Peach Pistil Carbohydrate and Moisture Contents and Growth during Controlled Deacclimation following Ethephon Application

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Abstract. Flower bud growth and carbohydrate content of pistils of two peach cultivars [*Prunus persica* (L.) Batsch. cvs. Jerseydawn and Jerseyglo] was studied during controlled postrest deacclimation in February and March at 7 and 21C following an application of ethephon (100 mg-liter⁻¹, in October. Ethephon-treated pistils contained more sorbitol and sucrose than untreated pistils, and levels of both sugars decreased during deacclimation. Sorbitol content decreased more rapidly at 21C than at 7C in February, but no difference was detected in March. Fructose content increased during deacclimation in February and was not affected by cultivar, ethephon treatment, or deacclimation temperature. In March, fructose increased in untreated 'Jerseydawn' pistils during deacclimation, but not in ethephon-treated pistils. In 'Jerseyglo', fructose was detected in all samples and declined during deacclimation. Glucose was not detected in treated pistils in February. In untreated pistils, glucose increased during deacclimation. In March, glucose was not detected in 'Jerseydawn' pistils reaclimated at 7C. At 21C, glucose was detected only in untreated pistils after 2, 3, or 4 days of deacclimation. In 'Jerseyglo', glucose was detected in all pistils. Moisture content of ethephon-treated pistils was lower than untreated pistils in both February and March. Pistil moisture content during deacclimation increased more slowly in ethephon-treated pistils than in untreated pistils in February, but not in March. Pistils sampled in March had a lower moisture content when reaclimated at 7C than at 21C. Pistil growth at 21C was slower in ethephon-treated buds than in untreated buds, but no difference was detected at 7C. The effects of a fall application of ethephon on the carbohydrate content of flower buds in relation to both winter deacclimation and growth in the spring are discussed. Chemical names used: (2-chloroethyl) phosphoric acid (ethephon).

Peach floral primordia supercool to between -10 and -30C during dormancy and, therefore, escape freezing injury (Quamme, 1978). The temperature to which a primordium will supercool varies with its water content, which appears to be controlled by freezing, preceding the low-temperature stress (Quamme, 1983). The capacity to supercool decreases as buds develop in the spring. In the mid-Atlantic region of the eastern United States, peach flower buds are susceptible to low-temperature injury from January through fruit set. Freezing may kill a large proportion of pistils, resulting in economic losses, and in some years, complete crop failure. Increasing cold hardiness and delaying bloom can increase crop yields and thereby decrease the magnitude of such losses (Durner and Gianfagna, 1988; Gianfagna et al., 1989; Proebsting and Mills, 1976).

The plant growth regulator ethephon, applied at low rates (100 mg-liter⁻¹) in the fall, reduces and delays peach flower bud development. Immediately after application, cell division is curtailed for ≈7 days (Herrera, 1986). In the spring, bloom has been delayed by as much as 10 days in New Jersey (Gianfagna et al., 1986) and by 16 days in New Zealand (Irving, 1987). The bloom delay increases the probability that the crop will avoid frost damage. In addition, fall-applied ethephon increases the intrinsic hardiness of both cherry (Proebsting and Mills, 1976) and peach (Durner and Gianfagna, 1988; Proebsting and Mills, 1969) flower buds. In peach, flower buds treated with ethephon supercool to lower temperatures and reaclimate

more slowly than untreated buds (Durner and Gianfagna, 1991). Quamme and Gusta (1987) have suggested that differences in osmotic potentials due to differences in sugar content of various floral parts may help regulate supercooling in flower buds. Durner (1989) and Durner and Gianfagna (1989) have shown that pistils from peach trees treated with ethephon in the fall have more sucrose, more sorbitol, and less water on a fresh-weight basis and are harder than untreated pistils.

The research reported here was initiated to determine if ethephon applied in the fall alters pistil carbohydrate content, moisture content, or growth during controlled deacclimation after the chilling requirement to break the rest period has been satisfied.

