Water supply from pearl millet by hydraulic lift can mitigate drought stress and improve productivity of rice by the close mixed planting

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ABSTRACT

The authors have proposed the close mixed planting technique using mixed seedlings of two different crop species that results in close tangling of their root systems. Especially, the combination of drought-adaptive upland crops (e.g. pearl millet or sorghum) and flood-adaptive lowland crop of rice would be beneficial to overcome the drought and flood conditions and to reduce the risks of crop failure. In our previous studies, we found that upland crop yield losses by flood stress was mitigated by mix-cropped rice, owing to the oxygen gas released from the rice roots into the aqueous rhizosphere. In the present study, we conducted two experiments to assess whether mixed cropping a drought-resistant cereal, pearl millet, would improve the performance of co-growing drought-susceptible crop, rice under drought conditions. In the field experiment, some grains were obtained from the rice plants mix-cropped with pearl millet under drought condition. However, no rice matured in the single cropping system. In the model experiment using deuterium analysis, it was confirmed that water absorbed by pearl millet roots from deep soil layer was utilized by rice, suggesting that mix-cropped rice could withstand drought stress and complete grain filling using water released into the upper soil layer by hydraulic lift.

1. Introduction

Food shortages caused by flooding have become common in the semi-arid African regions in recent years. Moreover, dry-spell durations have significantly increased in Southern and West African countries during 1961–2000 (New et al., 2006). One of the sub-Saharan countries in Southwestern Africa, Namibia has recently experienced several events of substantial flooding (Mendelsohn et al., 2013; Mizuochi et al., 2014). Moreover, prolonged periods of dry weather during the rainy season (dry spell) afflict the country’s main cropping areas of the populous northern region and have caused substantial losses of the production of pearl millet (Iijima et al., 2016).

In north-central Namibia, more than 90% of the farmers cultivate pearl millet as a staple food crop (McDonagh & Hillyer, 2003); 45% of the cultivated area is intercropped with cowpea (Matanyaire, 1998). Under such conditions, strong competition for limited soil water between intercropped pearl millet and cowpea may occur (Reddy et al., 1992). However, intercropping is also known to be an efficient cropping system in terms of natural resources as light, water, and nutrients utilization, when component crops with different root systems or leaf canopies exploit different soil layers or canopy heights (Hailu, 2015). Zegada-Lizarazu, Izumi, and Iijima (2006) and Zegada-Lizarazu, Kanyomeka, Izumi, and Iijima (2006) investigated the water sources of a pearl millet–cowpea intercropping system under drought condition with deuterium analysis and found that pearl millet developed deeper roots and changed water sources; as opposed to single-cropped plants. Therefore, their studies elucidated the beneficial interaction of this cropping pattern traditionally practiced in Namibia.

Recently, the authors have developed the new cropping concept of mixed cropping; the close mixed planting is a technique that two different crop species are sown or planted in a same place to enhance the root tangling of their root systems to utilize the released oxygen gas from lowland adapted rice to upland adapted pearl millet (Iijima et al., 2016, 2017). In the laboratory study, it was ascertained that oxygen gas (O₂) released from rice roots...
into the rhizosphere mitigated flood-induced damage of adjacent upland crops of sorghum and pearl millet (Iijima et al., 2016). The close mixed planting was also tested in the field conditions of Namibia to confirm the mitigation of flood stress of drought adaptive crops by the combination with rice (Awala et al., 2016). Under field condition, pearl millet and sorghum mix cropped with rice showed smaller yield reduction by flood stress during vegetative stage as compared to single cropping, and resulted in larger land equivalent ratio (LER), indicating a mixed planting advantage over single-stand planting (Awala et al., 2016). Furthermore, the farmers in Namibia have just started to practice the close mixed planting technique of pearl millet and sorghum as a way of ensuring crop security since the latter is more tolerant to waterlogging than the former (Awala et al., 2016).

