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Use of ^{13}C Isotope Discrimination Analysis to Quantify Distribution of Barnyardgrass and Rice Roots in a Four-Year Study of Weed-Suppressive Rice

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In a 4-yr field study, "weed suppressive" rice cultivars provided 30% greater control of barnyardgrass and sustained 44% less yield loss (relative to weed-free) compared to "nonsuppressive" tropical japonica rice cultivars. ^{13}C analysis revealed that rice root mass predominated vertically and laterally within the soil profile of plots infested with barnyardgrass. Among all cultivars, rice roots accounted for 75 to 90% of the total root mass in samples, and this was most concentrated in the surface 5 cm of soil in the row. Barnyardgrass roots were most prevalent in the surface 5 cm between rows where they accounted for 30% of total root mass. Overall, barnyardgrass root mass was about twice as high in nonsuppressive rice compared to suppressive rice. Weed suppression by indica/tropical japonica rice crosses generally was intermediate between that of the other two rice groups. At the 0- to 5-cm depth, between-rows, barnyardgrass root mass was correlated negatively with rice height ($r = -0.424$), yield ($r = -0.306$), and weed control ratings ($r = -0.524$) in weedy plots. Control ratings in weedy plots also were negatively correlated with rice percent height reduction ($r = -0.415$) and % yield loss ($r = -0.747$) relative to weed-free plots, and with barnyardgrass root mass as a percent of total root mass ($r = -0.612$). Control ratings were positively correlated with rice yield under weed pressure ($r = 0.429$) but were correlated with rice root mass in-rows only ($r = -0.322$). Clearly, rice root mass could not have been the major cause of the differences in barnyardgrass control between cultivars.

Nomenclature: Barnyardgrass, *Echinochloa crus-galli* (L.) Beauv.; rice, *Oryza sativa* L.
Key words: $^{13}C/^{12}C$ isotope ratio, $\delta^{13}C$, ^{13}C depletion, C_3 photosynthetic pathway, C_4 photosynthetic pathway, crop–weed interference, crop–weed root distribution, allelopathic rice, indica rice.

Effective weed control is an ongoing challenge in U.S. rice production. *Echinochloa* species are among the most troublesome weeds of rice in the United States and worldwide (Labrada 2007). Barnyardgrass is a dominant *Echinochloa* species in Arkansas and other southern states in the United States, while early watergrass [*Echinochloa oryzoides* (Ard.) Fritsch] and late watergrass [*E. oryzicola* (Vasinger) Vasinger (Stapf.) Koss] are prevalent in water-seeded rice systems in California (Bridges and Baumann 1992; Fischer et al. 2000; Smith 1988). Barnyardgrass is one of the two most competitive weed species in the southern United States and is particularly damaging early in the rice growing season (Smith 1988). Rice yields in California were reduced unless *Echinochloa* species were removed completely from fields for 30 d or more after planting (Gibson et al. 2002).

Weed-suppressive rice germplasm with high weed interference potential in drill-seeded systems of the southern United States has been evaluated for a number of years (Dilday et al. 2001). These efforts have identified Asian indica lines with suppressive activity against aquatic weeds and barnyardgrass (Dilday et al. 2001; Gealy and Fischer 2010; Gealy et al. 2003; Gealy et al. 2005a,b). However, before considering growing "weed suppressive" rice cultivars, U.S. farmers will need a high level of confidence that these cultivars will produce yields and grain quality similar to or better than those of existing cultivars. Unfortunately, plant type and grain quality of promising suppressive indica lines often have not met U.S. rice industry standards. For instance, 'Teqing' and 'PI 312777' are prone to lodging and have low milling yields (49 and 45% head rice, respectively) compared to the commercial cultivar 'Cypress' (61% head rice) (Gealy et al. 2003). PI 312777 was developed from the cross, T65*2/TN 1, and is also known as 'WC 4644' (Germplasm Resources Information Network [GRIN] 2010). To address the need for improved grain quality, crosses between high yielding nonsuppressive commercial cultivars (e.g., 'Katy' and 'Drew') and weed-suppressive indicas (e.g., PI 312777 and PI 338046; GRIN 2010) have been developed at Stuttgart, AR (K. Moldenhauer breeding program) and tested for weed suppression (Gealy and Moldenhauer 2005; Gealy et al. 2005b). 'RU 9701151' and 'STG96L-26-093' are selections from a cross between the suppressive indica, 'PI 338046', and Katy. RU9701151 has shown good milling yield (64% head rice) (Moldenhauer et al. 1999) and cooking quality (Dilday et al. 2001; Gealy et al. 2005b; Moldenhauer et al. 1999) and was also seen as a source of enhanced natural weed suppression.

Research in rice systems (Dingkuhn et al. 1999; Fischer et al. 1997; Fofana and Rauber 2000; Gealy et al. 2005a,b; Gibson et al. 1999; Gibson et al. 2001; Gibson et al. 2003; Perera et al. 1992; P'erez de Vida et al. 2006; Zhao et al. 2006) as well as other cereal crops (Hoad et al. 2008; Murphy et al. 2008; Vandeleur and Gill 2004) has identified crop traits that can confer natural competitiveness against weeds, including rapid early root and leaf growth, high tillering, large above-ground biomass, and tall plant height. The competitive effects from roots on the growth of target plants are reported to be greater than those from shoots for 70% of studies conducted, encompassing numerous species (Wilson 1988).

PI 312777 has suppressed barnyardgrass and aquatic weeds under a variety of conditions (Dilday et al. 2001; Gealy et al. 2003; Kong et al. 2006), as does one of its parental lines, 'TN 1' (Kim et al. 2005), which is also a parent of PI 338046 (GRIN 2010). Roots and other tissues of PI 312777 are known to release potent phytotoxic chemicals (allelochemicals) (Chen et al. 2008; Gu et al. 2009; Kato-Noguchi and Ino 2005; Kong et al. 2006; Okuno and Ebana 2003; Seal and Pratley 2010) that are active against weeds or other plants. Genetic control of this activity has been attributed to a number of quantitative trait loci identified in rice mapping

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populations (Lee et al. 2005; Okuno and Ebana 2003; Xiong et al. 2007; Zeng et al. 2003; Zhou et al. 2007). In rice (Chen et al. 2008; Khanh et al. 2007; Seal and Pratley 2010) and other small grains (Bertholdsson 2005, 2007), root exudates have been shown to enhance weed suppression by some cultivars and are being evaluated in breeding programs.

