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EVALUATING THE INFLUENCE OF TEMPERATURE ON REMONTANCY IN STRAWBERRY.

By

Emma Bradford

A THESIS

Submitted to
Michigan State University
In partial fulfillment of the requirements
For the degree of

MASTER OF SCIENCE

Plant Breeding, Genetics, and Biotechnology - Horticulture

2009

ABSTRACT

EVALUATING THE INFLUENCE OF TEMPERATURE ON REMONTANCY IN STRAWBERRY.

By

Emma Bradford

Fragaria ×ananassa Duch. ex Rozier (strawberry) cultivars are traditionally classified as short-day (Junebearing), day-neutral, or long-day (everbearing) plants based on when and how often flowering occurs during the growing season. We propose that the term remontant replace 'day-neutral' to describe strawberry genotypes producing multiple flowering cycles in a season, and present evidence that differences in remontancy across strawberry genotypes are primarily a function of differential temperature tolerance, and at temperatures above the threshold tolerance photoperiod becomes regulating. In support of this, the remontant 'Tribute' exhibited superior heat tolerance to the short-day cultivar 'Honeoye', while RH 30 exhibited intermediate heat tolerance. Individuals from the F_1 population 'Honeoye' × 'Tribute' were replicated through either crown division or runner propagation, and grown at 17, and 23°C under a 16 h photoperiod. Results show that temperature is the primary factor in determining photoperiod dependent flowering, and how an experimental unit is derived will have an effect on the number of runners and inflorescences produced.

AKNOWLEDGMENTS

I'd like to thank Dr. Ryan Warner for giving me the opportunity to study under him, for his unfaltering support, guidance, and patience throughout and for generally being a great guy.

Thanks go to Dr. Jim Hancock for introducing me to the wonderful world of strawberries. I especially appreciated the opportunity to make crosses and evaluate progeny, a process in which I not only learned a lot about making selections but also picked up some uniquely descriptive vocabulary.

Dr. Dechun Wang made a potentially hazardous subject, QTL mapping, a user friendly experience thanks to his unwavering availability to answer questions, and ease frustrations.

To my partner in crime, Travis Stegmeir, I'd like to extend a hearty thank you for being there and for sharing the most amazing office in PSSB with me.

Pete Callow, who is possibly the most entertaining and helpful lab and field technician, I thank for all his tips and advice on lab techniques, horticulture, and parenting.

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CHAPTER ONE

TEMPERATURE IS THE PRIMARY FACTOR CONTROLLING PHOTOPERIOD REQUIREMENTS FOR REPEAT FLOWERING (REMONTANCY) IN STRAWBERRY.

ABSTRACT

Fragaria ×ananassa Duch. ex Rozier (strawberry) cultivars are traditionally classified as short-day (Junebearing), day-neutral, or long-day (everbearing) plants based on when and how often flowering occurs during the growing season. We propose that the term remontant replace 'day-neutral' to describe strawberry genotypes producing multiple flowering cycles in a season, and present evidence that differences in remontancy across strawberry genotypes are primarily a function of differential temperature tolerance leading to photoperiodic sensitivity. To more clearly define the roles of temperature and day length in flowering control of strawberry, the short-day cultivar 'Honeoye', and two remontant genotypes, 'Tribute' and an elite clone of *Fragaria virginiana* Duch. ssp. *virginiana*, RH 30, were grown at 14 ,17, 20, 23, 26, or 29 °C, under a short (9 hr) or long (16 hr) photoperiod. 'Honeoye' and RH 30 exhibited similar flowering patterns in response to temperature, with RH 30 producing flowers at temperatures 3 °C warmer than the threshold temperature for flowering in 'Honeoye', regardless of photoperiod. 'Tribute' continued to produce flowers under all treatments except 29 °C under short days. Based on these results, we conclude that temperature is the primary factor in determining photoperiod dependent flowering.

Introduction

Strawberry cultivars have traditionally been classified into photoperiodic response groups for flowering. Junebearers are defined as facultative short day (SD) plants (Darrow, 1936), everbearers are classified as long day plants (LD) (Darrow and Waldo, 1934), and photoperiod insensitive varieties are defined as day neutral (DN) (Bringhurst and Voth, 1978). However, early on, Darrow (1936) described the influence of temperature on flower initiation in strawberry, indicating the potential difficulty in photoperiodic classification of cultivars. Flower induction of SD types can occur under any photoperiod if the temperature is cool enough, generally <15 °C (Guttridge, 1985). At high temperatures, inhibition of flowering in SD types is observed even under short photoperiods (Ito and Saito, 1962), and flowering of DN and LD types also decreases at high temperatures (Durner *et al.*, 1984; Heide, 1977; Serçe and Hancock, 2005a). In a controlled environment study, Durner *et al.* (1984) reported inconsistent effects of photoperiod on flowering of two SD cultivars grown under different temperature regimes, further suggesting the inadequacy of classifying cultivars into photoperiodic response groups to predict multiple flowering cycles. Sonsteby and Heide (2007a) concluded that seedlings of the F_1 hybrid 'Elan' were quantitative long-day plants, as plants produced more flowers under continuous light than under short-day conditions. However, flowering under long photoperiods was inhibited at 27 °C. Nishiyama and Kanahama (2002) also used a 24 h long-day treatment, but used two different temperature regimes, a 20 °C day temperature with a 15 °C night temperature and a 30 °C day temperature with a 25 °C night temperature, to determine that 'Summerberry' and 'Hecker' were long-day plants. However, plants were maintained at a temperature of 30 °C and an 8 h

photoperiod for 16 weeks to inhibit flowering prior to commencing the experiment. Maintaining the plants in a stressful environment may have influenced their results.

Strawberry cultivars exhibit considerable variation in the degree of repeat blooming, or remontancy. The same genotype may be remontant in some parts of the USA, but not in others (Durner *et al.*, 1984). Since cultivars that produce multiple crops during the summer can extend the growing season for farmers, understanding the genetic basis of repeat flowering has been an active area of investigation (Ahmadi *et al.*, 1990; Powers, 1954; Serçe and Hancock, 2005a; Shaw, 2003; Sugimoto et al, 2005; Weebadde *et al.*, 2008). Unfortunately, the genetic basis of remontancy remains poorly understood, with inconsistent inheritance ratios reported for different populations using the same genetic source of remontancy (Hancock *et al.*, 2002; Shaw, 2003; Shaw and Famula, 2005; Serçe and Hancock, 2005a) or in different trialing locations using the same clonally propagated segregating populations (Hancock et al, 2002; Weebadde *et al.*, 2008). For example, a clonally propagated mapping population derived from the DN 'Tribute' and SD 'Honeoye' grown in California, Oregon, Minnesota, Michigan, and Maryland exhibited 48-50% remontant individuals in MN, MD and MI, compared to 80% and 87% in OR and CA, respectively (Weebadde *et al.*, 2008). The range of latitude and, therefore, photoperiod covered by the three eastern sites was similar to the two western sites, while recorded temperatures were considerably higher in MN, MD, and MI compared to OR and CA during the experimental period, suggesting a strong influence of temperature on remontancy.

The objectives of the work presented here are to determine the effects of temperature and photoperiod on remontancy of 'Honeoye', 'Tribute' and another genetic source of remontancy, an elite clone of *Fragaria virginiana* Duch. ssp. *virginiana*, RH 30, previously classified as day neutral (Hancock *et al.*, 2002). Results of this work will allow us to identify permissive and inhibitive temperatures for remontancy in each genotype which we can subsequently use to evaluate remontancy in segregating populations derived from these parental genotypes. We have chosen to use established plants as our case study in order to determine the effects of temperature and photoperiod on re-blooming and not initial flower induction.