On the other hand, mix-cropped dryland cereals should interact with rice under drought condition. Very few drought studies were conducted using such cropping pattern combining flood-adaptive and drought-adaptive crops, and neither the results of field experiments nor the yield research on it was reported before. However, we found that the water availability of component crops imposed drought treatment was improved by the close mixed planting in lysimeter and pot experiment (Yamane et al., 2017). These results suggest that drought stress was mitigated by hydraulic lift (Vetterlein & Marschner, 1993), the passive transport of water through the root axis from deeper, wetter soil layers to drier, upper soil layers (Caldwell et al., 1998; Dawson, 1993; Liste & White, 2008; Sekiya et al., 2011). Water in the deep soil layer may be lifted up by pearl millet roots thus can be utilized by the shallow-root crops such as rice. Therefore, we conducted a field experiment to evaluate the effect of close mixed planting of pearl millet and rice on plant growth and productivity under drought condition. Further, a model experiment using deuterium analysis was conducted to investigate the possibility of water supply from pearl millet to close mixed planted rice via hydraulic lift.

2. Materials and methods

2.1. Field experiment

The experiment was conducted under a model sloped field at the University of Shiga Prefecture, Hikone, Japan (35°15′N, 136°13′E) in 2014. The field was specially constructed with a slope of 4° to simulate the topography of many pearl millet fields found in north-central Namibia (Iijima et al., 2013). We covered the field by three plastic rain shelters with same size to avoid rainfalls and to impose a drought stress as described below. Two water management regimes (main plot) as drought treatment and control were assigned to each half of rain shelter, and three cropping patterns (subplot), i.e. single cropping of pearl millet, single cropping of rice and mixed cropping of the both were randomly arranged. Therefore, this experiment was conducted as a split-plot design with three replications. The planting area including border plants of each replicate plot (rain shelter) was 12.0 m (L) × 5.0 m (W). Moreover, considering different water condition along the slope, sampling was done from three different positions, i.e. upper, middle and lower along a row. All the measurements or sampling activities were performed for each position. However, we did not treat the position along the slope as an experimental factor because they were fixed and could not be arranged randomly. A rotary tillage was conducted twice before cultivation. Property of the topsoil (0–20 cm) was light clay (clay 26.55%, silt 31.86%, sand 13.65%) with pH 6.8 (H2O) and EC of 35.80 ds m−1; total N, 1.8 g kg−1; organic carbon, 17.15 g kg−1 (C/N, 9.76); CEC, 11.52 cmol kg−1. As a basal dressing, chemical fertilizer was applied within the ratio of 4:4:4 g m−2 for N:P2O5:K2O, respectively, before the tillage practice, and no top dressing was done.

In this study, an early maturing cultivar pearl millet (Pennisetum glaucum (L.) R.Br), cv. Okashana2, which is cultivated in several Southern African countries including Namibia; and an upland rice cultivar, NERICA4 (interspecies of Oryza sativa L. and O. glaberrima Steud.) were used. The seedlings of the close mixed planting were grown in a green house. On 4 June, two pre-germinated seeds of NERICA4 were sown in individual cell compartments filled with nursery soil for rice. Twelve days after sowing (DAS), of rice, the seedlings were thinned to one plant per cell. In the same day, two pearl millet seeds were sown in each of the cell compartments containing the rice seedlings to prepare the seedlings of close mixed planting (Awala et al., 2016). This relay-planting method was used to minimize a competition for rice shoot growth. A single-cropped treatment of rice was also prepared by leaving some rice seedling trays without being mix-cropped. Similarly, pearl millet single crop treatment was prepared by sowing the seeds in sown in new cell compartments without rice seedlings, and thinning was done as in rice.

On 2 July (28 DAS for rice and 16 DAS for pearl millet) seedlings were transplanted into field plots. Three types of the seedlings, i.e. single-cropped pearl millet, single-cropped rice and mix-cropped pearl millet and rice were transplanted in rows from upper to lower parts of the slope at .5-m inter-row spacing and .4-m in-row spacing (5 hills m−2). Therefore, each subplot consists of three rows of each cropping pattern and was surrounded by border plants (single-cropped NERICA4). Further, each plot of drought treatment was surrounded by .45-m-wide plastic sheet buried at .25-m deep from the soil surface to prevent inflow of surface and below ground water. Until 41 days
after transplanting (DAT), surface irrigation was applied daily to all plots. From the following day (42 DAT) to harvest, no irrigation was done for the drought treatment plots, but irrigation was continued for the control plots. After the drought treatment, soil water content \((v/v)\) in 0–10-, 10–20-, 20–30-, and 30–40-cm layers was monitored by PR2/4 profile probe (Delta-T Devices Ltd, Cambridge CB25 0EJ, UK). Insect control was done as necessary using chemicals and weeds were manually removed as farmers conventionally do in Namibia. The averages of daily temperature and relative humidity during the experiments were 24.0 °C and 47.0%, respectively.