^{13}C isotope discrimination analysis has been adapted as a tool to quantify root distribution between C_3 (photosynthetic pathway) rice and C_4 grass weeds such as barnyardgrass under natural flooded field conditions (Gealy and Fischer 2010; Gealy and Gealy 2011). The method relies on the phenomenon that C_3 and C_4 plants both fix the common ^{12}C form of CO_2 and the much rarer ^{13}C form of CO_2 during photosynthesis, and that fundamental differences between the photosynthesis processes of the two plant types cause C_4 plants to fix a higher percentage of ^{13}C than C_3 plants (Ehleringer 1991; Farquhar et al. 1989). Thus, C_3 plant tissues are ^{13}C-depleted compared to those in C_4 plants. Rice mapping populations studies on $\delta^{13}C$ levels (an expression of ^{13}C:^{12}C isotope ratios) and associated crop productivity traits have indicated quantitative trait loci for $\delta^{13}C$ on five (Xu et al. 2009) or on six (Laza et al. 2006) of the 12 rice chromosomes. $\delta^{13}C$ analysis has also been used to determine the proportions of C_3 and C_4 plant roots in a number of systems (Derner et al. 2003; Eleki et al. 2005; Polley et al. 1992; Svejcar and Boutton 1985; Svejcar et al. 1988), and has been used in programs to improve water use efficiency in rice (Dingkuhn et al. 1991; Impa et al. 2005; Kondo et al. 2004; Scartazza et al. 1998).

Root distribution between barnyardgrass and weed-suppressive indica and nonsuppressive tropical japonica rice under natural field conditions is not well understood and is difficult to measure. The aim of this research was to determine the differences, if any, in weed interference activity and root distribution between barnyardgrass and three groups of rice cultivars differing in weed-suppression potential. Specific objectives were: (1) determine distribution of barnyardgrass and rice roots at different soil depths and locations (relative to rice rows) using ^{13}C isotope discrimination analysis; (2) determine above-ground productivity of barnyardgrass and rice; and (3) determine potential relationships between rice–weed interactions in above- and below-ground environments.

Materials and Methods

Field Plots. Rice was drill-seeded 2-cm deep from May 5 to May 21 during the 4-yr period from 2001 to 2004 at a density of 430 seeds m^{-2} into DeWitt silt loam soil (fine smectitic, thermic, Typic Albaqualfs) with 1.2% organic matter and pH 5.8 at the University of Arkansas Rice Research and Extension Center near Stuttgart, AR (34.49°N, 91.55°W) as described previously (Gealy and Fischer 2010). Plots consisted of nine, 3-m-long rice rows spaced 18 cm apart. Plots containing weed-free rice cultivars were paired with a weed-infested (weedy) counterpart containing the same cultivar. One or more plots of monoculture barnyardgrass were included in each replication as a weed-only standard. After planting, supplemental barnyardgrass seed was broadcast evenly over all weedy plots at a density of 11.5 kg barnyardgrass seeds ha^{-1} and rolled. Although the primary species present in weedy plots was barnyardgrass, other C_4 grass species such as sprangletop (*Leptochloa* spp.) and broadleaf signalgrass [*Urochloa platyphylla* (Nash) R.D. Webster] were sometimes observed and were not controlled. These species have since been shown to produce ^{13}C isotope discrimination signatures relatively close to those of barnyardgrass in flooded rice fields (Gealy and Gealy 2011), and thus should not alter ^{13}C-related inferences regarding root interaction. Rice plants emerged from May 14 to May 30. Barnyardgrass and other weeds were removed from weed-free plots by hand and by a POST application of propanil + quinclorac (4.4 + 0.275 kg ai ha^{-1}) (Scott et al. 2010). At the three- to four-leaf stage of barnyardgrass, weedy plots were sprayed POST with 1.1 kg ai ha^{-1} propanil (0.25× rate) to achieve mild stunting of barnyardgrass and with 0.55 kg ai ha^{-1} bentazon to kill broadleaf weeds (Scott et al. 2010). The barnyardgrass stunting caused by the low rate of propanil serves the purpose of reducing overall weed competition so that differences among rice cultivars can be more readily determined. Urea at 110 kg N ha^{-1} was broadcast over all plots before establishment of the permanent flood (June 15 to July 3).

Cultivar Selection. Five or more rice cultivars were evaluated in each of the 4 yr. Each was assigned to one of three groups based on its expected level of weed suppression or genetic pedigree. 'Kaybonnet' (Gravois et al. 1995), 'Lemont' (Bollich et al. 1985), and 'Francis' (Moldenhauer et al. 2007) (2003 and 2004 only) were included as "nonsuppressive" commercial southern long-grain standards. Asian indicas, 'PI 312777' (T65*2/TN1) and 'Teqing', and the proprietary commercial hybrid, 'RT-XL8' (2003 and 2004 only), were included as "suppressive" (or "weed-suppressive") cultivars (Gealy et al. 2003; Gealy et al. 2005b). In 2004 the proprietary commercial hybrid, 'RT Clearfield XL8', was planted at a density of 140 seeds m^{-2} (commercially recommended) as a substitute for RT-XL8 due to limited availability of seed. 'RU 9701151' (2001 and 2002 only) and 'STG96L-26-093' (2003 and 2004 only) were selections from a PI 338046/Katy cross (Gealy et al. 2005b), and for classification purposes, were considered to be "intermediate" between suppressive and nonsuppressive cultivar groups.

Above-Ground Plant Measurements. Rice data were obtained from both weedy and weed-free plots. The number of days from rice seedling emergence to 50% heading was estimated in each plot based on visual estimates recorded three times per week during the reproductive stage. Mature rice heights (height) in each weedy and weed-free plot were obtained by averaging 10 randomly selected plants measured (cm) to the tip of the tallest panicle. Rice "% height reduction" in weedy plots, calculated as 100 − (height in weedy plots/height in weed-free plots)(100), was used to indicate the reduction in height caused by weed interference. Rough rice yields (adjusted to 12% moisture) in weedy plots (yield) and their adjacent weed-free plots (weed-free yield) were determined from an interior 2-m section of the five middle rows of each plot and expressed in kg ha^{-1}. Rice "% yield loss" in weedy plots, calculated using the same approach as that for percent height reduction described above, was used to indicate the yield reduction caused by weed interference.

