Eur. J. Hortic. Sci. *84*(1), 39–47 | ISSN 1611-4426 print, 1611-4434 online | https://doi.org/10.17660/eJHS.2019/84.1.6 | © ISHS 2019

Original article – Thematic Issue

Effects of partial root drying on strawberry fruit

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Summary

Partial root-zone drying (PRD) is a well-established agricultural technique used to conserve water. Nitrogen plays a role in modifying both PRD-associated signaling and fruit quality. Here, we report the combined effects of PRD and nitrogen availability on water relations and fruit quality of strawberry plants (*Fragaria* × *ananassa*). Plants were subjected to PRD or common water deficit (DW) treatments with or without extra nitrogen supplied. PRD treatment resulted in a dramatic decrease in leaf conductance, whereas it had little effect on changes of leaf water potential. Strikingly, the inhibitory effect of PRD on leaf conductance was enhanced by nitrogen application. In the absence of nitrogen application, but not in its presence, PRD caused a significant decrease in fruit size. PRD did not improve fruit quality in comparison with its well-watered control; however, PRD in combination with nitrogen application resulted in increases in fruit firmness and vitamin C, soluble solid, and reducing sugar content, as compared with the control without nitrogen application, suggesting that PRD and nitrogen availability may jointly improve strawberry fruit quality formation. These findings provide guidelines for optimizing irrigation regimes to improve water use efficiency and fruit quality in strawberry farming.

Keywords
deficit watering, fruit quality, nitrogen application, partial root-zone drying, strawberry

Significance of this study

What is already known on this subject?

- Partial root drying (PRD) has been well known to be a technique in water-saving agriculture. Application of the PRD technique is based on root-to-shoot communication. Nitrogen has been reported to play an important role in the modification of root-to-shoot communication. No information is available about the combined effect of PRD and nitrogen regulation on fruit quality formation as well as water saving in strawberry plants.

What are the new findings?

- PRD technique can be exploited in water-saving production of strawberry fruits. PRD in combination with nitrogen regulation may jointly improve strawberry fruit quality formation and water use efficiency.

What is the expected impact on horticulture?

- These findings may be used to optimize irrigation regimes for improved water use efficiency and fruit quality in strawberry farming.

Introduction

In many regions of the world, agricultural production is greatly limited by water shortages. As water supplies continue to dwindle, it is increasingly important to develop strategies that improve irrigation efficiency. Partial root-zone drying (PRD), or similarly, regulated deficit irrigation (RDI), has been shown to be a technique to conserve water in agriculture (Davies and Zhang, 1991; Davies et al., 2000; Dodd, 2005; Ren et al., 2007). The theoretical basis for PRD is that the subset of roots growing in wet soil sustains normal plant growth and development, whereas the subset growing in dry soil triggers signals that regulate stomatal movement and reduce water consumption. Whereas PRD has been extensively studied in crop plants and some fruit tree species, with water conservation as a major objective, few studies have evaluated the effect of PRD on fruit quality in horticultural plants (Loveys et al., 2000, 2004; Stikic et al., 2003; Costa et al., 2007; Du et al., 2015; Galindo et al., 2017).

In crops, water conservation methods are largely based on promoting water use efficiency (WUE); in fruit crops, these methods aim to improve fruit quality, while promoting WUE. A few studies have evaluated the effects of PRD on fruit quality formation in *Solanum lycopersicum* (tomato) and several fruit tree species; however, these studies yielded ambiguous results, even for studies conducted on the same plant species (Verreynne et al., 2001; Costa et al., 2007; Stikic et al., 2014; Casassa et al., 2015; Boas et al., 2017; Coyago-Cruz et al., 2017; Galindo et al., 2017). There is a need to study the regulation of fruit quality in relation to different watering regimes and plant species.

PRD-induced signaling has been established to be mediated by root-to-shoot abscisic acid (ABA) communication. Additionally, pH has been suggested to be a co-signal of the ABA signal (Davies and Zhang, 1991; Bahrun et al., 2002). Since ABA signaling is pH-dependent, any factors that may affect the sub-cellular pH pattern may potentially modulate PRD-induced signaling, thereby modulating plant water relations. We have previously demonstrated that nitrogen nutrition may significantly modify PRD-induced ABA signaling (Jia and Davies, 2007). Nitrogen is a key nutrient influencing plant growth and development. A few studies have suggested that nitrogen availability might have significant effects on fruit quality formation. For example, tomato plants grown under low nitrogen conditions were reported to exhibit increases in fruit dry matter, and in soluble sugar and total ascorbic acid content, as well as in various pheno-

lic compounds (Benard et al., 2009). Given the importance of nitrogen in the regulation of both plant water relations and fruit quality formation, it is of particular interest to further investigate how PRD and nitrogen availability jointly affect fruit quality as well as plant water relations.

