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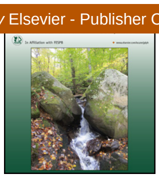

Short communication

Mixed cropping has the potential to enhance flood tolerance of drought-adapted grain crops

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Abbreviations:
ANOVA, analysis of variance
RGR, relative growth rate
ROL, radial oxygen loss

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ABSTRACT

Recently, the occurrences of extreme flooding and drought, often in the same areas, have increased due to climate change. Wetland plant species are known to oxygenate their rhizospheres by releasing oxygen (O_2) from their roots. We tested the hypothesis that wetland species could help upland species under flood conditions; that is, O_2 released from the wetland crop roots would ameliorate rhizosphere O_2-deficient stress and hence facilitate upland crop root function. Flooding tolerance of upland-adapted staple crops—pearl millet (*Pennisetum glaucum*) and sorghum (*Sorghum bicolor*) mix-cropped with rice (*Oryza* spp.) was investigated in glasshouse and laboratory. We found a phenomenon that strengthens the flood tolerance of upland crops when two species—one wetland and one drought tolerant—were grown using the mixed cropping technique that results in close tangling of their root systems. This technique improved the photosynthetic and transpiration rates of upland crops subjected to flood stress (O_2-deficient nutrient culture). Shoot relative growth rates during the flooding period (24 days) tended to be higher under mixed cropping compared with single cropping. Radial oxygen loss from the wetland crop roots might be contributed to the phenomenon observed. Mixed cropping of wet and dryland crops is a new concept that has the potential to overcome flood stress under variable environmental conditions.

1. Introduction

Various grain food crops adapted to environments with different water availability are used worldwide to provide food for humans (and animals). For example, pearl millet and sorghum have been used since ancient times because they are dryland-adapted food crops with high yield potential even under limited rainfall conditions (Rachie and Majmudar, 1980). They are the most widely cultivated grain crops in the semi-arid regions of Asia and Africa. More specifically, they are the major food crops in the Sahel of Africa, which account for more than 70% of all cereals grown in that region (Bhattacharjee et al., 2011). Although pearl millet is one of the most drought-resistant food crops, it is extremely susceptible to conditions caused by waterlogged soil (Zegada-Lizarazu and Iijima, 2005). Daily rainfall intensity and dry-spell duration have significantly increased in South and West African countries during 1961–2000 (New et al., 2006). The latest Intergovernmental Panel on Climate Change (IPCC) report also indicated that extreme precipitation events such as droughts and heavy rainfall have become more frequent throughout eastern Africa during the last 30–60 years (Lyon and DeWitt, 2012; Niang et al., 2014). Moreover, in case of southwest African country of Namibia, they have received to three episodes of substantial flooding (Mendelsohn et al., 2013) and two episodes of severe drought in the north central densely populated region since 2008. This has caused substantial loss of pearl millet production. Food shortages caused by flooding have become common in the semi-arid African regions in the recent years (Bhattacharjee et al., 2011; Newsham and Thomas, 2011).

Rice, the only flood-adapted major cereal, sequentially forms air channels in its root cortex (called aerenchyma) during root growth, and oxygen (O_2) is continuously supplied via the aerenchyma from the shoot to the root apical meristem when the soil is submerged in water. A barrier to radial oxygen loss (ROL) at the root surface helps in providing O_2 to the root apex, but this barrier will not be developed in the newly formed, young meristem regions.

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Therefore, O_2 is released into the rhizosphere near the root tips (Armstrong, 1979; Colmer, 2003; Yamauchi et al., 2013). Upland cereal species adapted to dry environments also form continuous channels for O_2 transport in their cortex tissues, but the amount of gas space is mostly much less than in wetland species (Armstrong, 1979; Justin and Armstrong, 1987), and as a result, their roots may not survive for long in flooded soil. If the O_2 released from the rice root tips can ameliorate rhizosphere O_2 deficiency stress for companion drought-adapted upland grain crops, flood-stressed grain production may become possible in drought-prone areas.

Major grain crops are occasionally mix-cropped with other species for risk management (Wolfe, 2000; Brooker et al., 2014). Mixed cropping of cereals and legumes is a commonly practiced cultivation technique worldwide because of the complementary effects for cereals, which benefit from utilizing the nitrogen that is biologically fixed by the legumes (Ehrmann and Ritz, 2014). Mixed cropping of wet- and dryland-adapted species may overcome the limitations imposed by both flood and drought conditions; Although similar combination has already been discussed before {For example, Setter and Belford (1990)}, there is no experimental evidence for this concept so far. In this study, we tested the hypothesis that wetland species could help upland species under O_2-deficient conditions.

