Photoperiod affects floral ontogeny in strawberry (*Fragaria × ananassa* Duch.) plug plants

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ABSTRACT

Strawberry (*Fragaria × ananassa* Duch.) plug plants of the short day (SD) cultivars 'Earliglow', 'Seneca', 'Jewel', 'Chandler' and 'Cavendish', and the long day (LD) cultivars 'Seascape', 'Fern' and 'Selva' were exposed to 0, 1, 2 or 4 weeks of short-days (8 h) at 15 °C followed by forcing in a long-day (16 h) greenhouse. Leaf, runner and flower growth were monitored weekly. Floral ontogeny and plant phenology of three week old plug plants was sensitive to pre-forcing short-day conditioning and the degree of sensitivity varied with cultivar and parameter examined. In all SD cultivars except 'Chandler' conditioning hastened flowering. The length of conditioning needed to enhance precocity and intensity of enhancement varied with cultivar. Conditioning did not alter the time of flowering for LD cultivars. SD conditioning enhanced leaf production under LD forcing in some cultivars. Each cultivar exhibited its own characteristic response to photoperiod for runner production regardless of the traditional photoperiodic category to which it belonged. The general classification for enhanced runner production of SD cultivars under LD and LD cultivars under SD is questionable since runner production responses of cultivars did not follow this categorization: runner production was enhanced by SD conditioning in the SD cultivar 'Chandler' and inhibited by SD in the LD cultivar 'Fern'. Runner and inflorescence production are not necessarily antagonistic processes in short-day cultivars, as sometimes suggested. Reduced runner formation was observed with a concomitant increase in inflorescence production in some cultivars. The reduction in runner production in other cultivars was a direct inhibitory response to short days rather than an inhibition caused by flowering. Runner production was reduced but flowering was not enhanced with short day conditioning. In addition, SD enhanced flowering in 'Chandler' did not inhibit runner production. Cultivars did not fall into specific photoperiod response categories (SD or LD) with respect to flowering either. All SD and one of three LD cultivars were vegetative at the start of the experiment. Inflorescence production occurred during long-day forcing in non-conditioned controls indicating that floral initiation occurred during the long days in the greenhouse. Nevertheless, altered flowering under LD forcing of SD conditioned plugs compared to controls in several cultivars indicated that floral ontogeny under long days was altered with pre-forcing, short-day conditioning. All cultivars except 'Seascape' and 'Cavendish' exhibited enhanced initiation and differentiation following SD conditioning. Each stage of floral development (induction/initiation, development and differentiation) was differentially affected by photoperiod and as many of these stages as possible should be evaluated to provide a clear description of any response. The only general description of flowering response to photoperiod in strawberry is that SD exposure enhances differentiation in both SD and LD cultivars. General categorizations for initiation and development should not be made as responses to photoperiod for these stages are cultivar specific.

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1. Introduction

Temperature and photoperiod are the two major environmental signals which regulate flower ontogeny in strawberry. Cultivars are often categorized as seasonal flowering (SF) (Junebearing), or recurrent flowering (RF) (everbearing, day-neutral, or perpetual-fruiting (remontant)) based on cropping season and growth responses to specific photoperiod and temperature treatments (Darrow and Waldo, 1934; Durner et al., 1984; Heide et al., 2013). SF cultivars (traditionally called Junebearers) are mono-cropping, producing a single crop in the spring (except in Florida and California, USA). Most cultivars that are SF are considered quantitative short-day

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plants at temperatures <20 °C: floral initiation is intensified by shorter daylengths even though floral initiation may occur under longer daylengths at cooler temperatures (<17 °C) (Darrow and Waldo, 1934; Durner, 1985; Durner and Poling, 1987; Heide et al., 2013). The critical photoperiod for flower formation (Borthwick and Parker, 1952; Jonkers, 1965) and the number of cycles needed (Austin et al., 1961; Greve, 1936; Hartmann, 1947) varies with cultivar and both are modified by temperature (Darrow, 1936; Ito and Saito, 1962; Jonkers, 1965). In general, shorter photoperiods and/or a greater number of short day cycles are needed for floral initiation at higher temperatures (>17 °C). Most SF cultivars are qualitative short day plants at higher temperatures (>20 °C) however, they fail to form flowers under any daylength at temperatures approaching 30 °C (Heide et al., 2013). Though this generalization applies to most SF cultivars, the photoperiod × temperature interaction response curve should be determined for each individual cultivar (Heide et al., 2013).

