Analysis of yield reduction factors in processing tomatoes under waterlogging conditions

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Abstract

Waterlogging conditions cause severe abiotic stress and reduce average yields in vegetable crops. Processing tomatoes are cultivated extensively worldwide, and are used in many food products. Recently, processing tomatoes have been cultivated in paddy fields in Hokkaido, northern Japan. Studies are needed to assess the responses of processing tomatoes to wet conditions. The goal of this study was to clarify the mechanisms of waterlogging injury, and to identify ways to mitigate wet injury in processing tomatoes. We used three cultivars in a two year pot experiment and a one year field experiment. Longer waterlogging treatments increased the severity of yield losses in both experiments. The waterlogging treatments initially caused reductions in fruit number and then in average fruit weight. The reductions in fruit number resulted from reduced fruiting ratios. The reductions in average fruit weight may have been triggered by multiple factors, including reductions in soil nutrients, reduced nutrient uptake due to hypoxia, and reductions in the photosynthetic rate. These results suggested that top-dressing with fertilizer after excess rain may help to mitigate yield losses. The waterlogging treatments also induced changes in fruit composition, with reduced water content and increased sugar/acid ratios. The responses to waterlogging treatment varied among cultivars, and we concluded that 'Natsunoshun' is a superior cultivar for cultivation in converted paddy fields that may become waterlogged after heavy rains.

Key words: fruit quality, fruiting ratio, root uptake, waterlogging injury, yield

1. Introduction

Processing tomato (*Solanum lycopersicum* L.) is a widely cultivated horticultural crop that contains many functional nutrients including lycopene and β-carotene, which are vital for human health (Dorais et al., 2008). After processing, these tomatoes are consumed habitually throughout the world in a wide variety of products including ketchup, sauce, juice, and puree (Mirondo and Barringer, 2015). Approximately 38.5 million tonnes of processing tomatoes are produced per year worldwide, with major production areas in California (USA), China, Italy, and Turkey (AMITOM, 2020). Japan is one of the smallest producing countries, with about 25,200 tonnes produced in 2019 (e-Stat, 2020). Processing tomatoes are grown mainly in the central regions of Japan in Nagano and Ibaraki prefectures (e-Stat, 2020). Hokkaido, a mainly agricultural region in northern Japan, has a 200% food self-sufficiency rate, but produces only 3% of domestic processing tomatoes (e-Stat, 2020). However, interest in growing processing tomatoes in Hokkaido has recently increased because temperatures in traditional growing areas are rising due to climate change. This is a serious worldwide problem because high temperatures are a major environmental factor limiting tomato productivity (Silva et al., 2017), even in Japan (Sato, 2006). The reproductive stage appears to be especially vulnerable to temperature increases (Hedhly et al., 2009).

The numbers of farming households in Hokkaido, especially in the paddy field areas, are decreasing due to aging of the population and farmers leaving the agriculture sector. Currently, the cultivation area per farmer in Hokkaido is more than 10 times the national average, so low-cost production systems with low labor inputs are needed. To realize this goal, the National Agriculture and Food Research Organization (NARO) Bio-oriented

Technology Research Advancement Institution ran a project in Hokkaido to promote the production of processing tomatoes and onions, which can generate high crop prices even in converted paddy fields, from 2016 to 2019 (Hokkaido Agriculture Research Center (HARC/NARO), 2018). Some Hokkaido municipalities, such as Numata and Iwamizawa, already have industrial processing plants for processing tomatoes grown on converted or redundant paddy fields (Takahashi and Shiwa, 2018). However, the paddy fields generally have clay soils with quite fine particles, and are unfit for vegetable production under waterlogged conditions.

Recently, water table control systems called farm-oriented enhancing aquatic systems (FOEAS) were developed by NARO and the Paddy Research Co., Ltd. These are designed to regulate the groundwater level to an optimum depth in paddy fields, and are expected to lead to improvements in crop quality and yields (Koshiyama, 2019). Processing tomato is one of the vegetable crops that will potentially benefit from these water table control systems (Jitsuyama et al., 2019). However, it is not feasible to install these systems in all converted paddy fields, and currently, these systems are installed in less than 10% of the total available area of converted paddy fields (Jitsuyama et al., 2019). Without these systems, heavy rains are likely to produce excess moisture conditions in the clay soils of the converted paddy fields. Therefore, while water table control systems provide the best way to realize vegetable cultivation in converted paddy fields, it will also be necessary to identify cultivars with tolerance to excess moisture.

The root’s activity is severely affected by salt, water deficiency, and waterlogging (Morard et al., 2000; Dresboll et al., 2013). Waterlogging results in hypoxia, which has negative effects on root development, plant growth, and longevity (Drew, 1997; Dat et al., 2004). Some research has focused on the effects of waterlogging or low oxygen conditions on table tomatoes or wild varieties (Dresboll et al., 2013; Horchani et al., 2010; Li et al., 2012; Morard and Silventre, 1996; Opeña et al., 1992), but the effects on processing tomatoes cultivated in converted paddy fields have not been investigated. In a previous study, we conducted pot experiments with the cultivar 'Natsunoshun', which is the main cultivar grown in Numata, central Hokkaido. We found that waterlogging treatment after the first flowering stage significantly reduced yields (Jitsuyama et al., 2019).

The goal of this study was to clarify the mechanisms of waterlogging injury in processing tomatoes, and we hope that the suggestions lead to identifying ways to mitigate the waterlogging injury. For these purposes, we investigated the processing tomato's response to waterlogging treatment using three cultivars of 'Natsunoshun', 'Suzukoma' and 'Lycoball', and clarified the differences between the tested cultivars in a two-year pot experiment and a one-year converted paddy field experiment.

2. Materials and Methods

2.1. Pot experiment

2.1.1. Plant materials and plant growth

The pot experiments were performed in 2017 and 2018 in a rain shelter at the Experimental Farm of the Field Science Center for the Northern Biosphere, Hokkaido University, Sapporo, Hokkaido, Japan (N43°07'15", E141°33'87"). Three cultivars of processing tomato (*Solunum lycopersicum* L.): 'Natsunoshun', 'Suzukoma' and 'Lycoball' were tested. 'Natsunoshun' was released from the Nagano Vegetable and Ornamental Crops Experiment Station in 2004 and is a high-yielding cultivar suited to mechanized harvesting (Figure 1A). 'Suzukoma' was released from NARO in 2013 and is suited to soilless culture systems with low node-order pinching and high-density planting (Figure 1B). ‘Lycoball’ was released from the Nagano Vegetable and Ornamental Crops Experiment Station in 2009; it is suitable for tomato juice processing and has a high lycopene content (Figure 1C). ‘Natsunoshun’ is currently the most widely grown processing tomato cultivar in Hokkaido because it is well adapted to the relatively cool summer climate (Yanokuchi et al., 2001).

From late April to early May of each year, seedlings were germinated and grown in 72-cell plug trays filled with potting soil (Nursery soil, Takii & Co., Ltd., Kyoto, Japan) that included basal fertilizer at rates of 320 mg·L^{-1} N, 210 mg·L^{-1} P_2O_5, and 300 mg·L^{-1} K_2O. No additional fertilizer was supplied to the pots during the experiment. These levels of fertilizer application were approximately one-tenth of the conventional levels for cultivation of ‘Natsunoshun’ (Chida et al., 2018). Eighty seedlings were used in each year for each cultivar. After germination, the apical meristems at the third leaf stage were pinched, creating two elongated lateral buds as the main stems of the plants. This is a ground creeping style of training. In early May, the seedlings were transplanted to 240 mm diameter poly-pots with the same nursery soil described above. Maintenance and insect and disease control were done according to standard practices, as described previously (Jitsuyama et al., 2019). Harvesting was done at the optimum time for each cultivar, when the fruits had matured to red (mid-September for ‘Suzukoma’, late September for ‘Natsunoshun’, and early October for ‘Lycoball’ in both years).

2.1.2. Waterlogging treatments

Four types of water stress treatments were created as follows:

CONT: each pot irrigated constantly 4–7 mm day^{-1} using irrigation pipes.

WET3: CONT conditions except for 3 consecutive days of excess soil moisture.

WET5: CONT conditions except for 5 consecutive days of excess soil moisture.

WET10: CONT conditions except for 10 consecutive days of excess soil moisture.

The WET treatments consisted of maintaining 2–3 cm of water on the soil surface. The pots had holes in the bottom to allow for drainage, so thick vinyl bags were used to prevent drainage during the WET treatments. The pots were inserted into the vinyl bags, which were held in place by additional pots (Fig. 1D). The water stress treatments were conducted at the flowering stage when 80% of plants had developed their first flower cluster. In 2017, the treatments were conducted between 17 July and 26 July [90–99 days after sowing (das)] and in 2018 they were conducted between 27 July and 5 August (86–95 das).

The following environmental parameters: soil volumetric water content, pF value, soil dissolved oxygen concentration, air and soil temperature, relative humidity, and cumulative day radiation were also measured. For these measurements, a soil moisture kit (SM150T, Delta-T Devices, Cambridge, UK), a pF meter (DIK-3162, Daiki Rika Kogyo, Co., Ltd., Saitama, Japan), a soil O_2 sensor (MIJ-03, Environmental Measurement Japan Co., Ltd., Fukuoka, Japan), a thermo recorder (R-71U, T AND D, Co., Ltd., Nagano, Japan), and an illuminance UV recorder that included a relative humidity sensor (R-74Ui, T AND D, Co., Ltd., Nagano, Japan) were used. The soil moisture was continuously measured using the kit, and the other soil measurements were conducted by inserting the O_2 sensor, thermo sensor, and pF meter into the pot soil to a depth of 15 cm. These measurements were taken once per day for each treatment, between 10:00 am and midday. The air temperature recorder and the illuminance UV recorder were each set separately at 30 cm above ground which were above the tomato plants, and their data were logged automatically every hour.

2.1.3. Fruit and plant measurements

At harvest time, from mid-September to early October, yield parameters (fresh fruit yield, number of fruits per plant, and average weight of fruit) and fruit harvest parameters (marketable fruit ratio and fruit water content) were measured. In this study, the yield parameters were calculated using sepal-detached fruit, including immature fruit and fruit with blossom-end rot (Fig. 1E). The marketable fruit ratio, immature fruit ratio, and blossom-end rot fruit ratio were calculated using the total fruit number as the denominator. The evaluation of whether or not a fruit was marketable was conducted according to the standards of fruit color and size created by the Numata town tomato processors in Central Hokkaido.

The number of flowers per plant was counted in late August, and calculated the fruiting ratio using the number of flowers as the denominator. The biomass traits (root and shoot dry weight, shoot water content, and leaf area) were also measured in late August. The crop growth rate (CGR) was calculated using all dried biomass including leaves, stems, flowers, fruits, and roots. These were measured in mid-July and again in late August. The dry weights were measured after drying at 80°C for 72 hr with a forced-air dryer. The leaf area of each plant was evaluated at the same times as the biomass traits using a WinRHIZO system (2004a,b, Regent Instruments Inc., Canada), and converted to the mean leaf area index (LAI). The net assimilation rate (NAR) was calculated as the ratio CGR/mean LAI. The plant area was calculated as the area of the top of the poly-pot, approximately 450 cm^2 per plant. The fruit growth rate (FGR) was calculated by using the total fruit weight per plant in mid-July and in late August. The fruit delivery ratio (FDR) was then calculated as FGR/CGR＊100.

2.1.4. Statistical analyses

The experimental design was a split-split plot design with five replications. Main plots, subplots, and sub-subplots were defined as the two experimental years (Y: 2017 and 2018), the four water stress treatments (T: CONT, WET3, WET5, and WET10) and the three cultivars (C: 'Natsunoshun', 'Lycoball', and 'Suzukoma'). The significance in the analysis of variance (ANOVA) was calculated as described by Little and Hills (1978) for the split-split plot design. Other statistical analyses, including the Student's t-test, Tukey-Kramer's test and Pearson's product-moment correlation analysis were done using Statcel4 (developed by Yanai, OMS, Japan), which is an add-in form in Microsoft Excel 2019 for Windows.

2.2. Field experiment

2.2.1. Plant materials and growth

The field experiment was performed in a converted paddy field at the Experimental Farm of the Field Science Center for the Northern Biosphere, Hokkaido University, Sapporo, Hokkaido, Japan (N43°07'56", E141°33'64") in 2019. We used the same three experimental cultivars of processing tomato as in the pot experiment: 'Natsunoshun', 'Lycoball', and 'Suzukoma'.

