

## Flowering and Fruiting on Command in Berry Crops

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**Keywords:** *Fragaria* × *ananassa*, *Rubus idaeus*, *Vaccinium corymbosum*, blueberry, blackberry, strawberry, flower bud initiation, photoperiod, off-season production, tunnels, primocane fruiting, day-neutral, everbearer

### Abstract

Many berry crops are managed by altering growth and environment in commercial production systems, to affect time of flowering and fruiting season. The effect of photoperiod, temperature, and production system on flower bud initiation and development is reviewed for strawberry, raspberry, blackberry and blueberry. While “flowering on command” is still a challenge, research and commercial production systems have been successful at scheduling fruit harvest for many of these crops. In strawberry and biennial cropping red raspberry, pre-conditioned plants, grown to maximize flower bud development, are commonly used along with staggered planting dates (often in tunnels) to time fruit harvest date. In primocane-fruiting raspberry, annual production systems with staggered planting dates, often in combination with pruning techniques, are used to target market windows. This system of production shows promise with primocane-fruiting blackberry. In southern highbush blueberry, cultivars are grown in warm regions using evergreening systems, pruning, and fertilization methods, to produce fruit at desired times. With a good understanding of plant physiology and the factors that affect flower bud initiation and development, bud break, and the production of high-quality fruit, it is possible to manipulate many berry crops to have fruit production target desirable market windows.

### INTRODUCTION

There are various ways to control flowering and fruiting season including use of plants with “pre-formed flower buds”, continuous cropping types or cultivars, climate modification (including protected culture), and growing crops at low-latitude or in a milder climate. A significant change toward protected cultivation and concomitant manipulation of the crop for off-season production, particularly in *Fragaria* and *Rubus*, led to a need to better understand the impacts of environmental manipulation on plant growth, flowering, and fruiting season. Considerable research toward this effort has occurred and is reported here.

Commercial production and/or research with use of protected structures are occurring in most berry crop production regions worldwide. The types of protected structures used include greenhouses (mainly limited to western Europe), low and high tunnels, shade structures, and row covers. Use of shade structures and net is relatively common in berry crops, depending on growing region. Tunnels are used to shelter plants from the environment, particularly rain and ultra-violet light, advance, delay, or extend the harvest season, and to create diffusing light to improve crop growth, yield, and quality, and to exclude or reduce some pests. Tunnels may be covered with plastic or shade cloth to manage the microclimate and crop growth. In warmer regions, tunnels may be used year round and can provide for a longer growing season in temperate climates. The choice of berry crops that may be grown in a particular region can be expanded. In colder regions, tunnels are typically used to extend the growing season - heating of tunnels for berry crops is not common at this time, nor is supplemental lighting. There is relatively little published research documenting the direct effects of tunnels on growth

and quality of berry crops, compared to field-grown plants, mainly due to the inherent problem with appropriately replicating the tunnels.

It is important to understand the factors that control quantity and rate of flower bud initiation, differentiation, and development to best manipulate fruiting season in protected structures or the open field, while still producing acceptable yield and quality.

Specific stages of reproductive development are often referred to as induction, initiation, differentiation, and development (Durner and Poling, 1988). While these stages are sometimes differentially regulated, depending on the crop, for the purposes of this overview, I will refer to floral induction/initiation (FBI) and flower bud differentiation (FBD).

In many berry crops FBI and FBD are clearly affected by photoperiod and temperature, with these often having interactive effects. Manipulation of photoperiod and temperature during the FBI period has been used successfully to alter fruiting season. In addition, cultural practices such as pruning, fertilization, and application of growth regulators are commonly used to modify growth and fruiting. I will briefly review the factors related to FBI, FBD, and fruiting season in *Fragaria*, *Rubus*, and *Vaccinium* and how this knowledge is being used in commercial situations to manipulate flowering and fruiting to target desired market windows.

### **STRAWBERRY (*FRAGARIA*)**

Strawberries have been classified according to their flowering response to photoperiod: short-day plants which initiate flower buds only under short days (SD, <14 h); long-day plants (LD, >12 h, Darrow, 1936); and day-neutral plants which are relatively insensitive to day length with regard to flowering. The minimum number of photo-inductive cycles required for FBI ranges from 7-24 (e.g., Hancock, 1999) with the number of required inductive cycles generally increasing with temperature (Ito and Saito, 1962).

The interaction between photoperiod and temperature has been reviewed (Darnell, 2003; Darnell and Hancock, 1996; Durner and Poling, 1988; Guttridge, 1969, 1985; Strik, 1985; Taylor, 2002). Research on photoperiod-temperature interactions (e.g., Darrow, 1936; Durner et al., 1984; Heide, 1977) suggests that FBI in SD strawberry is insensitive to photoperiod at low (~10-15°C) and high (>25°C) temperatures (Darnell, 2003). Recently, Bradford et al. (2010) found that the SD cultivar 'Honeoye' was insensitive to photoperiod at 14 to 20°C. Under SD conditions, the optimal temperature for FBI is 15-18°C (Heide, 1977), while little FBI occurs below 10°C and above 25°C (Durner and Poling, 1988; Heide, 1977; Sønsteby and Heide, 2006a; Verheul et al., 2007). Flower bud development is optimum at higher temps (19-27°C; e.g., Hartmann, 1947; Le Mière et al., 1996). Optimal night temperatures during SD also can vary among cultivars (Sønsteby and Heide, 2009c). In many SD strawberry cultivars, FBI will occur under LD at low temperatures (Heide, 1977; Ito and Saito, 1962; Verheul et al., 2007), with the temperature threshold varying by cultivar (Guttridge, 1985; Heide, 1977), and some cultivars in Nordic regions have no FBI under LD at temperatures as low as 9°C (Sønsteby and Heide, 2006a).

