1999 | 2000 |
| | $g\ m^{-2}$ | |
| '2470' | 445 (123.8)[a] | 1,316 (38.9) |
| '1406' | 381 (11.0) | 1,192 (180.3) |
| '96Y' | 244 (86.2) | 814 (123.7) |
| 'M-101' | 214 (87.5) | 855 (122.5) |
| 'S-201' | 81 (35.9) | 748 (57.3) |
| 'M-302' | 70 (7.7) | 767 (127.5) |
| 'M-202' | | 882 (146.8) |
| 'Italica livorna' | | 835 (74.1) |
| LSD (0.05) | 239[b] | 350 |

[a] Standard errors are given in parentheses.

[b] LSD in 1999 was calculated using log-transformed data and was then back-transformed for presentation.

## Statistical Analyses

Analysis of variance (ANOVA) was conducted by harvest each year to determine the effect of cultivar and environment (weedy or weed free) on watergrass DW and rice yields. Means were separated by least significant difference at the 0.05% level when ANOVA revealed significant ($P < 0.05$) differences among treatments. Pearson correlation coefficients were calculated for rice traits at H1 and H2 and rice grain yields in weed-free plots. Watergrass DW and rice yields in 1999 were $\log_{10}$-transformed to homogenize variances. Untransformed data are presented herein. Regression models between rice traits in monoculture at H1 and H2 and watergrass mean DW at final harvest were developed using forward (significance level for entry was 0.50) and backward (significance level for inclusion was 0.15) multiple stepwise regression techniques. Regression models with the lowest mean square error were then selected for each harvest. Regression analysis was also used to assess the relationship between mean watergrass DW and light interception in weed-free plots. Statistical analyses were conducted using SAS.[3]

# Results and Discussion

## Cultivar Interference with Watergrass Growth

Watergrass plant densities did not differ among cultivars at H1 in 1999 (36 plants $m^{-2} \pm 4.43$ SE) and 2000 (97 plants $m^{-2} \pm 10.2$ SE), suggesting that any subsequent differences in watergrass growth among cultivars could be attributed to crop interference. There were significant differences among cultivars in watergrass DW at H3 in 1999 and 2000 (Table 1). M-302 and S-201 were the most suppressive cultivars in both years, whereas 2470 and 1406 were the least suppressive in both years (Table 1). Dry weight of watergrass grown with the most suppressive cultivar was only 16% in 1999 and 57% in 2000 of the DW of watergrass grown with the least suppressive cultivar. Cousens and Mokhtari (1998) argued that consistency in competitive performance was essential for the adoption of more competitive cultivars as a tool to reduce farmers' reliance on herbicides. The authors found that the ability of wheat (*Triticum aestivum* L.) cultivars to tolerate weed pressure was not consistent over time, and they cautioned that farmers would not assume the risk inherent in relying on WT cultivars. But Cousens and Mokhtari (1998) suggested that the WSA of cultivars might be more consistent than their ability to tolerate competition with weeds, and Lemerle et al. (1996) found WSA to be more consistent than WT. In tropical rice, Fischer et al. (1997, 2001) reported that the rankings of their most and least weed-suppressive cultivars were consistent across years. Our work and that of Gibson et al. (2001) also support the idea that the WSA of water-seeded rice cultivars relative to each other is consistent over time.

## Relationship between Weed-free Rice Traits and Watergrass DW

Cultivar means for leaf area index (LAI), leaf DW, root DW, and total DW in monoculture were each negatively related to watergrass DW. But the best single-variable regression models at each harvest, based on the lowest mean square error, included either LAI or root DW. Leaf area index alone measured at H1 in 1999 and 2000 explained 79 and 73% ($P < 0.05$) of the variability in watergrass DW, respectively (Figure 1). Root DW explained 74% ($P < 0.05$) at H2 in 1999 and 84% ($P < 0.05$) at H1 in 2000 (Figure 2). Including LAI and root DW in a regression model explained only slightly more of the variability ($R^2 = 0.86$, $P < 0.05$) in watergrass DW at H1 in 2000 (data not shown). Forward and backward stepwise multiple regression analysis did not identify any other models in either year in which including other variables in addition to LAI or root DW significantly ($P < 0.05$) improved our ability to explain variability in watergrass DW.