Strawberries (*Fragaria* × *ananassa*) are widely consumed throughout the world. In many regions, strawberries are mainly grown in greenhouses or plastic tunnels, environments that fail to support the production of flavorful and nutritious fruit. Additionally, strawberries are highly sensitive to soil water deficits, and a decline in water supply may result in a serious decrease in both yield and fruit size (Serrano et al., 1992; Liu et al., 2007). Thus, improving strawberry fruit quality is a major objective in strawberry production. As ABA has been suggested to play important roles in the regulation of strawberry fruit development and ripening (Jia et al., 2011, 2017), PRD-induced ABA signaling may affect strawberry fruit growth and development, thereby affecting fruit quality formation. The effects of PRD have been studied in horticultural plants, but most work has focused on tomato and *Vitis vinifera* (grape). Nitrogen availability may affect strawberry fruit quality (Cantliffe et al., 2007; Ojeda-Real et al., 2009; Cardeñosa et al., 2015). In this study, we analyzed the combined effects of PRD application and nitrogen supplementation on strawberry plant water relations, especially with respect to fruit quality formation, under laboratory-controlled conditions.

Materials and methods

Plant materials and growth conditions

Strawberry seedlings (*Fragaria* × *ananassa* Ducherne 'Sweet Charlie') were propagated through runners. When the seedlings were grown to 3 to 5 leaves, they were planted with roots split or not in pots (diameter 350 mm; depth 380 mm) containing a mixture of nutrient soil, vermiculite, and organic fertilizer (7:2:1; v/v/v) (Figure 1). The organic fertilizer was fermented dairy manure mixed with turfy soil. The basic characteristics of the mixed substrate were as follows: pH 7.26; total nitrogen content, 680 mg kg^{-1}; alkali-hydrolyzable nitrogen content, 87.56 mg kg^{-1}; organic content, 1.22%; available phosphorous content, 12.32 mg kg^{-1}; and available potassium content, 80.14 mg kg^{-1}. The seedlings were grown in a controlled environment with the following conditions: 25°C:18°C (day:night), 60% humidity, 12-h photoperiod with a photosynthetic photon flux density (PPFD) of 450 µmol m^{-2} s^{-1}. Plants were watered daily to the drip point until flowering, and then different watering regimes were applied according to the various aims of the experiments (for details, see the description below).

Split-root experiment

A plastic trapezoidal board with its dimensions adjusted to the diameter of the top and bottom of the pot was mounted into the pot, so that the inside of the pot was isolated into two equal compartments. Both sides of the board were smeared with a small amount of universal glue. Two plastic bags with maximum volumes of about half the volume of the pot were selected, and one side of each bag was adhered to the plastic board. The bags were filled with soil, such that the two compartments were absolutely water tight, except for the bottom of the plastic bags, where four small holes (each 1 cm in diameter) were made to allow water dripping. Each young seedling of about two months old, propagated from runner, was transplanted into an individual pot in mid-August, 2017. The roots were equally divided into two parts, and each part was separately buried in the soil in the two compartments described above. Plants were grown and irrigated as described above, until different watering regimes were implemented in December, 2017. The experimental set-up is shown in Figure 1.