Trials on producing fruit through the winter on the SD cultivar 'Korona' in Norway have been successful using SD treatments to induce FBI (Sønsteby and Heide, 2006b). Productivity, however, was very dependent on plant quality; preconditioning plants to SD increased branch crown formation and subsequent yield. In 'Elsanta' temperature was positively correlated to rate of progress to fruiting, but crown size, while positively correlated to yield, was not related to time of fruiting. However, warmer temperatures reduced yield through a reduction in canopy size (Le Mière et al., 1998). Projections on the impact of climate change in the Huelva region of Spain include an expectation for greater yields in early season, but reduced overall yields with higher temperature in the SD cultivar 'Camerosa' (Palencia et al., 2009).

Mori (1998) found an inverse relationship between the number of achenes per fruit (for all flower positions) and temperature during the ovule/pistil FBD period. The highest number of achenes per fruit was found when temperatures were 16/11°C (day/night)

throughout FBD. The number of achenes per fruit is positively correlated with fruit size (Abbott et al., 1970; Strik and Proctor, 1988b).

There is still some question as to whether strawberry buds enter endodormancy; however, the strength of endodormancy varies with cultivar. In strawberry, chilling stimulates the development of previously initiated inflorescences (Tehranifar and Battey, 1997); but excessive chilling inhibits (Avigdori-Avidov et al., 1977; Tehranifar and Battey, 1997) and or delays (Durner and Poling, 1987) FBI. Thus excessive chilling reduces yield and delays harvest in SD strawberry.

Flower bud initiation in SD strawberry is regulated by an inhibitory LD process in the leaves (e.g., Guttridge, 1985), as evidenced by the positive effect of post-harvest defoliation in SD cultivars on FBI (e.g., Guttridge and Wood, 1961; Zhang et al., 1992) and phytochrome manipulation with red and far-red light (Collins, 1966; Vince-Prue and Guttridge, 1973). Inhibition of flowering can be mimicked by application of gibberellin (GA, e.g., Guttridge and Thompson, 1963). Applications of inhibitors of GA biosynthesis increase crown formation, flowering, and yield (Black, 2004; Hytönen et al., 2008). The synthesis of GA is blocked under SD in strawberry (Hytönen et al., 2009 in Sønsteby et al., 2009b).

Renovation immediately after harvest in SD strawberry (post-harvest defoliation) has been shown to increase yield in the autumn (Zhang et al., 1992), without a vernalization period. Delaying post-harvest defoliation in SD strawberry has reduced yield the following year (Guttridge and Wood, 1961; Zhang et al., 1992). Zhang et al. (1992) found that renovation from 2 to 4 weeks after last harvest in SD strawberry led to maximum yield. Early renovation increased yield from 12 to 41% compared to plants that were not defoliated.

Treatment of crowns of SD-strawberry with red light (600-702 nm) reduced or delayed FBI under SD (Takeda et al., 2008). Thus, SD-strawberry plugs grown at high density with crowns heavily shaded and receiving less red light, produced flowers under LD and temperatures  $>21^{\circ}\text{C}$  day/night (Takeda et al., 2008).

Light intensity has less of an effect than photoperiod in strawberry, but inflorescence number per plant may increase with light intensity (Chabot, 1978; Dennis et al., 1970), perhaps an indirect effect of increased vegetative growth. Shade during the growing season has reduced yield the following season (Ferree and Stang, 1988).

Hartz et al. (1991) found no effects of increased  $\text{CO}_2$  concentration during the FBI period on inflorescence or flower number in SD strawberry. However, this work was done in plastic tunnels where excessively high air temperatures may have limited FBI. In other studies, enrichment with  $\text{CO}_2$  has shown more promise for increasing yield of strawberries (Deng and Woodward, 1998).

In day-neutral (DN) strawberry, many cultivars respond as qualitative LD plants at high temperatures ( $>27^{\circ}\text{C}$ ), quantitative LD plants at lower temperatures (10 to  $25^{\circ}\text{C}$ ), and DN at temperatures below  $10^{\circ}\text{C}$  (Nishiyama and Kanahama, 2000; Sønsteby and Heide, 2007), although flowering of DN types decreases at high temperatures (Durner et al., 1984; Heide, 1977). The DN cultivar 'Tribute' was insensitive to photoperiod at 14 to  $23^{\circ}\text{C}$ , but required LD at higher temperatures (Bradford et al., 2010), similar to what has been observed by others (Sønsteby and Heide, 2007). Night interruption or day extension can be used to stimulate long day responses in a naturally short day (e.g., Kronenberg and Wassenaar, 1972). Temperature and cultivar differences in rate of FBD, strongly influence the expression of repeat flowering or remontancy (Bradford et al., 2010).

Strawberry cultivars that are classified as DN often vary in the degree of remontancy, by growing location or year (Durner et al., 1984). Understanding the genetic basis for remontancy is actively being investigated (e.g., Bradford et al., 2010; Serçe and Hancock, 2005; Shaw, 2003). With the variable response of FBI in remontant strawberry to temperature, there seems to be no basis for continuing to classify these plants as "day-neutral". Rather these strawberries respond more like LD plants at all temperatures except those less than  $10^{\circ}\text{C}$  when they are less sensitive to day length (Sønsteby and Heide, 2007).

Soil temperature may have a direct effect on FBI or an indirect one through effects on vegetative growth. Mulches that maintain soil temperatures below 25°C have increased reproductive development compared to mulches that promote higher soil temperatures (Fear and Nonnecke, 1989). Use of black polyethylene mulch and medium to high irrigation regimes increased flowers and fruit per plant in SD strawberry in a temperate climate compared to bare soil and low irrigation volume (Renquist et al., 1982).

Use of row covers and tunnels to manipulate the growing and fruiting season of strawberry has been successful. Remontant strawberries can have their fruiting season advanced or extended provided the row cover or tunnel provides a suitable temperature and day length that is adequate for FBI and fruiting. For example, flowering in DN strawberries ceases when temperatures get too high under tunnels in the UK and in the continental USA (Dale et al., 2002; Sønsteby and Heide, 2009b). In SD strawberry, placing row covers over plants from autumn to the beginning of bloom in spring increased mean temperature, leaf growth, and inflorescence and flower number (Gast and Pollard, 1991). Pritts et al. (1989) found that row covers applied in spring, before bloom, advanced ripening and increased yield of SD strawberry.

