



Temporary drought can selectively suppress *Schoenoplectus mucronatus* in rice

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ABSTRACT

Outdoor pot experiments were conducted in California to quantify differences in rice and *Schoenoplectus mucronatus* susceptibility to drought and to identify morphological and physiological traits that would favor rice over *S. mucronatus* under drought. Plants were grown in flooded soil for approximately 5 weeks, and then subjected to different drought periods after which pots were re-flooded. Chlorophyll fluorescence assays revealed that rice and *S. mucronatus* Fv/Fm first became <0.8 after leaf water potential (Ψ_{leaf}) had decreased to approximately -4 MPa and -2 MPa, respectively. Thus, by suffering less photosynthetic damage from drought, rice had better recovery after re-flooding than *S. mucronatus*. When drought reduced Ψ_{leaf} to -3 MPa, *S. mucronatus* re-growth was nearly suppressed but that of rice was unaffected. Rice plants depleted soil moisture 1.6 faster than *S. mucronatus* due to larger and deeper roots and a high water-spending strategy (when Ψ_{leaf} decreased from approximately -0.5 MPa to -2.5 MPa, ^{13}C increased from -27.8 to -27.4 and from -28.1 to -26.0 for rice and *S. mucronatus*, respectively). Rice under interspecific competition sustained its Ψ_{leaf} by extracting more water from greater depths, while causing severe moisture stress and photosynthetic damage to *S. mucronatus*. Thus temporary drought enhanced rice competitiveness over *S. mucronatus*, supporting the concept of using brief drought as a tool for *S. mucronatus* suppression in rice. The Ψ_{leaf} developed by the end of the drought period predicted rice yields ($R^2 = 0.77$, $P < 0.0001$) and the capacity of *S. mucronatus* to recover from drought upon irrigation resumption ($R^2 = 0.62$, $P < 0.001$). Brief (8–10 d) drought imposed on 5-week-old rice did not significantly depress late-season rice biomass growth or grain yields, while *S. mucronatus* never fully recovered from drought. Rice yields were only reduced after Ψ_{leaf} reached values below approximately -2.5 MPa. Longer drought (~ 20 d) delayed maturity and reduced rice yields by approximately 60–80%. The dry-down approach could help suppress weeds similar to *S. mucronatus* in organic rice where premium prices can compensate for lower grain yield.

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1. Introduction

In California, approximately 2.3 million metric tons of rice (*Oryza sativa* L.) are produced annually from 239,000 ha, of which approximately 5,700 ha are grown organically. While this only represents 2.4% of the total California rice land area, it is the largest area of organic rice production in the USA. Weeds in California rice fields can cause substantial yield loss and control is often herbicide dependent (Fischer et al., 2000). However, prohibited herbicide use among organic growers generates a need for alternative weed control strategies. Grasses (*Echinochloa* spp. and *Leptochloa fascicularis* (Lam.) Gray) and sedges (*Cyperus difformis* L. and

Schoenoplectus mucronatus (L.) Palla) are among the most troublesome weeds of California rice fields. Unlike the grasses, *C. difformis*, *S. mucronatus* cannot be suppressed by deep flooding of rice fields (Williams et al., 1990). *S. mucronatus* is an aquatic perennial that behaves as an annual in California rice fields. Research in Asian countries indicates that *S. mucronatus* competition can cause severe rice losses, even under transplanted conditions (Biswas and Sattar, 1993). *S. mucronatus* has a physiological mechanism for submergence tolerance by which it elongates in response to a decrease in free ABA induced by submergence (Lee et al., 1996). Inversely, ABA levels increase and stem elongation decrease under aerobic conditions. These results suggest that *S. mucronatus* may lose a component of early season competitiveness due to diminished plant growth under drained (aerobic) conditions.

With some success, California organic rice growers employ the concept of drying down rice fields during the early season attempting to suppress *S. mucronatus* interference with the crop. Their management decisions are based on empirical observations.

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Results are inconsistent, failures often occur, and variable yield loss results from this practice. Detailed studies on the ecophysiology underlying different rice and *S. mucronatus* responses to temporary drought are needed to optimize the dry-down practice and provide farmers with adequate criteria for establishing the intensity and duration of the moisture stress that would maximize suppression of this or similar aquatic weeds, while minimizing associated rice yield losses. Rice yield loss may increase with longer drought (Scartazza et al., 1998; Turner et al., 1986). However, drought during vegetative growth may affect yields less than drought during reproductive development (Lilley and Fukai, 1994b; O'Toole and Moya, 1981; O'Toole, 1982). Rice cultivars differ in physiological responses to moisture stress, and those that recover quickly after drought suffer lower yield losses (Lilley and Fukai, 1994b). Growth rates during recovery can be related to dehydration tolerance during water deficit and to water extraction ability. The maintenance of physiologically functional leaf area is relevant to drought tolerance and can be largely determined by the ability to extract water from deep soil layers through greater rooting depth and root length density (Lilley and Fukai, 1994a; Wade et al., 2000). Deep rooting in rice is considered part of a drought avoidance strategy that compensates for inability to regulate water loss (Yeo et al., 1997). Weeds of upland rice (*E. colona* (L.) Link, *Amaranthus spinosus* L., and *Rottboellia conchinchinensis* (Lour.) Clayton) are able to maintain higher water potentials than rice under water stress, and their competition can reduce rice water potential (Janiya and Moody, 1991). Rice competitiveness against these weeds improves under flooded conditions. Thus, it appears the effectiveness of drought as a weed management tool may depend on certain key morphological and physiological traits of the species involved.

