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Relating rice traits to weed competitiveness and yield: a path analysis

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Resistance to herbicides in the most important weeds threatens the sustainability of California rice. Weed-competitive rice cultivars could be a low-cost and safe nonchemical addition to an integrated weed management program. Trade-offs between competitiveness and productivity and inconsistent trait expression under weedy and weed-free conditions could complicate the breeding of competitive rice cultivars. A 2-year competition experiment was conducted in the greenhouse involving eight rice cultivars and two weed competition regimes (presence or absence of late watergrass) to examine the effects of rice weed-suppressive ability and tolerance to weed competition (weed tolerance) on rice yield. Competition reduced average rice yield from 32 to 48%, and watergrass biomass from 44 to 77%. Path analysis suggested that enhancing rice weed-suppressive ability and weed tolerance while minimizing possible productivity trade-offs should promote early (12 d after seeding) growth and light-capture traits followed by moderate growth rates before heading and a vigorous grain filling period. Crop growth rate (CGR) after heading was a relevant determinant of yield (direct path: 0.82, $P < 0.01$) and correlated ($r = 0.30$, $P < 0.01$) with weed tolerance. Late biomass accumulation was negatively correlated with harvest index and CGR during ripening ($r = -0.46$, $P < 0.01$); thus, late-season competitiveness can lower productivity. Rice traits conferring competitiveness were correlated across weed competition regimes ($r = 0.36$–0.81, $P < 0.01$). However, significant cultivar-by-competition and cultivar-by-year interactions suggest that selection efficiency would be greater when traits are identified under competition and in different environments. This study relates to the phenotypic expression of traits for competitiveness. Breeding competitive cultivars will require additional knowledge on trait heritability, genetic correlations with competitiveness, and on the effects of the environment upon gene expression.

Nomenclature: Late watergrass, *Echinochloa phyllopogon* (Stapf) Koss., ECHPH; rice, *Oryza sativa* L.

Key words: Crop interference, competitive cultivars, weed-suppressive ability, weed tolerance, yield penalty.

The sustainability of rice in California is threatened by the evolution of resistance to most available herbicides in late watergrass and early watergrass [*Echinochloa oryzoides* (Ard.) Fritsch], the most economically important weeds of this crop (Fischer et al. 2000; Hill et al. 2002). Crop interference has been proposed as a means to reduce the number of herbicide applications while maintaining good weed control, address public concerns regarding pesticide use, and reduce the selection pressure for resistance (Christensen 1994; Gibson and Fischer 2004). Competitive cultivars can suppress weed seed production, limit future weed infestations (Jordan 1993), fit easily into current agronomic practices, and become a safe and low-cost tool for integrated weed management in rice (Gibson et al. 2003). Several traits have been associated with irrigated rice competitiveness with weeds in previous studies (Fischer et al. 1997; Gibson et al. 2003; Ni et al. 2000). Negative correlations between competitiveness and rice productivity have been reported by some authors (Dingkuhn et al. 1999; Jennings and Aquino 1968; Kawano et al. 1974), and others have suggested that enhancing rice competitiveness and maintaining high yielding ability are compatible goals (Fischer et al. 1997, 2001; Gibson et al. 2001, 2003; Johnson et al. 1998). The reasons for these discrepancies have not been fully clarified, since most of these studies are based on the inspection of simple correlations and lack a mechanistic analysis of the relationships between plant characteristics that determine competitiveness and those that determine yielding ability. Crop competitiveness is a complex attribute that involves the ability to sustain yields despite the presence of weeds (weed tolerance) and the ability to suppress weed growth (Goldberg and Landa 1991; Jordan 1993). An analysis of the interrelationships between these processes and the factors determining yielding ability is required for the assessment of possible trade-offs between enhanced cultivar competitiveness and productivity. Moreover, early- and late-season crop growth contribute differently toward competitiveness and yield (Dingkuhn et al. 1991, 1999; Jordan 1992, 1993). Most studies fail to address this complexity, and the analysis of simple correlations does not adequately incorporate the effects of interrelations among traits, which is relevant to the definition of selection criteria for crop improvement. Simulation modeling can provide a process-based tool for designing rice cultivars that are more competitive with weeds (Bastiaans et al. 1997; Lindquist and Kropff 1996). However, current simulation models have limitations arising from insufficient understanding of key plant processes (Passioura 1996), and the availability of complex data sets for calibration and validation has limited their usefulness.

Path analysis (Li 1975) is an insightful tool to examine the effects of growth traits on rice competitiveness (Jordan 1992; Ogg and Seefeldt 1999), and to identify factors that may determine a trade-off between competitiveness and yielding ability. Path coefficients are used within a hypothetical network of causal relationships to compare the effects of a set of independent variables on a response (dependent) variable. The overall correlation between a causal and a response variable is partitioned into path coefficients corresponding to direct effects of one variable upon another, indirect effects mediated via other correlated variables also affecting the dependent variable, and other effects due to undetermined causes (residuals) (Wright 1921). Thus, additional information commonly hidden in simple correlation analysis can be obtained (Pantone et al. 1992; Smith et al. 1997). Path coefficients are standardized partial regression coefficients, and thus are independent of original units of measurement. This allows the relative importance of the hypothesized causal relationships to be directly compared. Ni et al. (2000) used path analysis to identify traits associated with rice weed-suppressive ability, but did not relate competitiveness to yield potential, nor did they establish the contribution of weed tolerance and early vs. late interference to overall competitiveness.

Although rice may have limited plasticity compared to late watergrass (Gibson and Fischer 2001; Gibson et al. 2004), plants often respond to the presence of neighbors with morphological and physiological alterations (Gibson and Fischer 2001; Gibson et al. 2001). Identifying traits for competitiveness under weed-free conditions would allow indirect selection for competitiveness in monoculture (Jannink et al. 2000; Lemerle et al. 1996), instead of the less-practical cultivar selection based on their performance under weedy conditions (Wall 1983). For this, weed-free and weedy traits must be correlated and their expression should be consistent across different growing conditions. In this study we present an approach to describe the outcome of late watergrass interference with eight rice cultivars and examine traits and processes associated with rice competitiveness using a series of path analyses. First, we quantify competition effects and establish the components of rice competitiveness. By assessing the contribution of key processes toward the grain-yielding ability of rice and rice growth at different stages, we uncover the sources of possible trade-offs between rice competitiveness and productivity. Then we identify traits involved in the ability of rice to suppress late watergrass throughout different growth stages or to sustain yield under competition. We also examined the consistency of expression among rice traits for competitiveness across weed competition regimes and years. Finally, we formulate a hypothesis for improving rice weed-suppressive ability and weed tolerance while minimizing possible trade-offs with productivity.