The seeds were sown in late April, and the seedlings were grown as described for the pot experiment. The paddy field was prepared with basal dressing chemical fertilizer (N:P:K=15:20:40 kg/10a) and plowed to a 20 cm depth. Elongated mounds of 110 cm width and 20 cm height were created mechanically and covered with biodegradable black mulching film (Kiemaru, Unyck, Tokyo, Japan). The seedlings were planted with spacing of 50 cm along the top of each mound. No top dressing was added during the cultivation. Bird repelling nets were used to protect the fruits (Fig. 1F). Harvesting was done at the optimum time for each cultivar: on 12 September (147 das) for ‘Suzukoma’, on 18 September (153 das) for ‘Natsunoshun’, and on 26 September (161 das) for ‘Lycoball’. Maintenance and insect and disease control were done according to standard practices, as described previously (Jitsuyama et al., 2019).

2.2.2. Waterlogging treatments and measurements

Three types of water stress treatments were created as follows:

CONT: field with natural precipitation (pF value greater than 2.0).

WET5: CONT conditions except for 5 consecutive days of excess irrigation.

WET10: CONT conditions except for 10 consecutive days of excess irrigation.

The WET treatments consisted of keeping the soil surface wet (pF value less than 1.7; Fig. 1G) and were conducted between 10 July and 19 July (83–92 das) at the flowering stage when 80% of plants had developed their first flower cluster. The waterlogging treatments were done using irrigation pipes near the planted mounds, and partitions between treatments were created by inserting plastic boards to a depth of 30 cm. The ten acre paddy field has a slight slant from the inlet to the outlet, and the treatments were ordered from the inlet as follows: CONT, WET5, WET10.

The environmental parameters (soil volumetric water content, pF value, soil dissolved oxygen concentration, air and soil temperature, relative humidity, cumulative day radiation) were measured as described for the pot experiment. At harvest, the yield parameters (fresh fruit yield, number of fruits per plant, and average weight of fruit) and fruit harvest parameters (marketable fruit ratio and fruit water content) were also measured as described for the pot experiment.

Soil components, soil properties, and soil microbial activity (see Table S2) were also measured before and after the waterlogging treatments. Three soil samples of 500g wet weight were taken from the center of the mound 25 cm from plants in each treatment area. The analyses were conducted by the Tokachi Federation of Agricultural Cooperatives.

A fruit composition analysis was conducted as described previously (Jitsuyama et al., 2019). Each replication was done using four fruits from a plant at harvest, and the average value of the four fruits was defined as the value of the replication. In summary, half of each fruit was squeezed to get the sap and juice, which were used to measure Brix and acidity with a Brix-acid meter (PAL-BX/ACID F5 Master Kit; ATAGO Co., Ltd., Tokyo, Japan). The other half of the fruit was freeze-dried and powdered, and 25 mg of each powdered sample was homogenized, extracted in hexane, dried, and re-mobilized in 100 μL chloroform and 900 μL acetonitrile. Then, 20 μL of the mixture was analyzed by high performance liquid chromatography to determine the lycopene and β-carotene contents, as described by Jitsuyama et al. (2019). The Beer-Lambert law was used to calculate the contents.

2.2.3. Statistical analysis

The experimental design was a split plot design with five replications (five plants per replication). The main plots and subplots were defined as the three water stress treatments (T: CONT, WET5, and WET10) and the three cultivars (C: 'Natsunoshun', 'Lycoball' and 'Suzukoma'). The significance in the ANOVA was calculated as described for the split-split plot design (Little and Hills, 1978). Other statistical analysis was done as described for the pot experiment.

3. Results

3.1. Pot experiment

3.1.1. Environment

When the air temperatures were averaged over the entire 6 months' duration of the pot experiment, they did not differ between years (2017: 19.7˚C, 2018: 19.2˚C, Student's t-test, $p>0.1$) (Table S1). However, during the 12-day period just before flowering (5–16 July), the average air temperature was higher in 2017 than in 2018 (2017: 25.0˚C, 2018: 18.5˚C, Student's t-test, $p<0.001$). The average total solar radiation over the 6-month duration of the experiment was also higher in 2017 than in 2018 (2017: 17.0 MJ・m^{-2}, 2018: 15.1 MJ・m^{-2}, Student's t-test, $p<0.05$).

The waterlogging treatments drastically altered the soil environments, including the water content, pF value, and oxygen concentration (Table S1). The average soil water contents during the waterlogging treatments were significantly higher than in the controls (2017; CONT: 16.6%, WET: 42.5%, 2018; CONT: 17.6%, WET: 42.9%, Tukey-Kramer's test, $p<0.05$). The soil water content affected the average pF values such that the pF values in the waterlogging treatments were significantly lower than in the controls (2017; CONT: 1.94, WET: 1.32, 2018; CONT: 1.86, WET: 1.33, Tukey-Kramer's test, $p<0.05$). Similarly, the soil water content affected the average oxygen concentrations, with significantly lower oxygen concentrations in the waterlogging treatments than in the controls (2017; CONT: 16.3%, WET: 0.6%, 2018; CONT: 18.2%, WET: 0.9%, Tukey-

Kramer's test, $p<0.05$). For the data shown here, the daily measurements in the WET10, WET5, and WET3 treatments (a total of 18 measurements) were used to calculate the WET means, and 10 daily measurements in the CONT treatment were used to calculate the CONT means.

3.1.2. Yield-related traits

The yield-related data from the pot experiment and the ANOVA used to compare the variables among experimental years, waterlogging treatments, and cultivars are shown in Table 1. The only significant effect of the experimental year was on yield ($p<0.05$); the yield in 2018 was lower than in 2017. The waterlogging treatments also significantly affected yields ($p<0.001$), and longer waterlogging treatments caused greater yield reductions. There were also significant effects of cultivar on yield ($p<0.01$), with the greatest yields from 'Natsunoshun' and the lowest yields from 'Lycoball'.

The waterlogging treatments also affected the number of fruits per plant ($p<0.01$), causing reduced numbers regardless of the duration of the treatment. The number of fruits per plant was also affected by cultivar ($p<0.001$), with 'Suzukoma' producing the largest numbers and 'Lycoball' producing the fewest. Based on the Tukey-Kramer's test ($p<0.05$), the average weight was reduced by waterlogging treatment for 5 days or more. The average weight was significantly lower in 'Suzukoma' than in other two cultivars ($p<0.05$).

The relationships between yield and number of fruits per plant and between yield and average weight of fruit are shown for each cultivar in Figure S1A–C. All cultivars showed significant relationships between both pairs of traits ($p<0.001$), however the correlation coefficients were different among cultivars. The correlation between yield and number of fruits per plant was strongest in ‘Lycoball’, whereas the correlation between yield and average weight of fruit was strongest in ‘Suzukoma’.

The waterlogging treatments and cultivar each significantly affected the marketable fruit ratio. The WET5 and WET10 treatments produced lower ratios than the CONT and WET3 treatments (p<0.001), and ‘Suzukoma’ had a higher ratio than the other two cultivars (p<0.001) (Table 1). The fruit water content was reduced by waterlogging treatment for 5 days or more, and was lower in ‘Lycoball’ than in the other two cultivars (Tukey-Kramer’s test, p<0.05).

The ANOVA analysis revealed significant interactions among experimental year, waterlogging treatment, and cultivar that affected both yield and the number of fruits per plant (p<0.05) (Table 1). There were also significant interactions between experimental year and cultivar that affected yield (p<0.01). The effect of experimental year was strongest in ‘Lycoball’, since the ‘Lycoball’ yield was significantly reduced in 2018 compared with 2017 (Figure 2A). The negative effects of waterlogging treatment on yield were similar between both years and among all three cultivars, except in the ‘Suzukoma’ CONT-treated plants in 2017. That year, the CONT-treated ‘Suzukoma’ plants had relatively low yields, similar to those of the WET5-treated plants (Figure 2B). There tended to be no clear effects of the waterlogging treatments on the number of fruits per plant, except for a slight negative effect on ‘Natsunoshun’ in 2017 and a stronger negative effect on ‘Suzukoma’ in 2017 (Figure 2C).

3.1.3. Flowering and fruiting ratio

The numbers of flowers per plant and the fruiting ratios in the pot experiment, along with the ANOVA results, are shown in Table 2. The experimental year had significant effects on the number of flowers (p<0.001) and the fruiting ratio (p<0.05), with more flowers per plant but lower fruiting ratios in 2017 than in 2018. The waterlogging treatment significantly and negatively affected the fruiting ratio (p<0.01) but didn't significantly affect the number of flowers per plant. The number of flowers per plant was significantly affected by cultivar (p<0.01), with 'Suzukoma' having the highest number and 'Lycoball' the lowest. There were no significant interactions among year, treatment, and cultivar in their effects on the number of flowers per plant. The only significant interactions affecting fruiting ratio were between experimental year and cultivar (p<0.05), and between waterlogging treatment and cultivar (p<0.05) (Table 2). The fruiting ratio in 2018 was greater than in 2017 in 'Natsunoshun' and 'Suzukoma' at significance levels of 5% and 1%, respectively (Fig. 3A). The waterlogging duration affected the fruiting ratios differently among cultivars: ratios were significantly reduced by three or more days of waterlogging treatment in 'Natsunoshun', five or more days in 'Lycoball', and ten days in 'Suzukoma' (Fig. 3B).

3.1.4. Plant biomass

The root dry weight, shoot dry weight, shoot water content, leaf area, net assimilation rate (NAR) and fruit dry matter distribution ratio (FDR) data from the pot experiment, along with the ANOVA results, are shown in Table 3. The only significant effect of experimental year was on the FDR (p<0.01): the FDR was higher in 2017 than in 2018. The waterlogging treatments had significant effects on root dry weight, shoot dry weight, leaf area, and FDR at the 0.1% significance level. All traits, including the shoot water content and the NAR, were reduced by the longer waterlogging treatments. The cultivar also significantly affected four traits: root and shoot dry weight, leaf area, and FDR.

‘Natsunoshun’ had the largest shoot dry weights ($p<0.001$) and leaf areas ($p<0.001$); ‘Lycoball’ had the largest root dry weights ($p<0.05$); and ‘Suzukoma’ had the highest FDR among all cultivars ($p<0.001$).

There were significant interactions between experimental year and treatment in their effects on root dry weight ($p<0.05$) and leaf area ($p<0.01$). In 2017, the root dry weight was reduced by waterlogging treatment for 3 or more days, however in 2018, 5 or more days of treatment were needed to reduce the root dry weight (Fig. 4A). The leaf area was similarly affected by year and treatment except that in 2018, 10 days of treatment were needed to significantly reduce leaf area (Fig. 4B). A significant interaction between experimental year and cultivar was detected for the FDR ($p<0.01$). The FDRs of ‘Natsunoshun’ and ‘Lycoball’ were lower in 2018 than in 2017, but there was no significant change for ‘Suzukoma’ (Fig. 4C). In root dry weight, there was a significant interaction between treatment and cultivar ($p<0.05$). The root dry weights of ‘Lycoball’ and ‘Suzukoma’ were reduced by the longer waterlogging treatments, however, that of ‘Natsunoshun’ was not affected by the treatment (Fig. 4D).

3.2. Paddy field experiment

3.2.1. Environment

The average air temperature in the paddy field during the summer of 2019 was 20.3˚C, and the average total solar radiation was 17.7 MJ・m^{-2} (Table S1). The average air temperature and total solar radiation during the waterlogging treatments at flowering (10–19 July) were 20.7˚C and 18.6 MJ・m^{-2}, and these were not significantly different from the averages for the total duration of the experiment ($p>0.1$, Student’s t-test).

As we found in the pot experiment, the waterlogging treatment changed the following soil parameters: the water content, pF value, and oxygen concentrations (Table S1). The average soil water contents were increased significantly by waterlogging [CONT: 13.9%, WET5: 31.5%, WET10: 41.3%, Tukey-Kramer, $p<0.05$ (CONT; n=42, WET5; n=5, WET10; n=10)]. The average pF values were significantly lowered by waterlogging [CONT: 2.11, WET5: 1.16, WET10: 1.09, Tukey-Kramer, $p<0.05$ (CONT; n=121, WET5; n=5, WET10; n=10)]. The average oxygen concentrations were also significantly lowered [CONT: 19.3%, WET5: 14.2%, WET10: 15.1%, Tukey-Kramer, $p<0.05$ (CONT; n=41, WET5; n=5, WET10; n=10)]. On the other hand, the soil temperatures at depths of 10 cm and 20 cm were not affected by the waterlogging treatments ($p>0.1$ CONT; n=10, WET5; n=5, WET10; n=10).