The objectives of this research were to quantify morphological and physiological characteristics of rice and *S. mucronatus* associated with differences in their responses to temporary drought, and thereby identify traits that would confer rice a competitive advantage over *S. mucronatus* when both species are grown together under imposed drought stress. This knowledge is relevant to optimize methodologies for incorporating the dry-down technique into low-input integrated weed management programs. It would also help identify other species in aquatic rice environments that could be susceptible to suppression through field dry down. This system has the additional benefit of potentially reducing water use as a result of the extended non-flood period.

2. Materials and methods

An experiment was conducted to study the differential ability of rice and *S. mucronatus* to recover, resume growth, and yield grain (rice) after temporary moisture stress as imposed by periods of drought followed by re-flooding. *S. mucronatus* seed was collected from a rice farm in the northern Sacramento Valley of California. The rice cultivar planted was the semidwarf, short-grain, early maturing, and early vigorous S-201 (Carnahan et al., 1980), which is the variety planted by some organic growers who have used moisture stress to suppress weeds.

2.1. General growing conditions and experimental design

The experiment was conducted at the Agronomy Field Headquarters, University of California, Davis (38°32'N and 121°47'W; elevation 18 m). Four equidistantly spaced plants of each species were grown outdoors in individual 1-m-deep and 15-cm-diameter PVC pots filled with 20 kg Stockton Clay Adobe soil (fine, montmorillonite, thermic, Typic Pelloxert) up to 8 cm from the brim of the pots. The species were also grown in mixtures with two plants of each per pot (total density four plants pot⁻¹). After

scarification of *S. mucronatus* seeds in 96% sulphuric acid for 1 min followed by thorough rinsing in deionized water, rice and *S. mucronatus* seed were germinated in Petri dishes placed in a growth chamber (28/17 °C day/night and 15-h photoperiod under 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetic photon flux density delivered by a mixture of incandescent and fluorescent lights). Germinated seeds were transferred into 30- by 20-cm plastic containers filled 5-cm-deep with the same soil and kept in the greenhouse at 17/35 °C average minimum/maximum daily temperatures; the soil was maintained constantly saturated. On June 24, 2002, 2–3-leaf seedlings were transplanted into the outdoor pots, which had been immersed in water before planting to saturate the entire soil column. Water was added several times per day to replenish evaporative losses and maintain the water depth. An 8-cm water depth was maintained after rice reached the 3–4-leaf stage. Ammonium sulphate and a commercial fertilizer mixture containing ammonium phosphate (Scotts Miracle-Gro Products Inc., Marysville, OH) were applied in solution to the surface of the soil to supply 168 kg N and 30 kg P ha⁻¹. In order to approximate the dry-down technique organic growers currently practice in the field, plants were kept flooded for the first 34 d after seeding, and then water was allowed to drain from pots through an opening practiced at the bottom to impose drought periods of 0, 8, 14, 20, and 26 d. Thus plants were subjected to mild, moderate, strong, and severe moisture stress according to visual symptoms. At the end of each drought regime, pots were re-flooded until final harvest. Control pots (0 d of stress) were kept permanently flooded. Recovery from drought after re-flooding was assessed by harvesting shoot biomass for each species and moisture regime at 103 d after seeding. Rice grain yield was measured at maturity as grams per pot at 14% moisture. Experimental treatments were a factorial combination of three main factors: growth regimes (two levels, monoculture or species mixture) by species (two levels, rice and *S. mucronatus*) by days of stress (five levels, 0, 8, 14, 20, and 26 d) and were arranged in a completely randomized design with five replications. Pots were spaced approximately 30 cm apart and surrounded by one external border row.

2.2. Destructive above- and belowground sampling and leaf water potential measurement

At 34 d after seeding (the time when drought was initiated, corresponding to 0 d of stress) and at the end of each drought treatment, plants were cut at ground level and shoot and root dry weight, and rooting depth were measured. Midday leaf water potentials (Ψ_{leaf}) were measured with a Scholander et al. (1965) pressure chamber (plant water status console 3005-Series; Soil Moisture Equipment Corp., Santa Barbara, CA, USA.) on the main tiller of each individual plant in each pot between 13:00 and 15:00 h (Bannister et al., 1999). Stems were cut at the base of each plant. Immediately upon excision, samples were wrapped in polythene wrap prior to insertion in the chamber to prevent water loss. Due to the succulent triangular stems of *S. mucronatus*, silicon gaskets were manufactured for use in the pressure chamber following Simonelli and Spomer (1980). Gaskets handled pressures consistently to -4 MPa. The term leaf water potential in this context refers here to the water potential measured on the transpiring rice or *S. mucronatus* shoots actually introduced in the pressure chamber. For root sampling, pots were split longitudinally and divided into three sections of equal length (top, center, bottom). Gravimetric soil moisture was determined from a 100-g soil core extracted towards the center of each section. Roots were gently washed over a 2-mm screen while keeping the soil column intact, and root dry weight and maximum rooting depth was measured within each section. Root and shoot mass was weighed after being oven-dried at 80 °C to constant weight. In all

treatments, rice and *S. mucronatus* biomass recovery from drought after re-flooding was assessed after maturity when rice grain was harvested; biomass recovery and rice grain yield were each measured on five replicate pots per treatment.