For extended off-season production and to schedule harvests, SD strawberry plants are pre-conditioned to increase the number of flower buds per plant and future production; these pre-conditioned plants are commonly called “waiting bed” plants. A forcing system for production of strawberries in winter in Japan has been described (Mochizuki et al., 2009). Nursery plants that are grown in pots or plug trays are subjected to slight nitrogen (N) deficiency to promote FBI; plant N status is tested using a petiole NO<sub>3</sub>-N sap test. Short-day, low temperature treatments are used to pre-condition nursery plants for promoting FBI. Plants are kept at temperatures above 5°C to avoid heavy dormancy and promote continued FBI. For growth and continued flowering and fruit production strawberries are grown under LD and mild temperatures (Mochizuki et al., 2009). Nitrogen fertilization timing and rate during the FBI period of nursery plants has influenced yield of SD strawberry (Desmet et al., 2009; Yamasaki and Yano, 2009). Fertilizer application during the early part of a SD night-chilling treatment, delayed FBI compared to delaying fertilizer application by 10 days (Yamasaki and Yano, 2009). Although lack of fertilizer N promoted FBI, once initiation started, fertilizer N was required for development of the floral organs (Yamasaki et al., 2002).

In field-grown strawberry, adequate plant N status is important for maximizing growth and FBI and FBD. However, in SD strawberry, foliar applications of urea in the autumn, during the period of FBI, had no effect on yield the following summer in field-grown plants (Strik et al., 2004). However, when granular fertilizer N was applied at renovation in perennial, SD strawberry systems, fertilizer use efficiency improved and plants produced more crowns (Strik et al., 2004), in accordance with Strik and Proctor (1988a) showing that number of crowns and leaves are related to the number of flowering sites.

Withholding N and P may not increase flowering in strawberry (Abbott, 1968). Increasing N from a low N status level has increased flower development in strawberry (e.g., Latet et al., 2002), but application of high rates of N can inhibit FBI and reduce yield (e.g., Darrow and Waldo, 1932). More commonly, in perennial strawberry systems, fertilizer N has little effect on yield (e.g., Blatt, 1981; Strik et al., 2004). While good nutrition during the autumn period of FBI is important in SD strawberry (Long, 1939; Lieten, 2002), fertilization in the spring when further FBI and FBD occurs has not been effective at increasing yield (Opstad and Sønsteby, 2008; Strik et al., 2004). When groups of SD strawberry with a low fertility regime were fertilized with additional N for a period of time relative to a 4-week SD floral induction period, extent and time of flowering were affected by time of N fertilization (Sønsteby et al., 2009b). Fertilization with N for 3 weeks starting 2 weeks before the FBI period, delayed flowering by 7 days. When plants were fertilized starting 1 week after the start of the SD period, flowering was advanced by 8 days and flower number was increased two-fold, relative to plants receiving no additional N, even though there was no treatment effect on the number of crowns. In

strawberry, FBI is thus limited when plants are at a high N status immediately before the SD flower inductive period, whereas high N status during the SD inductive period increases FBI (Sønsteby et al., 2009b; Lieten, 2002).

### **RASPBERRY (*RUBUS*)**

Raspberry growth (Dale, 1989) and control of the annual growth cycle (Carew et al., 2000) of raspberry have been reviewed. In “biennial fruiting” or floricanefruiting raspberries, FBI occurs under SD when temperatures are below 15°C (e.g., Williams, 1959, 1960; Sønsteby and Heide, 2008); but under LD when temperatures are below 12°C, FBI is inhibited at temperatures greater than 18°C (Sønsteby and Heide, 2008; Williams, 1960). Intermediate combinations of day length and temperature allow FBI to proceed slowly (Williams, 1960).

While tip primocane flowering can occur in a typical biennial cultivar (Dale, 2008; Keep, 1961; Sønsteby and Heide, 2008) under sub-optimal conditions for FBI, the key difference between biennial cultivars and annual or primocane-fruited cultivars is that, in the latter, FBI is not accompanied by dormancy. Attaining dormancy in biennial cultivars required 5-6 weeks of SD and low temperature (Sønsteby and Heide, 2008). Dormancy did not occur in ‘Glen Ample’ if temperatures were higher than 15°C under SD (Sønsteby and Heide, 2009c). The biennial-fruited cultivars thus have a low temperature requirement, and do not flower when temperatures are above 15°C, regardless of day length (Sønsteby and Heide, 2008). Under growing conditions of high autumn temperature, FBI may be reduced in these cultivars (Sønsteby and Heide, 2009c).

Normal flowering requires cessation of growth, bud dormancy, and sufficient chilling in biennial-fruited cultivars. Once fully dormant, 6 weeks (Williams, 1959) to 12 weeks of cold storage (at -2°C) is required to ensure bud break along the entire cane length and maximum yield (Sønsteby et al., 2009a). In contrast, others (Heiberg et al., 2008; Pitsioudis et al., 2002; Sønsteby et al., 2009a) have shown a negative effect of longer cold storage on yield. A vernalization period, after cold storage of long-canes, increased yield in ‘Glen Moy’ biennial raspberry with 1 week at 4°C and 16 h photoperiod giving best results (Brennan et al., 1999).

Bud break and perhaps FBI may also be resource limited in *Rubus*. Primocane removal or suppression has a positive effect on current and following season yield in floricanefruited red raspberry (e.g., Crandall et al., 1980; Williamson et al., 1979). Loss of primary buds on floricanes or the first emerging fruited laterals, either through winter cold injury or pruning, leads to compensation from later emerging laterals from secondary buds and a delay in flowering and production. This is used to advantage in warmer production regions to delay the crop on the floricanefruited cultivars of biennial or annual cultivars (Strik, pers. obs.).

Growing biennial fruited raspberries in open-field or tunnel systems for scheduling production is quite common. In these production systems primocanes must be grown in a nursery to promote maximum flower bud development. These “long canes” are then cold stored to ensure adequate chilling and are planted at various times to schedule harvest.

