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Low-temperature Injury to Strawberry Floral Organs at Several Stages of Development

Woon Kye Ki[1] and Michele R. Warmund[2]
Department of Horticulture, University of Missouri, Columbia, MO 65211

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Abstract. **Inflorescences of 'Earliglow' and 'Honeoye' strawberry *(Fragaria ×ananassa* Duch.) plants were subjected to controlled freezing tests to determine the cold tolerance of styles, anthers, and receptacles of individual flowers at various stages of development. Flowers of both cultivars tended to deacclimate as the stages of development progressed. Styles and receptacles generally exhibited injury at higher temperatures than anthers. The greatest deacclimation of styles and receptacles of primary flowers occurred at earlier developmental stages of 'Honeoye' than of 'Earliglow'. However, at the sixth stage of development, the critical temperature for receptacle injury in primary and secondary fruit was -3C for both cultivars.**

Strawberry flowers are frequently injured by low temperatures in the spring. Frosts can result in injury to reproductive organs in individual flowers, partial loss of flowers, or complete loss of the inflorescence (Ourecky and Reich, 1976). Generally, the primary flowers are the most susceptible to low temperatures (Havis, 1938). Fruit number and weight are substantially reduced when primary flowers are injured (Janick and Eggert, 1968). Boyce et al. (1985) found that yield was decreased by 30% when primary flowers of strawberry plants were removed during early bloom. The fruit weight produced from secondary and tertiary flowers did not compensate for the loss of yield from primary flowers.

Darrow (1966) reported that styles were the most susceptible floral organs to freezing injury. When pistil injury occurred after fertilization, embryos failed to develop normally, resulting in misshapen fruit. In contrast, other researchers (Havis, 1938; Perry and Poling, 1986) found that anthers in some cultivars exhibited browning injury before styles.

Our objective was to determine the susceptibility of styles, anthers, and receptacles of 'Earliglow' and 'Honeoye' flowers to low-temperature injury.

'Earliglow' and 'Honeoye' plants were obtained from a commercial nursery and stored at 3C for 2 weeks before planting. On 26 Mar. and 2 and 9 Apr. 1991, 300 plants of each cultivar were placed at a 15 × 15-cm spacing in a Menfro silt loam soil in Columbia, Mo. Three planting dates were used to ensure that all stages of development were sampled for freezing tests. One inflorescence at each of the six stages of development (Table 1) was collected on 17 and 24 Apr. and 1, 8, and 15 May 1991. Samples were stored at 100% relative humidity (RH) at 2C for 4 h before freezing. For each developmental stage, each inflorescence was placed in moist cheesecloth and wrapped in aluminum foil for each of 16 test temperatures. A 0.01-mm-diameter (30-gauge) copper-constantan thermocouple was attached to the base of the terminal flower to monitor tissue temperature. Thermocouple output was read on a digital thermometer (Omega Engineering, Stamford, Conn.). Samples were placed in a programmable freezer (Tenney Engineering, Union, N.J.) at -1C for 15 h before they were cooled at 0.5C/h. Inflorescences were removed from the freezer at 0.2C intervals at estimated temperatures to result in bud injury. The tissue was then placed in a Styrofoam cooler at 2C and allowed to thaw slowly for 24 h. Nonfrozen controls were stored at 2C during the freezing tests. Samples were then incubated at room temperature at 100% RH for 24 h. Flowers were examined under a microscope at × 40 or lower magnification and the first temperature was recorded at which oxidative browning injury (T,) was observed for the styles, anthers, and receptacle of primary, secondary, and tertiary flowers. Data for quaternary flowers were omitted because they were too small to be sampled or-were absent at several stages of development. Data for each of the floral organs were then analyzed as a three-way factorial arrangement of treatments at all stages of development. The linear statistical model contained the main effects of cultivar, developmental stage, floral position, and all interactions among these main effects.

Style injury was evaluated at five of six of the stages of inflorescence development since the styles had senesced on the primary fruit at stage 6. The main effects of stage

Table 1. Stages of inflorescence development of strawberry cultivars.

Stage	Flower ordinal no. Primary	Secondary	Tertiary
1	Tight bud	Tight bud	Tight bud
2	Tight white[z]	Tight bud	Tight bud
3	Full petal	Tight white	Tight bud
4	Petal fall	Full petal	Tight white
5	Immature fruit	Petal fall	Full petal
6	Immature fruit	Immature fruit	Petal fall

[z]White petals were visible between the separated sepals.

