DOI: 10.22620/agrisci.2025.44.002

Responses of tomato plants in mixed-planting with rice during reproductive stage transient flooding

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Abstract

Tomato is a nutritionally rich and economically important crop in the Philippines. Its production is challenging in hot and humid lowland areas due to transient waterlogging during monsoon months. This study investigates the potential of mixed-planting of tomato and rice in attempt to mitigate the adverse effects of transient flooding during reproductive stage. The experiments used split-plot in a randomized complete block design (RCBD) where water treatments (continuous aerobic, flooded-aerobic, and continuous flooding) were the main plots, and plant culture (monoculture and mixed-planting) were subplots. Results showed that tomato and NSIC Rc 216 mixed-planting significantly improved the soil oxygen levels and tomato's physiological responses compared to the monoculture and mixed-planting with NSIC Rc 25. The robust root system of NSIC Rc 216 facilitated a better oxygen diffusion via the radial oxygen loss (ROL) phenomenon, which enhance soil oxygenation and support tomato root respiration under waterlogged conditions. Consequently, the mixed-planting of tomato with NSIC Rc 216 exhibited higher stomatal conductance, prolonged resistance to wilting, and increased root and shoot growth under transient flooding during reproductive stage. Moreover, the study showed a positive correlation between soil oxygen concentration and rice total root length, highlighting the crucial role of rice roots in the maintenance of soil oxygen levels. These findings underscore the importance of selecting rice varieties with strong ROL capabilities for mixed-planting systems aimed at mitigating transient flooding stress in tomato cultivation.

Keywords: Tomato, ROL, rice, transient flooding, mixed-planting, reproductive stage

INTRODUCTION

Tomato (*Solanum lycopersicum* L.) is one of the high valued crops in the Philippines (Conde & De Asis, 2021) with high vitamin and mineral contents (Tareq et al., 2020) crucial to body's nutritional requirements (Pavithra & Sujatha, 2019). Tomato is considered to be one of the most profitable crops and the second most important fruit vegetable in the country after eggplant (Altoveros & Borromeo 2007). However, in 2022, the tomato production reached 216,610 MT, which was lower than the previous years (PSA, 2022). Tomato production is negatively affected in hot and humid lowland areas of tropics during monsoon months due to transient occurrences of waterlogging, as a consequence of heavy rainfall, improper irrigation, land unevenness, inadequate drainage, heavy soil composition, and flooding (Nicola et al., 2009). Waterlogging may cause yield loss in tomato from 10 to 40% in some cases (Ezin et al., 2010). In the plant rhizosphere, the waterlogging altered the morphological and physiological responses (Pavithra and Sujatha, 2019) due to the limitation of oxygen, a condition to which tomato is sensitive (Tareq et al., 2020).

Since the demand for production of tomato is predicted to increase due to population growth (Ohashi et al., 2022) and climate change, the efficient production technology needs to be developed. Mixed-planting can contribute to sustainable agricultural intensification by enhancing the efficiency of land and resource utilization in crop production (Martin-Guay et al., 2018, Tilman, 2020). As per definition, a mixed-planting involves two or more crop species or genotypes growing together at the same time (Brooker et al., 2015). It is prevalent in regions with extensive subsistence farming and limited agricultural mechanization, typically practiced by small-scale farmers who rely on labor-intensive, low-input methods that usually result in lower yield (Ngwira et al., 2012). Under these circumstances, the mixed-planting can increase the aggregate yield per unit input, shields from crop failure and market fluctuations, meets food preference and/or cultural demands, protects and improves soil quality, and increase income (Rusinamhodzi et al., 2012).

Rice, having a well-developed aerenchyma tissue both in root and stem can withstand the effect of waterlogging (Tareq et al., 2020). Research on mixed-planting with rice has mostly focused on pairing rice with drought-tolerant cereals and legume mixtures (Iijima et al., 2022). As rice is naturally tolerant to flooding, combining it with flood-sensitive crops can be a global strategy to improve climate change resiliency (Iijima et al., 2017). Awala et al. (2016) has highlighted the "radial oxygen loss" (ROL) phenomenon, where flood-adapted crops release oxygen to the rhizosphere, potentially mitigating the flooding effects on sensitive crops. Wang et al. (2024) published into diverse mixed-planting systems and the physiological mechanisms of crop interactions, highlighting how complementary root architectures and nutrient exchange can enhance overall crop productivity and resilience. Additionally, recent research on climate-resilient agricultural practices (Gupta et al., 2024) contributes on how innovative irrigation techniques and drought-resistant crop varieties can mitigate the impacts of climate change on agriculture. Recent literature (Chen et al., 2023) supports exploring innovative mixed-planting approaches to enhance yield and sustainability.

Earlier, we proposed a new idea related to the mixed-planting of tomato and rice during vegetative stage to leverage the oxygen released through ROL during flooding. Interestingly, the tomato plants survived during short-term transient flooding was able to yield at maturity when mixed-planted with NSIC Rc 216 (Pascua et al., 2024).

The purpose of this study was to assess the growth and yield of tomato mixed-planting with rice under transient flooding conditions during reproductive stage of tomato. This study seeks to contribute to the understanding of mixed-planting by exploring a novel approach.