Growing canes at high density will reduce subsequent yield (Dijkstra and Scholtens, 1993) and delay FBI (Brennan et al., 1999). While Wood et al. (1961) found that tipping of dormant long-canes increased yield, Brennan et al. (1999) found that the effect of tipping on uniformity of bud break and yield was cultivar dependent. Producing canes of adequate length to allow for removal of the tip of the cane which produces shorter, lower yielding laterals, was critical to higher yielding long cane systems (Sønsteby et al., 2009a).

Long-canes can be field-grown and dug and stored bare-root or grown in containers for off-season production. The disadvantages to growing long-cane raspberries in the nursery are the relatively small root systems after digging, increased risk of root and cane desiccation during cold storage, poor bud health or FBI due to high density

plantings, and thus relatively low yield (< 400 g/cane) compared to potted, long-cane plants (Sønsteby et al., 2009a).

Yield in long-cane production systems has ranged from 1 kg/cane (Heiberg et al., 2008; Pitsioudis et al., 2002) to 3.5 kg/cane (Sønsteby et al., 2009a) using container grown long-canines in tunnel production. In contrast, yield of bare-rooted long canes has ranged from 300-400 g/cane in grower fields to 900 g/cane in research trials in the UK (Raffle, 2004 in Sønsteby et al., 2009a).

A yield reduction when planting out bare-root canes compared to potted plants, may be due to the root pruning that occurs when digging long-cane nursery plants (Darnell et al., 2008). Root-pruned 'Cascade Delight' biennial raspberry canes had reduced yield due to a lower flower and fruit number compared to plants that were not root pruned. The lower concentration and content of carbohydrate in the root-pruned plants may have limited FBI or FBD (Darnell et al., 2008). Long-canines of 'Tulameen', either grown in pots or bare-root, were stored for 6 months at -1°C and planted in open field in mid-April or mid-May in Italy (Beccaro et al., 2004). Bare-root plants had a more concentrated fruiting period, but yield per cane was not provided in their paper.

Raspberries exhibit characteristics of a source limited plant even though they have a relatively high leaf to fruit ratio. Removal of primocanes, increases yield of the floricanes in the same season (Freeman et al., 1989). Removal of competing primocanes is thus common in long-cane systems in the fruiting stage.

The economics of growing biennial raspberries in containers with natural chilling in the field followed by delayed production in the greenhouse has been shown to be favorable (e.g., Pritts et al., 1999). The favorable economics of growing bare-root long-canines in staggered plantings to target high-priced markets is evidenced by this continuing to be a common commercial practice in many growing regions.

Primocane or annual fruiting raspberry cultivars are different from floricanefruiting cultivars as they have no low temperature requirement for FBI. Although flowering will occur on primocanes in the absence of chilling (Dale et al., 2005), chilling improves and advances flowering (Takeda, 1993; Vasilakakis et al., 1980). The rate of growth and flowering was increased with temperature with an optimum in the low to mid 20s °C range (Carew et al., 2003; Sønsteby and Heide, 2009a) although temperatures can be as high as 30°C (Sønsteby and Heide, 2009c). In 'Autumn Bliss' harvest was two months earlier when grown at 22°C than when grown at 15°C (Carew et al., 2000). In 'Polka', flowering was advanced and the number of flowers increased with increasing temperature up to an optimum of 27°C (Sønsteby and Heide, 2009a). In 'Heritage', grown under LD, flowering node number and flower number were improved and flowering was advanced at 29/24°C compared to 25.5/20°C (day/night) (Lockshin and Elfving, 1981). Low temperature, or a vernalization (6 to 8 weeks at ~7°C), at an early growing stage, advances flowering or fruiting in primocane-fruited raspberries (Carew et al., 2001; Neocleous et al., 2005; Takeda, 1993; Vasilakakis et al., 1980).

Primocane-fruited raspberry are generally thought to be DN with regard to FBI, although flowering was somewhat advanced by photoperiods of 11 and 14 h compared to 8 and 17 h (Carew et al., 2003; Sønsteby and Heide, 2009a). Sønsteby and Heide (2009a) found that flowering of 'Polka' was promoted by LD. Lower buds on primocanes, although shown to be at an advanced stage of flower development, remained dormant for several months at 21°C and required 4 to 6 weeks of chilling at 2 to 4°C for growth activation and flowering; the proportion of dormant buds on the primocane was affected by temperature and photoperiod (Sønsteby and Heide, 2009a). Thus, if primocane-fruited raspberries are field grown in a region where the growing temperatures are relatively cool (12 to 15°C), in staggered plantings for off-season production, for example, only a relatively small portion of the tip of the primocane will fruit, with the remaining portion of the cane requiring a dormant period before fruiting the following season (on the floricanes). Thus, primocane-fruited raspberries should be grown at relatively high temperature (~25°C) to have most of the cane producing fruit leaving a minimal number of dormant buds. Planting date should be considered to avoid lower temperatures. In

Mediterranean climates, an extended harvest season can be obtained by early planting in tunnels and late planting in the field (Oliveira et al., 1996, 2001). In addition, cultivars that require less chilling and grow well in most environmental conditions would be an advantage for expanding production (Pitsioudis et al., 2009).

Cultivar and growing conditions also interact to determine how much of the primocane of an annual type flowers and fruits in the first year. 'Heritage' produced the most flowering nodes per primocane at the highest N rate and growing temperature studied (Lockshin and Elfving, 1981). They also found that increased N rate shortened the time for flowering to occur in 'Heritage'. However, this was not observed in the primocane-fruiting cultivar 'Amity' (DeGomez et al., 1986). Also light intensity influenced the fruiting and the higher the light intensity, the shorter the time from planting to fruiting in 'Autumn Bliss' (Carew et al., 2000). While this may have been a photosynthetic response, enrichment with CO<sub>2</sub> when primocane-fruiting red raspberries were grown in tunnels, had inconclusive results (Mochizuki et al., 2010).

Time of FBI in the annual-fruiting cultivar 'Heritage' has been induced by applications of daminozide, ethephon (e.g., Crandall and Garth, 1981; McGregor, 1987), and paclobutrazol (Braun and Garth, 1986). In areas where there is insufficient chilling for normal bud break, chemicals have been used successfully to break dormancy, stimulate lateral development, and increase yield (e.g., Snir, 1983).

