Weed Science

www.cambridge.org/wsc

Mature tubers of purple nutsedge (*Cyperus rotundus*) confer flooding tolerance by adopting a low-oxygen quiescence strategy that may contribute to its emergence in rice fields

Shan-Chi Yi[1], Chen-Yang Wei[1], Yao Tong[1], Lin Xu[1], Dan-Li Fan[1], Shi-Xian Yu[1], Shu-Yu Liu[1], Ren-Hai Wu[2], Xiao-Liang Liu[3] and Wen-Wei Tang[4]

[1]Graduate Student, Guangxi Key Laboratory of Agro-Environment and Agric-Product Safety, National Demonstration Center for Experimental Plant Science Education, College of Agriculture, Guangxi University, Nanning, Guangxi, People's Republic of China; [2]Doctoral Researcher, Henan Key Laboratory of Crop Pest Control, Institute of Plant Protection, Henan Academy of Agricultural Sciences, Zhengzhou, Henan, People's Republic of China; [3]Assistant Professor, Guangxi Key Laboratory of Agro-Environment and Agric-Product Safety, National Demonstration Center for Experimental Plant Science Education, College of Agriculture, Guangxi University, Nanning, Guangxi, People's Republic of China and [4]Professor, Guangxi Key Laboratory of Agro-Environment and Agric-Product Safety, National Demonstration Center for Experimental Plant Science Education, College of Agriculture, Guangxi University, Nanning, Guangxi, People's Republic of China

Research Article

Cite this article: Yi S-C, Wei C-Y, Tong Y, Xu L, Fan D-L, Yu S-X, Liu S-Y, Wu R-H, Liu X-L, Tang W-W (2024). Mature tubers of purple nutsedge (*Cyperus rotundus*) confer flooding tolerance by adopting a low-oxygen quiescence strategy that may contribute to its emergence in rice fields. Weed Sci. doi: 10.1017/wsc.2024.74

Received: 6 June 2024
Revised: 25 August 2024
Accepted: 4 October 2024

Keywords:
Rice field weeds; soil flooding; tuber adaptation

Corresponding author:
Wen-Wei Tang; Email: wenweitg@163.com

Abstract

Purple nutsedge (*Cyperus rotundus* L.) is one of the world's resilient upland weeds, primarily spreading through its tubers. Its emergence in rice (*Oryza sativa* L.) fields has been increasing, likely due to changing paddy-farming practices. This study aimed to investigate how *C. rotundus*, an upland weed, can withstand soil flooding and become a problematic weed in rice fields. The first comparative analysis focused on the survival and recovery characteristics of growing and mature tubers of *C. rotundus* exposed to soil-flooding conditions. Notably, mature tubers exhibited significant survival and recovery abilities in these environments. Based on this observation, further investigation was carried out to explore the morphological structure, nonstructural carbohydrates, and respiratory mechanisms of mature tubers in response to prolonged soil flooding. Over time, the mature tubers did not form aerenchyma but instead gradually accumulated lignified sclerenchymal fibers, with lignin content also increasing. After 90 d, the lignified sclerenchymal fibers and lignin contents were 4.0 and 1.1 times higher than those in the no soil-flooding treatment. Concurrently, soluble sugar content decreased while starch content increased, providing energy storage, and alcohol dehydrogenase activity rose to support anaerobic respiration via alcohol fermentation. These results indicated that mature tubers survived in soil-flooding conditions by adopting a low-oxygen quiescence strategy, which involves morphological adaptations through the development of lignified sclerenchymal fibers, increased starch reserves for energy storage, and enhanced anaerobic respiration. This mechanism likely underpins the flooding tolerance of mature *C. rotundus* tubers, allowing them to endure unfavorable conditions and subsequently germinate and grow once flooding subsides. This study provides a preliminary explanation of the mechanism by which mature tubers of *C. rotundus* from the upland areas confer flooding tolerance, shedding light on the reasons behind this weed's increasing presence in rice fields.

Introduction

Purple nutsedge (*Cyperus rotundus* L.) is one of the most challenging weeds to control globally, due to its rapid and efficient regenerative capacity and the viability of its tubers, which serve as the primary reproductive organ (Peerzada 2017). This species has been shown to adversely affect the growth of dryland crops such as sugarcane (*Saccharum officinarum* L.), maize (*Zea mays* L.), soybean [*Glycine max* (L.) Merr.], cotton (*Gossypium hirsutum* L.), and peanut (*Arachis hypogaea* L.) (Du et al. 2019; Durigan 2005; Salgado et al. 2002; Silva et al. 2015; Tuor and Froud-Williams 2002). Additionally, it can negatively impact rice (*Oryza sativa* L.) seedlings through the release of aqueous extracts and leachates from its leaves and tubers. In particular, the lowland ecotype of *C. rotundus*, when present at a density of 80 tubers m^{-2} in transplanted rice fields, has been shown to reduce rice shoot and root biomass by 54% and 60%, respectively (Donayre et al. 2022; Quayyum et al. 2000). *Cyperus rotundus* was initially reported to occur only sporadically or at low densities in rainfed lowland rice fields in the Philippines during the 1970s (Carbonell and Moody 1983). However, by the 1990s, it had become a dominant weed in paddy fields rotated with vegetables (Baltazar et al. 1999a), leading to a reduction in transplanted rice

grain yield by 14% to 38% (Donayre et al. 2022). Since then, this weed has become increasingly prevalent in the Philippines' rice fields (Donayre et al. 2015), and reports of *C. rotundus* in rice fields have surfaced in more than 20 countries across tropical and subtropical regions (Kraehmer et al. 2016). In Latin America, for instance, *C. rotundus* is commonly found in both irrigated and dryland rice fields in countries like Mexico, Honduras, Nicaragua, Brazil, Costa Rica, and Peru (Gonzalez et al. 1983; Silveira and De Aquino 1983). Similarly, in Asia, it has become a pernicious weed in rice fields, including dry direct-seeded paddy fields in the hilly areas of Jiangsu, China (Yu et al. 2022); intermittent plots of alternate wet and dry irrigation rice fields in Chiba, Japan (Chapagain et al. 2011); and rice fields across five districts of Punjab, Pakistan (Rabbani and Baiwa 2001). It has been observed that in areas where *C. rotundus* is prevalent in rice fields, its presence can often be traced back to previous cropping practices or the transition from dry- to wetland preparation (Baltazar et al. 1999b; Donayre et al. 2015). This suggests that *C. rotundus* can survive and reproduce in both the aerobic environment of upland areas and the anaerobic conditions of flooded rice fields. Understanding how this upland weed, which primarily reproduces through tubers, has adapted and propagated to become a noxious weed in rice fields is crucial.

In the cultivation of rice, water management is crucial throughout the various developmental stages, playing a significant role in determining crop yield and quality (Zhu et al. 2024). Most of the growth stages of rice, including the seedling stage, tillering stage, heading stage, and flowering stage, need the soil to be kept completely flooded. However, certain stages, such as the end of tillering, filling, and ripening stages, necessitate drainage and drying in the sun (Li et al. 2018; Zhang 2021). While this water management strategy optimizes rice development, it also inadvertently creates conditions that favor the survival and spread of certain weeds. We hypothesize that *C. rotundus* is well adapted to thrive in both the flooded and drained conditions typical of rice fields.

Plants have developed two primary strategies to endure flooding: low-oxygen escape and low-oxygen quiescence (Akman et al. 2012; Bailey-Serres and Voesenek 2008; Voesenek and Baily-Serres 2015). The plants employing the low-oxygen escape strategy typically develop more aerenchyma and adventitious roots, which enhance shoot elongation, allowing the plants to reestablish air contact by utilizing energy and consuming carbohydrates (Luo et al. 2011; Voesenek and Baily-Serres 2015; Yu et al. 2012), as seen in deepwater rice (Hattori et al. 2011). In contrast, plants following the low-oxygen quiescence strategy are characterized by traits that enable them to accumulate more carbohydrates by reducing energy consumption and inhibiting growth. This approach supports long-term survival under flooded conditions, ensuring sufficient energy reserves for growth recovery after the removal of flooding (Luo et al. 2011; Nakamura and Noguchi 2020). Much of the research has focused on how *C. rotundus* plants survive and reproduce in the oxygen-deficient environment of flooded rice fields, particularly in relation to their morphological and physiological responses. These responses include changes in morphological and anatomical features, energy consumption and supply, and enzymes of the fermentation pathway. Peña-Fronteras et al. (2009) have reported that the flooding tolerance of lowland *C. rotundus* may be attributed to large carbohydrate content, amylase activity, and the ability to maintain high levels of soluble sugars in the tubers during germination and early growth. Fuentes et al. (2010) further suggested that higher carbohydrate content, larger stem diameters, and larger air spaces, along with the mobilization and utilization of carbohydrate reserves under hypoxia, were important adaptive traits for plants under flooded conditions. However, the specific adaptive strategies employed by *C. rotundus* tubers to thrive under the flooding conditions prevalent in rice fields remain to be elucidated.

Therefore, *C. rotundus* tubers at two different maturity levels, mature and growing tubers, were selected from upland areas for soil-flooding and recovery (removal of soil flooding) treatment to simulate water management in paddy fields. This study hypothesizes that *C. rotundus* tubers subjected to soil flooding and subsequent removal of flooding will exhibit specific response mechanisms. These mechanisms are expected to be evidenced by changes in tuber vigor, morphological structure, carbohydrate levels, and anaerobic respiration.

