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Will Tomato Mix-planted with Rice Survive under Vegetative Stage Transient Flooding?

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The production of tomatoes during the wet season is challenging due to its vulnerability to oxygen (O_2) deficiency due to seasonal flooding in some growing areas. In this study, tomato mix-planted with rice was done to assess tomato survival during transient flooding through sourcing of its O_2 requirements from the radial O_2 loss (ROL) in rice roots. The experiment was conducted in a screenhouse and laid out in a split-plot design in a randomized complete block design with water treatment as the main plot and plant culture treatment as the subplot with six replications. Three replications were sampled after the imposition of transient flooding at the vegetative stage, whereas the remaining three were sampled at maturity. Under transient flooding, tomato mix-planted with NSIC Rc 216 had higher shoot growth and yield than its monoculture, whereas those mix-planted with NSIC Rc 25 did not sustain the tomato growth. Soil O_2 concentration and stomatal conductance of the tomato mix-planted with NSIC Rc 216 was higher than its monoculture and tomato mix-planted with NSIC Rc 25. Low soil O_2 concentration caused low stomatal conductance and wilting of monoculture tomato and tomato mix-planted with NSIC Rc 25. In contrast, only tomato mix-planted with NSIC Rc 216 produced yield under transient flooding. This suggests that under mix-planting, the roots of rice partially provided O_2 to tomato roots to maintain their growth and development during transient flooding but it is genotype dependent.

Keywords: diamante tomato, mix-planting, radial oxygen loss, rice, transient flooding, vegetative stage

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INTRODUCTION

Tomato is the second most important vegetable crop in the world next to potato (FAO 2001) due to its nutritional value and wide variety of uses (Gorme *et al.* 2017). In the Philippines, tomato production was recorded at 222,000 MT (PSA 2022). The production of tomatoes during the rainy season is extremely challenging due to its vulnerability to oxygen (O_2) deficiency in growing areas experiencing transient flooding.

The occurrence of flooding stress is presumed to increase in the near future owing to the drastic climate change (Iijima *et al.* 2022). Flooding negatively affects tomato yield by 10–40% or in severe cases, 100% (Pavithra and Sujatha 2019). Susceptible crops under monocropping systems may be jeopardized by this abiotic stress. Monocropping is the planting of a single variety representing the same genotype with almost no variation. The downside of monoculture is that it is vulnerable to biotic and abiotic stresses (Liu *et al.* 2018). Thus, several strategies are being assessed to mitigate its effects including mix-planting or intercropping.

Mix-planting is widely practiced in tropical regions, where two or more different crop species are grown in the same field and time. It optimizes niche complementarity, resource sharing, and facilitation, where traits of different crops can be combined to overcome resource limitations. Complementarity effects occur when mix-planted plants with complementary traits interact, and a positive response results in increased crop productivity (Brooker *et al.* 2015).

Previous studies on intercropping with emphasis on positive ecology with rice have mainly focused on rice-drought tolerant cereals and rice-legumes mixed planting (Iijima *et al.* 2022). Rice is a semi-aquatic plant generally tolerant to flooding and partial submergence. Growing flood and drought-adapted crops together as mix-planting may be a continual global strategy to overcome the effects of climate change (Iijima *et al.* 2017). The flood mitigation effects on flood-sensitive crops could be attributed to the transferred O_2 from roots of flood-adapted crops lost in the rhizosphere termed "radial oxygen loss" (ROL) (Awala *et al.* 2016). A large amount of ROL *via* the intracellular spaces, usually around 20–40% (Armstrong 1979; Colmer 2003), happened during O_2 diffusion *via* aerenchyma cells in root respiration (Yamauchi *et al.* 2013). The ROL plays a key role in plant physiology and soil ecology by providing vital O_2 to the rhizosphere. This O_2 is crucial for aerobic respiration in root cells essential for energy production and overall root growth (Armstrong and Armstrong 2005). The ROL also helps mitigate the accumulation of toxic substances, such as sulfides, that can harm plant roots, thereby promoting a healthier root-soil environment (Colmer and Greenway 2011). The O_2 released through ROL facilitates the oxidation of ammonium to nitrate enhancing nutrient availability to plants (Armstrong *et al.* 1991). The oxygenation of the rhizosphere supports a diverse community of beneficial microorganisms involved in nutrient cycling like nitrification and nitrogen fixation (Kuzyakov and Blagodatskaya 2015). Furthermore, the presence of sufficient O_2 in the soil can sustain normal root growth and overall plant health, potentially benefiting neighboring plants through improved soil conditions (Armstrong 1979) and maintaining an oxygenated soil environment regulating soil processes – including organic matter decomposition and nutrient cycling – thus contributing to overall soil health (Armstrong and Drew 2002).