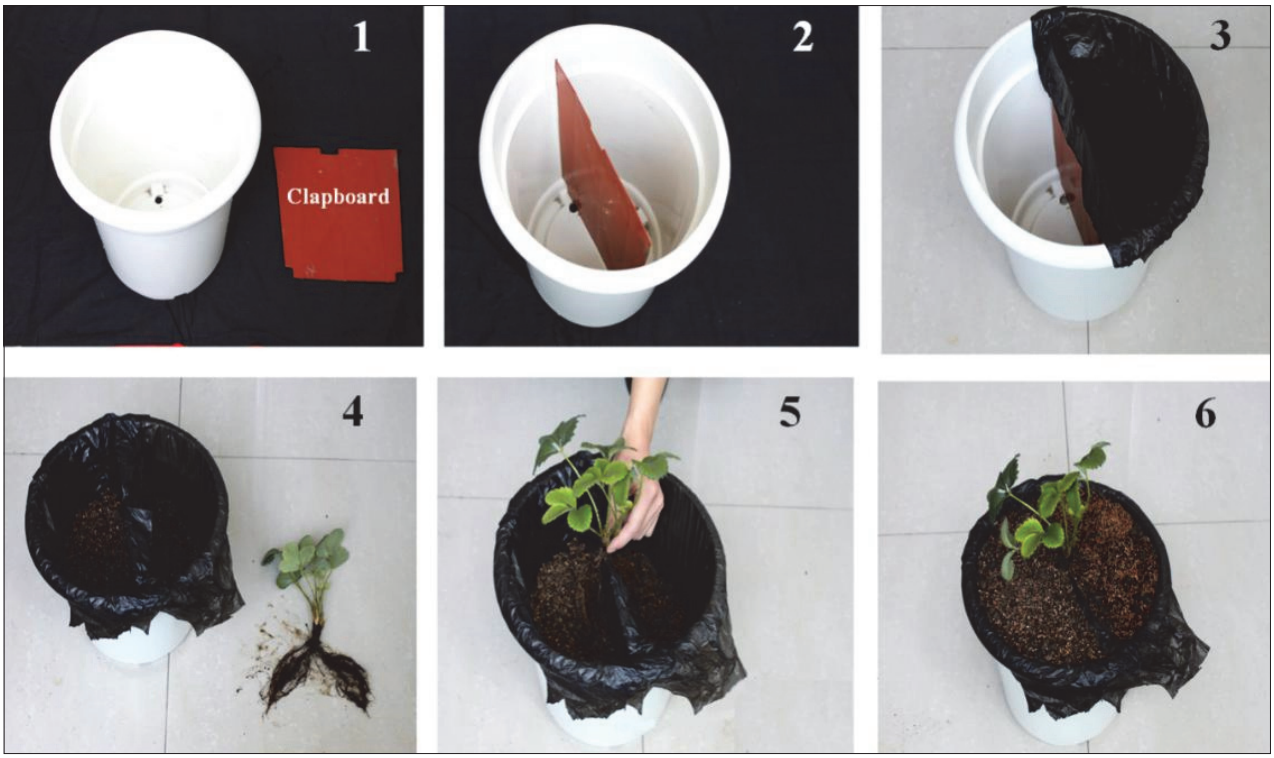


Figure 1. Graphic demonstration of split-root set-up. 1) Pot and clapboard used for split-root experiment; 2) Pot with clapboard installed inside; 3) Inside wall of the separated compartment sealed with plastic bag; 4) Pot and seedling ready for transplantation; 5) Transplantation of seedling, with roots separated into two compartments; 6) Seedling with split roots.

Watering regimes in combination with nitrogen application

Plants were divided into two groups, i.e., the split-root and non-split-root group. Plants were watered daily to the drip point until flowering, at about four months after transplantation. Strawberry fruit development, from fruit set to ripening, can be divided into three major stages, i.e., the green, white, and red fruit stages. Furthermore, the green stage can be divided into four substages (Jia et al., 2013). To avoid the effects of fruit number on fruit growth and development, only five fruits were retained per plant, and excess flowers were removed. Treatments were started when the first fruits of most plants were in the first or earliest stage. To investigate the synergistic effects of water stress and nitrogen treatment, individual plant was supplemented with 2 g NH_4NO_3 in each half of the separated root system. The amount of water loss per day per pot was estimated based on the weights of pots on successive days. This indicated that approximately 350 mL of water was lost per day. Water deficit treatment was started simply by watering withheld, and for the well-watered controls (i.e., both the split-root and non-split-root controls), 350 mL of water was replenished every two days in each individual pot. In the case of the split-root treatment group, water was withheld from one side, while 150 mL water was replenished every two days in the other side. In the case of deficit watering, water deficit was started simply by withholding water from whole pots until the soil water content decreased to about 20%. The soil water content was monitored using a 'WET-2 Sensor', as described below. Every two days, 100 mL water was replenished, to maintain the soil water content above 10% throughout the water deficit treatment. Each treatment consisted of six replicate plants.

Transient water deficit treatment

Well-watered plants were carefully removed from pots and transferred to larger pots containing dry fine soil to quickly absorb the soil moisture of the plants. After several changes of dry soil over a 16-h period, the plants were again transferred to the original pots and re-watered (Figure 6). Then, both control plants and the plants subjected to transient dehydration were well watered until the fruits of the plants of the water-deficit group turned red.

Determination of physiological parameters

Leaf conductance was determined using a 'SC-1 Leaf Prometer' (Decagon Devices, Inc.).

As leaf conductance changes with daily time course, measurements were taken between 10:00~11:00 am when a relatively high value was reached. For each plant, the area of fully expanded compound leaves was measured, and for each compound leaf, only the middle leaflet was measured. Each treatment consisted of six replicate plants, such that a total of 18 leaf samples were measured. Leaf water potential was determined using a pressure chamber (SEC3000, USA). Measurements were taken between 7:00~8:00 am when leaf potential became relatively steady. To determine the water potential of a leaf, the leaf must be detached from the plant. Because not much difference exists in the leaf water potential among different leaves from the same plant, only one fully expanded leaf was removed per plant, such that for each treatment, six samples were analyzed. Soil water content was determined using a 'WET-2 Sensor' (Delta-T Devices Ltd.). For both the non-split-root group and the split-root group of the well-watered control, soil water content was measured for three random pots, and for the split-root group subjected to water deficit treatment, measurements were taken at three random spots within each of the two compartments.

Determination of fruit firmness and fresh weight

Fruit firmness and fresh weight (FW) were assessed individually for 30 fruits, and individual fruit firmness was measured on the equatorial region of fruit using a penetrometer (Gaoke Inc., Jiangsu, China) using a sensor with a tip of around 3-mm in diameter.

Determination of fruit vitamin C content

The flesh of all fruit samples described in the previous section was frozen in liquid nitrogen and ground to a powder. Extraction and analysis of vitamin C content were performed as described (Hernandez et al., 2006). The liquid chromatographic method used to determine the vitamin C content consisted of an isocratic elution procedure with UV-visible detection.

