

Heat-stress Tolerance of Some Strawberry (*Fragaria × ananassa*) Cultivars

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Abstract

Physiological parameters were used to investigate genotypic variations in 15 strawberry cultivars ['Aromas', 'Camarosa', 'Carmine', 'Cal. Giant 3' (CG3), 'Cal. Giant 5' (CG5), 'Elsanta', 'Fern', 'Festival', 'Honeoye', 'Kabarla', 'Redlands Hope' (R.Hope), 'Ruby Gem', 'Selva', 'Sweet Charlie' and 'Whitney'] and their relationship to heat-stress tolerance (HST). Cold stored (frigo) strawberry seedlings were grown in pots for six weeks and then transferred to a growth chamber. The temperature in the growth chamber was increased stepwise from 35 to 40, 45 and 50°C to create a heat-stressed environment. Leaf relative water content (RWC), loss of turgidity and chlorophyll content were measured at each temperature. The 'Elsanta' and 'R.Hope' had the highest RWC, while the 'Festival' and 'CG3' had the lowest. However, 'Elsanta' and 'R.Hope' had the lowest loss of turgidity, while 'Festival' and 'CG3' had the highest. 'Elsanta' and 'R.Hope' showed the lowest chlorophyll content, and 'CG3' and 'Whitney' had the highest. To determine HST (LT₅₀), leaf discs of each cultivar were exposed to 35, 40, 45, 50, 55 and 60°C. A considerable decrease in the LT₅₀ was observed with increasing temperature in all cultivars. The LT₅₀ of the cultivars ranged from 51.8 to 52.9°C. Based on the data collected, 'Elsanta', 'R. Hope' and 'Camarosa' were determined to be relatively heat-tolerant cultivars, while 'Whitney', 'Fern', 'Festival' and 'CG3' were heat-sensitive cultivars.

Keywords: genotype, high temperature, leaf, LT₅₀, membrane injury

Introduction

Agriculture is one of the human activities most dependent on climate, and as a result, it is one of the sectors where climate change impacts are expected to be significant (Hertel *et al.*, 2010). These changes in climate have led to changes in the concept of stress in cultured crops. Stress in plants is defined by Hale and Orcutt (1987) as abnormal changes in physiological processes based on environmental and biological factors or a combination of both. In addition, stress can be classified in many different ways. Levitt (1980) analyzed stress in two categories: biotic and physicochemical effects. Based on this classification, high temperature stress can be examined as physicochemical effects. Heat stress is often defined as the increase in temperature above a threshold level for a period of time sufficient to cause irreversible damage to plant growth and development (Wahid *et al.*, 2007). As an abiotic stress factor, high temperatures have a negative effect on plant growth and development, and it limits crop production around the world.

High temperature stress causes physiological, biochemical and molecular changes in plant metabolism, such as lipid liquefaction or perturbation of membrane integrity (Levitt, 1980). Additionally, heat stress causes membrane lipid peroxidation and aggravated membrane injury in many plant species (Xu *et al.*, 2006). High temperatures (over 40°C) deactivate the PSII reaction centre,

and then the leaves lose the ability to dissipate heat (Shao *et al.*, 2007). Schöffl *et al.* (1999) reported that severe cellular injury and even cell death may occur within minutes at very high temperatures, which could be attributed to a catastrophic collapse of cellular organization.

According to the recent report of the Intergovernmental Panel on Climate Change (IPCC), 0.6°C of warming is expected globally by 2030 (IPCC, 2007). Thus, farmers need to be adaptable to climate change to maintain the quality of their products. According to Else and Atkinson (2010), adaptations could include using different cultivars, using more resource-efficient cropping systems or switching to crop types that better 'fit' a changing climate. Therefore, research on the mechanism of heat stress in plants is important to develop heat tolerant plants. In this regard, strawberries are an important horticultural crop that are cultivated almost everywhere in the world, and their production is increasing every year. Although strawberries are a temperate crop with optimum growth temperatures between 10-26°C (Ledesma *et al.*, 2004), as a field and greenhouse-grown crop it is often subject to high temperatures during cultivation. Even though some cultivation techniques are commonly used to reduce or limit damage from high temperatures, these strategies are not effective enough at the commercial scale to successfully protect the yield of this crop.