Materials and Methods

A study was conducted with late watergrass and eight rice cultivars to examine competition between both species, and to identify traits and processes associated with rice competitiveness using growth analysis and a series of path analyses.

General Growing Conditions

Competition between rice and late watergrass was studied in a greenhouse at the Rice Experiment Station near Biggs, CA in 2000 and 2001. Seeding dates were July 13, 2000 and May 25, 2001. Seeds of rice and watergrass were imbibed for 24 and 48 h, respectively, in deionized water and then seeded into 8.23 L pots filled with 7.48 kg Stockton Clay Adobe soil (fine, montmorillonite, thermic, Typic Pelloxert). Pots were seeded with a mixture of rice and watergrass or with each species individually. A plastic bag lined the interior of the pots to prevent contact between roots from adjacent pots. Nitrogen and phosphorous were applied in solution over the pots the day prior to seeding, pots were then watered to incorporate the nutrients. Target rates were equivalent to 168 kg N ha^{-1} and 30 kg P ha^{-1} following typical fertilization rates for rice production in California, and were applied within ± 9%. Five days after seeding (DAS) rice was thinned to a final stand of six equidistantly spaced plants per pot, which is equivalent to 210 plants m^{-2} to approximate the commercial seeding rate in California (200 plants m^{-2}). In the weedy pots, late watergrass was thinned to two plants per pot (equivalent to 70 plants m^{-2}) placed toward the center of the pots, but uniformly spaced with respect to rice plants in the same pot. The same spacing and density were used in control pots seeded only with watergrass. After thinning, a permanent flood was established and water level was gradually raised following plant growth up to a maximum of 8–10 cm above the soil surface. Pots were separated 30 cm from adjacent pots and spacing was increased by about 25% after each sampling date. The position of pots was randomized weekly within each bench. Average minimum and maximum daily temperatures from seeding to rice maturity were 15 and 33 C in 2000 and 17 and 35 C in 2001, respectively, and were representative of local climatic conditions (University of California 2005). The glasshouse intercepted approximately 10% sunlight at noon. Average photosynthetically active photon flux density in the greenhouse calculated from local weather station records (University of California 2005) was 1,076 $\mu mol\ m^{-2}\ s^{-1}$ in 2000 and 1,165 in 2001.

Experimental Design and Plant Material

Experiments involved a factorial combination of eight rice cultivars and two weed competition regimes (weedy and weed free). The two competition levels were either 2 or 0 plants of watergrass per pot. Treatments were arranged in a randomized complete block design with five blocks; each greenhouse bench was assigned to one replication (block). Four control pots with only two watergrass plants per pot were randomly placed in each bench. Watergrass seeds were collected from the Rice Experiment Station in the year previous to each experiment. The eight cultivars studied included a group of six experimental lines (EL) from a population originated by the introgression of *Oryza nivara* Sharma and Shastry into an *Oryza sativa* cv. M-202 background. The cultivar M-202 is a short-stature modern *japonica*-type cultivar widely used in California (Johnson et al. 1986). Cultivars M-202 and A-301 are known for their high and low initial vigor and competitiveness, respectively (Gibson et al. 2001). According to previous field records, plant height at heading among cultivars ranged from 82 to 121 cm, seedling shoot length measured 15 DAS ranged from 22 to 33 cm, and yields were from 6200 to 8300 kg ha^{-1}.

Sampling Procedure

Four sets of plants were started at the same time, allowing for destructive harvests to be conducted on all treatments and blocks at 12 DAS (five-leaf stage), 36 DAS (mid tillering), when rice was 10–20% headed (heading), and at maturity (final harvest). Except for cultivar EL 7, average heading dates were 86 ± 3 DAS in 2000 and 87 ± 1 DAS in 2001; "EL 7" headed 10 and 15 d earlier in 2000 and 2001, respectively. The following variables were measured at each sampling date on three randomly selected rice plants per pot: number of tillers per plant, biomass (dry weight) per tiller, length of the plant from the soil surface to the tip of the youngest fully extended leaf, area and dry weight of blades cut at the collar (leaves), root biomass (only at 12 DAS in weedy pots), and total aboveground biomass. The other three rice plants in each pot were dried and weighed in bulk. Aboveground biomass of the two watergrass plants was measured in the weedy pots. To determine biomass, plants were cut at soil surface and oven-dried at 60 C until constant weight. Root biomass was determined after gently washing soil over a 1 mm mesh. Leaf area was measured with the use of a LI-3100[1] leaf-area meter equipped with an 8.5 mm lens for 1 mm^2 resolution. At rice maturity, panicles were hand threshed and grain weights standardized to 13% moisture content. The following ratios were calculated from these measurements: specific leaf area (SLA, amount of leaf area per unit leaf dry weight) in $cm^2\ g^{-1}$, and harvest index (HI) or the amount of grain biomass per unit total aboveground biomass at maturity. Growth rates were defined and calculated following Hunt (1982). Crop growth rate is the absolute rate of growth within a period:

$$\mathrm{CGR} = (W_2 - W_1)/(t_2 - t_1) \qquad [1]$$

where W_2 and W_1 are the final and initial plant biomass, respectively, for the time interval $t_2 - t_1$. Relative growth rate is defined as the increase in total dry weight per unit of original weight per unit time:

$$\mathrm{RGR} = (\ln W_2 - \ln W_1)/(t_2 - t_1) \qquad [2]$$

Net assimilation rate is the rate of increase of plant weight per unit leaf area (L):

$$\mathrm{NAR} = [(W_2 - W_1)/(t_2 - t_1)] \times [(\ln L_2 - \ln L_1)/(L_2 - L_1)] \qquad [3]$$

and is dependent on the photosynthetic activity of leaves. All these rates were calculated for three distinct sampling intervals: 12 DAS to 36 DAS (vegetative stage), 36 DAS to heading (late vegetative and reproductive stage), and heading to maturity (grain-ripening stage) (IRRI 2005).