The rice roots developed under aerated conditions had a distinctive pattern, characterized by higher basipetal ROL rates diminishing toward the root tip showing weak or absence of barriers to ROL. Conversely, rice roots developed under stagnant, deoxygenated conditions have roots with developed strong barriers to ROL, which had lower ROL in basal zones but increased toward the root tip (Jimenez *et al.* 2021). These observations indicate that the majority of O_2 available under flooded soils grown to rice is due to ROL from roots.

In previous studies using pearl millet and sorghum, both mixed planted with rice and grown under vegetative stage flooding (Iijima *et al.* 2016) showed increased plant survival rates and made both crops produced higher grain yields relative to their monocropped counterparts grown under flooded conditions (Iijima *et al.* 2016). Similar results were observed in pearl millet mix-planted with rice under stagnant hydroponic culture (Iijima *et al.* 2017) and upland soybean mix-planted with rice under a short period of flooding between juvenile and early flowering stage (Iijima *et al.* 2022).

In this study, we hypothesized that tomato mix-planted with rice may source its O_2 from rice lost through ROL during transient flooding. If proven effective, tomato/rice mix-planting may partially solve problems in areas planted with the tomato occasionally experiencing transient floods. It is assumed that during flooding imposition, ROL from rice roots will serve as a source of O_2 to tomato roots to overcome anoxia. Thus, this study evaluated the growth, physiological, and yield responses of tomato mix-planted with rice under vegetative stage transient flooding.

MATERIALS AND METHODS

Plant Materials

A hybrid tomato variety and two rice varieties were used in the study. The tomato variety Diamante max F_1 is a high-yielding heat-tolerant hybrid with intermediate resistance to "kulot" or ToLCV (bacterial wilt), and its fruits are highly round and firm with excellent transportability and storability (PVPO 2024). The rice varieties used were NSIC Rc 216 (irrigated lowland variety) and NSIC Rc 25 (upland rice variety) (PhilRice n/d).

Experimental Design and Treatments

The experiment was arranged in a split-plot design in a randomized complete block with six replications. The water treatments were assigned as the main plot and the plant culture treatments as subplots. Water treatments were composed of continuous aerobic conditions (non-stress control treatment), flooded-aerobic (transient flooding), and continuous flooding (stress control treatment). The plant culture treatments were monoculture tomato (control), tomato mix-planted with NSIC Rc 216, and tomato mix-planted with NSIC Rc 25. Three replications (1 pot = 1 replication) were sampled after the imposition of transient flooding, whereas the remaining three replications were sampled during the maturity stage.

Soil and Pot Preparation

Loamy sand soil was sieved to remove debris and sun-dried for 2 d to reduce moisture content. Each pot (28 cm x 28 cm, H x D) contained 14.5 kg of soil.

Establishment of Tomato and Rice in a Single Pot

The rice was established 23 d ahead of the tomato. The rice seeds were soaked in tap water for 24 h and incubated for another 24 h for pre-germination. Pre-germinated rice seeds were sown in seedling trays containing 1:1:2 ratios of vermicompost, carbonized rice hull, and garden soil and grown for 21 d before transplanting. Rice plants were cultivated in continuously flooded (CF) conditions from transplanting until the transplanting of the tomato.

The tomato seeds were pre-germinated and sown in seedling trays containing the same media as that in rice 2 d after transplanting (DAT) of rice. The tomato seedlings were grown using the standard cultural management (DA-RFO2 2017). At 28 d old, the tomato seedlings were transplanted in pots containing earlier planted rice plants based on the treatment combinations (Table 1). For mix-planted treatment, each pot contained one plant each for tomato and rice variety. In monoculture, the pot contained two plants of tomato spaced 15 cm from each other.

Water Management

Soil moisture content (SMC) in pots containing the newly transplanted seedlings was maintained at 22% until 21 DAT of tomato. The 22% SMC was identified as the field capacity of the loamy sand used based on our estimation of its soil saturation point. The SMC estimate was calculated by subtracting the dry soil weight from the current weight to determine the weight of the water present in the soil. This weight of the water was then divided by the weight of the soil and expressed as a percentage. The imposition of water treatments was done at the vegetative stage (21 DAT) of the tomato. In the CF, SMC was maintained at 50% for 8 d, whereas in aerobic condition (AC), SMC was maintained at 22% (field capacity). In transiently flooded (TF), the SMC was maintained at 50% for 4 d and then allowed to decline and maintained at 22% SMC for another 4 d. Watering was done every two days to achieve the desired SMC (Suralta and Yamauchi 2008). The 50% SMC in flooded treatment was based on the 5-cm depth of excess water in the pot. A decreased volume of water was subsequently applied to sustain the target SMC. The volume of water was computed by subtracting the present weight of the pot from the target weight of the pot (computed based on the desired SMC).

Table 1. Treatment combinations used in the study.