MATERIALS AND METHODS

Plant Materials

A hybrid tomato variety and two rice varieties were used in the study. The tomato hybrid variety, Diamante max F_1, is a high yielding, heat tolerant hybrid with intermediate resistance to “kulot” or ToLCV and bacterial wilt. Its fruits are round, firm with excellent transportability and storability (East-West Seed, 2022). The used rice varieties were NSIC Rc 216 and NSIC Rc 25. The NSIC Rc 216 is an irrigated lowland rice variety while the NSIC Rc 25 is an upland rice variety (Pinoy Rice Knowledge Bank, 2022).

Experimental design and treatments

The experiment was laid-out in a split-plot Randomized Complete Block Design (RCBD) with six replications (1 pot = 1 replication). The water treatments were assigned as the main plot and the plant culture treatments as subplots (Table 1).

Table 1. Treatment combinations used in the study

Water regime	Plant culture combinations
Continuous Aerobic (22% SMC throughout the experiment)	Tomato (monoculture) Tomato + rice (NSIC Rc 216) Tomato + rice (NSIC Rc 25)
Flooded-Aerobic (Transient Flooding) (50% SMC for 4 days, 22% for 4 days)	Tomato (monoculture) Tomato + rice (NSIC Rc 216) Tomato + rice (NSIC Rc 25)
Continuous Flooding (50% SMC for 8 days)	Tomato (monoculture) Tomato + rice (NSIC Rc 216) Tomato + rice (NSIC Rc 25)

Water treatment was composed of continuous aerobic (non-stress control treatment), flooded-aerobic (transient flooding), and continuous flooding (stress control treatment). Plant culture treatments were: monoculture tomato (control), mixed-planting of tomato with NSIC Rc 216 or NSIC Rc 25. Three replications were sampled after water treatment during the reproductive stage, and the other three replications were sampled during the maturity stage.

Soil and pot preparation

Loamy sand soil was sieved to remove debris and sundried for two days to reduce moisture content. Each pot (28 cm x 28 cm, H x D) contained 14.5 kg soil.

Establishment of tomato and rice in a single pot

The rice was established 23 days ahead of 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 days before transplanting.

The tomato seeds were pre-germinated and sown in seedling trays containing the same media as that in rice at two days after transplanting (DAT) of rice. The tomato seedlings were grown using the standard management in AgriPinoy (2017). At 28 days old, the tomato seedlings were transplanted in pots which contained the preliminary planted rice plants according to the treatment combinations (Table 1). For mixed-planting treatment, each pot contained one plant per tomato and rice variety. In the monoculture, the pot contained two plants of tomato spaced at 15 cm apart from each other.

Water Management

Soil moisture content (SMC) was maintained at 22% until 21 DAT of tomato. The 22% SMC was identified as the field capacity of the used loamy sand based on our estimation of its 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 soil weight and expressed as percentage. The water treatment was done at the reproductive stage (31 DAT) of tomato. In the continuously flooded treatment SMC was maintained at 50% for eight days while in continuous aerobic, SMC was maintained at 22% (field capacity). In flooded-aerobic, SMC was maintained at 50% for four days and then allowed to decline and maintained at 22% SMC for another four days. Watering was done every two days to achieve the desired SMC (Suralta &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 level of SMC. The exact volume of water was computed by subtracting the present weight of the pot from the target weight of the pot (computed based on desired SMC).

Nutrient Management

Fertilizer application was based on the nutritional requirement of rice plants using a 90-60-60 kg NPK rate per hectare basis. Complete fertilizer (14% N, 14% P, 14% K) was applied before transplanting at the rate of 60 kg ha^{-1} (3.11 g pot^{-1}). Additional N (urea, 45% N) was applied at 7 and 30 DAT at the rate of 15 kg ha^{-1} (0.47 g pot^{-1}).

Harvesting

Matured tomato fruits from survived plants were harvested at stage of turning to pink from 115 to 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 tomato in which fruits were developed and hence mature at different times.

Soil O_2 Concentration Measurements

Soil water O_2 concentrations were measured during the transient flooding. An air stone attached to a hose was installed at the center of each pot between the tomato and rice plants at 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 into the tube containing the extracted soil water to measure the O_2 concentration using the Dissolved Oxygen (DO) sensor meter (Portable DO Meter AS720, AS ONE).

Stomatal Conductance Measurements

The stomatal conductance of the fully developed leaf of tomato was measured daily between 10:00 am to 3:00 pm after the application of water treatments using a leaf porometer (SC-1 Meter, METER GROUP) (Suralta *et al.* 2012).

Shoot Growth Measurements

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

Root Growth Measurements

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

Statistical Analysis

The analysis of variance (ANOVA) was conducted to examine the primary effects of water and planting culture treatments, along with their interactions using 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 for determining the relationship among selected traits.

RESULTS AND DISCUSSION

Effect of mixed-planting of tomato and rice on the soil oxygen concentration under transient flooding during reproductive stage

Figure 1 shows the soil oxygen concentration at the initial and after transient flooding. Immediately after the application of transient flooding, the average soil oxygen concentration was 3.36 mg L^{-1}. This value decreased rapidly a day after the flooding. Between monoculture tomato and tomato mixed-planting with rice varieties, the latter has evidently higher oxygen concentrations especially in treatment of mixed-planting with NSIC Rc216 (Figure 1A). After the transient flooding, the soil oxygen concentrations in the mixed-planting of tomato and rice remained higher, relative to the monoculture tomato which a low soil water oxygen (Figure 1B).