Competition Analysis

To quantify competition effects, we distinguish two components of rice competitiveness: The ability to reduce weed growth through competition (weed-suppressive ability) and the ability to sustain growth and grain filling in spite of weed presence (weed tolerance) (Goldberg and Landa 1991; Jannink et al. 2000). Weed suppressive ability is related to the vegetative growth of the crop, because fast and early rice growth will keep weeds at a disadvantage to capture resources. Cultivar differences in biomass accumulation under competition should reflect their relative weed-suppressive ability (Gaudet and Keddy 1988; Ni et al. 2000; Roush and Radosevich 1985). We used the watergrass shoot biomass at the time of heading (WG $\mathrm{Biom}_{\mathrm{Hd}}$; trait variables are designated by abbreviating the trait measured and the sampling date) to directly assess weed-suppressive ability. More weed mass present at heading indicated a lesser ability of rice to suppress weed growth. Weed tolerance was assessed as the unsuppressed shoot weed mass at heading per unit yield loss. A large value of this index of weed tolerance indicates that loss of yield was small relative to the amount of weed present, thus reflecting the ability of rice to tolerate the weed. We integrated the factors that affect rice competitiveness and yield under competition into a model represented in Figure 1, consisting of a two-stage path analysis, where unidirectional arrows correspond to the direct effects (paths) of hypothetically causative variables on the dependent variable, and double-headed arrows represent correlations among variables. The first stage represents vegetative growth from 36 DAS to heading. Plant mass at heading (dependent variable), both for rice and watergrass, is determined by mass at 36 DAS and relative growth rate between 36 DAS and heading (independent variables). Thus, competition effects are represented by the direct effects of mass and growth of each species on the mass of the other at the end of the stage. We incorporated the mass of weed-free rice at heading to statistically control for linear effects other than competition on rice mass, thus enhancing our ability to quantify competition impacts. The second stage represents reproductive growth between heading and maturity of rice. Yield under weedy conditions (dependent variable) is determined by the potential to produce grain in the absence of competition (weed-free yield) and by the fraction of this potential actually achieved when weeds are present. The ability to reach the yield potential depends on the amount of weed present and the tolerance of yield to competition (weed tolerance). Thus, rice and watergrass biomass at heading, weed tolerance, and weed-free yield are the independent variables in the second-stage path analysis (Figure 1). Watergrass mass at heading is the amount of watergrass that will be growing and competing for resources with rice during the grain filling period. Inflation due to multicollinearity was minimal, because only two direct effects were barely greater than one (Gravois and Helms 1992).

Competitiveness vs. Productivity Assessment

Biomass accumulation is a good measure of competitive success, because it reflects resource capture under the interference of neighbors (Gaudet and Keddy 1988; Roush and Radosevich 1985). However, it has been argued that enhancing rice competitiveness through excessive biomass growth may negatively affect its yield potential (Jennings and Aquino 1968). In order to assess interactions that can lead to negative effects of biomass accumulation on yield potential, we hypothesized a path analysis to explain weed-free grain yield as a function of biomass accumulation, the ability to partition biomass to grain (HI), and the rate of dry weight accumulation between heading and maturity