Selection and use of the heat-tolerant cultivars and/or developing heat-tolerant genotypes are the most effective

tive ways of avoiding heat damage. To this end, the physiological and molecular effects of heat stress in strawberry cultivars have been reported (Gulen and Eris, 2003; 2004; Ledesma *et al.*, 2004; 2008; Wang and Lin, 2006). However, to our knowledge, no previous studies have been published on the tolerance of common strawberry cultivars to heat stress. Therefore, this study was developed to determine the high temperature tolerance of 15 commonly grown strawberry cultivars in the laboratory. The main purpose of the work is to provide data for later, more detailed studies on strawberry heat-tolerance.

Materials and methods

Plant Material

Cold stored (frigo) strawberry seedlings of 'Aromas', 'Camarosa', 'Carmine', 'Cal. Giant 3' (CG3), 'Cal. Giant 5' (CG5), 'Elsanta', 'Fern', 'Festival', 'Honeoye', 'Kabarla', 'Redlands Hope' (R.Hope), 'Ruby Gem', 'Selva', 'Sweet Charlie' and 'Whitney' were planted in 14 cm × 12 cm pots containing a mixture of perlite, torf and garden soil (1:1:1). Plants were grown for six weeks (5-6 leaf stage) in a greenhouse with day/night temperature of 30/15°C and garden soil (1:1:1) (Tab. 1). The plants were watered with a nutrient solution as needed to avoid water stress.

High Temperature Treatments

The plants were transferred to a climate chamber with a relative humidity of 65%, a 16/8 h (light/dark) photoperiod regime and a 5500 lux light intensity. Then, the temperature was increased stepwise, 5°C every 24 h from 35 to 40, 45 and 50°C to impose heat stress gradually. Plants spent 24 h at each temperature in the climate chamber. Plants were watered with a nutrient solution. Control plants were kept in the greenhouse during the treatments with a 30/15°C day/night temperature. All temperature

treatments were replicated three times with all cultivars. Leaf RWC, loss of turgidity and chlorophyll content were measured in the leaves collected from heat treated and control plants.

Leaf RWC and loss of turgidity

Leaf RWC (%) and loss of turgidity were measured using the methods of Gulen and Eris (2003). Leaf discs of 1.5 cm diameter were cut from the fully expanded and uniform leaves of each of the three plants (replicates) per treatment. First, the fresh weight was recorded, and then samples were placed in a petri dish of distilled water for 4 h. After gently blotting the leaf surface with paper, turgid weights were recorded. At the end of this period, leaf samples were placed in an incubator at 70°C for 24 h, to determine the dry weight. Leaf RWC and loss of turgidity were measured as follow; $RWC(\%) = [(fresh\ weight - dry\ weight) / (turgid\ weight - dry\ weight)] \times 100$, loss of turgidity $(\%) = [(turgid\ weight - fresh\ weight) / turgid\ weight] \times 100$.

Chlorophyll Content

Chlorophyll content was determined using methods developed by Moran and Porath (1980). Three leaf discs of 0.5 cm diameter were taken from the fully expanded leaves of each treatment and soaked in 5 mL of dimethylformamide (DMF) for 72 h at 4°C (in the dark). The absorbance was read at 652 nm in spectrophotometer to measure chlorophyll content, which was calculated as $mg.gFW^{-1}$ (fresh weight).

Measurement of Heat-Stress Tolerance (HST)

Cell membrane injury and HST (LT_{50} ; assessed by electrolyte leakage) were determined by using the procedures of Arora *et al.* (1998) to assess the six temperature steps-35, 40, 45, 50°C. Strawberry leaf discs of 2 cm in di-

Tab. 1. Origin and response to day length of the 15 strawberry cultivars evaluated in this study