At 77 DAT, daily leaf water potential of the same leaves was also measured using a pressure chamber PMS Instruments Model 600 (Soilmoisture Equipment Corp.; Santa Barbara, USA). At 79 DAT, xylem sap from the stumps was collected following the method of Awala et al. (2016). The shoot samples were oven-dried for 72 h at 80 °C and, and sap exudation rate per shoot dry weight was calculated. At 119 DAT, five hills (equivalent to 1 m²) per plot were harvested and the samples were air-dried for 20 days, and grain yield was obtained after manual threshing and wind selection. Moreover, LER was determined by the following equation:

\[
LER = LER_r + LER_p \left( \frac{Y_{rm}}{Y_{rs}} + \frac{Y_{pm}}{Y_{ps}} \right)
\]

where \(LER_r\) and \(LER_p\) represent partial LER of rice and pearl millet, respectively. \(Y_{rm}\) and \(Y_{pm}\) represent the yields of rice and pearl millet as mixed crops, respectively, and \(Y_{rs}\) and \(Y_{ps}\) are the respective yields as single crops.

The data of leaf water potential and sap exudation rate were statistically tested by the two-way analysis of variance (ANOVA) with split-plot factorial design with the aid of Microsoft Excel 2008 for Mac (ver. 12.3.6).

### 2.2. Model experiment

The experiment was conducted in the crop science laboratory of the Kindai University, Nara, Japan from August to October 2015. The same cultivars of pearl millet and rice, i.e. Okashana2 and NERICA4, respectively, were used. Surface-sterilized seeds of rice were soaked in distilled water at 30 °C for 48 h to promote pre-germination. For pearl millet, surface-sterilized seeds were pre-germinated on paper towel in a petri-dish at 30 °C for 16 h. Thereafter, pre-germinated seeds were sown in cell compartments (one seed into one hole) filled with a growing medium (Metro-Mix 250, Sun GRO® Horticulture, USA). Seedlings for the close mixed planting of pearl millet and rice were prepared as in the field experiment. The rice seeds were sown and grown in a plant growth room having 28/23 °C \((d/n)\), 14 h photoperiod, and 318 ± 2 μmol m⁻² s⁻¹ photosynthetically active radiation above the leaf canopy.

Pearl millet was sown at 7 DAS of rice for the mix-cropped seedlings, and then transferred to a greenhouse. The seedlings were raised in solution culture using a plastic hydroponic reservoir \((.80 \times .67 \times .31 \text{ m}, L \times W \times H)\) in the growth chamber-controlled photoperiod, temperature, and photosynthetic active radiation as 14 h, 28/23 °C \((d/n)\) and 169 ± 6/551 ± 35 μmol m⁻² s⁻¹ (early morning and late afternoon/midday), respectively. Seedlings were grown under full strength Miyamoto’s culture solution (Miyamoto et al., 2001), which was renewed twice a week, until the time of transplanting.

Forty-three DAS of rice, the seedlings were transplanted into a container \((.135 \times .135 \times .105 \text{ m}, L \times W \times H)\) with two compartments (Figure 1) in a greenhouse. The upper compartment was filled with 230 g (.63 mL) of Metro-Mix 250, and the lower one was filled with .25 L of full strength of Miyamoto’s culture solution with aeration. The bottom of the upper compartment was perforated and a 40-mm long plastic tube with 5 mm diameter was inserted into 20 mm deep of the lower compartment. During transplanting, only one nodal root of pearl millet was guided to penetrate into the lower compartment. To prevent penetration of other roots, the tube was sealed with vaselin (224-00165, Wako Pure Chemical Industries Ltd, Kyoto, Japan) and thereafter.

Figure 1. Container with two compartments used in the model experiment.
covered with a waterproof film (BFR5, Nichiban Co., Ltd, Tokyo, Japan). After transplanting, .1 L of water was irrigated daily from the surface of the upper compartment, and the culture solution (pH adjusted 6.0–6.5) of the lower compartment was changed twice a week. The averages of daily temperature and relative humidity in the greenhouse during the experiments were 26.3 °C and 66.4%, respectively.