Water treatment	Plant culture treatment
Continuous aerobic (22% SMC throughout the experiment)	Tomato (monoculture)
	Tomato + rice (NSIC Rc 216)
	Tomato + rice (NSIC Rc 25)
Flooded-aerobic (50% SMC for 4 d, 22% for 4 d)	Tomato (monoculture)
	Tomato + rice (NSIC Rc 216)
	Tomato + rice (NSIC Rc 25)
Continuous flooding (50% SMC for 8 d)	Tomato (monoculture)
	Tomato + rice (NSIC Rc 216)
	Tomato + rice (NSIC Rc 25)

Nutrient Management

Fertilizer application was based on the nutritional requirement of rice plants using a 90-60-60 kg NPK rate on a per hectare basis. Phosphorous (solophos, 20% P) and potassium (muriate of potash, 60% K) were applied before transplanting at the rate of 60 kg ha^{-1}, whereas nitrogen (urea, 45% N) was applied at 7, 30, and 45 DAT at the rate of 30 kg ha^{-1}.

Harvesting

Matured tomato fruits from survived plants were harvested at turning to the pink stage from 115–146 DAS. This was done by twisting the fruits to separate the pedicel from the stem. Harvested fruits were placed in a plastic bag for further measurements. Harvesting was done in three batches due to the indeterminate nature of the tomato in which fruits were developed and, hence, matured at different times.

Soil O_2 Concentration Measurements

Soil water O_2 concentrations were measured during and after the imposition of transient flooding. Air stone attached to a hose was installed at the center of each pot between the tomato and rice plants at a depth of 30 cm. The soil water was extracted by a syringe attached to the tip of the hose and carefully placed in a tube. Thereafter, the sensor tip was inserted in the tube containing the extracted soil water to measure the O_2 concentration using the dissolved oxygen (DO) sensor (Portable DO Meter AS720, AS ONE) meter.

Stomatal Conductance Measurements

The stomatal conductance of the fully expanded (second-youngest) leaf of tomato was measured using a leaf porometer (SC-1 Meter, METER GROUP) daily between 10:00 AM–03:00 PM after the imposition of transient flooding (Suralta *et al.* 2012) in all treatments.

Shoot Growth Measurements

The number of days to wilting in tomato was recorded daily starting from the day of the imposition of flooding using the scale of Ezin *et al.* (2010) with slight modification**.** After the imposition of flooding treatments, the shoots of tomato from three replicates were cut and oven-dried for 72 h at 70 °C prior to recording of shoot dry weight. At maturity, the fruits of tomatoes were manually harvested, counted, and weighed using a digital weighing balance (Fuji SL-15).

Root Growth Measurements

The root system for both the tomato and rice plants was manually extracted, separated from each plant, and cleaned to remove debris (Suralta and Yamauchi 2008; Kono *et al.* 1987). Thereafter, the roots were kept separately in a plastic container containing 95% ethyl alcohol for further measurements. The total number of nodal roots was counted manually. For total root length (TRL), the roots were extracted and separated between the rice and tomato plants, cut into 3–5-cm lengths, washed with clean water, and spread without overlap on a clear sheet. The roots were scanned using EPSON v800 at 600 dpi. Scanned images were analyzed for TRL using WinRhizo v. 2016d (Régent Instruments, Québec, Canada). For the root length analysis, a pixel threshold value of 175 was set. After the scanning of roots, these were oven-dried for 48 h at 70 °C and recorded of the root dry weight (RDW).

Statistical Analysis

The analysis of variance was conducted to examine the primary effects of water and plant culture treatments, along with their interactions using the Statistical Tool for Agricultural Research (STAR). Differences in treatment means were assessed using the standard deviation of means and/or paired t-tests. Pearson correlation analysis was used to determine the relationship among selected traits.

RESULTS AND DISCUSSION

There are studies that have examined the mixed planting of rice-upland cereal crops and rice-legume crops subjected to flooding conditions for the survival of flood-susceptible crops (Iijima *et al.* 2016, 2017, 2022). However, the potential of mix-planting tomatoes with rice under similar conditions remains unexplored. In this study, tomato was mix-planted with rice and subjected to a 4-d transient flooding during the vegetative stage. We hypothesized that following transient flooding of tomato mix-planted with rice, the tomato will survive and produce yield due to the ROL from rice roots that will serve as a source of O_2 for its root requirement.

Effect of Mix-planting with Rice on the Soil O_2 Concentration and Root Growth of Tomato under Flooding

Figure 1 shows the dynamics of soil-dissolved O_2 concentration during and after transient flooding. Immediately after the imposition of transient flooding, the average soil O_2 concentration was at 4.3 mg/L (data not shown). However, this value decreased rapidly 1 d after the imposition of flooding. Between monoculture- and tomato mix-planted with rice varieties, the latter has evidently had higher O_2 concentrations especially the one mix-planted with NSIC Rc 216 (Figure 1A). After transient flooding, the soil O_2 concentrations increased rapidly in tomato mix-planted with rice – especially NSIC Rc 216 – relative to monoculture tomatoes, which maintained a low soil water O_2 (Figure 1B).