Cultivars	Response to Day Length	Parents	Origin
'Aromas'	Day-neutral	Cal 87.112-6 × Cal 88.270-1	California, USA
'Cal. Giant 3'	Short day	C1 × NWFV	California, USA
'Cal. Giant 5'	Short day	F39.1 × F15.1	California, USA
'Camarosa'	Short day	Douglas × Cal 85.218-605	California, USA
'Carmine'	Day-neutral	Rosa Linda × FL 93-53	Florida, USA
'Elsanta'	Short day	Gorella × Holiday	Netherlands
'Fern'	Day-neutral	Tufts × Cal 69.63-103	California, USA
'Festival'	Short day	Rosa Linda × Oso Grande	Florida, USA
'Honeoye'	Short day	Vibrant × Holiday	New York, USA
'Kabarla'	Day-neutral	-	Queensland, Australia
'Redlands Hope'	Day-neutral	Parker × Redlands Promise	Brisbane, Australia
'Ruby Gem'	Short day	Earlibrite × Carlsbad	Florida, USA
'Selva'	Day-neutral	Cal 70.3-117 × Cal 71.98-605	California, USA
'Sweet Charlie'	Short day	FL 80-456 × Pajaro	Florida, USA
'Whitney'	Day-neutral	89530-506 × 89542-504	California, USA

- not detected

ameter were taken from the uniform, individual and fully expanded leaves of each of three plants per cultivar. Leaf discs were lightly rinsed in deionized water, blotted with paper and placed in test tubes (one disc per tube) that contained 500 μ L of deionized water. Tubes were capped and placed in a thermostatically controlled water bath maintained at 25°C. The temperature was increased by 5°C at 30 min intervals up to 45°C, and then the bath temperature was increased by 1°C at 5 min intervals up to 60°C. Samples were allowed to equilibrate and then were held for 30 min at each temperature (35, 40, 45, 50, 55 and 60°C). Three tubes per temperature were removed and placed in an incubator. Three tubes of the control (un-stressed) discs remained at 30°C as controls. Tissue temperature was monitored with a copper-constant thermocouple inserted into the tubes. One hour after the the last sample was removed from the bath, 20 mL of deionized water was added to each test tube, and it was incubated overnight. The electrical conductivity of each sample was measured using a conductivity meter. Leaf discs were then heat killed in the same solution by autoclaving, and total conductivity was measured at room temperature. Percentage injury at each temperature was calculated from ion leakage data using the equation:

$$\% \text{ injury} = [(\% L_{(t)} - \% L_{(c)}) / (1 - \% L_{(c)})]$$

where % $L_{(t)}$ and % $L_{(c)}$ were the percentage ion leakage for the treatments and control samples, respectively (Arora *et al.*, 1992). HST (LT_{50}) was defined as the temperature at which 50% injury occurred. All temperature treatments, including the set of all cultivars, were replicated three times.

Statistical analysis

The experiment was arranged in a randomized block design with three replications. The data were analyzed using

SPSS 13.0, and mean separation was calculated with a Duncan test, where $p < 0.05$ was considered significant.

Results and discussion

Leaf RWC of all cultivars changed significantly depending on temperature (Fig. 1). In all cultivars, RWC decreased gradually from the control (30°C) to the highest temperature (50°C). Of all the cultivars, 'Elsanta' and 'R. Hope' had the highest RWC while 'Fern', 'Whitney', 'Festival' and 'CG3' had the lowest RWC even at 50°C. However, loss of turgidity in all cultivars increased as the temperature increased (Fig. 2). Loss of turgidity in the cultivars 'R. Hope', 'Elsanta' and 'CG3' was approximately 20-25% at 50°C, whereas it was the highest (60%) in the 'CG3', 'Festival' and 'Fern' cultivars. A two-way ANOVA showed significant effects of temperature, cultivar, and the interaction of temperature and cultivar on leaf RWC and loss of turgidity (Tab. 2). Primarily, high temperatures cause increases in transpiration, and this change leads to a reduction in the leaf RWC and the loss of turgidity (Cansev, 2012; Díaz-Pérez *et al.*, 1995). Cellular signal transduction is triggered and a series of genes are activated with the loss of water. This process is the activation of the stress response mechanism (Gonzalez and Gonzalez-Vilar, 2001). Else and Atkinson (2010) recently reported that increases in temperature cause an increase in evaporative demand, plant transpiration rates, and crop water use in soft fruits such as strawberries. Therefore, the measurement of RWC and loss of turgidity are useful indicators of the water balance in a plant. The RWC and loss of turgidity express the absolute amount of water and amount of water lost, respectively, which the plant requires to reach a level of full saturation artificially (Qariani *et al.*, 2000). Gulen and Eris (2003) reported that leaf RWC and loss of turgidity change significantly with high temperature