RF cultivars (traditionally called everbearers, day-neutrals and remontants) are qualitative long-day plants at high temperatures (27 °C), quantitative long-day plants at intermediate temperatures (between 10 and 27 °C) and day-neutral at temperatures below 10 °C (Sonsteby and Heide, 2007b). The major difference among RF cultivars is the temperature at which they become qualitative LD plants and the term 'photoperiod-insensitive permissive temperature range' (PIPR) was coined by Bradford et al. (2010). The original work by Durner et al. (1984) suggested that day-neutral cultivars were not day-neutral at all and determined that the PIPR for 'Tristar' and 'Hecker', two of the original LD (day-neutral) cultivars released in the US, was between 22/18 and 26/22 °C (day/night). At 26/22 plants required LD to flower and at 30/26 only 4 out of 10 plants flowered under LD. Night interruption (NI) at 30/26 did not simulate the critical daylength required for flowering in these 2 cultivars. Bradford et al. (2010) identified the PIPR for 'Tribute' another of the original US LD cultivars as 26 °C. In general, the critical photoperiod in RF cultivars is longer at higher temperatures (Heide et al., 2013).

Strawberry flowering is often divided into stages: induction, initiation, differentiation and development (Durner and Poling, 1985). Floral induction occurs in the leaf upon exposure to a stimulus which ultimately results in the production of a flower bud at a meristem (Durner and Poling, 1985). Initiation includes the physiological and morphological changes occurring in the meristem upon receipt of the stimulus from the leaf. Differentiation is the development of specific floral organs on a single flower or of flowers on a single inflorescence (Durner and Poling, 1985) and development is the macroscopic production of flowers. Induction may be monitored by evaluating leaf production rates during treatment that may or may not alter the flowering process (Durner and Poling, 1985). The evaluation process is time consuming and may not yield adequate data to allow induction estimates with short treatment periods (personal observation), thus this stage of strawberry floral ontogeny is not often studied. Initiation is monitored via meristem dissection or by inflorescence production over time, thus inferences regarding induction are often made using data which evaluates initiation. Differentiation is monitored by evaluating the number of flowers per inflorescence. Development is evaluated by rate of flower production under greenhouse or growth chamber conditions. Many studies of strawberry flowering do not discriminate among the various stages which may lead to generalized or erroneous statements about treatment effects (Durner and Poling, 1985).

Strawberry plugs (Poling and Parker, 1990) are utilized extensively in many commercial production schemes including Florida winter production (Bish et al., 1997, 2002), cold-climate plasticulture (Stevens et al., 2011) as well as most attempts at season extension in the US (Demchak, 2009; Jett, 2014; Kadir et al., 2006; Ballington et al., 2008; Fernandez and Ballington, 2003; Rowley et al., 2011; Poling, 2011; Takeda and Newell, 2006; Durner, 1999; Black et al., 2005; Takeda and Hokanson, 2002). In many cases plugs are manipulated by photoperiod or temperature to enhance fruiting (Black et al., 2005; Durner, 1999; Fernandez and Ballington, 2003; Takeda and Newell, 2006; Takeda and Hokanson, 2002). Conditioning is a time, labor and money intensive process which may (Durner, 1999; Fernandez and Ballington, 2003) or may not (Black et al., 2005; Takeda and Hokanson, 2002) improve fruiting for the desired market window.

Temperature and photoperiod during rooting and subsequent handling of tips or plugs influences flowering and productivity (Bish et al., 2002; Black et al., 2005; Durner, 1999; Durner et al., 2002; Fernandez and Ballington, 2003; Takeda et al., 2008). Jahn and Dana (1970) suggested that strawberry plants must exceed a certain minimum size before floral initiation can take place. Detailed studies of photoperiod or temperature influences on the floral stage of plugged plants is limited to one study (Verheul et al., 2006) utilizing 'Korona', a SF cultivar in which 4 week old plants were shown to be sensitive to photoperiod and temperature with respect to flowering.

This research documents the sensitivity of 3–4 leaf plug plants of five SF and three RF cultivars to photoperiod and evaluates three stages of floral ontogeny after photoperiod conditioning to illustrate (1) the importance of evaluating all floral stages and (2) the importance of careful tip and plug handling prior to planting in the field, high tunnel or greenhouse for fruit production.