2.3. Chlorophyll fluorescence and carbon isotope discrimination analysis

Chlorophyll fluorescence was measured on two rice and *S. mucronatus* plants per pot using a PAM-2000 Fluorometer (Heinz Walz, GmbH, Effeltrich, Germany) following Bilger et al. (1995) and avoiding obvious inconsistencies in the leaf surface such as fissures and spots. At each drought stress period, the fiber-optic cable was set to the third position on the leaf clip and samples were measured randomly at pre-dawn (04:00 and 05:00 h) to avoid variations in fluorescence due to radiation and to ensure that leaves were in a dark-adapted state. Measurements were taken for each individual plant on the green portion of the main stem (on one surface) of *S. mucronatus* or of the distal leaf (between the margin and midrib on the adaxial surface) on the main tiller of rice. Preliminary experiments in the laboratory revealed that there was no significant ($P > 0.05$) variation in fluorescence over the leaf surface, or between leaf and stem surfaces, for rice or *S. mucronatus*. Fluorescence measurements were used for the determination of Fm and Fo (maximum and minimum fluorescence after incubation in darkness). The maximum quantum yield (Fv/Fm) of photosystem II (PSII) was calculated as (Fm – Fo)/Fm (Lambers et al., 2008).

Carbon isotope discrimination analysis was conducted on monoculture shoot material from each dry biomass sampling and replicate. Samples were ground to pass a 0.5 mm screen and combusted in a Europa ANCA-GSL Elemental Analyzer prior to introduction into a Europa Hydra 20/20 Isotope Ratio Mass Spectrometer (Europa Scientific, Cheshire, UK) to determine $\delta^{13}\text{C}$ values:

$$\delta^{13}\text{C}_{\text{sample}} (\text{‰}) = \left[\frac{R_{\text{sample}} - R_{\text{standard}}}{R_{\text{standard}}} \right] \times 10^3 \quad (1)$$

where $\delta^{13}\text{C}_{\text{sample}}$ is the $^{13}\text{C}/^{12}\text{C}$ isotope ratio in parts per mil (‰), R_{sample} and R_{standard} are the $^{13}\text{C}/^{12}\text{C}$ molar abundance ratios of the plant material and a standard, respectively; for presentation purposes, all isotope ratios were expressed relative to the international PDB standard, a limestone fossil of *Belemnitella americana* Morton from cretaceous Pee Dee formation in South Carolina, USA (Kloppel et al., 1998; Lambers et al., 2008). One in-house standard was run for every six unknowns. Precision for the

$\delta^{13}\text{C}$ values was better than 0.01‰ based on repeated measurements of standards ($n = 19$ standards). All analyses were done at the University of California–Davis Stable Isotope Facility.

2.4. Statistical analyses

Data were subjected to analysis of variance (ANOVA); standard errors of the difference (s.e.d.) and the corresponding degrees of freedom (d.f.) for comparisons of main effects and/or factor interactions are presented. Treatment means were compared using Fisher's protected least significant difference ($\text{LSD} = t_{(d.f.)} \times \text{s.e.d.}$) with $P < 0.05$. Treatment means with their standard errors are also presented graphically. Pearson's correlation coefficient (r) and linear and non-linear (three-parameter logistic) regression were used to study associations between variables. Differences among regressions were tested using Chow's (1960) test of equality between coefficients. Monoculture and mixture treatments represented a replacement series (de Wit, 1960) with rice: *S. mucronatus* proportions of 1:0, 0.5:0.5, and 0:1. Thus, the effects of drought on aboveground biomass re-growth after re-flooding were also analyzed in terms of relative yields ($\text{RY}_a = \text{biomass per pot of species } a \text{ in mixture as a fraction of the biomass per pot of species } a \text{ in monoculture}$) and relative yield totals ($\text{RYT} = \text{RY}_a + \text{RY}_b$). An $\text{RYT} = 1$ suggests that the species are competing for the same resources; $\text{RYT} > 1$ indicates that more biomass is produced by mixtures than monocultures, suggesting that the species are making demands on different resources, avoiding competition, or maintaining a symbiotic relationship (Harper, 1977). Replacement diagrams plotting RY means (± 1 S.E.) against the proportion of rice:*S. mucronatus* plants per pot were analyzed graphically following Harper (1977); t -tests were used to assess if $\text{RYT} > 1$ and if $\text{RY}_{(50:50)}$ values differed from 0.5. Inspection of error distributions and scatter plots among variables suggested that assumptions of linearity and normality held reasonably well. Whenever needed, natural logarithm (ln) transformations were performed to homogenize variances. All analyses were conducted using the JMP (Version 7, 2007 Academic, SAS Institute Inc., Cary, NC) and the SigmaPlot (Version 10.0, 2006, Systat Software, Inc., San José, CA) software.

3. Results

3.1. Drought duration and plant growth

Drought periods were imposed to plants under conditions where daily temperature, relative humidity and vapor pressure

Table 1

Effect of drought periods (days of stress) imposed 34 d after seeding upon rice and *Schoenoplectus mucronatus* growing in monoculture and in interspecific mixture; plants were sampled at the end of each drought period.

Days of stress	Shoot dry weight			Root dry weight		
	Rice (g plant ⁻¹)	<i>S. mucronatus</i> (g plant ⁻¹)	Mean (g plant ⁻¹)	Rice (g plant ⁻¹)	<i>S. mucronatus</i> (g plant ⁻¹)	Mean (g plant ⁻¹)
0	1.77 ± 0.21	0.39 ± 0.08	1.08 ± 0.21 (0.73)	0.27 ± 0.03	0.03 ± 0.01	0.15 ± 0.04 (0.14)
8	2.20 ± 0.25	1.01 ± 0.13	1.60 ± 0.21 (0.96)	0.56 ± 0.03	0.11 ± 0.02	0.34 ± 0.08 (0.27)
14	2.06 ± 0.13	1.21 ± 0.16	1.64 ± 0.19 (0.97)	0.70 ± 0.09	0.17 ± 0.05	0.44 ± 0.10 (0.34)
20	2.29 ± 0.15	1.04 ± 0.25	1.67 ± 0.17 (0.98)	0.67 ± 0.08	0.16 ± 0.02	0.42 ± 0.09 (0.33)
26	2.13 ± 0.27	0.72 ± 0.21	1.42 ± 0.18 (0.88)	0.61 ± 0.04	0.13 ± 0.06	0.37 ± 0.09 (0.30)
Mean	2.09 ± 0.09 (1.13)	0.87 ± 0.09 (0.63)	1.48 ± 0.08	0.56 ± 0.04 (0.44)	0.13 ± 0.02 (0.11)	0.34 ± 0.04
s.e.d. species (shoot) = 0.049						
s.e.d. days of stress (shoot) = 0.077						
d.f. (shoot) = 76						
s.e.d. species (root) = 0.022						
s.e.d. days of stress (root) = 0.035						
d.f. (root) = 36						