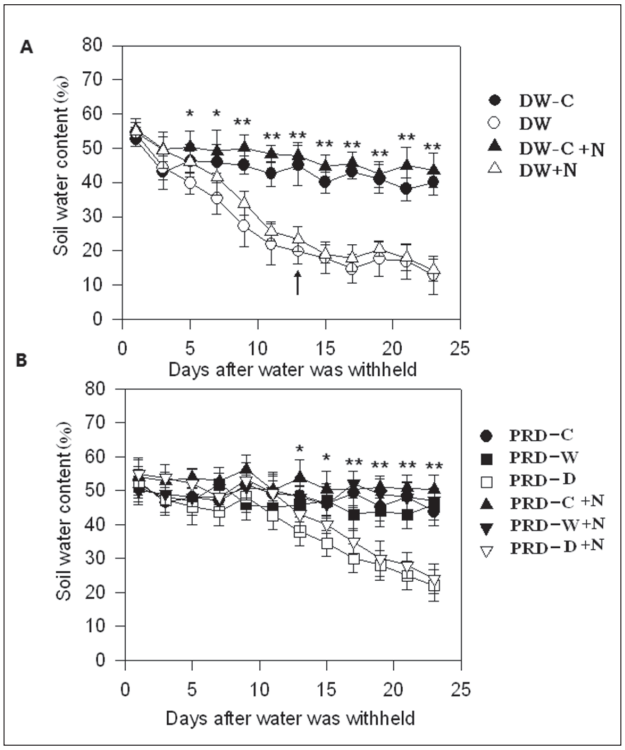


Figure 2. The effect of different watering regimes on changes in soil water content. A) Non-split-root plants. Water was withheld until the thirteenth day (arrow). DW-C, well-watered control; DW, deficit watering; DW-C+N, well-watered control with nitrogen application; DW+N, deficit watering with nitrogen application. B) Split-root plants. Water deficit treatment was started by withholding water from one side, while the other side was well watered. PRD-C, well-watered control; PRD-W, wet side in partial root-zone drying (PRD) group; PRD-D, dry side in PRD; PRD-C+N, well-watered control with nitrogen application; PRD-W+N, wet side in PRD with nitrogen application; PRD-D+N, dry side in PRD with nitrogen application. Values are means ± SD of six samples. Data were analysed using Student's *t*-test. Significant differences between the well-watered control and DW group are indicated by asterisks, * $P < 0.05$; ** $P < 0.01$; $n = 6$.

Determination of fruit soluble solid and reducing sugar content

Total fruit soluble solids were quantified on a separate aliquot of supernatant with a hand-held refractometer (Reichert A2R200, Reichert GmbH, Seefeld, Germany) and reported as °Brix. The reducing sugar content was quantified using dinitrosalicylic acid, according to Miller (1959). Reducing sugars were heated with 3,5 dinitrosalicylic acid, producing a red-brown product. The concentration of the coloured complex was determined spectrophotometrically by measuring the absorbance at 540 nM.

Determination of titratable acid content

The titratable acidity was determined by flow injection analysis with sodium hydroxide, and phenolphthalein was used as an indicator solution. As described by Rangel et al. (1998), a Crison (Barcelona, Spain) Model 2002 potentiometer equipped with a combined glass pH electrode and a Crison Model 2031 microburette were used.

Statistical analysis

To analyse physiological parameters and soil water content, the results of the water deficit treatment and its related controls were compared using Student's *t*-test. To analyse fruit quality parameters, significant differences among different treatments were compared using Fisher's LSD.

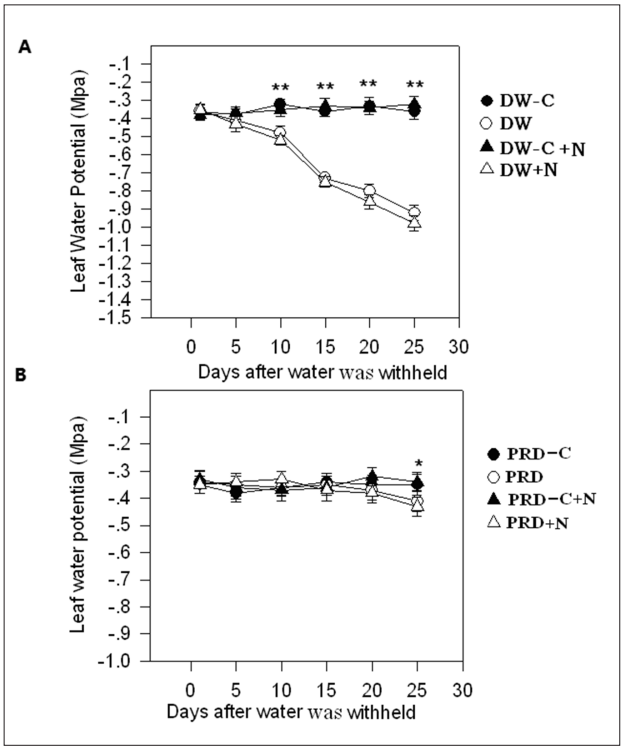


Figure 3. The effect of different watering regimes on changes in leaf water potential. A) Split-root treatment; DW-C, well-watered control; DW, deficit watering; DW-C+N, well-watered control with nitrogen application; and DW+N, deficit watering with nitrogen application. B) Non-split-root treatment. PRD-C, well-watered control; PRD, partial root drying; PRD-C+N, well-watered control with nitrogen application; PRD+N, partial root drying with nitrogen application. Values are means ± SD of six samples. Data were analyzed using Student's *t*-test. Significant differences between the well-watered control and DW groups are indicated by asterisks, * $P < 0.05$; ** $P < 0.01$.