In this study, the susceptibility of tomato plants to the transient flooding stress was mitigated by the mixed-planting with rice. However, the used varieties differed, the variety NSIC Rc 216 showed a better ability than NSIC Rc 25 to deliver oxygen to tomato through ROL at the beginning of flooding. NSIC Rc 216 is a variety developed and released for irrigated lowland conditions, which may partially explain its higher ability in providing oxygen support to the roots of tomato plants than the NSIC Rc 25 which is an upland variety. The higher ability of NSIC Rc 216 to release oxygen from its roots are linked to various morphological and metabolic adaptations, such as the formation of aerenchyma in its roots. These adaptations effectively enhance oxygen diffusion to the roots in waterlogged conditions, reducing the number of cells relying on oxygen for respiration (Suralta & Yamauchi, 2008). Additionally, it is important to note that the variations in the root ROL among different plant species can affect the physicochemical parameters and microbial communities within the rhizosphere (Colmer, 2003). Understanding these intricate interactions is crucial for enhancing crop resilience in transiently flood-prone areas and optimizing the agricultural practices.

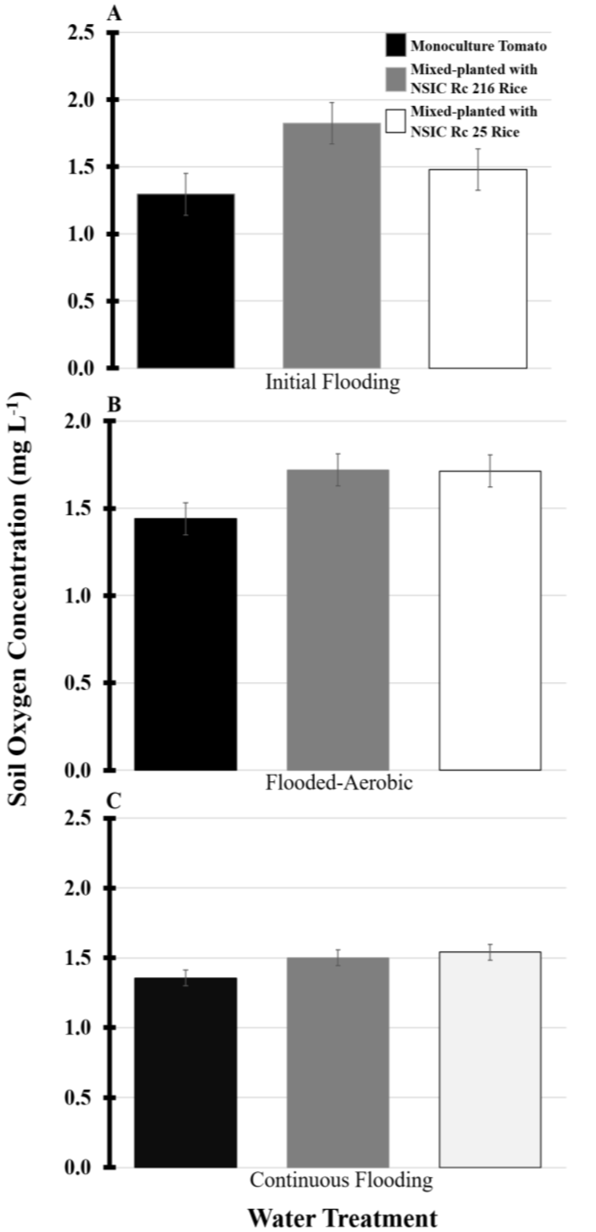

Figure 1. The soil oxygen concentrations in pots planted with tomato as influenced by mixed-planting with different rice varieties subjected to different water treatments. (A) At 4 days during initial flooding and (B and C) at 8 days after either transiently- and continuous flooding conditions during reproductive stage.

Root growth and development play a key role in a plant's ability to withstand soil abiotic stress conditions (Suralta et al., 2012). In this study, the root samples were extracted from all water treatments prior scanning in order to measure the total root lengths. Figure 2 shows the total root length of rice plants subjected to transient flooding. Interestingly, the total root length of NSIC Rc 216 was longer than that of NSIC Rc 25, which may partially explain the higher soil oxygen concentration of the NSIC Rc 216 during transient flooding, which alleviated tomato oxygen deficiency. This implied that the interaction of different crop species with intertwined root systems can lead to amplifying complementarity effects (Erhenhi et al., 2019). Furthermore, it is worth noting that the differences in the crop adaptation to various abiotic stresses can result in distinct optimal environmental characteristics. Plant root and shoot systems react differently to floods and drought conditions, consequently leading to variations in plant morphology and root system anatomy (Iijima et al., 2022). These facts indicate that revealing the complex interplay between plant species, their roots, and environmental factors will shed light on the importance of considering these dynamics in agricultural practices.