In the present study, the susceptibility of tomato plants to transient flooding was mitigated when mix-planted with rice. However, the benefit of mixed planting with rice was variety dependent as indicated by the better ability of NSIC Rc 216 over that of NSIC Rc 25 in providing O_2 to tomato roots through its ROL. The NSIC Rc 216 is a variety developed and released for irrigated lowland conditions, which may partially explain its better ability than NSIC Rc 25 – an upland variety – in providing O_2 to support the growth of tomato plants while under transient flooding. The better ability of NSIC Rc 216 to release O_2 from its roots is linked to various morphological and metabolic adaptations such as the aerenchyma formation in its roots. These adaptations effectively enhance O_2 diffusion to the roots in waterlogged conditions, reducing the number of cells depending on O_2 for respiration since aerenchyma formation was a result of root cortical

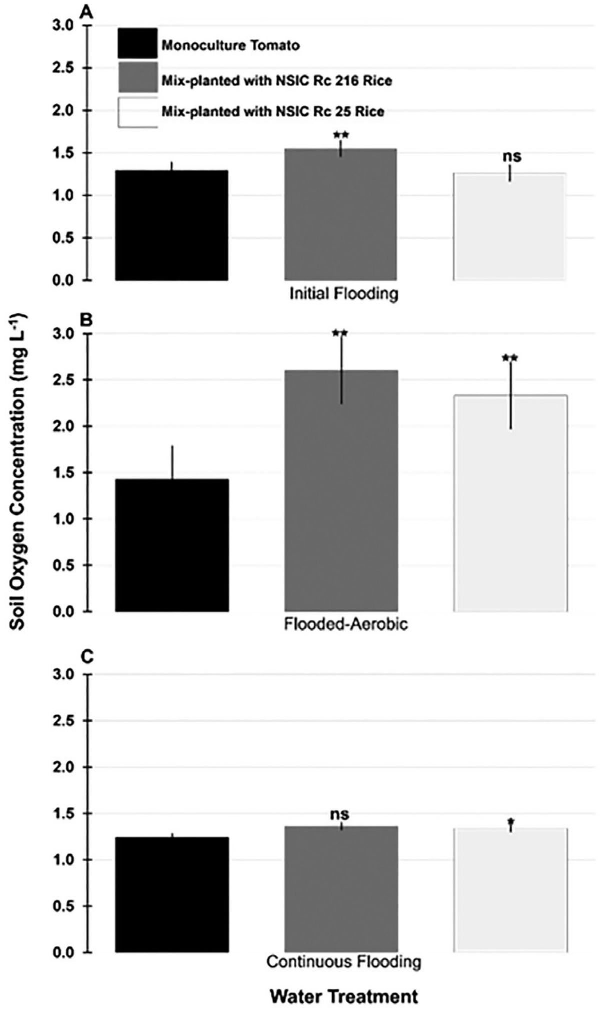

Figure 1. The soil O_2 concentrations in pots planted with tomato as influenced by mix-planting with different rice varieties and subjected to different water treatments [A] at 4 d during initial flooding and [B] at 8 d after either transiently- and continuous flooding conditions. No data for aerobic conditions since no available soil water can be extracted for O_2 concentration measurements. In each water treatment, ** and * indicate significant differences from monoculture tomatoes at $p < 0.05$ and $p < 0.01$, respectively.

disintegration (Suralta and Yamauchi 2008). Additionally, it is important to note that variations in ROL among different plant species can impact the physicochemical parameters and microbial communities within the rhizosphere (Colmer 2003).

Root growth and development are crucial in a plant's ability to withstand abiotic stressed growing environments (Suralta *et al.* 2012). In the present study, root samples were extracted from all water treatments prior to counting of the number nodal roots and measurement of various root lengths. Table 2 shows the different root traits of both tomato and rice plants subjected to transient flooding. Between transient flooding and CF treatments, transient flooding significantly influenced the RDW and TRL of tomatoes, depending on the companion rice variety used. Extended periods of flooding have led to a reduction in root growth (Erhenhi 2019). Remarkably, tomato mix-planted with NSIC Rc 216 had extensive TRL and heavier RDW than monoculture tomato and tomato mix-planted with NSIC Rc 25, with a respective decrease of 23, 6, 62, and 58%. This variation in RDWs was closely linked to available soil O_2 during the flooding period, as tomato plants mix-planted with NSIC Rc 216 had higher soil O_2 levels (Figure 1) and stomatal conductance (Figure 2) compared to the other stress treatments. Typically, under AC, the TRL of tomato was not significantly affected by the mix-planted rice but was generally shorter than that of the TRL of monoculture tomato. Thus, a careful balance between crops for mix-planting should be considered to avoid possible competition for nutrient uptake. A possible competition for soil resources was also evident in the current study as shown by the longer, broader, and heavier fruits observed in monoculture tomatoes compared to mix-planting with rice under non-stress (control) conditions (Table 4).