Results

To evaluate the effects of PRD and nitrogen treatment on the development of fruit quality, plants were divided into two groups, i.e., the split-root and non-split-root group, and each group was subjected to four different treatments, i.e., adequate or deficit watering, with or without nitrogen treatment. Figure 2 shows the changes in soil volumetric water content at various time-points throughout deficit watering (DW). In the non-split-root group (Figure 2A), the soil water content started to decline soon after watering was withheld. A dramatic decrease in soil water content may seriously impede fruit production. To avoid this, a limited amount of water was added when the soil water content decreased to about 20%, so that the soil water content was maintained above 10%. We did not detect any differences in the changes in soil water content between plants that had been treated with nitrogen and those that had not. By contrast, the soil water content of the PRD group (Figure 2B) remained unchanged until the 13th day after watering was withheld, and the decrease in soil water content did not always exceed 20%. Furthermore, we did not detect any differences in soil water content between the nitrogen treatment and non-treatment control plants subjected to PRD. As shown in Figure 3A, a significant decrease in leaf water potential was observed about 10 days after watering was withheld in the DW group. By contrast, withholding water did not result in a significant decrease in leaf water potential until the end of treatment under PRD conditions (Figure 3B).

As DW treatment caused a significant decrease in leaf water potential (Figure 3A) and a decrease in leaf water potential was predicted to cause a dramatic decrease in leaf conductance, we examined the effect of water deficit on leaf conductance only for the split-root group. The leaf water

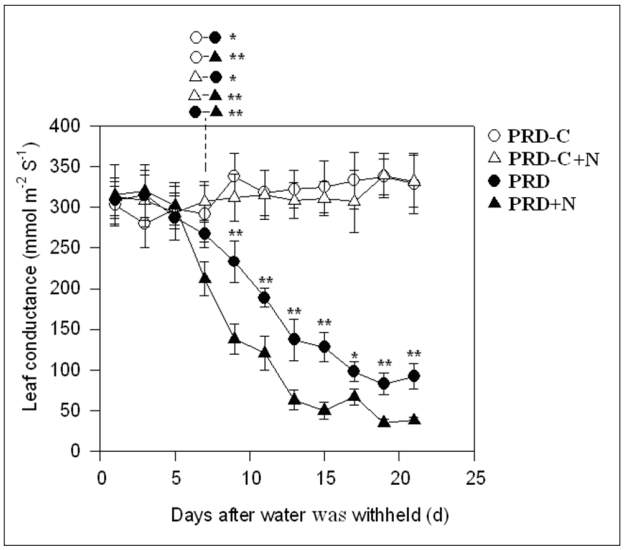


Figure 4. Changes in leaf water conductance in plants subjected to different watering regimes under split-root conditions. PRD-C, well-watered control; PRD-C+N, well-watered control with nitrogen application; PRD, partial root drying; and PRD+N, partial root drying with nitrogen application. Values are means ± SD of 18 samples. Data were analyzed using Student's *t*-test. Significant differences between treatments on the seventh day or between the effects of nitrogen application and non-application for the PRD treatment are indicated by asterisks, * $P < 0.05$; ** $P < 0.01$. The fourth measurement point is enlarged above the graph.

potential was not significantly altered for this group under which water deficit treatment (Figure 4). Whereas leaf conductance was unchanged under well-watered conditions, PRD treatment resulted in a dramatic decrease in leaf conductance. Furthermore, nitrogen application markedly promoted this decrease in leaf conductance.

DW treatment resulted in a dramatic decrease of nearly 30% in fruit fresh weight in comparison with the well-watered control (Figure 5A). PRD treatment also resulted in a decrease in fruit fresh weight, but the decrease was much lower than that caused by DW treatment. Nitrogen application promoted fruit growth and resulted in a significant increase in fruit fresh weight, and PRD did not result in a significant decrease in fruit fresh weight in the presence of nitrogen supplementation. Both in the presence and absence of nitrogen application, water deficit treatment caused a significant increase in fruit firmness. Moreover, nitrogen application also caused an increase in fruit firmness in comparison with seedlings not supplemented with nitrogen (Figure 5B). PRD treatment in conjunction with nitrogen supplementation did not affect fruit firmness, so that the fruit firmness was still larger than that of the well-watered control not supplemented with nitrogen.

There was no significant difference in the titratable acid content of fruit among the different watering regimes (Figure 5C). Also, nitrogen application had no significant effect on the titratable acid content. Whereas no significant differences were found in vitamin C content in plants subjected