Table 2. T_1 values of styles of 'Honeoye' and 'Earliglow' strawberry inflorescences exposed to freezing temperatures.

Cultivar	Flower ordinal no.[z]	Stage of inflorescence development 1	2	3	4	5
				T_1 (°C)		
Honeoye	1	−4.8	−5.2	−4.0	−3.6	−4.2
	2	−4.6	−5.3	−4.3	−5.2	−4.2
	3	−5.8	−5.6	−5.8	−5.6	−5.5
Earliglow	1	−4.6	−4.4	−4.7	−4.0	−4.0
	2	−4.7	−5.1	−5.2	−4.8	−4.2
	3	−5.4	−5.6	−5.6	−5.6	−5.2

Source	df	MS	LSD (0.05)
Cultivar (CV)	1	0.03[NS]	---
Stage (ST)	4	1.77**	0.3
Flower (FL)	2	19.64**	0.3
CV × ST	4	0.74*	0.4
CV × FL	2	0.24[NS]	---
ST × FL	8	0.79**	0.5
CV × ST × FL	8	0.41[NS]	---
Error	120	0.27	---

[z]1 = Primary, 2 = secondary, and 3 = tertiary flower or fruit.
[NS],*,**Not significant or significant at $P = 0.05$ or 0.01, respectively.

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[1]Postdoctoral Research Associate.
[2]Associate Professor.

Table 3. T_1 values of anthers of 'Honeoye' and 'Earliglow' strawberry inflorescences exposed to freezing temperatures.

Cultivar	Flower ordinal no.[z]	Stage of inflorescence development 1	2	3
			T_1 (°C)	
'Honeoye'	1	−4.8	−5.3	−4.7
	2	−5.3	−5.6	−5.2
	3	−5.8	−5.8	−5.8
'Earliglow'	1	−5.0	−5.2	−5.0
	2	−4.9	−5.7	−5.7
	3	−5.8	−5.8	−5.8
Source	df		MS	LSD (0.05)
Cultivar (CV)	1		0.05^{NS}	---
Stage (ST)	2		0.75*	0.3
Flower (FL)	2		4.72**	0.3
CV × ST	2		0.31^{NS}	---
CV × FL	2		0.03^{NS}	---
ST × FL	4		0.25^{NS}	---
CV × ST × FL	4		0.17^{NS}	---
Error	72		0.18	---

[z]1 = Primary, 2 = secondary, and 3 = tertiary flower or fruit.
NS,*,**Not significant or significant at $P = 0.05$ or 0.01, respectively.

Table 4. T_1 values of the receptacles of 'Honeoye' and 'Earliglow' strawberry inflorescences exposed to freezing temperatures.

Cultivar	Flower ordinal no.[z]	Stage of inflorescence development 1	2	3	4	5	6
				T_1 (°C)			
Honeoye	1	−4.8	−5.2	−4.0	−3.8	−3.7	−3.0
	2	−4.4	−5.3	−4.2	−5.2	−3.6	−3.0
	3	−5.8	−5.6	−5.8	−5.6	−5.3	−3.2
Earliglow	1	−4.6	−4.4	−4.7	−4.0	−3.8	−3.0
	2	−4.7	−5.1	−5.2	−4.8	−3.8	−3.0
	3	−5.4	−5.6	−5.6	−5.6	−5.1	−3.3
Source		df		MS		LSD (0.05)	
Cultivar (CV)		1		0.00^{NS}		---	
Stage (ST)		5		18.41**		0.3	
Flower (FL)		2		19.10**		0.3	
CV × ST		5		0.61^{NS}		---	
CV × FL		2		0.30^{NS}		---	
ST × FL		10		1.14**		0.5	
CV × ST × FL		10		0.34^{NS}		---	
Error		144		0.27		---	

[z]1 = Primary, 2 = secondary, and 3 = tertiary flower or fruit.
NS,**Not significant or significant at $P = 0.01$, respectively.

and flower and their interaction were significant (Table 2). T_1 values of styles of primary and secondary flowers were similar at all stages of development except stage 4. Styles of primary flowers were injured at a higher temperature than those of tertiary flowers. The interaction of cultivar and stage was also significant. T_1 values of 'Earliglow' styles were lower than those of 'Honeoye' at stage 3, but T_1 values for the cultivars were similar when compared at the same stages of development. Styles of primary and secondary flowers of 'Honeoye' deacclimated ≥ 1C between stages 2 and 3. Tertiary flowers of 'Honeoye' only deacclimated 0.3C across all stages of development. In 'Earliglow' inflorescences, the greatest deacclimation of styles occurred at later stages than those of 'Honeoye' flowers.