In Portugal, cutting 'Autumn Bliss' back to ground level in July or August, delayed harvest, but also reduced yield, particularly with the later cutting dates after which growth and FBI was not ideal under lower temperatures (Oliveira et al., 1996). Oliveira et al. (2004) compared three summer cane cutting dates (to ground level) in July along with four cane densities (8, 16, 24, and 32 canes/m row) and found that delaying cutting date delayed harvest and reduced yield per cane and per row. While yield per cane was highest at the lowest density, cane densities of 16 and 25 canes/m produced the highest yield per row; they did not have an un-cut control for comparison. Cutting canes to delay growth, coupled with primocane management such as tipping to increase yield, may allow for late-season production of primocane-fruiting raspberry in tunnels in temperate climates (Meesters and Pitsioudis, 1999; Oliveira et al., 1994).

Pruning primocanes at 40 cm increased yield, but delayed the crop of 'Heritage' (DeGomez et al., 1986). In comparison, cutting primocanes back to 10 or 15 nodes, rather than cutting back to ground level, increased harvestable yield and advanced the crop in Portugal (Oliveira et al., 1998). In their study, primocanes were cut back to 10, 15, or 20 nodes after fruit harvest on the primocane had started. While they stated that pruning or primocane tipping earlier may lead to inhibition of development of fruiting lateral branches (Oliveira et al., 1998), this has since not been observed in the industry; the commercial practice of tipping primocanes to induce lateral branches, increasing yield and delaying harvest as much as 3 weeks, is relatively common in some production regions with certain cultivars (Strik, pers. obs.). This practice only seems to work if the lower buds on the primocanes have not yet initiated a flower bud. While primocane-fruiting raspberries are commonly grown in annual production systems in many warmer regions, it is possible that a combination of cutting (to delay) or row covers (to advance) and primocane tipping may allow for manipulation of harvest season in perennial systems in warmer or temperate climates.

Spun-bound poly-propylene row covers placed over 'Heritage' rows before primocane emergence and removed when primocanes were ~50 cm tall advanced harvest by as much as 3 weeks and increased yield compared to un-covered plants (Pritts et al., 1992). While there was no treatment effect on flowering node number, the advanced harvest allowed them to pick more of the crop. In contrast, polyethylene row covers have had no effect on harvest date or yield in primocane-fruiting red raspberries (Pritts et al., 1992; Nonnecke and Taber, 1989); however, air temperature of un-covered plots was in optimal range for growth and node production (Nonnecke and Taber, 1989).

## **BLACKBERRY (*RUBUS*)**

There have been fewer studies on factors that affect flower bud development in biennial and annual blackberries. In biennial blackberry cultivars, FBI is generally thought to be a SD response. Rate of FBD varied with blackberry type and cultivar and with prevailing winter temperature (Takeda et al., 2002a). In ‘Marion’ and ‘Boysen’ trailing blackberry, sepal primordia were first observed microscopically in November and December with FBD continuing through winter in Oregon. In Arkansas, FBD in ‘Cherokee’ erect blackberry started later than in Oregon, due to colder average temperatures. ‘Chester Thornless’ semi-erect blackberry did not show evidence of FBD until spring (Takeda et al., 2002a). Where FBI and FBD occurs in a basipetal fashion in biennial raspberry (Robertson, 1957), this is not the case in blackberry (Takeda et al., 2002b).

Bud break and perhaps FBI may be resource limited in biennial blackberry as it is in raspberry. Yield for August-trained ‘Marion’ blackberry was 45% greater than for February-trained plants, due to a greater percent bud break and more fruit per lateral with canes more exposed to light in autumn and winter (Bell et al., 1995). Primocane removal during the fruiting season did not increase yield of the floricanes in ‘Marion’ (Strik, unpublished) likely because most primocane growth in trailing blackberry occurs after the fruiting season (Cortell and Strik, 1997) and primocanes are trained under the canopy of the floricanes. Growing trailing blackberries in an alternate year production system increases yield relative to an every-year production system (Strik et al., 2007), mainly due to higher cane numbers in the absence of floricanes; however, cutting primocanes in the non-production year reduced fruit per lateral if done too late (Bell et al., 1995). Loss of primary buds on floricanes, either through winter cold injury (Strik, pers. obs.) or pruning (Strik et al., 1996), leads to compensation from later emerging laterals from secondary buds and a delay in flowering and production.

The semi-erect cultivar ‘Loch Ness’ can be double cropped in a greenhouse by cutting back the fruiting laterals at just past the last harvested fruit; secondary laterals emerge from basal lateral buds and from buds on the main cane allowing for a second crop about two months later without chilling. The “second crop” can be stimulated by higher rates of fertilizer N and lower night temperatures (Pitsioudis et al., 2009).

In Mexico, specialized production systems have been developed to extend the season for erect blackberry cultivars such as ‘Brazos’ and ‘Tupy’. About 5-7 months after primocane emergence, a chemical defoliant (a combination of urea or ammonium sulfate, copper sulfate, and mineral oil) is applied two to three times. The plants are then pruned by topping canes and shortening laterals. Gibberellic acid and thidiazuron (TDZ) are used about 3 weeks after defoliation to improve flowering and promote bud break. Fruit harvest begins about 90 to 100 days after defoliation. After the first crop is finished, many growers prune again, removing the portion of the cane that fruited, and repeat the defoliation process to obtain multiple crops. Growers then mow the canes to ground level to repeat the cycle. Often plants are grown in tunnels to protect fruit from adverse weather conditions. Using these methods, the Mexican fruiting season extends from mid-October to early May for the export market and May through June for local markets (Strik et al., 2007).

Annual-fruiting blackberries recently released from the University of Arkansas (Clark et al., 2005) will produce fruit on the tip portion of the primocane in the current season and on the base of the floricanes the following season, if desired. Primocane-fruiting blackberries go through FBI and FBD after a short period of growth (Lopez-Medina et al., 1999); however, little is known at this time about the influence of temperature or day length on rate of flower bud development.