Leaf area index has been associated with WSA in tropical rice production systems (Fischer et al. 1997, 2001; Garrity et al. 1992). Leaf area growth rate has also been identified as the primary trait related to competitive ability in efforts to model rice–weed competition in the tropics (Bastiaans et al. 1997; Lindquist and Kropff 1996). Our research supports the idea that rapid leaf area expansion contributes to improved WSA in both temperate and tropical rice production systems. The strong relationship between rice LAI early in the season under weed-free conditions and watergrass DW (Figure 1) suggests that leaf area could be used as a valuable selection index for improving the suppressive ability of water-seeded rice. Leaf area might be particularly useful as a selection index if it can be measured nondestructively using image analysis techniques (Beverly and Van Iersel 1998; Ngouajio et al. 1998, 1999). Such an approach would allow breeders to rapidly screen large numbers of rice lines.

Rice LAI measured at H2 was not significantly related to watergrass DW, suggesting that differences among cultivars in early leaf area growth rates are more important to WSA than are differences in growth later in the season. At H1, LAI was greater in 1999 than in 2000 for the most suppressive cultivars (Figure 1). This may help explain why reductions in watergrass DW were greater in 1999 than in 2000 (Table 1) and reinforces the idea that accelerating the rate of canopy closure could improve control of these weed species. Watergrass plants that emerge with the crop may lessen the effects of shading by altering biomass partitioning, leaf morphology, and leaf physiology to increase light cap-

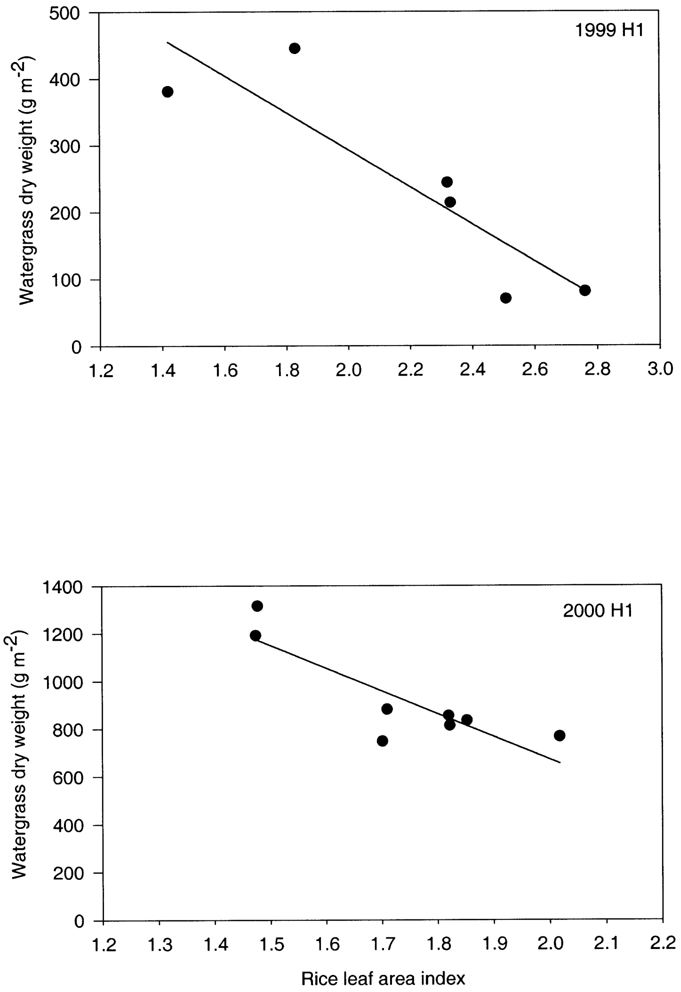

FIGURE 1. Relationship between watergrass (*Echinochloa* spp.) dry weight at final harvest and rice (*Oryza sativa* L.) leaf area index in weed-free plots at H1 in 1999 and 2000. Data points are the means for each cultivar. Estimates of the regression model with standard errors in parentheses: $y$ = 851 (162.1) − 279 (72.4) $x$ in 1999, $R^2$ = 0.79; $y$ = 2,587 (416.3) − 958 (238.8) $x$ in 2000, $R^2$ = 0.73.