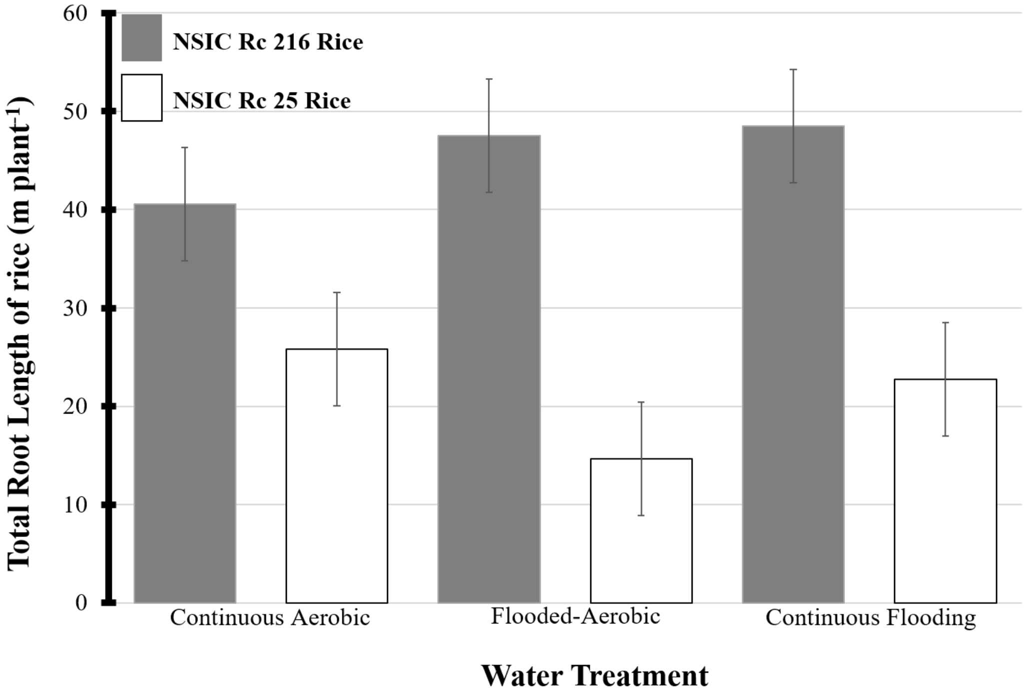

Figure 2. Total root length of two rice varieties under mixed-planting with tomato under various water treatments during reproductive stage.

Relationship between root growth of rice and soil oxygen concentration during transient flooding

The study found a positive correlation (r=0.48) between rice root length and soil oxygen concentration during transient flooding (Figure 3), especially under transient-aerobic conditions, while continuous flooding showed a negative relationship. These suggest that rice roots were a primary source of soil oxygen, which benefits tomato by improving the rhizosphere microenvironment, as demonstrated by Iijima et al. (2016). During transient flooding, the rice root growth is crucial for maintaining the soil oxygen levels through ROL, which supports the respiration and metabolism of both rice and tomato roots. Continuous flooding, however, still leads to prolonged hypoxia, a stunted root growth and possibly reduced ROL as the new formed rice roots tended to adapt to flooding and minimized the oxygen loss. This may consequently reduce the diffusion of oxygen to the soil and negatively affect the tomato plants.

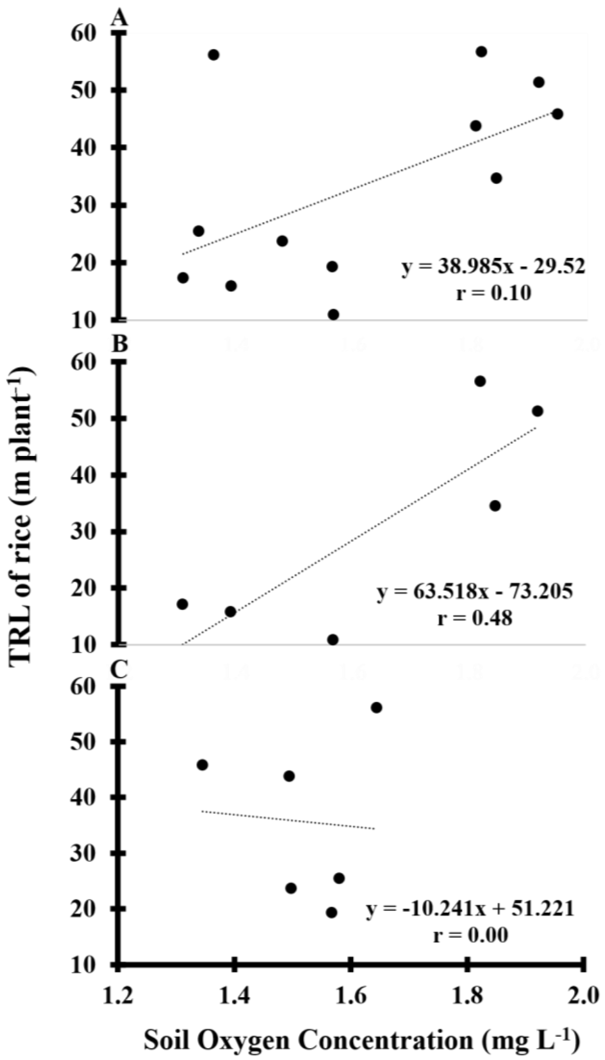

Figure 3. The relationship between the soil oxygen concentrations and TRL of rice in mixed-planting with different rice varieties subjected to various water treatments during tomato reproductive stage. (A) at 4 days during initial flooding of flooded-aerobic and continuous flooding (B) flooded-aerobic condition (C) continuous flooding.

The results highlight the importance of using rice varieties with strong ROL capabilities, such as NSIC Rc 216, and how long it can provide the oxygen to the roots of the flood-sensitive crops in a transiently flood-prone mixed-planting systems and to enhance its resilience and productivity. Understanding the link between the root growth and soil oxygenation is essential for sustainable agriculture in challenging environments.