The chilling requirement of the floricanes of ‘Prime-Jim’ seemed to range from 100 to 300 h (Carter et al., 2006); however the researchers also felt there may not be a chilling requirement as bud break was variable. Chilling of root cuttings of primocane-fruiting blackberry genotypes enhanced primocane growth and flowering (Lopez-Medina and Moore, 1999). Our preliminary work indicates primocane growth and flowering from the crown may respond to chilling in ‘Prime-Jan’ (Thompson and Strik, unpublished).



Primocane-fruiting blackberries show great promise for extended season production through growth of different genotypes/cultivars, advancing production through use of tunnels or row covers and delaying production by mowing primocanes during the growing season (Strik and Thompson, 2009).

Soft-tipping the primocane of annual blackberries at 1 m induced branching and increased flower and fruit number and yield three-fold without affecting fruiting season (Strik et al., 2008). Use of spun-bound row covers from late winter, before primocane emergence, through to ~60 cm primocane height, advanced flowering and fruiting by two weeks in Oregon (Strik et al., 2008). When primocanes were mowed back to ground level when height averaged ~0.5 m, fruit production was delayed by about four weeks (Thompson et al., 2009). Tipping the main cane and tipping the branches that were produced increased the number of flower buds, fruit, berry weight, and yield relative to tipping just the main cane, without affecting fruiting season. Producing primocane-fruiting blackberry in an un-heated tunnel extended the harvest season about 3 weeks in Oregon's temperate climate (Thompson et al., 2009). Growth and production ceased due to cool night temperatures rather than through reproductive development ceasing (Strik, pers. obs.).

A better understanding is needed of how plant water status, plant nutrition, and other cultural factors affect FBI, flowering time, and fruit quality in blackberry.

### **BLUEBERRY (*VACCINIUM*)**

In blueberry, FBI occurs under short day length in late summer and early fall (northern hemisphere), usually on the tip of the current season's shoot (Aalders and Hall, 1964; Bañados and Strik, 2006; Gough et al., 1978). Eight weeks of 8-, 10-, or 12-h photoperiod increased FBI compared to 14- or 16-h photoperiods (Hall et al., 1963). Six weeks of 8-h photoperiod in the fall promoted FBI in rabbiteye blueberry (Darnell, 1991). In southern highbush blueberry, Spann et al. (2003) found that FBI occurred in plants exposed to 8-h photoperiods, but not in plants exposed to 16-h photoperiods. Length of exposure to short days had no impact on the number of flower buds in southern highbush, but did affect flower bud quality, depending on temperature (Spann et al., 2004). Flower bud number was positively correlated with length of exposure to SD in northern highbush (Bañados and Strik, 2006). However, FBI appeared incomplete in plants exposed to only four weeks of short days and bloom was delayed compared to plants exposed to eight weeks.

There is limited information on the interaction between photoperiod and temperature on FBI in blueberry. In southern blueberry, FBI was reduced at 28°C compared with 21°C under a short day photoperiod (Spann et al., 2004); also, flowers that developed at the higher temperature remained in a dormant-like state, showing no further development, or abscised. They hypothesized that higher temperatures not only inhibited FBI in southern highbush, but impaired FBI as well, resulting in failure to open. In early-, mid-season, and late-season northern highbush blueberry cultivars, FBI only occurred under SD (at constant temp 22°C) with the number of flower buds correlated to the length of exposure. Plants grown under SD for four or more weeks ceased growth and entered endo-dormancy, whereas those grown under LD conditions had continuous growth and did not initiate flower buds or go dormant (Bañados and Strik, 2006).

Flower bud initiation proceeds basipetally with the number of floral buds per shoot affected by cultivar, climate, and production practices. Shoot growth often slows under short days, but this may be a response to a reduction in daily photosynthesis rather than a direct photoperiodic response.

Flower bud development continues until temperatures become too cool in fall. The chilling requirement for northern highbush cultivars ranges from 800-1500 h (at 0 to 7°C; Norvell and Moore, 1982), whereas southern highbush and rabbiteyes have a chilling requirement of 200-600 (Williamson et al., 2002) and 300-600 (Darnell and Davies, 1990), respectively. When northern highbush blueberries received chilling at 1, 6 or 12°C for 1000 hours, only chilling at a constant 6°C resulted in bud break (Norvell and Moore,

1982). Chilling for 1000 h at 6°C or at 6/1°C resulted in similar bud break (Norvell and Moore, 1982), even though the latter temperature regime provided only 500 h of chilling. In northern highbush blueberry, after 900 h of cold storage (4°C) to satisfy chilling, bud break and bloom occurred after 6 and 26 days, respectively, with little difference among cultivars (Bañados and Strik, 2006).

Blueberry growth and development is reviewed by Darnell (2006). Insufficient chilling in blueberry causes delayed and erratic bud break and a reduction in the number of buds that break (Darnell and Davies, 1990; Norvell and Moore, 1982). In general, the rate and amount of bud break increased as constant chilling in the range of 0.6 to 15°C increased (Darnell and Davies, 1990). Flower buds appear to have a lower chilling requirement than vegetative buds. In regions with borderline chilling units, use of hydrogen cyanamide (Dormex) to help break vegetative buds stimulates the development of shoots along with flower/fruit thus improving yield and quality (Krewer et al., 2007; Williamson et al., 2002).

Flower bud number in blueberry is dependent on photoperiod, temperature, and cultural practices that affect the time of growth cessation including nitrogen fertilization rate and timing and pruning (Bañados, 2006; Gough et al., 1978). In northern highbush blueberry, FBI and FBD required at least two weeks of shoot cessation before a flower bud could be visually identified at the apex (Bañados and Strik, 2006).

Decreasing light intensity reduced FBI and flower bud number (Hall, 1958) and rate of fruit maturation (Aalders et al., 1969). In rabbiteye blueberry 83% of the flower buds were found in the top 0.6 m of the canopy; thus relatively few buds were formed in the lower canopy where light levels were less than 9 to 18% of full sun (Yáñez et al., 2009). Use of shade nets can be used to delay harvest in blueberry, but shade can reduce photosynthesis and percent soluble solids of fruit (Lobos et al., 2009) and FBI, reducing next year's crop.

