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Cite this article: Galvin LB, Inci D, Mesgaran M, Brim-DeForest W, Al-Khatib K (2022) Flooding depths and burial effects on seedling emergence of five California weedy rice (Oryza sativa spontanea) accessions. Weed Sci. 70: 213-219. doi: 10.1017/wsc.2021.82

Received: 26 June 2021 Revised: 3 November 2021 Accepted: 6 December 2021 First published online: 10 January 2022

Associate Editor:

Prashant Jha, Iowa State University

Kevwords:

Conspecific; weedy (red) rice

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Flooding depths and burial effects on seedling emergence of five California weedy rice (Oryza sativa spontanea) accessions

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Abstract

Weedy rice (Oryza sativa f. spontanea Roshev.) has recently become a significant botanical pest in California rice (Oryza sativa L.) production systems. The conspecificity of this pest with cultivated rice negates the use of selective herbicides, rendering the development of nonchemical methods a necessary component of creating management strategies for this weed. Experiments were conducted to determine the emergence and early growth responses of O. sativa spontanea to flooding soil and burial conditions. Treatment combinations of four flooding depths (0, 5, 10, and 15 cm) and four burial depths (1.3, 2.5, 5, and 10 cm) were applied to test the emergence of five O. sativa spontanea accessions as well as 'M-206', a commonly used rice cultivar in California, for comparison. Results revealed that burial depth had a significant effect on seedling emergence. A 43% to 91% decrease in emergence between seedlings buried at 1.3 and 2.5 cm depending on the flooding depth and accession and an absence of emergence from seedlings buried at or below 5 cm were observed. Flooding depth did not affect emergence, but there was a significant interaction between burial and flooding treatments. There was no significant difference between total O. sativa spontanea emergence from the soil and water surfaces regardless of burial or flooding depths, implying that once the various accessions have emerged from the soil they will also emerge from the floodwater. Most accessions had similar total emergence compared with M-206 cultivated rice but produced more dry weight than M-206 when planted at 1.3 cm in the soil. The results of this experiment can be used to inform stakeholders of the flooding conditions necessary as well as soil burial depths that will promote or inhibit the emergence of California O. sativa spontanea accessions from the weed seedbank.

Introduction

Most rice (Oryza sativa L.) producers in California practice aerial, wet direct seeding with pre-germinated rice seeds, incorporate continuous annual flooding, and typically do not practice crop rotation (Kanapeckas et al. 2018). Minimal crop rotation and a recent lag in voluntary adherence in purchasing certified seeds have been credited to the most recent appearance of weedy rice, also known as "weedy red rice" (Oryza sativa f. spontanea Roshev.), in California (De Leon et al. 2019; Scherner et al. 2018). Roughly 5,600 ha spread across all nine rice-growing counties in California had been infested with one or more of five O. sativa spontanea accessions as of 2019 (Karn et al. 2020). Five prevalent accessions had been documented at the time of this study in 2018 and were simply referred to as accessions 1, 2, 3, 4, and 5 (De Leon et al. 2019). As of 2021, there were seven accessions identified that are thought to be the result of hybridization between various wild, weedy, and cultivated rice from across the United States and are genetically and phenotypically different from one another (De Leon

Oryza sativa spontanea was first documented in California in 1920 but was eradicated by the 1970s through the use of direct water-seeding methods, herbicides, and certified seeds (Kanapeckas et al. 2016). An O. sativa spontanea infestation was again reported in 2003, suspected to be accession 3 (De Leon et al. 2019), but did not become a weed of concern until 2016 (Espino et al. 2018). California O. sativa spontanea has several traits that warrant concern, including conspecific features with cultivated rice, early maturity (Zhao et al. 2015), high shattering (>25%) (USDA 2015), some level of seed dormancy (3+ yr), and subsequent seedbank persistence (Espino et al. 2018). Additionally, there is evidence indicating a competitive

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Table 1. Descriptions of California Oryza sativa spontanea accessions and cultivated rice M-206 (De Leon et al. 2019; Karn et al., 2020).