2. Materials and methods

2.1. Plant materials

Pearl millet (*Pennisetum glaucum* cv. Okashana 2) and sorghum (*Sorghum bicolor* cv. Macia), which are adapted for drought-prone semi-arid environments, were used as the upland crops (hereinafter called 'millets'). These are recommended crop cultivars widely grown in semi-arid southern African countries, as drought-tolerant crops. Rice (*Oryza sativa* cv. Nipponbare and interspecies of *O. sativa* and *Oryza glaberrima* cv. NERICA4) was used as the flood-tolerant crop. Nipponbare is extensively used as an experimental material in Japan. NERICA4 is an upland cultivar being promoted in West African countries such as Benin, Guinea, and Mali for cultivation.

2.2. Pre-germination

Seeds were surface-sterilised with 2.5% (v/v) sodium hypochlorite for 5 min and rinsed in running water for 20 min. Rice seeds were soaked in distilled water, whereas the pearl millet and sorghum seeds were sown on paper towels in Petri dishes. The seeds were pre-germinated in a dark incubator at 30 °C for 14, 24, and 48 h for pearl millet, sorghum, and rice, respectively.

2.3. Seedling establishment

Pre-germinated seeds were sown in a growing medium (Metro-Mix 250 Series; peat moss 43–47%, vermiculite 41–45%, bark ash 3–7%, pearlite 5–9%; N, P_2O_5, K_2O = 60, 70, 100 mg L^{-1}; Sun GRO® Horticulture, USA) in cell trays. One (single-species crop) or two (mixed cropping rice and upland crop) seeds were planted per cell (37 mm long × 37 mm wide × 46 mm deep, with a 5-mm diameter hole at the bottom). The cells were placed on plastic trays and maintained in 3–5-mm deep water. The seedlings were grown in a plant-growth room having 28/23 °C day/night temperature, 14-h photoperiod, and 318 ± 2 μmol m^{-2} s^{-1} photosynthetically active radiation above the leaf canopy. Seeds of millets were relay-planted into the same cell compartments containing the rice seedlings at 1 week after the rice seeds were sown. A week later (14 days after sowing the rice seeds), the seedlings used in Exp. 1, were transferred to a natural sunlight glasshouse with lighting supplemented by metal halide lamps to extend the photoperiod to 14 h. The temperature was controlled within 25–30 °C by using a gas heating system and automatic roof and window opening system. The cell trays containing the seedlings were cut into individual cell compartments, and then placed on plastic disposal dishes (80 × 80 × 25 mm, length × width × height) to allow the mixed-seedlings to form entangled root mats as shown in Fig. 1. The mixed-seedlings were grown for 3 weeks on hydroponic boxes containing 30 L (maximum depth, 15 mm) of Hoagland solution (Hoagland and Arnon, 1950) circulated at about 2.4 L min^{-1} for continuous O_2 supply. The nutrient solution was at quarter, half, and full strength concentrations during the first, second, and third weeks, respectively. Light penetration to the root mats was prevented by covering the cell trays with grey plastic mulch leaving the plant shoots exposed. The culture was renewed every 3–4 days, and the pH was adjusted and maintained at 6.5 during nursery and subsequent experimental periods. The photosynthetically active radiation in early morning and late afternoon, and midday was 142–464 and 386–947 μmol m^{-2} s^{-1}, respectively.

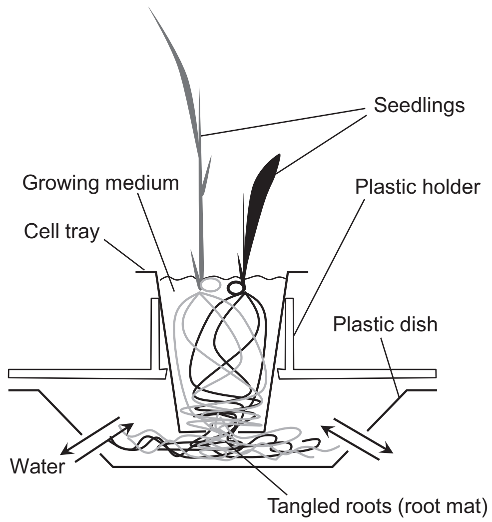

Fig. 1. Schematic diagram of the mixed-seedling system to enhance the intertwining of the roots of the two species (Exp.1). Pre-germinated seeds of pearl millet or sorghum were relay-planted into the same cell compartments containing the rice seedlings at 1 week after the rice seeds were sown. Fourteen days after sowing the rice seeds, all cell trays containing the seedlings were cut into individual cell compartments, which were placed on plastic dishes, the seedlings were then grown further under hydroponic nutrient culture to form entangled root mats.