Materials and Methods

Plant Sourcing and Collection

Tubers of *C. rotundus* were collected from a sugarcane field in Fusui, Guangxi, China (22.541°N, 107.838°E), where *C. rotundus* is the predominant weed species, characterized by extensive coverage and high density. Subsequently, the collected tubers were propagated in the Agricultural Science Experimental Field at Guangxi University, Nanning, China.

Experimental Design

The experiment was conducted in the greenhouse of the College of Agriculture, Guangxi University (22.850°N, 108.295°E) from August to December 2022. The soil used in the experiment was a mixture of peat, roseite, and sand (2:1:1), which was mixed, packed in bags, and sterilized in an autoclave. A total of 720 mature tubers (0.8 to 1.2 g, with hard, black-brown coats) and 720 growing tubers (0.1 to 0.3 g, with a softer texture and brown coats that could be pared by hand) of *C. rotundus* were collected for the experiment.

The experimental design aimed to simulate paddy water management conditions, involving both soil-flooding (maintaining a water layer) and drainage (recovery from soil flooding) treatments for *C. rotundus* tubers. Mature and growing tubers of *C. rotundus* were placed in plastic pots (17-cm lower diameter by 18-cm height by 20-cm upper diameter) with a bottom layer of 8 cm of soil and a top layer of 6 cm of soil. Water was then slowly added to cover the soil surface, maintaining a water level 3 cm above the soil.

Mature and growing tubers were subjected to four soil-flooding treatments: (1) no soil-flooding treatment as control (soil flooding 0 d, CK), (2) complete soil flooding under 3-cm-deep water for 30 d (SF-30), (3) complete soil flooding under 3-cm-deep water for 60 d (SF-60), and (4) complete soil flooding under 3-cm-deep water for 90 d (SF-90). Each treatment had three replicates, with 20 tubers per replicate.

Subsequently, mature and growing tubers were subjected to four treatments to investigate their recovery following different durations of soil flooding: (1) no soil-flooding treatment as control (CK), (2) removal of SF-30 (RSF-30), (3) removal of SF-60 (RSF-60), and (4) removal of SF-90 (RSF-90). To ensure consistency across the trials, all four treatments were sampled on the same day. Tubers in Treatment 4 were subjected to 90 d of soil flooding before sampling. Similarly, tubers in Treatment 3 underwent 60 d of soil flooding, and those in Treatment 2 experienced 30 d of soil flooding before being sampled. No further flooding was applied

https://doi.org/10.1017/wsc.2024.74 Published online by Cambridge University Press

after the sampling. The water was removed from all recovery treatments on the same day at the end of their respective soil-flooding durations, and the recovery duration was monitored for 30 d. Three replicates were conducted for each treatment, with each replicate comprising 20 tubers.

Sampling and Data Collection

After the soil-flooding treatments, an assessment was conducted of the number of viable tubers, identified by their firm texture when pressed with fingers and the absence of any signs of rot or softening. Additionally, the fresh weight of the tuber samples was measured. Based on the data, the survival rate and the fresh weight retention rate were calculated. The fresh weight retention rate was determined using Equation 1:

$$y = \frac{A_1 - A_0}{A_0} \times 100\% \quad [1]$$

where y represents fresh weight retention rate; A_0 is fresh weight of *C. rotundus* tubers after soil-flooding treatments, and A_1 is the fresh weight of *C. rotundus* tubers before soil-flooding treatments. One portion of the fresh samples was used for the observation of morphological characteristics and determination of tuber vigor, while another portion of samples was frozen in liquid nitrogen and stored at −80 C for further research.

After the recovery treatments following soil flooding, the emergence rate of *C. rotundus* tubers was recorded within 30 d. The germination rate was assessed after 30 d of recovery treatments, with both sprouted tubers and established seedling tubers counted as germinated. Additionally, samples were collected at two critical growth stages: the sprouting phase, when tubers had just begun to develop buds and the seedling rate ranged from 10% to 20%; and the seedling stage, when *C. rotundus* tubers were observed to successfully produce seedlings 30 d post-recovery (i.e., 30 d after water removal). One portion of the fresh samples was randomly selected for the observation of morphological characteristics (three tubers) and determination of tuber vigor (three tubers), while another portion of samples was frozen in liquid nitrogen and stored at −80 C for further research.

Measurement of Growth Parameters

Growth parameter data were collected at 30 d after recovery treatments from soil flooding: (1) plant height (length from stem base to top of plant with a ruler), (2) total fresh weight, (3) aboveground and belowground fresh weight, (4) root to shoot ratio (belowground fresh weight/aboveground fresh weight), (5) fresh weight of new tuber, (6) number of new tubers, and (7) single-tuber growth rate. The single-tuber growth rate was calculated using Equation 2.

$$y = \frac{a - b}{N} \times 100\% \quad [2]$$

where y represents the single-tuber growth rate, a is fresh weight of *C. rotundus* plants after 30 d of recovery, b is fresh weight of original *C. rotundus* tubers, and N is total number of tubers in each plastic pot. Each replicate had 20 tubers, and each treatment had three replicates. Principal component analysis (PCA) method and membership function analysis (MFA) (Liu 2022) were employed to evaluate the recovery capability of *C. rotundus* tubers after all recovery treatments.

Staining and Determination of Tuber Vigor

Tuber vigor was determined by the TTC (2,3,5-triphenyltetrazolium chloride) method (Lin et al. 2019). For each treatment, three tubers were randomly selected and sliced into thin sections (1 mm) using a double-edged razor blade. Each slice was then fully immersed in a solution containing 0.5% TTC and 75 mM phosphate buffer (pH 6.8). The slices were incubated in the dark at 37 C for 3 h. After incubation, the reaction was stopped by adding 2 ml of 1 mol L^{-1} sulfate buffer. Images of the stained tuber slices were taken with a Canon digital camera (EOS Digital 70D, Canon, Tokyo, Japan). The red extract solution of tubers was extracted using ethyl acetate, followed by spectrophotometric determination at 485 nm.

Observation of Morphological Characteristics

The anatomical structure of tubers was observed through paraffin sectioning. Three tuber samples were randomly selected for each treatment and then washed and cut into small pieces no larger than 5 mm by 5 mm by 5 mm using a double-edged razor blade. Samples were first soaked in 15% hydrofluoric acid for 2 d and then fixed in 70% formaldehyde–alcohol–acetic acid for about 2 d before rinsing and sectioning. The tuber samples were fixed, dehydrated, and then embedded in paraffin following the method of Cheng et al. (2018). The cross sections of *C. rotundus* tubers, 10-μm thick, were cut with a Leica RM 2255 microtome (Leica, Bensheim, Germany) and observed under bright-field illumination using an upright fluorescence microscope (Zeiss, Jena, Germany). The staining intensity of sclerenchymal fibers in each cross section was measured using Image J software v. 1.43u (National Institutes of Health, Bethesda, MD, USA) and expressed as integrated density. Three cross sections were randomly selected for measurement in each treatment.

Measurement of Malondialdehyde (MDA) and Hydrogen Peroxide (H_2O_2) Content

The concentration of MDA was determined using the thiobarbituric acid (TBA) method, as described by Yan (2017) with modifications. The tuber samples were homogenized in trichloroacetic acid (10% TCA) solution, and the mixture was centrifuged at 4 C, 10,000 × *g* for 20 min. The resulting supernatant was reacted with 0.67% TBA solution at 100 C for 20 min, then cooled to room temperature, and the absorbance was measured at 450 nm, 532 nm, and 600 nm. The H_2O_2 content was measured spectrophotometrically following the reaction with potassium iodide (KI) (Yiu et al. 2009). The tuber samples were homogenized in 0.1% TCA solution, and the mixture was centrifuged at 4 C, 10,000 × *g* for 10 min. The supernatant was then mixed with phosphate buffer and KI solution, and the mixture was incubated at 28 C for 1 h. The absorbance was read at 390 nm, and the H_2O_2 content was quantified by using a standard curve.

Determination of Nonstructural Carbohydrates

The nonstructural carbohydrate content, including starch and soluble sugar, was determined by an improved sulfuric acid–anthrone colorimetric method (Wu et al. 2019). The dried sample was extracted three times with 80% ethanol, and then the supernatant was used for the determination of soluble sugars, while the residue was used for the determination of starch content. For soluble sugar determination, the supernatant was mixed with anthrone solution for 10 s, quickly cooled on ice, and then boiled in

https://doi.org/10.1017/wsc.2024.74 Published online by Cambridge University Press

water for 10 min. The absorbance was measured at 620 nm after cooling. For starch determination, the residue was mixed with distilled water and boiled for 15 min, followed by the addition of 9.2 mol L^{-1} perchloric acid after cooling, and then boiled again for 10 min. The absorbance was measured at 620 nm after cooling. Starch and soluble sugar content were quantified using a standard glucose curve.

The determination of structural carbohydrate lignin content was carried out in accordance with the acetyl bromide method (Liu 2018). The tuber samples were extracted three times with 95% ethanol, and the deposit was washed with ethanol:*n*-hexane solution. The dried samples were treated with 25% bromoacetyl glacial acetic acid solution at 70 C for 30 min, and the reaction was halted by the addition of NaOH. Acetic acid and hydroxylamine hydrochloride were then added to the mixture, and the absorbance of the centrifuged supernatant was measured at 280 nm.

Measurement of Ethanol and Lactic Acid Contents and Alcohol Dehydrogenase (ADH) and Lactate Dehydrogenase (LDH) Activities

The ethanol and lactic acid contents, along with the activities of ADH and LDH were determined by assay kits (BC5100, BC2230, BC1080, and BC0680, Solarbio Science & Technology, Beijing, China). The measurement procedure was performed in accordance with the manufacturer's instructions, which included the preparation of sample extracts, the addition of reagents, and the measurement of absorbance or fluorescence.