Effect of mixed-planting with rice on the stomatal conductance of tomato under transient flooding during reproductive stage

Stomatal conductance, a critical indicator of efficient water uptake and root system development in response to water stress (Suralta et al., 2012), was quantified in both monoculture and tomato`s mixed-planting with different rice varieties. Under transient-aerobic condition, tomato with NSIC Rc 216 exhibited a higher stomatal conductance than either in monoculture and mixed-planted with NSIC Rc 25. This indicated that the roots of tomato mixed-planted with NSIC Rc 216 functioned well in taking up water and nutrient during transient flooding because of higher availability of soil oxygen supplied via ROL and rice variety in comparison to NSIC Rc 25 (Figure 4). Understanding the relationship between stomatal conductance and root respiration is pivotal in comprehending plant responses to stress caused by flooding. Previous research showed that there is often a delicate balance between achieving efficient water uptake, as reflected by stomatal conductance, and the oxygen-dependent processes associated with root respiration (Smith & Brown, 2019). The rate of photosynthesis and stomatal regulation are critical aspects of plant physiology affected by abiotic stress. Water stress, for example, can significantly curtail photosynthesis. Plants respond by swiftly closing their stomata to conserve moisture, thereby reducing transpiration, which in turn affects the exchange of CO_2 within the leaves.

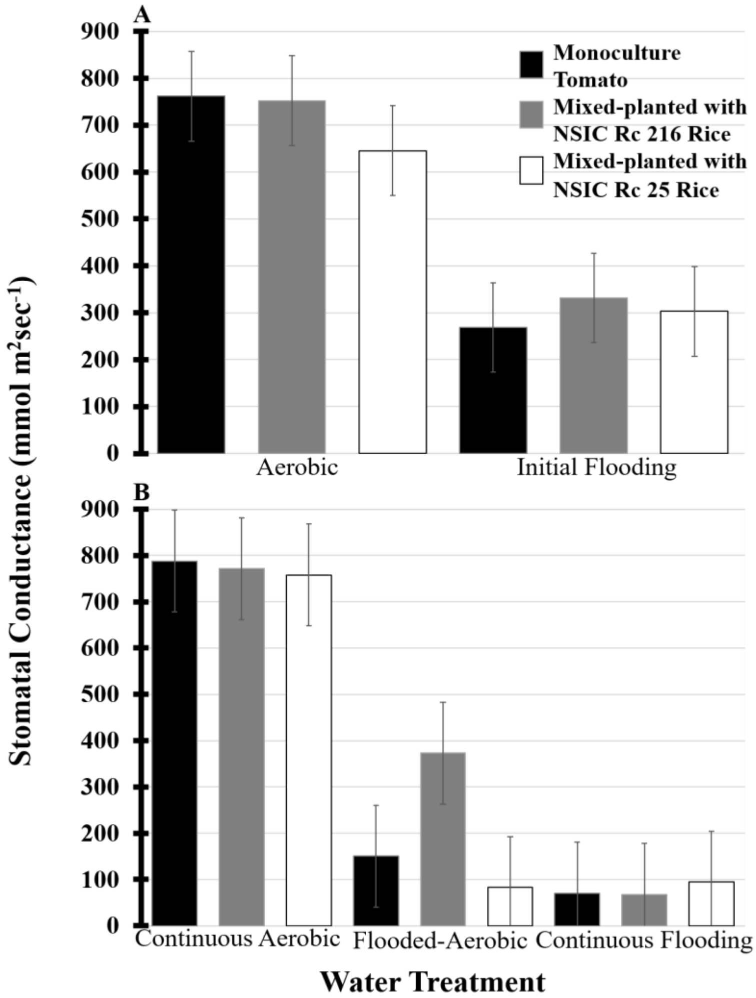

Figure 4. The stomatal conductance of tomato as influenced by the mixed-planting with different rice varieties and subjected to different water treatments during reproductive stage. (A) At 4 days during initial flooding and (B) at 8 days after either transiently- and continuous flooding conditions.

This reduction in stomatal conductance is linked to decreased photosynthesis in plants growing under abiotic stress conditions (Suralta et al., 2018; Zhang et al., 2017; Suralta et al., 2010).

Several studies underscored the far-reaching influence of abiotic stress on plant processes. Water stress, in particular, has a profound impact on photosynthetic enzymes and their efficiency, resulting in suppressed metabolic processes and damage to the photosynthetic machinery (Saxena et al., 2019). On the other hand, flooding restricts the availability of oxygen in the root zone, compelling plants to shift from aerobic to anaerobic respiration, thereby affecting energy metabolism and various biochemical and developmental processes (Pan et al., 2021).

The consistently higher stomatal conductance in mixed-planted tomato with rice variety NSIC Rc 216 during and after transient flooding than in tomato mixed-planted with NSIC Rc 25 indicated a higher availability of soil oxygen in the root zones in the former combination than in the latter. This indicates that tomato roots respiration under transient flooding was less constrained in the presence of NSIC Rc 216 and consequently supports the maintenance of its stomatal conductance. This partially underscores the intricate balance which plant must maintain, firstly between the soil oxygen availability in order to support the root respiration, and secondly, the uptake of water in order to maintain the stomatal conductance and to mitigate the impact of transient flooding on the overall growth and development (Pan et al., 2021).