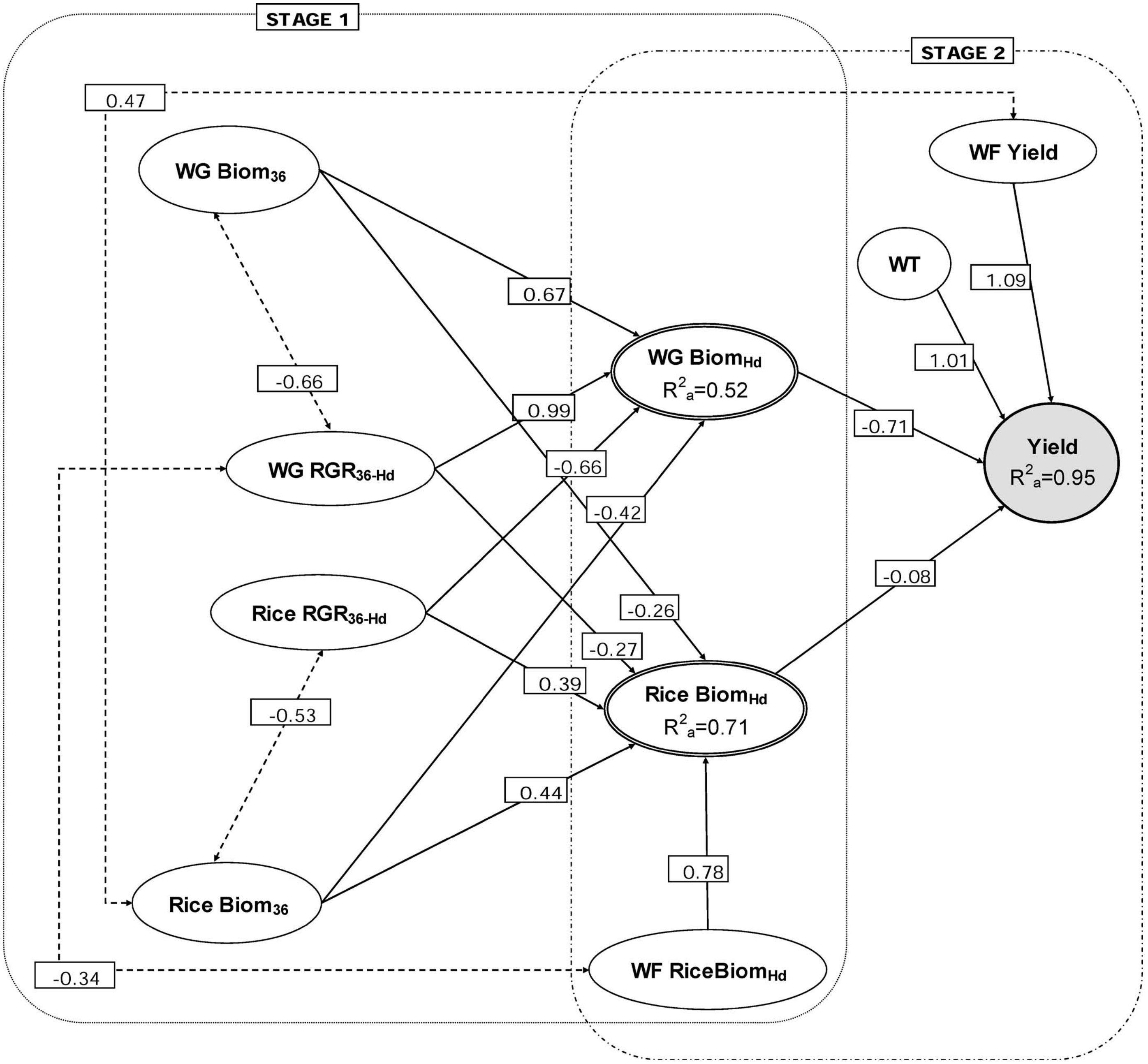

FIGURE 1. Path diagram showing the hypothesized direct and indirect effects on rice grain yield under watergrass competition (Yield) of yield potential, weed tolerance, weed-suppressive ability given by early- and late-season shoot growth of rice, and watergrass competition. Stage 1 represents vegetative growth from 36 d after seeding (DAS) to heading, and Stage 2 corresponds to the reproductive growth between heading and maturity of rice. Only correlations (dashed lines with double-headed arrows) and direct path (unidirectional arrows) coefficients significant at the 0.01 level are included in the diagram. Variables are WF Yield, rice grain yield weed-free; WT, weed tolerance; WG Biom_{36} and WG Biom_{Hd}, watergrass shoot biomass by 36 DAS and by heading, respectively; WG $\text{RGR}_{36\text{-Hd}}$, watergrass shoot relative growth rate between 36 DAS and heading; Rice Biom_{36} and Rice Biom_{Hd}, rice shoot biomass under competition by 36 DAS and by heading, respectively; Rice $\text{RGR}_{36\text{-Hd}}$, rice shoot relative growth rate between 36 DAS and heading; and WF Rice Biom_{Hd}, weed-free rice shoot biomass at heading; R^2_a, adjusted coefficient of determination. Weed tolerance (WT) was defined as the mass of weed per unit decrease in rice yield relative to the weed-free pots.

(Rice $\text{CGR}_{\text{Hd-Mt}}$) (Figure 2). These causative variables are considered to be key determinants of rice grain yielding ability (Akita 1994, Dingkuhn et al. 1991, Jennings and Aquino 1968, Kropff et al. 1994, Peng et al. 2000). In this analysis, biomass was partitioned into an early and a late component: Rice biomass measured by 36 DAS (Rice Biom_{36}) and rice biomass at heading (Rice Biom_{Hd}), respectively. A strong genetic correlation between early and late biomass accumulation would complicate breeding for these traits separately. Thus, we explored the correlation between two variables representing these processes in the competition model of Figure 1, Rice Biom_{36} and RGR between 36 DAS and heading (Rice $\text{RGR}_{36\text{-Hd}}$), by partitioning it into components due to the experimentally controlled effects and due to the residuals. This analysis is presented in Figure 3.

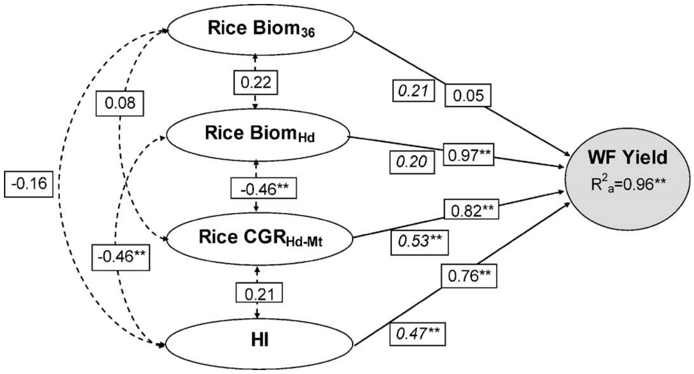

FIGURE 2. Path diagram showing the hypothesized direct and indirect effects on rice grain yield potential of early- and late-season rice biomass, rate of dry-matter accumulation after heading, and the ability to partition carbohydrates to grain measured in monoculture. Variables (measured in monoculture) are WF Yield, rice grain yield weed-free; Rice Biom$_{36}$ and Rice Biom$_{Hd}$, rice shoot biomass by 36 d after seeding and by heading, respectively; Rice CGR$_{Hd\text{-}Mt}$, absolute crop growth between heading and maturity; and HI, harvest index. Path coefficients are values on the unidirectional arrows; double-headed arrows (dashed lines) are correlations between independent variables. Indirect effects result from multiplying the correlation coefficient between two independent variables by the corresponding path coefficient of one variable toward WF Yield; correlation coefficients between WF Yield and a particular independent variable (values in italics below unidirectional arrows) are the sum of all direct and indirect effects involving WF Yield and that variable (Li 1975). R^2_a is the adjusted coefficient of determination. Asterisks (*, **) indicate significance at the 0.05 and 0.01 probability levels, respectively.

Identifying Traits Predicting Rice Competitiveness

Identifying morphological traits predicting rice competitiveness would help define selection criteria for crop improvement. The model presented in Figure 1 was used to identify indicators of rice competitiveness. Also, an additional path analysis model relating early rice biomass accumulation with traits measured under watergrass competition by 12 DAS was used to identify early predictors of rice competitiveness (Figure 4), because these traits would relate to plant weed-suppressive ability during the critical period of rice competition with weeds (Gibson et al. 2002), and would be convenient early selection criteria. Breeding and crop management will ultimately seek to achieve trait expression under competition. Therefore, we conducted our analyses using the phenotypic expression of rice traits under competition, not under monoculture.

Assessing Consistency of Trait Expression

Cultivar differences for individual traits involve genetic and environmental effects. In our study, the latter mainly resulted from watergrass competition and differences between years. Consistency of trait expression across environments was assessed by comparing the contributions of cultivar and environmental effects toward each trait and by correlating trait expression under monoculture and under competition. Our study examined relationships between plant characteristics under fertility and crop density levels representative of those that maximize productivity of modern irrigated rice in California. It is unlikely that weed management will involve drastic changes in these variables without incurring problems of lodging, sterility, diseases, and nutrient deficiency or lower nutrient use efficiency.