On the other hand, the TRL of tomatoes was severely reduced under continuous flooding regardless of the plant culture conditions relative to their counterparts under AC. This implied that tomato is sensitive to flooding, as in the case of monoculture, and the inability of rice roots to sustain enough supply of O_2 from its ROL under long-term flooding is due possibly to the development of a barrier to ROL.

Moreover, the rice root growth was also analyzed to check its impact on mix-planting with tomato roots during transient flooding. Interestingly, NSIC Rc 216 displayed a greater number of nodal roots than NSIC Rc 25 due to their differences in the number of tillers per plant which was higher in the former than the latter genotype (Figure 3C). This higher number of nodal roots partially contributed to the increase in the total nodal root length and TRL for NSIC Rc 216, which may explain the higher soil O_2 concentration of the former than the latter rice variety during transient flooding which alleviated the O_2 deficiency experienced by tomato during the condition. This implies that the interaction of different crop species with intertwined root systems can lead to amplifying complementarity effects (Erhenhi *et al.* 2019).

Effect of Mix-planting with Rice on the Stomatal Conductance of Tomato under Flooding Condition

Stomatal conductance, a critical indicator of efficient water uptake and function of the root system in response to water stress (Suralta *et al.* 2012), was quantified in both monoculture tomato and tomato mix-planted with rice varieties. Tomato mix-planted with NSIC Rc 216 exhibited a significantly higher stomatal conductance

Table 2. Root growth of tomato and rice, as influenced by mix-planting with different rice varieties and subjected to various flooding conditions.

Water (W)	Plant culture (P)	Total root length (tomato, cm plant^{-1})	Root dry weight (tomato, g plant^{-1})	No. of nodal root (rice, plant^{-1})	Total nodal root length (rice, cm plant^{-1})	Total root length (rice, cm plant^{-1})
Aerobic	Tomato (monoculture)	6259± 662	0.305 ± 0.03	–	–	–
	Tomato + NSIC Rc 216	3222 ± 1035	0.185 ± 0.01	72 ± 21	9583 ± 1717	57536 ± 6714
	Tomato + NSIC Rc 25	3576 ± 398	0.309 ± 0.08	90 ± 7	8185 ± 2501	44176 ± 15690
Flooded-aerobic	Tomato (monoculture)	882 ± 134	0.034 ± 0.01	–	–	–
	Tomato + NSIC Rc 216	1147 ± 534	0.036 ± 0.01	169 ± 6	9167 ± 1272	63958 ± 27996
	Tomato + NSIC Rc 25	438 ± 266	0.015 ± 0.01	124 ± 45	5928 ± 1918	32707 ± 13233
Continuous flooding	Tomato (monoculture)	719 ± 151	0.029 ± 0.01	–	–	–
	Tomato + NSIC Rc 216	882 ± 591	0.041 ± 0.02	156 ± 12	10613 ± 2430	52986 ± 18250
	Tomato + NSIC Rc 25	1213 ± 822	0.040 ± 0.02	128 ± 38	4779 ± 1321	25568 ± 6090
	W	**	**	**	ns	ns
	P	**	*	**	*	*
	W x P	**	**	*	ns	ns

Values are means of three replications ± standard deviations; [**] highly significant at $p < 0.05$; [*] significant at $p < 0.05$; [ns] not significant

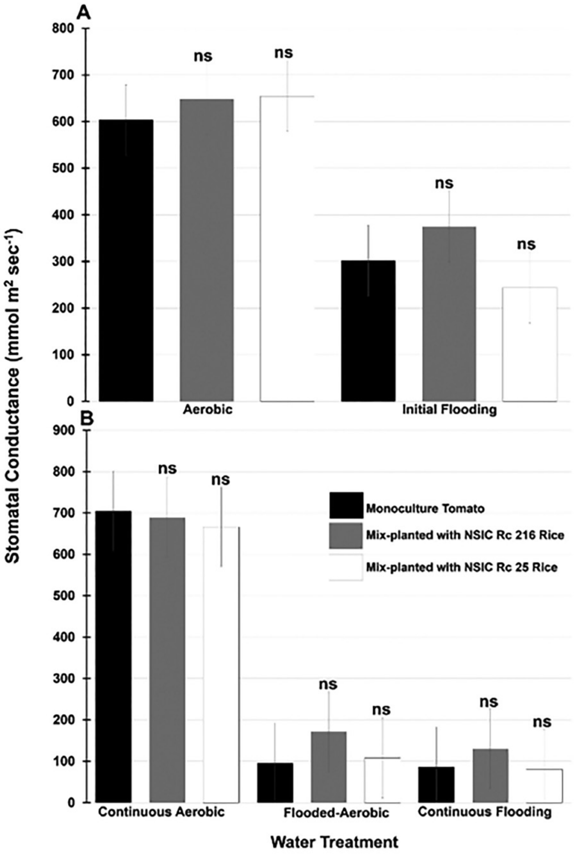

Figure 2. The stomatal conductance of tomato, as influenced by mix-planting with different rice varieties and subjected to different water treatments [A] at 4 d during initial flooding and [B] at 8 d after either transiently- and continuous flooding conditions. In each water treatment, [ns] indicates no significant differences from monoculture tomatoes at $p < 0.05$.