2.4. Physiological response of the mixed-seedlings under O_2-deficient nutrient culture (Exp. 1)

The effects of an O_2-deficient root environment on the physiological status of the mixed-seedlings were investigated in glasshouse experiments. This experiment was conducted at Kinki University, Japan (34° 40′ N, 135° 44′ E, 172 m ALT), which is located in a temperate climate zone. Four-week-old millet and 5-week-old rice seedlings were transplanted into plastic boxes filled with either air-bubbled (control) or N_2-bubbled (flooded/hypoxic) Hoagland solution (40 L) at full strength and grown for 24 days. The shoots of the mixed-seedlings were fixed into holes drilled through floating Styrofoam platforms fitted in each box. Diffusion of atmospheric gases into the culture medium was minimised by sealing the spaces between the platform and the box and around the planting holes. Hypoxic condition (6 ± 0.2 μM O_2), defined as "flood stress", was induced by daily bubbling of the culture solution with N_2 gas flowing at 6 L min^{-1} for 20 min, whereas air-bubbling was done continuously for the control treatment. Photosynthetic (CO_2 flux) and transpiration rates of the uppermost, fully expanded leaf were measured using a portable photosynthesis analyser (LCpro SD, ADC BioScientific, UK).

2.5. Oxygen concentration in the water culture of the mixed-seedlings (Exp. 2)

In Exp. 2, time course analysis of O_2 consumption rates of the mixed-seedlings was conducted in the growth room used for seedling establishment. Two-week-old seedlings of rice, as described in the 'seedling establishment section', were grown for 3 more weeks inside the room by using the same nutrient culture system that was used for Exp. 1. Four-week-old pearl millet and 5-week-old rice seedlings were then transferred into plastic pots (150 mm high × 110 mm diameter) filled with 800 mL of distilled water. The root system of the seedlings (Fig. 1) was completely submerged in water during the measurement. The dissolved O_2 concentration in the water was measured continuously for 16 h using a fiber optic oxygen-sensing probe {FireSting O_2 Fiber-Optic O_2 Meter with the OXROB3 (PyroScience GmbH, Germany)}. The O_2 probe was fixed at about 13 ± 2 mm above the root mat situated at the bottom of the pot. The distilled water was open to the air, but the container was wrapped in aluminium foil to darken the root environment, while leaving the shoot system exposed to light. The O_2 concentration of the distilled water without plants was also measured as the control.

2.6. Plant harvesting and RGR determination

In experiment 1, the plants were harvested just before the flooding treatment and then at the end of the experiment. The shoot samples were oven-dried at 80 °C for 72 h, weighed, and the shoot dry weights were determined. The dry weights from the two sampling regimes were then used to calculate crop relative growth rate (RGR, Malik et al., 2011). In experiment 2, plants were harvested only at the end of the experiment.

2.7. Statistical analysis

All statistical analyses were performed using Excel Statistics Version 2012 software (SSRI). An analysis of variance (ANOVA) was performed, and all plant growth and physiological parameters among treatment means were compared using Tukey–Kramer test at the 5% level. The number of replicates in each experiment was indicated in each Figure and Table.