Statistical Data Analyses

Statistical analyses were performed using SPSS v. 26.0 (SPSS Inc., Chicago, IL, USA) and GraphPad Prism v. 8 (GraphPad Software, San Diego, CA, USA) for figure creation. Data were analyzed using one-way ANOVA followed by Duncan's multiple-range test for comparisons among multiple treatments or independent-sample *t*-tests for comparisons between two treatments; statistical significance was set at $P < 0.05$. Each group of data was checked for normal distribution and tested for homogeneity of variance before conducting Duncan's multiple-range test and independent-sample *t*-tests. Normal distribution was confirmed by examining the histogram for a bell-shaped curve. For Duncan's multiple-range test, the variance result (Levene's test) based on the median showed that $P > 0.05$ satisfied the homogeneity of variance hypothesis; groups with the same letter indicated no significant difference, while different letters denoted significant differences. For independent-sample *t*-tests, Levene's test for equality of variances showed $P > 0.05$, confirming homogeneity. Significance was determined at $P < 0.05$ (*), $P < 0.01$ (**), and $P < 0.001$(***).

Results and Discussion

Growth Response of Mature and Growing Tubers under Soil Flooding

Mature tubers of *C. rotundus* only exhibited a darker epidermal surface after soil flooding, with no significant change in hardness compared with the pre–soil flooding period, whereas most growing tubers decayed or even perished, with their internal structure largely destroyed and the previously tender white epidermis turning into a grayish-brown mutilated outer skin (Figure 1A). Correspondingly, the fresh weight retention rate of mature tubers gradually decreased with prolonged soil flooding but remained at 93% after 90 d of flooding, with a survival rate consistently maintained at 100%. In contrast, the survival rate of growing tubers dropped to 5% after 90 d of flooding, with the fresh weight retention rate decreasing to 22% (Figure 1B).

During the subsequent recovery period, the germination rate of mature tubers after 30, 60, and 90 d of soil flooding was significantly higher than that of growing tubers by 62%, 60%, and 67%, respectively (Figure 1B). Mature tubers began to emerge about 1 wk after all treatments, with the highest emergence rate maintained under the RSF-30 treatment, whereas the emergence rate of growing tubers was severely affected, with only minimal germination under the RSF-30 treatment (Figure 1C). Further related growth data also revealed that mature tubers exhibited strong recovery growth, with the best recovery growth capacity under the RSF-60 treatment (Tables 1 and 2). As the duration of soil-flooding treatment increases, the height of mature tubers groups during the recovery period is suppressed to a certain degree. Specifically, the plant height under the RSF-90 treatment during the recovery period is reduced by 30%. However, the total fresh weight, aboveground and belowground fresh weight, new tuber fresh weight, and single-tuber growth rate under RSF-30 and RSF-60 showed faster recovery ability compared with CK and RSF-90. Notably, the single-tuber growth rate of RSF-60 was nearly double that of CK. However, the growth of growing tubers was significantly inhibited ($P < 0.05$; Table 1), likely due to their low survival rate under soil-flooding treatments. In addition, the extreme infestation with *C. rotundus* plants was observed in rice fields converted from dryland in Guangxi, China (Figure 1D). These results indicate that mature tubers could survive prolonged soil flooding, whereas growing tubers cannot. It is further suspected that the emergence of *C. rotundus* in rice fields may result from the sprouting and growth of mature tubers that have survived in the flooded environment.

Responses of Tuber Vigor in Mature Tubers under Soil Flooding

The tuber vigor of mature tubers was significantly affected by soil-flooding and recovery treatments (Figure 2). The vigor of mature tubers decreased sharply in the initial stage of soil flooding, being only 13% of CK at SF-30, and subsequently leveled off at SF-60 and SF-90 (Figure 2A and 2C). During the recovery period, tuber vigor increased, with the RSF-60 and RSF-90 treatments surpassing the CK level at the seedling stage. However, the RSF-30 treatment, despite showing some recovery, did not fully return to the CK level at the same stage (Figure 2B and 2D). Especially, under RSF-60 conditions, the vigor at the sprouting and seedling stages was approximately 1.6 and 1.7 times higher than that of CK, respectively (Figure 2D). Collectively, despite an initial decline at the onset of soil flooding, the vigor of mature tubers stabilized in the later stage. This resilience allowed for a gradual recovery during the sprouting and seedling stages of the recovery period, indicating that mature tubers are capable of withstanding prolonged soil flooding.

Responses of Morphological Traits in Mature Tubers under Soil Flooding

Previous research suggests that the formation of aerenchyma and apoplastic barriers can be considered to be a structural adaptation for flooding tolerance in plants (Evans 2003; Yang et al. 2013). In our study, no aerenchyma was observed in the internal structure of mature tubers of *C. rotundus*, even after 90 d of soil flooding

https://doi.org/10.1017/wsc.2024.74 Published online by Cambridge University Press

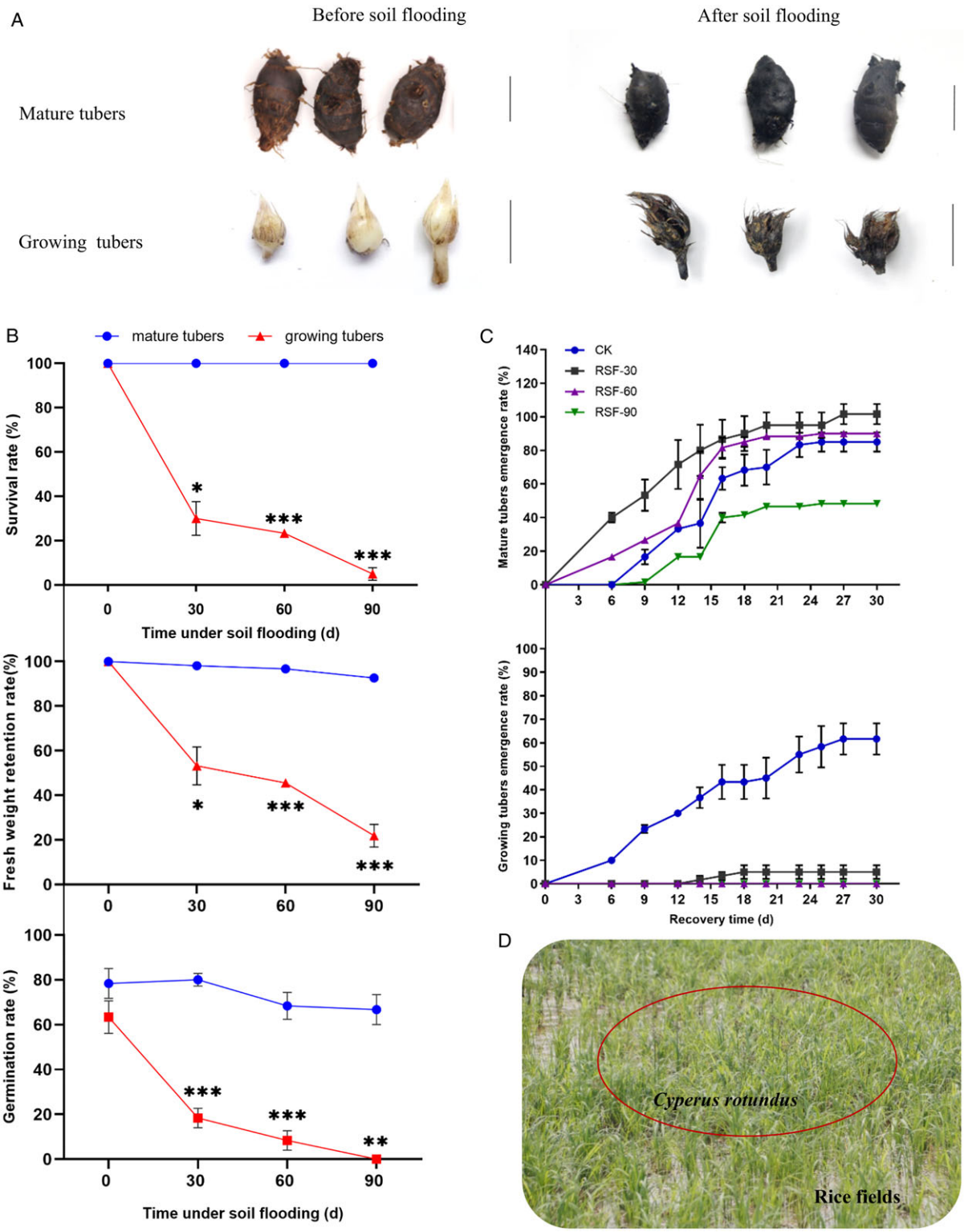

Figure 1. Phenotypic differences of mature tubers and growing tubers of *Cyperus rotundus* under soil flooding. (A) Phenotypic changes in mature tubers and growing tubers of *Cyperus rotundus* before and after soil flooding. Scale bars: 1 cm. (B) The survival rate, fresh weight retention rate, and emergence rate of mature tubers and growing tubers under soil-flooding treatments. (C) The emergence rate of mature tubers and growing tubers within 30 d after recovery treatments. (D) *Cyperus rotundus* appears in rice fields converted from dryland. Abbreviations: CK, no soil-flooding treatment; RSF-30, the removal of soil flooding at 30 d post-flooding; RSF-60, the removal of soil flooding at 60 d post-flooding; RSF-90, the removal of soil flooding at 90 d post-flooding. Data are shown as the means ± SE ($N = 3$). Independent-sample *t*-tests were used to determine differences at: *P < 0.05; **P < 0.01; ***P < 0.001.