2. Materials and methods

Dormant strawberry crowns of 'Chandler', 'Fern', 'Selva', 'Seascape' (Indiana Berry and Plant Company, Huntingburg, Indiana, USA), 'Earliglow', 'Cavendish', 'Seneca' and 'Jewel' (Nourse Farms Inc., Deerfield, Massachusetts, USA) were planted in 16.5 cm plastic pots in Pro-Mix BX (Premier Tech Horticulture, Québec, Canada) in April. Plants were placed in an open ended greenhouse and inflorescences removed as they appeared. Plants were allowed to runner and runner tips were rooted under mist in mid-July (daylength ~15 h) in 5 × 5 cm, 64-plug trays in Pro-Mix BX. Four-week-old plug plants with 3–4 expanded leaves were selected for experimental use. Five plugs per cultivar were dissected under a stereoscope on 8 August and the number of leaves and the number of leaf initials in the terminal bud were determined. The floral or vegetative nature of the terminal meristem was also observed (floral status).

Beginning 8 August plugs of each cultivar were exposed to 0, 1, 2 or 4 weeks of short days (8 h) (SD) at an average daily temperature of 15 °C (maximum 20 °C, minimum 12 °C). All treatments were given in growth chambers (Precision Instruments, Cole-Parmer, Vernon Hills, Illinois, USA) illuminated with cool white fluorescent and incandescent lights approximately 0.5 m above the plant canopy.

Control plugs (0 SD cycles) of all cultivars were maintained in the greenhouse at ambient temperatures (25 °C, average daily temperature) and 16 h long days (natural photoperiod extended to 16 h with 1000 W sodium vapor lamps set 1.5 m above the top of the plants) (LD). After plants received the appropriate photoperiod treatment, 6 single plant replicates for each cultivar/photoperiod combination were potted separately in 16.5 cm plastic pots in Pro-Mix BX and moved to the LD greenhouse for forcing. Plants were irrigated twice daily as needed and fertilized twice a week with Hydrosol (Scotts-Sierra, Marysville, Ohio) supplemented with calcium nitrate and magnesium sulfate providing 100 ppm N.

Observations of plant growth and development in the LD greenhouse were made at weekly intervals for 16 weeks following conditioning. The following data were collected: the number of

fully expanded leaves, the number of runners, the number of inflorescences and the total number of fully open flowers produced per plant. The number of flowers per inflorescence was calculated as the total number of flowers per plant/the number of inflorescences per plant. Data are presented for plants after 11 weeks of LD forcing. All plants had produced new leaves equal to at least the number of leaf primordia observed at dissection by this time. In addition, conditioning effects observed by week 11 did not change with continued observation. Initiation was evaluated via inflorescence counts, differentiation via flowers per inflorescence and development via precocity. Precocity was estimated as the length of time under LD after conditioning until the primary flower bud of the first inflorescence had fully emerged from the crown.

Data were subjected to a test for normality using the Shapiro–Wilks test of the UNIVARATE procedure of SAS (SAS Institute, Cary, North Carolina, USA). Nearly all data were found to be from a non-normal distribution. The Rank Transformation (Conover and Iman, 1981) was applied to all data, and ranked data tested for normality. Rank-transformed data passed the Shapiro–Wilks test for normality, thus only rank-transformed data was used in analyses. Transformed data were subjected to an analysis of variance using the ANOVA procedure of SAS (SAS Institute, 2014) and means were separated with Fisher's Protected LSD at the 0.05 level where appropriate. Means were back-transformed for presentation and discussion.

3. Results

3.1. Dissections

All terminal meristems of 'Cavendish', 'Chandler', 'Earliglow', 'Jewel', 'Seneca', and 'Seascape', were vegetative upon dissection at the commencement of the conditioning treatments. Many 'Fern' (80%) and 'Selva' (60%) plugs were floral at dissection.