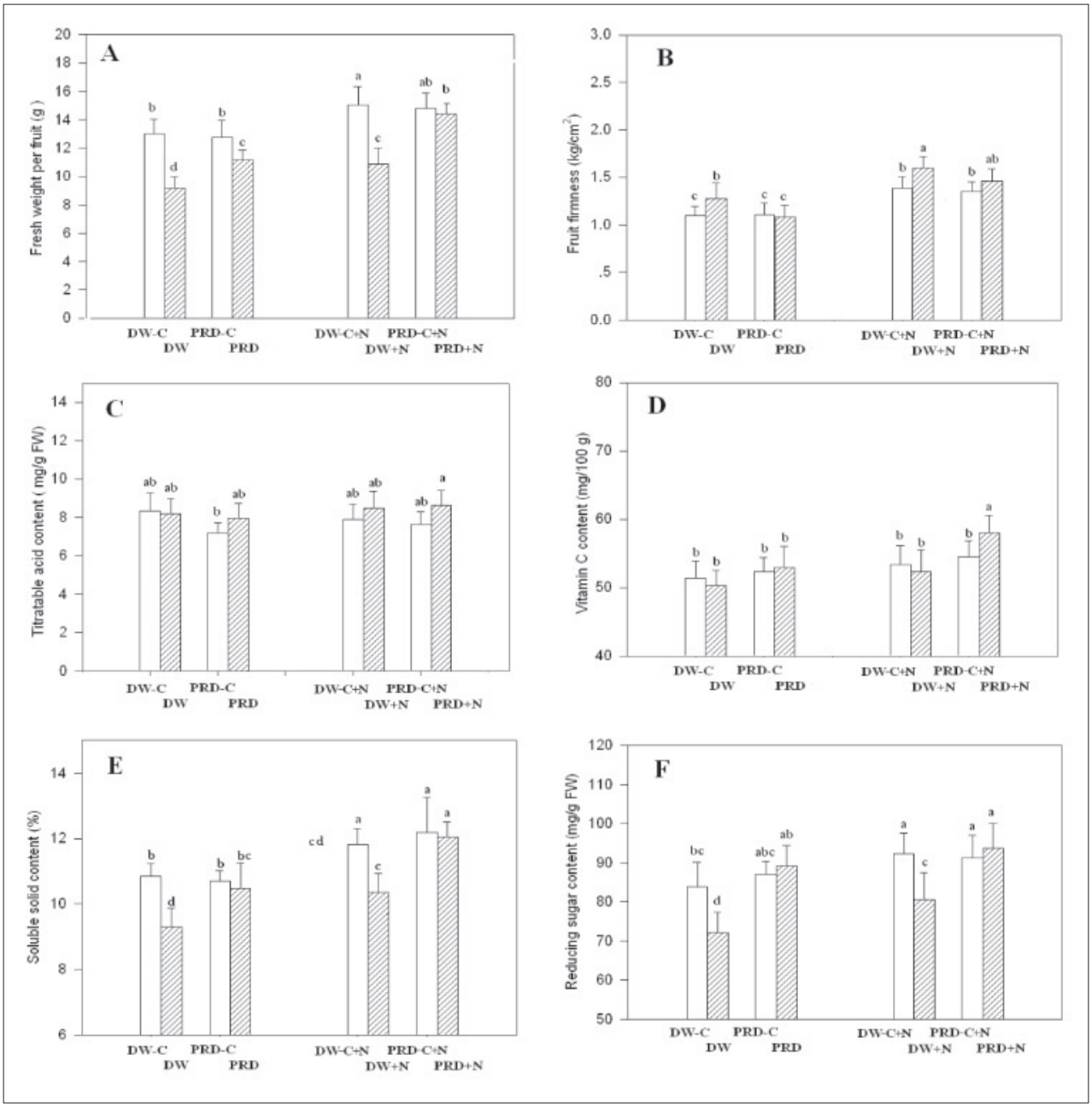


Figure 5. Effect of different watering regimes and nitrogen application on fruit quality parameters. A) fruit fresh weight; B) fruit firmness; C) titratable acid content; D) vitamin C content; E) soluble solid content; and F) reducing sugar content. DW-C, well-watered control; DW, deficit watering; DW-C+N, well-watered control with nitrogen application; DW+N, deficit watering with nitrogen application; PRD, partial root drying; PRD+N, partial root drying with nitrogen application; PRD-C, well-watered control; and PRD-C+N, well-watered control with nitrogen application. Values are means ± SD of 30 samples. Different lowercase letters indicate significant differences as determined by Fisher's LSD ($P < 0.05$).

to the different watering regimes, nitrogen application and PRD treatment jointly resulted in a significant increase in the vitamin C content compared to both the DI and PRD controls (Figure 5D).

Both in the presence and absence of nitrogen application, DW treatment caused a significant decrease in the soluble solid content (Figure 5E). PRD treatment had no effect on the soluble solid content as compared to the controls. Nitrogen application caused an increase in soluble solid content. Whereas DI resulted in a significant decrease in the soluble solid content compared to the control, PRD did not affect soluble solid content compared to the control (Figure 5E).