Three plots, replicated seven times, were set up as follows: non-hydraulic lift (non-HL), no nodal root penetration; control, one root penetration with frequent irrigation; and drought, one root penetration with limited irrigation. From 54 DAS of rice no irrigation was done during 10 days for the drought plot. Water content (w/w) and water potential of the upper compartment one day before the sampling (64 DAS) in the non-HL, control and drought plot was 223% and −15.1 kPa, 280% and −9.1 kPa, and 40% and −689 kPa, respectively. In the same day, water potential and stomatal conductance of the uppermost fully expanded leaf was measured from 09:00 to 11:00 by microvoltmeter (HR-33T Dew Point Microvoltmeter, Wescor, USA) and leaf porometer (AP4, Delta-Devices Ltd, UK), respectively.

Procedure of the deuterium analysis was followed by Araki and Iijima (2005), Iijima et al. (2005) and Zegada-Lizarazu, Izumi, et al. (2006). At 63 DAS of rice, .2 L of deuterium water (5 atom% D2O) was supplied to the lower compartment at 1700, and the shoot samples were collected the following day. Collected leaves and stems were cut in 10-mm-long pieces which were put into three centrifuge tubes, and centrifuged at 15,000 rpm for 5 min in 20 °C. Extracted liquid was again centrifuged at 15,000 rpm for 10 min and kept in refrigerator set at 4 °C. Irrigation water (non-labeled water) supplied to the upper compartment was also collected and kept in the same way as the extracted liquid. The atom% of the samples, irrigated water and supplied deuterium water was determined by stable isotope ratio mass spectrometer (IsoPrime100 IRMS system, Isoprime Ltd, UK) and the atom% excess values was calculated as follows:

\[
\text{atom}\%\ \text{excess} = \text{atom}\%\ \text{of the samples} - \text{atom}\%\ \text{of irrigated water}
\]

Shoot and root samples were oven-dried at 80 °C for 72 h and weighed. The data were analyzed by Student’s t-test, one way ANOVA and post hoc test (Tukey–Kramer test) using an add-in program for Excel (Excel Toukei ver. 6.0, Esumi Software Co., Ltd, Tokyo, Japan).

3. Results
3.1. Field experiment

Soil water content (v/v) at 10, 20, 30, and 40 cm depth in the center of the control and drought plots is shown in Figure 2. Regardless of the water management, water content was the lowest and the highest in the 0–10- and 30–40-cm layer, respectively. In the drought plot the water content started to decrease from just after the onset of the drought treatment (42 DAT) in the 0–10-cm layer. However, in the lower part of the field, soil water content was maintained for a while. In the 10–20-cm layer of the drought plot, water content started to decrease from about 5 days after the onset of the drought treatment. At 20–30- and 30–40-cm layers, the water contents of the control tended to be higher in the middle part than in the others.

Leaf water potential of rice at 77 DAT was significantly lower in the drought plot than in the control (p < .01) in all the positions of the field, whereas no significant difference was found between the cropping patterns (Figure 3-upper). In pearl millet, difference in the leaf water potential between the water managements was relatively small (Figure 3-lower). Those in the drought plot were significantly lower than in the control in the upper (p < .1) and middle (p < .05) part of the field, whereas in the lower part it tended to be higher in the drought plot, especially in the mixed cropping. Xylem sap exudation rate per shoot dry weight at 79 DAT was considerably reduced by the drought treatment in both the crops (Figure 4) and was significantly lower (p < .01) regardless of the position of the field. Main effect of the cropping pattern and interaction with the water management were also significant.
However, in the drought treatment, sap exudation rate of rice tended to be higher in the mixed cropping treatment than in the single cropping treatment. The shoot dry weight in the same day was not significantly different between the water managements, but was significantly different between the cropping patterns, i.e. those in the mixed cropping was significantly smaller than in the single cropping in any cases (data not shown). Therefore, xylem sap exudation rate per plant always showed the same trend (data not shown).