Materials and Methods

Ethephon (100 mg-liter⁻¹) was applied to runoff to mature 'Jerseydawn' and 'Jerseyglo' peach trees on 17 Oct. 1988 to delay bloom the following spring. Polyoxyethylenepolypropoxypropanol alkyl 2-ethoxyethanol/dihydroxypropane (Regulaid) was added at 0.1% (v/v) to assist spreading and was also used alone as a control.

Sampling dates, cultivars, and deacclimation times and temperatures are summarized in Table 1. On each date, fifty 30-cm-long terminal shoots were randomly sampled 1 m from the

Table 1. Sampling date, cultivar, and reaclimating time for field studies of deacclimation of peach flower buds treated the previous fall with ethephon for bloom delay. Deacclimation was tested at 7 and 21C in all cases.

Date (1982)	Cultivar	Reaclimating time (days)
6 Feb.	Jerseydawn	0, 1, 2
	Jerseyglo	0, 1, 2
6 Mar.	Jerseydawn	0, 1, 2, 3, 4
20 Mar.	Jerseyglo	0, 1, 2, 3

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ground from the periphery of five trees per cultivar per treatment. Twig bases were recut, and twigs placed in tap water in beakers and maintained at 7C or in the laboratory at 21C. After each deacclimation treatment, pistils were isolated from three 10-bud replicates per cultivar per treatment for carbohydrate analysis. Tissues were homogenized, boiled in 80% (v/v) ethanol for 30 min, centrifuged for 20 min at $1000 \times g$, decanted, and the supernatant retained. The residue was re-extracted twice with boiling 80% ethanol, and the combined supernatants were evaporated to dryness *in vacuo*. The sample was then redissolved in 4 ml of water and filtered through a 0.45- μ m filter. Sucrose, glucose, fructose, and sorbitol contents were determined by high-performance liquid chromatography using a Waters Sugar-Pak I column at 70C. The mobile phase was 50 mg-liter⁻¹ of the disodium-calcium salt of ethylenediaminetetraacetic acid in water, and the injection volume was 8 μ l. Sugars were identified and quantified from retention times and peak areas of standards. Results are presented as nanomoles of sugar per milligram of sample fresh weight. Three additional 10-bud replicates per cultivar and treatment were dissected to determine pistil water content on a percent fresh-weight basis. Samples were weighed fresh and then dried at 60C until stable dry weights were obtained, usually 48 h.

Carbohydrate, pistil fresh weight, and water content data were tested with an analysis of variance using the Type III sums of squares of the General Linear Models procedure of SAS (SAS Institute, Cary, N.C.). Data for February and March were analyzed separately. A completely random factorial model, including cultivar, ethephon treatment, deacclimation temperature, and length of deacclimation, was used in the analysis. Interactive or main effect means of qualitative factors were separated with Fisher's Protected LSD. Main effects of length of deacclimation were analyzed with least squares linear regression using the regression procedure of SAS. When a significant interaction between a qualitative factor and length of deacclimation was detected, regression equations were developed for each qualitative factor. Parameter estimates were then compared to determine if resulting equations were significantly different using the method of Weisberg (1985).

Results

February. No main or interactive effects of cultivar were detected for any variable. The following main effects were detected: ethephon treatment on sorbitol and sucrose, deacclimation temperature on sucrose, and length of deacclimation on sucrose and fructose. The significant interactions detected were: deacclimation temperature $\times$ length of deacclimation on sorbitol, ethephon treatment $\times$ length of deacclimation on glucose and percent moisture, and ethephon treatment $\times$ deacclimation temperature $\times$ length of deacclimation on pistil weight.

Sorbitol content. Ethephon-treated pistils contained more sorbitol than untreated pistils (113 and 88 nmoles-mg⁻¹ fresh weight, respectively), and sorbitol content decreased more rapidly at 21C than at 7C ($P = 0.001$) (Fig. 1).