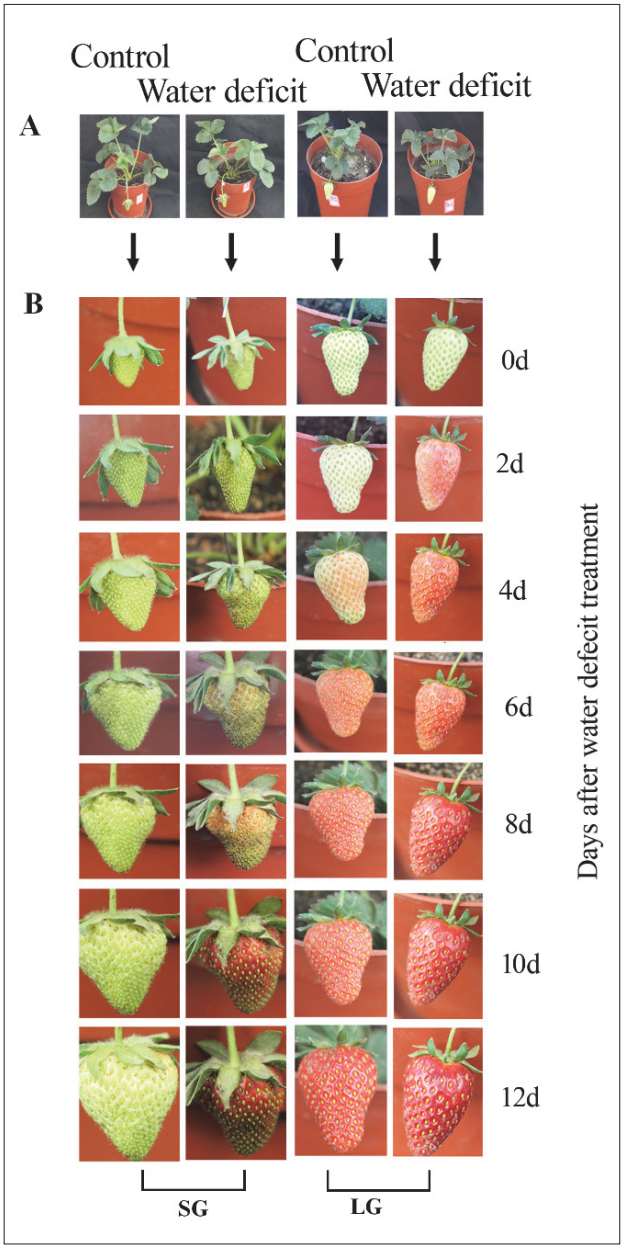


Figure 6. Effect of water deficit on fruit growth and ripening. Plants were subjected to transient water deficit by root drying and water withholding. A) Photographs showing individual fruits attached to plants just before water deficit treatment. SG (small green) and LG (large green) refer to the fruits' developmental stage when the water deficit treatment started. B) Photographs showing fruits' developmental progress, as affected by water deficit.

DW treatment resulted in a decrease in reducing sugar content compared to the well-watered control both in the presence and absence of nitrogen application (Figure 5F). Unexpectedly, nitrogen application caused an increase in the reducing sugar content, and PRD had no effect on the reducing sugar content compared to the PRD control (Figure 5F).

Given that DW caused a dramatic increase in fruit fresh weight (Figure 5A), soluble solid content (Figure 5E), and reducing sugar content (Figure 5F), we speculated that a decrease in fruit water status, as caused by DW, might greatly accelerate fruit ripening, and thus sugar accumulation. To test this possibility, we further investigated strawberry fruit development and ripening following a decrease in fruit water potential. Strawberry plants were first subjected to a transient water deficit treatment (only 16 hours versus the long-term DW treatment of several weeks), after which plants were again re-watered well. As shown in Figure 6, before water deficit started, the control and treatment fruits were basically identical at each developmental stage. Strikingly, two days after the water deficit started, the fruits quickly became fully red, whereas the control fruits were only at the white stage (for LG). The effect of water deficit on fruit development was most pronounced in the earlier developmental stages; for instance, when water deficit was applied at the LG stage, the fruits ripened fully about 3 days before the control fruit, whereas when water deficit was applied at the SG stage, the fruits ripened fully 12 days before the control fruit. Therefore, strawberry fruit development and ripening is quite sensitive to a decrease in fruit water potential; a small decrease in fruit water potential was enough to affect fruit-ripening and thus fruit quality formation.

Discussion

PRD has emerged as a promising strategy to conserve water in agriculture (Davies et al., 2000; Zegbe et al., 2006; Costa et al., 2007). Although the PRD technique has been applied to some horticultural plants, particularly grapevine and tomato, the effects of PRD on fruit quality are not clear (Davies and Zhang, 1991; Davies et al., 2000; Loveys et al., 2000; McCarthy et al., 2002; Cifre et al., 2005).

A number of studies have shown that mild water deficit, as controlled by PRD or regulated deficit irrigation (RDI), results in an increase in yield and improves berry quality (Matthews and Anderson, 1988; Santos et al., 2005). For example, a study by Pulupol et al. (1996) reported that fruits from tomato plants (*Lycopersicon esculentum* Mill. 'Virosa') subjected to DI treatment had significantly higher concentrations of sucrose, glucose, and fructose than did well-watered control fruits, and similarly, Davies et al. (2000) reported that PRD treatment greatly increased the soluble solid content of tomato fruit (*Lycopersicon esculentum* L.). Besides tomato, PRD and regulated deficit irrigation (RDI) have been reported to cause an increase in anthocyanins and total phenols in the grape berry skin (Matthews and Anderson, 1988; Santos et al., 2005, 2007), in soluble solid content in apple (*Malus domestica*) 'Braeburn' (Mpelasoka and Behboudian, 2002) and citrus 'Marisol Clementines' (Verreynne et al., 2001). In the present study, we did not find that water deficit was able to induce soluble solid or sugar accumulation, and conversely, we found that water deficit treatment resulted in a dramatic decrease in soluble solid (Figure 5F) and reducing sugar (Figure 5F) content, as well as in fruit size, as reflected by fresh weight (Figure 5A). To explore the underlying cause for this, we investigated fruit

development and ripening in response to changes in fruit water potential, and found that strawberry fruit ripening was quite sensitive to changes in fruit water potential, with a decrease in fruit water potential greatly accelerating fruit ripening (Figure 6). As water deficit may lead to a decrease in fruit water potential, we speculated that the reduced soluble solid and sugar content as well as fruit size was possibly due to the accelerated fruit ripening, because shortening the ripening process would be expected to reduce assimilate transport from the leaves to fruits.