After barnyardgrass plants headed (typically at early rice heading), weedy plots received a visual control rating in which 0% indicated no apparent difference in biomass and growth compared to barnyardgrass plants in monoculture plots, and

100% indicated complete control. After barnyardgrass plants had reached ~maximum above-ground biomass production, and just prior to rice harvest (usually following root sampling described in section below), the total above-ground barnyardgrass plant tissue ("shoots") in two 0.25 m by 0.25 m quadrats in weedy rice plots (barnyardgrass shoot mass) and in monoculture plots (i.e., barnyardgrass shoot mass in rice-free, weed-only check) was harvested, composited, dried to a constant weight at 60 C, weighed to an accuracy of 1 mg, and expressed as g m^{-2}. Total above-ground rice biomass was not determined. Barnyardgrass "% shoot mass loss" was calculated as

$$100-(\text{barnyardgrass shoot mass in weedy plots} / \text{barnyardgrass shoot mass in rice}-\text{free plots})(100) \quad [1]$$

to indicate the reduction in barnyardgrass shoot mass caused by rice.

Root Sampling and Analysis. Methods follow those in Gealy and Fischer (2010). Roots of barnyardgrass and rice from these plots were quantified from soil cores using ^{13}C discrimination analysis. After the permanent flood had been drained (September 7 to September 19), just prior to rice harvest, and preceding the barnyardgrass shoot sampling (described in section above), soil cores were sampled from plots (September 13 to October 17). Weedy plots of rice were sampled from within the five middle rows lying at least 30 cm from the front and back ends of plots to avoid edge effects. Four soil cores (10 cm-diameter by 15 cm-deep) were taken randomly within plots from each of two locations with respect to the rice rows. The locations were the mid point between rice rows ("between-row") and directly over the rice row ("in-row"). The cores were extracted using a lever-action hole cutter and were cut into soil depth sections of 0 to 5 cm (nearest soil surface) and 5 to 15 cm. Subsamples from each plot were immediately composited, placed in sealed plastic bags, and stored in a freezer at −12 C. Weed-free rice plots and weed-only barnyardgrass plots were similarly sampled within a rectangular area equivalent to that described for the weedy plots of rice in order to obtain monoculture root tissues. Henceforth, the four subsampled and composited soil cores described above are referred to as "samples."

The soil samples containing mixtures of barnyardgrass and rice root tissues were thawed, extracted from soil with tap water and mechanical agitation, captured on stacked sieves with 2 mm and 1.4 mm opening size, respectively, rinsed thoroughly with pressurized water, and subsequently hand-cleaned to remove any remaining foreign material. Root samples were not rinsed with dilute acid to remove soil carbonates as has been done previously (Svejcar and Boutton 1985), because soil carbonate formation on roots is minimal in the pH 5.8 soil used in our study (Gealy and Fischer 2010; unpublished data). Roots were dried at 60 C to a constant weight and weighed to the nearest 1 mg to obtain the total sample mass. Root samples were ground to a powder through 40-mesh screen with 2-mm openings.

The ^{13}C isotope procedures described in Gealy and Fischer (2010) were also used for this study. Briefly, all powdered root tissue samples were submitted to the Stable Isotope Laboratory at the University of Arkansas (http://www.uark.edu/ua/isotope), combusted in an elemental analyzer (Carlo Erba NC2500 elemental analyzer, CE Elantech, Inc. [formerly, Thermo Scientific/Carlo Erba], Lakewood, NJ) in a stream of helium, and analyzed for $\delta^{13}C$ using an isotope ratio mass spectrometer (Deltaplus isotope ratio mass spectrometer, Finnigan MAT, San Jose, CA) via a Conflo II interface. Raw $^{13}C/^{12}C$ isotope ratios were acquired by comparison with a reference gas injection and were normalized by comparison with in-house isotope standards. $^{13}C/^{12}C$ isotope ratios were expressed relative to the international Pee Dee Belemnite (PDB) limestone fossil standard as $\delta^{13}C$ in ‰ (Farquhar and Lloyd 1993; O'Leary 1993):

$$\delta^{13}C_{\text{sample}}(‰) = \left[\left(R_{\text{sample}} - R_{\text{standard}}\right)/R_{\text{standard}}\right] \times 10^3 \quad [2]$$

where $\delta^{13}C_{\text{sample}}$ is the isotope ratio in parts per thousand (‰), and R_{sample} and R_{standard} are the $^{13}C/^{12}C$ molar abundance ratios of the plant material and the PDB standard, respectively.

Instead of using linear regressions obtained from standard concentrations (Gealy and Fischer 2010) to determine the masses of barnyardgrass and rice roots in samples, we used a more accurate method that corrects mathematically for the presence of residual soil in root samples (Gealy and Gealy 2011). These equations were derived from independent "mixing equations" for carbon fraction (C fraction) and $^{13}C/^{12}C$ ratios. Full derivations and spreadsheet calculations for these equations are published in the text or appendices of this reference.

The variable names and definitions used in Equations 3 and 4 below are as follows: f and f_s are the respective C fractions, and M and M_s are the respective masses of the "total sample" and "soil component" (in g) in the sample mixture; and f_1 and f_2 are the respective C fractions, and M_1 and M_2 are the respective masses of the "C_3 root component (rice)" and "C_4 root component (barnyardgrass)" in the sample mixture. R, R_1, R_2, and R_s are $^{13}C/^{12}C$ ratios in the carbon present in the total sample, the C_3 and C_4 root components, and the soil component, respectively. Similarly, δ, δ_1, δ_2, and δ_s are $\delta^{13}C$ levels in the carbon contained in the total sample, the C_3 and C_4 root components, and the soil component, respectively. All data for pure rice and barnyardgrass (e.g., plant type "1" and "2," respectively) values were obtained from plants grown in monoculture plots. When available, data from individual cultivars from a given year were used to calculate results in Equation 3 for the same year. Otherwise, averages over all rice cultivars available in a given year were used. Root-free field soil in these studies had C fraction values (f_s = 0.008335) and $\delta^{13}C$ values (δ_s = −21.27‰) that were considered constants.

We used an approximation to determine the true C fraction values of rice (f_1) and barnyardgrass (f_2) roots. In this correction procedure, these root C fraction values were set equal to the values of their respective shoot C fractions obtained from the same plant or from the same species grown in the same year. When shoot analyses from the same year were not available, shoot C fractions of barnyardgrass and rice cultivars from a previous study (Gealy and Gealy 2011) were used instead. Root and shoot C fractions were shown to be similar when rice and barnyardgrass plant samples were vigorously re-washed to remove soil from roots (data not shown). Barnyardgrass root mass, M_2, was calculated according to the following equation.