compared to both monoculture tomatoes and those mix-planted with NSIC Rc 25 under transient flooding. This suggests that the presence of NSIC Rc 216 rice positively influenced stomatal conductance in tomatoes, potentially enhancing its ability to regulate water loss and uptake to minimize leaf wilting due to flooding stress. This increase in stomatal conductance in tomato mix-planted with NSIC Rc 216 could be attributed to the O_2 released through ROL (Figure 1). However, the amount of O_2 released through ROL was not significantly related to the overall root system development in terms of TRL (Table 3) but possibly due to differences in exodermal suberin (Watanabe *et al.* 2013) of rice roots developed during AC prior to exposure to transient flooding. The efficient water and nutrient uptake observed in tomato mix-planted with NSIC Rc 216 could be attributed to the availability of soil O_2 supplied by the roots of this rice variety, possibly *via* ROL. Rice plants are known for their ability to release O_2 through their roots *via* ROL, which can create O_2-rich zones in the surrounding soil, even under flooded conditions (Colmer 2003). This O_2 availability may have enhanced the activity of aerobic microorganisms, promoted nutrient availability, and facilitated water uptake by neighboring tomato plants (Zan *et al.* 2021).

The higher stomatal conductance in tomato mix-planted with NSIC Rc 216 rice compared to monoculture and/or tomato mix-planted with NSIC Rc 25 during transient flooding (Figure 2) indicates the availability of O_2 within the root zone (Figure 1), which supports normal function of tomato roots for taking up water. This also indicates that tomato root respiration was less constrained in the presence of NSIC Rc 216 and consequently supports the maintenance of higher stomatal conductance. This partially underscores the intricate balance that plants must maintain between soil O_2 availability to support root respiration and water uptake to maintain stomatal conductance to mitigate the impact of transient flooding on overall growth and development (Pan *et al*. 2021).

However, it is interesting to note that the full recovery of tomato plants mix-planted with rice following transient flooding was not fully achieved. The incomplete recovery within this period suggests a residual effect of flooding even after the stress was withdrawn. Voesenek *et al.* (2004) demonstrated that flooding can have prolonged effects on plant physiology, including alterations in root morphology and stomatal conductance, which may persist even after the removal of the stressor. Setter and Waters (2003) and Colmer and Voesenek (2009) have shown that flooding stress can lead to alterations in gene expression related to O_2 sensing and signaling, further indicating the lasting impact of flooding on plant physiology. Therefore, the incomplete recovery observed in our study underscores the lingering impact of transient flooding on tomato plants and emphasizes the need for further investigation of the long-term effects of such stress events.

Furthermore, the recovery period in the stomatal conductance of tomatoes following transient flooding highlights the resilience of the plants in response to stress. This recovery phase signifies the plant's ability to adapt and restore normal physiological functioning after experiencing the challenges posed by transient flooding. These insights contribute to a deeper understanding of the intricate interplay between root dynamics, stomatal regulation, and resilience mechanisms in plants subjected to transient flooding, thereby enriching our comprehension of their adaptive strategies and potential applications in agriculture.

Relationship between Root Growth of Rice and Soil O_2 Concentration during Transient Flooding under Tomato/Rice Mix-planting

During and after the imposition of transient flooding, there was a strong positive correlation between the number of nodal roots and the total nodal root length of rice and soil O_2 concentrations (Table 3). The relationship between the TRL and soil O_2 concentration tended to be positive under mix-planting during the transient flooding only. This partially suggests that the number and length of nodal roots are the primary source of soil O_2 released through ROL that effectively enhanced the growth of the intercropped tomato by influencing the microenvironments in the rhizosphere (Iijima *et al.* 2016).