Data were $\ln(X+1)$ transformed to homogenize variances. Values are means \pm S.E.; numbers in italics are $\ln(X+1)$ transformed means and s.e.d. (standard error of the difference) values for significant ($P < 0.001$) effects in ANOVA tests; P of overall ANOVA tests was < 0.001 . Effect of growth regime (monoculture vs. mixture) and factor interactions with shoot growth were not statistically significant ($P > 0.05$). Roots were sampled only in the monoculture treatments, not under competition.

deficit (VPD, a measure of dryness of the air) averaged 22.9 ± 0.2 °C, $55.2 \pm 1.0\%$ and 0.98 ± 0.05 kPa, respectively. Although rice plants accumulated considerable more above- and belowground biomass than *S. mucronatus*, drought affected rice and *S. mucronatus* growth similarly ($P > 0.05$), whereby more than 8 d of stress arrested growth of both species (Table 1). Rice had approximately four times more root biomass (Table 1) and greater rooting depth than *S. mucronatus* ($P < 0.0001$) throughout the entire drought season (Fig. 1a).

3.2. Soil moisture depletion and plant stress

Soil in all pots dried progressively with longer drought (Fig. 1b) causing increasing moisture stress in plants (Fig. 1c). With greater

and deeper root mass (Table 1; Fig. 1a), rice plants were able to rapidly deplete soil moisture and almost dry out the top 25 cm of the soil column (Fig. 1b). *Schoenoplectus mucronatus* monoculture pots were occupied by fewer and shallower roots and had wetter soil than rice (Fig. 1b), thus *S. mucronatus* plants were able to maintain higher Ψ_{leaf} than rice throughout the stress periods ($P < 0.0001$, Fig. 1c). However, soil moisture depletion by the 1:1 competition mixture became similar to that of monoculture rice ($P > 0.05$, Fig. 1b). Thus *S. mucronatus* in competition had its roots within a much drier surface soil layer (Fig. 1b) than in monoculture and became more drought stressed (lower Ψ_{leaf}) than the competing rice plants ($P < 0.0001$, Fig. 1c). Also, before extreme drought was reached, rice experienced less stress when grown in mixture with *S. mucronatus* than in monoculture ($P < 0.0001$, Fig. 1c).