Effect of mixed-planting with rice on the growth of tomato under transient flooding during reproductive stage

Tomato plants in monoculture showed similar responses towards transient and continuous flooding with signs of initial wilting of leaves within two days after flooding and completely wilted at seven and six days after flooding, respectively (Table 2). Ezin et al. (2010) showed that the wilting and yellowing of tomato plants under flooded conditions was attributed to reduced soil oxygen that triggered the transport of toxic substances from the soil, through the roots, and up to the leaves. For monoculture tomato subjected to continuous flooding, the typical consequences were severe starting within 3 days and resulted in the death of the plants and thus, yield loss. This outcome was primarily due to the excess water saturation of the soil, which hindered gas diffusion and diminished the oxygen supply to the roots (Bhatt et al., 2014). In contrast, the mixed-planted tomato, in particular with the NSIC Rc 216 variety exhibited an adaptation to both transient and continuous flooding. The tomato plants showed initial wilting after 4 days of flooding but did not wilt completely either under transient and continuously flooded conditions indicating that root respiration continued because of continuing oxygen supply from the rice roots especially in mixed-planted with NSIC Rc 216. This rice variety is bred for irrigated lowland environments with a characteristically shorter plant height and vigorous tillering ability, and hence better adaptation to continuously flooded conditions. On the other hand, tomato with NSIC Rc 25 exhibited an adaptation in the transient flooding which showed a partial wilting starting at three days after transient flooding, although did not wilt completely. However, under continuously flooded condition, tomato mixed-planted with NSIC Rc 25 wilted completely at six days after flooding indicating the poor ability of rice variety to supply oxygen to the roots of tomato under such conditions.

Table 2. Days to wilting and the total root length of tomato as influenced by mixed-planting with different rice varieties subjected to various water treatments during reproductive stage.

Water (W)	Plant culture (P)	Days to start wilting	Days to complete wilting	Total Root Length (tomato, m plant^{-1})
Continuous Aerobic	Tomato (monoculture)	-	-	18.03 ± 4.90
	Tomato + NSIC Rc 216	-	-	7.93 ± 4.88
	Tomato + NSIC Rc 25	-	-	7.01 ± 2.22
Flooded-Aerobic	Tomato (monoculture)	2 ± 0	7 ± 1	3.36 ± 0.37
	Tomato + NSIC Rc 216	4 ± 1	x	4.36 ± 2.97
	Tomato + NSIC Rc 25	3 ± 1	x	2.34 ± 1.13
Continuous Flooding	Tomato (monoculture)	2 ± 0	6 ± 0	2.78 ± 1.21
	Tomato + NSIC Rc 216	4 ± 1	x	3.37 ± 3.08
	Tomato + NSIC Rc 25	3 ± 1	6 ± 0	0.87 ± 0.24
W				**
P				*
W x P				*

*Legend: x - Did not wilt during flooding; * significant; ** highly significant at p<0.05*

The extended periods of flooding led to a noticeable reduction in root growth (Erhenhi, 2019). The transient flooding significantly influenced the total root length of tomato, depending on the companion rice variety. Remarkably, tomato mixed-planted with NSIC Rc 216 had longer total root length compared to the monoculture cultivation and tomato with NSIC Rc 25, with had of 23 and 46% lower total root length. This variation in the total root length was closely linked to the difference in soil oxygen, as tomato plants with NSIC Rc 216 demonstrated higher soil oxygen levels (Figure 1) and stomatal conductance (Figure 4) compared to the other treatments.

Relationship between stomatal conductance and the total root length of tomato during transient flooding

There was a positive relationship (r=0.42) between the total root length and stomatal conductance in tomato plant growing under transient flooding-aerobic condition which agreed with previous findings (Bishop et al., 2012) (Figure 5). The stomatal conductance of tomato plants is influenced by the capacity of the roots to absorb water from the soil. A well-developed root system expressed by the total root length enables efficient water uptake, leading to increased stomatal conductance. This indicates that tomato plants which had better growth during transient flooding, especially those which were mixed-planted with NSIC Rc 216, had the advantage of greater recovery in stomatal conductance when the soil water level fluctuated and anaerobic to aerobic conditions followed.

Conversely, there was a negative correlation between the stomatal conductance and the total root length in tomato mixed-planted with rice under continuous flooding conditions. This may be partially attributed to the limited oxygen availability in the soil under prolonged flooding, leading to reduced root growth and development. And as stated above, the rice roots also would adapt to the prolonged flooding by producing roots with higher aerenchyma and reduced ROL (Colmer, 2003) which limited soil oxygen availability to tomato roots in the long run. Under flooding conditions, plants often experience oxygen deficiency, which can negatively affect root respiration and growth (Jackson & Armstrong, 1999) and consequently restricts the uptake of water, leading to decreased stomatal conductance. The positive relationships during transient flooding-aerobic conditions suggest that the root growth plays a crucial role in enhancing stomatal conductance and efficacy of water uptake during periods of fluctuating water levels in the soil (Suralta et al., 2018).

Effect of mixed-planting with rice on the yield of tomato under transient flooding during reproductive stage

The yield of tomato in monoculture or mixed-planted with rice was higher under aerobic condition (Table 3). Under transient flooding condition, tomato mixed-planted with NSIC Rc 216 had higher yield in both the transient and continuous flooding treatments compared to the monoculture counterparts. On the other hand, the yield of tomato mixed-planted with NSIC Rc 25 also produced, however, only minimal yield under transient flooding condition. Furthermore, tomato mixed-planted with NSIC Rc 216 had produced minimal yield under continuous flooding conditions indicating that this variety did not sufficiently support tomato growth and yield.