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$$M_2 = M\left(\frac{\left(\frac{f_s(R_s-R)}{R_s+1}+\frac{f_1(R-R_1)}{R_1+1}\right)(f-f_s)-\left(\frac{f_s(R_s-R)}{R_s+1}\right)(f_1-f_s)}{\left(\frac{f_2(R_2-R)}{R_2+1}+\frac{f_s(R-R_s)}{R_s+1}\right)(f_1-f_s)-\left(\frac{f_s(R_s-R)}{R_s+1}+\frac{f_1(R-R_1)}{R_1+1}\right)(f_s-f_2)}\right) \quad [3]$$

This equates to Equation 23 in Gealy and Gealy (2011).

For any $^{13}C/^{12}C$ ratio (R_i), its $\delta^{13}C$ value (δ_i) can be expressed relative to the R value of the PDB standard (R_{pd}) according to the definition:

$$R_i \equiv P_{pd}[1+(\delta_i/1{,}000)] \quad [4]$$

this equates to Equation 25 in Gealy and Gealy (2011).

Note that this is a "generalized" rearrangement of Equation 2. Substituting this definition for the R values in Equation 3 yields equations that express $^{13}C/^{12}C$ ratios in terms of R_{pd}, the fixed standard ($^{13}C/^{12}C$ = 0.0112372; molar abundance ratio basis), and $\delta^{13}C$ values.

The mass of rice roots (M_1) can be obtained from the same general equations (Equations 3 and 4) after exchanging the f_i and R_i indices for plant "1" and plant "2" (i.e., the original f_1 and R_1 values become f_2 and R_2, respectively, while the original f_2 and R_2 values become f_1 and R_1, respectively). The f_s and f values and the R_s and R values are left unchanged.

Soil mass (M_s) was calculated as follows:

$$M_s = M - M_1 - M_2 \quad [5]$$

This equates to Equation 11 in Gealy and Gealy (2011).

Occasionally, slightly negative values for M_1 or M_2 were produced by Equation 3. This problem was most likely caused by mis-estimations of the true values of δ_1 or δ_2 obtained from monoculture plant standards. Similar negative values for soil mass (M_s) were also occasionally produced, apparently resulting from mis-estimation of one or both of the true C fraction values of f_1 or f_2 obtained from monoculture standards. The anomalous mass results described above were corrected as described in Supplemental Appendix 1B of Gealy and Gealy (2011), which increased the apparently negative mass values to approximately zero.

Root mass values were expressed using two distinct approaches. The first was as "mass per sample" (g sample^{-1}), which shows how the total mass of rice and barnyardgrass roots is distributed laterally and vertically within the plots. The second approach was "mass density" (mg L^{-1} soil), which shows how the root mass per volume (i.e. density) changes within plots and is particularly useful with soil depth. When expressed on a mass density basis, the mass per sample at the 0- to 5-cm depths doubles in relation to the respective values at 5 to15 cm because twice as much soil volume was sampled at the deeper depth. Root "mass per sample" values for rice (M_1) and barnyardgrass (M_2) were also expressed as their percentages of the total root biomass, rice root mass% and barnyardgrass root mass%, respectively.

Experimental Design. The experimental layout was a randomized complete block with four replications in 2001 and three replications in 2002, 2003, and 2004. For above-ground rice and barnyardgrass response variables, data were analyzed using the SAS GLIMMIX procedure (SAS Institute, Inc., Cary, NC: version 8.2). Years and replications were considered to be random effects. Means were separated at the 0.05 level using least squares means with the Tukey-Kramer adjustment. Two separate analyses were conducted; one with rice cultivars considered as individuals and one with cultivars divided into the three weed suppression groups, "nonsuppressive," "suppressive," and "intermediate."

For the below-ground measurements (i.e., root data from soil samples), a split-split plot design was used to model the response variables using the SAS PROC GLIMMIX procedure. Location was the first split and soil depth was the second split. Years and replications were considered to be random effects. Means were separated at the 0.05 level using least squares means with the Tukey-Kramer adjustment. A multivariate analysis was conducted using PROC CORR (SAS Institute, Inc., Cary, NC: version 8.2) to determine correlations among variables. Only the below-ground data from the 0- to 5-cm depth between-rows are presented from the correlation analyses.

Results and Discussion

Above-Ground Plant Measurements. In both weedy and weed-free plots, Lemont was the shortest cultivar, Kaybonnet and the two intermediate cultivars were tallest, and PI 312777 and Francis were midway in between (Table 1). With cultivars analyzed as groups, rice heights in weedy and weed-free plots were greater in the intermediate group than in the other two groups, but rice percent height reduction was similar among groups, averaging 3 to 7%.

Time to 50% heading in weedy plots ranged from 80 d in RT XL8 to 90 d in Lemont, but was similar among the three cultivar groups, averaging about 86 d (data not shown). Rice typically headed 1 to 2 d earlier in weed-free plots than in weedy plots.

Average weedy rice yield for PI 312777 was 2.2 and 1.7 times greater than for Lemont and Kaybonnet, respectively (Table 1). Teqing yield was similar to that of PI 312777. Yield of Francis, which was evaluated in only 2 of the 4 yr, was indistinguishable from all of the suppressive cultivars. Francis has excellent yield potential in weed-free production systems (Moldenhauer et al. 2007). Yields of the intermediate suppression cultivars were indistinguishable from those of the suppressive and nonsuppressive cultivars, usually falling midway between these groups.

Weed-free yields were similar among all the cultivars with the exception that yields of Lemont and STG96L-26-093 were lower than Teqing and RT CLXL8 by an average of 28% and the yield of Kaybonnet was 21% less than Teqing. When analyzed as a group, weed-free yields of the suppressive cultivars averaged about 20% more than nonsuppressive and intermediate groups.

Yield losses for Lemont and Kaybonnet were 2.7 and 2.3 times greater, respectively, compared with PI 312777. Similarly, the yield loss due to barnyardgrass interference in nonsuppressive cultivars was 1.8 times greater than in suppressive cultivars.

Visual control ratings were higher for PI 312777 (68%) than for Lemont (45%) and Kaybonnet (47%) (Table 1), and the trends in barnyardgrass shoot mass among these three cultivars were similar to those for the control ratings. Francis appeared to be atypical of the nonsuppressive rice group. Its visual control ratings and barnyardgrass shoot mass values usually were more similar to the suppressive and intermediate groups than to Lemont and Kaybonnet, although Francis was statistically indistinguishable from all of the cultivars.