Accession	Hull color	Awns	Grain type	Shattering	1,000-seed weight ^a	Dormancy ^b
					g	
M206	Straw	Absent	Medium	None	26.36 ± 0.3	None
Type 1	Straw	Absent	Short	High	19.88 ± 0.2	High
Type 2	Bronze	Absent	Medium	High	27.04 ± 0.3	Low
Type 3	Straw	Long	Medium	High	25.87 ± 0.3	High
Type 4	Black	Long	Short	High	26.02 ± 0.2	High
Type 5	Straw	Partial	Medium or Long	High	26.68 ± 0.3	Low

^aAverage observed 1,000-seed weight includes SE.

advantage of O. sativa spontanea in an elevated CO_2 environment (Ziska et al. 2010) as well as an ability for higher uptake of nitrogen compared with cultivated relatives (Chauhan and Johnson 2011). In the southern United States alone, O. sativa spontanea is one of the primary economic constraints to production (Ziska et al. 2015) and caused up to \$274 ha⁻¹ in economic losses before the introduction of imidazolinone-resistant rice cultivars (Burgos et al. 2008). There is a zero-tolerance policy for O. sativa spontanea in California rice fields cultivated for quality assurance programs, potentially causing massive financial losses if O. sativa spontanea is found (Blank 2019).

There are multiple cultural factors that contribute to the contemporary difficulty in controlling O. sativa spontanea in California in addition to the biological traits that limit control of these weeds. These include absence of herbicide-tolerant rice varieties, a reduced number of herbicides available for weed control compared with the southern U.S. rice-growing region, and a lack of crop rotation beyond continuously flooded rice (Al-Khatib 2017). The California Department of Food and Agriculture (2017) issued into law in 2019 that all rice planted in California must come from certified sources as a means to combat seed lots contaminated with O. sativa spontanea. Flooding has been suggested as an effective method of controlling rice weeds in the absence of chemical control options (Chauhan 2012b; Dorji et al. 2013; Ziska et al. 2015). The efficacy of flooding as a control strategy for O. sativa spontanea, however, has not been well studied in California rice systems. We hypothesized that California O. sativa spontanea accessions are well adapted to flooding due to the rice production culture in California, and consequently, flooding would not be a solitary control option for O. sativa spontanea.

Several studies have indicated that burial depth has an effect on seedling emergence patterns and is important for understanding seed longevity and persistence in the seedbank (Benvenuti et al. 2001; Ghosh et al. 2017). Several O. sativa spontanea accessions from Arkansas, Louisiana, and Mississippi (southern United States) were able to emerge from depths as great as 7.5 cm in clay and silt loam soils in dry direct-seeded conditions in the absence of standing water (Gealy et al. 2000). Drill-seeded, or dry directseeded rice, is less common in California than wet direct-seeded rice. California rice growers who practice wet direct seeding do not have the option of changing their planting depths, unlike farmers in the southern United States who practice dry direct seeding. It is important, however, to acknowledge that tillage depth is an important factor in weed suppression in both climates (Zhang et al. 2019). Information about seed survivability at various soil tillage depths can be used to determine how deep O. sativa spontanea seeds should be tilled into the soil or whether to implement preplant control options, such as a stale seedbed (Rathore et al. 2013). This illustrates how the rice-growing culture and production practices are different between the two U.S. regions, equating to the likelihood that California *O. sativa spontanea* may exhibit differential emergence responses when buried at depth compared with the southern *O. sativa* accessions studied by Gealy et al. (2000).

The objectives of this study were to determine the effects of flooding and burial depth on the emergence of the five California *O. sativa spontanea* accessions and determine whether there are differences in total emergence between these accessions. 'M-206', a medium-grain, medium-maturity rice cultivar developed at the Rice Experiment Station in Biggs, CA, was used for comparison in this experiment due to its consistent use by California rice producers and its close genetic relationship with accession 3 (De Leon et al. 2019). The overall goal of this research was to provide information to support future tillage and flooding-depth management strategies aimed at reducing *O. sativa spontanea* in California rice production systems.