The soil component in field experiment before and after flooding treatment are shown in Table S2. The waterlogging treatments had significant effects on the pH, soluble zinc, hot water soluble boron and total nitrogen, but not on the other composition, soil property and microbial activity. The soils in WET5 and WET10 had significantly lower soluble zinc, hot water soluble boron and total nitrogen than soil in control ($p<0.05$), and significantly higher pH than the control soil ($p<0.05$).

3.2.2. Yield and parameters related to yield

The data related to yield in the field experiment (yield, number of fruits per plant, average weight of fruit, marketable fruit ratio, and fruit water content), along with the ANOVA results, are shown in Table 4. The waterlogging treatments significantly affected all of these parameters. The WET10 plants had lower yields than the other treatments ($p<0.001$), the WET5 and WET10 plants had lower numbers of fruits per plant ($p<0.01$), and the

WET10 plants had lower average fruit weights ($p<0.001$). These parameters were also affected by cultivar. ‘Natsunoshun’ had the highest yields while ‘Suzukoma’ had the lowest ($p<0.001$), ‘Lycoball’ had the lowest number of fruits per plant ($p<0.01$), and ‘Suzukoma’ had the lowest average fruit weight ($p<0.001$).

The relationships between fruit yield and number of fruits per plant and between fruit yield and average weight of fruit are shown for each cultivar in Fig. S2. ‘Natsunoshun’ and ‘Lycoball’ showed the strongest correlations between fruit yield and number of fruits per plant (number of fruits: $p<0.001$, weight of fruits: $p<0.05$). On the other hand, ‘Suzukoma’ showed the strongest correlation between fruit yield and average weight of fruit (number of fruits: $p<0.01$, weight of fruits: $p<0.001$).

The marketable fruit ratios and fruit water contents were also affected by waterlogging treatment and cultivar. The WET10 plants had lower marketable fruit ratios and fruit water contents than those in the other treatments ($p<0.001$). Among the cultivars, ‘Lycoball’ had the lowest marketable fruit ratio ($p<0.001$) and ‘Suzukoma’ had the lowest fruit water content ($p<0.001$). The ANOVA did not reveal any interactions between waterlogging treatment and cultivar in any of the traits related to yield.

The reduced yields and parameters related to yield in the WET-treated plants may have been due, at least in part, to reduced transpiration rates. During the waterlogging treatments, we observed that the plants became wilted after around 5 days of waterlogging treatment (Fig. S3A and B). We did not measure root dry weights in the field experiment, but the development of adventitious roots in the WET-treated plants (Fig. S3C and D) suggested that the plants were responding to reduced efficiencies in the function of the below-ground roots.

3.2.3. Fruit composition

The fruit composition parameters: brix, acidity, sugar/acid ratio, and lycopene and β-carotene contents of the field-grown tomatoes, along with the ANOVA results for these parameters, are shown in Table 5. The waterlogging treatments had significant effects on the brix levels and the sugar/acid ratios, but not on the other parameters. The WET10 plants had significantly higher brix levels ($p<0.001$) and sugar/acid ratios ($p<0.01$) than the CONT plants. The cultivars had significant effects on brix, acidity, sugar/acid ratio, and β-carotene content. 'Suzukoma' had the highest brix level among the cultivars ($p<0.001$) and 'Lycoball' had the highest acidity ($p<0.001$). The sugar/acid ratios differed significantly among all three cultivars, with the highest in 'Suzukoma' and the lowest in 'Lycoball' ($p<0.001$). The β-carotene content was highest in 'Lycoball' ($p<0.001$). No interactions were found by ANOVA between treatment and cultivar in their effects on the brix, acidity, or sugar/acid ratios, however, significant interactions were detected in their effects on the lycopene ($p<0.05$) and β-carotene ($p<0.01$) contents. The lycopene contents were increased by longer waterlogging treatments in 'Lycoball', but not in the other two cultivars (Fig. 5A). Conversely, the β-carotene contents in 'Natsunoshun' and 'Suzukoma' were increased by longer waterlogging treatments, but that of 'Lycoball' did not change (Fig. 5B).

3.2.4. Fruit quality

Fruit quality data for the field cultivated tomatoes, along with the ANOVA results for those variables, are shown in Table 6. The waterlogging treatments had significant effects on the marketable fruit ratio and the immature fruit ratio, but not on the blossom-end rot fruit ratio. The WET10 plants had significantly lower marketable fruit ratios than plants in the other treatments (*p*<0.001), and significantly higher immature fruit ratios than the WET5 plants (*p*<0.001). 'Lycoball' had a much lower marketable fruit ratio than the other two cultivars (*p*<0.001), whereas 'Suzukoma' had a much lower immature fruit ratio than the other two cultivars (*p*<0.001). The ANOVA detected significant interactions between treatment and cultivar in their effects on immature fruit ratio and blossom-end rot fruit ratio (*p*<0.01). The blossom-end rot fruit ratio was increased by the waterlogging treatments in 'Natsunoshun' and 'Lycoball', but not in 'Suzukoma' (Fig. 6A). Similarly, the immature fruit ratio was increased by the longer waterlogging treatment in 'Natsunoshun' and 'Lycoball', but not in 'Suzukoma' (Fig. 6B).

4. Discussion

4.1. What kinds of environment aggravate the processing tomatoes' wet injury?

The wet conditions used in this study drastically reduced the fruit yield of processing tomatoes in both the pot and converted paddy field experiments (Table 1, Table 4). An important question is, what kinds of environmental factors affect the severity of the wet injury? The soil types, temperature and radiation could also be impactful factors, however, a very clear result from this study was that the longer the waterlogging treatment, the greater the effect on yield. The 10-day waterlogging treatment in the converted paddy field and the 3-day waterlogging treatment in the pot experiment significantly reduced yields. In previous studies, severe damage and yield reductions were reported after 3 to 5 days of wet conditions in the field (Jitsuyama et al., 2019; Higashio et al., 2012).

Our biomass analysis in the pot experiment showed that 3 days of waterlogging treatment reduced the root and shoot biomass and leaf area, and prolonged treatment was linked to smaller plant size (Table 3). We also found interactions between experimental year and treatment in both root dry matter and leaf area: the effect of the waterlogging treatment was greater in 2017 than in 2018 (Fig. 4A, B). Therefore, environmental differences between the two years might provide information on what environmental factors can aggravate the tomatoes' wet injury.

In the pot experiment, the water treatments were the same between years, and the profiles of the air temperature and the accumulated light intensity were similar between years. Therefore, the greatest environmental difference between 2017 and 2018 was in the average temperatures from early July to mid-August; temperatures during this period were higher in 2017 than in 2018. Possibly, these higher temperatures aggravated the yield reduction due to waterlogging. In the case of soybeans, if the ambient temperature was higher, the wet injury became more severe (Jitsuyama, 2013; Matsukawa et al., 1983). It has also been shown that in tomatoes, heat and waterlogging are the two biggest challenges to production (Opeña et al., 1992).

The value of growth ratio per leaf area, NAR, was reduced by waterlogging treatment for more than 5 days (Table 3). Although it was not significant, the NAR was lower in 2017 than in 2018 at a specific period, possibly because the water available for photosynthesis was limited by the hotter weather. Tomato fruits after fruit set are the strongest sink organs (Wardlaw, 1990). The waterlogging treatment reduced not only the source organs, the leaves, but also the FDR (Table 3). The excess moisture also drastically reduced the root dry weight (Table 3). These results suggest that the higher temperatures may have aggravated the tomatoes' wet injury because the smaller roots could not satisfy the higher transpiration demands. This phenomenon would lead to reduced photosynthetic efficiency and reduced translocation.

Both fruit number and fruit size contribute to yield. We found that in the pot experiment, fruit number was reduced after only 3 days of waterlogging, whereas fruit size was not reduced unless the plants were exposed to 5 or more days of waterlogging (Table 1). Similarly, in the field experiment a shorter period of waterlogging was needed to reduce the fruit number than was needed to reduce the average weight of the fruit (Table 4). These results suggest that fruit number is more sensitive to waterlogging than fruit size. In brief, the facts support the hypothesis that excess moisture affects how many flowers develop into fruits.

The fruit number is determined by flower number and the number of flowers that develop into fruit. The ANOVA showed that the waterlogging treatment affected the fruiting ratio more than it affected the number of flowers (Table 2). Thus, the fruit number was reduced because fewer flowers developed into fruits. In a previous study using only ‘Natsunoshun’, the fruit number was more closely related to the fruiting ratio than to the number of flowers (Jitsuyama et al., 2019). We did not detect an interaction between experimental year and treatment in their effects on the number of flowers or the fruiting ratio (Table 2), so it is difficult to explain what environmental factors might aggravate the tomatoes’ lower fruiting ratio after waterlogging.

4.2. What kinds of tomato traits tend to aggravate wet injury?

Next, we considered what kinds of tomato cultivar traits might aggravate wet injury. In particular, we focused on the specific traits that were linked to the lower fruiting ratios after waterlogging. The fruits of ‘Suzukoma’ were relatively small (average weight less than 40 g per fruit) but it had relatively large numbers of fruits per plant and marketable fruit ratios (Table 4, Fig. 1B). Therefore, the relationship between yield and yield components differs between ‘Suzukoma’ and the other two cultivars (Fig. S1). The other cultivars, ‘Natsunoshun’ and ‘Lycoball’, produce relatively large fruits of more than 70 g per fruit (Table 4). The total yield of ‘Natsunoshun’ was larger than that of ‘Lycoball’, because the fruit number per plant affected the yield (Table 1, Table 4). All three cultivars showed interactions with waterlogging treatment (cultivar x treatment) in their effects on fruiting ratio (Table 2), but ‘Natsunoshun’ was more sensitive than the other two (Fig. 3B). The results indicate that the yield reduction in ‘Natsunoshun’ after waterlogging was largely due to the reduction in fruiting ratio. In the pot experiment, the difference in yield between the CONT and WET3 treatments was significant in 2017 but not in 2018, in both ‘Natsunoshun’ and ‘Lycoball’ (Fig. 2B). The total yield in 2017 was much higher than in 2018 (Table 1), and thus, the results show that the effect of waterlogging was exaggerated in the high-yield year.

The ANOVA results showed that one of the parameters whose interaction between treatment and cultivar was significant is the root dry weight (Table 1). Whereas the fruiting ratio in ‘Natsunoshun’ was more sensitive to waterlogging than it was in the other two cultivars (Fig. 3B), the other two cultivars showed more sensitivity to waterlogging in their root dry weights (Fig. 4D). Therefore, there appeared to be no relationship between the fruiting ratio reduction and the stress-responsiveness of the root biomass. On the other hand, it is possible that the nutritional status of the plant may affect the fruiting ratio. Cultivation under low nutrient conditions resulted in incomplete flower development, smaller ovaries, and higher rates of flower abscission in tomato (Saito and Ito, 1967). The waterlogging treatment in the field experiment significantly reduced the total nitrogen and nitrate contents of the soil (Table S2). This was likely due to denitrification by anaerobic bacteria (Nishio, 1994) and of the leaching of nitrogen by excess moisture (Tokuda, 2018). One of the main factors contributing to yield reduction in tomato is nitrogen deficiency (Higasa and Imada, 1993), and nutritional uptake of the root depends on the oxygen concentration at the root zone (Morard and Silventre, 1996). Thus, even before the root biomass was affected by waterlogging, the treatment caused a reduction in nutrient uptake by the roots under the low oxygen conditions, and a reduction in nitrogen availability. Therefore, topdressing of nitrogen just after waterlogging may be affective in mitigating the wet injury. Previous studies in wheat and soybean have also shown that nitrogen topdressing is effective in the mitigation of wet injury (Sugimoto et al., 1988).

There was no significant interaction between treatment and cultivar in any other parameter related to biomass, however, we detected significant interactions in the immature fruit ratio and the blossom-end rot fruit ratio (Table 6). In our previous study, the reduction in the marketable fruit ratio caused by waterlogging was accompanied by reductions in the blossom-end rot fruit and immature fruit ratios (Jitsuyama et a., 2019). In this study, 'Natsunoshun' and 'Lycoball' showed increased immature fruit and blossom-end rot fruit ratios after waterlogging (Fig. 6-A, B). Generally, blossom-end rot in tomato is induced by calcium deficiency (Manishi et al., 1996). We detected no significant changes in the exchangeable calcium content of the soil after waterlogging, but we did find changes in the boron content (Table S2). Boron affects calcium uptake and utilization in the plant body (Bose and Tripathi, 1996). Therefore, the frequency of blossom-end rot may have been affected by the lower soil boron content after waterlogging. Our previous study showed that a lack of moisture may delay fruit maturation and increase morbidity due to blossom-end rot (Jitsuyama et al., 2019). This suggests that a declined water uptake in the root may have increased the immature fruit and blossom-end rot ratios in ‘Lycoball’, since the root mass of ‘Lycoball’ was reduced by the waterlogging treatment (Fig. 4D). In summary, the delayed maturation and morbidity due to blossom-end rot may be caused by both root mass reduction and root malfunction resulting from hypoxia.