Table 1. Above-ground rice and barnyardgrass measurements from field plots.[a,b,c]

	Rice						Barnyardgrass		
	Mature height			Yield				Shoot mass	
Rice cultivar (or group)	Weedy	Weed-free	Height reduction relative to weed-free	Weedy	Weed-free	Yield loss relative to weed-free	Visual control rating	Weedy	Mass loss relative to rice-free
	cm	cm	%	kg ha^{-1}	kg ha^{-1}	%	%	g m^{-2}	%
Analysis with cultivars considered as individuals									
Nonsuppressive									
Lemont	84 c	96 d	11[c] a	2,390 b	5,800 b	58.7 b	45[c] b	165	47.1
Kaybonnet	114[c] ab	120[c] ab	5 a	3,040[c] ab	6,130[c] ab	49.1 b	47 b	163	41.2
Francis	107 b	109 c	2 a	4,780 ab	7,310 ab	38.0 ab	58 ab	148	55.5
Intermediate									
RU 9701151	119 a	127 a	6 a	4,260 ab	6,560 ab	27.8 ab	59 ab	154	66.0
STG96L-26-093	122 a	126 a	3 a	4,030 ab	5,600 b	34.6 ab	61 ab	188	50.8
Suppressive									
PI 312777	106[c] b	108 c	2[c] a	5,240[c] a	6,870 ab	21.7 a	68 a	70	79.3
Teqing	106 b	112[c] bc	5 a	4,890 a	7,760[c] a	32.5 ab	60[c] ab	79	76.0
RT CL XL8	118 ab	118 a-c	0 a	4,880 ab	8,090 a	41.7 ab	61 ab	111	57.9
RT XL8	111 ab	111 bc	0 a	5,440 a	7,320 ab	32.6 ab	64 ab	125	62.0
	$P < 0.0001$	$P < 0.0001$	$P = 0.0165$	$P < 0.0029$	$P = 0.0003$	$P = 0.0081$	$P = 0.0003$	$P = 0.276$	$P = 0.532$
Analysis with cultivars considered as weed-suppressive groups									
Nonsuppressive	101 b	109 b	7	3,130 b	6,080 b	50.6 b	48 b	159 a	46.7
Intermediate	120 a	126 a	5	4,150 ab	6,230 b	31.2 ab	60 a	170 a	58.8
Suppressive	107 b	111 b	3	5,060 a	7,380 a	28.2 a	63 a	82 b	74.3
	$P = 0.0046$	$P = 0.0019$	$P = 0.097$	$P = 0.0037$	$P = 0.0069$	$P = 0.0118$	$P = 0.0025$	$P = 0.0477$	$P = 0.1204$

[a] Plants were grown in field plots in 2001, 2002, 2003, and 2004 in a standard drill-seeded, flooded rice production system at Stuttgart, AR.
[b] Means within columns followed by the same letter are not different according to a least squares means test at $P \leq 0.05$ unless otherwise noted.
[c] The following additional pairs within columns are significantly different: cultivar main effect; rice height and yield in weedy plots (PI 312777, Kaybonnet); rice height and yield in weed-free plots (Teqing, Kaybonnet); rice % height reduction (PI 312777, Lemont); and visual control rating for barnyardgrass (Teqing, Lemont).

When analyzed as groups, the suppressive cultivar group had about 30% (15 percentage points on the visual scale) greater control than the nonsuppressive group (Table 1). Barnyardgrass shoot mass of the suppressive group was approximately half that of both the nonsuppressive and intermediate groups. Previously, barnyardgrass suppression by F_3 progeny from a PI 312777/Lemont cross was intermediate to that by the parents (Gealy et al. 2005a).

Our field study results for rice percent yield loss and barnyardgrass percent shoot mass loss (Table 1; cultivars considered as groups; columns 6 and 9) are comparable to those previously reported from a greenhouse study in California, in which competition from late reduced average rice yield from 32 to 48% and the rice reduced the weed's biomass 44 to 77% (P'erez De Vida et al. 2006).

Rice cultivars with early growth, height development, and light-capture, greater leaf area, and a vigorous grain filling period have had competitive advantages against *Echinochloa* spp. (Caton et al. 1999; Gibson et al. 2003; P'erez de Vida et al. 2006). Ability to compete against weeds has also been associated with high yields. Cultivars that were most competitive against *Echinochloa* spp. were high-yielding (Gibson et al. 2003). Minimal yield loss to rice cultivars growing under weed pressure has previously been associated with weed suppression (Fofana and Rauber 2000), which was demonstrated by the suppressive cultivar group in our study (Table 1). Selection efficiency for *Echinochloa* spp. suppression traits was considered to be best achieved under weed pressure and in a variety of environments (P'erez de Vida et al. 2006).

Minimal yield loss under weed pressure has been reported previously for PI 312777 and other indicas (Gealy et al. 2003; Gealy et al. 2005b). Even after application of the low-dose of 1.1 kg ha^{-1} propanil, the PI 312777 rice yield loss due to barnyardgrass was 22% (Table 1), which would be economically prohibitive for most farmers. In similar field tests in China, weed-suppressive rice was used effectively with a combination of cultural management options (Kong et al. 2008). Suppressive rice varieties such as PI 312777 and Huagan-1 substantially reduced weeds, and when they were treated with low-dose bensulfuron-methyl (25 g ai ha^{-1}), weeds were nearly eliminated with no reduction in yield. In a nonsuppressive variety, yields were reduced up to 60% (Kong et al. 2008). These data agree with reports that weed-suppressive cultivars are not likely to control barnyardgrass by themselves and could be compatible with reduced herbicide/minimum input systems (Gealy et al. 2003; Gealy et al. 2005b; Kong et al. 2008) or with organic production systems (Texas Organic; W. Yan, personal communication) that can tolerate lower yields and quality because these deficiencies will be offset by a premium price for the crop.