Materials and Methods

Seed Material and Pretreatment Protocols

Localized seed collections were organized by University of California Cooperative Extension staff during a field survey conducted in 2016 (Espino et al. 2018). Seed multiplication of all *O. sativa spontanea* accessions was done in controlled greenhouse environments on the University of California Davis campus from 2016 to 2019 with plants physically separated to reduce the likelihood of cross-pollination. All plants were grown in 3.79-L pots that were submerged in trays with 5 cm of standing water maintained consistently throughout the plants' life cycles. Table 1 describes each *O. sativa spontanea* accession as well as M-206, a common cultivar in California.

The accessions described in Table 1 were the only well-documented O. sativa spontanea in California at the time of study and have varying levels of dormancy (Espino et al. 2018). Each O. sativa spontanea accession was primed by placing seeds into separately sealed plastic bags with a dry paper towel and setting them in a dark incubation chamber for 5 d at 50 C (Shiratsuchi et al. 2017; Waheed et al. 2012). Following the dry-hot incubation period for dormancy breaking, all seeds, including M-206, were wetted by saturating the paper towel within each plastic bag with deionized water. This mimicked common practices for pregerminating cultivated varieties for wet direct-seeded practices (Linquist et al. 2018). The plastic bags were subsequently placed back into the dark chamber for 3 d at 30 C. Deionized water was added as needed to ensure the paper towel remained saturated, and all seeds received constant moisture for the duration of the germination process.

bDormancy is quantified by length of time seeds can remain viable in the soil seedbank. High, dormancy is greater than 5 yr; low, dormancy is 1-3 yr in the soil (Espino et al. 2018).

Plant Growth Conditions

Field soil from a site historically planted in rice (>5 yr before experimentation) at the Rice Experiment Station in Biggs, CA (39.4654°N, 121.7339°W), was used for this study. Soil from this site is described as Esquon-Neerdobe clay soils, taxonomically defined as fine, smectitic, thermic Xeric Epiaquerts, moderately deep to a duripan, and contains 20% sand, 30% silt, 50% clay, and 2.65% soil organic matter, with a pH of 5.88, 0.06% total N, 13 ppm Olsen-P, and 250 ppm K. Clear 46 by 66 by 38 cm polycarbonate tubs were filled half full, ~0.04 m³, with soil that was wetted and leveled before planting to ensure all seeds were buried and flooded to consistent depths.

Once seeds had germinated (within incubated plastic bags), those with radicles protruding 1 to 3 mm from the seed coat were planted. Seeds were placed on the soil surface and then covered with soil to the designated burial-depth level (Chauhan 2012b). Irrigation water from a municipal tap was applied immediately after seed burial to achieve the desired flooding depth.

Experimental Design

The experiment was repeated in time to expose O. sativa spontanea accessions to various conditions; Run 1 commenced in July and Run 2 in August of 2018. Four flooding depths of 0 (fully saturated soil absent of standing water), 5, 10, and 15 cm in combination with four burial depths of 1.3, 2.5, 5, and 10 cm were used. Treatments were arranged as a factorial split plot in a randomized complete block design with four replicates. Each tub (block) was planted with 15 seeds of each accession as well as M-206 and incorporated a single flooding depth and burial depth. All accessions were buried at the same depth using a grid with 5 cm of separation to help demarcate different O. sativa spontanea seedlings from one another upon soil emergence. Each burial by flooding combination was replicated four times for each run, equating to 64 tubs in total for each run. Tubs were placed outside to capture diurnal temperature swings that may play a role in O. sativa spontanea emergence (Boddy et al. 2012).

Data Collection

Water temperature was recorded hourly from a single treatment combination replicate with HOBO® Pendant™ MX2201 (Onset Computer, 470 MacArthur Boulevard, Bourne, MA 02532, USA) water temperature data loggers. Ambient air temperature was also recorded hourly with a single HOBO® MX100 temperature data logger. Average minimum and maximum ambient air temperatures were 15 and 39 C, respectively, for Run 1 (July) and 13 and 34 C, respectively, for Run 2 (August). There was an absence of rainfall typical of this region during the summer months for both runs.