3. Results and discussion

3.1. Physiological response of the mixed-seedlings under O_2-deficient nutrient culture (Exp. 1)

To prove the hypothesis, we first prepared a seedling mix of the wetland-adapted (rice) and dryland-adapted (pearl millet and sorghum) crop species as shown in Fig. 1. This mixed-seedlings system was intended to enhance the intertwining of the roots of the two species. It involved growing the mixed-seedlings in a small container to allow the development of a dense root mat under the container. In this way it was hoped to ameliorate the adverse effect of O_2 deficiency for the upland species by re-oxidation of reduced phytotoxins in the rhizosphere, and by satisfying most of the rhizosphere O_2 demand, buffer the dryland species own internal O_2 supply from being lost to the soil. However, this needs to be proven under field soil condition, which is completely different from a nutrient culture condition. In fact, a part of the mixed-seedling roots were suspended in the solution culture, even though the major part of the tangled roots remained in soil in cell trays. In this study we flushed the culture with N_2 gas to reduce O_2 level in the solution, thus creating O_2-deficient condition in the growing medium. Although the agar: water method has been used in many studies as standard procedure, this method was not suitable for our long period (24 days) experiment (with up to 52 days old millets and 59 days old rice). Microorganisms could have grown rapidly in the growing medium if we had used nutrient solution with agar. This N_2 flushing method and the partial growth of the root system in soil inside cell tray should help providing basic understanding about rhizosphere interaction between the wetland and dryland species. After 2 weeks of O_2 deficiency treatment, the photosynthetic rate, an indicator of plant leaf physiological activity (Fig. 2a,b), was significantly higher in the mixed-seedlings than in the single-species seedlings for both pearl millet and sorghum. The transpiration rate, an indicator of physiological activity of the entire root system in terms of water and nutrient uptake, of millets showed a trend similar to that of the photosynthetic rate (Fig. 2c,d). The increased physiological activity of both the leaf and root systems implied that the mixed-seedlings were effective for millets. Mixed cropping often causes the competition among the component species. Biomass production at the end of experiment 1 indicated that competition occurred between rice and sorghum, which was shown by the ratio of mixed to single plants (Table 1). Pearl millet did not show any biomass reduction caused by the competition with rice during the entire growth period of 52 days (4 weeks nursery plus 24 days experiment). Therefore, only pearl millet was used in the subsequent experiment 2. In experiment 1, shoot relative growth rates during the flooding period (24 days) tended to be higher under mixed cropping compared with those under single cropping. The ratios of mixed cropping to single cropping were similar for both pearl millet and sorghum. The results of experiment 1 indicated that mixed-seedling enhanced physiological activities under O_2-deficient condition, resulting in an increased trend of biomass production.

3.2. Oxygen concentration in the water culture of the mixed-seedlings (Exp. 2)

Rice seemed to have facilitated the growth of both pearl millet and sorghum by modifying their rhizosphere microenvironments. We investigated this phenomenon by following changes in the O_2 concentration in an open-water system with either no root systems (control), rice-single, pearl millet-single, or a mixture of rice and pearl millet. Initially, in all cases (Fig. 3) there was net O_2 consumption from the water and in the case of the pearl millet-single treatment, all the O_2 had been scavenged from the water in about 5 h. There was only a slight decline in the no-plant control treatment. In the other two cases, however, the decline in O_2 was eventually arrested before all the O_2 had been removed: in the case of the rice-single treatment, the concentration stabilized at ca. 60 μM and we suggest that ROL from the roots at this point was just balancing the O_2 consumption rate. The rice-pearl millet mix stabilized at a much lower figure (ca. 5 μM) which we interpret as the point at which ROL from the rice roots was just able to balance the additional consumption due to the pearl millet roots. In view of the complete scavenging of O_2 in the pearl millet-single treatment, this would seem to indicate that some ROL from the rice roots was now being utilized by the pearl millet. After 11 h there was apparently either an increase in ROL from the rice or perhaps a reduction in consumption by the rice, the pearl millet or both which was reflected in a small increase in the O_2 concentration in the medium. However, since the rise coincided with the beginning of the light period, when any potential decline in respiration could have been expected to be reversed (by renewed photosynthate transport to the roots) we interpret the effect as being due to