Sucrose content. Ethephon-treated pistils contained more sucrose than untreated pistils (53 and 48 nmoles-mg⁻¹ fresh weight, respectively), and sucrose content decreased during deacclimation ($Y = 83 - 32X$, $R^2 = 0.79$, $P > F = 0.001$, where $Y =$ nmoles-mg⁻¹ fresh weight and $X =$ days of deacclimation). Pistils reaclimated at 7C contained more sucrose than those reaclimated at 21C (52 and 49 nmoles-mg⁻¹ fresh weight, respectively).

Fig. 1. Sorbitol content of peach pistils in February during deacclimation at 7 or 21C. Symbols represent means of twelve 10-bud observations.

Fig. 2. Moisture content of peach pistils in February during deacclimation as affected by a fall application of ethephon. Symbols represent means of twelve 10-bud observations.

Fructose content. Fructose content of pistils increased during deacclimation ($Y = 6 + 7X$, $R^2 = 0.19$, $Pr > F = 0.001$).

Glucose content. Glucose was not detected in ethephon-treated pistils. In untreated pistils, glucose content increased during deacclimation ($Y = 2 + 3X$, $R^2 = 0.12$, $Pr > F = 0.039$).

Pistil moisture content. Ethephon-treated pistils increased in moisture more slowly during deacclimation than untreated pistils ($P = 0.001$) (Fig. 2).

Pistil fresh weight. At 7C, ethephon-treated pistils were smaller (33 mg) than untreated pistils (49 mg), and no effect of ethephon was detected on the rate of pistil growth ($Y = 31 + 10X$, $R^2 = 0.31$, $Pr > F = 0.001$). However, at 21C, ethephon-treated pistils were smaller and grew more slowly (11 mg-day⁻¹) than untreated pistils (31 mg-day⁻¹) ($P = 0.001$) (Fig. 3).

March. Significant main effects of ethephon treatment and deacclimation temperature were detected for sorbitol, sucrose, and moisture content. A main effect of length of deacclimation on sucrose was also detected. No main or interactive effects of cultivar were detected for these variables. A significant interaction among cultivar, ethephon treatment, deacclimation temperature, and length of deacclimation was detected for fructose, glucose, and pistil fresh weight.

Sorbitol content. Ethephon-treated pistils contained more sorbitol than untreated pistils (47 and 34 nmoles-mg⁻¹ fresh weight, respectively). Pistils reaclimated at 7C contained more sorbitol

Fig. 3. Fresh weight of peach pistils in February during deacclimation at 21C as affected by a fall application of ethephon. Symbols represent means of twelve 10-bud observations.

than those reaccimated at 21C (48 and 32 nmoles·mg⁻¹ fresh weight, respectively).

Sucrose content. Ethephon-treated pistils contained more sucrose than untreated pistils (31 and 23 nmoles·mg⁻¹ fresh weight, respectively), and pistils reaccimated at 7C contained more sucrose than those reaccimated at 21C (30 and 24 nmoles·mg⁻¹ fresh weight, respectively). Sucrose content decreased during deacclimation ($Y = 43 - 16X + 3X^2$, $R^2 = 0.51$, $Pr > F = 0.001$).

Fructose content. In eight of the 10 ethephon-treated 'Jerseydawn' pistil samples, no fructose was detected. In the two samples where fructose was detected, there was no trend; with 1 day of deacclimation at 7C, an average of 10 nmoles·mg⁻¹ fresh weight (SE = 0.7, n = 3) was detected, and after 4 days at 21C, an average of 14 nmoles·mg⁻¹ fresh weight (SE = 8.7, n = 3) was detected. With such a high standard error, the latter figure is not statistically different from zero. In untreated pistils, fructose increased with deacclimation ($Y = 2 + 6X$, $R^2 = 0.37$, $Pr > F = 0.003$). In 'Jerseyglo', fructose was detected in all samples. More fructose was present at 21C than at 7C (34 and 25 nmoles·mg⁻¹ fresh weight, respectively), and fructose declined with deacclimation ($Y = 37 - 5X$, $R^2 = 0.17$, $Pr > F = 0.005$).