Seedling emergence from both the soil and water surfaces was recorded daily when possible. Emergence from the soil surface was defined by a visible cotyledon of 3 mm or greater extending from the soil surface. Emergence from the water was noted when a leaf visibly permeated the water surface. Any non-rice weeds were immediately removed by hand, while copper sulfate (CuSO4; Millipore Sigma, PO Box 14508, St Louis, MO 63178, USA) was applied in liquid formulation at a rate of 13.45 kg ha⁻¹ to each tub at 2, 9, and 16 d after planting to prevent algal growth. Plants were harvested at the soil surface at 21 d after planting and then placed in paper bags that were dried at 70 C for 3 wk, after which dry biomass was determined.

Data Analysis

Oryza sativa spontanea emergence from the soil and water and the dry weight data were analyzed using PROC MIXED in SAS v. 9.4 (SAS Institute, 100 SAS Campus Drive, Cary, NC 27513, USA). Burial depth, flooding depth, accession, and their associated interactions were included as fixed effects. There were two-way interactions between flood and run for both emergence from the soil and emergence from the water, but experimental run alone was not a significant factor. There were no significant differences in experimental run in the dry weight analysis. A two-tailed t-test analysis using R programming software (R Core Team 2021) indicated a significant difference of 2 C in ambient air temperature as well as water temperature between the two experimental runs. Experimental run was incorporated as a random intercept to account for the variation of replicates in time in an outdoor setting (Yang 2010). Residuals were visually inspected to ensure assumptions of ANOVA with respect to homogeneity and normality. Initial analysis included all treatments; however, to create a less skewed distribution of the data, the 5- and 10-cm burial depths were excluded from the analysis due to complete lack of emergence from those treatment groups for all accessions, including the control group, M-206. Treatment effects and interactions were subjected to a type III ANOVA followed by a Tukey honestly significant different post hoc test at a significance level of 0.05. A one-tailed, Welch two-sample t-test was conducted using R (R Core Team 2021) to determine differences between emergence from the soil and water surfaces.

Results and Discussion

Burial depth alone had significant influence (P < 0.0001) over emergence from the soil and water surfaces and dry weight. However, once the 5- and 10-cm burial depths were removed from the analysis due to a lack of data, burial alone was no longer significant for any of the measured variables. Burial by flood interactions had significant effect on emergence from the soil (P < 0.0001) and emergence from the water (P < 0.0001), but not on dry weight (P = 0.0975). Burial by accession interactions also had significant effect on emergence from the soil (P = 0.0203), emergence from the water (P = 0.0116), and dry weight (P = 0.0091). There were no significant three-way interactions. Results from the *t*-test comparing total emergence from the soil and water surfaces showed no significant differences between them regardless of burial depth, flooding depth, or accession, including M-206.

Seedling Emergence from Soil and Water Surfaces

Burial had significant effects on emergence (P < 0.0001) of all accessions as well as M-206. No pre-germinated seeds buried at or deeper than 5 cm in the soil emerged, regardless of flooding depth or accession (Figure 1). Reduction in weed emergence with increasing soil burial depth may be due to several factors such as increased soil physical impediment or decreased oxygen concentrations in deeper soil depths leading to hypoxia (Ismail et al. 2012; Setter et al. 1988). Accessions 2 and 5 have a short dormancy period (Table 1), so burial at 5 cm or deeper may be a control option for these specific California *O. sativa spontanea* seeds present in the soil seedbank (Marambe 2009). Accessions from the southern United States have been found to emerge from 7.5 cm in dry drill-seeded conditions absent of standing water (Gealy et al 2000). In California mostly wet direct seeding with standing water is implemented, that is, seeds are not planted into

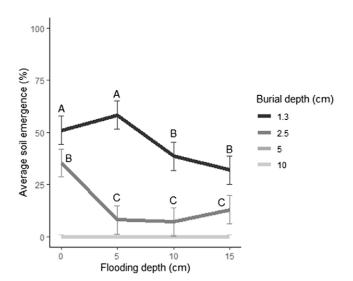


Figure 1. Burial and flooding depth interactive effects on pooled emergence from the soil surface for all accessions of weedy rice. Different letters indicate significant differences between treatment means, and error bars represent standard error.

the soil, but are situated on the soil surface. The difference in emergence depths of the regionally different accessions highlights the effects of cultural management practices and their effects on field ecology of weeds (Chauhan 2012a).