Nitrogen application has frequently been reported to adversely affect fruit quality formation (Cantliffe et al., 2007; Wold and Opstad, 2007; Ojeda-Real et al., 2009; Cardeñosa et al., 2014). Consistent with these reports, the present study showed that nitrogen application could significantly affect strawberry fruit quality formation. While the nitrogen application may affect many fruit quality parameters, the greatest impact was found on fruit size, one of the most important fruit quality parameters. Over application of nitrogen has been commonly reported to produce a negative effect on fruit quality formation in many plant species (Cantliffe et al., 2007; Wold and Opstad, 2007; Ojeda-Real et al., 2009; Cardeñosa et al., 2014). In strawberry, however, the situation was more complicated than as expected. Nitrogen is known to be essential for robust plant growth, and fruit growth and development depend on plant robust plant growth. Strawberry is characterized by successive rounds of flowering and fruit production, which rely on adequate nutrient supplementation. Alternatively, fruit quality formation, especially fruit size, may be tightly correlated to the vegetative growth. Nitrogen application promoted vegetative growth and hence had a great influence on fruit size. Strikingly, strawberry fruit ripening was found to be quite sensitive to water deficit treatment (Figure 6), such that fruit size was also found to be quite sensitive to water deficit owing to the reduced growth time from fruit set to ripening. Nitrogen application not only resulted in an increase in fruit size (Figure 5A), but also in fruit firmness (Figure 5B) and soluble solid and reducing sugar content (Figure 5E, F). Besides the direct effects of nitrogen application on fruit development and quality formation, nitrogen application may potentially play a role in modulating the PRD-induced root-to-shoot signaling.

In the absence of nitrogen supplementation, PRD resulted in a decrease in fruit size, as reflected by fresh weight, in comparison with the control grown under the same conditions. However, PRD did not negatively affect fruit size when the plants were supplemented with nitrogen (Figure 5A). A reason for this may be that nitrogen application resulted in an increase in stomatal sensitivity to the root-sourced signal, thereby maintaining the leaf and fruit water potential at relatively high values (Figures 3 and 4). These findings suggest that PRD and nitrogen application indeed have joint effects on both water conservation and fruit quality improvement.

The effect of PRD on fruit development and ripening is complex. Theoretically, under PRD conditions, the water potential of leaves should not be decreased significantly, because, on the one hand, the signals originating in the drying parts of the roots are expected to result in a significant decrease in transpiration, and on the other hand, the well-watered part of roots is expected to maintain normal water transport from roots to leaves (Davies and Zhang, 1991; Bahrun et al., 2002). However, practically, whether a leaf's water potential decreases is determined by the balance between the rates of transpiration and water transport into the leaf, such that even under PRD conditions, a leaf's water potential and fruit water potential may possibly decrease. Whether or how a fruit's water potential changes under PRD conditions is associated with many factors, such as plant species, developmental stage, and environmental and soil conditions. The effect of PRD on grape berry quality has been proposed to be caused by improved exposure of berry clusters to solar radiation, because PRD led to a decrease in vegetative growth (Costa et al., 2007; Santos et al., 2005, 2007). Unlike grapes and the fruit of most fruit tree species, which develop and ripen over several months, strawberry fruit develops and ripens within about one month, and the ripening from the white stage to the full red stage takes only about one week (Jia et al., 2013; Han et al., 2015). Additionally, strawberry fruit ripening is regulated by ABA, which coincides with the key signal mediating PRD-induced root-to-shoot signaling. Given the differences in the patterns of fruit growth and development between strawberry and other fruit, the effect of DI and PRD on strawberry fruit quality formation is likely mediated via different mechanisms from other fruit trees, and this may be why DI or PRD have been commonly reported to have different effects on fruit quality in different studies (Mpelasoka et al., 2002; Zegbe et al., 2006; Santos et al., 2007; Adak et al., 2018).

In summary, whereas PRD has been demonstrated to be an important water-saving technique in agriculture, its effect on fruit quality formation has not been conclusively established. The effect of PRD on fruit quality formation may be influenced by many factors, such as plant species, developmental stage, and environmental and soil conditions, and the combined effects of PRD and these factors merit further investigation. In the current study, we examined the combined effect of PRD and nitrogen availability on strawberry fruit quality formation. We found that PRD is an effective technique to conserve water in strawberry production, but that in the absence of nitrogen application, PRD had a negative effect on fruit size. However, when nitrogen was applied, PRD not only had no negative effect on fruit size, but also resulted in an increase in soluble solid and sugar content in comparison with the well-watered control without nitrogen application. Thus, PRD and nitrogen may jointly promote strawberry fruit quality formation. These findings should be used to optimize watering regimes in strawberry production.

Acknowledgments

This work was supported by the National Natural Science Foundation of China (Grant No. 31471851, 31672133) and the Beijing Municipal Natural Science Foundation (Grant No. 6171001).

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Received: Mar. 3, 2018
Accepted: Oct. 9, 2018

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