4.3. Root mass reduction by wet injury

As mentioned above, the root malfunction due to hypoxia must be considered the first step in the wet injury of processing tomato, because root mass reduction had not occurred when the waterlogging treatment began. Generally, the root system is the first organ to be affected by physiological stress under waterlogging conditions (Drew,1997; Dat et al., 2004), and the phenomenon is accompanied by oxidative damage (Li et al., 2012) under the changes of soil microbiota and soil redox potential (Moriyama et al., 2018). This damage induces root rot, which limits the uptake of water and nutrients, and these biological disorders result in biomass reduction (Ma et al., 2005). Five days of waterlogging conditions severely hampered root elongation in table tomato (Dresboll et al., 2013). Root rot may cause localized increases in carbon dioxide, methane gas, and volatile fatty acids produced by fermentative metabolic processes (Pezeshki, 2001). We did detect a foul odor from the root systems of the waterlogged plants, whose root dry weights were drastically reduced by the waterlogging treatments (Table 3).

As described above, the fruiting ratio might be less affected by root damage, however, the reduction in water uptake must affect translocation to the fruits, eventually affecting fruit size. The leaves under the waterlogging treatment showed severe wilting symptoms (Fig. S3A, B), and the water contents in the stem and fruit were also reduced after prolonged waterlogging conditions (Table 1, Table 3). These data provide evidence of reductions in water uptake. From the viewpoint of root biomass, 'Natsunoshun' was less affected by the excess moisture, and may have physiological or morphological traits that reduce the negative effects of waterlogging. The results also suggested that the other cultivars which have larger roots could also have higher root plasticity leading to adaptations to waterlogging. From a different angle, however, 'Natsunoshun', with its small root system, has superior stability against waterlogging in another way. There is a soybean cultivar whose root system is quite small, but its wet tolerance is markedly strong, and expresses no reduction in hypoxia (Jitsuyama, 2017). Some tomato cultivars can adapt to excess soil moisture by growing adventitious roots, triggered by anoxia or hypoxia (Jackson and Drew,1984; Colmer and Voesenek, 2009). In this study, adventitious roots were found at the bases of stems after 3 days or more of waterlogging (Fig. S3C, D), however, we did not observe differences among cultivars in the frequency of adventitious root formation.

4.4. Effects of waterlogging on fruit composition

We found that the fruit water contents decreased significantly with longer waterlogging treatments (Table 1, Table 4), and this tendency was similar to the reductions in average fruit weight after waterlogging. The results suggest that the reduction in fruit size by waterlogging was caused by the reduction in water translocation to the fruits. Moreover, in the field experiment, the fruit sugar/acid ratio increased with longer waterlogging treatments (Table 5). This suggests that changes in the fruit composition were at least in part due simply to increased concentrations of solids and solutes as a result of the reduced water content. The relationship between acidity and waterlogging treatment was not significant (the correlation between fruit water content and brix was described by y=-

1.239x+122.2, R^2=0.8258***; the correlation between fruit water content and acid was described by y=-0.018+2.462, R^2=0.0078 ns). Therefore, the increased sugar/acid ratios in the fruits may be due to the increased or concentrated sugar in the fruits. Generally, tomato fruit quality is highly responsive to fluctuations in soil water (Zushi and Matsuzoe, 1998), and sweeter fruits can be produced using conditions of deficit irrigation (Lu et al., 2021). In contrast to dry conditions, the condition was 'wet' in this study, however, the water uptake by the root was restricted by the waterlogging treatment.

Processing tomato fruits have more carotenoids, such as lycopene, than table tomato fruits (Sass-Kiss et al., 2005) because they are harvested when completely mature. In this study, the overall contents of lycopene and β-carotene showed no significant changes after the waterlogging treatments (Table 5). This result was in line with that for acidity and differed from the results for the sugar/acid ratios (Table 5). Interestingly, however, we did find interactions between treatment and cultivar in their effects on each carotenoid (Table 5). Waterlogging increased the lycopene content in 'Lycoball' (Fig. 5A) and increased the β-carotene contents in 'Natsunoshun' (Fig. 5B). A previous study of table tomato showed that hypoxia in the root zone at the flowering stage caused a decrease in the lycopene content of the fruits (Horchani et al., 2010). Thus, our results for 'Lycoball' were in complete contrast to the results from the previous study. The accumulation of carotenoids in tomato fruits is affected by not only the irrigation conditions but also by other environmental factors such as illuminance, ambient temperature, and fertilization (Dumas et al., 2003; Taber et al., 2008). These results suggested that the variable factors of the changes in carotenoid levels appeared to be a specific response to waterlogging treatment depending upon cultivars rather than these environmental conditions. Our results indicated that the waterlogging conditions affected not only the fruit number and size of the processing tomatoes, but also aspects of fruit quality.

5. Conclusion

Although it was not clarified in our previous study (Jitsuyama et al., 2019), this trial shed light on the mechanisms that result in wet injury of processing tomatoes after waterlogging. At the onset of the waterlogging treatment, reduced soil nutrient levels and hypoxia cause reductions in nutrient uptake by the roots, leading to lower fruiting ratios and reductions in fruit numbers. If the waterlogging situation continues, the root biomass will be reduced, leading to further limitations in the uptake of nutrients and water, resulting in lower photosynthetic ability, and finally, drastic reduction of fruit size and total yields.

In regions where processing tomatoes are cultivated in converted paddy fields, such as central Hokkaido, excess moisture conditions for more than 5 days should be avoided by any means. This could be achieved by using engineering works such as FOEAS. However, if waterlogging cannot be avoided, the topdressing of fertilizer after the water has receded might be effective in mitigating the damage to yields, especially during hot summers. The choice of cultivar can also reduce the negative effects of waterlogging. 'Natsunoshun' is a high-yielding cultivar that produces fruit with a long shelf life. 'Natsunoshun' showed less root damage after waterlogging than the other two cultivars. Therefore, although its fruiting ratio is sensitive to waterlogging, 'Natsunoshun' has superior root characteristics for cultivation in converted paddy fields.

In this study, the cultivation conditions were quite different between the pot and field experiments, especially in the nutrition conditions and the spaces available for root growth. Nevertheless, each cultivar's responses to the excess moisture were similar between experiments, with significant correlations (data not shown). Therefore, pot experiments may be useful in preliminary surveys for selecting cultivars that can acclimate to waterlogging conditions. In the field, the planting density is higher and this may add further detrimental effects such as rebound of raindrops on the tomato fruits. Thus, further studies are needed to improve the production of processing tomatoes in converted paddy fields.

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Figure legends

Fig. 1 Plant growth conditions and fruit characters.

(A - C) Reddish mature fruits of ‘Natsunoshun’(A), ‘Suzukoma’ (B) and ‘Lycoball’ (C). (D) In the pot experiment, the ‘WET’ treatments were achieved using pots inserted in vinyl bags, as illustrated by the upper photo and the lower diagram. (E) Damaged fruits, either undeveloped or displaying blossom-end rot. Scale bars represent 1 cm. (F) Cultivation of ‘Natsunoshun’ in the field experiment. (G) The WET10 waterlogging treatment in the field experiment.

Fig. 2. Interactions among variables affecting yield parameters in the pot experiment.

(A) Y x C interactions in their effects on yield. (B) Y x T x C interactions in their effects on yield. (C) Y x T x C interactions in their effects on the number of fruits. Data represent means from 4 replications, and bars show standard errors. Different letters above the bars indicate significant differences among treatments and growth stages at the 5% level (Tukey-Kramer test).

Fig. 3. Interactions among variables affecting fruiting ratios in the pot experiment.

(A) Y x C interactions in their effects on fruiting ratio (B) T x C interactions in their effects on fruiting ratio. Data represent means from 4 replications, and bars show standard errors. Different letters above the bars indicate significant differences among treatments and growth stages at the 5% level (Tukey-Kramer test).

Fig. 4. A-D. Interactions among variables affecting root dry weight and the fruit delivery ratio (FDR) in the pot experiment.

(A) Y x T interactions in their effects on root dry weight. (B) Y x T interactions in their effects on leaf area. (C) Y x C interactions in their effects on FDR. (D) T x C interactions in their effects on root dry weight.

Data represent means from 4 replications, and bars show standard errors. Different letters above the bars indicate significant differences among treatments and growth stages at the 5% level (Tukey-Kramer test).

Fig. 5. Interactions among variables affecting the fruit lycopene and *β*-carotene contents in the pot experiment.

(A) T x C interactions in their effects on the lycopene content. (B) T x C interactions in their effects on the *β*-carotene content.

Data represent means from 5 replications, and bars show standard errors. Different letters above the bars indicate significant differences among treatments and growth stages at the 5% level (Tukey-Kramer test).

Fig. 6. Interactions among variables affecting the blossom-end rot ratio and the immature fruit ratio in the field experiment.

(A) T x C interactions in their effects on the blossom-end rot ratio. (B) T x C interactions in their effects on the immature fruit ratio.

Data represent means from 5 replications, and bars show standard errors. Different letters above the bars indicate significant differences among treatments and growth stages at the 5% level (Tukey-Kramer test).

Fig. S1. Relationships between the average fruit weight and yield (●) and between the fruit number per plant and the yield (○) in the pot experiment.

(A) ‘Natsunoshun’. (B) ‘Lycoball’. (C) and ‘Suzukoma’.

Each value represents the average of two years. The asterisks ***, **, and * represent significance in the regression analysis at the 0.1%, 1%, and 5% levels using Pearson’s correlation coefficient.

Fig. S2. Relationships between the average fruit weight and yield (●) and between the fruit number per plant and the yield (○) in the field experiment.

(A) ‘Natsunoshun’. (B) ‘Lycoball’ (C) ‘Suzukoma’.

The asterisks ***, **, and * represent significance in the regression analysis at the 0.1%, 1%, and 5% levels using Pearson’s correlation coefficient.

Fig. S3. Plants grown in the field and pot experiments.

(A) A ‘Natsunoshun’ plant before the waterlogging treatment in the field. (B) A wilted ‘Natsunoshun’ plant at day 5 of the WET10 treatment in the field. (C) The base of a ‘Natsunoshun’ plant from the CONT treatment at the flowering stage in the pot experiment. D: The base of a ‘Natsunoshun’ plant from the WET3 treatment in the pot experiment. Adventitious roots are shown at the base of the stem. Scale bars represent 1 cm.