Colmer et al. (1998) showed that rice grown under stagnant (oxygen deficient growing conditions) had developed a more barrier to ROL compared to those grown under aerated conditions which improved the transport of atmospheric oxygen 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 to tomato growth before flooding.

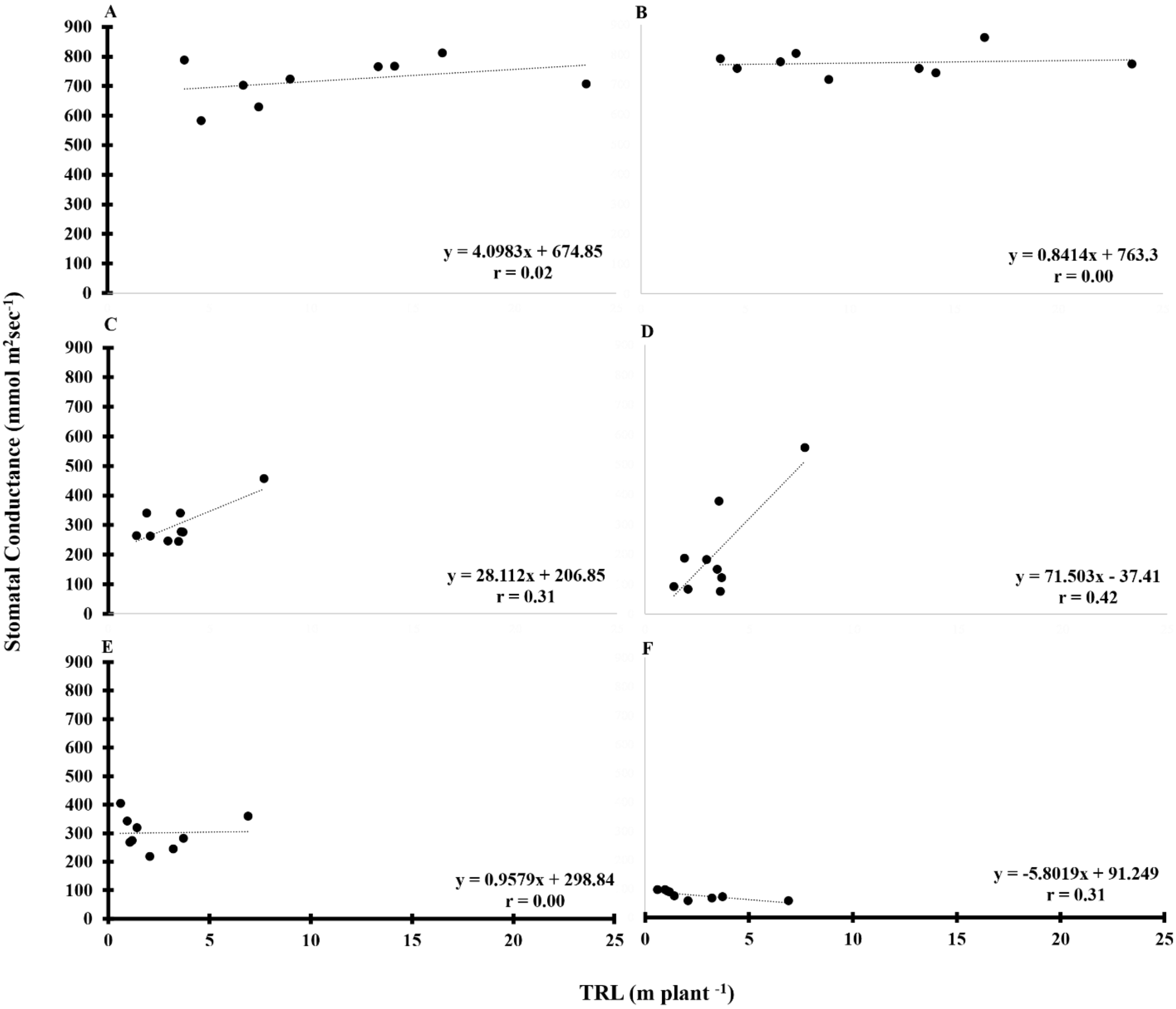

Figure 5. The correlation of stomatal conductance and TRL of tomato in mixed-planting with different rice varieties subjected to various water treatments during reproductive stage. Continuous Aerobic (A) during and (B) after transient flooding; flooded-aerobic (C) during and (D) after transient flooding; continuous flooding during (E) and (F) after transient flooding.

This may suggest that the existing roots of NSIC Rc 216 may have low barrier to ROL during the early period of flooding and hence more oxygen were leaked into the soil. As the flooding progressed, however, the roots of NSIC Rc 216 may have started to form barrier to ROL resulting in minimal amount of oxygen leaked to the soil (Figure 1). Thus, the tomato plants mixed-planted with this rice variety had shown a decrease in yield in comparison to their transiently flooded counterparts.

Flooding can reduce the number and size of tomato fruits due to restricted nutrient uptake of the roots due to hypoxia and decreased soil nutrient levels (Tareq et al., 2020). A prolonged flooding can exacerbate yield reductions (Ide et al., 2022). Based on the data obtained by Tareq et al. (2020), the reduction of photosynthesis and the effect of flooding conditions may result in significant decrease in number of flowers and fruits.