Root Analysis. Root mass and density among all of the rice cultivars were similar (cultivar main effect; Table 2). Barnyardgrass root mass and density were greatest in Lemont, and Kaybonnet typically followed a similar trend. These cultivars averaged more than twice the respective barnyardgrass root masses among the suppressive cultivars, as well as Francis. Barnyardgrass root mass and density in the "intermediate" line STG96L-26-093 were among the lowest of all rice cultivars, along with PI 312777, Teqing, RT XL8, and Francis (Table 2). Barnyardgrass root mass% in Lemont (25%) was nearly twice that in suppressive and intermediate cultivars (10 to 15%). Clearly, root mass alone was not

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Table 2. Root distribution in weedy plots with rice cultivars identified individually.[a,b,c]

Cultivar	Rice	Barnyardgrass	Rice	Barnyardgrass	Rice	Barnyardgrass
	Root mass		Fraction of total root mass		Root mass density	
	g sample^{-1}		(%)		mg L^{-1}	
"Nonsuppressive"						
Lemont	2.94	0.83[c] a	74.7 a	25.3 a	1,610	464[c] a
Kaybonnet	3.46	0.61 ab	80.5 a	19.5 a	1,910	336 a
Francis	3.50	0.28[c] ab	86.6 a	13.4 a	1,930	159 ab
"Intermediate"						
STG96L-26-093	3.28	0.21 b	89.5 a	10.5 a	1,790	112 b
RU 9701151	3.09	0.37 ab	86.2 a	13.8 a	1,720	209 a
"Suppressive"						
PI 312777	2.78	0.29[c] ab	85.9 a	14.1 a	1,600	160[c] ab
Teqing	2.86	0.36[c] ab	85.4 a	14.6 a	1,610	194[c] ab
RT CL XL8	3.04	0.24 ab	86.9 a	13.1 a	1,560	119 ab
RT XL8	3.58	0.11 b	89.9 a	10.1 a	2,000	49 b
	P = 0.7584	P = 0.0032	P = 0.0424	P = 0.0424	P = 0.8747	P=0.0041

[a] Plants were grown in field plots in 2001, 2002, 2003, and 2004 in a standard drill-seeded, flooded rice system at Stuttgart, AR. Means within columns followed by the same letter are not different according to a least squares means test at the P values noted.

[b] Data presented are from the cultivar main effect. Means are across in-row and between-row locations and the 0 to 5 cm and 5 to 15 cm soil depths. All mass and mass density values were determined using soil correction equations in Gealy and Gealy (2011). Location and soil depth main effects, and the location by soil depth interaction were generally similar to those shown in Table 3 where rice cultivars were classified into "suppressive," "intermediate," or "nonsuppressive" groups. Thus, they were not presented here.

[c] The following additional pairs within columns are significantly different: barnyardgrass root (Lemont, Francis), (Lemont, PI 312777), and (Lemont, Teqing); barnyardgrass root mass density (Lemont, PI 312777), and (Lemont, Teqing).

responsible for cultivar differences in suppression of barnyardgrass root mass.

There was no cultivar by depth interaction for rice root mass (data not shown). However, means of rice root mass% for all cultivars except PI 312777 trended higher at 5 to 15 cm compared to 0 to 5 cm. These increases ranged from 3.5% for Teqing and 6.4% for RU 9701151 to 19% for Lemont and 26% for Francis. Rice root mass% for Francis and PI 312777 responded differently at the two soil depths. Root mass% of Francis at 0 to 5 cm was much greater than at 5 to 15 cm (97 vs. 77%), whereas PI 312777 root mass% was similar at the two soil depths (87 vs. 85%) ($P = 0.0310$; data not shown). These data suggest that PI 312777 may support root proliferation at both shallow and deeper depths, thus exploiting this space at the expense of barnyardgrass growth. Francis and PI 312777 may be using different rooting strategies to achieve crop productivity or weed suppression. In contrast to our results, PI 312777 and PI 338046 were reported to produce more root mass than common commercial cultivars in a pot study (Dilday et al. 2001). These cultivars also appear to produce a greater number of fibrous surface roots (Gealy and Fischer 2010; unpublished data) that could add substantially to the total root area while adding minimally to the mass.

Methods used to measure these below-ground variables were time-consuming and labor-intensive (Gealy and Fischer 2010), so sample size and replications had to be minimized. This probably reduced the number of differences ($P = 0.05$) that we detected among cultivars when they were considered as individuals. In an earlier study using ^{13}C analysis to evaluate root distribution between sorghum and cotton, similar limitations caused authors to consider $P < 0.10$ to be significant (Derner et al. 2003).

When root data were analyzed with rice cultivars grouped into weed suppression levels, rice root mass and density were similar among the three weed suppression groups (cultivar group main effect; Table 3). Barnyardgrass root mass and density in nonsuppressive rice were more than twice the levels present in suppressive rice, and the barnyardgrass root mass% showed a similar trend (Table 3). The barnyardgrass mass and mass density levels in intermediate rice were not different from those in the other two rice groups, but their means were most similar to means of suppressive rice. Total root masses were similar among the cultivar groups averaging 3.5 g sample^{-1} (Table 3) and roughly paralleled the rice root mass values.

Rice root mass and density were 5.8 and 7 times greater, respectively, in-row than between-row (location main effect; Table 3). Barnyardgrass root mass and density were similar at the two locations. Barnyardgrass root mass% between-rows was more than 2½ times the level found in-rows (Table 3), indicating that a relatively small amount of barnyardgrass roots had encroached into the rice row. Total root mass and density were 4.6 and 5.3 times greater, respectively, in-row than between-row. Rice was the predominant component of total root mass. Thus, barnyardgrass accounted for only 8.5 and 22.7% of the root mass in-row and between-row, respectively.

In nonsuppressive rice, there was a trend ($P = 0.2656$) toward production of greater barnyardgrass root mass density in-row compared to suppressive rice, both in-row (2.4 times) and between-row (2.9 times) (cultivar group by location interaction; Table 3).

Rice root mass and density were about 4.8 and 9.7 times greater, respectively, at the 0- to 5-cm depth compared to the 5- to 15-cm depth, and the corresponding "barnyardgrass" and "total root" values were nearly identical to these (depth main effect; Table 3). Rice was the predominant component of total root mass at both soil depths. Barnyardgrass accounted for 19 and 12%, respectively, of the root mass at the 0- to 5-cm depth and 5- to 15-cm depth, suggesting that the surface 5 cm may be a key to its interactions with rice.