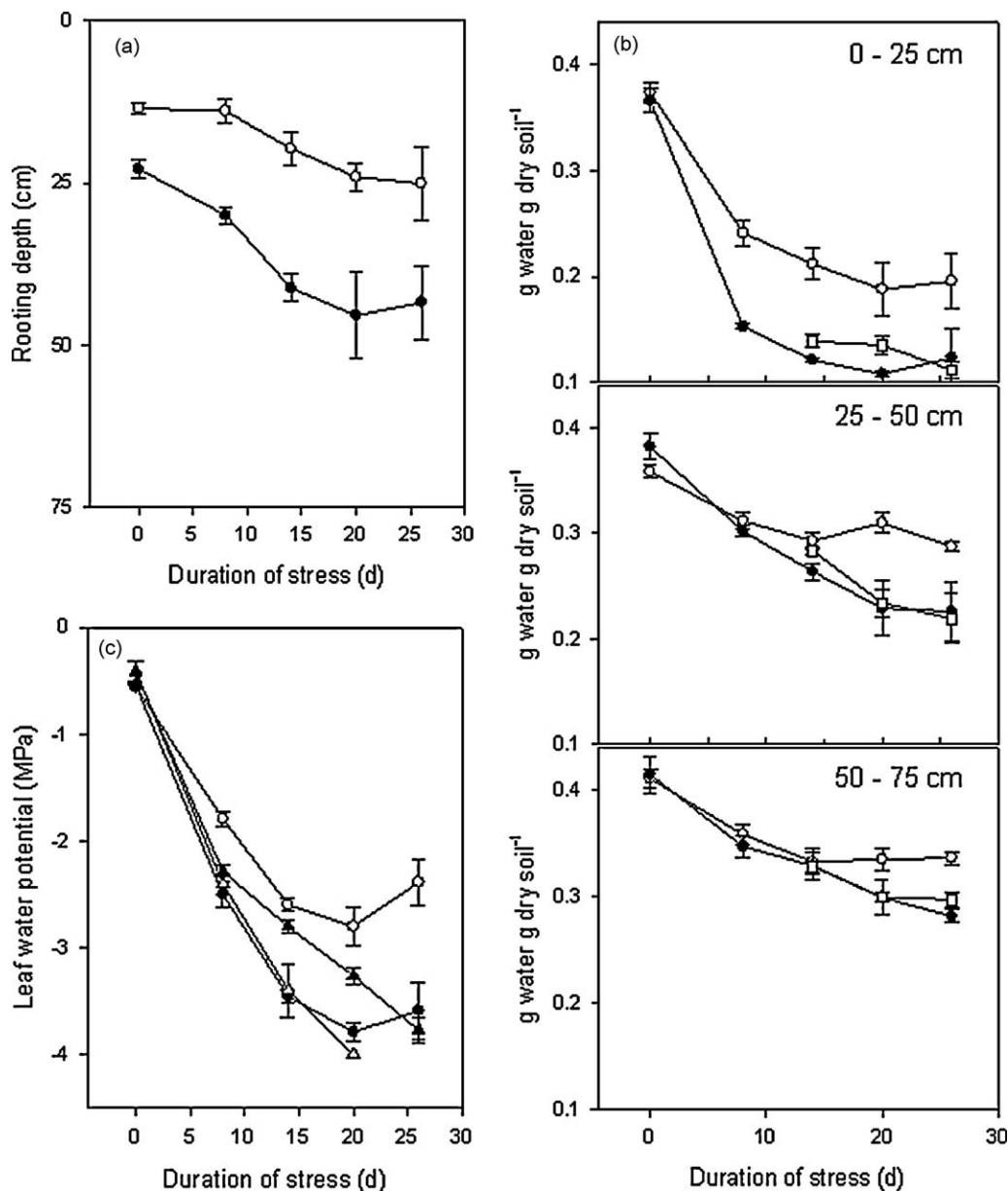


Fig. 1. Changes in rooting depth (a), soil moisture (b), and plant moisture stress (c) for rice (●) and *Schoenoplectus mucronatus* (○) growing in pots in monoculture and under interspecific competition (rice: ▲, *S. mucronatus*: △, and both species mixed: □) with the duration of stress. Moisture stress was initiated 34 d after seeding; vertical error bars are \pm S.E. of the mean ($n = 5$), s.e.d. are standard errors of the difference. Total rooting depth, data were $\ln(X)$ transformed for ANOVA, main effects were significant with $P < 0.0001$, s.e.d. (duration of stress) = 0.13, s.e.d. (species) = 0.082, 36 d.f. The species \times duration of stress interaction effects on gravimetric soil water content throughout the soil column were significant with $P < 0.0001$ in an ANOVA test (data for species in competition were superimposed to the plot and were not part of the same ANOVA), pooled s.e.d. = 0.008, 36 d.f. The species \times competition regime \times duration of stress interaction effects on midday leaf water potential (moisture stress) were significant with $P < 0.0001$, pooled s.e.d. = 0.166, 76 d.f.

3.3. Physiological effects of drought

Foliar tissues of both species became increasingly chlorotic and necrotic with longer stress duration (not shown). Chlorophyll fluorescence measurements on the basal healthy-appearing portion of the foliar structures revealed deterioration of photosynthetic integrity with increasing moisture stress (Fig. 2a). As Ψ_{leaf} decreased, the more rapid reduction of Fv/Fm values below healthy levels (~ 0.8) in *S. mucronatus* than in rice suggests *S. mucronatus*' photosynthetic tissues were more moisture stress sensitive than those of rice. It was only when Ψ_{leaf} decreased to values approaching -4 MPa that Fv/Fm in rice green tissue was significantly reduced below healthy values, yet PSII damage was already detected in *S. mucronatus* when Ψ_{leaf} decreased below -2 MPa (Fig. 2a).

Carbon isotope discrimination analysis on plants growing in monoculture also detected differences in physiology and water use strategies under moisture stress between *S. mucronatus* and rice

