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Responses of two strawberry cultivars to severe high temperature stress at different flower development stages

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ABSTRACT

Prolonged heat stress negatively affects fruit set and fruit development in strawberry (*Fragaria* x *ananassa* Duch.), but the effect of a one-time severe heat stress at different stages of flower development is poorly understood. We hypothesized that strawberry is negatively affected by acute and severe heat stress but the response varies by floral development stage and by cultivar. Two Japanese cultivars, 'Nyoho' and 'Toyonoka', which were previously reported to differ in their tolerance to prolonged high temperatures, were heat stressed at 42 °C for 4 h at 12, 9, 6, 3, and 0 days before anthesis (DBA) of the primary flower. Data on the percentage fruit set and fresh weight, diameter, and length of all developed fruits were then collected. In terms of fruit set from primary to tertiary flowers, two heat-sensitive floral development stages were observed in 'Nyoho': at 12 DBA and 0 DBA (or at anthesis). In 'Toyonoka', the heat-sensitive floral development stages were at 9 DBA and 0 DBA. Fresh weight and fruit size were larger in primary and secondary fruits of 'Nyoho' when the heat stress was applied during the earlier floral development stages but tertiary fruits were larger when heat stress was applied during the later floral development stages. For 'Toyonoka', the fresh weight and fruit size of primary fruits were smallest when the heat stress was applied at 9 and 0 DBA. These findings confirm our hypotheses and will be helpful in predicting yield losses in open-field strawberry production when a sudden heat wave occurs during the crop's flowering and fruiting season from late winter to early summer.

1. Introduction

High temperature stress (HTS) is one of the most important abiotic stresses that affect reproductive growth in plants. Low fruit set, flower and fruit abortion, and pollen and ovule infertility are some of the negative effects that have been reported across a wide range of crops (Gupta et al., 2015; Turner and Wien, 1994; Mutters and Hall, 1992; El-Abd et al., 1986; Sato et al., 2000; Tao et al., 2008). Several studies have also shown that the response to HTS differ at specific stages of flower development. In peanut, a reduction in fruit set was caused by exposure of plants to ≥39 °C for 1 day, but the percentage of reduction was greater at 3 days before and at anthesis than prior to or after these two stages (Vara Prasad et al., 2001). Maize plants were shown to be most sensitive to heat stress at 15 days before anthesis than at 15 days from the start of silking as evidenced by the higher percentage of kernel abortion and final kernel number (Rattalino Edreira et al., 2011). Gross and Kigel (1994) found that in the common bean, heat stress during microsporogenesis resulted in sterile pollen that failed to dehisce during anthesis, whereas heat stress during anthesis reduced the ability of the pollen to penetrate the stigma resulting in low fruit set.

The strawberry has been shown to respond negatively to HTS (Ledesma et al., 2008; Pipattanawong et al., 2009). Temperatures above 30 °C reduce fruit set and fruit size (Ledesma et al., 2008; Kadir et al., 2006). Moreover, it was reported that plants exposed to high temperatures from flower bud initiation to emergence had lower fresh weight of fruits compared to plants grown at lower temperatures (Mori, 1998). Plants grown at 30/25 °C from when the primary flower became visible was found to have smaller berries (Ledesma et al., 2008). However, there were cultivar differences in the response to heat stress: fruit set was much lower in 'Toyonoka' than in 'Nyoho' at the high temperature treatment. The heat sensitivity of 'Toyonoka' was later reported to be due to poor pollen performance at high temperatures compared to 'Nyoho' (Ledesma

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and Sugiyama, 2005) and could also be due to the lower expression of heat shock proteins in this cultivar (Ledesma et al., 2004).

Only a handful of studies have so far examined how a short, one-day exposure to high temperature stress can damage key stages in plant reproduction. Rudich et al. (1977) found that a tomato cultivar had reduced fruit set when exposed to 40 °C for 4 h 9 days before anthesis, whereas no reduction was observed at 7, 2, and 0 days before anthesis. A study done on *Arabidopsis* revealed that when flowers at various stages of development were heat shocked at 42 °C for 4 h, two heat-sensitive stages were found: during pollen mother cell development and subsequent meiotic processes (early stage) and during anther dehiscence (late stage) (Kim et al., 2001). Exposure of rice plants to a one-day heat stress of 35 °C during the near-flowering and early grain set stages significantly reduced grain yield in several genotypes. However, genotypic differences in the response to the heat stress were found (Talukder et al., 2014). Gross and Kigel (1994) also reported that even just a one-day exposure to moderate heat stress reduced fruit set in the heat-sensitive cultivar of the common bean but not in the heat-tolerant one.

The Intergovernmental Panel on Climate Change (IPCC) reports that the occurrence of heat wave events (short periods of extremely high temperatures) have been increasing since the 1950s and is "very likely" to continue into the late 21st century, especially in Europe and North America where most of the world's strawberry production currently takes place (IPCC, 2013; Hancock, 1999). It is important to determine how such short-term HTS can affect strawberry productivity because the productive season for June-bearing cultivars begins in late winter and lasts through early summer, a period when extreme changes in temperatures can occur (Kadir et al., 2006). Furthermore, strawberry production also exists in subtropical (Mackenzie et al., 2011) and tropical (Aspuria et al., 1996) areas where heat stress can be more severe. The objectives of this study were 1) to determine the effect of a single-day extreme HTS event on strawberry flowers at different stages of development and 2) to determine if there are cultivar differences in the response to this acute and severe HTS.