(Figure 3A), which is similar to findings in both submerged and unsubmerged terrestrial environments (Wei et al. 2022). Thus, the result indicated that aerenchyma formation is not responsible for the survival of *C. rotundus* mature tubers under soil-flooding conditions. Notably, significant changes were observed in the lignified sclerenchymal fibers on the epidermis of mature tubers during both the soil flooding and the recovery period (Figure 3B–E). The intensity of sclerenchymal fibers gradually increased by

https://doi.org/10.1017/wsc.2024.74 Published online by Cambridge University Press

Table 1. Plant growth parameters of *Cyperus rotundus* at 30 d after recovery treatments from soil flooding.[a]

Type of tuber	Treatment[b]	Plant height	Total fresh weight	Aboveground fresh weight	Belowground fresh weight	Root–shoot ratio	New tuber fresh weight	New tuber no.	Single-tuber growth rate
		cm	g				g		%
Mature tubers	CK	21.46 ± 0.75 a	24.11 ± 0.85 b	4.10 ± 0.37 a	20.01 ± 0.33 c	5.09 ± 0.40 b	1.11 ± 0.19 ab	20.00 ± 2.05 a	1.53 ± 0.17 b
	RSF-30	20.82 ± 0.45 a	29.01 ± 0.42 a	4.90 ± 0.08 a	24.11 ± 0.18 b	4.92 ± 0.06 b	1.56 ± 0.31 a	23.67 ± 0.27 a	2.73 ± 0.11 a
	RSF-60	16.35 ± 1.23 b	30.49 ± 1.04 a	4.85 ± 0.58 a	25.64 ± 0.62 a	5.70 ± 0.53 b	1.32 ± 0.19 a	19.67 ± 1.52 a	2.87 ± 0.32 a
	RSF-90	15.16 ± 0.25 b	21.11 ± 0.45 b	1.16 ± 0.14 b	19.95 ± 0.21 c	17.19 ± 1.96 a	0.27 ± 0.04 b	9.50 ± 1.44 b	0.07 ± 0.01 c
Growing tubers	CK	18.84 ± 1.67 a	6.88 ± 0.85 a	1.65 ± 0.29 a	5.23 ± 0.63 a	3.17 ± 0.38 b	0.18 ± 0.00 a	11.00 ± 0.71 a	2.50 ± 0.63 a
	RSF-30	8.62 ± 1.96 b	1.41 ± 0.25 b	0.07 ± 0.03 b	1.34 ± 0.23 b	19.14 ± 2.30 a	0.00 ± 0.00 b	0.00 ± 0.00 b	−2.96 ± 0.32 b
	RSF-60	0.00 ± 0.00 c	0.58 ± 0.17 c	0.00 ± 0.00 b	0.58 ± 0.17 b	—	0.00 ± 0.00 b	0.00 ± 0.00 b	−4.06 ± 0.27 c
	RSF-90	0.00 ± 0.00 c	0.34 ± 0.04 c	0.00 ± 0.00 b	0.34 ± 0.04 c	—	0.00 ± 0.00 b	0.00 ± 0.00 b	−4.44 ± 0.05 c

[a]Data are shown as the mean ± SD ($N \geq 3$). A different letter in the same column of mature or growing tubers represents a significant difference ($P < 0.05$, one-way ANOVA).
[b]Treatment: CK, no soil-flooding treatment; RSF-30, the removal of soil flooding at 30 d post-flooding; RSF-60, the removal of soil flooding at 60 d post-flooding; RSF-90, the removal of soil flooding at 90 d post-flooding.

approximately 60% at SF-60 and 400% at SF-90 (Figure 3D). During the subsequent recovery period, the intensity of sclerenchymal fibers of in the RSF-30 and RSF-60 treatments can return to the levels comparable to CK at the seedling stage. However, the RSF-90 treatment, despite showing some recovery, did not fully reach the CK level (Figure 3E). Lignin, a key component in sclerenchymal fiber formation (Novo-Uzal et al. 2012), exhibited similar alterations across treatments. Specifically, it significantly increased to 1.1 times that of CK after 90 d of soil flooding. Notably, the RSF-60 treatment facilitated lignin levels to recover to those of the CK during the seedling phase (Figure 3F and 3G). These results indicated that the regulation of lignified sclerenchymal fibers on the epidermis and the level of lignification in the tubers act as a barrier to protect the mature tubers of *C. rotundus* from flooding stress. This is consistent with previous studies indicating that lignified peripheral mechanical tissue in *C. rotundus* may enhance plant adaptation to flooding environments (Wei et al. 2022; Zheng et al. 2024).

We also determined the content of two signaling molecules associated with lignin, MDA and H_2O_2 (Veal and Day 2011), in mature tubers of *C. rotundus* during the soil flooding and recovery period. As the duration of soil flooding increased, both MDA and H_2O_2 contents in the mature tubers steadily rose, reaching 1.3 and 4.7 times the levels of CK by 90 d of soil flooding, respectively (Figure 4A and 4C). During the recovery period (RSF-30, RSF-60, and RSF-90), both MDA and H_2O_2 levels decreased, with a particularly rapid decline in H_2O_2 content, suggesting that cellular peroxidation and oxidation gradually diminished (Figure 4B and 4D). Although the H_2O_2 content did not return to the level as the same period of CK at the seedling stage of RSF-30 treatment (Figure 4D), the MDA content of mature tubers was restored to the CK level (Figure 4B). These results suggested that soil flooding can regulate the content of MDA and H_2O_2, affecting the degree of cellular peroxidation and oxidation. Additionally, MDA and H_2O_2 may act as molecular signals that collectively affect the level of lignification and the development of sclerenchymal fibers, contributing to the formation of protective barriers that shield mature tubers from flooding stress. This morphological adjustment represents a structural manifestation of flooding tolerance as well (Yang et al. 2013). Furthermore, identifying molecular signals such as MDA and H_2O_2 that trigger these morphological changes could offer new avenues for intervention. By manipulating these signaling pathways, it may be possible to inhibit the formation of protective structures in weeds, thereby reducing their survival and competitiveness under flooded conditions.

Responses of Nonstructural Carbohydrate in Mature Tubers under Soil Flooding

Carbohydrate reserves, critical energy sources for plants under flooding conditions, are often positively correlated with higher levels of flooding tolerance (Yuan et al. 2023). Under soil-flooding conditions, the soluble sugar content of nonstructural carbohydrates in mature tubers of *C. rotundus* dropped sharply in the initial stage, with only 51% of CK at SF-30, and subsequently maintained a steady rate at SF-60 and SF-90 (Figure 5A). Conversely, the starch content of mature tubers increased with prolonged soil flooding, surpassing CK levels by greater than 50% at SF-90 (Figure 5C). During the following recovery period, soluble sugar content at the seedling stage of RSF-30, RSF-60, and RSF-90 increased by greater than 120% compared with that of CK in the same period (Figure 5B). Starch content in mature tubers increased under the RSF-30 and RSF-60 treatments but decreased under RSF-90. In particular, the starch content at the sprouting and seedling

https://doi.org/10.1017/wsc.2024.74 Published online by Cambridge University Press

Table 2. Evaluation results of mature tubers of *Cyperus rotundus* at 30 d after recovery treatment from soil flooding.

Treatment[a]	PCA[b]		MFA[c]		Comprehensive ranking
	Rating value	Ranking	Rating value	Ranking	
CK	−0.047	3	0.552	3	3
RSF-30	0.059	2	0.894	2	2
RSF-60	0.104	1	0.940	1	1
RSF-90	−0.115	4	0.116	4	4

[a]Treatment: CK, no soil-flooding treatment; RSF-30, the removal of soil flooding at 30 d post-flooding; RSF-60, the removal of soil flooding at 60 d post-flooding; RSF-90, the removal of soil flooding at 90 d post-flooding.
[b]PCA, principal component analysis.
[c]MFA, membership function analysis.