Effect of Mix-planting with Rice on the Growth and Yield of Tomato under Flooding

Monoculture tomato and tomato mix-planted with NSIC Rc 25 had similar responses to transient and continuous flooding, which showed an initial wilting of their leaves within the first few days and completely wilted at 7 and 9 d after flooding, respectively (Table 4). Aside from the obvious lack of O_2 in the soil, Ezin *et al.* (2010) also showed that the wilting and yellowing of tomato plants was due to the transport of toxic substances from the soil, through the roots, and up to the leaves. For monoculture tomatoes enduring prolonged flooding, typically spanning 2–3 d, the consequences were severe, resulting in substantial plant mortality and consequently, producing no yield at all. This outcome was primarily due to the excess water saturation of the soil, which hindered gas diffusion and diminished the O_2 supply to the roots (Bhatt *et al.* 2014). In contrast, tomato mix-planted with rice particularly NSIC Rc 216 exhibited partial adaptation to flooding (Figure 3). Although the tomato plants showed

Table 3. The relationship between soil O_2 concentrations and root traits of rice in mix-planted with different rice varieties under subjected to various flooding conditions.

Water (W)	Plant culture (P)	Soil O_2 content *vs.* number of nodal roots		Soil O_2 content *vs.* total nodal root length		Soil O_2 content *vs.* total root length	
		DTF	ATF	DTF	ATF	DTF	ATF
Continuous aerobic	Tomato (monoculture) Tomato + NSIC Rc 216 Tomato + NSIC Rc 25	–	–	–	–	–	–
Flooded-aerobic	Tomato (monoculture)	–	–	–	–	–	–
	Tomato + NSIC Rc 216 Tomato + NSIC Rc 25	0.59*	0.71*	0.48^{ns}	0.72*	0.47^{ns}	$–0.00^{ns}$
Continuous flooding	Tomato (monoculture)	–	–	–	–	–	–
	Tomato + NSIC Rc 216 Tomato + NSIC Rc 25	0.49^{ns}	0.02^{ns}	0.29^{ns}	$–0.16^{ns}$	0.13^{ns}	$–0.27^{ns}$

[–] No water sample extracted to soil O_2 content; [DTF] during transient flooding; [ATF] after transient flooding; [*] significant at $p < 0.05$; [ns] not significant

Table 4. Yield and yield components of tomato as influenced by mix-planting with different rice varieties and subjected to various flooding conditions.

Water (W)	Plant culture (P)	Days to start of wilting	Days to complete wilting	Shoot Dry Weight (g plant^{-1})	Days to recover from the start of transient flooding	Fruits (no. plant^{-1})	Fruit weight (g plant^{-1})
Continuous aerobic	Tomato (monoculture)	–	–	5.05 ± 1.4	–	6.0 ± 1.5	207.7 ± 30.0
	Tomato + NSIC Rc 216	–	–	5.12 ± 0.4	–	6.0 ± 2.1	124.0 ± 28.8
	Tomato + NSIC Rc 25	–	–	6.50 ± 0.6	–	6.0 ± 1.5	159.7 ± 12.9
Flooded-aerobic	Tomato (monoculture)	2.0 ± 0.6	7.0 ± 1.7	2.34 ± 0.1	–	–	–
	Tomato + NSIC Rc 216	4.0 ± 1.0	–	2.36 ± 0.4	8 ± 1	2.0 ± 0.6	41.0 ± 16.7
	Tomato + NSIC Rc 25	2.0 ± 0.6	9.0 ± 0.6	1.63 ± 0.6	–	–	–
Continuous flooding	Tomato (monoculture)	3.0 ± 1.5	7.0 ± 0.6	2.18 ± 0.7	–	–	–
	Tomato + NSIC Rc 216	4.0 ± 0.6	–	2.54 ± 0.4	14.0 ± 0	1.0 ± 1.7	21.0 ± 36.4
	Tomato + NSIC Rc 25	2.0 ± 0.6	9.0 ± 0.6	2.83 ± 0.9	–	–	–
	W	ns	ns	**	*	*	*
	P	**	*	ns	*	ns	*
	W x P	ns	ns	ns	*	ns	*

Values are means of three replications ± SD; [*] highly significant at $p < 0.01$; * significant at $p < 0.05$; [ns] not significant; [–] tomato plant does not completely wilt

initial wilting after 4 d of flooding, they did not completely wilt under either transient or CF treatments. This can be attributed to the higher ROL in the roots of NSIC Rc 216 developed under AC prior to exposure to transient flooding as evidenced by high soil O_2 concentration during the condition (Figure 1).

