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Screening Thermal Shock as an Apple Blossom Thinning Method. II. Pollen Tube Growth and Spur Leaf Injury in Response to Temperature and Duration of Thermal Shock

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***Abstract*. Blossom thinning can confer significant benefits to apple growers, including increased fruit size and annual bearing. However, current blossom thinning practices can damage spur leaves and/or fruit. We evaluated the use of short duration forced heated air treatments [thermal shock (TS)] as a blossom thinning strategy for 'York Imperial'. Using a variable-temperature heat gun, TS treatments were applied to solitary blossoms 24 hours after pollination. Effects of output temperature (five levels) and treatment duration (four levels) were evaluated using a completely randomized design with a factorial treatment structure. Short duration treatments (0.5 and 1.0 seconds) were ineffective for arresting pollen tube growth in vivo. TS temperature required to inhibit stylar pollen tube growth was inconsistent across years. In 2014, TS temperatures ≥56 °C inhibited pollen tubes from reaching the style base at 2.0 and 4.0 second durations. However, in 2015, TS temperatures ≥81 °C at 4.0 seconds prevented pollen tubes from reaching the style base. Inconsistent effects of TS across years were attributed to treatments being applied too late due to optimal conditions for pollen tube growth during the intervening 24-hour period after pollination. Excessive injury to spur leaf tissue was observed at temperatures higher than 84 °C and 70 °C (2.0 and 4.0 seconds, respectively). Pollen tube growth was reduced or arrested at temperature and duration combinations that caused minimal visible injury to spur leaves. Identifying and exploiting structural differences between apple blossoms and vegetative spur leaves may provide insight for the future development of TS or other attempts at developing selective thinning technologies.**

Early thinning reduces competition among fruit, which increases fruit cell division and size potential (Lakso et al., 1996). Although existing chemical and mechanical blossom thinners may reduce the apple fruit set, blossom thinners are destructive by nature and can cause injury to nontarget tissues. Blossom thinner product development has been limited due to the risk of crop damage and high costs of product registration. More than 150 blossom thinning chemistries have been screened since 1990; however, a limited number of blossom thinning chemicals are registered for commercial apple production use in the United States, and the use of these products is restricted to specific states (Kon and Schupp, 2018). Although conventional apple growers have several effective postbloom chemical thinning products available, postbloom chemical thinning agents are not compatible with the specifications of organic production systems. In the United States, organic apple growers can only use OMRI-approved formulations of liquid lime sulfur, mechanical thinning devices, pruning, and/or hand thinning to reduce the crop load (Kon and Schupp, 2018). Therefore, developing organically approved and/or nonchemical crop load management strategies remains a research priority.

We investigated the use of short duration forced heated air treatments [thermal shock (TS)] as a blossom thinning strategy (Kon et al., 2020). Temperature stress in plants involves complex interactions of the intensity, duration, and rate of temperature change (Wahid et al., 2007). Although reproductive tissues are more sensitive to chronic heat stress when compared with vegetative tissues (Snider and Oosterhuis, 2011), information comparing tissue sensitivity to short duration TS is limited. Morphological characteristics of reproductive (Francescatto et al., 2016) and vegetative (Schechter et al., 1992) tissues can vary widely due to multiple interrelated factors, including environmental, genetic, physiological, and nutritional factors. To the best of our knowledge, limited research of floral structure differences among new cultivars has been conducted. Structural characteristics may influence the sensitivity of tissues to TS. In an effort to identify an alternative apple crop load management strategy, the effects of TS temperature and treatment duration on pollen tube growth in vivo and visible spur leaf injury were evaluated.

Materials and Methods

Trials were conducted in 2014 and 2015 at the Pennsylvania State University's Fruit Research and Extension Center in Biglerville, PA. Experiments were performed using 'York Imperial'/'Bud. 9' planted in 2004 at 1.5 × 4.6-m spacing.