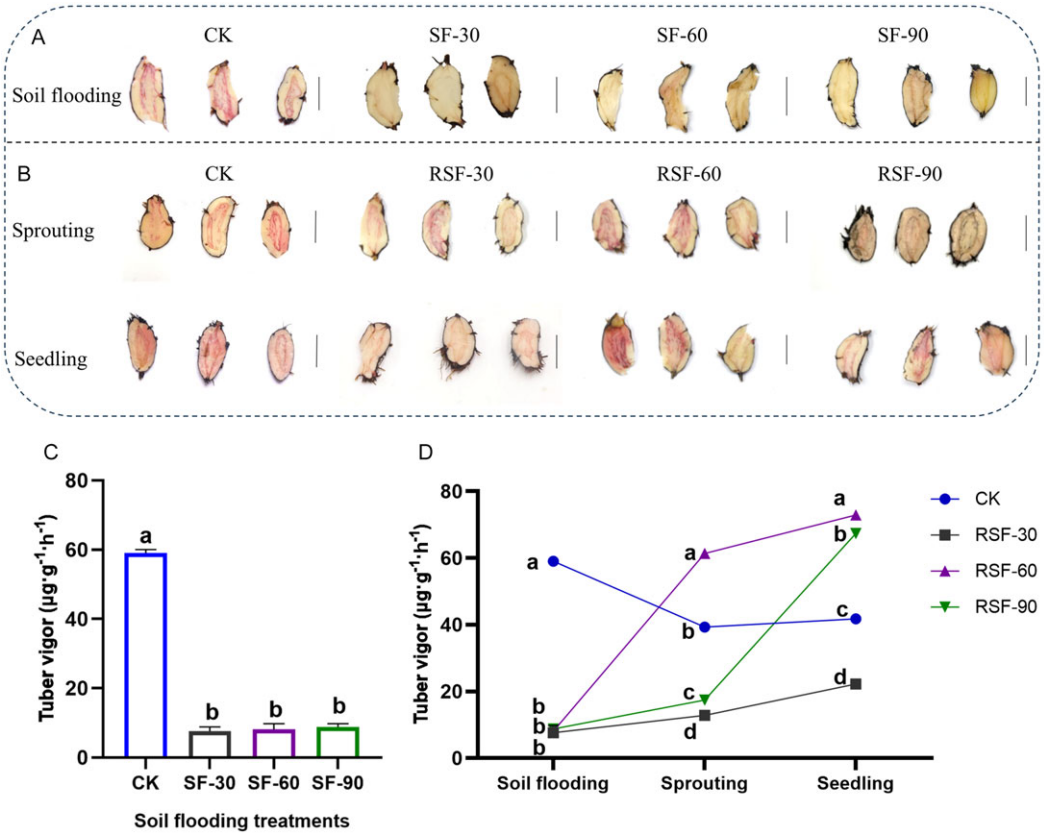

Figure 2. Vigor of mature tubers of *Cyperus rotundus* under soil flooding. (A) Staining chart of mature tubers under soil-flooding treatments. (B) Staining chart of mature tubers at the sprouting and seedling stages of recovery treatments. (C) Changes in tuber vigor of mature tubers under soil-flooding treatments; different letters above bars indicate significant differences ($P < 0.05$, one-way ANOVA). (D) Changes in vigor of mature tubers after recovery treatments; different letters in each column indicate significant differences ($P < 0.05$, one-way ANOVA). Values are means ± SE ($N = 3$). Abbreviations: CK, no soil-flooding treatment; SF-30, soil flooding for 30 d; SF-60, soil flooding for 60 d; SF-90, soil flooding for 90 d; RSF-30, the removal of soil flooding at 30 d post-flooding; RSF-60, the removal of soil flooding at 60 d post-flooding; RSF-90, the removal of soil flooding at 90 d post-flooding.

stages of RSF-60 returned to CK levels (Figure 5D). These results indicated that nonstructural carbohydrates of mature tubers were altered and remobilized by the soil-flooding environment. Similar to the strategy employed by *Sub1A* rice, which remains stunted to conserve energy during flash flooding at the seedling stage (Nagai et al. 2010), these mature tubers conserved energy during flooding and reactivated growth post-flooding, ensuring their survival and subsequent development.

Respiratory Responses in Mature Tubers under Soil Flooding

Fermentation serves as a crucial energy-generating mechanism in soil-flooding conditions (Tadege et al. 1999), primarily through the action of two key enzymes—ADH and LDH, which reflect plants' adaptability to such low-oxygen conditions. Under soil-flooding conditions, the ethanol content and ADH activity in mature tubers of *C. rotundus* both increased with the duration of flooding. By SF-90, they were approximately 5 times and 2 times higher than that in CK, respectively (Figure 6A and 6C). Notably, the ethanol content of mature tubers returned to or fell below the level of the same period of CK at the sprouting and seedling stages of RSF-30, respectively (Figure 6B). The ADH activity of mature tubers also declined at the seedling stage after RSF-30, RSF-60, and RSF-90 compared with SF-30, SF-60, and SF-90 (Figure 6D). While LDH activity varied across different soil-flooding time treatments (Figure 6G), lactic acid content did not show significant changes

https://doi.org/10.1017/wsc.2024.74 Published online by Cambridge University Press

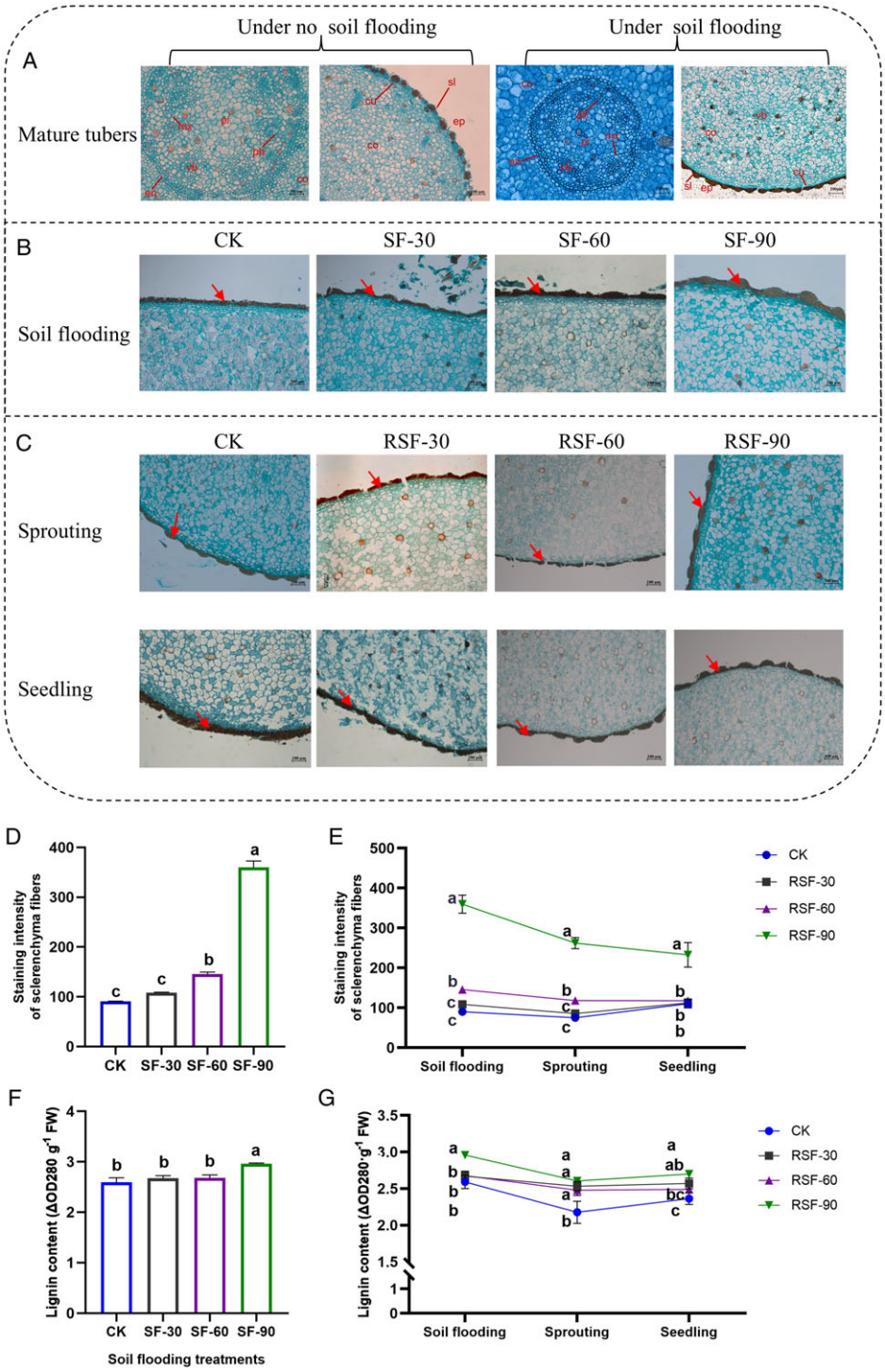

Figure 3. Responses of morphological traits of mature tubers of *Cyperus rotundus* under soil flooding. (A) Anatomical structure of the inner structure of tubers under no soil flooding and under soil flooding. Abbreviations: co, cortex; cu, cuticle; en, endodermis; ep, epidermis; sl, sclerenchymal fibers; mx, metaxylem; ph, phloem; pi, pith; vb, vascular bundles. (B) Photograph of changes in sclerenchymal fibers in mature tubers under soil-flooding treatments. (C) Photograph of changes in sclerenchymal fibers in mature tubers at the sprouting and seedling stages after the recovery treatments. The red arrows represent sclerenchymal fibers. Staining: saffron and solid green. (D) Changes in staining density of sclerenchymal fibers in mature tubers under soil-flooding treatments. (E) Changes in staining density of sclerenchymal fibers of mature tubers after recovery treatments. (F) Changes in lignin content in mature tubers under soil-flooding treatments. (G) Changes in lignin content in mature tubers after recovery treatments. Values are means ± SE ($N = 3$). (D and F) Different letters above bars indicate significant differences ($P < 0.05$, one-way ANOVA). (E and F) Different letters in each column indicate significant differences ($P < 0.05$, one-way ANOVA). Abbreviations: CK, no soil-flooding treatment; SF-30, soil flooding for 30 d; SF-60, soil flooding for 60 d; SF-90, soil flooding for 90 d; RSF-30, the removal of soil flooding at 30 d post-flooding; RSF-60, the removal of soil flooding at 60 d post-flooding; RSF-90, the removal of soil flooding at 90 d post-flooding.

https://doi.org/10.1017/wsc.2024.74 Published online by Cambridge University Press