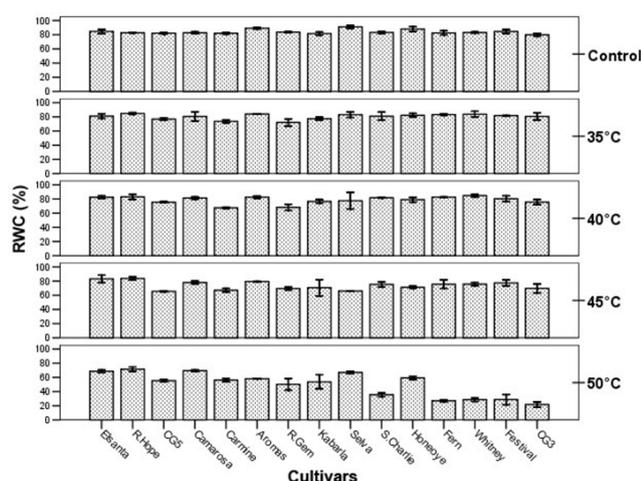


Fig. 1. Leaf relative water content (RWC) of 15 strawberry cultivars in heat-stressed and control samples. The data are presented as the mean \pm S.E.M. (Standard Error of Means) of three replicates

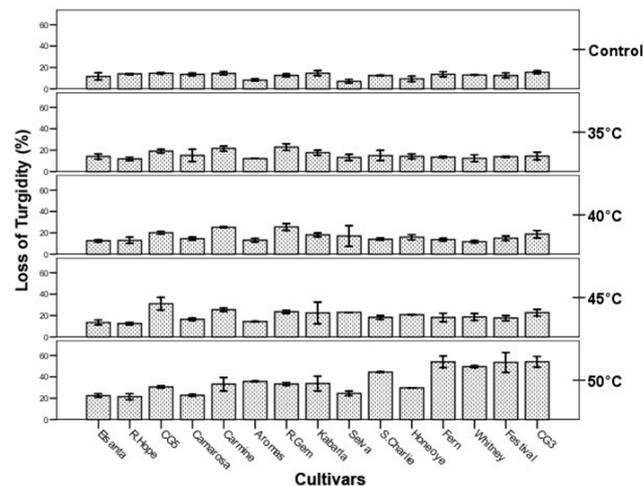


Fig. 2. Loss of turgidity of 15 strawberry cultivars in heat-stressed and control leaf samples. The data are presented as the mean \pm S.E.M. (Standard Error of Means) of three replicates

Tab. 2. Analysis of variance (ANOVA) of temperature (T), cultivar (Cv.), and their interaction for leaf relative water content (RWC), loss of turgidity, chlorophyll content and heat-stress tolerance (HST; LT₅₀)

Dependent variable	Independent variable		
	Temperature (T)	Cultivars (Cv)	T x Cv.
RWC	578.152	32.545	20.686
	(<i>p</i> < 0.001)	(<i>p</i> < 0.001)	(<i>p</i> < 0.001)
Loss of Turgidity	399.353	23.633	14.371
	(<i>p</i> < 0.001)	(<i>p</i> < 0.001)	(<i>p</i> < 0.001)
Chlorophyll Content	366.879	45.497	9.164
	(<i>p</i> < 0.001)	(<i>p</i> < 0.001)	(<i>p</i> < 0.001)
LT ₅₀	37312.059	19.940	7.345
	(<i>p</i> < 0.001)	(<i>p</i> < 0.001)	(<i>p</i> < 0.001)

Numbers represent F values at the 0.05 level (n=9)

treatments of strawberry cv. ‘Camarosa’. Reduction of leaf RWC due to increases in heat stress was also observed in tall fescue and perennial rye-grass leaves (Xu *et al.*, 2006). In this study, the linear increase in leaf RWC and linear decrease in leaf RWC and loss of turgidity were detected in 15 strawberry cultivars. There was a significant variation in the level of leaf RWC and loss of turgidity with variations in genotype in response to high temperatures.