Plant water deficit during the FBI period reduced flower bud number and fruit number the following season (Mingeau et al., 2001).

Summer pruning of vigorous growth in highbush blueberry leads to the production of lateral shoots, depending on pruning date (Bañados et al., 2009). Longer lateral length was positively correlated with the number of flower buds (Bañados, 2006; Bañados et al., 2009).

Pruning in summer delayed FBD and subsequently fruit harvest the following year by 1 to 2 weeks, depending on pruning date, compared to un-pruned plants (Bañados et al., 2009). Dormant pruning has been shown to advance fruit harvest, relative to un-pruned plants, an indirect effect due to lower yield on pruned plants (Strik et al., 2003). Producing too much fruit on young plants reduced growth and subsequent yield (Strik and Buller, 2005), due to a reduction in the number of shoot growth flushes and shoot number on plants that had a competing sink strength of fruit (Strik et al., 2006).

Row covers have been used to advance or delay the crop of blueberries (Hicklenton et al., 2003), but this is not yet a commercial practice. Use of un-heated, closed tunnels advanced FBI by 38-39 days for 'Emerald' and 'Jewel' compared to outdoor plants (Ogden and Iersel, 2009). Tunnels have been used successfully to advance the crop of blueberries from 1 to 5 weeks (Bal, 1996; Baptista et al., 2006; Ciordia et al., 2006) and to extend the harvest season up to five months (Bal, 1996).

Although, protected structures can be used to modify fruiting season in blueberry, more commonly blueberries in warmer regions are grown in evergreen systems. In the evergreen blueberry production system leaves are retained longer in fall and winter allowing for continued perception of the SD photoperiod and therefore continued FBI, increasing flower bud number relative to plants grown in the dormant system (Reeder et al., 1998; Swain and Darnell, 2002). Evergreen systems in combination with pruning and fertilization programs can be used to manipulate the harvest season; some cultivars are more adapted to this production system than others.

## CONCLUSIONS

In many berry crops, flower bud initiation and differentiation are clearly affected by photoperiod and temperature with these often having interactive effects. Separating out the direct effects of light intensity on FBI compared to indirect effects through increased photosynthesis and plant reserves or carbohydrate status has been difficult. Cultural practices such as pruning, fertilization, and application of growth regulators have been successfully used to manipulate fruiting season in berry crops. However, the opposing effects of needing adequate nitrogen (N) for plant health and good FBI and excessive N promoting excessive growth and reducing FBI are not well researched in many berry crops.

In strawberry and biennial cropping red raspberry, pre-conditioned plants are commonly used along with staggered planting dates (often in tunnels) to time harvest date. The nursery plants in these systems must be grown under optimal conditions to promote good FBI and FBD and thus maximize potential yield per plant.

More information is needed about the chilling requirement of many berry crops. Equal hours of chilling in cold storage are not “equal” to similar hours in the field. At present, little is known about the effect of fluctuating temperatures and how to best simulate more “natural” chilling - this would have a large impact on off-season production systems.

In primocane-fruiting raspberry, annual production systems with staggered planting dates, often in combination with pruning techniques, are used to target market windows. This system of production shows promise in primocane fruiting blackberry; however, manipulation of this crop in perennial systems is underway at present.

Row covers have been used to advance and/or increase crop in various berry crops, but yield responses depend on crop, cultivar, time of row cover application and removal, and climate. Tunnels covered with plastic and sometimes also shade cloth are relatively common in off-season production systems to assist in climate modification and protection from harmful environmental effects.

With blueberry production expanding worldwide, rapid advancements are being made in manipulating southern highbush blueberry cultivars, using evergreening systems, pruning, and fertilization methods, to produce fruit during high-priced markets. Such systems are only possible in warmer growing regions.

With a good understanding of plant physiology and the factors that affect FBI, FBD, bud break, and the production of high-quality fruit, it is possible to manipulate many berry crops to time fruit production for desirable market windows. Economical systems have been developed in many production regions and research in this area is ongoing.

## Literature Cited

- Aalders, L.E. and Hall, I.V. 1964. A comparison of flower bud development in the lowbush blueberry, *V. angustifolium* Ait. under greenhouse and field conditions. Proc. Amer. Soc. Hort. Sci. 85:281-284.
- Aalders, L.E., Hall, I.V. and Forsyth, F.R. 1969. Effects of partial defoliation and light intensity on fruit set and berry development in the lowbush blueberry. Hort. Res. 9:124-129.
- Abbott, A.J. 1968. Growth of the strawberry plant in relation to nitrogen and phosphorus nutrition. J. Hort. Sci. 43:491-504.
- Abbott, A.J., Best, G.R. and Webb, R.A. 1970. The relationship of achene number to berry weight in strawberry fruit. J. Hort. Sci. 45:215-222.
- Avigdor-Avidov, H., Goldschmidt, E.E. and Kedar, N. 1977. Involvement of endogenous gibberellins in the chilling requirements of strawberry (*Fragaria* × *ananassa* Duch.). Ann. Bot. 41:927-936.
- Bal, J.J.M. 1996. Blueberry culture in greenhouses, tunnels, and under raincovers. Acta Hort. 446:327-332.
- Bañados, M.P. 2006. Dry weight and <sup>15</sup>N-nitrogen and partitioning, growth, and