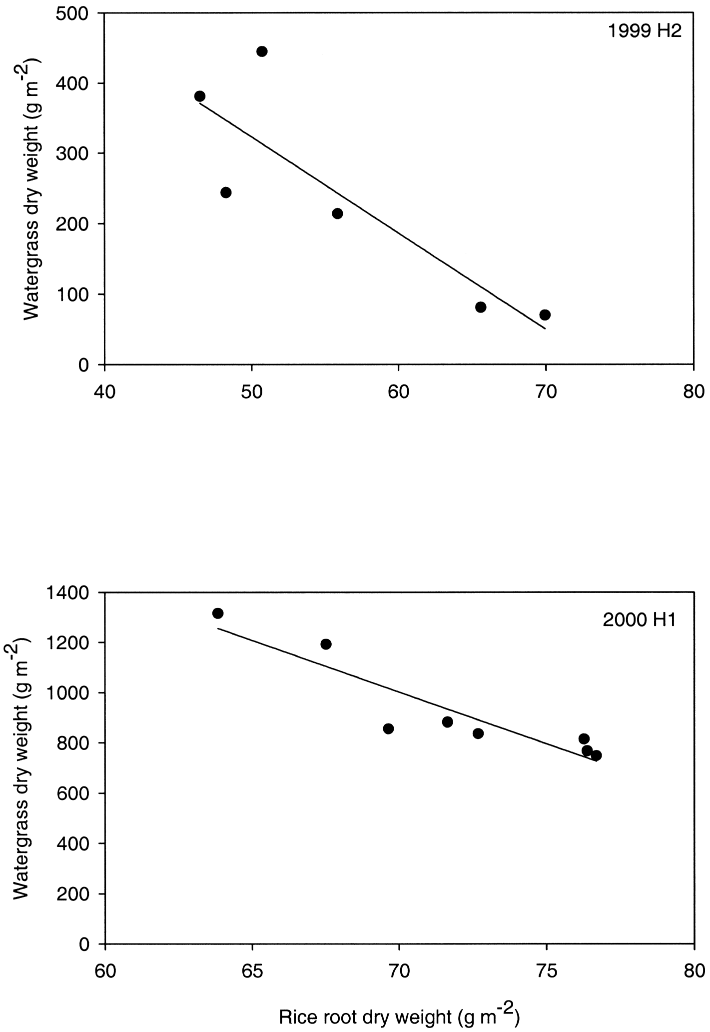

FIGURE 2. Relationship between watergrass (*Echinochloa* spp.) dry weight at final harvest and rice (*Oryza sativa* L.) root dry weight in weed-free plots at H2 in 1999 and at H1 in 2000. Data points are the means for each cultivar. Estimates of the regression model with standard errors in parentheses: $y$ = 1,006 (228.8) − 13.7 (4.03) $x$ in 1999, $R^2$ = 0.74; $y$ = 3,887 (529.8) − 41.2 (7.36) $x$ in 2000, $R^2$ = 0.84.

ture (Gibson and Fischer 2001). Watergrass plants may also avoid or escape shading by growing above the crop. Severe light reductions must be imposed on the weed early in the season to substantially interfere with this plastic response to shade. Gibson et al. (2002) examined the effect of delayed watergrass emergence on the ability of the crop to suppress the weed. Delaying the emergence of watergrass by 15 d relative to seeding the crop reduced watergrass DW by almost 75%. When watergrass emergence was delayed by 30 d or more, the crop alone was able to completely suppress the weed. The ability of the crop to interfere with watergrass growth was directly related to the length of the period between canopy closure and watergrass emergence. Accelerating the rate of canopy closure with more competitive rice cultivars may impose shading early enough to limit the ability of watergrass plants to acclimate to or avoid shading by the crop.