Materials and Methods

During the summer of 2007, runners of *Fragaria ×ananassa* (Duch. ex Rozier) 'Tribute' and 'Honeoye', and *Fragaria virginiana* ssp. *virginiana* elite clone RH 30 (Hancock *et al.*, 2001) were rooted in 10-cm square pots. After ca. 4 weeks, the connecting stolons were severed, and the plants were transplanted into 3.79 L pots filled with soilless media containing (v/v) 70% peat moss, 21% perlite and 9% vermiculite (Sure-Mix, Michigan Grower Products, Galesburg, MI). On 25 October 2007, 72 plants consisting of a single crown of each genotype were selected, and any flowers or runners present were removed. On 2 November 2007, twelve plants of each type were placed in one of six glass glazed greenhouses set to a constant temperature of 14, 17, 20, 23, 26, or 29 °C. Air temperature in each treatment was measured by a Type E thermocouple (TT-E-40; Omega Engineering, Stamford, CT.) placed in an aspirated tube. Thermocouples were connected to a data logger (CR10; Campbell Scientific, Logan, UT) and data were

recorded every 10 s. Weekly temperature averages for each temperature were within ± 1.0 °C of the setpoint each week during the experimental period. Vapor pressure deficit was maintained between 0.7 and 1.0 kPa at each temperature by steam injection. Within each temperature treatment, half of the plants were maintained under a 9-hr photoperiod (plants were covered with an opaque cloth from 1700 to 0800 HR daily) and half were maintained under a 16-hr photoperiod (ambient daylight supplemented with 50 μmol m^{-2} s^{-1} photosynthetically-active radiation supplied by high-pressure sodium lamps from 0600 to 2200 HR daily; lamps were programmed to turn off when ambient irradiance outside the greenhouse exceeded 400 μmol m^{-2} s^{-1}). Plants were overhead irrigated with reverse osmosis water supplemented with a water-soluble fertilizer to provide the following (mg L^{-1}): 125 N, 13 P, 125 K, 15 Ca, 1 Fe, 0.1 B, 0.1 Mo, 0.5 Mn, 0.5 Zn and 0.5 Cu (MSU Special; Greencare Fertilizers, Chicago, IL).

Data collection and analysis

Every 10 to 15 days during the experiment, the number of inflorescences per plant, flowers per inflorescence, and runners were determined. Inflorescences were counted once all flower buds within the inflorescence were clearly distinguishable. After each data collection, inflorescences, runners and any dead leaves were removed. Data collected during the first 49 days of the experiment were not included in the data analysis, as it was assumed that any flowers or runners produced during this period were induced in conditions prior to initiation of the experiment. Therefore, only data collected between days 63 and 178 were included for statistical analysis. Analyses of covariance

with temperature as the covariate were conducted using PROC GLM in the SAS software package (SAS v. 8.2; SAS Institute, Cary, N.C.).

Results

Flowering

Genotype, temperature and photoperiod interacted to impact the number of flowers ($P<0.001$) and inflorescences ($P=0.003$) produced. Under long days, 'Honeoye' flower and inflorescence number were greatest at 14 and 17 °C, decreased as temperature increased to 20 °C, and flowering was completely inhibited at 23, 26 and 29 °C (Figs. 1.1A and 1.2). Under short days, 'Honeoye' flower number increased as temperature increased from 14 to 20 °C (Fig. 1.1A). Flower number decreased as temperature further increased to 23 or 26 °C, and flowering was inhibited at 29 °C. Under 14 and 17 °C, 'Honeoye' produced more flowers under LD than SD, while under temperatures of 20 to 26 °C flower production was greater under SD. Inflorescence production in 'Honeoye' lagged about 84 days behind RH 30 and 'Tribute' (Fig. 1.2), and was highest under long days at 14 and 17°C. At 20 and 23°C, 'Honeoye' produced more inflorescences under short days than long days and at temperatures of 26°C or more, inflorescence production in 'Honeoye' is inhibited under both photoperiods. The genotype RH 30 displayed a similar trend for flower production, producing more flowers per plant under long days than short days at 14 °C and 17 °C, similar numbers under both photoperiods at 20°C, and more flowers under short days than long days at 23 to 29 °C (Figs. 1B and 2). RH 30 was the only genotype to produce flowers under short days at 29 °C. In contrast to both 'Honeoye' and RH 30, 'Tribute' produced more flowers under long days than short days,

regardless of temperature (Figs. 1C and 2). 'Tribute' was also the only genotype to produce flowers under long days at 29 °C. Flower production in 'Tribute' was similar as temperature increased from 14 to 23 °C under long days, but decreased ca. 30% as temperature further increased to 26 or 29 °C.

The observed differences in flower production could be due to variations in inflorescence production, the number of flowers produced per inflorescence, or both. In general, the differences in flower production were more strongly associated with variation in inflorescence number than flowers per inflorescence, as patterns of inflorescence number and flower number were very similar across temperature for each genotype and photoperiod (Figs. 1.1 and 1.3). This was particularly true at temperatures of 20 °C or lower. Flower number per inflorescence was similar for 'Honeoye' at temperatures of 20 °C or less, regardless of photoperiod (Fig. 1.4A). As temperature increased from 23 to 26 °C, 'Honeoye' flower number per inflorescence decreased from 8 to 3 flowers under short days. RH 30 flower number per inflorescence was similar between 14 and 20 °C under long days, but decreased as temperature further increased to 23 or 26 °C (Fig. 1.4B). Under short days, RH 30 flower number per inflorescence was similar between 14 and 23 °C, decreasing as temperature increased to 26 or 29 °C. At 14 and 17 °C, RH 30 produced more flowers per inflorescence under long days than short days, and more flowers per inflorescence under short days than long days at temperatures of 23 to 29°C. Under long days, flower number per inflorescence for 'Tribute' was relatively constant across the entire temperature range (Fig. 1.4C). Under short days, 'Tribute' produced fewer flowers per inflorescence at 26 or 29 °C than under cooler temperatures.

Runner production

Temperature, photoperiod and genotype interacted to influence the number of runners produced ($P<0.001$). 'Honeoye' did not produce runners at 14°C, or 17°C, regardless of photoperiod (Fig. 1.5A). Under short days, 'Honeoye' did not produce runners, regardless of temperature. The number of runners produced increased as temperature increased from 20 to 26 °C, but declined as temperature increased from 26 to 29 °C (Fig. 1.5A). In contrast to 'Honeoye', RH 30 did produce runners under short days, but only at temperatures of 23 to 29 °C (Fig. 1.5B). Runner production for RH 30 increased with temperature from 17°C to 29°C under long days. RH 30 produced far more runners than either cultivar under long days and temperatures ≥ 20 °C. The cultivar 'Tribute' produced very few runners under short days, and only if the temperature was 23 °C or greater (Fig. 1.5C). Runner production for 'Tribute' under long days was lower than either 'Honeoye' or RH 30 at temperatures ≥ 23 °C, with a maximum of seven runners per plant produced at 23 °C.

Discussion

Repeat flowering in strawberry is often referred to as 'day-neutrality' (Hancock, 1999). We propose that the term remontancy more accurately describes the repeat flowering pattern of strawberry, and should be employed instead of day-neutrality. The genetics of remontancy in strawberry have proven difficult to dissect, with contrasting reports of whether this trait is controlled by a single dominant gene (Bringhurst and Voth, 1978; Ahmadi *et al.*, 1990), complimentary dominant genes (Ourecky and Slate, 1967) or quantitative inheritance (Powers, 1954; Hancock *et al.*, 2002; Serçe and Hancock, 2005a;

Shaw, 2003; Weebadde *et al.*, 2008). To identify the genetic basis of remontancy, understanding the influence of environmental variables on this trait is critical to identify the appropriate screening environment. Utilizing genotypes previously defined as short day ('Honeoye') and day-neutral ('Tribute' and RH 30) (Serçe and Hancock, 2005a) , we have shown that temperature is a primary factor determining whether these genotypes exhibit remontancy, with each genotype possessing an unique threshold temperature above which photoperiod becomes regulating. We have determined permissive and inhibitive temperatures for remontancy in these genotypes under both long and short day conditions.

Growing plants under short days compared to long days improved 'Honeoye' heat tolerance by ca. 3 °C. That is, plants grown under long days at 20 °C produced similar numbers of flowers and inflorescences as plants grown under short days at 23 °C (Figs. 1.1A and 1.2). Plants produced few or no flowers and inflorescences at temperatures of 26 and 29 °C, regardless of photoperiod. Defining 'Honeoye' as a short-day plant is inconsistent with the flowering pattern observed in this study. RH 30 was previously defined as 'day-neutral' (Serçe and Hancock, 2005a). However, in our study the flowering pattern in response to temperature and photoperiod was very similar to 'Honeoye', previously defined as a short-day cultivar, but shifted up by 3 °C. 'Honeoye' flower production under long days decreased as temperature increased above 17 °C, while RH 30 flower production under long days continued to increase up to 20 °C before declining with a further temperature increase (Fig. 1.1A and B). Similarly, under short days, 'Honeoye' flower production increased up to 20 °C, then declined, while RH 30

flower production increased up to 23 °C before declining with further temperature increase (Fig. 1.1A and B). Durner *et al.* (1984) cautioned that the flowering classification of strawberry genotypes must be regional due to inconsistent performance across locations.