Table 3. Yield of tomato as influenced by mixed-planting with different rice varieties subjected to various water treatments during reproductive stage

Water (W)	Plant Culture (P)	Fruit Weight (kg pot^{-1})
Continuous Aerobic	Diamante	0.17 ± 0.03
	Diamante + NSIC Rc 216	0.14 ± 0.04
	Diamante + NSIC Rc 25	0.13 ± 0.04
Flooded-Aerobic	Diamante	0.00 ± 0.00
	Diamante + NSIC Rc 216	0.07 ± 0.03
	Diamante + NSIC Rc 25	0.04 ± 0.04
Continuous Flooding	Diamante	0.00 ± 0.00
	Diamante + NSIC Rc 216	0.02 ± 0.01
	Diamante + NSIC Rc 25	0.00 ± 0.00
W		**
P		ns
W X P		ns

*Legend: ** highly significant at p<0.05; ns not significant*

The magnitude of changes in reproductive growth varies with plant type and variety, as well as with the time and duration of flooding. Also, the decrease in the yield was also associated with few in number and small in size fruits (Ezin et al, 2010). The low productivity could also be linked to fruits shed by plant before harvest (Tareq et al., 2020).

Awala et al. (2016) showed that the mixed-planting of crops adapted to aerobic soil with rice under flooding conditions were more productive compared to their monoculture counterparts. Under favorable conditions, however, a careful balance between crops for mixed-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 heavier fruits observed in monocultures tomato compared to mixed-planted under aerobic non-stress (control) conditions.

Relationship between total root length and yield of tomato during transient flooding

Figure 6 shows a positive relationship (r=0.09) of total root length of tomato and its yield indicating that the well-developed root system based on the total root length, was related to higher fruit yield. The enhanced root growth, facilitated by higher soil oxygen concentrations released from the roots of NSIC Rc 216, could contribute to maintaining fruit yield even when plants are exposed to transient flooding conditions. Longer roots enable better water and nutrient uptake, crucial for fruit development under transiently flooded conditions.

The enhanced root growth in tomato plants mixed-planted with NSIC Rc 216 was partially attributed to improved soil oxygenation, which supported the aerobic respiration in roots during transient flooding conditions and improved root growth when exposed back to aerobic soil conditions. This oxygenation may be facilitated by the ROL from the rice roots, particularly from varieties adapted to lowland conditions such as NSIC Rc 216. The formation of aerenchyma and other morphological adaptations in NSIC Rc 216 enable efficient oxygen transport to the rhizosphere, mitigating the hypoxic stress of tomato roots. Moreover, the increased root length and associated higher fruit yield suggest that the physical presence of extensive root systems can improve soil structure and moisture retention, further supporting plant health and productivity. This interaction of root length and yield demonstrates the potential benefits of mixed-planting systems, where companion plants like rice can enhance the resilience and output of sensitive crops like tomatoes.

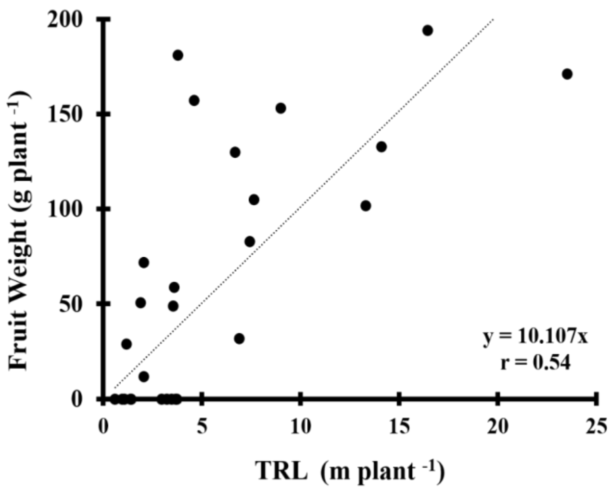

Figure 6. The relationship between yield and TRL of tomato influenced by mixed-planting with different rice varieties subjected to various water treatments during reproductive stage

CONCLUSIONS

The ROL from rice roots can be a source of oxygen for tomato roots under mixed-planting at short-term transient flooding during reproductive stage. However, the survival of tomato plants under short-term flooding in the mixed-planting was dependent on rice genotype. Therefore, the difference in soil oxygen concentration brought about by the difference in ROL between the two rice varieties influenced the tomato roots functions for water uptake, and possibly the nutrients during transient flooding. A higher stomatal conductance in tomato mixed-planted with rice prevented severe wilting and resulted in higher photosynthetic activity and yield. This was clearly exhibited by the higher yield of tomato mixed-planted with NSIC Rc 216 rice compared to those combined with NSIC Rc 25. The superior root system of NSIC Rc 216, in terms of total root length, provided higher amount of ROL during the initial transient flooding. The yield of tomato, however, was further reduced by continuous flooding regardless of rice variety.

ACKNOWLEDGMENTS

The authors thank Ms. Imeldalyn G. Pacada of PhilRice for the use of screenhouse. Special thanks to CLSU Futures Thinking: SPRice UP Pinas 2040 for the use of pots. Sincere appreciation to Mr. Blacer, Mr. Marzan, Mr. Bildua, and Mr. Bruno III for their invaluable support in the study.

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