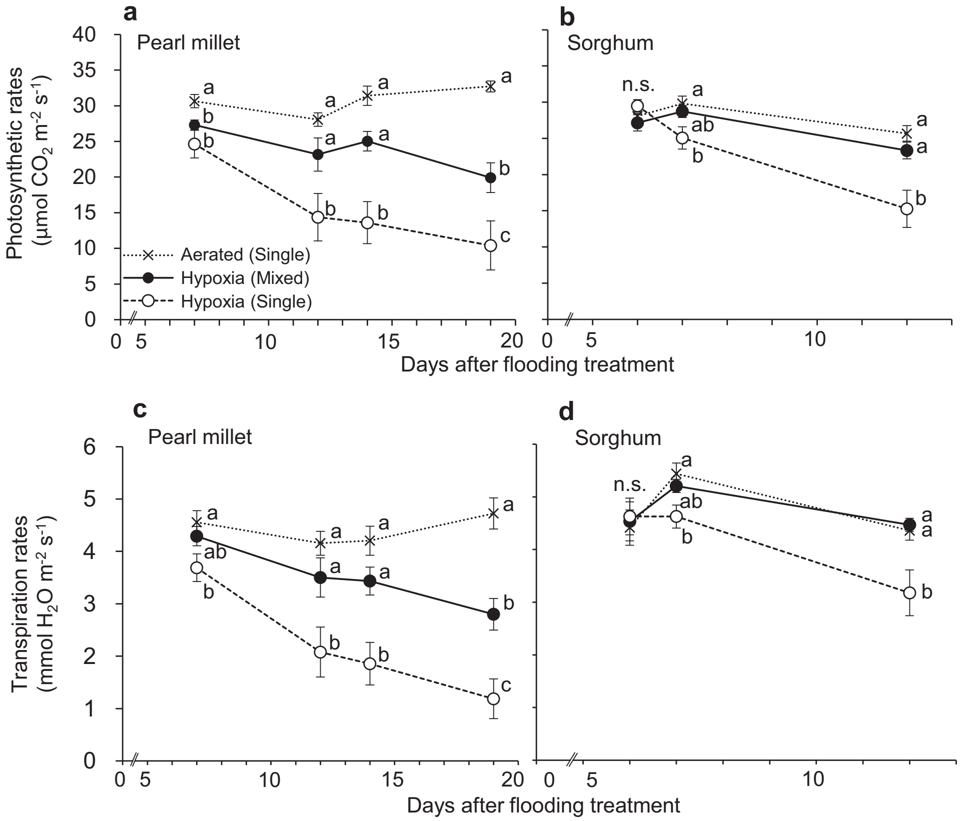

Fig. 2. Photosynthetic and transpiration rates of pearl millet (PM, $n = 9–11$) (a, c) and sorghum (S, $n = 6–8$) (b, d) as influenced by mix-cropping with rice cv. NERICA4 (N4) under root O_2 deficiency stress, Exp. 1. Four-week-old millets and 5-week-old rice were transferred into plastic boxes filled with either air-bubbled (Aerated) or N_2-bubbled (Hypoxia) solution culture and grown for 24 days in a glasshouse. Photosynthetic and transpiration rates were measured in the uppermost, fully expanded leaves. Error bars indicate standard error of the means. Different letters indicate significant difference by Tukey–Kramer test at $P < 0.05$ level.

Table 1
Growth traits of the mixed-seedling at harvesting in Experiment 1 and 2.

Treatment			RGR (g g^{-1} d^{-1})	Ratio to single plant	Shoot biomass (g plant^{-1})†	Ratio to single plant	Leaf no.	Ratio to single plant	Tiller no.	Ratio to single plant
Exp. 1										
Aerated	PM single		0.096		32.9 ± 1.6		14.8 ± 0.6		1.1 ± 0.4	
	Mixed	PM	0.103	1.07	33.4 ± 1.9	1.01 ns	13.8 ± 0.3	0.93 ns	1.8 ± 0.2	1.64 ns
		R(N4)			2.5 ± 0.2		8.5 ± 0.2		1.9 ± 0.1	
Flooded	PM single		0.058		14.1 ± 2.1		12.5 ± 0.5		1.0 ± 0.4	
	Mixed	PM	0.069	1.19	15.8 ± 0.8	1.12 ns	13.7 ± 0.7	1.09 ns	1.3 ± 0.5	1.30 ns
		R(N4)			1.3 ± 0.2		9.2 ± 1.0		1.8 ± 0.6	
Ratio to aerated	PM single				0.43**		0.84*		0.91 ns	
	Mixed	PM			0.47**		0.99 ns		0.72 ns	
		R(N4)			0.50**		1.08 ns		0.95 ns	
Aerated	S single		0.080		21.9 ± 1.2		15.0 ± 0.3		0.0 ± 0.0	
	Mixed	S	0.091	1.14	18.2 ± 1.1	0.83*	14.1 ± 0.2	0.94*	0.0 ± 0.0	
		R(N4)			2.3 ± 0.2		9.8 ± 0.2		2.1 ± 0.1	
Flooded	S single		0.063		14.7 ± 0.9		14.1 ± 0.4		0.0 ± 0.0	
	Mixed	S	0.076	1.20	12.7 ± 1.0	0.86 ns	13.3 ± 0.4	0.94 ns	0.0 ± 0.0	
		R(N4)			2.0 ± 0.4		9.3 ± 0.4		1.7 ± 0.4	
Ratio to aerated	S single				0.67**		0.94 ns			
	Mixed	S			0.70**		0.94 ns			
		R(N4)			0.90 ns		0.95 ns		0.78 ns	
Exp. 2										
Flooded	PM single				28.2 ± 4.6		11.4 ± 0.7		2.4 ± 0.3	
	R(Ni) single				2.5 ± 0.2		8.1 ± 0.3		3.8 ± 0.3	
	Mixed	PM			23.8 ± 4.8	0.84 ns	11.2 ± 0.8	0.98 ns	2.9 ± 0.4	1.21 ns
		R(Ni)			2.0 ± 0.1	0.80*	7.6 ± 0.2	0.94 ns	3.3 ± 0.2	0.87 ns