Classifying strawberry genotypes in photoperiodic categories appears inadequate for predicting reblooming behavior across a range of geographic regions. We were able to accurately determine the threshold temperature for remontancy of 'Honeoye' and RH 30. Flower production in 'Tribute', however, followed a different trend. 'Tribute', classified as a day-neutral plant, preferentially produced flowers under long days regardless of temperature, and flower production under short days declined as temperature increased. Based on the same trends, Sonsteby and Heide (2007b) used the term quantitative long-day plant to describe European everbearing cultivars which produced a higher number of flowers under long photoperiods than under short photoperiods at high temperatures. Other authors have concluded that traditional Junebearing varieties should be classified as facultative short-day plants (Darrow, 1966), or single cropping (Durner *et al.*, 1984; Nicoll and Galletta, 1987). Day-neutral plants (or everbearers) have been more problematic to classify as they tend to differ in strength of rebloom and fruit quality. Several attempts have been made to categorize cultivars based on different fruiting, and flowering trends (Darrow, 1966; Nicoll and Galletta, 1987). After evaluating remontancy of eleven strawberry genotypes in a controlled environment, Nicoll and Galletta (1987) proposed classifying genotypes as Junebearing, weak day-neutral, intermediate day-neutral, and strong day-neutral. The temperature environment chosen for their study was

22 °C day/18 °C night (under a 9-hr photoperiod plus night interruption lighting), for a 24-hr average temperature of 19.5 °C. Employing this classification system to the current study, 'Honeoye' would be classified as Junebearing, while RH 30 would be classified as a strong day-neutral. If, however, 23 °C were used as the screening environment, RH 30 would be classified as a Junebearer, highlighting the critical influence of temperature on remontancy. Utilizing genotypes previously defined as short day ('Honeoye') and day-neutral ('Tribute' and RH 30) (Serçe and Hancock, 2005a), we have shown that temperature is a primary factor determining whether these genotypes exhibit remontancy. According to our results, all genotypes are photoperiod insensitive at permissive temperatures, however, we propose that each genotype possesses an unique temperature threshold above which flowering become daylength dependent.

Therefore, we suggest that multiple cropping of strawberry is primarily a function of temperature, with each genotype possessing a unique temperature threshold above which photoperiod becomes regulating, and genotypes should be classified based on relative heat-tolerance for remontancy. A multiple cropping genotype in one region may act as a single cropping genotype in a warmer region, as alluded to by Durner *et al.* (1984). Genotypes should be screened for remontancy in several regions, including warm regions, to ensure consistent multiple cropping across locations and years.

'Tribute' was the most heat-tolerant genotype under long days, producing similar numbers of flowers across the entire temperature range. All genotypes reached a temperature where flowering was inhibited except 'Tribute' grown under long days.

'Tribute' produced more flowers under long days than short days, regardless of temperature. RH 30 exhibited intermediate heat-tolerance between 'Honeoye' and 'Tribute', with threshold temperatures of 20 °C under long days and 23 °C under short days. This may explain the inconsistent field performance in successive years of progeny utilizing RH 30 as a genetic source of remontancy, performing as a strong remontant one year, and more as a single cropper the next (J.F.H. unpublished data).

Newly produced lateral meristems can form either a lateral crown, from which an inflorescence develops, or a runner. Our results suggest that once flowering is initiated, as long as the temperature is permissive, development of inflorescences remains the default pathway. If, however, temperature is too high, flowering is inhibited in subsequent meristems and runners are produced. No genotype produced runners at 14 °C (Fig. 5), and generally few or no runners were produced when temperature was 20 °C or less, regardless of genotype or photoperiod, similar to the results of Hartmann (1947) and Smeets (1980). This is in contrast to the results of Durner *et al.* (1984) who, using different genotypes, observed runner production in everbearing and day-neutral varieties across a range of temperatures, from 18/14 °C to 30/26 °C day/night under both short days and night-interruption (NI) lighting treatments, and in Junebearing varieties at all temperatures under NI and warm temperatures under short days.

It is not known whether the reduction in flowering at high temperatures is due to a lack of floral initiation, or failed development of an initiated inflorescence prior to macroscopic visibility. Taylor (2002) suggested that flowering inhibition of mature strawberry plants

may be due to early developmental arrest of initiated flowers rather than failed initiation, and that microscopic dissection should be conducted in addition to counting inflorescences to describe meristem fate. In support of this are the results of Downs and Piringer (1955) who, in a summer experiment in Beltsville, MD using a greenhouse lacking temperature control, reported the presence of flower primordia following dissection but no macroscopic flower buds on two Junebearing genotypes, Howard 17 and Klondike, under an 11-hr photoperiod. These results suggest that high temperatures prevented floral development even under short day conditions.

Early research on flowering control in strawberry defined the interaction of photoperiod and temperature, as Darrow and Waldo (1934) reported that at temperatures above 15 °C, a photoperiod of 10 h or less is required for flower initiation, while photoperiod did not influence flower initiation at temperatures below 15 °C, results that were confirmed by numerous other groups (Darrow, 1936; Ito and Saito, 1962; Darrow, 1966; Durner *et al.*, 1984; Nicoll and Galletta, 1987). Our results show that further increases in temperature inhibit flowering under short day conditions as well. Breeding efforts over the past few decades have aimed to incorporate novel germplasm into commercial strawberry cultivars to improve 'day-neutrality'. Several genetic sources of remontancy have been described and reviewed by Ahmadi *et al.* (1990). The most recent genetic source of remontancy to be introduced into commercial strawberry cultivars is a native genotype of *Fragaria virginiana* (Mill) ssp. *glauca* (S. Watson) from the Wasatch mountains of Utah (Bringhurst and Voth, 1984), and 'Tribute' is thought to have received its genes for remontancy from a breeding parent derived from this genotype (Draper *et al.*, 1981).

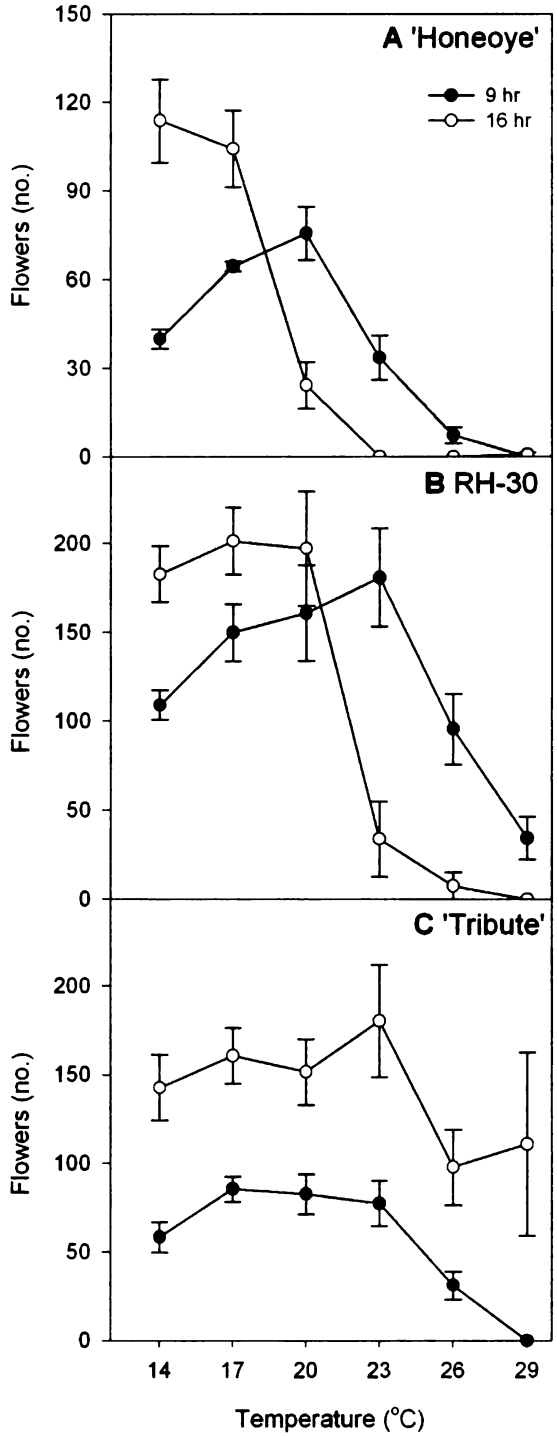
Performance of modern remontant varieties has been inconsistent across regions. Controlled environment studies on additional remontant cultivars and the wild sources of remontancy will aid in dissecting the relative contributions of temperature and photoperiod on flowering control.