An alternative or supplemental approach to using LAI as a selection index would be the measurement of light intercepted by the crop canopy. In this study, light interception by cultivars in weed-free plots 32 d after seeding (DAS) in 1999 was negatively correlated with watergrass DW and explained 61% of the variation in final watergrass DW (P = 0.07) (Figure 3). Light interception 35 DAS in 2000 explained 56% of the variation in watergrass (P = 0.03). The relationship between light interception and watergrass DW suggests that competitive genotypes might be selected in the field on the basis of rates of canopy closure, as suggested by Fischer et al. (1997). Such an approach would allow growers to screen genotypes under field conditions without detailed morphological analyses.

Competitive ability in rice has been primarily associated with traits related to light capture (Dingkuhn et al. 1999; Fischer et al. 1997, 2001; Khush 1996), and our results support the importance of competition for light. But rice root DW in weed-free plots was linearly related to watergrass DW at H2 in 1999 and H1 in 2000 (Figure 2). Watergrass species are very responsive to nitrogen, and higher rates of nitrogen increase the interference of watergrass species with rice yields (Gibson et al. 1999; J. E. Hill, unpublished data; LeStrange 1981). Gibson et al. (1999) examined the relative contribution of full and shoot-only interference by rice to late watergrass growth and concluded that competition for

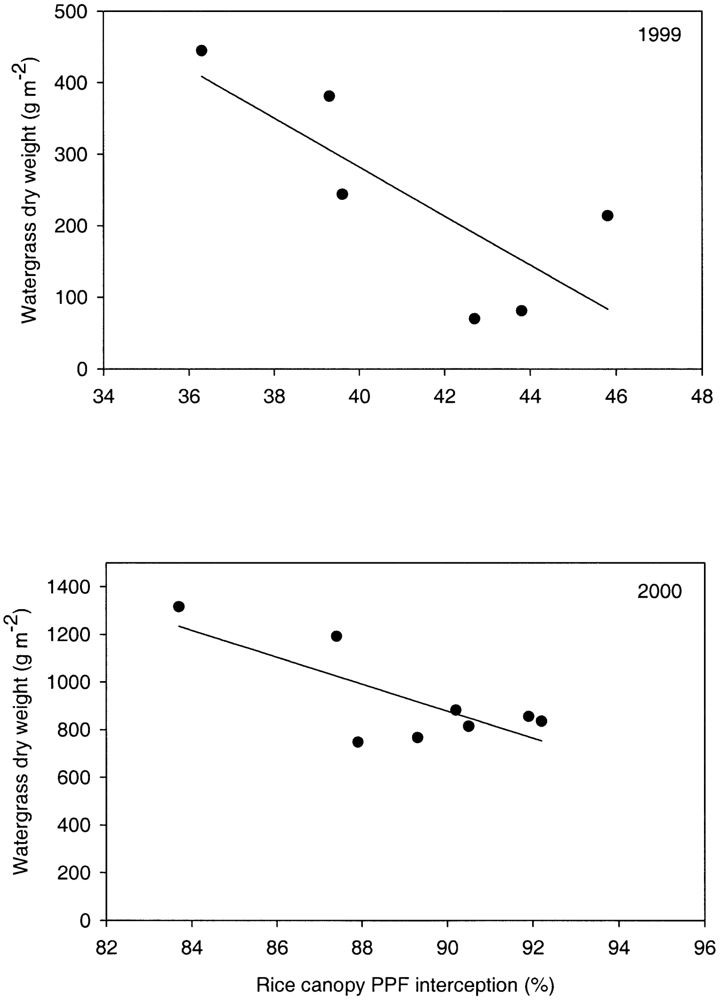

FIGURE 3. Relationship between watergrass (*Echinochloa* spp.) dry weight at final harvest and percent photosynthetic photon flux interception by rice (*Oryza sativa* L.) canopies in weed-free plots 1 wk before H1 in 1999 and 2000. Values are the means for each cultivar. Estimates of the regression model with standard errors in parentheses: $y = 1{,}652\ (571.1) - 34\ (13.8)\ x$ in 1999, $R^2 = 0.61$; $y = 5{,}968\ (1{,}813.8) - 57(20.3)\ x$ in 2000, $R^2 = 0.56$.