Expt. 1: Effects of TS temperature and treatment duration on stigmatic receptivity of 'York Imperial' apple. Eighty spurs on 2- to 3-year-old wood were selected when king blossoms were at the late balloon stage. All side blooms were removed and selected king blossoms were emasculated. The spur was excluded from pollinators with a bag made of spunbonded rowcover material to prevent unregulated pollination. Treatments were randomly assigned to solitary blossoms and flagged. On the following day, blossoms were hand-pollinated with 'Rome Beauty' pollen. A range of TS treatments were applied to solitary blossoms 24 h after pollination using a variable-temperature heat gun set to an air flow rate of 0.50 $m^3 \cdot min^{-1}$ (Milwaukee 8988-20; Brookfield, WI). Effects of output temperature (five levels) and treatment duration (four levels; 0.5, 1, 2, or 4 s) were evaluated using a completely randomized design with a factorial treatment structure and replicated four times. A gas-powered generator supplied electricity to the heat gun in the field. A data-logging thermocouple (EL-GFX-TC; Lascar Electronics Inc., Erie, PA) was used to monitor the output temperature of the heat gun. The thermocouple probe was attached to the heat gun 2 cm from the heat gun outlet. For a given treatment, a nominal heat value was set on the heat gun, and the actual thermal output was recorded. After the heat gun temperature stabilized, all replicates of a given heat treatment were applied in ascending order. The start and stop times were recorded. The heat gun was positioned perpendicular to the calyx when heat treatments were applied to the pistil. The distance of the heat gun aperture from the pistil was held constant at 2 cm. To control the duration of

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the TS treatment, a quartz metronome was used as an auditory timing aid. All treatments were applied within 1 h. The mean and SD were determined for each level of the factor temperature. Descriptive statistics of TS treatments are provided in Table 1. In all subsequent tables, mean TS output temperatures are presented as the explanatory variable.

Blossoms were collected 24 h after treatments were applied, placed in a labeled vial containing 5% sodium sulfite, and stored at 4 °C until analysis. A modified version of the method of Embree and Foster (1999) was used to visualize pollen tube growth. Before microscopic examination, samples were autoclaved at 121 °C for 10 min to soften tissues. Blossoms were rinsed with distilled deionized water and the style was removed with a scalpel at the junction with the hypanthium. Styles were rinsed, separated, and soaked in a water-soluble fluorescence solution of 0.01% Aniline Blue stain in 0.067 M K_2HPO_4 on a microscope slide. Styles were squashed between two microscope slides and incubated overnight at room temperature. Samples were observed using fluorescence microscopy at ×100 (BX51; Olympus Optical Co., Tokyo, Japan). A high-pressure mercury vapor light source and ultraviolet/DAPI longpass filter cube was used (part 19000; Chroma Technology Corp, Bellows Falls, VT). Style damage was visually rated (1–6 scale; 1 = no visible injury; 2 = trace to 10% style damage; 3 = 11% to 25% style damage; 4 = 26% to 50% style damage; 5 = 51% to 75% style damage; 6 = 76% to 100% style damage). Pollen density on the stigmatic surface was visually rated using a 0 to 10 scale (0 = no pollen tubes visible on the surface and 10 = 91% to 100% of the surface covered by pollen tubes) described by Yoder et al. (2009). Pollen tubes that entered the style and the number that reached the style base were counted. The longest pollen tube length and style length were measured with an ocular micrometer.

Table 1. Expt. 1: Descriptive statistics for thermal shock (TS) output temperatures applied to 'York Imperial' apple blossoms in 2014 and 2015.[z]

Nominal treatment	Mean (°C)	SD
2014		
Control	18[y]	–
49	41[x]	0.4
66	56	0.5
82	73	1.1
93	83	0.8
2015		
Control	23	–
49	51	3.6
66	66	4.4
82	81	3.5
93	89	3.8

[z]In both years, all treatments were applied within 1 h.
[y]Control treatment = ambient air temperature at timing of treatment.
[x]All heat treatments were applied with a variable temperature. Distance from the heat gun aperture and the pistil was 2 cm.

Table 2. Expt. 2: Descriptive statistics for thermal shock (TS) output temperatures applied to 'York Imperial' apple spur leaves in 2014 and 2015.[z]

Nominal treatment	Mean (°C)	SD
2014		
Control	28[y]	–
49	56[x]	0.9
66	70	1.2
82	81	2.2
93	92	1.9
2015		
Control	28	–
49	57	3.1
66	71	3.6
82	84	2.8
93	94	3.3

[z]In both years, all treatments were applied within 1 h.
[y]Control treatment = ambient air temperature at timing of treatment.
[x]All heat treatments were applied with a variable temperature heat gun. Distance from the heat gun aperture and the pistil was 2 cm.