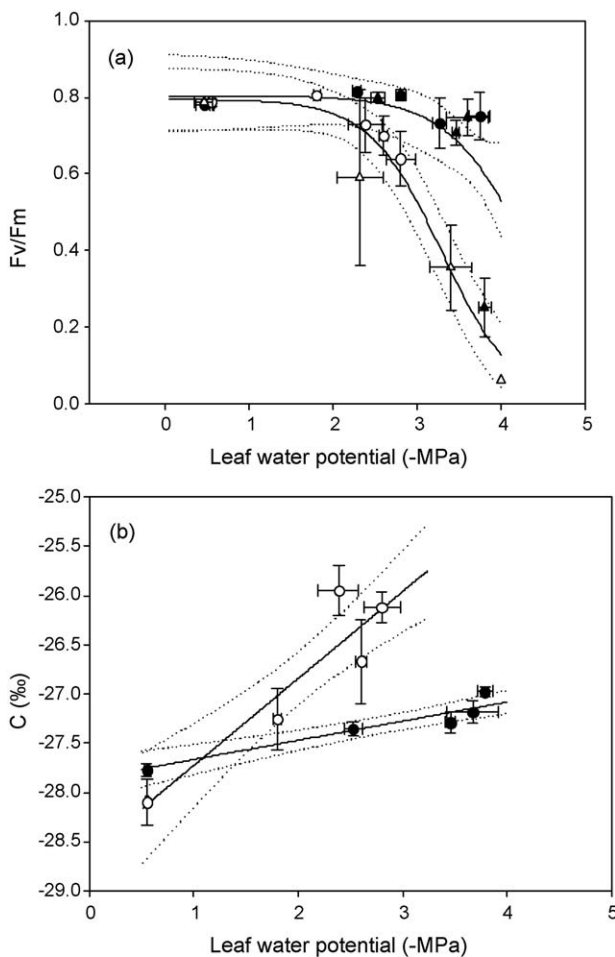


Fig. 2. Chlorophyll fluorescence (a) and carbon isotope discrimination (b) measured on rice and *S. mucronatus* as a function of moisture stress (midday leaf water potential) caused by drought periods imposed 34 d after seeding; the species grew in pots either in monoculture (rice: ●, *S. mucronatus* ○) or under interspecific competition (rice: ▲, *S. mucronatus*: △). Data points are bivariate treatment means ($n = 5$) and error bars are \pm S.E. of the mean, the solid lines are regressions fitted to the raw data and the dotted lines represent 95% confidence limits for the fitted lines. Chlorophyll fluorescence (Fv/Fm): rice, $Y = 0.80/(1 + \exp(-(X - 4.31)/-0.48))$, $R^2 = 0.26$ ($P < 0.001$); *S. mucronatus*, $Y = 0.79/(1 + \exp(-(X - 3.29)/-0.43))$, $R^2 = 0.77$ ($P < 0.0001$), regressions for each species differ ($P < 0.0001$) according to a test of equality (Chow, 1960) between coefficients (F for 3 and 95 d.f. = 14.14). Carbon isotope discrimination ($\delta^{13}\text{C}$): rice, $Y = -27.68 + 0.19X$, $R^2 = 0.59$ ($P < 0.0001$); *S. mucronatus*, $Y = -28.61 + 0.88X$, $R^2 = 0.59$ ($P < 0.0001$), regressions for each species differ ($P < 0.001$) according to Chow's (1960) test of equality between coefficients (F for 2 and 46 d.f. = 26.52).

(Fig. 2b). Discrimination ratios were consistent with those observed in C_3 species (Lambers et al., 2008), with $\delta^{13}\text{C}$ ranging between -26.97 ± 0.05 and -27.78 ± 0.12 for rice and -25.95 ± 0.69 to -28.10 ± 0.33 for *S. mucronatus*. As drought progressed and Ψ_{leaf} decreased, both species discriminated less against the heavier isotope (less negative $\delta^{13}\text{C}$) but the discrimination reduction was more pronounced for *S. mucronatus* than for rice ($P < 0.01$), which had a more negative $\delta^{13}\text{C}$ by drought's end ($P < 0.01$).

3.4. Shoot biomass recovery after drought, competition and rice yield

Following the re-flooding of pots after each drought period, aboveground biomass from growth recovery was measured for each species. Re-growth was negatively affected by prolonged drought (Fig. 3a) but there was a clear difference between species

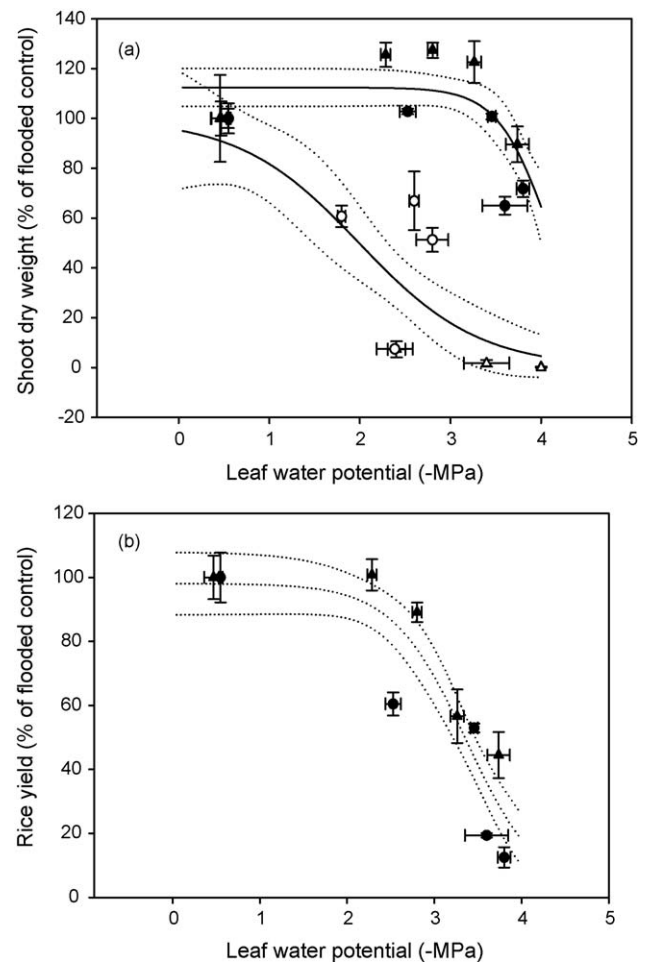


Fig. 3. Relationships between moisture stress (midday leaf water potential) caused by drought periods and biomass re-growth (a) or rice grain yield (b) measured at rice maturity after resuming irrigation at the end of each drought period imposed 34 d after seeding rice and *S. mucronatus* into pots; the species grew either in monoculture (rice: ●, *S. mucronatus*: ○) or under interspecific competition (rice: ▲, *S. mucronatus*: △). Data points are bivariate treatment means ($n = 5$) and error bars are \pm S.E. of the mean, the solid lines are three-parameter logistic functions fitted to the raw data and the dotted lines represent 95% confidence limits for the fitted lines. Biomass (% of flooded control pots): rice, $Y = 112.44/(1 + \exp(-(X - 4.08)/-0.28))$, $R^2 = 0.44$ ($P < 0.0001$); *S. mucronatus*, $Y = 100/(1 + \exp(-(X - 1.99)/-0.66))$, $R^2 = 0.62$ ($P < 0.001$), regressions for each species differ ($P < 0.0001$) according to a test of equality between coefficients (Chow, 1960) with F for 3 and 95 d.f. = 82.97; absolute values \pm SE (g plant^{-1}) for the controls are: rice monoculture = 14.8 ± 0.61 , rice in competition = 20.36 ± 1.39 , *S. mucronatus* monoculture = 3.29 ± 0.2 , and *S. mucronatus* in competition = 7.21 ± 1.26 . Rice grain yield (% of flooded control pots), $Y = 98.09/(1 + \exp(-(X - 3.37)/-0.43))$, $R^2 = 0.77$ (47 d.f., $P < 0.0001$); absolute yields \pm SE (g plant^{-1}) for the controls are: rice monoculture = 27.71 ± 2.16 and rice in competition = 37.92 ± 2.86 .