3.2. Precocity

3.2.1. Short-day cultivars

Conditioning did not affect precocity in the short-day cultivar 'Chandler' which flowered after an average of 11.2 weeks of forcing. In all other short-day cultivars, conditioning hastened flowering. The length of conditioning needed to enhance precocity and intensity of enhancement varied with cultivar (Table 1). 'Cavendish' plants conditioned for 1, 2 or 4 weeks flowered 4.4 weeks earlier than controls. 'Earliglow' required 4 weeks of conditioning for accelerated flowering (2 weeks). 'Jewel' flowering was accelerated by almost 2 weeks with 1 or 2 weeks of conditioning but not with 4 weeks and 'Jewel' plants conditioned for 4 weeks did not differ from those conditioned for 0, 1 or 2 weeks. 'Seneca' flowering was accelerated by 2 weeks with 1 week of conditioning and by 3 weeks when conditioned for 2 or 4 weeks.

3.2.2. Long-day cultivars

Conditioning did not alter the time of flowering for any of the long-day cultivars (Table 1). All 'Fern' plants flowered during the first week of forcing, 'Selva' flowered after 5.5 weeks of forcing and 'Seascape' flowered after 6.6 weeks of forcing.

3.3. Leaf production

3.3.1. Short-day cultivars

Conditioning did not affect leaf production in 'Cavendish' or 'Jewel'. Plants of 'Chandler', 'Earliglow' and 'Seneca' conditioned for 4 weeks produced significantly more leaves than those conditioned for 0, 1 or 2 weeks (Table 1).

3.3.2. Long-day cultivars

Conditioning did not affect leaf production in 'Seascape' (Table 1). In both 'Fern' and 'Selva' plants conditioned for 4 weeks produced significantly more leaves than those conditioned for 0, 1 or 2 weeks (Table 1).

3.4. Runner production

3.4.1. Short-day cultivars

'Cavendish' control plants produced runners (1.2 per plant) while conditioned plants did not (0.1 per plant) (Table 1). 'Chandler' plants conditioned for 4 weeks produced more runners (6.0) than those conditioned for 0, 1 or 2 weeks (3.4) (Table 1). All 'Earliglow' plants produced an average of 1.9 runners regardless of conditioning. 'Jewel' plants conditioned for 0 or 1 week produced an average of 0.8 runners per plant while plants conditioned for 2 or 4 weeks did not runner. 'Seneca' control plants produced 2.0 runners per plant while plants conditioned for 2 or 4 weeks produced significantly fewer runners (0.2 per plant). Plants conditioned for 1 week (1.2 runners per plant) were intermediate and not statistically different from plants conditioned for 0, 2 or 4 weeks.

3.4.2. Long-day cultivars

No effect of conditioning on runner production was observed for 'Seascape' or 'Selva' while conditioning reduced runner production in 'Fern' (Table 1).

3.5. Inflorescence and flower production

3.5.1. Short-day cultivars

Conditioning of 'Cavendish' plugs did not influence the production of inflorescences (1.5) or flowers per inflorescence (5.1) (Table 1). In 'Chandler', plants conditioned for 2 or 4 weeks produced more inflorescences and flowers per inflorescence (0.8 and 10.6 inflorescences and flowers per inflorescence, respectively) than those given 0 or 1 week of conditioning (0.2 and 4.5 inflorescences and flowers per inflorescence, respectively) (Table 1). All 'Earliglow' plants produced an average of 1.0 inflorescence. Plants conditioned for 4 weeks produced 3 times the number of flowers per inflorescence (19.3) compared to those conditioned for 0, 1 or 2 weeks (9.2) and the difference was significant. Conditioning of 'Jewel' plugs did not influence inflorescence production (1.2 per plant) (Table 1). Control plants produced on average 4.8 flowers per inflorescence while conditioned plants produced 8.0 flowers per inflorescence and the difference was significant (Table 1). 'Seneca' plants conditioned for 4 weeks produced significantly more inflorescences (1.7) than those conditioned for 0, 1 or 2 weeks (0.9). Conditioned plants produced significantly more flowers per inflorescence (13.2) compared to controls (8.6) (Table 1).

3.5.2. Long-day cultivars

'Fern' plants conditioned for 4 weeks produced an average of 3.2 inflorescences, which was significantly more than plants conditioned for 0 or 1 week (1.3). Plants conditioned for 2 weeks produced an average of 2.5 inflorescences which as not different from any other treatment. Plants conditioned for 4 weeks produced more flowers per inflorescence (8.0) than those conditioned for 0, 1 or 2 weeks (6.3) (Table 1). 'Seascape' plugs produced an average of 2.0 inflorescences per plant and 5.5 flowers per inflorescence regardless of conditioning treatment (Table 1). In 'Selva', there was no effect of conditioning on the number of inflorescences (1.5) (Table 1). Plants conditioned for 4 weeks produced more flowers per inflorescence (8.3) than those conditioned for 0, 1 or 2 weeks (5.9) (Table 1).

