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Temperature effects on pistil viability and fruit set in sweet cherry

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ABSTRACT

Field observations suggest high air temperatures during bloom decrease fruit set of many sweet cherry (*Prunus avium* L.) cultivars. We investigated the role of temperature on stigma receptivity and ovule viability in four sweet cherry cultivars that exhibit variability in productivity and fertility: 'Sweetheart' (self-fertile, high productivity), 'Benton' (self-fertile, low productivity), 'Rainier' (self-sterile, high productivity), and 'Tieton' (self-sterile, low productivity). The development of the stigmatic surface, and pollen hydration, germination and tube growth in vivo, were evaluated by hand pollination and used as proxies for stigma receptivity. In addition, the senescence of primary and secondary ovules was analyzed with fluorescence microscopy. The stigmatic papillae began deteriorating by the second day after anthesis and had collapsed by the sixth day post-anthesis across cultivars. Pollen hydration exhibited 5 stages related to the length-width ratios of 2.5:1, 2:1, 1.75:1, 1.5:1 to 1:1. Maximum pollen hydration and pollen germination occurred on the stigmas within 2 days of bloom, depending on cultivar and air temperature. Pollen hydration and germination, and ovule senescence accelerated under warmer temperatures. At 7 days post-anthesis and under 24 °C approximately 80% of 'Rainier' ovules were viable compared to 30% in the three other cultivars. Under moderate temperature (18 °C) which mimicked the field average flowering temperature, ovule of the two high productivity cherry cultivars, 'Rainier' and 'Sweetheart', kept full viabilities for 3–4 days post-anthesis while only 1 day for the two low productivity cultivars 'Benton' and 'Tieton'. These results reveal that low commercial productivity of sweet cherry cultivars in the Pacific Northwest (PNW) of U.S. is likely due to rapid ovule senescence, a condition exacerbated in warm conditions.

1. Introduction

The Pacific Northwest (PNW) region is one of the most important sweet cherry production area in the world that contributes to more than 75% sweet cherries production in U.S. Sweet cherry anthesis in PNW usually occurs within the first two weeks of April depending on cultivars and years. The thermal unit accumulation between bloom initiation and full bloom was 43 growing degree days (GDD) in 'Sweetheart' and 106 GDD in 'Kordia' cherries which were calculated with the base temperature of 4.5 °C (Whiting et al., 2015). The variations of first bloom date and flowering period of cherries could have adverse impact on flower qualities and pollination (Zhang and Whiting, 2012). Successful pollination results in fertilization and fruit set that is accelerated by the endogenous hormones GA and auxin produced by the embryo (Rodrigo and Herrero, 1996; Sanchez et al., 2004). Most commercial sweet cherry genotypes exhibit gametophytic self-incompatibility, requiring pollen from compatible genotypes for fertilization (Choi and Andersen, 2001). Therefore, honey bee (*Apis mellifera* L.) pollinators and bloom overlap with pollinizers are important (Afik et al., 2008; Someriville, 1999; Imani et al., 2013). Sweet cherry fruit set has been reported to range from 0% to 70% (Sutyemez, 2011). Fruit set of self-fertile sweet cherry genotypes is generally higher than that of self-incompatible cultivars (Tosun and Koyuncu, 2007; Beyhan and Karakaş, 2009; Sutyemez, 2011). In the PNW, the commercial productivity of several sweet cherry cultivars with outstanding fruit attributes (e.g., 'Tieton', 'Regina' and 'Benton') is poor, generally lower than 10% (Whiting and Zhang, unpublished), considered the upper threshold for low fruit set (Bekefi, 2004).

The effective pollination period (EPP) reflects the influence of genotype and environment on pollination, and therefore fruit set and production. Williams defined EPP as ovule longevity as minus the time between pollination and fertilization that does not exceed the stigma's receptive period (Williams, 1965; Ortega et al., 2004; Tonutti et al., 1991). Collectively, stigma receptivity, pollen tube kinetics and ovule longevity determine the EPP in cherry. Pollen germination on the stigma and pollen tube growth to ovules requires 2–5 days depending

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on cultivar and temperature (Sutyemez, 2011). The duration of EPP in sweet cherry varies among cultivars, locations and years (Sanzol and Herrero, 2001). In 'Bing' cherry, the EPP was reported ranging from 4 to 7 days of different years in Pullman, USA (Toyama, 1980).

Three steps in the fertilization process are a function of stigma receptivity: pollen grain adhesion, pollen germination, and pollen tube penetration (Hedhly et al., 2003). Stigmas lose the capacity to support pollen tube penetration first, pollen germination second and pollen adhesion last (Sanzol et al., 2003b). Stigma receptivity is associated with the exfoliation of cuticles, production of stigma secretions and integrity of papillae structures (Harrison, 2000; González et al., 1995). In *Prunus* fruit crops, stigma becomes receptive post anthesis, and receptivity decreases with time (Hedhly et al., 2003; Ortega et al., 2004; Yi et al., 2006). Stigma receptivity is also sensitive to environmental changes and pathogens (Nicholson and Hammerschmidt, 1992). Pistils of *Prunus* species contain two ovules in a single carpel, the secondary ovule will lose viability before the primary ovule (Rodrigo and Herrero, 1998). The primary ovule is penetrated by the pollen tube to complete fertilization (Bradbury, 1929; Arbeloa and Herrero, 1991). Ovule degeneration has been reported to be associated with internal callose formation but not internal starch formation (Pimienta and Polito, 1982; Rodrigo and Herrero, 1998). Pimienta and Polito (1982) demonstrated that the EPP of species in which the embryo sac maturity and fertilization happen within days of pollination was strongly affected by ovule longevity.