Barnyardgrass root mass was greatest in the nonsuppressive group at 0 to 5 cm, which was 2.2 times and 8.9 times greater

Table 3. Root distribution in weedy plots with rice cultivars classified as "suppressive," "intermediate," or "nonsuppressive" groups.[a,b]

	Root mass: Rice	Root mass: Barnyardgrass	Root mass: Total	Barnyardgrass fraction of total root mass	Root mass density: Rice	Root mass density: Barnyardgrass	Root mass density: Total
	g sample^{-1}			%	mg L^{-1}		
Cultivar group main effect							
Nonsuppressive	3.26	0.63 a	3.90	20.2	1,790	349 a	2,150
Intermediate	3.20	0.30 b	3.49	12.5	1,760	166 ab	1,920
Suppressive	2.90	0.30 b	3.20	14.1	1,630	162 b	1,790
	P = 0.4260	P = 0.0404	P = 0.0951	P = 0.1234	P = 0.6077	P = 0.0319	P = 0.1607
Location main effect							
In-row	5.32 a	0.46	5.78 a	8.5 b	3,030 a	256	3,280 a
Between-row	0.91 b	0.36	1.27 b	22.7 a	429 b	195	624 b
	P = 0.0005	P = 0.2766	P = 0.0005	P = 0.0032	P = 0.0005	P = 0.2535	P = 0.0005
Cultivar group by location interaction							
Nonsuppressive: In-row	5.69	0.75	6.45	11.3	3,220	425	3,650
Intermediate: In-row	5.32	0.30	5.61	6.2	3,010	166	3,170
Suppressive: In-row	4.97	0.32	5.29	8.0	2,860	177	3,030
Nonsuppressive: Between-row	0.83	0.50	1.35	29.1	366	272	646
Intermediate: Between-row	1.07	0.30	1.37	18.8	513	166	673
Suppressive: Between-row	0.83	0.28	1.10	20.2	410	146	555
	P = 0.3994	P = 0.2696	P = 0.2366	P = 0.1977	P = 0.4193	P = 0.2656	P = 0.2444
Depth main effect							
0–5 cm	5.16 a	0.67 a	5.84 a	19.2 a	3,140 a	410 a	3,540 a
5–15 cm	1.07 b	0.14 b	1.22 b	11.9 b	324 b	41 b	364 b
	P < 0.0001	P ≤ 0.0001	P < 0.0001	P < 0.0001	P < 0.0001	P < 0.0001	P < 0.0001
Cultivar group by depth interaction							
Nonsuppressive: 0–5 cm	5.39	1.07 a	6.47	25.8 a	3270	648 a	3,920
Intermediate: 0–5 cm	5.12	0.48 bc	5.59	16.5 ab	3110	290 bc	3,400
Suppressive: 0–5 cm	4.97	0.48 b	5.45	15.3 ab	3020	292 b	3,310
Nonsuppressive: 5–15 cm	1.13	0.19 bc	1.33	14.5 b	319	49 bc	374
Intermediate: 5–15 cm	1.27	0.12 bc	1.39	8.4 b	406	43 bc	443
Suppressive: 5–15 cm	0.82	0.12 c	0.94	12.8 b	243	32 c	275
	P = 0.8442	P = 0.0009	P = 0.3619	P = 0.0281	P = 0.8012	P = 0.0002	P = 0.232
Location by depth interaction							
In-row: 0–5 cm	9.31 a	0.78	10.1 a	8.0 c	5,650 a	474	6,130 a
Between-row: 0–5 cm	1.01 b	0.57	1.58 b	30.4 a	616 b	346	962 b
In-row: 5–15 cm	1.34 b	0.13	1.47 b	8.9 c	403 b	38	441 b
Between-row: 5–15 cm	0.81 b	0.15	0.97 b	15.0 b	242 b	44	287 c
	P < 0.0001	P = 0.1115	P < 0.0001	P < 0.0001	P < 0.0001	P = 0.1207	P < 0.0001

[a] Plants were grown in field plots in 2001, 2002, 2003, and 2004 in a standard drill-seeded, flooded rice system at Stuttgart, AR. Means within columns followed by the same letter are not different according to a least squares means test at the P values noted.
[b] All mass and mass density values were determined using soil correction equations in Gealy and Gealy (2011).

than the suppressive group at 0 to 5 cm and 5 to 15 cm, respectively (cultivar group by depth interaction; Table 3). The root mass density values for these respective treatments were 2.2 and 20.3 times greater than for the suppressive group at 0 to 5 cm. The reason for the relative doubling of the root mass density difference due to depth compared to the root mass was that the same root mass is distributed throughout twice the volume of soil at 5 to 15 cm compared to 0 to 5 cm. The barnyardgrass root mass% in the nonsuppressive group at 0- to 5-cm was about twice the average level present in the three cultivar groups at 5 to 15 cm.

Consistent with the results above, rice roots predominated vertically and laterally within the soil profile (location by depth interaction; Table 3). Rice root mass in-row at the 0- to 5-cm soil depth was 7 to 11 times greater than for all other location by depth combinations and total root mass followed a similar pattern. Barnyardgrass accounted for 30% of the total root mass at 0 to 5 cm between rows, which was twice the level found between-rows at 5 to 15 cm, and about 3½ times the levels in-row (Table 3). Clearly, barnyardgrass roots encroached most successfully into potential rice root space between rows near the soil surface. Rice root mass density in-row at 0 to 5 cm was 9 to 23 times greater than for the other treatment combinations. The location by depth interactions for barnyardgrass root mass and mass density were not significant.

Root samples obtained in-rows at the 0- to 5-cm depth retained 4.4 g soil (sample)$^{-1}$ (~24% of total sample mass), which was 19 to 34 times more soil contamination ($P < 0.0001$) than that found in the other combinations of location and depth (location by depth interaction; data not shown). This large amount of soil was apparently associated with the large mass of rice roots growing in rice rows near the soil surface, and was difficult to remove using our standard rinsing procedures. There was a tendency ($P = 0.2262$) toward greater in-row retention of soil mass for the suppressive cultivar group than for the other groups (cultivar group by location interaction; data not shown). Detection of these sizeable soil quantities demonstrates the benefit of mathematically correcting for soil when estimating rice and

Table 4. Root masses summed over full 15-cm soil depth with cultivars identified individually.[a,b]

Cultivar	Location in plot	Rice	Barnyardgrass	Total
		—g (combined sample from 0–15 cm)$^{-1}$—		
Lemont	In-row	10.0	2.03	12.0
Lemont	Between-row	1.7	1.30	3.0
Kaybonnet	In-row	11.8	1.61	13.4
Kaybonnet	Between-row	2.0	0.83	2.9
Francis	In-row	13.1	0.27	13.3
Francis	Between-row	0.9	0.86	1.7
STG96L-26-093	In-row	11.5	0.25	11.7
STG96L-26-093	Between-row	1.6	0.58	2.1
RU 9701151	In-row	9.7	0.89	10.7
RU 9701151	Between-row	2.6	0.60	3.3
PI 312777	In-row	9.3	0.56	9.8
PI 312777	Between-row	1.8	0.59	2.4
Teqing	In-row	9.6	0.88	10.5
Teqing	Between-row	1.8	0.54	2.4
RT CL XL8	In-row	10.4	0.41	10.8
RT CL XL8	Between-row	1.8	0.54	2.3
RT XL8	In-row	13.9	0.20	14.0
RT XL8	Between-row	0.5	0.23	0.6
		$P = 0.1671$	$P = 0.2126$	$P = 0.2969$

[a] Plants were grown in field plots in 2001, 2002, 2003, and 2004 in a standard drill-seeded, flooded rice system at Stuttgart, AR. Means within columns followed by the same letter are not different according to a least squares means test at the P values noted.