Table 1
Precocity, leaf, runner, inflorescence and flower production of the short-day cultivars 'Cavendish', 'Chandler', 'Earliglow', 'Jewel' and 'Seneca' and the long-day cultivars 'Fern', 'Seascape' and 'Selva' strawberry plug plants after 11 weeks of long day (16 h) forcing in a greenhouse (20 °C) as affected by the number of pre-forcing short day (8 h) cycles (weeks) at 15 °C.

Short day cultivars

Weeks of short day cycles	Precocity	Leaves	Runners	Inflorescences	Flowers/inflorescence
	Cavendish				
0	10.4 a[a]	13.3	1.2 a	0.8	5.6
1	5.2 b	13.8	0.2 b	1.6	4.0
2	6.7 b	15.5	0.0 b	1.7	5.2
4	6.2 b	17.0	0.0 b	1.8	5.7
	Chandler				
0	12.3	10.8 b	2.8 b	0.2 b	4.0 b
1	12.0	11.0 b	3.3 b	0.2 b	5.0 b
2	9.7	11.3 b	4.0 b	0.8 a	8.8 a
4	10.8	15.7 a	6.0 a	0.7 a	12.4 a
	Earliglow				
0	9.3 a	10.8 b	2.3	1.0	9.3 b
1	9.3 a	11.2 b	2.2	1.2	7.3 b
2	8.2 ab	12.2 b	1.7	1.0	11.0 b
4	7.3 b	14.7 a	1.0	1.0	19.3 a
	Jewel				
0	9.8 a	11.8	1.0 a	1.2	4.8 b
1	8.0 b	15.2	0.7 a	1.0	9.0 a
2	8.2 b	14.2	0.0 b	1.3	9.5 a
4	8.7 ab	15.3	0.0 b	1.7	5.5 a
	Seneca				
0	11.2 a	13.2 b	2.0 a	0.7 b	8.6 b
1	9.3 b	13.7 b	1.2 ab	1.0 b	12.5 a
2	8.2 c	15.5 b	0.2 b	1.0 b	15.3 a
4	8.3 c	22.3 a	0.3 b	1.7 a	11.8 a

Long day cultivars

Weeks of short day cycles	Precocity	Leaves	Runners	Inflorescences	Flowers/inflorescence
	Fern				
0	2.3	14.3 b	2.3 a	1.3 b	7.7 b
1	0.1	12.7 b	0.3 b	1.3 b	6.4 b
2	0.3	14.5 b	0.2 b	2.5 ab	4.9 b
4	1.2	20.2 a	1.0 b	3.2 a	8.0 a
	Seascape				
0	7.2	11.2	0.0	2.0	5.6
1	4.8	12.0	0.5	2.0	5.4
2	4.3	11.7	0.3	1.8	5.4
4	6.0	13.3	0.7	2.0	5.7
	Selva				
0	7.2	10.3 b	1.3	1.2	7.0 b
1	8.9	11.4 b	1.1	1.0	5.2 b
2	6.4	11.3 b	0.4	1.8	5.6 b
4	4.0	16.2 a	1.0	2.2	8.3 a

[a] Mean separation within column and cultivar by Fisher's protected LSD, $\alpha = 0.05$. Lack of letters indicates not significant.

4. Discussion

Floral ontogeny and plant phenology of three week old plug plants was sensitive to short-day photoperiod conditioning and the degree of sensitivity varied with cultivar and parameter examined. Dissection of apical meristems prior to conditioning confirmed a vegetative state in the cultivars 'Cavendish', 'Chandler', 'Earliglow', 'Jewel', 'Seneca', and 'Seascape', thus floral growth responses are attributed to conditioning treatment rather than photoperiod or temperature effects on physiology during plug propagation. Since many 'Fern' (80%) and 'Selva' (60%) plugs were floral at dissection, floral growth responses in these two cultivars observed after conditioning may not be wholly attributable to treatment, but rather may be carry over effects of photoperiod or temperature during plug propagation.