Figures

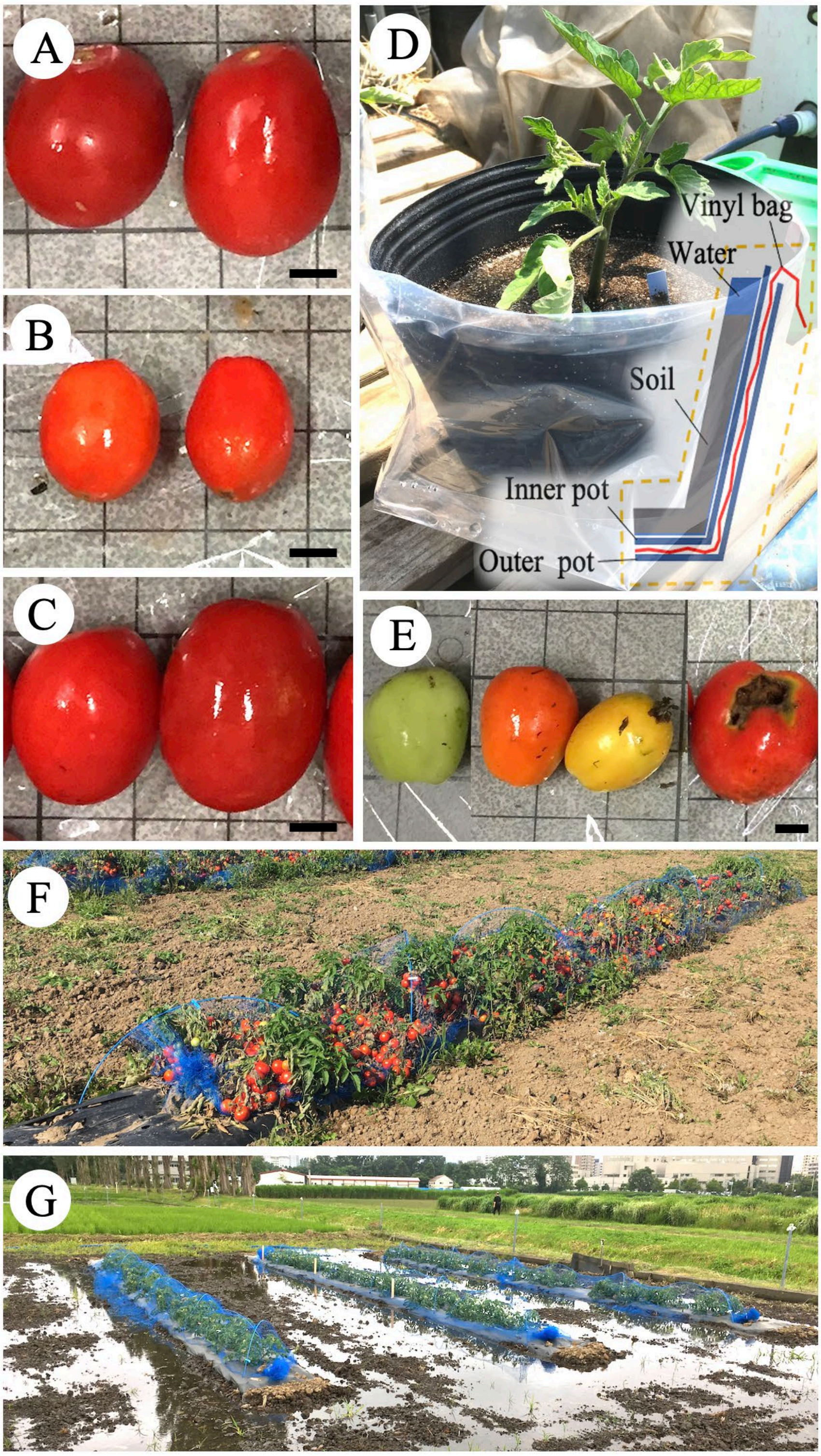

Figure 1.

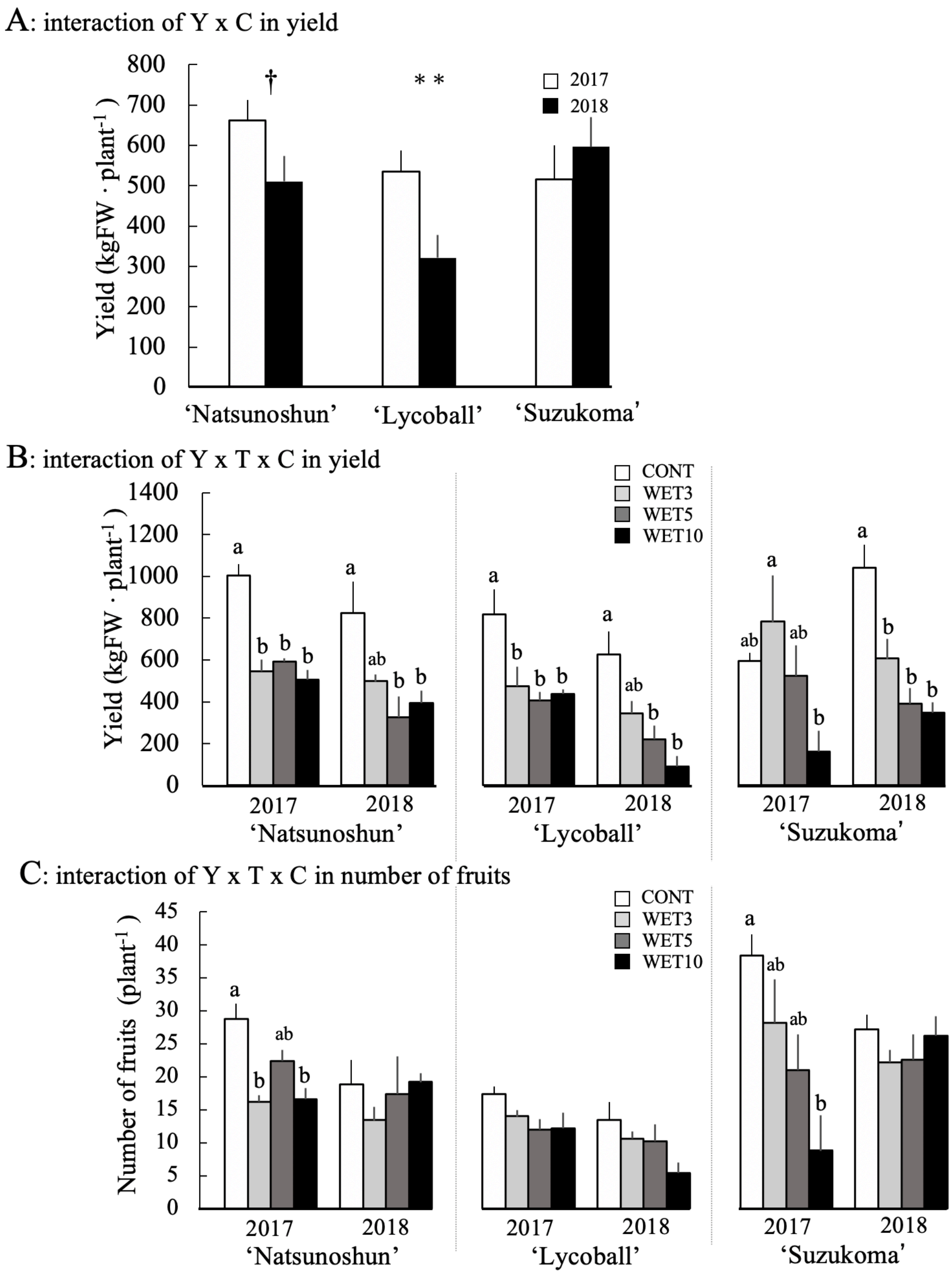
A: interaction of Y x C in yield
Yield (kgFW · plant-1)
800
700
600
500
400
300
200
100
0
†
* *
2017
2018
'Natsunoshun'
'Lycoball'
'Suzukoma'
B: interaction of Y x T x C in yield
Yield (kgFW · plant-1)
1400
1200
1000
800
600
400
200
0
CONT
WET3
WET5
WET10
2017
2018
'Natsunoshun'
'Lycoball'
'Suzukoma'
C: interaction of Y x T x C in number of fruits
Number of fruits (plant-1)
45
40
35
30
25
20
15
10
5
0
CONT
WET3
WET5
WET10
2017
2018
'Natsunoshun'
'Lycoball'
'Suzukoma'

Figure 2.

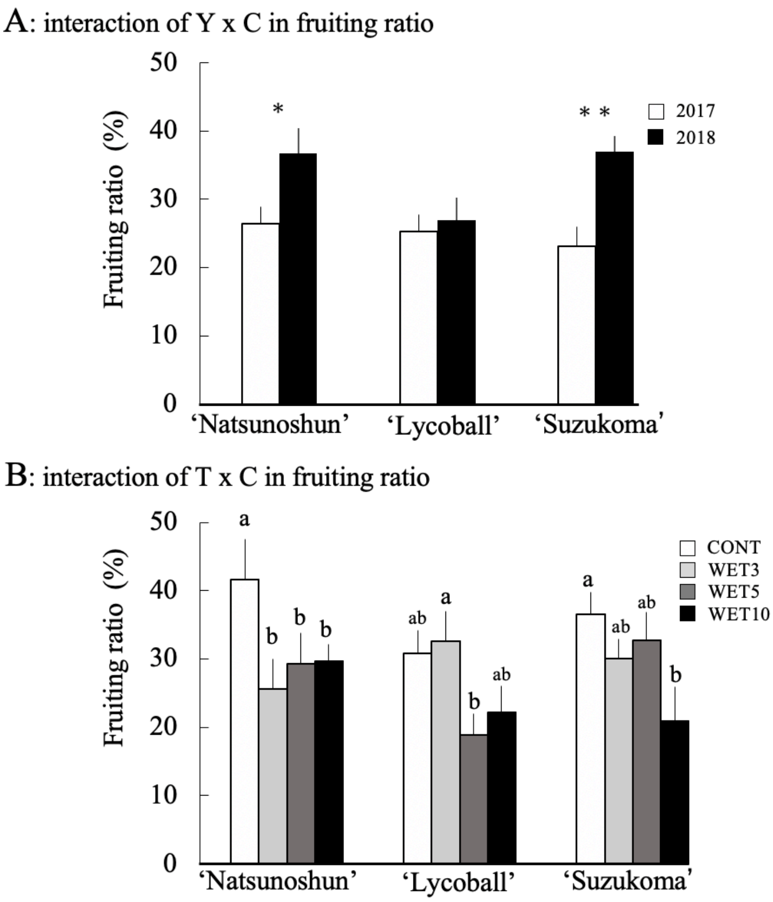
A: interaction of Y x C in fruiting ratio
Fruiting ratio (%)
0
10
20
30
40
50
*
* *
2017
2018
'Natsunoshun'
'Lycoball'
'Suzukoma'
B: interaction of T x C in fruiting ratio
Fruiting ratio (%)
0
10
20
30
40
50
CONT
WET3
WET5
WET10
a
b
b
b
ab
a
b
ab
a
ab
ab
b
'Natsunoshun'
'Lycoball'
'Suzukoma'

Figure 3.

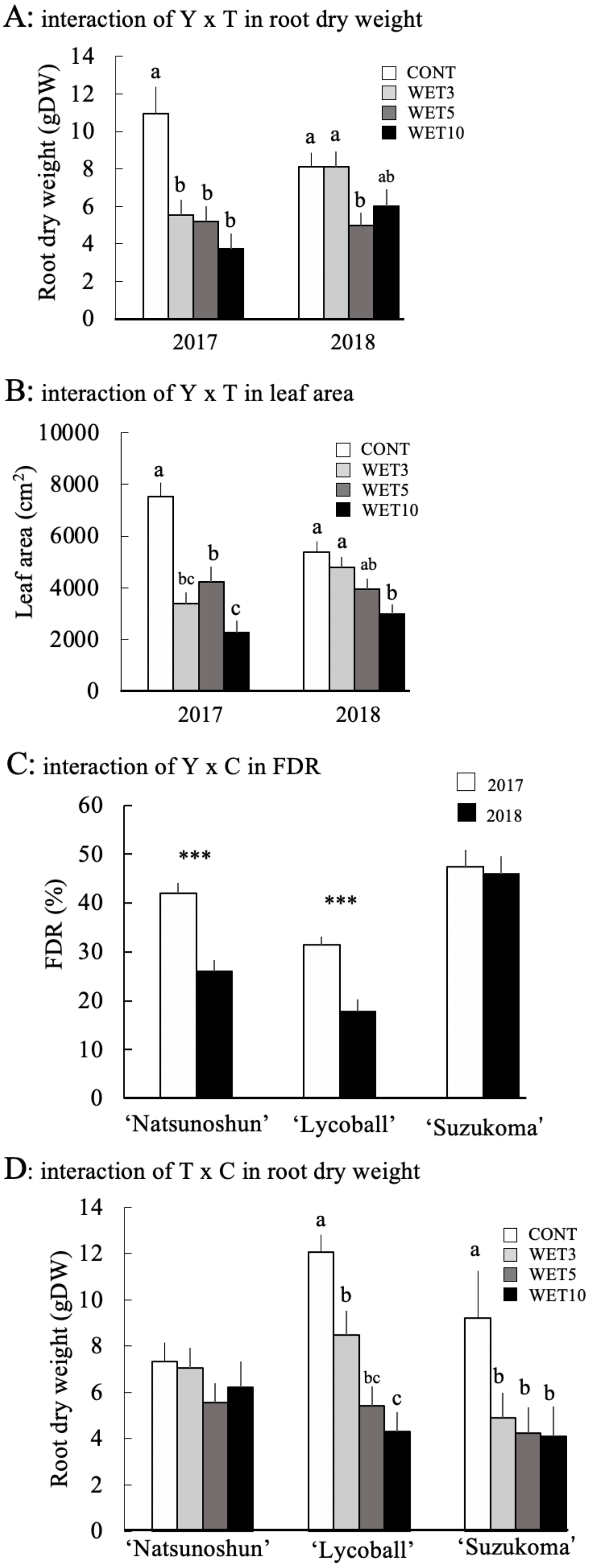
A: interaction of Y x T in root dry weight
Root dry weight (gDW)
0
2
4
6
8
10
12
14
CONT
WET3
WET5
WET10
a
b
b
b
a
a
b
ab
2017
2018
B: interaction of Y x T in leaf area
Leaf area (cm2)
0
2000
4000
6000
8000
10000
CONT
WET3
WET5
WET10
a
bc
b
c
a
a
ab
b
2017
2018
C: interaction of Y x C in FDR
FDR (%)
0
10
20
30
40
50
60
2017
2018
***
***
'Natsunoshun'
'Lycoball'
'Suzukoma'
D: interaction of T x C in root dry weight
Root dry weight (gDW)
0
2
4
6
8
10
12
14
CONT
WET3
WET5
WET10
a
b
bc
c
a
b
b
b
'Natsunoshun'
'Lycoball'
'Suzukoma'

Figure 4.