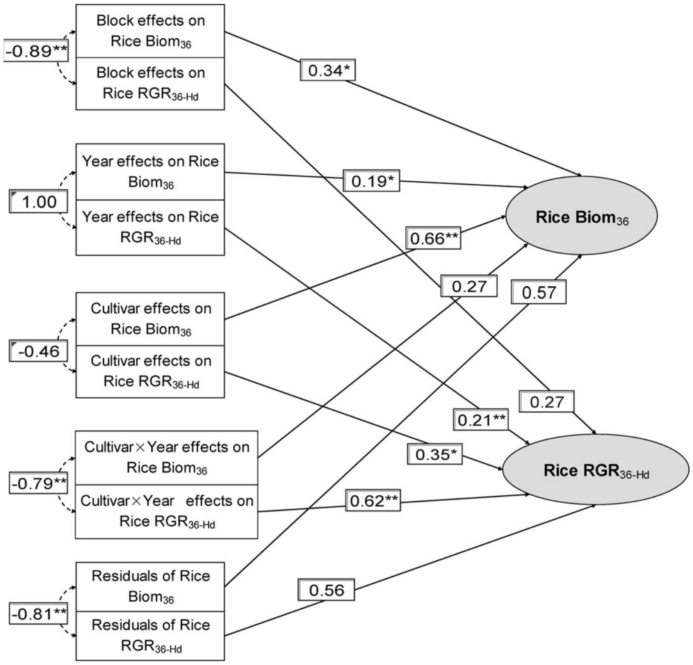

FIGURE 3. Partitioning of the total correlation under weedy conditions between rice shoot biomass by 36 d after seeding (Rice Biom$_{36}$) and rice shoot relative growth rate between 36 d after seeding and heading (Rice RGR$_{36\text{-}Hd}$) into components due to experimentally controlled effects and residuals. Components of covariance (and correlation) between the two variables due to the different effects were obtained by performing a multivariate analysis of variance (MANOVA) on the two variables, with cultivar, year, cultivar by year, and block within year as effects. Contributions of main effects and interactions (unidirectional arrows) were calculated as the proportion of the total sum of squares (SS) explained by each effect ($\sqrt{(\text{Effect SS/Total SS}}$). Correlations between the exogenous variables due to each effect are indicated by double-headed arrows and were calculated from cross products and sums of squares derived from the MANOVA (Johnson and Wichern 2002). The total correlation between Rice Biom$_{36}$ and Rice RGR$_{36\text{-}Hd}$ is given by the sum of all possible paths between these two variables; the value of each path results from multiplying the correlation due to a given effect by the values on the unidirectional arrows joining that effect with each dependent variable. Asterisks (*, **) indicate significance at the 0.05 and 0.01 probability levels, respectively.

Data Analysis

ANOVA was conducted for each harvest to determine cultivar and competition effects and their interaction each year as well as year-by-treatment interactions. Path analysis was used to identify rice plant traits related to competitiveness with watergrass and to assess trade-offs between competitiveness and productivity. Path analyses were based on hypothesized models where independent variables were causally related to a dependent variable. Multiple linear regression was used to calculate the path coefficients, which represented the direct effects of the causative variables on the dependent variable. Coefficients for path analysis models having more than one dependent variable were calculated by performing one multiple linear regression for each dependent variable, where all variables with direct paths towards the dependent variable were considered explanatory variables (Li 1975). Path analysis partitioned the correlations between the dependent variable and each of the causative variables into direct and indirect effects. An indirect effect between one causative variable and the dependent variable through a second causative variable was calculated by multiplying the correlation between the causative variables by

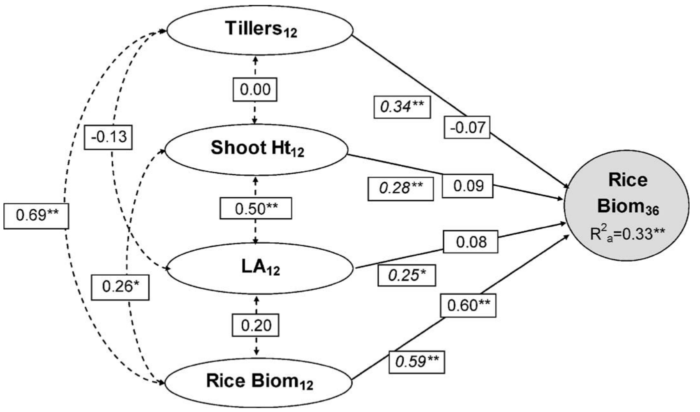

FIGURE 4. Path diagram showing the hypothesized direct and indirect effects on early rice biomass of rice traits measured by 12 d after seeding (DAS). Variables (measured under competition) are Rice Biom$_{36}$, rice shoot biomass by 36 DAS; Tillers$_{12}$, number of tillers per plant; Shoot Ht$_{12}$, seedling height; LA$_{12}$, leaf area per pot; and Rice Biom$_{12}$, aboveground biomass. Path coefficients are values on the unidirectional arrows; double-headed arrows (dashed lines) are correlations between independent variables. Indirect effects result from multiplying the correlation coefficient between two independent variables by the corresponding path coefficient of one variable toward Rice Biom$_{36}$; correlation coefficients between Rice Biom$_{36}$ and a particular independent variable (values in italics below unidirectional arrows) are the sum of all direct and indirect effects involving Rice Biom$_{36}$ and that variable (Li 1975). R^2_a is the adjusted coefficient of determination. Asterisks (*, **) indicate significance at the 0.05 and 0.01 probability levels, respectively.

the direct path from the second causative variable to the dependent variable [please refer to Pantone et al. (1992) for an example of path analysis calculations]. The path analysis of Figure 1 involves exogenous (predictors that do not appear as responses in the model) and endogenous variables, where an indirect effect can also result from the multiplication of two consecutive direct paths, one linking an exogenous with an endogenous variable, and one from the endogenous variable toward the dependent variable. The sum of all direct and indirect effects yields the total correlation between a causative variable and the dependent variable. The effect from residual variation due to unknown factors can be calculated as $\sqrt{1 - R^2}$ (Williams et al. 1990). Pairwise correlations were used to explore relationships between variables and for the calculation of indirect effects in path analysis. To avoid multicollinearity problems, independent variables with correlations above 0.80 with other explanatory variables were not included in path analysis (Ogg and Seefeldt 1999). When two variables were highly correlated, we selected the one making the strongest contribution to the model. After checking that path coefficients were consistent across years, all multiple regressions were performed with data from both years together.

The total correlation between the variables representing early and late biomass accumulation (Rice Biom$_{36}$ and Rice RGR$_{36\text{-Hd}}$) was partitioned into components due to the experimentally controlled effects (block, cultivar, year, and cultivar-by-year interaction) and due to the residuals. Components of covariance (and correlation) between these variables due to the different effects were obtained by performing a multivariate analysis of variance (MANOVA) with the two variables as responses, and with cultivar, year, cultivar by year, and block within year as effects. Correlations between these variables due to each effect were calculated by saving the *E* and *H* matrices (Johnson and Wichern 2002) from the MANOVA and dividing the cross products by the square root of the product of the sums of squares. Each correlation has as many degrees of freedom as the effect generating it. This is presented as a path diagram in Figure 3, where the contributions of main effects and interactions (unidirectional arrows) were calculated as the proportion of the total sums of squares (SS) explained by each effect in the model $\sqrt{\text{Effect SS/Total SS}}$, which is equivalent to the standardized coefficients used in path analysis. The total correlation between Rice Biom$_{36}$ and Rice RGR$_{36\text{-Hd}}$ is given by the sum of all possible paths between these two variables. For example, the path between Rice Biom$_{36}$ and Rice RGR$_{36\text{-Hd}}$ via residual effects can be calculated as the Residual effect of Rice Biom$_{36}$ on Rice Biom$_{36}$ by the correlation between Residual of Rice Biom$_{36}$ and Residual of Rice RGR$_{36\text{-Hd}}$ (double-headed arrow) by the Residual effect of Rice RGR$_{36\text{-Hd}}$ on Rice RGR$_{36\text{-Hd}}$ (Figure 3).