Grain yield of pearl millet harvested at 119 DAT tended to be higher in the drought than in the control plot and in single than in the mixed cropping at any part of the field (Table 1-lower). On the other hand, rice yield was severely reduced by drought (Table 1-upper). Nevertheless, some rice grains were obtained by the close mixed planting treatment in the upper part of the field, whereas that in single cropping was zero. In the middle part of the field, a significant interaction between water management and cropping pattern was found. Total LERs of the control were nearly 1 or less (Table 2) indicating that yield advantage of the mixed cropping was not clear. On the other hand, in the drought treatment that in the middle part of the field exceeded 3 due to high partial LER of rice. Moreover, total LER and partial LER of rice in the upper part could not be calculated or ‘infinite’ because the denominator, i.e. yield of single-cropped rice was zero.

### 3.2. Model experiment

Leaf stomatal conductance of rice at 62 DAS was significantly lower in the drought plot than in the control and non-HL plots (Figure 5-upper). Those in the control and non-HL plots were not significantly different. In pearl millet no significant difference was found among the three plots (Figure 5-lower). Leaf water potential of rice measured in the same day (Figure 6) was lower in the drought plot than in the control despite no significant difference.

Deuterium water concentration extracted from rice plant at 63 DAS was more than two times and significantly larger in the drought than in the control plot (Figure 7), indicating that deuterium water supplied to the lower compartment was absorbed by pearl millet roots, and was further utilized by rice roots. On the other hand, deuterium water concentration in the control did not significantly differ from the non-HL plot. In both the shoot and root dry weights of rice and pearl millet sampled at the same day no significant difference was observed among the three plots (data not shown). Other growth parameter such as plant height, number of leaves and tiller number did not show any significant difference among the plots for both the crops (data not shown).
higher than that of single-cropped one under short-term flood stress condition, resulting in high total LER value as 2.55 (Awala et al., 2016). In this study, using the same cropping pattern but under drought condition, yield advantage was shown in the lower and middle parts of the field when evaluated with the total LER values (Table 2), but it was not

**Table 1.** Grain yield (g m⁻²) of single- and mix-cropped rice (upper) and pearl millet (lower) harvested from three parts of the field at 119 DAT.

|          | Lower | Middle | Upper |
|----------|-------|--------|-------|
|          | Single | Mixed | M/S   | Single | Mixed | M/S   | Single | Mixed | M/S   |
| Rice     |        |        |       |        |        |       |        |        |       |
| Control  | 69.7   | 40.5   | .58   | 90.5   | 37.4   | .41   | 70.5   | 45.6   | .65   |
| Drought  | 16.1   | 10.5   | .65   | .1     | .25    | 2.50  | 0      | 4.6    | na*   |
| D/C      | .23    | .26    |       | .01    |        |        |        |        | .10   |
| Water    |        |        |       |        |        |       |        |        |       |
| C × W    | *      |        |        | **     |        | **    |        |        |       |
| Pearl millet |      |        |       |        |        |       |        |        |       |
| Control  | 488.6  | 209.2  | .43   | 498.1  | 213.6  | .43   | 422.2  | 192.9  | .46   |
| Drought  | 603.4  | 279.7  | .46   | 486.2  | 266.3  | .55   | 521.4  | 223.3  | .43   |
| D/C      | 1.24   | 1.34   | .98   | 1.25   | 1.24   | 1.16  |        |        |       |
| Water    |        |        |       |        |        |       |        |        |       |
| C × W    | **     |        | **    |        |        |       |        |        |       |

*Not available because the yield of single-cropped rice was not acquired.

* and ** show significant difference at *p < .05* and *p < .01* level between the cropping patterns, respectively.

**Table 2.** Partial and total land equivalent ratio (LER) for mixtures of rice and pearl millet harvested from three parts of the field at 119 DAT.

|          | Lower | Middle | Upper |
|----------|-------|--------|-------|
|          | Rice  |        |       |        | Pear millet |        |       |        |
| Control  | .58   | .43    | .65   | .43    | .46          |       |       |       |
| Drought  | .65   | 2.50   | na*   | .46    | .35          | .43   |       |       |
| D/C      | 1.12  | 3.05   | na*   | 1.27   | 1.24         | na*   |       |       |

*Not available because the yield of single-cropped rice was not acquired.