Further support for the importance of temperature on remontancy in strawberry comes from a quantitative trait locus analysis (QTL) analysis for repeat blooming utilizing phenotypic data for a 'Honeoye' × 'Tribute' mapping population grown at five different locations throughout the United States (Weebadde *et al.*, 2008). Runner plants of the same genotypes were grown in CA (Watsonville), MD (Beltsville), MI (Benton Harbor), MN (Victoria), and OR (Corvallis) for phenotypic analysis. The percentage of remontant individuals varied by location, with 48-50% of plants repeat flowering in the MD, MI, and MN locations, 80% in OR, and 87% in CA. The latitudinal range covered by the three eastern U.S. locations is similar to that of the CA and OR sites, indicating that differences in photoperiod alone cannot explain the observed differences in flowering. However, weather station data from each location indicated that the CA and OR sites were considerably cooler (both day and night temperatures) than any of the eastern sites. A QTL explaining 36% of the phenotypic variation for remontancy identified in the MD, MI and MN populations, but not in CA or OR, was suggested as a potential locus for heat tolerance. The identification of permissive and inhibitive temperatures for repeat flowering of 'Honeoye' and 'Tribute' will allow us to test this hypothesis utilizing the same 'Tribute' × 'Honeoye' population in controlled environments.

Runner formation was photoperiod and temperature sensitive, consistent with previous studies indicating that runner formation is stimulated by high temperatures and long days (Darrow, 1936; Durner *et al.*, 1984; Heide, 1977). Runners were only formed under long days in 'Honeoye' and 'Tribute' (Fig. 1.4). Similarly, Serçe and Hancock (2005b) did not observe runner development under 12 hr days, regardless of temperature. RH 30 did produce runners under short days at 23 and 26 °C, however runner production was greatly reduced compared to long days at similar temperatures. The inhibition of runner formation under short photoperiods appears to be related to gibberellin metabolism. Hytönen *et al.* (2009) determined that strawberry 'Korona' formed branch crowns but not runners under a 10 or 14 hr photoperiod (18/15 °C day/night in all photoperiods), and formed runners under an 18 hr photoperiod. This corresponded to reduced concentration of the active gibberellin GA_1 in axillary buds of plants exposed to short photoperiods. Branch crown formation was promoted under an 18 hr photoperiod following application of the gibberellin synthesis inhibitor prohexadione-calcium. Subsequent GA_3 application restored the development of runners and inhibition of branch crown formation. Application of GA_3 marginally promoted runner formation under short days, though to a lesser extent than long day exposure, indicating an additional role for photoperiod beyond GA metabolism in vegetative meristem differentiation. Our results suggest that flowering inhibits formation of runners, and that flowering is primarily controlled by temperature. If temperature is inhibitive for flowering, runner formation is then promoted in a photoperiod-dependent manner.

In conclusion, we propose that the term remontant replace 'day-neutral' to describe repeat flowering of strawberry within a growing season. Our results indicate that temperature plays a primary role in determining remontancy in strawberry, and that each genotype possesses a unique temperature threshold above which photoperiod becomes a regulating factor. Evaluating strawberry responses to temperature and identifying the threshold temperature at which photoperiod affects remontancy will likely be a better predictor of repeat flowering performance in the field across locations.

Figure 1.1 The effect of temperature on the number of flowers produced for strawberry genotypes (A) 'Honeoye', (B) RH 30 and (C) 'Tribute' under a 9-hr (filled circles) or 16-hr (empty circles) photoperiod during a 16 week period. Error bars represent standard error of the mean (n=6).



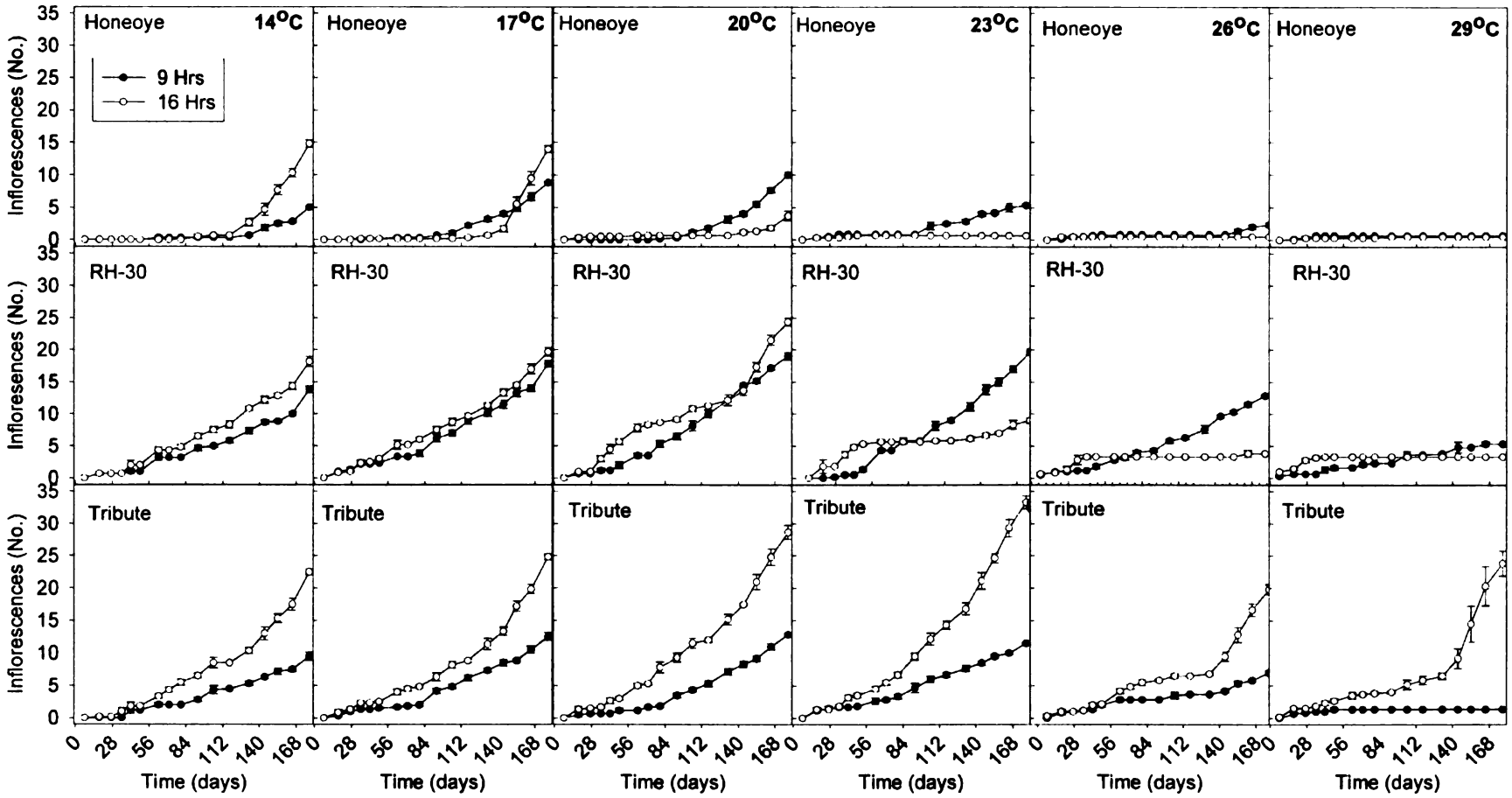


Fig. 1.2 Influence of temperature and photoperiod on cumulative mean inflorescence production on short-day 'Honeoye', remontant 'Tribute', and wild clone of *Fragaria virginiana* ssp.*virginiana* RH 30.

Figure 1.3 The effect of temperature on the number of inflorescences produced for strawberry genotypes (A) 'Honeoye', (B) RH 30 and (C) 'Tribute' under a 9-hr (filled circles) or 16-hr (empty circles) photoperiod during a 16 week period. Error bars represent standard error of the mean (n=6).