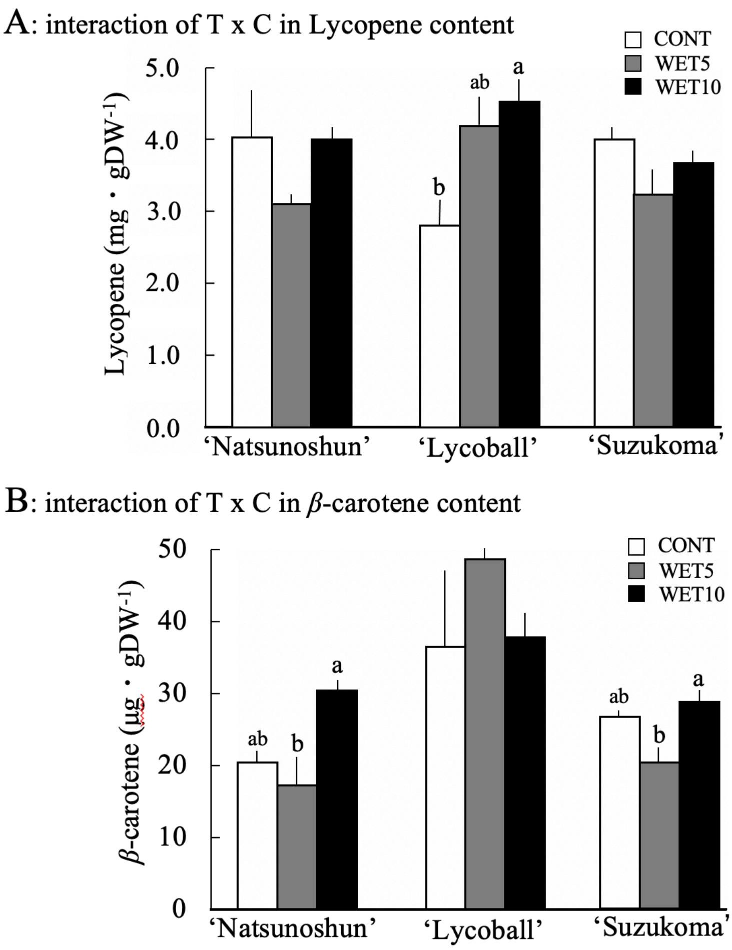
A: interaction of T x C in Lycopene content
Lycopene (mg・gDW-1)
5.0
4.0
3.0
2.0
1.0
0.0
CONT
WET5
WET10
a
ab
b
'Natsunoshun'
'Lycoball'
'Suzukoma'
B: interaction of T x C in β-carotene content
β-carotene (μg・gDW-1)
50
40
30
20
10
0
CONT
WET5
WET10
a
ab
b
ab
b
a
'Natsunoshun'
'Lycoball'
'Suzukoma'

Figure 5.

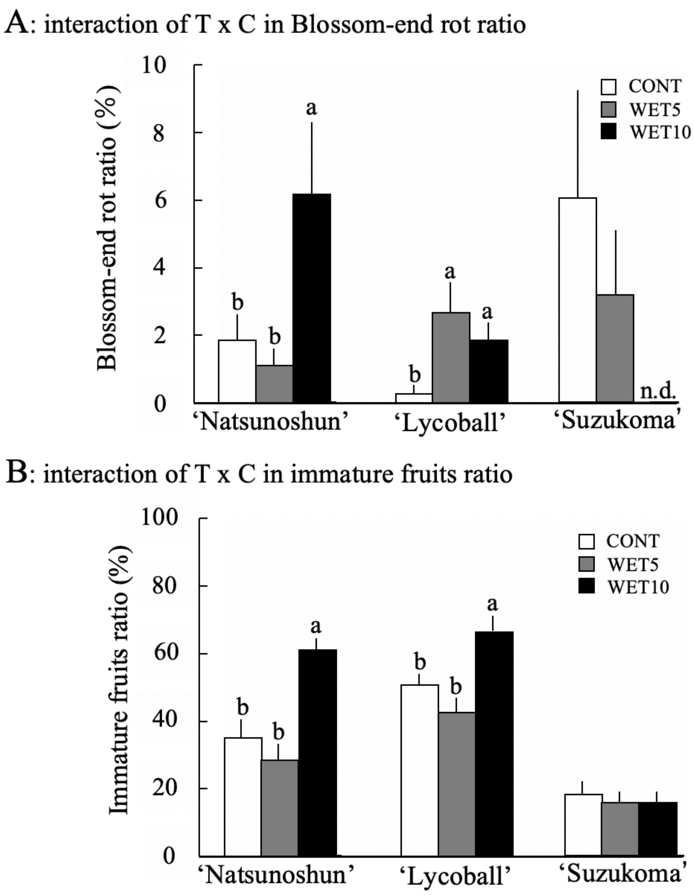
A: interaction of T x C in Blossom-end rot ratio
Blossom-end rot ratio (%)
10
8
6
4
2
0
CONT
WET5
WET10
a
b
b
a
a
b
n.d.
'Natsunoshun'
'Lycoball'
'Suzukoma'
B: interaction of T x C in immature fruits ratio
Immature fruits ratio (%)
100
80
60
40
20
0
CONT
WET5
WET10
a
b
b
a
b
b
'Natsunoshun'
'Lycoball'
'Suzukoma'

Figure 6.

Tables

Table 1 Yield, number of fruits per plant, average weight of fruit, marketable fruit ratio, and fruit water content in the pot experiment. Analysis of variance was used to compare the variables among treatment and cultivar under different environments for the 2 years.

	Yield (gFW·plant^{-1}) [z]		Number of fruits (plant^{-1})		Average weight of fruit (gFW) [y]		Marketable fruit ratio (%) [x]		Fruit water content (%) [y]	
Year (Y)										
2017	570.6 (37.3)		19.7 (1.4)		31.6 (1.6)		24.8 (2.7)		92.9 (0.1)	
2018	475.8 (39.8)		17.2 (1.1)		27.7 (1.9)		30.0 (3.1)		92.5 (0.2)	
Treatment (T)										
CONT	817.5 (50.1)	a	24.0 (1.9)	a	38.3 (2.5)	a	39.4 (3.9)	a	93.4 (0.2)	a
WET3	541.9 (48.3)	b	17.4 (1.6)	b	32.4 (2.1)	a	38.0 (4.0)	a	93.3 (0.2)	a
WET5	410.3 (38.7)	bc	17.6 (1.7)	b	23.6 (1.8)	b	18.6 (4.0)	b	92.3 (0.2)	b
WET10	323.1 (35.3)	c	14.7 (1.7)	b	23.1 (2.6)	b	13.1 (2.4)	b	91.7 (0.3)	b
Cultivar (C)										
'Natsunoshun'	586.1 (41.6)	a	19.1 (1.1)	b	31.2 (1.8)	a	23.2 (3.2)	b	93.0 (0.2)	a
'Lycoball'	427.7 (41.8)	b	11.9 (0.8)	c	33.7 (2.7)	a	19.3 (3.1)	b	92.1 (0.3)	b
'Suzukoma'	555.9 (55.5)	ab	24.3 (1.8)	a	23.1 (1.6)	b	39.3 (3.7)	a	92.9 (0.2)	a

ANOVA [w]	*df*	*MS*	Sig.	*MS*	Sig.	*MS*	Sig.	*MS*	Sig.	*MS*	Sig.
Y	1	269558	*	180	ns	-	-	0.12	ns	-	-
T	3	1397432	***	463	**	-	-	1.08	***	-	-
C	2	282787	**	1556	***	-	-	0.77	***	-	-
Y×T	3	61811	ns	213	ns	-	-	0.04	ns	-	-
Y×C	2	239524	**	63	ns	-	-	0.04	ns	-	-
T×C	6	68168	ns	86	ns	-	-	0.02	ns	-	-
Y×T×C	6	98029	*	126	*	-	-	0.11	ns	-	-
error	63										

[z] Each value represents the average (S.E.). Different letters within each column indicate significant differences at the 5% level according to the Tukey-Kramer's test. (Year: n=60, Treatment: n=30, Cultivar: n=40.) (For average fruit weight and fruit water contents: 2017: n=56, WET5: n=29, WET10: n=27, 'Suzukoma': n=36.)

[y] ANOVA could not be performed due to lack of replicates because some individuals died. Annual differences were analyzed using Student's t-test.

[x] Statistical analysis was performed after converting the percentage values to arcsine values.

[w] ANOVA was done by the split-split plot design (Little and Hills, 1978) (n=5).

df: degree of freedom, *MS*: mean square, Sig. : Significance (***, **, and * indicate significance at the 0.1%, 1%, and 5% levels, respectively. ns, not significant.)

Table 2 Number of flowers per plant and fruiting ratio in the pot experiment. Analysis of variance was used to compare the variables among treatment and cultivar under different environments for the 2 years.

	Number of flowers (plant^{-1}) [z]		Fruiting ratio (%) [y]	
Year (Y)				
2017	79.0 (3.5)		25.0 (1.5)	
2018	53.8 (3.1)		33.5 (1.9)	
Treatment (T)				
CONT	71.7 (5.7)		36.3 (2.6)	a
WET3	65.0 (5.4)		29.4 (2.3)	ab
WET5	68.3 (5.3)		27.0 (2.5)	b
WET10	60.7 (4.3)		24. (2.3)	b
Cultivar (C)				
'Natsunoshun'	66.4 (4.2)	b	31.6 (2.4)	
'Lycoball'	51.7 (3.6)	c	26.1 (2.0)	
'Suzukoma'	81.1 (4.4)	a	30.1 (2.1)	

ANOVA[x]	*df*	*MS*	Sig.	*MS*	Sig.
Y	1	19076	***	0.33	*
T	3	666	ns	0.13	**
C	2	8628	***	0.04	ns
Y×T	3	1375	ns	0.02	ns
Y×C	2	857	ns	0.08	*
T×C	6	747	ns	0.05	*
Y×T×C	6	613	ns	0.04	ns
error	63				

[z] Each value represents the average (S.E.). Different letters within each column indicate significant differences at the 5% level according to the Tukey-Kramer's test (Year: n=60, Treatment: n=30, Cultivar: n=40).

[y] Statistical analysis was performed after converting the percentage values to arcsine values.

[x] ANOVA was done by the split-split plot design (Little and Hills, 1978).

df: degree of freedom, *MS*: mean square, Sig. : Significance (***, **, and * indicate significance at the 0.1%, 1%, and 5% levels, respectively. ns, not significant.)

Table 3 Root dry weight, shoot dry weight, shoot water content, leaf area, NAR, and FDR in the pot experiment. Analysis of variance was used to compare the variables among treatment and cultivar under different environments for the 2 years.