The amount of chlorophyll in the leaves after high temperatures was examined in the cultivars (Fig. 3). In general, leaf chlorophyll content varied following high temperature treatment. The chlorophyll content increased gradually from 2.8 mg/g FW (in the control) to 5 mg/g FW (at 50°C) in ‘SweetCharlie’ and ‘Whitney’ cultivars, which were the highest values. On the other hand, ‘Fern’ had the lowest leaf chlorophyll content with approximately 2-2.5 mg/g FW. In addition, the relative increase in chlorophyll content was compared between control and heat-stressed leaves of each cultivar. The smallest relative increase in chlorophyll content was found in ‘Elsanta’ and ‘R. Hope’ (10% and 12%, respectively), while the greatest increase was found in ‘CG3’ and ‘Whitney’ (42% and 44%, respectively). A two-way ANOVA showed a signifi-

cant effect of temperature, cultivar and the interaction of temperature and cultivars on chlorophyll content (Tab. 2). Increased total chlorophyll content is a typical response of plants to stress conditions (Romero-Aranda *et al.*, 2001). As a response to high temperatures, Gulen and Eris (2003) reported an increase in chlorophyll content in strawberry cv. ‘Camarosa’ under gradual and sudden heat treatments. Similarly, in the present study, the chlorophyll content of all cultivars increased with heat stress. In comparing the percent increase in chlorophyll content between control and highest temperature, the cultivars that had the highest increase were ‘CG3’ and ‘Whitney’. On the other hand, the smallest increase was found in cvs. ‘Elsanta’ and ‘R. Hope’. The amount of increase in chlorophyll content with heat-stress was correlated with the heat-tolerance of the cultivars. Liu and Huang (2000) reported a relationship between chlorophyll content and heat-tolerance in *Agrostis palustris*, which supports our findings. In contrast to those findings, Chaitanya *et al.* (2001) observed a heat-stress induced reduction in chlorophyll content in mulberry plants. Therefore, the physiological responses of plants to stress conditions strongly depend on the species, strength of the stress and its source (Dekov *et al.*, 2000).

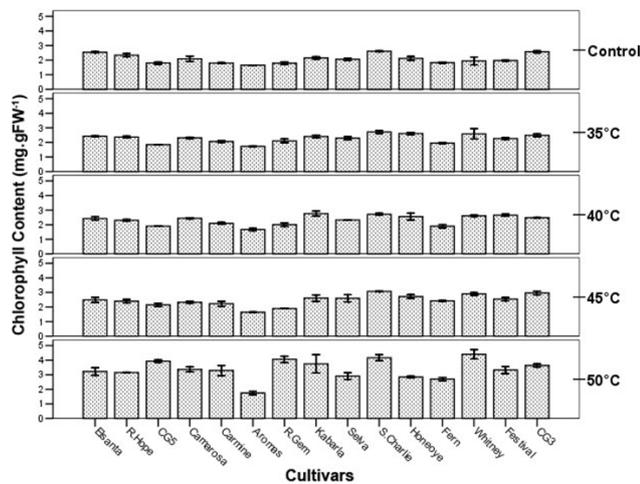


Fig. 3. Chlorophyll content of 15 strawberry cultivars in heat-stressed and control samples. The data are presented as the mean ± S.E.M. (Standard Error of Means) of three replicates