There was significant (P < 0.0001) burial depth by flooding depth interactions on soil surface emergence. There was no statistical difference in emergence from the soil when no flood (0 cm) and 5-cm flooding were applied to seeds buried at 1.3 cm (Figure 1). Similarly, there was no statistical difference between emergence from the soil at 10- and 15-cm flooding depths when seeds were buried at 1.3 cm (Figure 1). At this same burial depth, there was a difference (P = 0.0017) between total seedling emergence from shallow flooding (0- and 5-cm) and deeper flooding (10- and 15-cm) depths, with a 20% decrease in emergence from the soil when flooding increased from 5 to 10 cm (Figure 1). The decrease in emergence from the soil with increasing flooding depth supports the current practice of using deep flooding as a weed suppression method in flooded rice systems (Ismail et al. 2012). Our research suggests that the flood must be at least 10 cm to have an impact on California O. sativa spontanea seeds located at the soil surface (1.3 cm).

Seeds buried at 2.5 cm in combination with no flooding exhibited significantly higher emergence from the soil (P < 0.0001) than at other flooding levels at the same burial depth. Average seedling emergence decreased from 35% at 0-cm flooding to 8% at 5-cm flooding when seeds were buried at 2.5 cm (Figure 1). There was no significant difference in average seedling emergence when 5-, 10-, and 15-cm flooding was applied in combination with 2.5-cm burial. Most California rice producers will apply a winter flood to encourage decomposition of postharvest rice straw and weed seed decay and to provide habitat for migratory birds (Aghaee and Godfrey 2017). Tillage in the fall is important for incorporation of said rice straw and reducing nitrogen requirements in the following spring (Linquist et al. 2008). A 5-cm flooding depth in combination with deep tillage (>10 cm) could be used to prevent emergence of O. sativa spontanea accessions and potentially decrease seed viability over time (Zhang et al. 2019).

There was significant burial by flooding depth interactions (P < 0.0001) on emergence from the water surface (Figure 2).

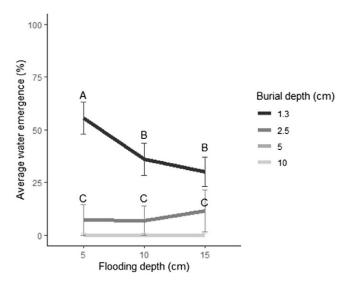


Figure 2. Pooled emergence from the water surface for all accessions of weedy rice. Different letters indicate significant differences between treatment means, and error bars represent standard error.

There was no significant difference in overall accession emergence from the water between the 10- and 15-cm flooding depths when seeds were buried at 1.3 cm (Figure 2). There was a significant difference (P < 0.050) in emergence from the water between these two flooding depths and the 5-cm flooding depth when accessions were buried at 1.3 cm. This is similar to total emergence from the soil for the same treatment groups. Emergence from the water decreased from 55% at 5-cm flooding to 36% at 10-cm flooding, but only a 6% decrease in emergence was seen going from 10- to 15-cm flooding depths (Figure 2).