		Root dry weight (gDW·plant^{-1}) [z]		Shoot dry weight (gDW·plant^{-1}) [y]		Shoot water content (%) [x]		Leaf area (cm^2)		NAR [w] (gDW·m^{-2}·day^{-1}) [x]		FDR [v] (%) [u]	
Year (Y)													
2017		6.4 (0.6)		46.2 (2.5)		84.7 (0.9)		4535 (358)		6.3 (0.3)		40.3 (1.7)	
2018		6.8 (0.4)		45.7 (2.3)		85.1 (0.9)		4278 (228)		6.7 (0.2)		29.9 (2.2)	
Treatment (T)													
CONT		9.5 (0.8)	a	60.5 (3.0)	a	87.2 (0.3)	a	6464 (388)	a	7.2 (0.3)	a	42.0 (2.6)	a
WET3		6.8 (0.6)	b	49.4 (3.2)	b	86.0 (0.5)	a	4086 (321)	b	7.2 (0.3)	a	40.1 (3.0)	a
WET5		5.1 (0.5)	b	41.1 (2.6)	bc	85.0 (1.1)	ab	4085 (352)	b	5.8 (0.4)	b	32.3 (2.4)	ab
WET10		4.9 (0.6)	b	32.6 (2.5)	c	80.9 (2.1)	b	2627 (307)	c	5.7 (0.3)	b	26.0 (2.8)	b
Cultivar (C)													
'Natsunoshun'		6.6 (0.5)		52.7 (2.7)	a	85.7 (1.0)		4998 (312)	a	6.6 (0.3)		34.0 (2.0)	b
'Lycoball'		7.6 (0.6)		48.0 (3.1)	b	83.5 (1.3)		4500 (399)	ab	6.5 (0.3)		24.6 (1.9)	c
'Suzukoma'		5.6 (0.8)		37.0 (2.4)	b	85.5 (0.8)		3448 (347)	b	6.4 (0.3)		46.7 (2.4)	a
ANOVA [t]	*df*	*MS*	Sig.	*MS*	Sig.	*MS*	Sig.	*MS*	Sig.	*MS*	Sig.	*MS*	Sig.
Y	1	6.0	ns	8.1	ns	-	-	171413	ns	-	-	0.4594	**
T	3	139.4	***	4249.5	***	-	-	75745133	***	-	-	0.2470	***
C	2	38.3	*	2592.2	***	-	-	25039339	***	-	-	0.6031	***
Y×T	3	47.8	*	296.6	ns	-	-	18081689	**	-	-	0.0092	ns
Y×C	2	8.2	ns	134.5	ns	-	-	6149285	ns	-	-	0.1050	**
T×C	6	23.2	*	229.7	ns	-	-	4297877	ns	-	-	0.0196	ns
Y×T×C	6	16.3	ns	135.9	ns	-	-	1672048	ns	-	-	0.0267	ns
error	63												

[z] Each value represents the average (S.E.). Different letter within each column indicate significant differences at the 5% level according to the Tukey-Kramer's test. (Year: n=60, Treatment: n=30, Cultivar: n=40.) (For the shoot water content in 2017: n=57, WET10: n=27, 'Suzukoma': n=37, NAR in 2017: n=56, 2018: n=58, WET3: n=29, WET10: n=25, 'Lycoball': n=39, 'Suzukoma': n=35.)

[y] Did not include fruit.

[x] ANOVA could not be performed due to lack of replicates because some individuals died . Annual differences were analyzed using Student's t-test.

[w] Net Assimilation Rate

[v] Fruit Dry matter distribution Ratio

[u] Statistical analysis was performed after converting the percentage values to arcsine values.

[t] ANOVA was done by the split-split plot design (Little and Hills, 1978).

df: degree of freedom, *MS*: mean square, Sig. : Significance (***, **, and * indicate significance at the 0.1%, 1%, and 5% levels, respectively. ns, not significant.)

Table 4 Yield, number of fruits per plant, average weight of fruit, marketable fruit ratio, and fruit water content in the field experiment. Analysis of variance was used to compare the variables among treatment and cultivar.

	Yield ($gFW \cdot plant^{-1}$) [z]		Number of fruits ($plant^{-1}$)		Average weight of fruit (gFW)		Marketable fruit ratio (%) [y]		Fruit water content (%)	
Treatment (T)										
CONT	8544 (954)	a	127.4 (10.5)	a	68.7 (5.3)	a	47.6 (4.3)	a	95.4 (0.1)	a
WET5	6684 (456)	a	100.3 (5.9)	b	68.6 (4.4)	a	52.2 (3.5)	a	95.1 (0.1)	a
WET10	4103 (288)	b	87.2 (4.5)	b	49.0 (4.2)	b	28.0 (3.3)	b	94.7 (0.1)	b
Cultivar (C)										
‘Natsunoshun’	8211 (926)	a	112.3 (10.1)	a	71.9 (3.8)	a	47.6 (4.9)	a	95.3 (0.1)	a
‘Lycoball’	6393 (691)	ab	84.7 (7.0)	b	74.6 (2.9)	a	28.2 (2.7)	b	95.2 (0.1)	a
‘Suzukoma’	4727 (376)	b	117.9 (5.4)	a	39.7 (2.4)	b	51.9 (3.3)	a	94.7 (0.1)	b

ANOVA[x]	*df*	*MS*	Sig.	*MS*	Sig.	*MS*	Sig.	*MS*	Sig.	*MS*	Sig.
T	2	74593700	***	6302.8	**	1918.3	***	0.29	***	2.148	***
C	2	45551797	***	4758.7	**	5648.3	***	0.27	***	1.699	***
T×C	4	5633882	ns	162.1	ns	119.8	ns	0.02	ns	0.007	ns

[z] Each value represents the average (S.E.). Different letters within each column indicate significant differences at the 5% level according to the Tukey-Kramer’s test (Treatment: n=15, Cultivar: n=15).

[y] Statistical analysis was performed after converting the percentage values to arcsine values.

[x] ANOVA was done by the split plot design (Little and Hills, 1978) (n=5).

df: degree of freedom, *MS*: mean square, Sig. : Significance (*** and **, indicate significance at the 0.1%, and 1% levels, respectively. ns, not significant.)

Table 5. Brix percent, acid percent, sugar/acid ratio, Lycopene content, and β-carotene content of fruit in the field experiment. Analysis of variance was used to compare the variables among treatment and cultivar.

	Brix (%) [zy]	Acid (%) [y]	Sugar-acid ratio	Lycopene ($mg \cdot gDW^{-1}$)	*β*-carotene ($\mu g \cdot gDW^{-1}$)
Treatment (T)					
CONT	4.1 (0.2) b	0.75 (0.02)	5.6 (0.3) b	3.6 (0.3)	27.6 (3.2)
WET5	4.4 (0.2) ab	0.76 (0.03)	6.1 (0.4) ab	3.5 (0.2)	28.2 (3.9)
WET10	4.9 (0.2) a	0.74 (0.03)	6.9 (0.3) a	4.1 (0.1)	32.3 (1.9)
Cultivar (C)					
‘Natsunoshun’	4.1 (0.1)b	0.68 (0.02)b	6.2 (0.2) b	3.7 (0.2)	22.5 (2.1)b
‘Lycoball’	4.1 (0.1)b	0.85 (0.02)a	4.9 (0.2) c	3.9 (0.3)	40.9 (3.1)a
‘Suzukoma’	5.2 (0.1)a	0.72 (0.02)b	7.5 (0.2) a	3.7 (0.1)	24.8 (1.3)b

ANOVA [x]	*df*	*MS*	Sig.	*MS*	Sig.	*MS*	Sig.	*MS*	Sig.	*MS*	Sig.
T	2	2.47	***	0.002	ns	6.47	**	1.504	ns	0.2470	ns
C	2	6.32	***	0.120	***	25.81	***	1.491	ns	0.6031	***
T×C	4	0.05	ns	0.009	ns	0.68	ns	2.223	**	0.0196	*

[z] Each value represents the average (S.E.). Different letters within each column indicate significant differences at the 5% level according to the Tukey-Kramer’s test (Treatment: n=15, Cultivar: n=15).

[y] Statistical analysis was performed after converting the percentage values to arcsine values.

[x] ANOVA was done by the split plot design (Little and Hills, 1978) (n=5).

df: degree of freedom, *MS*: mean square, Sig. : Significance (***, **, and * indicate significance at the 0.1%, 1%, and 5% levels, respectively. ns, not significant.)

Table 6. Marketable fruit ratio, immature fruit ratio, and blossom-end rot fruit ratio in the field experiment. Analysis of variance was used to compare the variables among treatment and cultivar.

		Marketable fruit ratio (%) [y]		Immature fruit ratio (%) [y]		Blossom-end rot fruit ratio (%) [y]	
Treatment (T)							
CONT		47.6 (4.3)	a	35.5 (4.1)	ab	2.7 (5.3)	
WET5		52.2 (3.5)	a	29.8 (3.2)	b	2.5 (4.4)	ns
WET10		28.0 (3.3)	b	47.5 (6.0)	a	2.7 (4.2)	
Cultivar (C)							
‘Natsunoshun’		47.6 (4.9)	a	43.0 (4.0)	a	3.0 (0.9)	
‘Lycoball’		28.2 (2.7)	b	52.3 (3.2)	a	1.7 (0.5)	ns
‘Suzukoma’		51.9 (3.3)	a	17.6 (1.7)	b	3.2 (1.4)	
ANOVA[x]	*df*	*MS*	Sig.	*MS*	Sig.	*MS*	Sig.
T	2	0.05	***	0.29	***	0.001	ns
C	2	0.31	***	0.27	***	0.011	ns
T×C	4	0.03	†	0.02	**	0.057	**
error	24						

[z] Each value represents the average (S.E.). Different letters within each column indicate significant differences at the 5% level according to the Tukey-Kramer’s test (Treatment: n=15, Cultivar: n=15).

[y] Statistical analysis was performed after converting the percentage values to arcsine values.

[x] ANOVA was done by the split plot design (Little and Hills, 1978) (n=5).

df: degree of freedom, *MS*: mean square, Sig.: Significance (***, **, and † indicate significance at the 0.1%, 1%, and 10% levels, respectively. ns, not significant.)

Supplemental Tables and Figures

Table S1. Environments on the ground (A) and under the ground (B) in a two-year pot experiment and a one-year converted paddy field experiment.

A Site	Year	Average air temperature (˚C) Total experimental period		Average air temperature (˚C) Before flowering (5-16 July)		Average total solar radiation (MJ・m^{-2})	
Pot exp.	2017	19.7	ns	25.0	**	17.0	*
	2018	19.2		18.5		15.1	
Field exp.	2019	20.3		-		17.7	

B Site	Year	Treatment	Average soil water content (%)		pF		Average oxygen concentration (%)	
Pot exp.	2017	CONT	16.6	*	1.94	*	16.3	*
		WET	42.5		1.32		0.6	
	2018	CONT	17.6	*	1.86	*	18.2	*
		WET	42.9		1.33		0.9	
Field exp.	2019	CONT	13.9	*	2.11	*	19.3	*
		WET5	31.5		1.16		14.2	
		WET10	41.3		1.09		15.1	

Each value indicates the mean,.

** and * represent significant differences at 1% and 5% level (Student's t-test). ns, not significant.

Table S2. Soil components in the field experiment before and after waterlogging treatments.

		pH		common counts (mg / 100gFW soil)							
				P		K		Mg		Ca	
before treatment	CONT	*5.5 (0.00)*	b	*12.9 (0.4)*		**46.2 (2.3)**		**116.4 (2.9)**		**737.9 (17.9)**	
after treatment	CONT	*5.6 (0.09)*	b	*12.7 (0.8)*	ns	**50.9 (8.1)**	ns	**118.7 (6.4)**	ns	**745.1 (11.4)**	ns
	WET5	6.0 (0.09)	a	*15.6 (1.2)*		**44.2 (2.9)**		**128.0 (1.4)**		**679.1 (2.4)**	
	WET10	6.2 (0.00)	a	*15.6 (1.1)*		**38.0 (2.7)**		**136.3 (6.0)**		**741.3 (33.3)**	

		common counts							
		Mg / K		Ca / Mg		lime saturation degree (%)		base saturation (%)	
before treatment	CONT	5.9 (0.2)		4.5 (0.07)		**73.3 (2.5)**		**92.1 (3.2)**	
after treatment	CONT	5.7 (1.1)	ns	4.6 (0.23)	ns	**77.2 (1.1)**	ns	**97.4 (2.2)**	ns
	WET5	6.8 (0.5)		3.8 (0.03)		**69.7 (0.5)**		**90.7 (0.7)**	
	WET10	8.5 (0.9)		4.0 (0.37)		**76.0 (3.7)**		**97.8 (3.1)**	

		trace element (ppm)							
		Cu		Zn		Mn		B	
before treatment	CONT	5.9 (0.1)	a	11.9 (0.5)	a	117.5 (3.9)		**2.0 (0.05)**	a
after treatment	CONT	5.8 (0.1)	ab	11.5 (0.3)	a	118.3 (9.4)	ns	**1.8 (0.13)**	ab
	WET5	5.4 (0.1)	b	9.7 (0.1)	b	120.0 (1.7)		**1.2 (0.18)**	c
	WET10	5.5 (0.1)	ab	9.8 (0.4)	b	113.3 (1.7)		**1.3 (0.02)**	bc

		N							
		hot water extractable N (mg / 100gFW soil)		total N (%)		nitrate N (mg / 100gFW soil)		ammonia N (mg / 100gFW soil)	
before treatment	CONT	5.7 (0.8)		0.26 (0.003)	a	12.0 (1.6)	a	2.2 (0.7)	
after treatment	CONT	5.4 (0.3)	ns	0.26 (0.003)	a	8.0 (2.5)	ab	1.7 (0.4)	ns
	WET5	*4.4 (0.2)*		0.24 (0.003)	b	4.2 (0.7)	b	1.2 (0.4)	
	WET10	*4.3 (0.1)*		0.24 (0.003)	b	3.6 (0.8)	b	1.2 (0.2)	

		soil property						α-glucosidase activity (pmol/gFW·min)	
		phosphate absorption coefficient		CEC (me / 100gFW soil)		tentative specific gravity			
before treatment	CONT	1416.7 (24.5)		36.0 (0.4)		0.79 (0.01)		647.3 (155.7)	
after treatment	CONT	1389.0 (34.0)	ns	34.5 (0.4)	ns	0.79 (0.01)	ns	915.3 (98.4)	ns
	WET5	1360.0 (12.2)		34.7 (0.2)		0.76 (0.02)		698.0 (32.0)	
	WET10	1396.7 (20.6)		34.8 (0.4)		0.78 (0.02)		823.0 (133.4)	

Each value indicates the mean (± S.E.) (n=3), and different letters in each column represent significant differences at the 5% level (Tukey-Kramer's test). P: available phosphoric acid, K: exchangeable potassium, Mg: exchangeable magnesium, Ca: exchangeable calcium, Cu: soluble copper, Zn: soluble zinc, Mn: easy reducible manganese, B: hot water soluble boron, N: nitrogen. The α-glucosidase activity represents microbial activity.