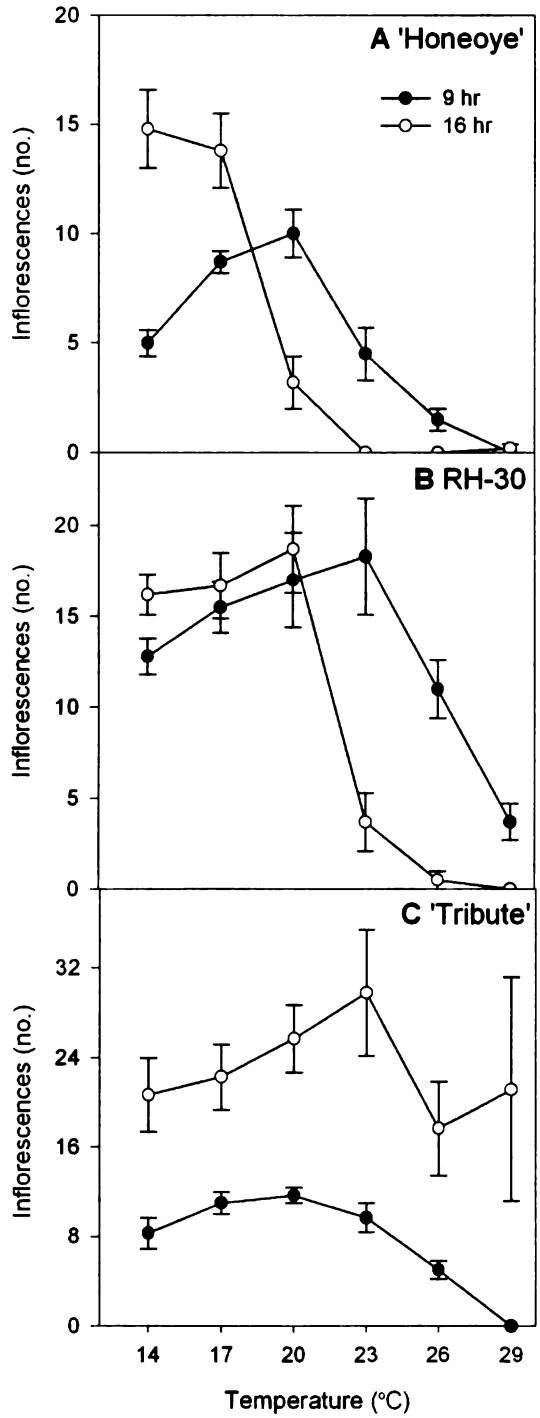


Figure 1.4 The effect of temperature on the number of flowers per inflorescence for strawberry genotypes (A) 'Honeoye', (B) RH 30 and (C) 'Tribute' under a 9-hr (filled circles) or 16-hr (empty circles) photoperiod during a 16 week period. Error bars represent standard error of the mean (n=6).

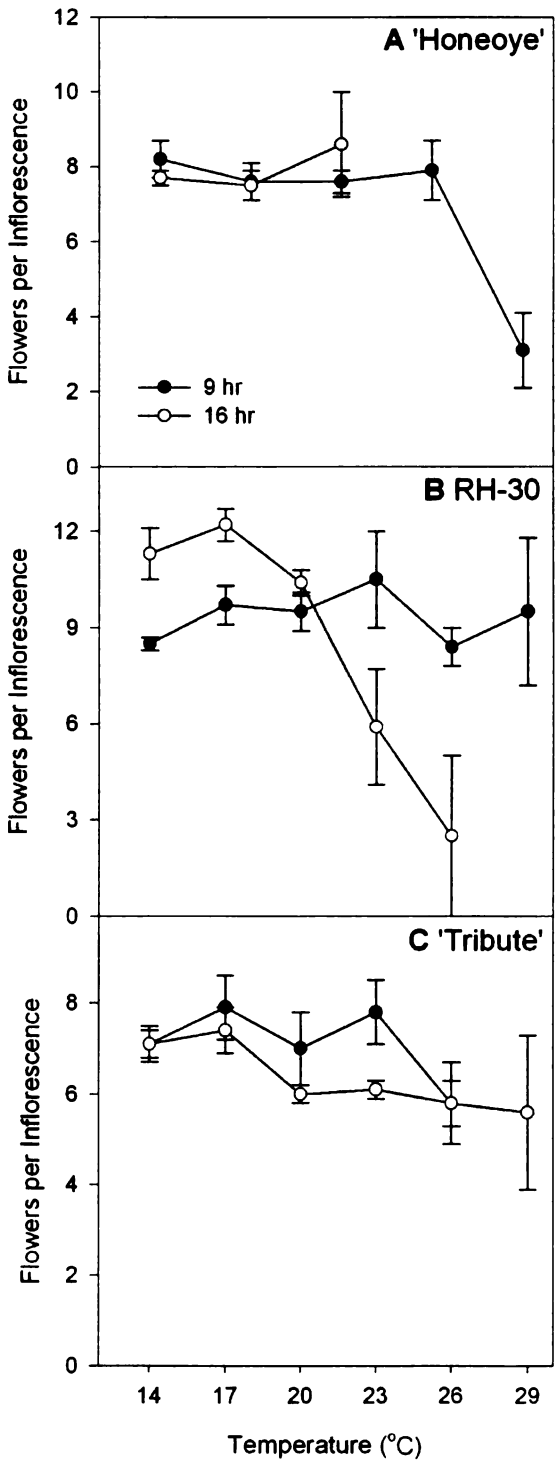
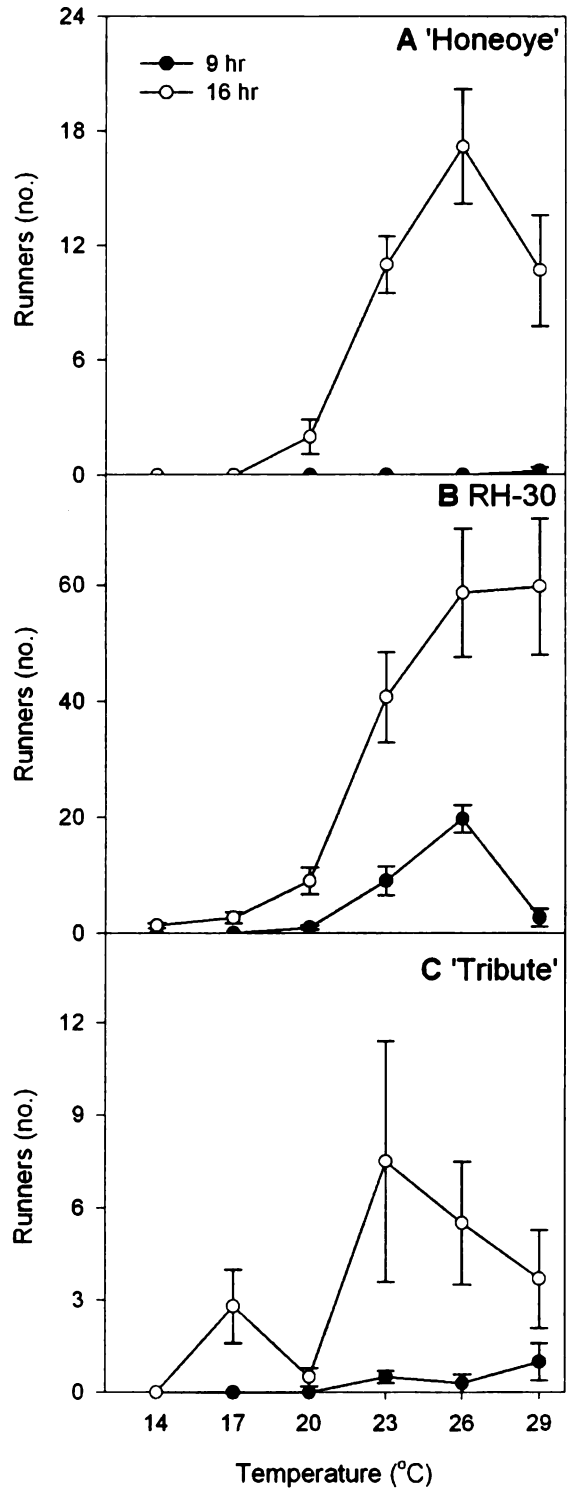


Fig. 1.5 The effect of temperature on the number of runners per plant for strawberry genotypes (A) 'Honeoye', (B) RH 30 and (C) 'Tribute' under a 9-hr (filled circles) or 16-hr (empty circles) photoperiod during a 16 week period. Error bars represent standard error of the mean (n=6).



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CHAPTER TWO

INFLUENCE OF TEMPERATURE ON REMONTANCY AND RUNNERING IN THE STRAWBERRY F_1 POPULATION 'HONEOYE' × 'TRIBUTE'

ABSTRACT

Previously, we identified the threshold temperatures for repeat flowering (remontancy) of 'Honeoye' and 'Tribute' under long photoperiods. To further explore the role of temperature in controlling flowering, individuals from the F_1 population 'Honeoye' × 'Tribute' were replicated through either crown division or runner propagation, and grown at 17, and 23°C under a 16 h photoperiod. Remontancy class for each individual genotype was determined using flowering data obtained from five different field trial locations MD, MI, MN, OR, and CA. Results indicate that remontant types (RM) produced more total inflorescences than non-remontant (NRM) types regardless of temperature or propagule type, and NRM types produced the most runners. In addition, how an experimental unit is derived will have an effect on the number of runners and inflorescences produced. Runner derived plants have an affinity to produce more runners, and plants obtained through crown division produce more inflorescences.