In Exp. 1, millets (pearl millet and sorghum) were harvested at 28 and 52 days after sowing (DAS) for the estimation of relative growth rates (†shoot biomass at 52 DAS). In Exp. 2, pearl millet was harvested only once at 29 DAS. RGR, relative growth rate; PM, Pearl millet; R(N4), rice cv. NERICA4; S, Sorghum; R(Ni), rice cv. Nipponbare; ns, not significant. Values are means ± standard error of the survived plants (PM, $n = 8–11$; S, $n = 6–8$ in Exp. 1; $n = 8$ in Exp. 2). †Dry weight (Exp.1) or fresh weight (Exp.2). Asterisks indicate significant difference by *t*-test at $P < 0.01$(**) or $P < 0.05$(*) level.

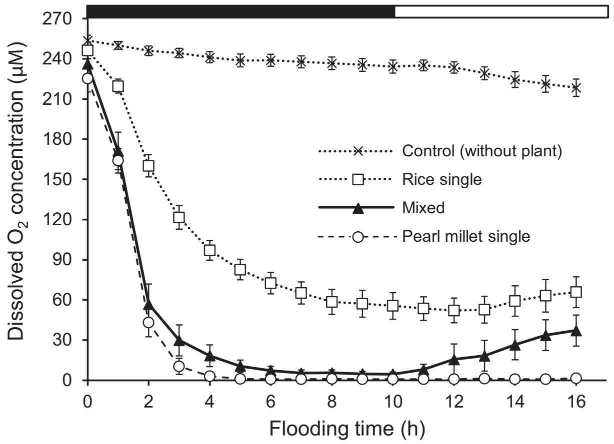

Fig. 3. Dissolved O_2 concentration in an open-water system ($n=8$) as influenced by mixed-seedling growth, Exp. 2. Four-week-old pearl millet and 5-week-old rice seedlings were transferred into plastic pots filled with 800 mL of distilled water. The dissolved O_2 concentration in the water was measured continuously for 16 h, during the dark phase from 0 to 10 h and subsequent light phase. Black and white bars at the top indicate periods of dark and light, respectively. Error bars indicate standard error of the means.

a contribution from photosynthetic O_2 production. Further study is necessary to discuss the enhancement of O_2 diffusion to the roots by photosynthesis.

3.3. Future implications

In this study, we demonstrated that the mixed-seedling cropping technique ameliorate the adverse effects of rhizosphere low O_2 stress on upland crop growth. The nutrient solution experiments can only demonstrate the possible principle. To draw final conclusions the hypothesis needs to be tested in a soil system, where O_2 diffusion would be slower than in water culture and the O_2 demand would be higher owing to soil microorganisms. In soil, microorganisms can rapidly consume the O_2 released from rice roots; therefore, rhizosphere O_2 concentration in soil would likely be much less than in a nutrient solution, which could affect rice mitigation efficiency. At present, simultaneous occurrence of floods and droughts in the same place has become common globally. Under such weather conditions, crop cultivation techniques that might accommodate both extremes of water abundance are required to stabilize cereal production. Field evaluation on the proposed mixed-seedlings is necessary to apply any practical models in farm fields. The mixed-seedling cropping technique may provide one of the agronomic countermeasures to ensure constant staple food production under flood conditions.

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