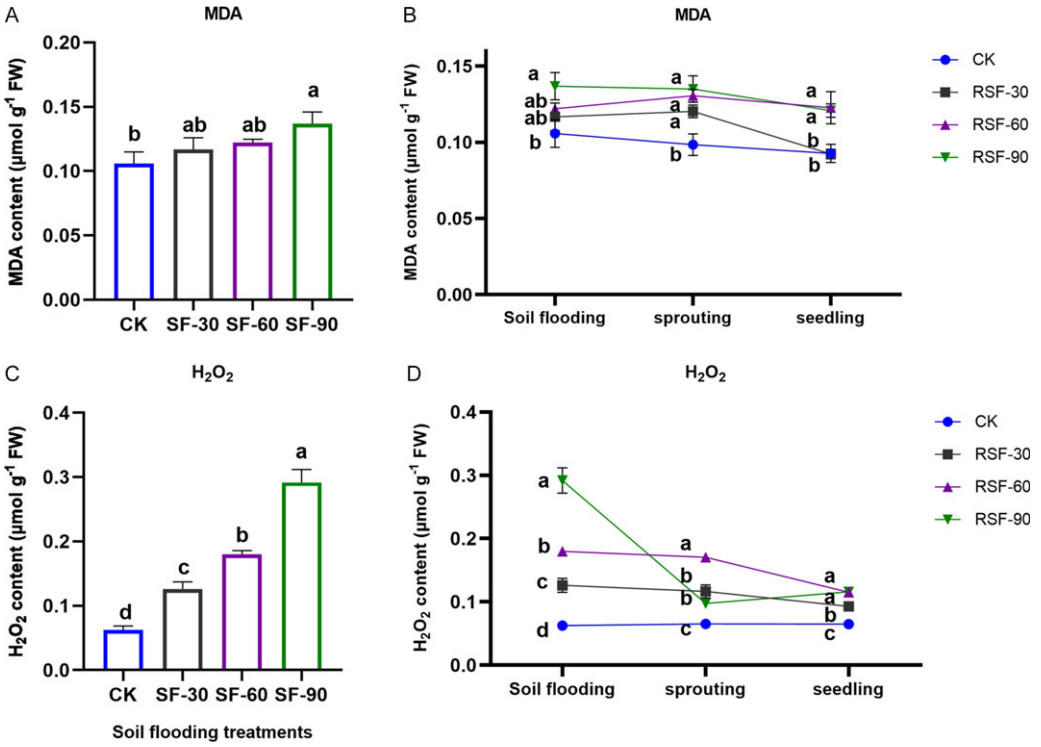

Figure 4. Responses of malondialdehyde (MDA) and hydrogen peroxide (H_2O_2) of mature tubers of *Cyperus rotundus* under soil flooding. Changes in MDA content of mature tubers under soil-flooding treatments (A) and after recovery treatments (B). Changes in H_2O_2 content of mature tubers under soil-flooding treatments (C) and after recovery treatments (D). Values are means ± SE ($N = 3$). (A and C) Different letters above bars indicate significant differences ($P < 0.05$, one-way ANOVA). (B and D) Different letters in each column indicate significant differences ($P < 0.05$, one-way ANOVA). Abbreviations: CK, no soil-flooding treatment; SF-30, soil flooding for 30 d; SF-60, soil flooding for 60 d; SF-90, soil flooding for 90 d; RSF-30, the removal of soil flooding at 30 d post-flooding; RSF-60, the removal of soil flooding at 60 d post-flooding; RSF-90, the removal of soil flooding at 90 d post-flooding.

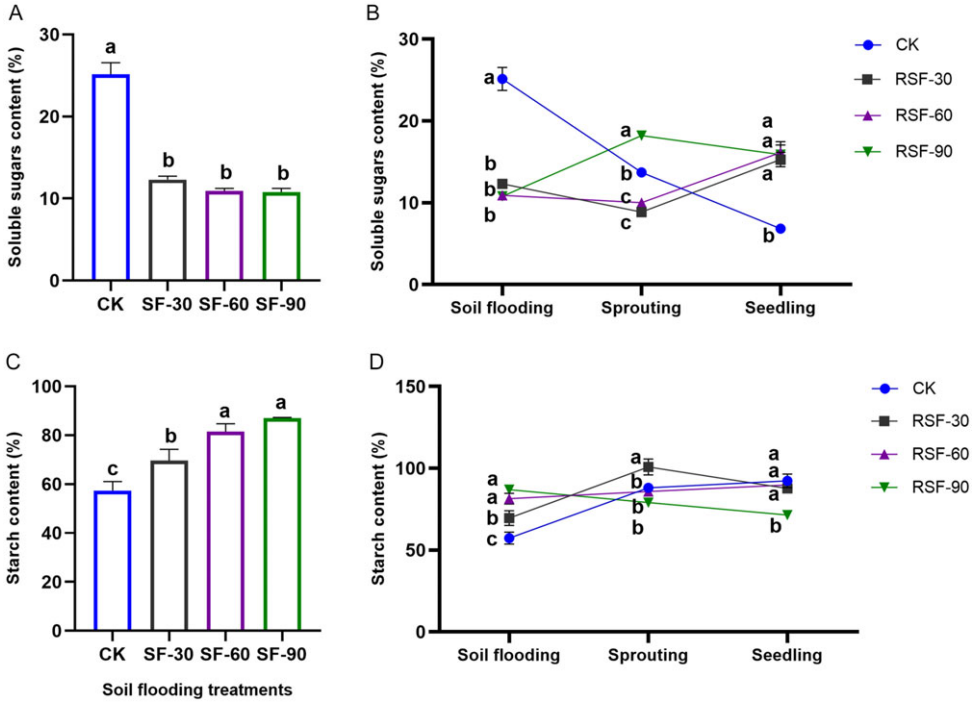

Figure 5. Responses of nonstructural carbohydrate of mature tubers of *Cyperus rotundus* under soil flooding. Changes in soluble sugar content of mature tubers under soil-flooding treatments (A) and after recovery treatments (B). Changes in starch content of mature tubers under soil-flooding treatments (C) and after recovery treatments (D). Values are means ± SE ($N = 3$). (A and C) Different letters above bars indicate significant differences ($P < 0.05$, one-way ANOVA). (B and D) Different letters in each column indicate significant differences ($P < 0.05$, one-way ANOVA). Abbreviations: CK, no soil-flooding treatment; SF-30, soil flooding for 30 d; SF-60, soil flooding for 60 d; SF-90, soil flooding for 90 d; RSF-30, the removal of soil flooding at 30 d post-flooding; RSF-60, the removal of soil flooding at 60 d post-flooding; RSF-90, the removal of soil flooding at 90 d post-flooding.

https://doi.org/10.1017/wsc.2024.74 Published online by Cambridge University Press