INTRODUCTION

The cultivated strawberry, *Fragaria ×ananassa* Duch., arose from the accidental hybridization of two American species *Fragaria virginiana* Duch. and *Fragaria chiloensis* (L.) Duch.. It was discovered in 1766 by French botanist Antoine Nicholas Duchesne, possibly in the royal garden at Versailles where Duchesne studied, but systematic efforts to improve *Fragaria ×ananassa* through plant breeding did not begin until the early 1800's (Hancock 1999).

Fragaria ×ananassa cultivars are classified by when and how often they flower during a growing season. Historically, cultivars have been divided into two main flowering types, 'Junebearers'(JB; or short-day (SD)) which produce one flush of flowers per season during the spring, and 'Everbearers' (EB; or long-day (LD)) which, in addition to a spring crop, produce another crop of fruit during the long days of summer (Darrow 1934). Because floral induction is regulated by both genetic and environmental factors, more recent classification systems have been proposed. Bringhurst and Voth (1978) described everbearing cultivars derived from a cross using a multiple cropping clone of *F. virginiana* ssp. *glauca* as 'day-neutral' (DN). Others have described flowering as a quantitative rather than a qualitative trait with plants displaying a continuum of flowering responses ranging from strictly SD types to strongly DN (Nicoll 1987).

Early investigations reported the influence of temperature on flower initiation in strawberry, indicating the potential difficulty in photoperiodic classification of cultivars (Darrow 1936). Guttridge (1985) found that SD types can be induced to flower under any photoperiod given that temperatures are 15 °C or less. At temperatures higher than

this, flowering in SD types is inhibited even under short photoperiods (Ito 1962), and flower numbers decrease for DN and LD types (Durner et al., 1984; Heide, 1977; Serçe and Hancock, 2005a). As photoperiod appears not to be the only factor controlling repeat flowering, we propose that the term 'remontancy' be used to describe cultivars classified as DN. This terminology describes the flowering behaviour only and not the putative underlying mechanism responsible for repeat flowering. Results from Weebadde et al. (2008) further support a role for temperature in controlling repeat flowering in strawberry. In this study, an F_1 population was produced by crossing the SD 'Honeoye' by the DN 'Tribute'. The population was grown in five different locations: MD, MI, MN, CA, and OR and evaluated weekly for flowering. Genotypes were considered to be DN if they produced flowers after June 15th. A higher percentage of DN progeny were recorded in CA and OR compared to MD, MN, and MI. Field-collected weather data indicated that the CA and OR sites were considerably cooler than the eastern locations, while covering a similar latitudinal (and thus, photoperiodic) range. Therefore, the observed differences in flowering patterns of the population across location suggest that high temperatures, rather than long photoperiods, may be the factor inhibiting flowering in SD types.

To test this hypothesis, the SD parent 'Honeoye', the DN parent 'Tribute', and a putative DN clone of *Fragaria virginiana* ssp.*virginiana,* RH 30, were grown in six different temperatures, 14, 17, 20, 23, 26, and 29°C, under a 9 or 16 h photoperiod (Chapter 1). Results from this study indicate that flowering in 'Honeoye' is inhibited at temperatures of 20°C or more under long days. At temperatures of 17°C or less, 'Honeoye' produced flowers regardless of daylength, whereas 'Tribute' produced flowers in temperatures up

to 29°C under long days. RH 30 behaved much as 'Honeoye', but its flowering was inhibited at the higher temperature of 23°C.

The previous study indicated that both 'Honeoye' and 'Tribute' were remontant at 17 °C under long photoperiod, while only 'Tribute' was remontant under long days at 23 °C. The objective of the current study is to determine if the flowering patterns observed across locations for 'Honeoye' × 'Tribute' population individuals by Weebadde et al. (2008) resulted from variation in heat-tolerance among population individuals. That is, do individuals classified as DN exhibit greater heat-tolerance than individuals classified as SD?

Materials and Methods

During the summer of 2007, plants of the segregating population 'Honeoye' × 'Tribute' (Weebadde et al., 2008) were dug and transferred from the Southwest Research and Extension Centre in Benton Harbor, MI, to the Horticulture Teaching and Research Centre in Holt, MI. Plants were potted in one gallon round pots using soilless media containing (v/v) 70% peat moss, 21% perlite and 9% vermiculite (Sure-Mix, Michigan Grower Products, Galesburg, MI) and maintained in an unheated greenhouse. In October 2008, these plants were moved to a 26°C heated greenhouse and given supplemental light to induce runner production (Chapter 1). On 27 January 2009, individuals which had not yet produced runners were replicated through crown division to produce four replicates of each genotype, and potted as above. For individuals that did produce runners, the runners were removed and potted as above to produce four replicates of each genotype. Sixty-

five genotypes were replicated through crown divisions. Of these, twenty-three were classified as non-remontant and forty-two were classified as remontant. Ninety-three genotypes were replicated through runner plants: sixty-nine classified as non-remontant, and twenty-four classified as remontant. Both types of propagule were placed in a misted propagation house to root.

On 23 February 2009, two plants of each genotype were placed in one of two glass glazed greenhouses set to a constant temperature of 17 and 23°C and a 16 h photoperiod. Air temperature in each treatment was measured by a Type E thermocouple (TT-E-40; Omega Engineering, Stamford, CT.) placed in an aspirated tube. Thermocouples were connected to a data logger (CR10; Campbell Scientific, Logan, UT) and data were recorded every 10 s. Weekly temperature averages for each temperature were within ± 1.0 °C of the setpoint each week during the experimental period. Vapor pressure deficit was maintained between 0.7 and 1.0 kPa at each temperature by steam injection. To maintain a 16 h daylength, ambient daylight was supplemented with 50 μmol m^{-2} s^{-1} photosynthetically-active radiation supplied by high-pressure sodium lamps from 0600 to 2200 HR daily; lamps were programmed to turn off when ambient irradiance outside the greenhouse exceeded 400 μmol m^{-2} s^{-1}.

Two representatives of each genotype were arranged in a randomized complete block design within each temperature. Plants were overhead irrigated with reverse osmosis water supplemented with a water-soluble fertilizer to provide the following (mg L-1): 125 N, 13 P, 125 K, 15 Ca, 1 Fe, 0.1 B, 0.1 Mo, 0.5 Mn, 0.5 Zn and 0.5 Cu (MSU Special; Greencare Fertilizers, Chicago, IL).

Data collection and analysis

Every 7 d during the experiment, the number of inflorescences and runners per plant were determined. Inflorescences were counted once all flower buds within the inflorescence were clearly distinguishable. After each data collection, inflorescences, runners and any dead leaves were removed. Data collected during the first 49 days of the experiment was assumed to be the result of conditions prior to initiation of the experiment and therefore was analyzed seperately (Chapter 1, (Serçe 2005).

Analyses of variance were performed on the total number of inflorescences and runners produced between days 56 and 77 by each genotype. Fixed factors used in the analysis were temperature (17°C, 23°C), remontancy class (remontant, non-remontant), and propagule (crown divisions, runner plants). The dependent variables were total inflorescences, and total runner production between days 56 and 77. Remontancy class was determined using flowering data obtained from five different growing regions MD, MI, MN, OR, and CA (Weebadde, 2008). As growing conditions in OR and CA were considered to be permissive, a genotype was determined to be remontant (RM) if it flowered in at least two of the eastern regions MN, MD, and MI, and non-remontant (NRM) if flowering only occurred in CA and/or OR.

Results

Flowering

Remontancy class and propagule type (Crown division (CR) or runner plants (RU)) interacted to influence inflorescence production both during the early (days 1-49) and late

(days 50-77) periods of the experiment (Table 1). RM types produced more total inflorescences than NRM types in both temperature treatments, regardless of propagule type, from day 50-77 (Table 1). Among the RM genotypes, CR plants produced more total inflorescences than RU plants, during both the early and late periods of the experiment.

There was considerable variation in the percentage of individuals producing inflorescences, both across remontancy class, and across propagule type within a remontancy class (Table 2, Figs. 2.1, 2.2). At 17 °C, 79% of RM CR plants, and 36% of RM RU plants flowered as opposed to 18% of NRM CR plants, and 16% of NRM RU plants (Table 2, Figs. 2.1, 2.2). At 23°C, 58% of RM CR plants while only 22% of RM RU plants flowered. Very few NRM plants flowered at 23 °C, with only 11% of NRM CR plants and no NRM RU plants producing flowers. RM types derived from crown divisions produced the most inflorescences, and had the highest flowering percentages in both temperatures.