There was no significant difference (P > 0.05) in emergence from the water between the 5-, 10-, and 15-cm flooding depths when accessions were buried at 2.5 cm (Figure 2). These results mirror emergence from the soil patterns that occurred at the 2.5-cm burial depth with increasing flooding depth. Results from the *t*-test showed no significant differences (P = 0.2786, n = 576) in emergence between soil and water surfaces. The similarities between emergence from the soil and water surfaces imply that once O. sativa spontanea emerges from the soil, it has a high likelihood of also emerging through floodwaters at or below 15 cm. Some rice cultivars have been found to increase coleoptile elongation in the presence of floodwater containing low oxygen concentrations (Turner et al. 1981). This response could be an explanation for the similarities observed between soil and water surface emergence patterns of these weedy accessions. It is possible that the lack of crop rotation and consistent flooding have produced selective pressure on California O. sativa spontanea accessions, making them more likely to emerge from floodwaters compared with types from the southern United States, where dry seeding is the norm (Ismail et al. 2012).

Differences between Oryza sativa spontanea Accessions

There were significant interactions (P = 0.0203) between burial depth and accession that influenced emergence from the soil surface. There was no significant difference between average emergence from the soil surface for accessions 1, 2, 3, 5, and M-206 when buried at 1.3 cm (Figure 3). Accession 4 had significantly lower emergence from the soil than other accessions, with 26% less

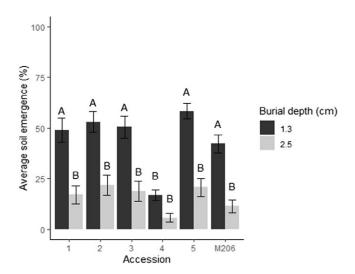


Figure 3. Average emergence from the soil surface of each *Oryza sativa spontanea* accession and cultivated rice M-206 when planted at 1.3- or 2.5-cm burial depths. Different letters indicate significant differences between treatment means, and error bars represent standard error.

emergence (P = 0.006) compared with M-206 (Figure 3). There was no significant difference between emergence from the soil of all accessions, including M-206, at 2.5-cm burial (Figure 3). Accession 4 is phenotypically very different from the other accessions despite its close genetic relationship with accession 3 (De Leon et al. 2019). Based on greenhouse growth observations, accession 4 has a dwarf-like growth habit, long awns with a high shattering rate, a high tiller and panicle number, and low shoot and root dry weight compared with the other *O. sativa spontanea* accessions. Karn et al. (2020) found that accession 4 growth is greatly reduced in the presence of competition from other rice plants. The planting density of this experiment could be a partial factor in the reduced emergence rate of accession 4 in addition to the biological differences with other accessions.

There were significant interactions (P = 0.0116) between soil burial depth and accession for emergence from the water. Accession 5 had 54% emergence from the water surface, significantly more (P = 0.0405) emergence compared with M-206, 35%, when buried at 1.3 cm in the soil regardless of flooding depth (Figure 4). Accessions 1, 2, 3, and 5 had 42%, 47%, 50%, and 54% emergence from the water, respectively, and were not significantly different from each other; however, only accessions 1, 2, and 3 were not significantly different from M-206 (Figure 4). Accession 4 was again significantly different from all other accessions, with only 16% emergence from the water surface when buried at 1.3 cm regardless of flooding depth. There was no significant difference between emergence from the water of all accessions, including M-206, at 2.5-cm burial depths (Figure 4).

Similar patterns of emergence from the soil and water surfaces were demonstrated through the burial by flooding interactions as well as the burial and accession interactions. Several factors may have contributed to rapid growth after germination in the presence of a flood, including early maturation (Zhao et al. 2015) and morphological features such as rapid shoot elongation and vertical leaf position (Voesenek et al. 2006). The general ability to emerge from the soil and floodwaters at equivalent or greater rates compared with M-206 highlights the *O. sativa spontanea* accessions' probable adaptation to the continuous annual flooding

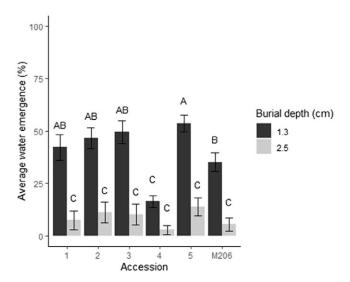


Figure 4. Pooled emergence from the water surface of each *Oryza sativa spontanea* accession and cultivated rice M-206 when planted at 1.3- or 2.5-cm burial depths. Different letters indicate significant differences between treatment means, and error bars represent standard error.