[b] All mass values were determined using soil correction equations in Gealy and Gealy (2011).

C_4 weed root masses (Gealy and Gealy 2011), instead of relying on traditional standard curves (Gealy and Fischer 2010).

To better understand the total root mass present in the 15-cm sampling depth, data were analyzed with cultivars classified as individuals using the sum of the root masses from 0 to 5 cm and 5 to 15 cm as a new dependent variable (Table 4). Rice root mass was similar among cultivars (cultivar by location interaction), which is consistent with results from Table 2. Rice root mass ranged from ~4 to 30 times greater in-row than between-row, averaging 9 times greater (Table 4). Barnyardgrass root mass for all cultivars and locations was usually similar, but trended greater for Lemont in-row than for other treatments such as Francis, STG96L-26-093, and PI 312777 in-row, and PI 312777 and Teqing between-row.

Other ^{13}C discrimination studies have also shown differential distribution of C_4 and C_3 plant roots with depth or location in field plots (Derner et al. 2003; Eleki et al. 2005; Polley et al. 1992). However, in these studies, the proportion of roots near the soil surface generally was much greater for C_4 plants than for C_3 plants. These results contrast with those in the present study in which C_3 rice plants comprised the predominant root mass near the soil surface in mixtures with C_4 barnyardgrass. This may be due, in part, to the excellent suitability of rice to flooded culture and its natural ability to interfere with weeds in this environment.

In general, correlations between the variables in this study were low or not significant, but several important relationships became evident. Barnyardgrass root mass (0- to 5-cm depth; between-rows) was correlated ($P \leq 0.05$) negatively with rice yield in weedy plots ($r = -0.306$), rice height in weedy plots ($r = -0.424$), and visual control rating ($r = -0.524$), and was positively correlated with rice percent height reduction ($r = 0.653$), rice percent yield loss ($r = 0.478$), and barnyardgrass shoot mass ($r = 0.0377$). Barnyardgrass root mass also was slightly positively correlated with rice root mass ($r = 0.266$), which does not support the hypothesis that high rice root mass is associated with reduced barnyardgrass growth. The correlation between barnyardgrass root mass and shoot mass was small and nonsignificant at the 0- to 5-cm depth, between-rows ($r = 0.222$; $P = 0.0612$), but was significant at the same depth, in-rows ($r = 0.452$). Visual control rating was negatively correlated with the barnyardgrass root mass% ($r = -0.612$), barnyardgrass shoot mass ($r = -0.435$), rice yield in weed-free plots ($r = -0.300$), rice percent yield loss ($r = -0.747$), and rice percent height reduction ($r = -0.415$). The correlation between visual control rating and rice root mass was nonsignificant at the 0- to 5-cm depth, between-rows ($r = 0.0839$), but was significant at the same depth, in-rows ($r = -0.322$). Visual control rating was positively correlated with rice yield in weedy plots ($r = 0.429$), but it was not correlated with rice root mass ($r = 0.084$), or rice height in weedy plots ($r = 0.204$) or weed-free plots ($r = -0.016$). These results suggest that rice root mass alone was not a major cause of barnyardgrass shoot and root suppression in this study, and that rice percent yield loss and percent height reduction were reasonably good indicators of a cultivar's weed control potential. However, with the exception of Lemont, PI 312777 was among the shortest of the cultivars tested (Table 1), even though its weed suppression capacity was among the greatest (Tables 1 and 2), which is similar to a previous report (Gealy et al. 2003).

Our root mass results (Tables 2–4) appear to contrast with several previous rice reports. Gibson et al. (2003) found that root biomass of semi-dwarf rice in weed-free plots was inversely related to biomass of *Echinochloa* spp. The most suppressive cultivars reduced weed biomass up to 84% compared to the least suppressive cultivar. Similarly, competitive differences were observed among rice cultivars in low-input systems, where weed biomass was negatively correlated with early rice root growth and with rice root and shoot growth at later growth stages (Fofana and Rauber 2000). Root interference by *Echinochloa* spp. against rice was more important than shoot interference in both transplant- (Perera et al. 1992) and water-seeded rice (Gibson et al. 1999).

Results from our field study demonstrated that relatively high levels of suppression were achieved with weed-suppressive cultivars. Performance of the two indica/tropical japonica crosses often was intermediate between the "nonsuppressive" and "suppressive" commercial cultivars evaluated. More recent crosses incorporating PI 312777 and newer commercial cultivars into the PI 312777/Katy lines have shown improved suppression (Gealy et al. 2010; Gealy, unpublished data).

^{13}C analysis revealed that under weed pressure, rice roots dominated the below-ground environment, particularly in the row near the soil surface. However, rice root mass generally did not differ among cultivars, even though barnyardgrass root mass was much lower in the presence of the suppressive cultivar group compared to the nonsuppressive group. Shoot competition may have favored suppressive cultivars over nonsuppressive cultivars, or below-ground interference may be aided by release of barnyardgrass-inhibitory allelochemicals as has been shown for PI 312777 (Kong et al. 2006). Genetic control of rice root morphology was thought to be independent from that of the allelopathic component of barnyardgrass suppression in allelopathic rice (Bach-Jensen et al. 2001). Potential differences in root length or root area among cultivars, which could differentially affect interference against barnyardgrass, were not detectible in these studies because the ^{13}C method does not account for these traits. However, our results do show that this ^{13}C discrimination method can be a useful tool for quantification of root mass distribution patterns of rice and C_4 barnyardgrass under field conditions. They also suggest that even the most suppressive cultivars are vulnerable to weed pressure and may benefit from additional traits such as early crop vigor and an integrated approach that includes other weed control tactics in order to achieve complete weed control.

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Erratum

Gealy, D. R., K. A. K. Moldenhauer. 2012. Use of ^{13}C Isotope Discrimination Analysis to Quantify Distribution of Barnyardgrass and Rice Roots in a Four-Year Study of Weed-Suppresive Rice. Weed Sci. 60:133–142.

Equation [4] should read:

$$Ri \equiv R_{\mathrm{pd}}\ [1 + (\delta_i/1{,}000)]$$

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