in biomass recovery from drought, which reflected their relative sensitivity to stress as revealed by the Fv/Fm responses (Fig. 2a). *S. mucronatus* showed a systematic decline in biomass recovery that started already after mild stress (approximately $\Psi_{\text{leaf}} < -0.5$ MPa), but rice only showed reduced biomass when Ψ_{leaf} decreased below -3 MPa (Fig. 3a). Thus, under the time course of moisture stress development in this experiment, the level of stress (Ψ_{leaf}) developed in rice after approximately 2 weeks of stress in monoculture (Fig. 1c) still allowed for considerable rice biomass recovery (Fig. 3a). Whereas, *S. mucronatus* never recovered from Ψ_{leaf} values caused by more than 8 d of stress in monoculture (Figs. 1c and 3a).

Extended drought adversely affected rice yields. The level of moisture stress (Ψ_{leaf}) developed in rice by the end of a drought period was a strong predictor ($R^2 = 0.77$, $P < 0.0001$) of yields to be realized after pots were re-flooded (Fig. 3b). However, yield reductions only occurred when rice midday Ψ_{leaf} decreased below approximately -2.5 MPa (Fig. 3b), which should have occurred sometime after 8 d of stress (Fig. 1c). Rice yields correlated well with the extent of biomass produced by stressed plants after re-flooding ($r = 0.68$; $P < 0.0001$, $n = 50$). Extended drought also delayed rice anthesis (not shown) and affected fecundity, thus no rice grain was formed following 20 and 26 d of stress.

Aboveground biomass recovery after re-flooding was also measured in pots where both species were growing in mixtures under interspecific competition. Although the total rice density in this experiment approximates 57 plants m^{-2} , which is on the low side of a conventional seeding rate in California, it was not possible to fully represent in this experiment all rice: *S. mucronatus* mixtures that may actually appear in the field. Thus, observations on species interactions in this study only intend to strengthen inferences made regarding relative rice and *S. mucronatus* differences in response to moisture stress. When biomass recovery was analyzed using relative yields (RY) in a replacement series (de Wit, 1960; Harper, 1977), both species in the continuously irrigated 50:50 mixture pots grew better than expected (above the diagonal equivalence lines) and the mixture produced more total biomass than either monoculture resulting in $\text{RYT} > 1$ ($P < 0.01$) (Fig. 4, no stress). However, after a brief period of 8 d of stress, the plot of rice RY departs upwards ($P < 0.01$) from the diagonal line while that of *S. mucronatus* falls below ($P < 0.01$) the corresponding diagonal (Fig. 4, 8 d of stress). Diagonal lines indicate expected yields for plants that have equivalent competitiveness (Harper, 1977). According to Harper (1977), this type of replacement diagram suggests rice became a superior ($P < 0.01$) competitor over *S. mucronatus* when moisture stress was imposed for any period longer than 8 d of stress (Fig. 4). As shown earlier, the stress level developed with more than 8 d of drought (Fig. 1c) was strongly suppressive of *S. mucronatus* ability to recover growth (Fig. 3a).

4. Discussion

Differences between rice and *S. mucronatus* in response to drought resulted from different root mass distribution, physiology, and water use strategies that together determined greater moisture stress tolerance in rice than in *S. mucronatus*.

4.1. Rooting patterns and moisture stress

S. mucronatus roots were mostly superficial, while rice root mass was larger and deeper, which favored more rapid soil moisture depletion by rice and conferred drought tolerance to rice plants (Fukai and Cooper, 1995; O'Toole, 1982). Assuming that rooting patterns in mixture resembled those in monoculture, *S. mucronatus* growing with rice had roots in the upper soil layer that was dried out by rice. Thus *S. mucronatus* suffered severe moisture stress and was strongly suppressed by rice competition.

4.2. Physiological responses to drought

The Fv/Fm ratio is correlated with the quantum yield of leaf photosynthesis (Kao and Forseth, 1992) and can be used as indicator of PSII damage to assess plant responses to various stresses (Jiang and Huang, 2000; Meinander et al., 1996). Reductions of the Fv/Fm value below 0.8 suggest PSII damage due to stress induced photoinhibition in plants (Garg et al., 2002; Lambers et al., 2008). Drought stress caused visible foliar damage to both species, but the Fv/Fm ratios indicated functionality of the photosynthetic area available to support plant re-growth following flood resumption was more affected in *Schoenoplectus mucronatus* than in rice. Besides this difference in tissue susceptibility to drought, both species exhibited different control of transpirational losses as suggested by carbon isotope discrimination analysis. Greater stomatal conductance to CO_2 increases intracellular CO_2 concentration and allows for greater biochemical discrimination by Rubisco against the heavier ^{13}C isotope (Lambers et al., 2008). Carbon isotope discrimination in rice has been directly associated with stomatal conductance (Scartazza et al., 1998). Since stomatal conductance is directly proportional to water loss, ^{13}C