Glucose content. In 'Jerseydawn' pistils, glucose was not detected at 7C. At 21C, glucose was not detected in ethephon-treated pistils and, in untreated pistils, was detected after 2, 3, or 4 days of deacclimation (mean glucose content = 10 nmoles·mg⁻¹ fresh weight). In untreated 'Jerseyglo' pistils, the mean glucose content was 8 nmoles·mg⁻¹ fresh weight. In ethephon-treated pistils, glucose increased with deacclimation ($Y = 4 + 5X$, $R^2 = 0.26$, $Pr > F = 0.011$).

Moisture content. Ethephon-treated pistils contained less water than untreated pistils (75.6% and 76.6% moisture, respectively). Pistils reaccimated at 7C contained less water than those reaccimated at 21C (75.0% and 77.2% moisture, respectively).

Pistil fresh weight. At 7C, untreated 'Jerseydawn' pistils grew slowly (4 mg·day⁻¹), while treated pistils did not grow (Fig. 4A). Initially, pistils from ethephon-treated buds grew slowly at 21C, and after 3 days, their growth rate increased (Fig. 4B). Untreated 'Jerseyglo' pistils were much larger than treated pistils ($P = 0.01$) (Fig. 4 C and D). At 7C, ethephon-treated pistils grew slowly (7 mg·day⁻¹), while untreated pistils did not grow

(Fig. 4C). At 21C, treated pistils grew more slowly (42 mg·day⁻¹) than untreated pistils (89 mg·day⁻¹) ($P = 0.001$) (Fig. 4D).

Discussion

These results confirm our previous reports (Durner, 1989; Durner and Gianfagna, 1989) that a fall application of ethephon increases the sorbitol and sucrose content of peach pistils. We reported earlier (Durner and Gianfagna, 1991) that ethephon enhanced flower bud hardiness in peach by lowering the mean low-temperature freezing exotherm (LTE) of pistils, increasing the number of buds that supercool after deacclimation, and reducing the rate of deacclimation. The research reported here was performed concurrently with the hardiness work to study alterations in carbohydrates, pistil moisture, and pistil growth, induced by ethephon, that may be related to differences in hardiness.

Quamme and Gusta (1987) proposed that peach flower primordia have an intrinsic resistance to ice nucleation, a resistance that may be due to the formation of discontinuities in the liquid phase between the water in the supercooled primordium and the ice in surrounding tissues. This system may prevent nucleation of pistil water by ice from bud scales or vascular traces (Cary, 1985). Pistils have also been found to have lower water and osmotic potentials than the surrounding tissue within the bud (Quamme and Gusta, 1987). Lower pistil water content could, therefore, lead to deeper supercooling (Quamme, 1983). Ethephon-treated pistils contained less water than untreated pistils. The reduced osmotic potential of flower primordia could be due to higher sucrose levels in the primordia compared to the vascular tissues below the buds or the bud scales (Quamme and Gusta, 1987). High levels of sucrose in pistils could depress their supercooling point as well. Ashworth and Abeles (1984) have found that increasing the sucrose concentration of an aqueous solution will depress the nucleation temperature of the solution in small pores. Ethephon-treated pistils contained more sorbitol and sucrose than untreated pistils. The lower LTEs observed in ethephon-treated buds (Durner and Gianfagna, 1991) may be due to the combined effects of decreased moisture and increased sucrose and sorbitol in the treated pistils. Durner (1989) previously reported increased sorbitol and sucrose with decreased moisture in reaccimating buds after a fall application of ethephon. Treated buds in that study were harder than untreated buds.

Proebsting et al. (1982) showed that the ice nucleation temperature for developing peach flower buds increases as buds develop. Ethephon-treated pistils increased in fresh weight more slowly and also rehardened more slowly than untreated pistils (Durner and Gianfagna, 1991). Treated pistils were also smaller than untreated pistils and their reduced size may account for their decreased mean LTE. The reduced growth rate of treated pistils may contribute to the reduced rate of deacclimation observed in treated buds. Reduced growth could also account for some of the delay in bloom associated with fall ethephon applications.