Expt. 2: Effects of TS temperature and treatment duration on the visible spur leaf injury of 'York' apple. Sixty flowering spurs on 2- to 3-year-old-wood were selected. Spurs were manipulated to permit unobstructed airflow to test leaves. At each spur, all blossoms were removed, three fully expanded spur leaves were selected, and the rest were removed. Treatments were randomly assigned to spurs and flagged. Using the methods described in Expt. 1, TS treatments were applied to persisting spur leaves at each spur. Spur leaf blades were held in a fixed position perpendicular to the heat gun aperture using forceps. The adaxial surface of the leaf was treated. Descriptive statistics of TS treatments are provided in Table 2. One week after treatment, leaf injury was visually rated (1–6 scale; 1 = no visible injury; 2 = trace to 10% leaf damage; 3 = 11% to 25% leaf damage; 4 = 26% to 50% leaf damage; 5 = 51% to 75% leaf damage; 6 = 76% to 100% leaf damage). Leaf injury ratings correspond with the extent of discolored leaf surface.

Statistical analysis. Effects of output temperature (five levels) and treatment duration (four levels; 0.5, 1, 2, or 4 s) were evaluated using a completely randomized design with a factorial treatment structure. The experiment was replicated three times. The PC version of SAS (version 9.3; SAS Institute, Cary, NC) was used for all statistical analysis. Main effects and interactions were determined using an analysis of variance. In several cases, the interaction between temperature and duration was significant. In these instances, regression analysis was conducted using PROC GLM at each level of duration.

Results and Discussion

Expt. 1: Effects of TS temperature and treatment duration on stigmatic receptivity of 'York' apple. Visible injury to styles were influenced by the interaction between temperature and duration in both years (Table 3). As the TS temperature increased, greater visible injury to styles were observed; however, the magnitude of the observed increase in injury was greater with longer treatment durations (Table 4). Specialized glandular cells in the style (transmitting tissue) were shown to provide resources to support pollen tube growth (Losada and Herrero, 2014). In chemical thinning trials, stylar browning corresponded with blossom thinner efficacy (Rom and McFerson, 2003). Regardless of treatment, it was rare to observe styles with more than 75% of the style exhibiting injury (injury rating = 6). Because apple styles are fused at the base, basal portions of the style presumably have greater thermal tolerance when compared with the upper style.

The interaction between temperature and duration was significant for all response variables evaluated, with two exceptions: pollen density rating (means not presented, 2014 and 2015) and the number of pollen tubes entering the style (2014 only). Pollen was applied to all blossoms 24 h before TS application. This provided ample time for pollen grains to germinate. Losada and Herrero (2014) showed that apple pollen germination occurred within 2 h after deposition on the stigmatic surface. Pollen tube cell walls contain callose (Currier, 1957), which is a polysaccharide and plant cell constituent. Stigmatic and stylar transmitting tissues are devoid of callose (Losada and Herrero, 2014). When viewed via fluorescence microscopy and stained with Aniline Blue, callose present in germinated pollen glows vividly. During this experiment, callose tissue from germinated pollen grains was still visible despite visible damage to the stylar tissue. When chemical blossom thinners were applied to blossoms that were hand-pollinated 24 h before treatment, pollen tubes were still visible but were brown and faded (Embree and Foster, 1999). Injury similar to germinated pollen tubes with TS treatments described by Embree and Foster (1999) were observed.

The number of pollen tubes that penetrated the style was not influenced by the TS temperature, duration, or interaction between temperature and duration in 2014. This corresponds with the limited effect of TS treatments on pollen germination and is a function of the delayed application timing (24 HAP) evaluated in this experiment. In 2015, there was no relationship between the TS temperature and pollen tubes entering the style at 0.5 s duration. However, at 2.0 and 4.0 s durations, the number of visible pollen tubes entering the style was reduced linearly as temperature increased. At the highest temperature evaluated (89 °C), the number of pollen tubes entering the style was reduced 43% and 83% at 2 and 4 s treatment durations, respectively.