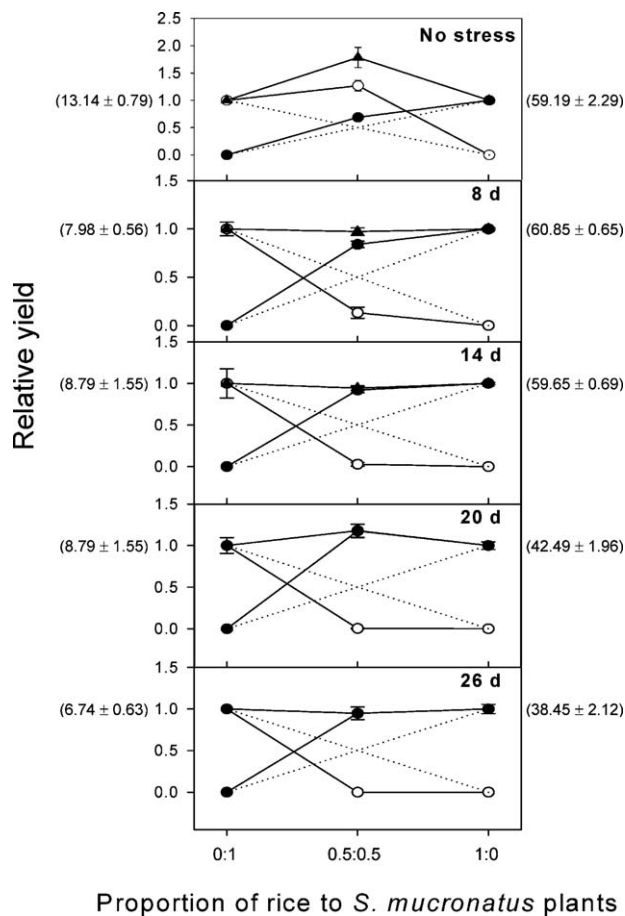


Fig. 4. Replacement-series diagrams with relative shoot biomass yields ($\text{RY} = \text{competition/monoculture}$) for rice (●) and *S. mucronatus* (○) growing in monoculture and in 50:50 mixture; total plant density per pot was four plants. Triangles (▲) are relative yield totals ($\text{RYT} = \text{RY}_{\text{rice}} + \text{RY}_{\text{S. mucronatus}}$). Absolute yields \pm S.E. (g pot^{-1}) are given in brackets. Plants were irrigated either continuously (no stress) or during 34 d after seeding followed by 8, 14, 20 or 26 d of stress by drought; aboveground biomass from both species was harvested at rice maturity. Dotted diagonal lines are theoretical RY values assuming all individuals have equivalent competitiveness (Harper, 1977); vertical bars are \pm S.E. ($n = 5$).

discrimination provides an integrated measure of water loss per unit of carbon assimilated over time (Dingkuhn et al., 1991; Ehleringer, 1991; Farquhar et al., 1982) and a useful tool to compare water use between plants (Kloppel et al., 1998). As drought progressed, the pronounced discrimination decrease (less negative δ^{13}) observed in *S. mucronatus* suggested this species exerted control of transpirational losses relative to carbon assimilation. Whereas, the small change in rice δ^{13} over the drought period revealed little adjustment in water spending by rice. Wopereis et al., 1996 found no transpiration differences between flooded and moisture stressed rice plants, suggesting lack of transpiration control in rice. High transpiration rates in rice are correlated with greater water extraction from soil (Kamoshita et al., 2000). Thus under the conditions of our experiment, rice behaved like plants that resist drought by maximizing water use rather than water use efficiency through stomatal closure (Jones, 1993). Therefore, rice was a water spender and drove the soil moisture depletion that inhibited *S. mucronatus* growth and competitiveness when both species grew in mixture.

4.3. Recovery after drought

Rice had better biomass recovery after drought than *S. mucronatus*. It has been shown that the extent of drought-induced photosynthetic damage and green leaf area retention in upland rice lines subjected to early season water stress relates to their growth recovery and yielding ability when stress is relieved (De Datta et al., 1988; Fukai and Cooper, 1995; Garg et al., 2002). The greater sensitivity of *S. mucronatus* foliar tissue to drought stress must have contributed to its weaker post-flood recovery and to its susceptibility to rice competition. Competition was intense under drought when the superior soil moisture extraction ability of rice drove *S. mucronatus* Ψ_{leaf} values in competition below monoculture levels. After 8 d of stress, the photosynthetic integrity of the remaining *S. mucronatus* green tissue was sufficiently damaged that longer drought was not needed to confer substantial competitive advantage to rice during re-growth. Thus drought enhanced rice competitiveness against this emergent aquatic weed that is adapted to flooded environments (Hwang et al., 1996).

Tissue resilience and soil water extraction ability contributed towards rice tolerance to brief initial drought as expressed by its biomass recovery and yielding ability. In this study, rice yield was somewhat more sensitive to declining Ψ_{leaf} than was total shoot biomass recovery. Rice yields may be less affected by early vs. late moisture stress, since water deficits during flowering can inhibit pollination and grain formation, but early moisture stress may delay maturity and thus also affect yields as observed in our study (Fukai and Kamoshita, 2005; O'Toole, 1982).

In summary, larger and deeper roots and a high water-spending strategy allowed rice to extract soil moisture faster than *S. mucronatus*. Rice green tissue sustained less photosynthetic damage than *S. mucronatus* as Ψ_{leaf} decreased. This enabled rice to accumulate more biomass than *S. mucronatus* after re-flooding. Temporary drought considerably enhanced rice competitiveness by quickly stressing *S. mucronatus* and causing drastic loss of its photosynthetic ability, while rice maintained higher Ψ_{leaf} by extracting water from greater depths. Therefore morphological and physiological differences between these species support the concept of using temporary moisture stress as a tool for *S. mucronatus* suppression in rice. It appears that drought should be imposed briefly and early to cause minimum delays in rice maturity, but intensely enough to substantially damage *S. mucronatus*. Leaf water potential at the end of a moisture stress period predicted *S. mucronatus* growth recovery and rice yields upon irrigation resumption after drought. Further studies should identify weeds with similar characteristics to *S. mucronatus* and

suggest further opportunities for aquatic weed suppression and control of wetland weeds eventually moving into rice fields.

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