The shoot dry weight of the tomato was significantly reduced by both transient and continuous flooding conditions relative to the non-stress (control) conditions (Table 4), as similarly shown by Erhenhi *et al.* (2019). Furthermore, the yield of tomatoes in monoculture or mix-planted with rice under AC produced fruits with heavier weight compared to tomato mix-planted with rice. Under flooding, however, only the tomato mix-planted with NSIC Rc 216 yielded fruit in both the transient and continuous flooding. Furthermore, the tomato mix-planted with NSIC Rc 216 under transient flooding also produced more fruits relative to its CF counterparts. This indicates that mix-planting tomato with a suitable rice variety may not be enough to support its growth and yield under prolonged flooding. Colmer *et al.* (1998) showed that rice grown under stagnant (O_2 deficient growing conditions) had developed a strong barrier to ROL compared to those grown under aerated conditions, which improved the transport of atmospheric O_2 from the base to the nodal roots to the growing tips. In this study, rice was initially grown under aerobic (partially saturated) soil conditions to simulate a favorable growing environment for tomato growth prior to the imposition of flooding. This may suggest that the roots of NSIC Rc 216 intercropped to tomato developed during AC may have an initially low barrier to ROL during the early period of transient flooding. However, as the duration of flooding has extended, the newly developed roots of NSIC Rc 216 may have started to form a strong barrier to ROL leading to a smaller amount of O_2 concentration leaking into the soil (Figure 1). Flooding can reduce the number and size of tomato fruits (Tareq *et al.* 2020) due to the restricted nutrient uptake by the roots due to hypoxia and decreased soil nutrient levels. Prolonged flooding durations can exacerbate yield reductions (Ide *et al*. 2022).

CONCLUSION

The ROL from rice roots can be a source of O_2 for tomato roots under mix-planting during transient flooding. Consequently, the difference in soil O_2 concentration as

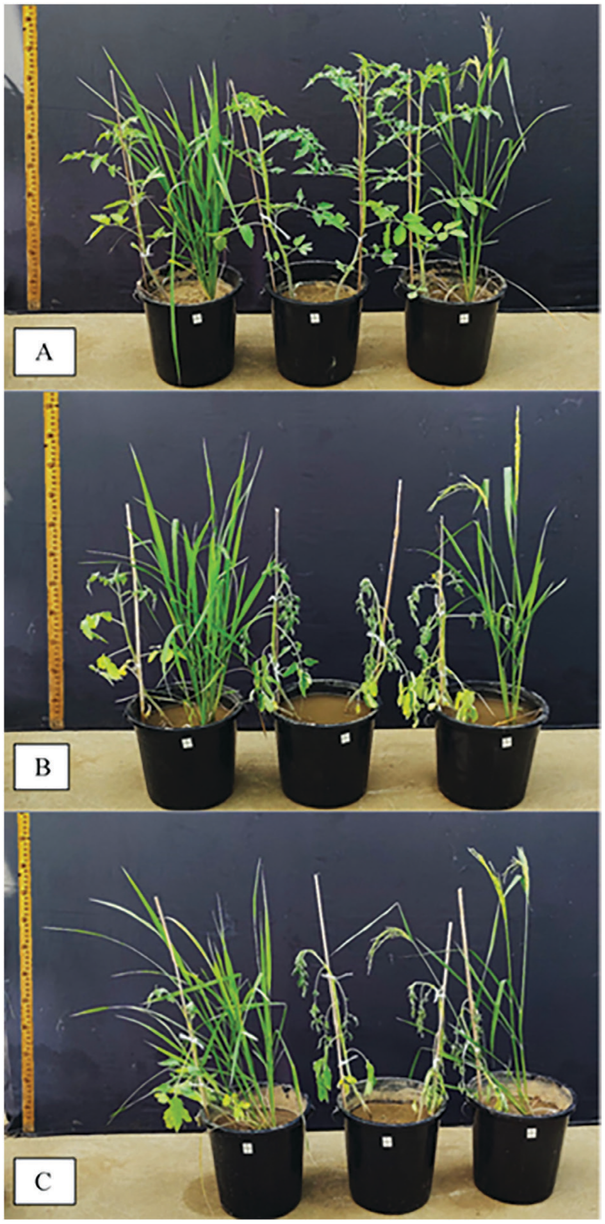

Figure 3. Tomato plants (Diamante max F_1) at five days after imposition of transient flooding: [A] aerobic, [B] flooded-aerobic, and [C] continuous flooding condition. In each photo, left to right: tomato mix-planted with NSIC Rc 216 rice; monoculture tomato and tomato mix-planted with NSIC Rc 25 rice.

possibly brought about by the difference in ROL between the two rice varieties would influence the tomato roots to continue their functions in taking up water and possibly nutrients during transient flooding to maintain the higher stomatal conductance in tomato mix-planted with rice. This consequently mitigated the impact of transient flooding to leaf wilting in tomatoes under the tomato/rice mix-planting and thus supports its higher photosynthetic activity and yield. However, the performance of tomato mix-planted with rice under transient flooding was genotype-dependent. Furthermore, tomato mix-planted with rice can only perform better under transient flooding but not under continuous flooding, which may indicate that rice can only support the partial O_2 requirements of tomato during short transient flooding after heavy rainfall enough to survive until flooding has subsided or the rice used in this study may have limited capacity to support tomato under prolonged flooding. Thus, further studies are needed to explore potential rice genotypes as a source of O_2 to tomatoes under transient flooding and/or how long it can support tomatoes when prolonged flooding has occurred, and the ability of roots to form aerenchyma during transient flooding and their ability to develop a barrier to ROL under continuous flooding.

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