belowground resources played a major role in that interference. Other researchers (Assemat et al. 1981; Perera et al. 1992) have also concluded that root competition is an important component of the interaction between rice and watergrass species. Fofana et al. (1995), working in West Africa, reported that weed biomass was negatively correlated with rice root growth early in the season and with root and shoot growth later in the season. Fofana and Rauber (2000) reported that rice root growth was negatively correlated with weed biomass in West Africa and suggested that screening cultivars for root development might increase rice competitiveness with weeds. There is substantial variation in root growth and morphology (Slaton et al. 1990) and in nutrient uptake rates (Teo et al. 1995) among rice cultivars. But screening for root growth under field conditions can be laborious and would likely face considerable resistance from rice breeders. It might be possible to overcome this hurdle by screening for cultivars with a high root growth rate under greenhouse conditions. Also, the use of molecular markers to screen for root traits may become a possibility given the notable progress that has been made in the past decade in rice molecular genetic mapping (Nagamura et al. 1997).

## Relationship Between Rice Yields and Traits Related to Weed Suppression

Rice weed-free plant densities did not differ among cultivars at H1 in 1999 (334 plants $m^{-2}$ ± 16.8 SE) or 2000 (464 plants $m^{-2}$ ± 28.0 SE). Delayed planting in 2000 may have exposed germinating seeds to higher temperatures, resulting in greater initial rice densities in 2000 (Caton et al. 1998). All cultivars used in this study had high weed-free yields, particularly in 1999 (Table 2). Lower yields in 2000 than in 1999 may be the result of delayed planting of early-maturity rice varieties in 2000. This shortens the growing season and can also result in lower yields because of heat stress caused by flowering occurring later in the summer than usual (Brandon et al. 1981).

Watergrass significantly reduced rice yields in both years (Table 2); average rice yield reductions were greater in 2000

TABLE 2. Rice (*Oviza sativa* L.) yields in weed-free (WF) and weedy (W) plots in 1999 and 2000.

| | Rice yield | | | | | |
|---|---|---|---|---|---|---|
| | 1999 | | | 2000 | | |
| Cultivar | W | WF | Mean | W | WF | Mean |
| | $g\ m^{-2}$ | | | | | |
| ‘2470’ | 1,143 (149.1)[a] | 872 (171.3) | 1,008 (118.3) | 932 (29.0) | 517 (47.3) | 724 (82.5) |
| ‘1406’ | 1,201 (32.2) | 885 (183.1) | 1,043 (109.1) | 799 (27.6) | 394 (41.9) | 597 (80.0) |
| ‘M-101’ | 1,028 (11.1) | 633 (190.8) | 831 (82.5) | 856 (33.9) | 451 (27.7) | 653 (79.1) |
| ‘96Y’ | 1,260 (55.5) | 993 (220.3) | 1,127 (117.8) | 893 (82.4) | 552 (75.9) | 723 (82.7) |
| ‘M-302’ | 1,060 (31.5) | 918 (183.1) | 988 (47.3) | 876 (47.5) | 543 (85.5) | 710 (80.7) |
| ‘S-201’ | 1,276 (176.9) | 937 (99.4) | 1,106 (118.2) | 1,010 (53.7) | 536 (125.0) | 773 (109.4) |
| ‘M-202’ | | | | 962 (51.5) | 387 (100.5) | 675 (130.8) |
| ‘Italica livorna’ | | | | 909 (110.7) | 466 (48.9) | 687 (100.6) |
| Mean | 1,161 (40.9) | 873 (62.9) | | 905 (21.8) | 481 (26.8) | |
| LSD (0.05) environment | | | 155[b] | | | 68 |
| LSD (0.05) cultivar | | | NS[c] | | | NS |
| LSD (0.05) E × C | | | NS | | | NS |

[a] Standard error are given in parentheses.

[b] LSDs in 1999 were calculated using log-transformed data and were then back-transformed for presentation.

[c] NS, not significant.

than in 1999 (47 and 25%, respectively). We attribute this to greater watergrass DW in 2000 than in 1999 (Table 1). There were no significant cultivar by environment (weedy vs. weed free) interactions for yields in either year, and no significant differences among cultivars in mean yields were detected (Table 2). Also, despite the different levels of watergrass DW among cultivars (Table 1), cultivars did not differ significantly in percent yield reduction (100 × (rice yield in weed-free plots − rice yield in weedy plots)/rice yield in weed-free plots) in 1999 or 2000 (data not shown). This may result from insufficient experimental precision in detecting small differences in yield among these high-yielding cultivars or may perhaps reflect the different levels of WT among cultivars.