Runnering

Temperature interacted with remontancy class (type), and propagule interacted with remontancy class to influence runner production (Table 1). More runners were produced at 23°C than at 17°C regardless of remontancy class or propagule (Table 1). A higher percentage of NRM types produced runners than RM types (Table 2, Figs.2.1, 2.2), and runner derived plants produced more runners than plants derived from crown divisions

(Table 1). At 23°C NRM types produced more runners then RM types, and runner derived plants at 23°C produced more runners overall.

Discussion

The objective of this experiment was to test whether observed differences in flowering behaviour of individuals across different field trialling sites may be related to differences in heat-tolerance. Based on previous results (Chapter 1) 17°C was chosen as a permissive temperature at which both RM and NRM types would repeat flower, while at 23°C NRM plants would be inhibited from flowering.

NRM types grown at 23°C produced the most runners regardless of propagule type. As lateral buds can either develop into an inflorescence (short shoot) or into a runner (long shoot) (Hytönen 2009) the more runners a plant produced, the fewer lateral buds could potentially develop into inflorescences. Furthermore, all plants grown at 23°C, regardless of remontancy class or propagule type, produced more runners than those grown at 17°C. This is in agreement with the previous study (Chapter 1) which showed an increase in runner production in all three varieties as temperature and daylength increased.

RM types generally produced more inflorescences than NRM types, and NRM types produced more runners than RM types, regardless of temperature. These findings, however, may have been confounded by the different ratios of propagule type for each remontancy class. Because NRM plants runner more easily than RM plants, 78% of the NRM plants were derived from runners as opposed to 46% runner derived RM plants. The most inflorescences were produced by crown derived RM types at 23°C.

Although the results do show NRM types being inhibited at 23°C, with only 11% of NRM CR and no NRM RU plants flowering, these percentages were not significantly different from those found at 17°C, where only 18% of NRM CR and 11% of NRM RU plants flowered. This lack of significance may due to the fact that the plants grown at 17°C developed at a slower rate than those grown at 23°C. In the previous study (Chapter 1), 'Honeoye' took 112 days to repeat flower. The current study had to be terminated after only 77 days due to loss of temperature control in the greenhouses because of rising outside temperatures. Had the experiment continued, it is possible that a higher percentage of NRM types would have flowered. Alternately, this discrepancy may be because the NRM types in the population have a higher temperature threshold than that of its NRM parent 'Honeoye'. The progeny may have inherited some heat tolerance from the RM parent 'Tribute'. It is also possible that the results were confounded by the disparaging ratios of propagule represented in each flowering type.

The results show that the way an experimental unit is produced, whether by runners or crown division, influences the number of inflorescences and runners produced. Because plants derived from crown divisions had a greater affinity for inflorescence production than those obtained from runners, and runner derived plants preferentially produced runners, the prior life history of a fully grown strawberry plant impacts how it performs under experimental conditions. Another problem that strawberry researchers encounter in trying to obtain replicates is the fact that RM types produce few to no runners (Dale 2002). This results in a discrepancy in the number of RM and NRM types represented in experiments using runner derived plants.

Sonsteby and Heide (2007a) chose to use seedlings in an attempt to avoid these complications, but as strawberries are octoploid heterozygotes, it is impossible to recover the exact genetic profile of the parent in the progeny, as each round of self-pollination decreases heterozygosity by 50% (Fehr 1987). Thus, the alleles of interest may be lost when selfing heterozygous octoploids.

To lessen the impact of genetic variation between sibs, it may be possible to use immature runner plants obtained from one seedling plant so that all replicates are identical clones. Also, because strawberry seedlings have the ability to runner prior to flowering (Lacey, 1973), it is possible that this phenomenon occurs regardless of seedling remontancy class; therefore plants may be obtained without any one remontancy class being preferentially represented. Future studies in this area would be helpful in answering this question, and determining whether replicates obtained in this way are immature enough to be placed in experimental conditions without their previous life history confounding the data obtained.

Table 1. Effect of temperature, remontancy class, and propagule type on inflorescence and runner production of F_1 strawberry 'Honeoye' × 'Tribute' individuals.

Temp	Remontancy Class	Propagule Type	N	Experimental Period (days) 1-49 Inflorescences Mean	std.err	50-77 Inflorescences Mean	std.err	1-49 Runners Mean	std.err	50-77 Runners Mean	std.err
17°C	Non-Remontant	Crown	22	0.27	0.10	0.23	0.11	0.86	0.42	0.05	0.05
		Runner	87	0.52	0.06	0.22	0.06	3.93	0.40	1.32	0.20
	Remontant	Crown	48	1.88	0.23	1.96	0.23	0.35	0.13	0.10	0.05
		Runner	39	0.67	0.10	0.74	0.24	3.36	0.43	1.15	0.39
23°C	Non-Remontant	Crown	18	0.50	0.17	0.17	0.12	1.17	0.34	1.50	0.68
		Runner	59	0.53	0.08	0.00	0.00	6.39	0.58	4.31	0.50
	Remontant	Crown	24	1.46	0.30	2.04	0.50	0.08	0.06	0.17	0.13
		Runner	23	0.57	0.19	0.96	0.62	6.09	0.69	3.00	0.69
Source						*P*-value					
Temperature (T)				0.55		0.98		0.00		0.00	
Remontancy Class (RC)				0.00		0.00		0.12		0.03	
Propagule Type (PT)				0.00		0.00		0.00		0.00	
T × RC				0.11		0.41		0.85		0.04	
T × PT				0.84		0.97		0.00		0.01	
RC × PT				0.00		0.00		0.65		0.87	
T × RC × PT				0.26		0.68		0.56		0.83	

Table 2. Effect of temperature, remontancy class, and propagule type on the percentage of F_1 strawberry 'Honeoye' × 'Tribute' individuals producing inflorescences or runners.

Temp	Remontancy Class	Propagule Type	N	Experimental Period (days) 1-49 Flowering (%)	Experimental Period (days) 50-77 Flowering (%)	Experimental Period (days) 1-49 Runnering (%)	Experimental Period (days) 50-77 Runnering (%)
17°C	Non-Remontant	Crown	22	27	18	27	5
		Runner	87	47	16	71	49
	Remontant	Crown	48	81	79	19	8
		Runner	39	59	36	82	33
23°C	Non-Remontant	Crown	18	39	11	50	39
		Runner	59	46	0	86	80
	Remontant	Crown	24	71	58	8	8
		Runner	23	43	22	96	61

Figure 2.1: The effect of temperature, remontancy class, and propagule type on cumulative percent of replicates flowering in the segregating population 'Honeoye' × 'Tribute' under a 16 h photoperiod.