In 2014, a linear reduction in the pollen tube length with 2 and 4 s treatment durations was observed (Table 4). At 2 and 4 s durations, temperatures ≥56 °C resulted in the pollen tube length being less than 50% of the average style length (9.2 mm) and prevented

Table 3. Main effects and interactions of thermal shock temperature and duration on stylar browning rating, pollen density on the stigma, number of pollen tubes penetrating the style, length of the longest pollen tube, and the number of pollen tubes at the style base of 'York Imperial' apple blossoms in 2014 and 2015.

Response variable	Significance ($P > F$)		
	Temperature	Duration	Interaction
	2014		
Stylar browning	<0.0001	0.5275	0.0129
Pollen density	0.3026	0.2887	0.4379
No. pollen tubes in style	0.4671	0.3417	0.2499
Length of longest pollen tube	<0.0001	0.6896	0.0038
No. pollen tubes at style base	<0.0001	0.4519	0.0191
	2015		
Stylar browning	<0.0001	0.0048	<0.0001
Pollen density	0.2414	0.8484	0.4648
No. pollen tubes in style	0.0010	0.1675	0.0038
Length of longest pollen tube	<0.0001	0.0195	<0.0001
No. pollen tubes at style base	0.4055	0.1436	0.0088

Table 4. Effects of thermal shock temperature and duration on pollen density and the number of pollen tubes penetrating the style of hand-pollinated 'York Imperial' apple blossoms in 2014 and 2015.[z]

	Duration (s)							
	0.5	1.0	2.0	4.0	0.5	1.0	2.0	4.0
Mean temperature (°C)	Stylar browning (1–6)[y]				No. pollen tubes penetrating style			
				2014				
18	1.1	1.1	1.3	1.9	15.9	16.8	13.9	9.9
41	1.0	1.0	1.1	1.0	14.4	19.6	16.0	19.1
56	1.2	1.0	2.8	4.8	12.8	16.8	12.3	13.0
73	1.0	2.6	4.8	5.0	16.8	14.9	7.4	23.0
83	3.0	5.0	5.0	5.0	14.8	14.4	23.0	18.0
Significance	Q[x]	Q	L	L	–	–	–	–
P value	0.0038[w]	<0.0001	<0.0001	<0.0001	–	–	–	–
r^2	0.50	0.87	0.69	0.62	–	–	–	–
				2015				
23	1.6	1.6	1.5	1.4	20.1	16.8	25.0	21.5
51	1.5	1.2	1.6	1.3	17.4	23.1	14.9	21.2
66	1.2	1.7	2.3	3.2	24.3	24.6	22.5	10.4
81	1.5	2.4	3.7	4.3	15.9	20.0	8.7	8.8
89	1.2	2.8	4.3	4.9	21.5	17.1	14.3	3.6
Significance	NS	L	Q	Q	NS	Q	L	L
P value	–	0.0383	<0.0001	<0.0001	–	0.0442	0.0290	<0.0001
r^2	–	0.22	0.76	0.89	–	0.31	0.24	0.56

[z]All thermal treatments were applied with a variable temperature heat gun at 2 cm distance from the pistil and blossoms were hand pollinated 24 h before treatment.
[y]Style damage was visually rated (1–6 scale; 1 = no visible injury; 2 = trace to 10% style damaged; 3 = 11% to 25% style damaged; 4 = 26% to 50% style damaged; 5 = 51% to 75% style damaged; 6 = 76% to 100% style damaged).
[x]In cases where a significant interaction was observed, each level of duration was analyzed separately.
[w]*P* value is for the model.
L = linear model; Q = quadratic model; NS = nonsignificant.

pollen tubes from reaching the style base. Although a minor reduction in the pollen tube length was observed with increased temperature at 0.5 s treatment duration, these short duration treatments did not affect the number of pollen tubes that reached the style base.

In 2015, there was no relationship between TS temperature and pollen tube length with shorter treatment durations (0.5 and 1.0 s; Table 5). However, at 2 and 4 s durations, curvilinear reductions were observed in the pollen tube length with increasing TS temperature. The average style length in 2015 was 8.8 mm (data not presented), and high temperatures (≥81 °C) at 4.0 s duration limited the pollen tube length to 50% of the average style length. The TS temperature did not influence the number of pollen tubes that reached the style base with 0.5, 1.0, and 2.0 s treatment durations. At 4.0 s duration, a curvilinear reduction in the number of pollen tubes that reached the style base was observed.