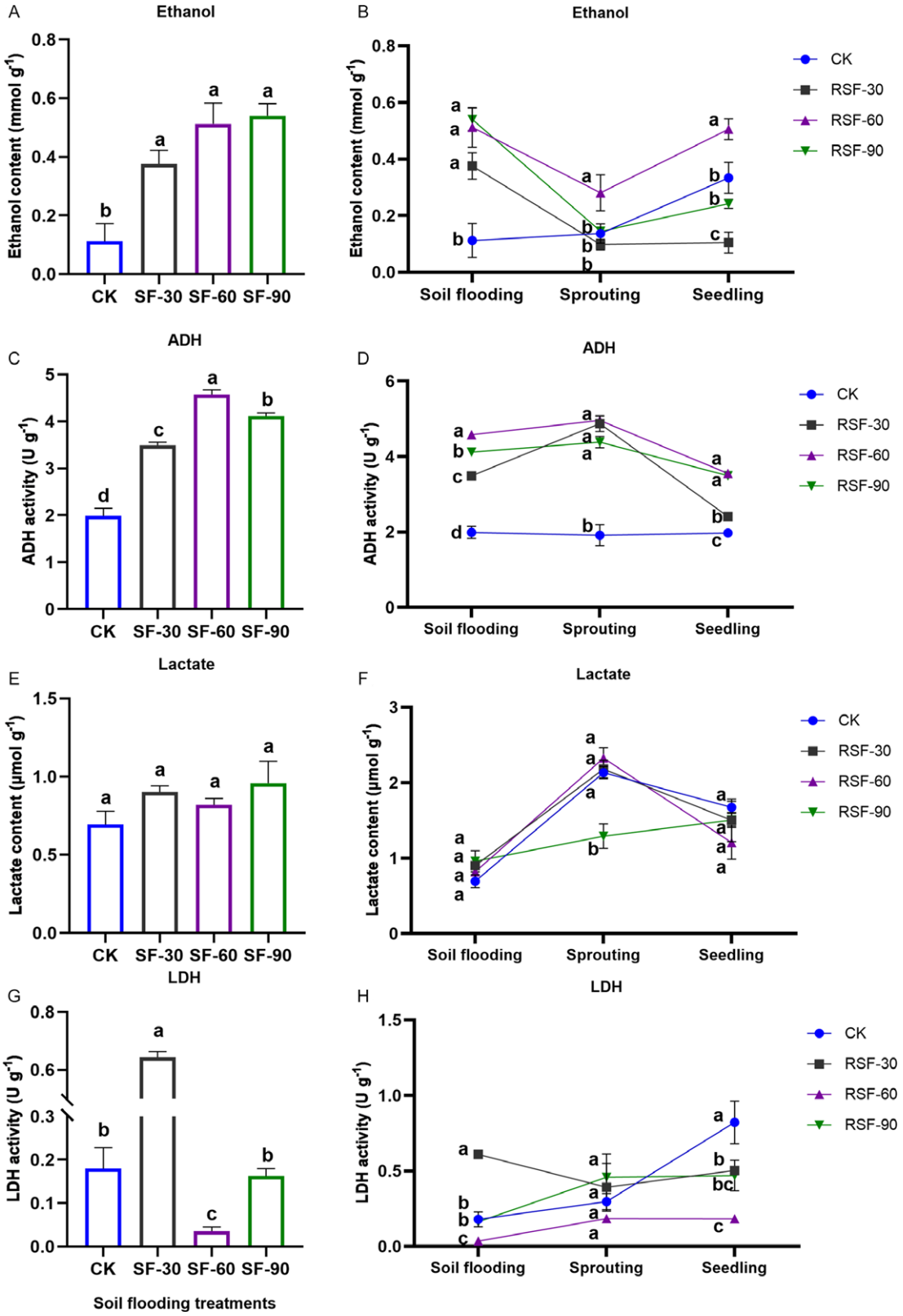

Figure 6. Respiratory response of mature tubers of *Cyperus rotundus* under soil flooding. Changes in ethanol content of mature tubers under soil-flooding treatments (A) and after recovery treatments (B). Changes in alcohol dehydrogenase (ADH) activity of mature tubers under soil-flooding treatments (C) and after recovery treatments (D). Changes in lactic acid content of mature tubers under soil-flooding treatments (E) and after recovery treatments (F). Changes in lactate dehydrogenase (LDH) activity of mature tubers under soil-flooding treatments (G) and after recovery treatments (H). Values are means ± SE ($N = 3$). (A, C, E and G) Different letters above bars indicate significant differences ($P < 0.05$, one-way ANOVA). (B, D, F, and H) Different letters in each column indicate significant differences ($P < 0.05$, one-way ANOVA). Abbreviations: CK, no soil-flooding treatment; SF-30, soil flooding for 30 d; SF-60, soil flooding for 60 d; SF-90, soil flooding for 90 d; RSF-30, the removal of soil flooding at 30 d post-flooding; RSF-60, the removal of soil flooding at 60 d post-flooding; RSF-90, the removal of soil flooding at 90 d post-flooding.

https://doi.org/10.1017/wsc.2024.74 Published online by Cambridge University Press

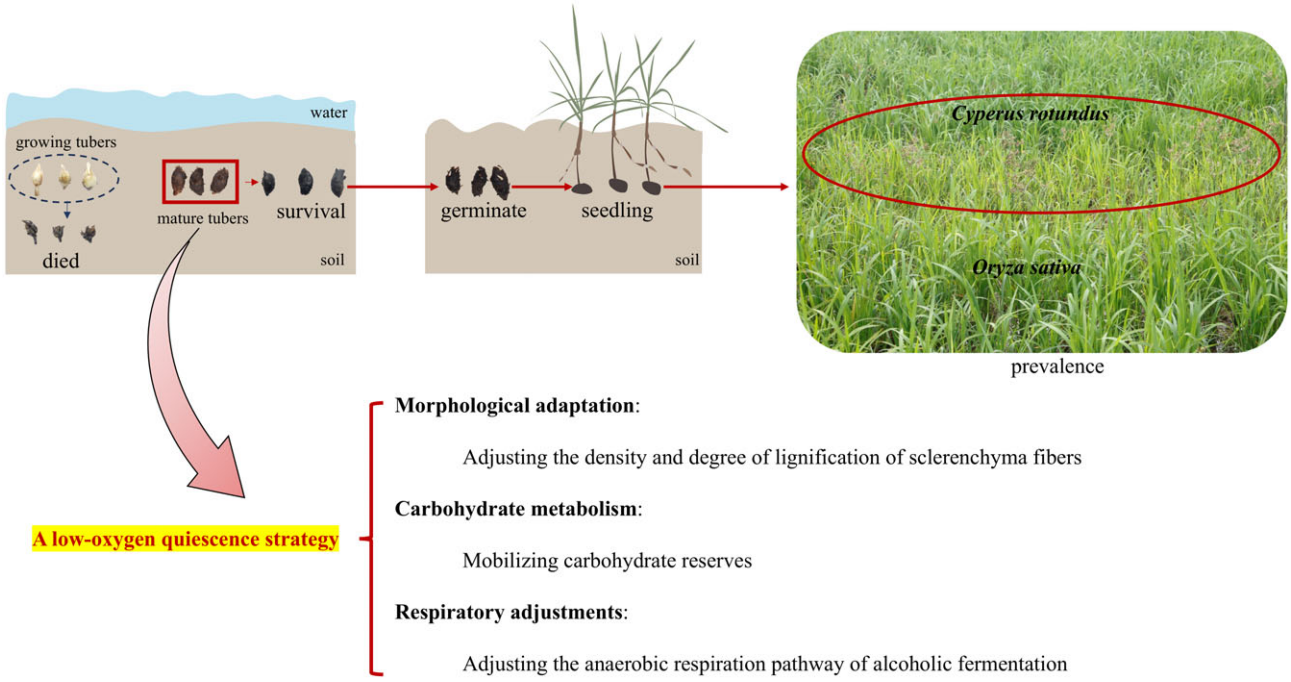

Figure 7. Mature tubers of *Cyperus rotundus* from the upland are tolerant to soil flooding through adoption of a low-oxygen quiescence strategy, thus explaining the emergence of *Cyperus rotundus* from the upland in rice fields.

($P = 0.078$; Figure 6E). During recovery, lactate content and LDH activity in mature tubers showed an increase compared with the soil-flooding treatment, except in the RSF-30 treatment. However, these levels remained either equal to or notably lower than those observed in the sprouting and the seedling stages of RSF-30 and RSF-60 relative to CK (Figure 6F and 6H). Moreover, LDH activity was consistently lower than ADH activity across treatments, suggesting that alcohol fermentation is the primary anaerobic respiratory pathway. These results indicated that mature tubers of *C. rotundus* enhance their resilience to soil flooding by upregulating the alcohol fermentation pathway, allowing them to resume growth once the flooding subsides and reducing the accumulation of toxic substances. Similar findings were reported for lowland ecotypes of *C. rotundus* by Fuentes and Peña-Fronteras and colleagues (Peña-Fronteras et al. 2009; Fuentes et al. 2010), and for *Distylium chinense* by Sun et al. (2020). Both showed a relatively modest ethanol fermentation energy yield for flooding tolerance. This metabolic adaptation thus emerges as a critical flooding-tolerance mechanism.

Our findings, combined with previous research, suggest that mature tubers of *C. rotundus* can endure soil-flooding conditions. This tolerance may be attributed to the mature tuber's adoption of a low-oxygen quiescence strategy (Figure 7), characterized by three primary adaptations. (1) Morphological adaptations: mature tubers developed lignified sclerenchymal fibers, which subsequently accumulated lignin content and acted as a protective barrier; (2) Carbohydrate metabolism: mature tubers conserved energy by reducing the utilization of soluble sugars and increasing starch reserves for energy storage. (3) Respiratory adjustments: mature tubers heightened ADH activity to strengthen the anaerobic respiration pathway of alcoholic fermentation, thus alleviating the energy crisis imposed by flooding to some degree.

Cyperus rotundus primarily affects regions with temperate and tropical monsoon climates, which are also the main rice-cultivating areas. Changes in cultivation practices, such as converting upland fields to paddy fields or implementing paddy–upland rotations, can leave a significant number of *C. rotundus* tubers behind. These tubers have the potential to serve as seedbanks for the proliferation of *C. rotundus* during rice production. Given the water management measures of actual rice cultivation fields (Zhang 2021), it is common for the water layer to be absent at the end of the tillering and yellow ripening stage, which provides favorable environmental conditions for germination and growth of mature tubers. Further, during this period, mature tubers can germinate rapidly and grow in the paddy field through enhanced consumption of soluble sugars, weakened alcoholic fermentation, and reduced levels of lignification (Figure 7). Once *C. rotundus* plants grow above the water surface, they can ensure high photosynthetic productivity and utilize the ability of clonal integration to co-resist flooding adversity, thereby expanding their reproduction (Zhang et al. 2010).

In conclusion, this study revealed that mature tubers from the upland are tolerant to soil flooding through adoption of a low-oxygen quiescence strategy. This finding not only sheds light on how *C. rotundus* from the upland emerges in rice fields and becomes a noxious rice weed but also opens new avenues for future research. Specifically, further exploration of the genetic basis of flood tolerance in *C. rotundus* tubers could offer valuable insights for the development of flood-resistant crop varieties. Understanding how these mechanisms can be harnessed or mitigated could have significant implications for weed management in rice fields and the improvement of agricultural practices.

Funding statement. This research was funded by the Six Special Actions of the Vanguard of Science and Technology to Strengthen Agriculture and Enrich the People (no. GKM202416), the Innovation Project of Guangxi Graduate Education (no. YCBZ2023027), and the Guangxi Natural Science Foundation (no. 2021GXNSFAA220098).