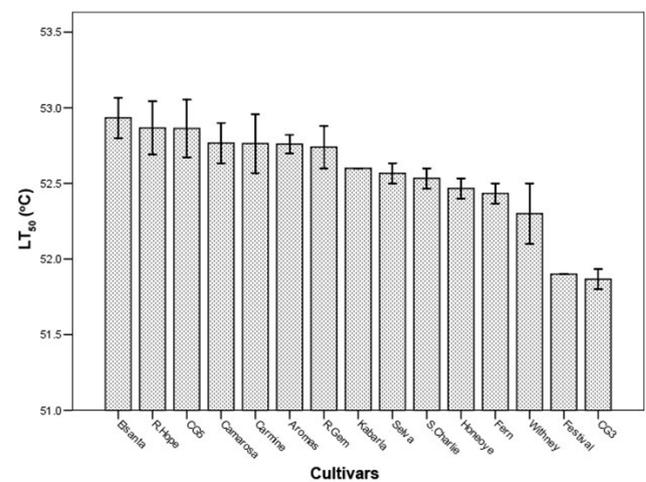


Fig. 4. Heat stress tolerance (HST; LT₅₀) of 15 strawberry cultivars in heat-stressed and control leaf samples. The data are presented as the mean ± S.E.M. (Standard Error of Means) of three replicates

The heat-stress tolerance (HST; defined as LT_{50}) of 15 strawberry cultivars was assessed by measuring electrolyte leakage from the cell membrane, which is an indication of injury of the cell membrane (Fig. 4). Heat-acclimation caused an increase in heat-tolerance of all cultivars (measured as an increase in LT_{50}), which was highest in 'Elsanta' (ave. 52.94°C), 'R. Hope' and 'CG5' (ave. 52.88°C). Meanwhile, 'CG3', 'Festival' and 'Whitney' had the lowest heat-tolerance with a LT_{50} value of approximately 51.85°C. 'Kabarla', 'Selva', 'Sweet Charlie', 'Honeyoye' and 'Fern' had moderate heat-tolerance, while 'Camarosa', 'Carminé', 'Aromas' and 'Ruby Gem' were more tolerant than these five cultivars to high temperatures with LT_{50} values close to those of the heat-tolerant cultivars. A two-way ANOVA showed a significant effect of temperature, cultivars and the interaction of temperature and cultivars on the heat-tolerance (Tab. 2).

Stress responses in plants are common for tolerance to difficult conditions. Tolerance to high temperature stress is the ability of a plant or a tissue to grow at temperatures. While a plant is undergoing a stress response to tolerate difficult conditions, both reversible and irreversible damage occurs. An ion leakage test is known to be an effective measurement of cell membrane thermostability and a primary indicator of damage under stressful conditions (Arora, 1998; Fan *et al.*, 2012). Thus, an ion leakage test is commonly used to determine the tolerance of various plant species to many stress factors, such as cold (Arora *et al.*, 1992; Barronco *et al.*, 2005; Eris *et al.*, 2007; Cansev *et al.*, 2009), salinity (Sudhakar *et al.*, 2001; Gulen *et al.*, 2006; Turhan *et al.*, 2008) and high temperatures (Gulen and Eris, 2003; 2004). In this study, HST gap was found to be 1.09°C between relatively sensitive and tolerant cultivars. Meanwhile, the annual mean maximum and minimum temperatures have increased by 0.35 and 1.13°C from 1979 to 2003 (International Rice Research Institute). This temperature increase has exposed many of the world's crops to heat-stress during at some point in their life cycle (Peng *et al.*, 2004; Shah *et al.*, 2011). The HST of a cultivar, indicated as LT_{50} , is defined as the temperature which 50% of a population died due to high temperatures. Measuring the LT_{50} is important for screening genotypes in stress physiology studies as well as breeding and developing new cultivars that are tolerant to a given stressor. This is the first study to report data evaluating the heat-tolerance of different strawberry cultivars.

Conclusions

To summarize, the LT_{50} showed the heat-tolerance between 51.8 and 52.9°C in the strawberry cultivars. The cultivars 'Elsanta', 'R. Hope' and 'Camarosa' were determined as relatively heat-tolerant, while 'Whitney', 'Fern', 'Festival', and the 'CG3' were relatively heat-sensitive among the 15 strawberry cultivars evaluated. There are genotypic variations for response to heat-stress among the 15 strawberry

cultivars assessed, likely due to having different metabolic activities for their defence mechanisms and accumulation of heat-specific or heat-shock proteins. Further study of the molecular behaviour of these plants could help to explain HST of strawberry plants.

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