Leaf growth of 'Cavendish' (SD), 'Jewel' (SD) and 'Seascape' (LD) was not affected by pre-forcing conditioning. All other cultivars produced significantly more leaves after 4 weeks of conditioning compared to 0, 1 or 2 weeks of conditioning. Previous reports indicated that leaf production in LD cultivars is generally enhanced during or following SD exposure (Nishiyama et al., 2003, 2006; Sonsteby and Heide, 2007a,b) and remains constant (Jahn and Dana, 1966; Durner and Poling, 1987; Konsin et al., 2001; Kurokura et al., 2005) or increases (Hytonen et al., 2004; Sonsteby and Heide, 2006) in SD cultivars.

Cultivars did not fall into short-day or long-day categories based on runner production following SD conditioning. Runner production in SD cultivars is normally associated with LD or high temperature and is often inhibited following SD treatment (Heide et al., 2013). The SD cultivars in this study did not categorically respond this way. Three SD cultivars ('Cavendish', 'Jewel' and 'Seneca') exhibited this behavior, one ('Earliglow') had no response, and one ('Chandler') exhibited significantly enhanced runner production following SD treatment. Sonsteby and Heide

(2007b) asserted that runner production in LD cultivars was primarily a response to high temperature and SD, however, results were inconsistent among three of their experiments for 5 of the 6 LD cultivars they studied. Only the LD cultivar 'Elan' exhibited consistent runner production under SD and high temperature conditions (Sonsteby and Heide, 2007a,b). Nishiyama et al. (2003) reported enhanced runner production in the LD cultivar 'Summerberry' under shorter 8 to 16 hr photoperiods compared to longer 20 or 24 h photoperiods. In a later study, (Nishiyama et al., 2006) fewer runners were produced under 12, 14, 15 or 16 h daylengths compared to 13 h. Both Durner et al. (1984) and Bradford et al. (2010) observed enhanced runner production under LD at high temperature (26/22 and 30/26 °C (Durner and Poling, 1987); 23–29 °C (Bradford et al., 2010)) in LD cultivars. The discrepancy among these studies is likely related to cultivar differences and not due to differences in experimental LD conditions such as daylength extension vs night interruption, light source, and light levels during interruption or extension. The major difference among these studies was runner production or lack thereof under SD conditions. All cited studies recorded runner production under LD conditions, albeit at different temperatures and at varying runner production rates. SD conditioning in this present study reduced runner production in 'Fern', the parent contributing the LD photoperiodic flowering nature to 'Elan' which has been shown to runner significantly under SD at higher (27 °C) temperatures (Sonsteby and Heide, 2007a). In addition, runner production in the LD cultivars 'Seascape' and 'Selva' was not affected by conditioning. The general categorization for enhanced runner production of SD cultivars under LD (Heide et al., 2013) and LD cultivars under SD (Sonsteby and Heide, 2007b) is questionable since runner production responses of cultivars in this study and others (Nishiyama et al., 2006; Durner et al., 1984; Bradford et al., 2010) did not follow this categorization.

Runner and inflorescence production are not necessarily antagonistic processes in short-day cultivars, as suggested by Bradford et al. (2010). Even though reduced runner formation was observed with a concomitant increase in inflorescence production (Table 1) in some cultivars ('Seneca' (SD) and 'Fern' (LD)), in other cultivars ('Cavendish' and 'Jewel' (both SD)) the reduction in runner production was a direct inhibitory response to short days rather than inhibition caused by flowering: runner production was reduced but flowering was not enhanced with short day conditioning (Table 1). In addition, SD enhanced flowering in 'Chandler' did not inhibit runner production: both inflorescence and runner production were enhanced with short-day conditioning.

Cultivars did not fall into specific photoperiod response categories (SD or LD) with respect to flowering either. All short-day cultivars and the long-day cultivar 'Seascape' were vegetative at the start of the experiment yet inflorescence production occurred during long-day forcing in non-conditioned controls. Thus floral initiation occurred during the long days in the greenhouse. Nevertheless, altered flowering of conditioned plugs compared to controls under LD forcing in several cultivars indicates that floral ontogeny under long days was altered by pre-forcing, SD conditioning. This highlights the importance of plug handling during production since the flowering under one photoperiod (in this case LD greenhouse forcing) can be modified by pre-forcing photoperiod (in this case different lengths of time under SD) even if altered meristems are not visible prior to forcing.