There were no significant negative correlations between weed-free rice traits and weed-free rice yields in 1999 and 2000. On the contrary, S-201, one of the most suppressive cultivars in both years, had the highest weed-free yields in both years (Table 2). Competitive ability has been linked to lower potential yields for some crop species (Callaway 1992; Jannink et al. 2000). For example, researchers have found that height can be associated with competitiveness in rice but that it is inversely correlated with yield (Jennings and Aquino 1968; Jennings and De Jesus 1968; Jennings and Herrera 1968). But those studies focused on the differences between tall (> 170 cm at maturity) varieties and semidwarfs (80 to 90 cm at maturity). Our results support the idea that, among semidwarf cultivars with relatively small differences in height (cultivars ranged in height from 80 to 100 cm), rice plant height may not be related to differences in WSA (plant height was not linked to WSA in our study). Fischer et al. (1997, 2001) reported no correlation between the competitive ability of rice and rice yields in field studies with junglerice [*Echinochloa colona* (L.) Link] or two *Brachiaria* species. The authors linked competitive ability with rice tillering and leaf area but not with height. Similarly, Ni et al. (2000) found significant differences in WSA among semidwarf cultivars of similar height and suggested that high-yielding competitive cultivars could be developed for tropical rice production. Although additional work should be conducted to determine the genetic correlations between yield and competitive traits, our work supports the idea that high-yielding weed-suppressive semidwarf cultivars could be developed for California rice production.

It should be noted that the successful development of an indirect breeding program depends in part on two factors not considered in this study: heritability of traits and effect of local conditions on trait expression (Jannink et al. 2000). In our study, increased WSA in rice was a function of two traits (LAI and root DW), which could be identified under weed-free conditions. Determining whether these traits have high heritability and are expressed relatively independently of environmental conditions will require further study before an indirect breeding program could begin. Although the cultivars in this study performed similarly in relation to each other in both years, there were temporal differences in the magnitude of watergrass suppression (Table 1). Dry weight of watergrass grown with S-201 was 18% in 1999 and 57% in 2000 of the DW of watergrass grown with the least suppressive cultivar. Temporal factors may influence the expression of traits related to WSA and the effectiveness of WSA as a tool for weed management. But if competitive cultivars are used as one tool in a weed management system that includes herbicides, tillage, fertility, and water management (Gibson and Fischer 2002), then rice growers will be able to adjust their reliance on competitive cultivars according to environmental conditions.

Herbicide resistance, concerns about human and ecosystem health, and economic constraints on herbicide development challenge the continued sustainability of weed management in California rice (Fischer et al. 2000; Hill and Hawkins 1996). An increased reliance on the crop for weed control has been suggested as a low-cost, environmentally benign approach that could be readily integrated by growers into existing agronomic practices (Gibson and Fischer 2002). Competitive rice cultivars have the potential to reduce seed production by weeds that escape herbicide control, reduce herbicide loads in the environment, and lessen selection pressure for resistance to herbicides (Gibson and Fischer 2002; Gibson et al. 2001; Maxwell et al. 1990). This study supports research conducted in tropical rice (Fischer et al. 1995, 1997, 2001; Fofana and Rauber 2000; Garrity et al. 1992; Johnson et al. 1998; Ni et al. 2000) that suggested that competitive high-yielding cultivars could be developed for rice production. Furthermore, this study suggests that an indirect selection program based on one or two rice traits (leaf area and root DW) has great potential for developing high-yielding weed-suppressive cultivars for water-seeded rice production.

## Sources of Materials

[1] LI-COR 3000 leaf area meter, Li-COR Inc., P.O. Box 4425, Lincoln, NE 68504.

[2] Linear AccuPAR ceptometer, Decagon Devices, Inc., P.O. Box 835, Pullman, WA 99163.

[3] SAS software, version 8.02, Statistical Analysis Systems Institute Inc., SAS Campus Drive, Cary, NC 27512.

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