Bold values: Higher than the reference value.

Italic values: Lower than the reference value (Tokachi Agricultural Cooperative Association).

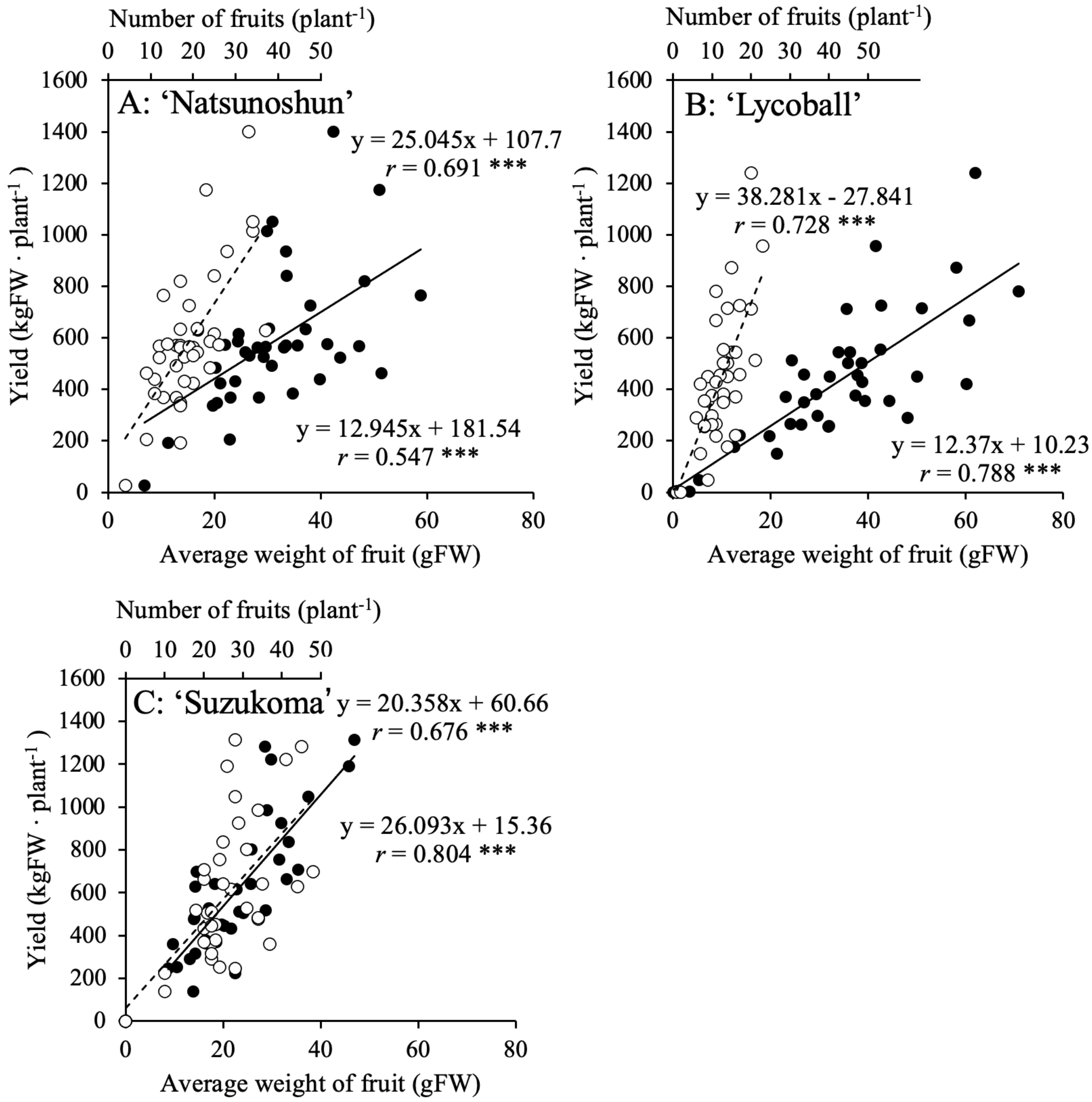
A: ‘Natsunoshun’
y = 25.045x + 107.7
r = 0.691 ***
y = 12.945x + 181.54
r = 0.547 ***
B: ‘Lycoball’
y = 38.281x - 27.841
r = 0.728 ***
y = 12.37x + 10.23
r = 0.788 ***
C: ‘Suzukoma’
y = 20.358x + 60.66
r = 0.676 ***
y = 26.093x + 15.36
r = 0.804 ***
Number of fruits (plant-1)
Yield (kgFW · plant-1)
Average weight of fruit (gFW)

Figure S1.

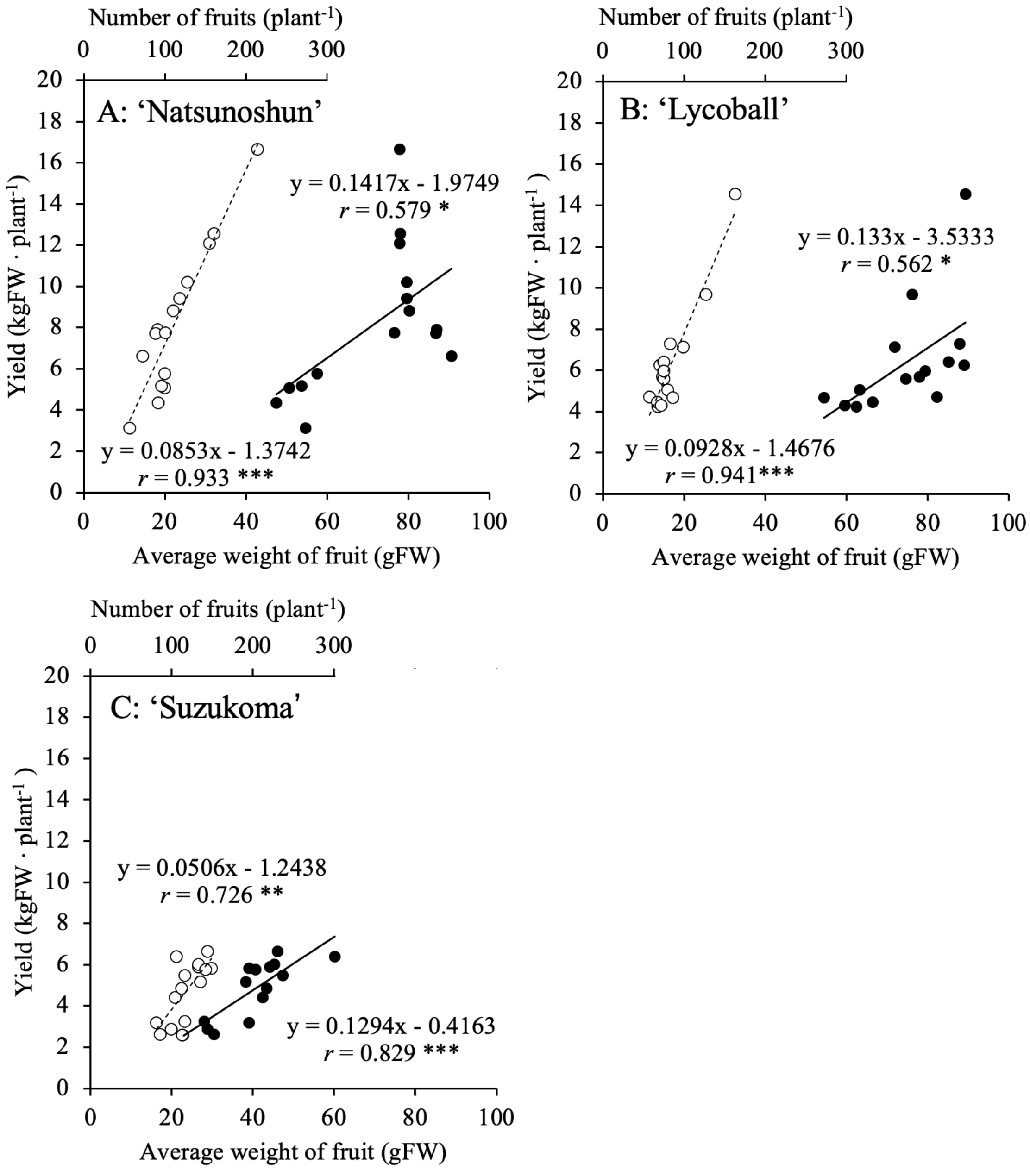
Number of fruits (plant-1)
A: 'Natsunoshun'
y = 0.1417x - 1.9749
r = 0.579 *
y = 0.0853x - 1.3742
r = 0.933 ***
Yield (kgFW · plant-1)
Average weight of fruit (gFW)
B: 'Lycoball'
y = 0.133x - 3.5333
r = 0.562 *
y = 0.0928x - 1.4676
r = 0.941***
C: 'Suzukoma'
y = 0.0506x - 1.2438
r = 0.726 **
y = 0.1294x - 0.4163
r = 0.829 ***

Figure S2.

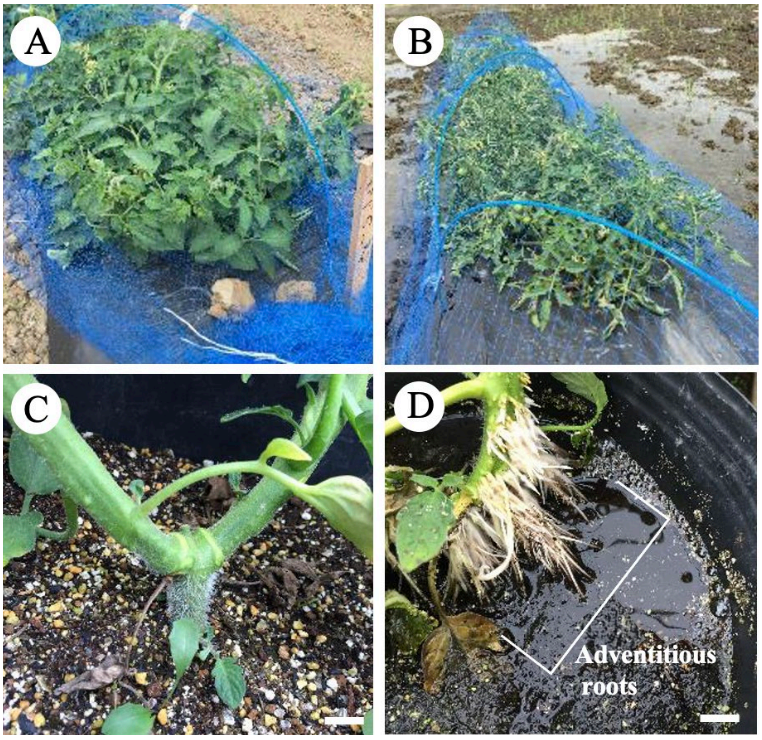

Figure. S3