Environmental conditions during anthesis, pollinator activity, and genotype are the three factors affecting pollination (Hedhly et al., 2003; Mohamed, 2008). Warm pre-bloom temperatures can accelerate sweet cherry anthesis, but not floral organ development, resulting in reduced pistil weight (Rodrigo and Herrero, 2002). Pollen germination rate on the stigma surface is increased by warm temperatures. Sweet cherry pollen tube growth through the style was slowed by 6 days at 10 ℃ versus 30 ℃ (Hedhly et al., 2003). However, Cerović et al. (2000) reported ovule senescence of plum was accelerated under constant warm temperature of 20 ℃ and the EPP was not be prolonged by pollen tube growth alone. Cold temperatures will extend the sweet cherry EPP by increasing ovule longevity but it also slows pollen tube growth (Sanzol et al., 2003b). Given the conflicting reports of genotype and temperature on stigma receptivity and ovule longevity in determining the EPP we proposed to further define this relationship in four sweet cherry cultivars: 'Sweetheart' (self-fertile, high productivity), 'Benton' (self-fertile, low productivity), 'Rainier' (self-sterile, high productivity), and 'Tieton' (self-sterile, low productivity).

2. Materials and methods

2.1. Plant material

This research was conducted in 2011 at two locations: Washington State University's Roza research farm in Prosser, USA (Latitude 46°19′32″, Longitude -119°43′00″) and a commercial orchard in The Dalles, Oregon, USA (Latitude 45°34′38″, Longitude -121°12′42″). Four sweet cherry cultivars were selected; two genotypes with high productivity, 'Sweetheart' (self-fertile) and 'Rainier' (self-sterile), and two genotypes with low productivity, 'Benton' (self-fertile) and 'Tieton' (self-sterile). At 10% bloom, thirty, two-year-old flowering branches per cultivar were randomly collected from the outer canopy of fifteen trees, placed in water and delivered to the lab immediately. Flowers that were older or younger than the unopened 'half white' stage (Zhang et al., 2015) were removed. The remaining flowers were emasculated by removing the stamens and perianths to prevent self-pollination. An additional 3 branches with intact flowers, the controls, were covered by mesh veils and isolated from treated flowers in the growth chambers to prevent inadvertent pollen transfer.

Thirty branches were randomly divided into three groups, placed in buckets of water and cultivated in three controlled environment chambers (Adaptis, A1000, Canada). Each chamber was programmed to mimic either a cool (lowest: 4 °C, highest: 12 °C), average (lowest:6 °C, highest: 18 °C), or warm (lowest:12 °C, highest: 24 °C) spring (Fig. 1). These three temperature regimes were based on the historical air temperatures in the Prosser region during the first two weeks of April (i.e., the weeks prior to anthesis). Yearly average minimum, medium and maximum hourly temperatures of this pre-bloom period were designated low, moderate and high for programming the growth chambers. All chambers were held at 70% relative humidity with a daily day/night light cycle of 0 (photosynthetic photon flux density PPFD = 0 μmoles m^{-2} s^{-1}, 12 h, 19:00-6:00), 1 (PPFD = 320 μmoles m^{-2} s^{-1}, 2 h, 7:00 and 18:00) and 2 (PPFD = 700 μmoles m^{-2} s^{-1}, 10 h, 8:00-17:00).

2.2. Observation of stigma surface

Sampling for stigma surface evaluation of the unemasculated flowers held at moderate temperatures began day one of anthesis and continued for 1-day intervals for six days. Stigma development was observed using both scanning electron and light microscopy of longitudinal sections.

The pistil of five fresh flowers of each cultivar was severed and the stigma was observed directly under the Hitachi S-570 scanning electron microscope (Hitachi Ltd., Tokyo, Japan). Images were digitally captured using Quartz PCI 4.2 imaging software (Quartz Imaging

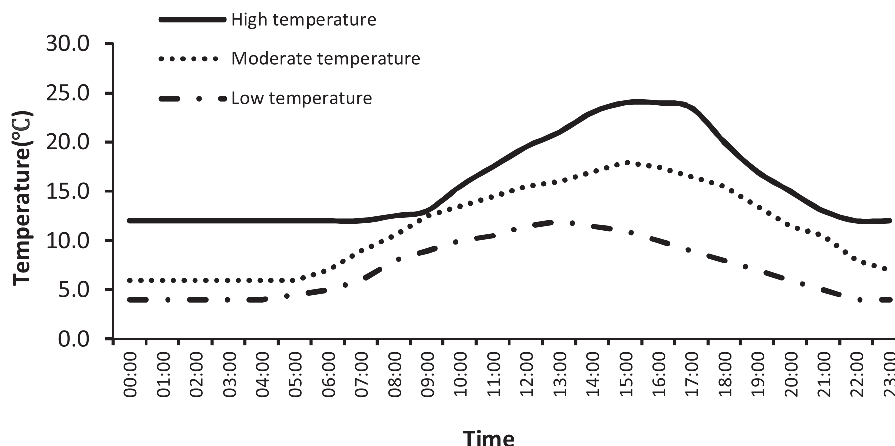

Fig. 1. Diurnal variation in air temperature in controlled environment chambers mimicking field environment of the past 10 years.

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