The changes in sugar content of treated and untreated buds at the two incubation temperatures adds complexity to the system. Sorbitol is the primary translocated carbohydrate in the *Rosaceae*, which includes *Prunus* (Bielecki, 1982). It is metabolized to glucose via an NADP-dependent sorbitol dehydrogenase (Yamaki, 1984) or via a sorbitol oxidase (Yamaki, 1980). An NAD-dependent sorbitol dehydrogenase catalyzes the interconversion of sorbitol and fructose (Negro and Loeschner, 1979). Since no reports on sorbitol metabolism in peach leaves are in

Fig. 4. Pistil fresh weight of 'Jerseydawn' (A and B) and 'Jerseyglo' (C and D) peach during controlled deacclimation in March at 7C (A and C) or 21C (B and D) as affected by a fall application of ethephon. Symbols represent means of three 10-bud observations.

the literature, we must make a corollary with the work on apples and apricots. Young leaves can synthesize (to a limited degree) and use sorbitol. Mature leaves synthesize sorbitol but cannot use it (Bielecki and Redgwell, 1985). The two pathways appear independent and involve different enzyme systems (Keller, 1989). In apricots (*P. amreniaca*), nectaries metabolize sorbitol (Bielecki and Redgwell, 1980); thus, we assume that peach pistils also metabolize sorbitol.

Ethephon-treated pistils metabolized sorbitol at rates similar to untreated pistils during deacclimation at 7 and 21C; yet, treated pistils grew much more slowly than untreated pistils (Fig. 4). The fate of the energy released during metabolism is unknown. Even though we did not detect decreased sorbitol catabolism in ethephon-treated buds at 7 or 21C, sorbitol catabolism may be slower in ethephon-treated buds at temperatures below 7C, accounting for decreased pistil growth. This slowing could delay the transition from the hardy to the nonhardy condition, and also delay bloom. The enhanced sorbitol levels in ethephon-treated buds might be due to inhibited catabolism or enhanced anabolism, but whether or not metabolism is directly affected by ethephon treatment via some effect on the enzyme system is not known. Ethephon could indirectly enhance carbohydrate levels by reducing the demand for carbohydrates or products of carbohydrate catabolism by inhibiting some unknown metabolic process. If sorbitol content per pistil is considered rather than content per milligram fresh weight, there are similar quantities of sorbitol in treated and untreated pistils (≈ 450 nmoles/pistil). The sorbitol in treated pistils is more concentrated; thus, ethephon's effect on sorbitol content may be indirect due to its effect on pistil size.

Sorbitol in apple trees has been shown to increase during

exposure to low temperatures and to decrease during exposure to higher temperatures (Raese et al., 1978; Williams and Raese, 1974). In loquat, sorbitol synthesis via sorbitol-6-phosphate dehydrogenase increased upon exposure to low temperatures (Hirai, 1983). The increase was due to an increase in the amount and activity of the enzyme. In our study, we have shown that sorbitol levels in peach pistils are affected by temperature. Sorbitol levels were higher at 7C than at 21C. Sorbitol decreased more slowly at 7C than at 21C, regardless of ethephon treatment (Fig. 1). These differences support the hypothesis that sorbitol catabolism increases with temperature (Raese et al., 1978; Williams and Raese, 1974). The decrease in sorbitol levels from February to March in our study also supports this hypothesis.

An increasing fructose and decreasing sorbitol content in untreated pistils was observed during deacclimation in February, and the rate of sorbitol decline was greater at 21C than at 7C. This change suggests an increased level or activity of the NAD-dependent sorbitol dehydrogenase at higher temperatures. Glucose was not detected in ethephon-treated pistils in February, while fructose was. The consistent presence of fructose during deacclimation coupled with the lack of glucose under conditions when sorbitol decreased suggests that sorbitol catabolism in peach pistils is via the NAD-dependent sorbitol dehydrogenase. If the NADP-dependent sorbitol dehydrogenase or the sorbitol oxidase were involved, glucose should have been detected.

Increased pistil sorbitol and sucrose content, together with reduced moisture, pistil size, and growth rates during deacclimation, may account for the increased hardness and delayed bloom often observed in peach following a fall application of ethephon.

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