Competing interests. The authors declare no competing interests.

https://doi.org/10.1017/wsc.2024.74 Published online by Cambridge University Press

References

Akman M, Bhikharie AV, McLean EH, Boonman A, Visser EJ, Schranz ME, van Tienderen PH (2012) Wait or escape? Contrasting submergence tolerance strategies of *Rorippa amphibia*, *Rorippa sylvestris* and their hybrid. Ann Bot 109:1263–1275

Bailey-Serres J, Voesenek LACJ (2008) Flooding stress: acclimations and genetic diversity. Annu Rev Plant Biol 59:313–339

Baltazar AM, Martin EC, Casimero MC, Bariuan FV, Obien SR, De Datta SK (1999a) Major weeds and dominance patterns in rainfed rice-onion cropping system. Philipp Agric Sci 82:166–177

Baltazar AM, Martin EC, Casimero MC, Bariuan FV, Obien SR, De Datta SK (1999b) Major Weeds in Rainfed Rice-Onion Cropping Systems in the Asian Site in the Philippines. IPM CRSP Working Paper 98-1. Blacksburg, VA: IPM CRSP, Office of International Development. 24 p

Carbonell PU, Moody K (1983) Weed control practices in irrigated and rainfed rice farms in Nueva Ecija, Philippines. Philippine Agriculturist (Philippines) 66:458–469

Chapagain T, Riseman A, Yamaji E (2011) Achieving more with less water: alternate wet and dry irrigation (AWDI) as an alternative to the conventional water management practices in rice farming. J Agric Sci 3:3–13

Cheng K, Du H, Ouyang Y (2018) Paraffin embedding rice tissues and sectioning. BioProtoc, 10.21769/BioProtoc.1010140

Donayre DKM, Jimenez JJL, Latonio AMLS, Martin EC, Chauhan BS (2022) Lowland ecotype *Cyperus rotundus* L. affects growth and yield of rice under flooded conditions in the Philippines. Philipp J Sci 151:1087–1097.

Donayre DKM, Martin EC, Casimero MC, Juliano LM, Beltran JC (2015) Prevalence of lowland ecotype *Cyperus rotundus* L. and weed management of rice farmers in Aliaga, Nueva Ecija, Philippines. IAMURE Int J Ecol Conserv 13:14–28

Du L, Li X, Chen J, Jiang X, Ju Q, Qu C, Qu M (2019) Density effect and economic threshold of purple nutsedge (*Cyperus rotundus* L.) in peanut (*Arachis hypogaea* L.). Int J Plant Prod 13:309–316

Durigan JC (2005) Effects of plant densities and management of purple nutsedge on sugarcane yield and effect of growth stages and main way of herbicides contact and absorption on the control of tubers. J Environ Sci Health B 40:111–117

Evans DE (2003) Aerenchyma formation. New Phytol 161:35–49

Fuentes RG, Baltazar AM, Merca FE, Ismail AM, Johnson DE (2010) Morphological and physiological responses of lowland purple nutsedge (*Cyperus rotundus* L.) to flooding. AoB Plants 2010:plq010

Gonzalez J, Garcia E, Perdomo M (1983) Important rice weeds in Latin America. Pages 119–132 *in* Proceedings of the Conference on Weed Control in Rice, International Rice Research Institute and International Weed Science Society. Manila, OR: International Rice Research Institute

Hattori Y, Nagai K, Ashikari M (2011) Rice growth adapting to deepwater. Curr Opin Plant Biol 14:100–105

Kraehmer H, Jabran K, Mennan H, Chauhan BS (2016) Global distribution of rice weeds—a review. Crop Prot 80:73–86

Li D, Nanseki T, Chomei Y, Yokota S (2018) Production efficiency and effect of water management on rice yield in Japan: two-stage DEA model on 110 paddy fields of a large-scale farm. Paddy Water Environ 16:643–654

Lin H, Xiong J, Zhou H, Chen C, Lin F, Xu X, Oelmüller R, Xu W, Yeh K (2019) Growth promotion and disease resistance induced in *Anthurium* colonized by the beneficial root endophyte *Piriformospora indica*. BMC Plant Biol 19:1–10

Liu C (2018) Preliminary Study on the Mechanism of Promoting Wound Cupping of Yam Tuber Treated by Temperature and Chemical Agent. Master's thesis. Hubei: Huazhong Agricultural University. 66 p

Liu S (2022) Evaluation of the Fecundity of *Cyperus rotundus* L. and Its Effect in Maize Rhizosphere Soil Bacteria. Master's thesis. Guangxi: Guangxi University. 85 p

Luo F, Nagel KA, Scharr H, Zeng B, Schurr U, Matsubara S (2011) Recovery dynamics of growth, photosynthesis and carbohydrate accumulation after de-submergence: a comparison between two wetland plants showing escape and quiescence strategies. Ann Bot 107:49–63

Nagai K, Hattori Y, Ashikari M (2010) Stunt or elongate? Two opposite strategies by which rice adapts to floods. J Plant Res 123:303–309

Nakamura M, Noguchi K (2020) Tolerant mechanisms to O_2 deficiency under submergence conditions in plants. J Plant Res 133:343–371

Novo-Uzal E, Pomar F, Gómez Ros LV, Espiñeira JM, Ros Barceló AR (2012) Evolutionary history of lignins. Adv Bot Res 61:311–350

Peerzada AM (2017) Biology, agricultural impact, and management of *Cyperus rotundus* L.: the world's most tenacious weed. Acta Physiol Plant 39:270

Peña-Fronteras JT, Villalobos MC, Baltazar AM, Merca FE, Ismail AM, Johnson DE (2009) Adaptation to flooding in upland and lowland ecotypes of *Cyperus rotundus,* a troublesome sedge weed of rice: tuber morphology and carbohydrate metabolism. Ann Bot 103:295–302

Quayyum HA, Mallik AU, Leach DM, Gottardo C (2000) Growth inhibitory effects of nutgrass (*Cyperus rotundus*) on rice (*Oryza sativa*) seedlings. J Chem Ecol 26:2221–2231

Rabbani N, Baiwa R (2001) Weeds distribution in rice fields of 5 districts of Punjab. Pak J Bot 33:94–102

Salgado TP, Alves P, Rossi CVS (2002) Effect of purple nutsedge (*Cyperus rotundus*) tuber density on the initial growth of cotton plants. Planta Daninha 20:405–411

Silva DV, Freitas MAMD, Silva GSD, Souza MDF, Silva AAD, Ferreira LR, Sediyama T, Cecon PR (2015) Growth and yield of maize in purple nutsedge interference. Semina: Cienc Agrar 36:3077–3084

Silveira Filho A, De Aquino ARL (1983) Weed control and rice production in Brazil. Pages 133–138 *in* Proceedings of the Conference on Weed Control in Rice, Philippines, International Rice Research Institute. Manila, OR: International Rice Research Institute

Sun L, Li X, Wang X, Xiang L, Yang J, Min Q, Chen G, Chen F, Huang C, Wang G (2020) Growth and respiratory metabolic adaptation strategies of riparian plant *Distylium chinense* to submergence by the field study and controlled experiments. Plant Physiol Biochem 157:1–12

Tadege M, Dupuis I, Kuhlemeier C (1999) Ethanolic fermentation: new functions for an old pathway. Trends Plant Sci 4:320–325

Tuor FA, Froud-Williams RJ (2002) Interaction between purple nutsedge, maize and soybean. Int J Pest Manag 48:65–71

Veal E, Day A (2011) Hydrogen peroxide as a signaling molecule. Antioxid Redox Signal 15:147–151

Voesenek LACJ, Baily-Serres J (2015) Flood adaptive traits and processes: an overview. New Phytol 206:57–73

Wei H, Deng W, Zheng H, Zhou C, Liu Z, Yang C, Zhang X, Tan D (2022) Anatomical and histochemical structures of *Cyperus rotundus* L. facilitate success in amphibious environments. Flora 295:152150

Wu Y, Sun M, Zhang J, Zhang L, Ren Z, Min R, Wang X, Xia Y (2019) Differential effects of paclobutrazol on the bulblet growth of oriental lily cultured in vitro: growth behavior, carbohydrate metabolism, and antioxidant capacity. J Plant Growth Regul 38:359–372

Yan X (2017) Study on the Dormancy Characteristics of Different Potatoes. Master's thesis. Shannxi: Northwest A&F University. 57 p

Yang C, Zhang X, Liu G, Bao M, Zhou Z (2013) Progress on the structure and physiological functions of apoplastic barriers in root. Bull Bot Res 33:114–119

Yiu J, Juang L, Fang DY, Liu C, Wu S (2009) Exogenous putrescine reduces flooding-induced oxidative damage by increasing the antioxidant properties of Welsh onion. Sci Hortic 120:306–314

Yu J, Zhang G, Zhu A, Zhang X, Wang H, Zhao L, Yao K, Lou Y, Shu Z (2022) Chemical technology of the weed control in dry direct-seeded rice fields in Jiangsu hilly area. J Weed Sci 40:34–41

Yu X, Luo N, Yan J, Tang J, Liu S, Jiang Y (2012) Differential growth response and carbohydrate metabolism of global collection of perennial ryegrass accessions to submergence and recovery following de-submergence. J Plant Physiol 169:1040–1049

Yuan LB, Chen MX, Wang LN, Sasidharan R, Voesenek LACJ, Xiao S (2023) Multi-stress resilience in plants recovering from submergence. Plant Biotechnol J 21:466–481

https://doi.org/10.1017/wsc.2024.74 Published online by Cambridge University Press

Zhang X (2021) Effects of Different Irrigation Models on Rice Growth and Gas Emissions. Master's thesis. Heilongjiang: Northeast Agricultural University. 85 p

Zhang X, Fan D, Xie Z, Xiong G, Li Z (2010) Clonal integration enhances performance of *Cynodon dactylon* subjected to submergence. Chin J Plant Ecol 34:1075–1083

Zheng H, Wang Y, Xu J, Zhu T, Qin G, Zhou C, Yang C, Tan D, Zhang X, Wei H (2024) Anatomical and histochemical features of amphibious *Cyperus rotundus*. Acta Prataculturae Sin 33:155–164

Zhu H, He X, Wang X, Long P (2024) Increasing hybrid rice yield, water productivity, and nitrogen use efficiency: optimization strategies for irrigation and fertilizer management. Plants 13:1717

https://doi.org/10.1017/wsc.2024.74 Published online by Cambridge University Press