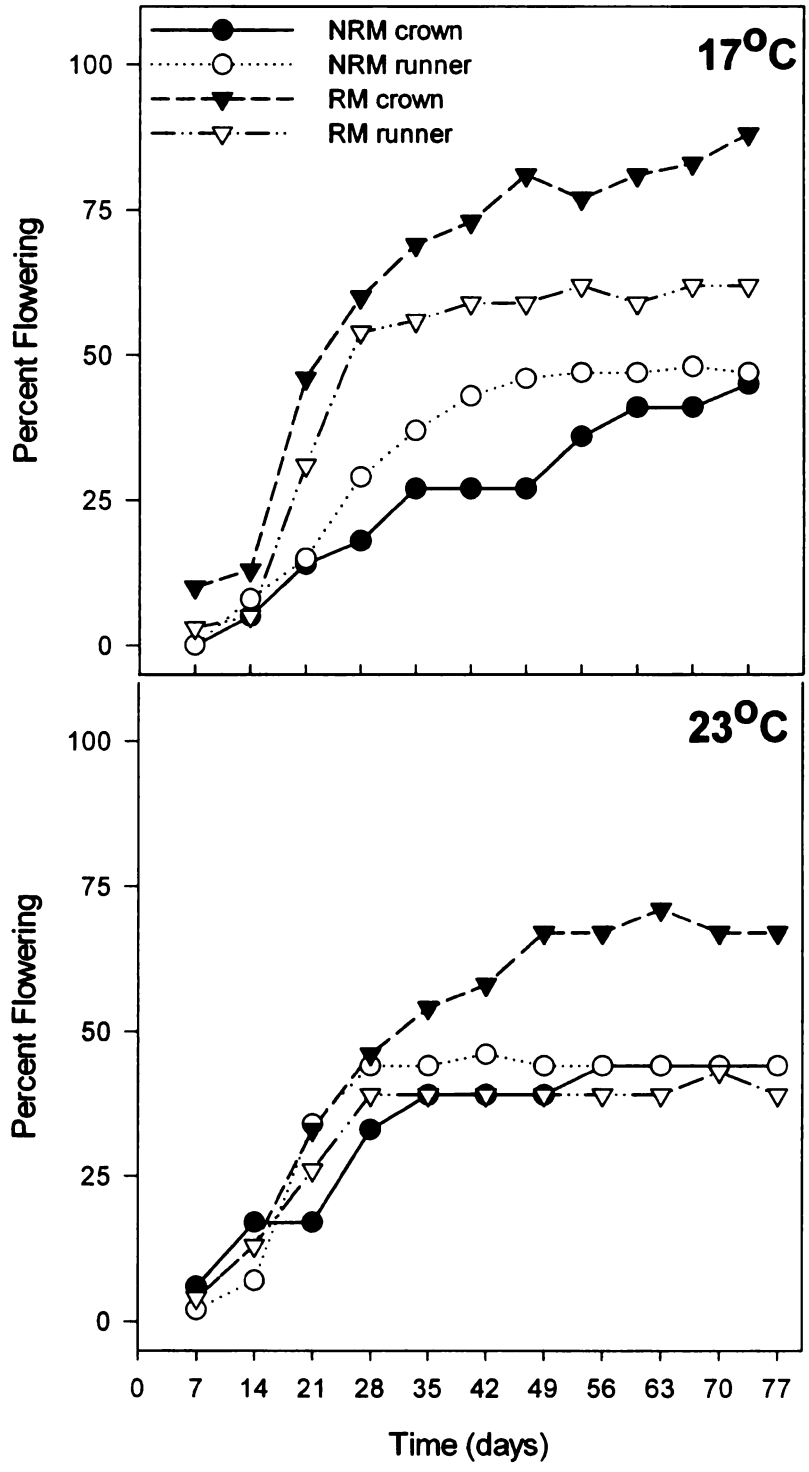
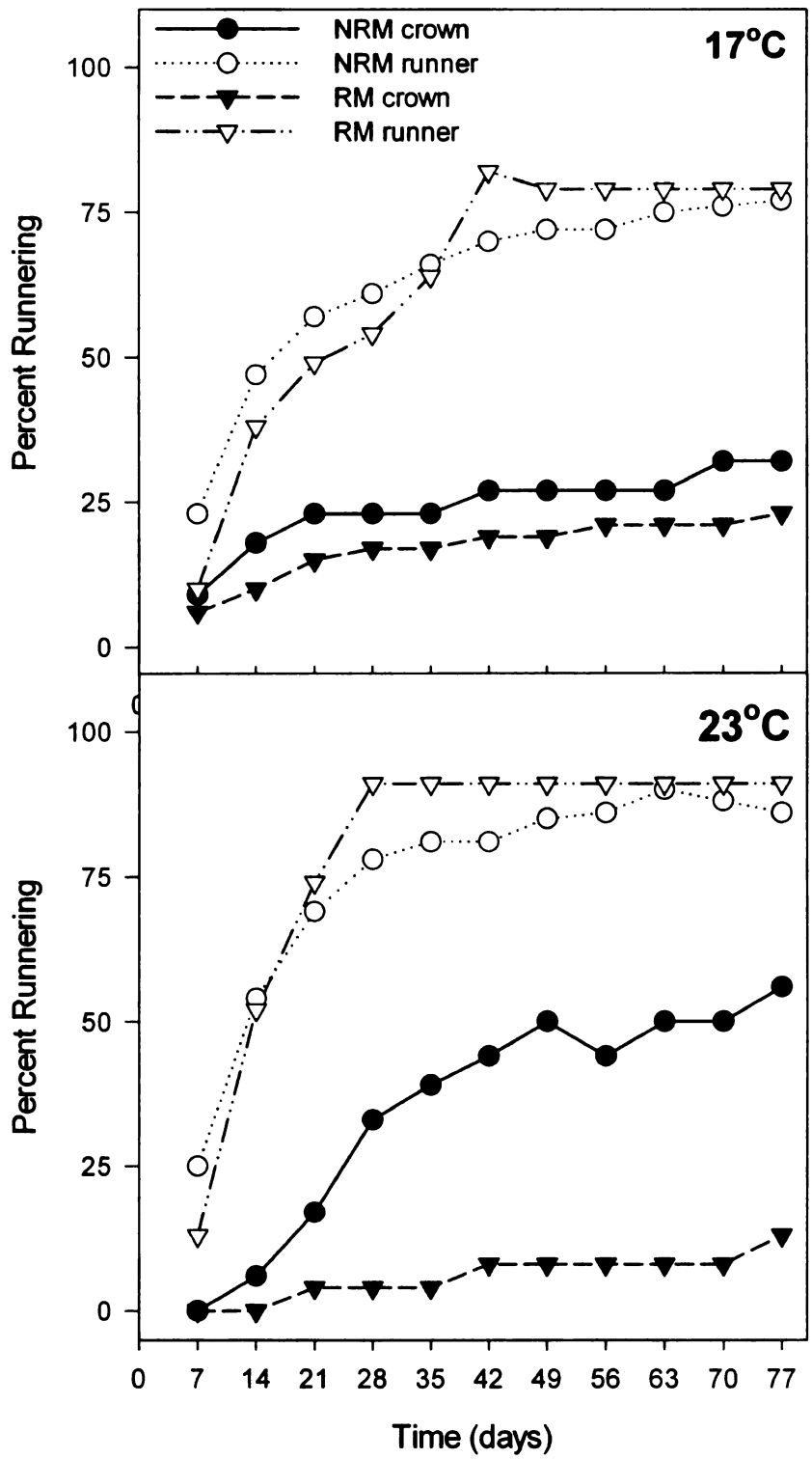


Figure 2.2: The effect of temperature, remontancy class, and propagule type on cumulative percent of replicates runnering in the segregating population 'Honeoye' × 'Tribute' under a 16 h photoperiod.



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APPENDIX

Weebadde *et al.* (2008) successfully identified a major QTL for remontancy in the segregating population 'Honeoye' × 'Tribute'. The marker closest to this QTL is AFLP band aggcat187T. As this marker was found to be present in the remontant parent, 'Tribute', but was absent in the non-remontant parent, 'Honeoye', it could provide a useful marker to genetically screen for remontantcy. A re-investigation of the segregation ratios of the marker in 65 individuals of the mapping population (29 RM, 36 NRM) revealed that of the 29 individuals classified as RM the marker was present in 9, and of the 36 that were classified as NRM, the marker was absent in 20 individuals. Therefore, it was concluded that the AFLP marker (aggcat187T) was not closely linked to the major QTL for remontancy in this population.

Table A. 1. Segregation of the AFLP marker, aggcat187T, in sixty-five individuals of the mapping population 'Honeoye' × 'Tribute'.

Genotype	Phenotype	Marker
Honeoye	NRM	Absent
Tribute	RM	Present
1	RM	Present
2	RM	Absent
3	NRM	Present
4	RM	Absent
5	RM	Present
6	NRM	Present
7	NRM	Present
8	RM	Absent
9	NRM	Absent
10	NRM	Absent
11	NRM	Absent
12	NRM	Absent
13	RM	Absent
14	RM	Present
15	RM	Present
16	NRM	Absent
17	NRM	Absent
18	RM	Present
19	NRM	Present
20	RM	Absent
21	NRM	Present
22	NRM	Present
23	NRM	Absent
24	NRM	Present
25	NRM	Present
26	RM	Absent
27	RM	Absent
28	RM	Present
29	RM	Absent
30	NRM	Absent
31	NRM	Absent
32	RM	Absent

Genotype	Phenotype	Marker
39	NRM	Present
40	NRM	Present
41	RM	-
42	NRM	Absent
43	RM	Present
44	NRM	Present
45	RM	Absent
46	RM	Absent
47	RM	Absent
48	NRM	Present
49	NRM	Absent
50	RM	Absent
51	NRM	Present
52	NRM	Present
33	NRM	Absent
34	RM	Absent
35	NRM	Absent
36	RM	Absent
37	NRM	Absent
38	NRM	Absent
53	NRM	Absent
54	RM	Present
55	RM	Present
56	NRM	Absent
57	RM	Present
58	RM	Present
59	NRM	Absent
60	NRM	Absent
61	RM	Present
62	RM	Absent
63	NRM	Present
64	NRM	Absent
65	RM	Absent

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