Consistency of trait expression across weed competition regimes and years was examined by subjecting each characteristic involved in the path analyses of this study to a three-factor ANOVA. The contributions of main effects (rice cultivar, weed competition regime, and year) and interactions were compared for each trait in terms of the proportion of the total SS explained by each effect in the model (Table 1).

Inspection of error distributions and scatter plots among variables suggested that assumptions of linearity and normality held reasonably well. All analyses were conducted with the use of the JMPin software (Version 4.0.3 Academic, SAS Institute Inc.).

Results and Discussion

Competition and Yielding Ability in the Presence of Weeds

Competition reduced ($P < 0.05$) rice productivity and suppressed watergrass. Watergrass competition led to grain yield losses ranging from 32 to 48% among cultivars across both years. In turn, rice competition suppressed watergrass biomass by about 44–77%. Cultivars differed ($P < 0.05$) for all growth variables measured and competition effects first became significant ($P < 0.05$) on most traits by 36 DAS (data not shown). Similarly, junglerice [*Echinochlea colona* (L.) Link] competition reduced rice growth by 40 d after emergence in field studies in the tropics (Fischer et al. 1997).

Under competition, both early rice shoot biomass (Rice Biom$_{36}$) and aggressive rice growth between 36 DAS and heading (Rice RGR$_{36\text{-Hd}}$) acted as significant ($P < 0.01$) weed suppressors (direct paths = −0.42 and −0.66, respectively) and as promoters (direct paths = 0.44 and 0.39, respectively) of rice shoot mass at heading (Figure 1). Conversely, early weed shoot mass accumulation by 36 DAS (WG Biom$_{36}$) and relative weed growth rate before heading (WG RGR$_{36\text{-Hd}}$) can reduce late rice growth (direct paths = −0.26 and −0.27, respectively; $P < 0.01$) and support more weed competition subsequently (direct path from WG Biom$_{\text{Hd}}$ to final grain yield = −0.71, $P < 0.01$). The model in Figure 1 also shows the relevance of early growth on yield under competition. By having significant ($P < 0.01$) negative impacts on WG Biom$_{\text{Hd}}$, Rice Biom$_{36}$ and Rice

TABLE 1. Correlations (*r*) between trait expression in monoculture and in competition, and proportion (*p*) of the total sums of squares (SS)[a] explained by the main effects of cultivar (Cv), competition regime (WC), and year (Yr) and by factor interactions (Cv by WC, Cv by Yr, WC by Yr, Cv by WC by Yr) for the following rice characteristics: Number of tillers per plant by 12 d after seeding (DAS) (Tillers$_{12}$); shoot height at 12 DAS (Shoot Ht$_{12}$); leaf area per pot at 12 DAS (LA$_{12}$); shoot biomass accumulated by 12 DAS, 36 DAS, and heading (Rice Biom$_{12}$, Rice Biom$_{36}$, and Rice Biom$_{Hd}$, respectively); relative rice growth rate between 36 DAS and heading (Rice RGR $_{36\text{-}Hd}$); biomass accumulation rate from heading to maturity (Rice CGR$_{Hd\text{-}Mat}$); harvest index (HI); grain yield; and weed tolerance (WT)

Trait	CV	WC	Yr	Cv by WC	Cv by Yr	WC by Yr	Cv by WC by Yr	Residual	Mono-culture vs. competition
	p								*r*
Tillers$_{12}$	0.39**	0.05	0.68**	0.15	0.19*	0.02	0.12	0.53	0.70**
Shoot Ht$_{12}$	0.74**	0.02	0.46**	0.09	0.30**	0.05	0.05	0.36	0.81**
LA$_{12}$	0.49**	0.04	0.55**	0.20	0.28**	0.03	0.10	0.54	0.62**
Rice Biom$_{12}$	0.58**	0.04	0.53**	0.14	0.29**	0.01	0.11	0.46	0.76**
Rice Biom$_{36}$	0.54**	0.47**	0.01	0.24**	0.23**	0.17**	0.11	0.53	0.37**
Rice RGR$_{36\text{-}Hd}$	0.34**	0.51**	0.22**	0.17	0.40**	0.05	0.22**	0.53	0.38**
Rice Biom$_{Hd}$	0.57**	0.74**	0.02	0.16**	0.15**	0.05*	0.07	0.26	0.79**
Rice CGR$_{Hd\text{-}Mat}$	0.41**	0.52**	0.15**	0.19	0.17	0.08	0.18	0.64	0.36**
HI	0.39**	0.25**	0.65**	0.04	0.25**	0.03	0.12	0.52	0.66**
Yield	0.31**	0.85**	0.24**	0.06	0.08	0.02	0.06	0.32	0.74**
WT	0.40*	—	0.23**	—	0.26	—	—	0.80	—

[a] $p = \sqrt{(\text{effect SS/total SS})}$.

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

RGR$_{36\text{-}Hd}$ under competition had indirectly positive impacts on rice yield under competition ($-0.42 \times [-0.71] = 0.30$ and $-0.66 \times [-0.71] = 0.47$). These traits also had significant positive impacts on weedy Rice Biom$_{Hd}$; but only weak indirect effects on yield through Rice Biom$_{Hd}$ due to the weak direct path between Rice Biom$_{Hd}$ and yield (Figure 1). Thus, after accounting for weed tolerance, WG Biom$_{Hd}$, and for yield potential (which incorporates the effect of biomass accumulated in the absence of weed interference as discussed later), Rice Biom$_{Hd}$ did not contribute much to yield under competition. Conversely, Rice Biom$_{36}$ had a positive impact on yield through its large negative impact on weed mass.