The TS temperature effects on the number of pollen tubes that reached the style base were not consistent among years. In 2014, TS temperatures ≥56 °C prevented pollen tubes from reaching the style base at 2 and 4 s durations. However, much higher temperatures were required to prevent pollen tubes from reaching the style base in 2015. The reasons for this inconsistency are unclear. Although TS treatments were applied at the same timing in each year (24 h after pollination), the rate of pollen tube growth in vivo may have been more rapid in 2015 due to warm temperatures during the 24-h period following pollination (mean temperature = 19.8 °C). Perhaps the pollen tubes penetrated far enough into the style to avoid injury caused by TS treatments. At constant temperatures higher than 24 °C, pollen tubes reached the style base of 'Golden Delicious' within 24 h (Yoder et al., 2009). The maternal cultivar can influence pollen tube growth rates (Yoder et al., 2013). Pollen tube growth rates of 'York Imperial' have not been evaluated, thereby making a direct comparison difficult. During pollen tube growth, the cytoplasm and sperm cells are positioned near the apex of the pollen tube. Deposits of callose (i.e., callose plugs) isolate the actively growing portion of the pollen tube (Losada and Herrero, 2014). To arrest the growth of pollen tubes with a blossom thinner, the actively growing pollen tube tip or adjacent transmitting tissue must be disrupted or damaged. It is possible that our treatments were applied too late to have an impact in 2015 because the pollen tube growing point had progressed beyond the more distal regions of the stylar tissue that were affected by treatment.

Expt. 2: Effects of TS temperature and treatment duration on visible spur leaf injury of 'York Imperial' apple. Relationships between visible injury and TS treatments for spur leaves were very consistent in both years of this trial (Table 6). At 0.5 s duration, the

Table 5. Effects of thermal shock temperature and duration on the length of the longest pollen tube and number of pollen tubes at style base of hand-pollinated 'York Imperial' apple blossoms in 2014 and 2015.[z]

	Duration (s)							
	0.5	1.0	2.0	4.0	0.5	1.0	2.0	4.0
Mean temperature (°C)	Length of longest pollen tube (mm)				No. pollen tubes at style base			
				2014				
18	8.7	8.7	8.2	8.9	3.2	3.1	4.5	4.1
41	10.0	9.1	8.6	8.6	5.0	6.2	5.1	2.5
56	9.1	8.1	6.2	4.3	4.4	3.7	0.0	0.1
73	8.9	8.4	3.3	3.9	3.9	2.4	0.2	0.0
83	7.5	7.5	5.3	3.8	3.3	1.2	0.1	0.0
Significance	Q	NS	L	L	NS	Q	L	Q
P value	0.0337[y]	–	0.0048	0.0006	–	0.0097	0.0003	<0.0001
r^2	0.35	–	0.40	0.51	–	0.44	0.55	0.78
				2015				
23	8.7	9	8.9	8.9	4.8	2.7	5.5	4.1
51	8.92	9.2	9	8.7	3.9	8.5	3.7	9.5
66	9.1	9.1	8.1	7.6	5.8	4.1	6.4	2.7
81	8.8	8.8	7.4	4.4	6	7.5	2.65	1.5
89	8.4	8.3	5.5	1.3	8.8	4.1	1.8	0.05
Significance	NS	NS	Q	Q	NS	NS	NS	Q
P value	–	–	0.0025	<0.0001	–	–	–	0.0018
r^2	–	–	0.51	0.77	–	–	–	0.52

[z]All thermal treatments were applied with a variable temperature heat gun at 2 cm distance from the pistil and blossoms were hand pollinated 24 h before treatment.
[y]*P* value is for the model.
L = linear model; Q = quadratic model; NS = nonsignificant.