2. Materials and methods

This study was conducted at the Graduate School of Agricultural and Life Sciences, University of Tokyo. Rooted runners of 'Nyoho' and 'Toyonoka' were obtained from a commercial nursery. These two cultivars were chosen due to their previously reported different responses to prolonged heat stress, so it was important to find out if such responses also extended to acute heat stress. The runners were transplanted into 15-cm plastic pots and grown in a greenhouse under natural light conditions and an average day/night temperature of 26/15 °C from August 2002 until the onset of flowering (October 2002). The growing medium used was a mixture of soil compost (Soil Mix; Sakata, Yokohama, Japan), granulated soil-derived potting material (Engei-baido; Kureha, Tokyo, Japan), and vermiculite at a 4:1:1 ratio.

To determine which flower stage(s) was most sensitive to HTS, strawberry plants of both cultivars were heat stressed at 42 °C for 4 h in a growth cabinet at different stages of flower development. Designation of stages was based on the number of days to anthesis of the primary flower: Stage 1 was 12 days before anthesis (DBA) when the first inflorescence had just become visible, Stage 2 was 9 DBA, Stage 3 was 6 DBA, Stage 4 was 3 DBA, and Stage 5 was the day of anthesis (0 DBA).

The HTS treatment was achieved by ramping up the temperature in the growth cabinet from 26 °C to 42 °C at increments of 4 °C/h, held at 42 °C for 4 h, then brought back to 26 °C at increments of 4 °C/h. Five plants were used for each stage of flower development for each cultivar. After the HTS treatment, plants were returned to the greenhouse and allowed to continue flowering from October 2002 to January 2003. For the control, five plants from each cultivar were not heat stressed and allowed to grow normally in the greenhouse. The control plants were at the same stage as Stage 1 when the HTS treatments commenced. All flowers that opened post-HTS, including Stage 5 flowers, were pollinated with a paintbrush. Data on percentage total fruit set as well as fresh weight of fruit, fruit size (diameter at the widest side and length), and percentage fruit set from the primary to tertiary flowers were gathered from all treatments to determine if the higher flower positions (i.e., secondary and tertiary) were also as affected as the primary position.

Data were analyzed by one-way or two-way ANOVA and means were compared by Fisher's LSD using the IBM SPSS Statistics 23 software (New York, USA).

Table 1
Mean total fruit set (%) of 'Nyoho' and 'Toyonoka' exposed to high temperature stress at different flower development stages.

	Stages (% total fruit set)					
Cultivar	Control	1	2	3	4	5
Nyoho	89.67^{a,d}	74.11^{a,b}	71.56^{b}	75.05^{a,b}	73.56^{b}	61.89^{c}
Toyonoka	93.50^{d}	66.54^{b,c}	71.82^{b}	88.33^{a,d}	78.07^{b}	76.11^{b}
Significance[a]						
Cultivar (C)	NS					
Stages (S)	**					
C × S	NS					

[a] ,*,**, or NS indicates significance at $P \leq 0.05$ (*) or $P \leq 0.01$ (**). Superscript letters signify statistical differences among means. Degrees of freedom = 11.

3. Results

3.1. Fruit set

High temperature stress reduced total fruit set percentage (fruit set from all flowers that developed in the first inflorescence, including quaternary flowers) in both 'Nyoho' and 'Toyonoka' (Table 1). There was no significant difference between the two cultivars in response to HTS, indicating that total fruit set in both cultivars at the different stages were similarly affected by HTS; the two cultivars differed in total fruit set at Stage 5 only. Significant differences were found among the stages of each cultivar (Table 1). In 'Nyoho', total fruit set in the control plants (no HTS) did not differ from that of Stage 1 (S1) and Stage 3 (S3) plants (12 and 6 DBA, respectively), but it was significantly higher than Stage 2 (S2), Stage 4 (S4), and Stage 5 (S5) plants (9, 3, and 0 DBA, respectively).No significant differences in total fruit set were found among the stages only (control not included) except for S5, which had the lowest fruit set of them all. In 'Toyonoka', total fruit set in the control was higher than all the stages except S3. Among the stages only, S1 and S2 fruit set were lower than S3; no significant differences were found between S4 and S5. The interaction of Cultivar and Stages was also not significantly different.

Regression and correlation analyses of the effect of HTS on the relationship between the different flower stages and total fruit set at each stage revealed that although the regression line trended negatively (i.e., decreasing total fruit set with increasing stage, data not shown), no strong linear correlations were found in either Nyoho ($R^2 = 0.260$) or Toyonoka ($R^2 = 0.278$).

The percentage fruit set of primary to tertiary flowers only is shown in Table 2. Cultivar differences in the response to HTS were highly significant in primary flowers, whereas it was only significant and not significant in the secondary and tertiary flowers, respectively. The effect of HTS on fruit set of primary flowers was more severe in 'Nyoho' than in 'Toyonoka' at S3, S4, and S5. In 'Nyoho', no fruit set was observed in plants exposed to HTS at S4 and S5. In 'Toyonoka', however, HTS did not significantly affect fruit