Trade-Offs Between Competitiveness and Productivity

By partitioning the correlations between yield and each of the causative variables into direct and indirect effects, the path analysis in Figure 2 revealed that HI was actually a stronger determinant of yield than apparent on the basis of the overall correlation between HI and yield. In the absence of weed interference, there was a strong positive and significant ($P < 0.01$) direct effect (direct path = 0.76) of HI on weed-free yield (Figure 2). However, HI also affected weed-free yield indirectly through Rice Biom$_{Hd}$ and Rice CGR from heading to maturity (Rice CGR$_{Hd\text{-}Mt}$), because these variables were correlated. The indirect effect through Rice Biom$_{Hd}$ (-0.45) is the product of the negative correlation between Rice Biom$_{Hd}$ and HI ($r = -0.46$, $P < 0.01$) and the direct path from Rice Biom$_{Hd}$ to yield (0.97, $P < 0.01$) (Pantone et al. 1992). The sum of all direct and indirect effects yields the total correlation of 0.47 ($P < 0.01$) between HI and weed-free yield. The low correlation between HI and yield, relative to the direct effect, results from a negative indirect effect of HI on yield through Rice Biom$_{Hd}$ (Figure 2). Negative indirect effects through Rice Biom$_{Hd}$ also affected the correlation between weed-free yield and Rice CGR$_{Hd\text{-}Mt}$ (Figure 2), although Rice CGR$_{Hd\text{-}Mt}$ was a most relevant determinant of weed-free yield (path coefficient = 0.82, $P < 0.01$). The relative importance of the direct effects on yield was Rice Biom$_{Hd}$ $\geq$ Rice CGR$_{Hd\text{-}Mt}$ $>$ HI $\gg$ Rice Biom$_{36}$.

Negative indirect effects on yield through Rice Biom$_{Hd}$ are attributed to the impact of excessive vegetative biomass that increases canopy self shading and respiratory costs, which lower photosynthetic capacity and grain filling rates during the ripening stage (Akita 1994; Dingkuhn et al. 1991; Jennings and Aquino 1968). Competitiveness usually involves a differential contribution of early- and late-season effects (Fofana and Rauber 2000; Gibson et al. 2002; Jordan 1992, 1993). Thus, it would be logical to infer that if there is a productivity trade-off from enhanced competitiveness this may depend on differential yield penalties associated with early- or late-season biomass accumulation. Figure 2 suggests that yield penalties associated with early rice biomass accumulation would be lower than those associated with the amount of rice biomass accumulated by heading (total negative effects of Rice Biom$_{36}$ and Rice Biom$_{Hd}$ on grain yield were $-0.16 \times 0.76 = -0.12$ and $-0.46 \times 0.76 + (-0.46) \times 0.82 = -0.73$, respectively (Figure 2). Therefore, enhancing early-season rice competitiveness would carry a lower yield penalty than improving its late-season competitiveness. The feasibility of implementing this concept in breeding competitive rice cultivars would depend on the type of correlation that may exist between the processes of early and late biomass accumulation. Rice Biom$_{36}$ and Rice RGR$_{36\text{-}Hd}$ are expressions of these processes, and both had significant and large negative direct effects on weed mass (Figure 1). However, these two traits were negatively correlated ($r = -0.53$, $P < 0.01$). Breaking this correlation would allow increased competitiveness through the best combination of early suppressive ability and sufficient but not excessive late rice shoot mass. However, optimizing this combination would be difficult if the correlation is mostly genetic. Exploring the nature of the correlation by partitioning it among the experimental factors—cultivar (which incorporates the genetic component), year, cultivar by year, and block—revealed that the relationship between Rice $RGR_{36\text{-}Hd}$ and Rice $Biom_{36}$ was mostly due to year (because there were only 2 years, the correlation due to year is identical to 1.0 and its significance is based on the effects of year on each response), blocks, errors, and interaction effects (Figure 3).

This analysis suggests potential for breaking the negative correlation between Rice $Biom_{36}$ and Rice $RGR_{36\text{-}Hd}$ through selection and breeding.

Predictors of Early-Season Weed-Suppressive Ability

Weed biomass at heading (WG $Biom_{Hd}$) had a strong negative effect (direct path = -0.71, $P < 0.001$) on yield under competition (Figure 1). Weed mass at 36 DAS (WG $Biom_{36}$) was a strong determinant of WG $Biom_{Hd}$ (direct path = 0.67, $P < 0.001$) and had also a negative direct effect on Rice $Biom_{Hd}$ (-0.26, $P < 0.01$). Therefore, morphological traits predicting Rice $Biom_{36}$ would be expressions of early plant vigor associated with competitiveness during a period when watergrass competition is most susceptible to suppression. This agrees with Gibson et al. (2002), who demonstrated that suppressing watergrass during the first 30 DAS prevents rice yield losses from watergrass competition in California. In our study, rice shoot mass by 12 DAS (Rice $Biom_{12}$) had a significant direct effect on Rice $Biom_{36}$ (direct path = 0.60, $P < 0.01$), whereas seedling shoot height (Shoot Ht_{12}) and leaf area (LA_{12}) were significantly correlated with Rice $Biom_{36}$ ($r = 0.28$, $P < 0.01$, and $r = 0.25$, $P < 0.05$, respectively) mostly due to positive indirect effects through Rice $Biom_{12}$ ($0.26 \times 0.59 = 0.15$ and $0.20 \times 0.59 = 0.12$, respectively), which were the largest effects for those variables (correlations result from adding all direct and indirect effects for a given variable) (Figure 4). Early leaf-area development and height growth could have provided light-capture advantage under competition, thus promoting rice biomass accumulation during critical early competition stages. Height growth before 36 DAS and early LA have also been related to rice competitiveness in other studies (Fischer et al. 1997, 2001; Ni et al. 2000), and early LA explained most of the weed-suppressive ability of similar cultivars competing against early and late watergrass in California (Gibson et al. 2003). Increasing a canopy's specific leaf area (SLA, $cm^2\ g^{-1}$) would reduce the amount of photosyntates needed to produce a given LA for early light capture and ground coverage; this has been a key strategy for improving competitiveness in tropical upland rice (Dingkuhn et al. 1999). However, in our study SLA did not contribute to competitiveness or was eliminated due to collinearity, because SLA and LA were positively correlated ($r = 0.43$–0.56, $P < 0.01$). Early tillering ability has been related to rice competitiveness in several studies (Dingkuhn et al. 1999; Fischer et al. 1997; Jennings and Aquino 1968). However, the number of tillers per plant contributed little toward early competitiveness in our study (Figure 4), which agrees with a preliminary field study by Gibson et al. (2003) in California.

Late-Season Weed-Suppressive Ability

Rice cultivars with late-season competitiveness would contribute to weed management by suppressing late-emerging weeds and herbicide-resistant weeds that have escaped early weed control. Path analysis suggested that late-season competitiveness against watergrass depended on the extent of growth achieved by 36 DAS, and on the rate of biomass accumulation thereafter (Figure 1). These traits have been associated with competitiveness in previous studies (Fischer et al. 1997; Holt and Orcutt 1991; Ni et al. 2000; Roush and Radosevich 1985). Compared to early-season competitiveness, enhancing late-season competitiveness through resource capture bears a greater yield penalty due to the adverse effects of excessive vegetative growth on HI and grain filling (Figure 2). High Rice CGR during the ripening phase could allow rice to maintain a moderately high HI in spite of high biomass production (Peng et al. 2000).