**4. Discussion**

Previously, our research group reported that the yield of mixed-cropped pearl millet with rice was significantly higher than that of single-cropped one under short-term flood stress condition, resulting in high total LER value as 2.55 (Awala et al., 2016). In this study, using the same cropping pattern but under drought condition, yield advantage was shown in the lower and middle parts of the field when evaluated with the total LER values (Table 2), but it was not
accompanied by the improvement of absolute yield by mixed cropping, suggesting an interspecific competition with rice instead (Table 1). Of course, this new cropping system is still in development, hence further researches focusing on raising of seedlings, nutrient management, and selection for suitable cultivars of the component crops will be needed to reduce competition and to enhance their complementarity.

Anyway, as is already mentioned, this cropping system was originally devised to introduce into sloped seasonal wetlands commonly seen in the fields of small holder farmers in Namibia to cope with extreme weather conditions and to reduce risk of complete crop failure (Awala et al., 2016). In fact, small holder farmers in Namibia have suffered from three episodes of substantial flooding since 2008 (Mendelsohn et al., 2013), hence it is undoubtedly true that the pearl millet single cropping is nowadays quite risky. Diangar et al. (2004) reported that there was no yield advantage to intercropping millet but farmer might prefer intercropping with cowpea as a strategy to ensure food security in semiarid areas of Senegal. With the same reason, close mixed planting of pearl millet with rice will be acceptable by Namibian farmers.

Another finding to be appreciated was that mixed cropped rice could produce some grains under a severe drought condition of the upper part where no yield would have been acquired from single cropping (Table 1).

Deuterium analysis in the model experiment indicated that water absorbed by one deep nodal root of pearl millet was released into the upper shallow root zone, and thereafter absorbed by rice, when both the crops were cultivated under drought condition (Figure 7), suggesting hydraulic lift under drought condition. On the other hand, that in the control with no significant difference from the non-HL plot indicates almost no hydraulic lift had occurred under well-watered condition. Rostamza et al. (2013) reported that pearl millet had a more plastic response than sorghum to moisture around the nodal roots due to faster growth and progression through ontogeny for earlier nodal root branch length and partitioning to nodal root length from primary roots, independent of shoot size. Hence, we suppose that pearl millet utilizes water in shallow zone under no drought stress and gradually shifts to deep water as a gradient of soil water potential between shallow and deep layer increases. Leaf stomatal conductance in the drought plot with no significant difference from that in the control (Figure 5-lower) also suggests that water uptake by deep roots contributed to drought avoidance. In contrast, significantly lower stomatal conductance in rice (Figure 5-upper) implies that water supply was not sufficient to maintain transpiration, resulting in stomatal closure to maintain leaf water potential under drought condition (Figure 6). Nevertheless, no morphological trait was significantly decreased by 10-day drought stress, suggesting that drought stress could be mitigated by the hydraulic lift of pearl millet roots. Further studies will be necessary to quantify the water supply by this phenomenon.

In a field study of maize–soybean intercropping in Zimbabwe, Mudita et al. (2008) discussed that one possible mechanism of yield improvement of cereal in intercrop was hydraulic lift. Pang et al. (2013) also reported that hydraulic lift by deep rooting legume species improved water relations of shallow one. Vetterlein and Marschner (1993) that firstly observed the hydraulic lift of pearl millet in a pot experiment mentioned that water release from the roots would be expected to be much smaller under field conditions. Nevertheless, in our field experiment, higher xylem sap exudation rate in the mix-cropped rice than in the single-cropped one was observed under drought condition (Figure 4-upper), suggesting that more soil water was supplied even in the upper part of the field where the severest drought was imposed. This additional water, which might be absorbed and lifted up by the deep roots of pearl millet could help the panicle development and/or grain filling of rice even if it was small amount, as Sekiya et al. (2011) mentioned that the influence of hydraulic lift in an agricultural situation might be unexpectedly high.

Moreover, Sekiya et al. (2011) suggested that shoot removal of a donor plant might have enhanced vegetable growth of neighboring plant through a reduction in soil water competition and/or a continued water supply even during daylight. These seem to be worthy because maturity of pearl millet is generally earlier than that of rice. In Namibia, farmers generally conduct ear reaping, but if they cut down pearl millet shoot in harvest, more benefit on rice production will be expected. Therefore, studies on harvesting time and method of pearl millet will be meaningful to obtain more rice yield with this mixed cropping system.

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