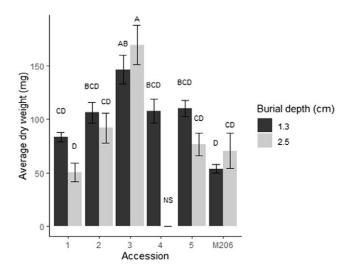


Figure 5. Pooled seedling dry weight of the five *Oryza sativa spontanea* accessions and cultivated rice M-206 when planted at either 1.3- or 2.5-cm burial depths. Accession 4 did not have enough plant material at the 2.5-cm burial depth to produce significant dry weight results. Different letters indicate significant differences between treatment means, and error bars represent standard error.

common in the majority of California rice-cropping systems (Delouche et al. 2007).

Biomass Production

Average dry weight was significantly affected by burial and accession interactions (P = 0.0091). Weedy accessions 2 (106.2 mg; P = 0.0371), 3 (146.4 mg; P = 0.0003), 4 (107.5 mg; P = 0.0427), and 5 (110.0 mg; P = 0.0255) yielded significantly greater dry weight compared with M-206 (53.72 mg) at 1.3-cm burial. Accession 1 (83.44 mg) was not significantly different (P = 0.2400) from M-206 at the same burial depth (Figure 5). Accession 1 has a short-grain seed size (Karn et al. 2020), and the 1,000-seed weight is less than the other weedy accessions,

including M-206 (Table 1). The 1,000-seed weight may account for the reduced dry weight accumulated during early stages of development (Roy et al. 1996). This research highlights the importance of early-season control and seedbank management of these accessions to prevent *O. sativa spontanea* from gaining a competitive advantage over cultivated varieties (Kanapeckas et al. 2018).

Accession 3 (169.5 mg; P = 0.0028) accumulated significantly more dry weight compared with M-206 (70.42 mg) and accessions 1 (50.44 mg; P < 0.0001), 2 (91.81 mg; P = 0.0070), and 5 (76.48 mg; P = 0.0013) when all accessions were buried at 2.5 cm. There was not enough plant material from accession 4 for statistical analysis of the data (Figure 5). It is assumed that accession 3 has existed in the rice-growing region of California for considerably longer than the other *O. sativa spontanea* accessions included in this experiment (Kanapeckas et al. 2016). Accession 3 is a genetic divergent from California cultivated rice (De Leon et al. 2019) and was first reported in 2003 (Espino et al. 2018). This accession may have had a longer period of time to adapt to California production systems, which would explain its ability to produce more dry weight in early growth stages compared with M-206 and other *O. sativa spontanea* accessions.

The greatest total emergence of any O. sativa spontanea occurred at shallow burial (1.3-cm) and shallow flooding (0- to 5-cm) depths in this experiment. Emergence and dry weight varied among the different California O. sativa spontanea accessions depending on flooding depth, burial depth, and accession. Burial depth played the most important role in emergence patterns, demonstrated by the lack of emergence from depths greater than 5 cm in the soil. Flooding depth alone did not significantly influence emergence, nor did an increase in flooding depth at 1.3-cm burial depth cause a consistent decline in emergence patterns of weedy accessions or M-206. Deep flooding in general is an important weed control tool for California rice producers to control grass-type weeds, but flooding alone will not greatly reduce O. sativa spontanea emergence. Burial depth information could be used to promote O. sativa spontanea emergence when implementing a stale seedbed methodology, currently one of the only conventional practices available for controlling this pest in California rice-cropping systems (Karn et al. 2020). Results from this study could also be used by growers to determine how deep they must bury weed seeds to avoid bringing them to the surface during soil cultivation, rendering O. sativa spontanea seeds inactive and potentially nonviable over time.

Acknowledgments. This research was supported by the California Rice Research Board and the Melvin D. Androus Endowment. The authors acknowledge John Madsen for technical support. No conflicts of interest are declared.

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