Anthers were evaluated at only three stages of development (Table 3). Cultivars were similar in anther injury. However, anthers of primary flowers had the highest T_1 values, those of secondary flowers had intermediate T_1 values, and anthers of tertiary flowers had the lowest T_1 values. Anthers of flowers at stage 2 had lower T_1 values than those at stage 1 or 3. The reason for this is unclear. None of the interactions were significant.

Receptacle damage was recorded at all six stages of development (Table 4). Receptacles of inflorescences of both cultivars were similar in hardiness. However, the stage and flower and their interaction were significant. Receptacles of primary flowers were more susceptible to low-temperature injury than those of tertiary flowers, except at stage 6. Primary and secondary flowers had similar T_1 values, except at stage 4. In primary flowers of 'Honeoye', receptacles deacclimated the most (1.2C) between stages 2 and 3, while those of 'Earliglow' deacclimated 0.7C between stages 3 and 4 and 0.8C between stages 5 and 6. The hardiness of receptacles in secondary flowers of both cultivars decreased by ≥ 1C between stages 4 and 5. However, the greatest loss of receptacle hardiness was in the tertiary flowers of both cultivars. Tertiary flowers of 'Honeoye' and 'Earliglow' deacclimated by 2.1 and 1.8C between stages 5 and 6, respectively. At stage 6, both primary and secondary flowers were injured at -3C. Thus, almost a complete crop failure could occur when the temperature drops to the T_1 value of the primary fruit when the inflorescence is at the sixth stage of development.

In this study, styles and receptacles of primary flowers of 'Honeoye' deacclimated the most at earlier stages of development than 'Earliglow' floral organs. However, 'Honeoye' generally suffers less blossom kill due to frost injury than does 'Earliglow' in field trials (Kaps et al., 1990). 'Earliglow', an early season cultivar, blooms ≈5 days before 'Honeoye' (J. Scheerens, personal communication). Thus, 'Earliglow' inflorescences would be at a more advanced stage of floral development with greater susceptibility to frost injury when exposed to low temperatures than those of 'Honeoye'. 'Honeoye' inflorescences may escape early frost damage in some years because they bloom later than 'Earliglow'.

Results from this study indicate that anther injury may not be a reliable indicator of crop loss from low-temperature injury, since style and receptacle injury generally occur before anther injury in 'Earliglow' and 'Honeoye' inflorescences. Further, anther injury can only be evaluated at early stages of floral development. Conflicting reports of floral structure susceptibility to freezing temperatures may be attributed to cultivar differences (Darrow, 1966; Havis, 1938; Perry and Poling, 1986).

Boyce and Strater (1984) demonstrated that strawberry flowers that were inoculated with ice were injured at a higher temperature than noninoculated flowers that supercooled. Styles and receptacle tissue of inoculated and noninoculated flowers subjected to subfreezing temperatures at full bloom had T_{50} values of -2.1 and -4.9C, respectively. In our experiment, styles and receptacles of flowers at full bloom had T_1 values in the range of -4.0 to -5.5C. Although samples were wrapped in moist cheesecloth that froze at about -5C, flowers were not inoculated with ice or ice-nucleation-active (INA) bacteria in our study. Naturally occurring populations of INA bacteria that limit supercooling have been reported on strawberries (Lindow et al., 1978). However, the INA bacteria population on the strawberry flowers in our study may not have been sufficient to prevent supercooling. Alternatively, the reason that floral organs survived relatively low temperatures may be attributed to the detachment of the inflorescence from the plant before freezing. Yelonsky (1988) reported that detached citrus flowers supercooled to a lower temperature than those attached to the tree.

Cold injury is often evaluated by determining the temperature at which 50% of the flowers are injured (T_{50} value). While T_{50} values have been used to determine the relative difference among cultivars (Boyce and Marini, 1978; Boyce and Strater, 1984), these values do not indicate the first temperature at which potential marketable yield was lost. Thus, T_1 values for primary, secondary, and tertiary flowers may be more useful than T_{50} values in estimating the potential crop loss after a low-temperature episode.

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