A Framework for Enhancing Weed Suppression by Rice

Cultivar competitiveness alone cannot eliminate weeds in rice, but a delay in weed emergence provides California flooded rice with enough competitive advantage to prevent further weed establishment (Gibson et al. 2002). In our study, light-capture traits (LA, height) and biomass measured within 2 wk after seeding were good predictors of early competitiveness, and early LA development would lead to a more rapid canopy closure. Therefore, combining early biomass, which carries a low yield penalty, with a moderate growth rate during later stages would enhance early rice weed-suppressive ability to exclude weeds by the end of a brief initial weed-free period (Gibson et al. 2002) and ensure the maintenance of a competitive status without the yield trade-off from excessive late biomass production. Weed control would only be required to provide a brief initial weed-free period. This agrees with Dingkuhn et al. (1999), who suggested that trade-offs between rice competitiveness and yield potential could be reduced by expressing traits for light capture at an early developmental stage.

Tolerance of Weed Competition

In this experiment, weed tolerance contributed significantly to the ability of rice to yield under competition (Figure 1). According to Jordan (1993), differences in weed tolerance should not be confounded with differences in weed-suppressive ability. The absence of significant correlations between weed tolerance and variables of Stage 1 in Figure 1 suggests that our weed tolerance index was in fact rather independent of weed suppression, and that it probably relates to late-season processes at the time of grain filling. Crop growth rate between heading and maturity was a relevant component of yield (Figure 2), and was correlated under competition with weed tolerance ($r = 0.30$, $P < 0.01$). It has been demonstrated that rice tolerance to drought stress and defoliation is related to the ability for remobilizing stem carbohydrates toward grain filling (Ingram et al. 1995). Therefore, the high grain filling rates and long grain filling duration sought for high productivity in modern rice varieties (Dingkuhn et al. 1991; Peng et al. 2000) may have contributed tolerance to stress by weed competition. Further studies to understand the physiological components of tolerance would be relevant. However, enhancing weed tolerance may be insufficient as a single strategy to improve crop competitiveness. Weed tolerance needs the complement of weed-suppressive ability and/or additional weed control, because unsuppressed weeds can produce seed and cause a weed population buildup capable of inflicting substantial yield losses even to cultivars with high weed tolerance (Callaway and Forcella 1993, Jannink et al. 2000, Jordan 1993).

Traits and Environmental Effects

Correlations between traits in monoculture and competition ($r_{\text{M-C}}$) suggested that Rice Biom_{Hd}, yield, and HI were consistently expressed among cultivars across weed competition regimes (Table 1). Most other traits exhibited moderate to low $r_{\text{M-C}}$ values except traits measured by 12 DAS, which had not yet been modified by competition. Early-season biomass accumulation (Rice Biom_{36}), which was a determinant of early weed-suppressive ability (Figure 1), was differently affected by competition among cultivars as suggested by the low $r_{\text{M-C}}$ and by the rather large effect of the cultivar-by-competition interaction relative to cultivar effects for this trait (Table 1). The $r_{\text{M-C}}$ for the absolute rate of weight increase during grain filling (Rice $\text{CGR}_{\text{Hd-Mt}}$) was comparatively low, although this trait was not affected by interactions. The rather high error term for this variable suggests that improved precision in its determination may lead to a more consistent expression across competition regimes. Some authors have identified monoculture traits that are predictive of rice competitiveness in mixed stands (Dingkuhn et al. 1999; Gibson et al. 2003). However, other studies suggest that this may not be possible when cultivars differ strongly in their plastic responses to competition (Fischer et al. 1997, 2001). Wall (1983) suggested that trait evaluation under competition might be more efficient than evaluation in monoculture for selecting competitive genotypes.

Cultivar-by-year interactions affected ($P < 0.05$) many plant traits except yield, overall weed tolerance, and Rice $\text{CGR}_{\text{Hd-Mat}}$ (Table 1). Also, certain cultivars ('M-202' and the experimental lines, except 'EL 7') consistently exhibited in both years less yield reductions and more weed suppression ($P < 0.05$) than 'A-301', which was a cultivar chosen for its low competitiveness (data not shown). Other studies have reported consistent expression of cultivar competitiveness across years (Fischer et al. 1997, 2001; Gibson et al. 2001 and 2003). Jannink et al. (2000) found that early soybean height, which was genetically correlated with weed suppression, was a consistent predictor of competitiveness across environments. However, genetic correlations between traits and competitiveness may vary between crop lines derived from different crosses (Jannink et al. 2000), suggesting the need for studies involving different rice germplasm and competing species.

In conclusion, rice and weed responses to competition obtained in this greenhouse study were commensurate with field observations in California and elsewhere. Ranges of trait expression reflected the variability of the rice genotypes used, and predictions beyond these ranges would require the use of ecophysiological modeling or studies with different sets of cultivars. Nevertheless, the study provides a good model for the analysis of traits, competitiveness, and yield trade-offs. This analysis suggests that improving the competitiveness of California water-seeded rice while minimizing possible trade-offs with productivity would involve combining early light capture, moderate relative growth rates before heading, and a vigorous grain filling period. Early growth is critical for watergrass suppression. Selection for cultivars with rapid early growth followed by moderate late biomass accumulation should be feasible. Most cultivars in our study were highly productive and fairly weed suppressive. However, path analysis was useful to uncover trade-offs between competitiveness and productivity and to detect opportunities for mitigation. Productivity penalties from enhanced competitiveness may have to be compensated by the benefits of cheaper, safer, or improved weed management (Jannink et al. 2000). Enhancing rice competitiveness by selecting traits in monoculture could be possible. However, cultivar-by-competition and cultivar-by-year interactions caution that trait evaluation under competition might be more efficient than evaluation in monoculture and that rice traits for competitiveness need to be identified under a range of growing environments. Further knowledge is needed on trait heritability, genetic correlations with competitiveness, and environmental dependency of expression. Competitive cultivars would be a relevant addition to tactics for integrated weed management and should contribute to delay the evolution of herbicide resistance.

Sources of Materials

[1] LI-COR 3100 leaf-area meter, Li-COR Inc., P.O. Box 4425, Lincoln, NE 68504.

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