Table 6. Effects of thermal shock temperature and duration on visible injury ratings of 'York Imperial' apple spur leaves in 2014 and 2015.[z]

	Duration (s)			
	0.5	1.0	2.0	4.0
Mean temperature (°C)	Visible leaf injury (1–6)			
			2014	
28	1	1	1	1
56	1	1	1	1.3
70	1	1	2.7	4.3
81	1.3	2	3.3	5.3
92	1.3	2.3	5	6
Significance	NS	L	Q	Q
P value	–	0.0004[y]	<0.0001	<0.0001
r^2	–	0.73	0.89	0.95
			2015	
28	1	1	1	1
57	1	1	1.1	1.2
71	1	1	2	4.2
84	1	1.2	4.7	5.1
94	1	1.9	5	6
Significance	–	L	L	Q
P value	–	0.0127	<0.0001	<0.0001
r^2	–	0.48	0.92	0.95

[z]One week after treatment, leaf injury was visually rated (1–6 scale: 1 = no visible damage; 2 = trace to 10% damage; 3 = 11% to 25% damage; 4 = 26% to 50% damage; 5 = 51% to 75% damage; 6 = 76% damage to 100% damage).
[y]*P* value is for the model.
L = linear model; Q = quadratic model; NS = nonsignificant.

TS temperatures did not influence visible spur leaf injury. Although spur leaf injury increased when temperatures increased at 1.0 s duration, none of the temperatures evaluated resulted in >33% injury to spur leaves. Apple fruit growth rate is strongly related to spur leaf area because the fruit growth rate increased with increasing leaf number (Yuan and Greene, 2000). Ferree and Palmer (1982) demonstrated that the removal of >33% of the spur leaf area had negative consequences for the fruit set, fruit size, and mineral nutrition. At 2.0 and 4.0 s, visible injury to spur leaf tissue exceeded a rating of 4 (4 = 26% to 50% damage) at temperatures higher than 84 °C and 70 °C, respectively.

Unfortunately, TS effects on net photosynthesis (P_n) were not evaluated. As documented in studies with photosynthetic inhibitors, it is possible that TS could influence P_n without exhibiting visible injury (Byers et al., 1990). A transient reduction in P_n during early fruit development can induce fruit abscission. However, many plants are capable of compensating for some level of leaf removal and/or damage, including apple. Defoliation of up to 20% of the leaf area was compensated for, and minor leaf removal did not influence P_n (Flore and Irwin, 1983; Hall and Ferree, 1976). Spur defoliation did not influence flower bud formation, but defoliation significantly inhibited the flower formation of bourse shoots (Elsysy and Hirst, 2017). The effects of TS on spur leaf P_n and impact on bourse leaves should be evaluated in future work because these may contribute to the mode of action of TS and/or potential as a thinning strategy.

Conclusions

At the range of TS temperatures tested, short duration forced air treatments (0.5 and 1.0 s) were ineffective for arresting pollen tube growth in vivo and had negligible effects on spur leaf injury. A minimum TS treatment duration of 2 s was required to elicit a meaningful reduction in pollen tube growth in vivo. Leaf injury responses to TS were consistent in both years of this trial, suggesting that TS strategies based on forced air have an upper threshold of 70 °C for 2 s to avoid visible leaf injury.

TS was inconsistent across years for reducing pollen tube growth in the style, and we speculated that the lower efficacy in 2015 was primarily attributed to the timing of treatment (24 h after pollination). Based on the 2014 outcomes, 56 °C for 2 s would prevent fertilization, which is a temperature well below that required to damage leaves. Use of a pollen tube growth model (Yoder et al., 2013) and the ability to apply TS treatments rapidly would be essential to its successful deployment as a thinner. Pollen tube growth rates in vivo are complex and dependent on multiple factors, including maternal cultivar, pollen genotype, and temperature (DeLong et al., 2016). The use of pollen tube growth models as timing aids for TS should be considered for future work. The strong interaction between temperature and duration involved in arresting pollen tube growth suggests that longer durations may be a strategy for extending the efficacy of TS during seasons when ambient temperatures favor rapid pollen tube growth.

Blossom thinning using chemical and thermal treatments is a time-sensitive operation, and efficacy is influenced by environmental conditions. TS is perhaps even more time sensitive because the effects of TS last only seconds. Regardless of the method of heat transfer, the canopy structure and distance of the heat source from the target are important considerations. The relatively recent adoption of high-density orchards with narrow "tree wall" canopies could facilitate the application of TS to whole-plant canopies. Vision systems and end effectors, which are used to detect and remove blossoms with selective or semi-selective mechanical thinners, are undergoing development (Lyons et al., 2015; Pflanz et al., 2016; Wouters et al., 2015). Based on this research, TS may have some utility for future nonchemical selective thinning technologies for apple.

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