All cultivars except 'Seascape' and 'Cavendish' exhibited enhanced initiation and differentiation following SD conditioning. Four of five short day cultivars ('Chandler', 'Earliglow', 'Jewel' and 'Seneca') produced significantly more flowers per inflorescence with increased length of short day conditioning. In the other short-day cultivar 'Cavendish', though inflorescence and flower production among conditioning treatments was not statistically significant, conditioned plugs produced twice as many

inflorescences as control plugs (Table 1). These results generally agree with reports that both flower initiation (Sonsteby et al., 2013; Sonsteby et al., 2009; Bradford et al., 2010; Hytonen et al., 2004; Manakasem and Goodwin, 2001; Verheul et al., 2006) and differentiation (Sonsteby and Ness, 1998; Manakasem and Goodwin, 2001; Verheul et al., 2006) of SD cultivars are generally enhanced with exposure to short days. Exposure to SD at warm temperatures (Bradford et al., 2010) or for extended periods (Verheul et al., 2006) have both been shown to reduce differentiation and several authors (Miere et al., 1996; Hytonen et al., 2004) reported no effect of photoperiod on differentiation. In the LD cultivars 'Fern' and 'Selva', exposure to 4 weeks of SD enhanced differentiation (Table 1). That SD conditioning generally enhances differentiation in LD cultivars is supported by observations from other studies (Bradford et al., 2010; Manakasem and Goodwin, 2001). Bradford et al. (2010) observed that 'Tribute' (a quantitative LD plant at 23 °C) produced more flowers per inflorescence under SD compared to LD at 23 °C and Manakasem and Goodwin (2001) observed more flowers per inflorescence under SD compared to LD at a temp of 18/13C (day/night) in 'Hecker', 'Brighton' and 'Aptos', LD cultivars from California.

Floral development measured as precocity was enhanced by SD in several of the SD cultivars in this study and this has been previously reported for other SD cultivars (Sonsteby et al., 2013; Heide et al., 2013). Floral development in LD cultivars of this study was not affected by SD treatment. Precocity of LD cultivars may or may not be delayed by SD exposure depending on cultivar (Heide et al., 2013; Hamano et al., 2015; Sonsteby and Heide, 2007a,b; Nishiyama et al., 2003).

Cultivar sensitivity to conditioning was observed in the number of weeks of conditioning required to induce altered flowering compared to non-conditioned controls. 'Jewel' and 'Seneca' responded with 1 week of conditioning, 'Chandler' with 2 weeks, and 'Earliglow' with 4 weeks of conditioning. That cultivars differ widely in the length of exposure time required to elicit flowering responses is widely reported (Heide et al., 2013).

Each stage of floral development described by Durner and Poling (1985) as induction/initiation, development and differentiation are differentially affected by photoperiod and as many of these stages as possible should be examined to provide a clear description of any response(s). Omitting one or more stages may lead to erroneous or incomplete conclusions. For example, development as measured by precocity was enhanced by SD exposure in several SF cultivars ('Cavendish', 'Earliglow', 'Jewel') while initiation measured by inflorescence production was not affected by SD (Table 1). If precocity had not been calculated, an important effect of photoperiod on the flowering response to photoperiod in 'Cavendish', 'Earliglow', and 'Jewel' would have been overlooked. Similarly in the SD cultivar 'Chandler, development (11.2 weeks to flower) was not affected by SD while initiation and differentiation were significantly enhanced by 2 or 4 weeks of SD prior to forcing (Table 1). Many flowering studies in the literature evaluated only one or two of the stages (usually initiation and differentiation) by evaluating inflorescence and flower number production responses to treatment.

5. Summary

This study verifies plug plant sensitivity to photoperiod with respect to floral ontogeny and plant phenology and that the degree of sensitivity varies with cultivar and parameter examined. Cultivars do not always fall into short-day or long-day categories based on growth responses including flowering and runner production. When evaluating flowering responses to photoperiod in strawberry, each specific stage of floral development (induction/initiation, differentiation and development) should be evaluated since each stage is differentially affected by photope-

riod. Based on the results in this study as well as others previously cited, the only general description of flowering responses to photoperiod in strawberry is that SD exposure enhances differentiation in both SD and LD cultivars. General categorizations for initiation and development should not be made as responses to photoperiod for these stages are cultivar specific.

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