- development of young and mature blueberry plants. Ph.D. thesis, Oregon State University, 172p.
- Bañados, M.P. and Strik, B. 2006. Manipulation of the annual growth cycle of blueberry using photoperiod. *Acta Hort.* 715:65-71.
- Bañados, P., Uribe, P. and Donnay, D. 2009. The effect of summer pruning date in ‘Star’, ‘O’Neal’ and ‘Elliott’. *Acta Hort.* 810:501-507.
- Baptista, M.C., Oliveira, P.B., Lopes da Fonseca, L. and Oliveira, C.M. 2006. Early ripening of southern highbush blueberries under mild winter conditions. *Acta Hort.* 446:191-196.
- Beccaro, G., Bounous, G., Baudino, M. and Giordano, R. 2004. Modification of the bearing period of red raspberry cv. Tulameen with cold stored bare root and potted long-canes planted at different dates. *Acta Hort.* 649:297-299.
- Bell, N., Strik, B. and Martin, L. 1995. Effect of date of primocane suppression on ‘Marion’ trailing blackberry. I. Yield components. *J. Amer. Soc. Hort. Sci.* 120:21-24.
- Black, B.L. 2004. Prohexadione-calcium decreases fall runners and advances branch crown of ‘Chandler’ strawberry in a cold-climate annual production system. *J. Amer. Soc. Hort. Sci.* 129:479-485.
- Blatt, D.R. 1981. Effect of nitrogen source, rate and time of application on fruit yields of the Micmac strawberry. *Commun. Soil Sci. Plant Anal.* 12:511-518.
- Bradford, E., Hancock, J.F. and Warner, R.M. 2010. Interactions of temperature and photoperiod determine expression of repeat flowering in strawberry. *J. Amer. Soc. Hort. Sci.* 135:102-107.
- Braun, J.W. and Garth, J.K.L. 1986. Growth and fruiting of ‘Heritage’ primocane fruiting red raspberry in response to paclobutrazol. *HortScience* 21:437-439.
- Brennan, R.M., McNicol, R., Gillespie, T. and Raffle, S. 1999. Factors affecting out-of-season *Rubus* production. *Acta Hort.* 505:115-120.
- Carew, J.G., Gillespie, T., White, J., Wainwright, R., Brennan, R. and Battey, N.H. 2000. The control of the annual growth cycle in raspberry. *J. Hort. Sci. & Biotech.* 75:495-503.
- Carew, J.G., Mahmood, K., Darby, J., Hadley, P. and Battey, N.H. 2001. The effects of low temperature on vegetative growth and flowering of the primocane fruiting raspberry ‘Autumn Bliss’ raspberry. *J. Hort. Sci. & Biotech.* 76:264-270.
- Carew, J.G., Mahmood, K., Darby, J., Hadley, P. and Battey, N.H. 2003. The effect of temperature, photosynthesis photon flux density, and photoperiod on the vegetative growth and flowering of ‘Autumn Bliss’ raspberry. *J. Amer. Soc. Hort. Sci.* 128:291-296.
- Carter, P.M., Clark, J.R., Drake Particka, C. and Yazzetti Crowne, D. 2006. Chilling response of Arkansas blackberry cultivars. *J. Amer. Pom. Soc.* 60:187-197.
- Chabot, B.F. 1978. Environmental influences on photosynthesis and growth in *Fragaria vesca*. *New Phytol.* 80:87-98.
- Ciordia, M., Garcia, J.C. and Diaz, M.B. 2006. Off-season production of southern highbush blueberries in the north of Spain. *Acta Hort.* 715:317.
- Clark, J.R., Moore, J.N., Lopez-Medina, J., Finn, C. and Perkins-Veazie, P. 2005. ‘Prime-Jan’ (‘APF-8’) and ‘Prime-Jim’ (‘APF-12’) primocane-fruiting blackberries. *HortScience* 40:852-855.
- Collins, W.B. 1966. Floral initiation in strawberry and some effects in red and far-red radiation as components of continuous white light. *Can. J. Bot.* 44:663-668.
- Cortell, J. and Strik, B. 1997. Effect of florican number in ‘Marion’ trailing blackberry. I. Primocane growth and cold hardiness. *J. Amer. Soc. Hort. Sci.* 122:604-610.
- Crandall, P.C. and Garth, J.K.L. 1981. Yield and growth response of ‘Heritage’ raspberry to daminozide and ethephon. *HortScience* 16:654-655.
- Crandall, P.C., Chamberlain, J.D. and Garth, J.K.L. 1980. The effects of chemical primocane suppression on growth, yield, and chemical composition of red raspberries. *J. Amer. Soc. Hort. Sci.* 105:194-196.
- Dale, A. 1989. Productivity in red raspberries. *Hort. Rev.* 2:185-228.

- Dale, A. 2008. Raspberry production in greenhouses: physiological aspects. *Acta Hort.* 777:219-223.
- Dale, A., Luby, J.J. and Hancock, J.F. 2002. Breeding day neutral strawberries for northern North America. *Acta Hort.* 567:133-136.
- Dale, A., Pirgozliev, S., King, E.M. and Sample, A. 2005. Scheduling primocane-fruiting raspberries (*Rubus idaeus* L.) for year-round production in greenhouses by chilling and summer-pruning of canes. *J. Hort. Sci. & Biotech.* 80:346-350.
- Darnell, R.L. 1991. Photoperiod, carbon partitioning, and reproductive development in rabbiteye blueberry. *J. Amer. Soc. Hort. Sci.* 116:856-860.
- Darnell, R.L. 2003. The Strawberry. A Book for Growers, Others. N.F. Childers (ed.), Dr. Norman F. Childers Publications, Gainesville, FL, p.3-10.
- Darnell, R.L. 2006. Blueberry botany/environmental physiology. p.5-13. In: N.F. Childers (ed.), Blueberries. For Growers, Gardeners, Promoters. Dr. Norman F. Childers Publications, Gainesville, FL.
- Darnell, R.L. and Davies, F.S. 1990. Chilling accumulation, budbreak, and fruit set of young rabbiteye blueberry plants. *HortScience* 25:635-638.
- Darnell, R.L. and Hancock, J.F. 1996. Balancing vegetative and reproductive growth in strawberry. p.144-150. In: M.V. Pritts, C.K. Chandler and T.E. Crocker (eds.), Proc. IV N.A. Straw. Conf., Hort. Sci. Dept., Univ. Fla. Gainesville, Fla.
- Darnell, R.L., Alvarado-Raya, H.E. and Williamson, J.G. 2008. Root pruning effects on growth and yield of red raspberry. *HortScience* 43:681-684.
- Darrow, G.M. 1936. Interrelation of temperature and photoperiodism in the production of fruit buds and runners in the strawberry. *Proc. Amer. Soc. Hort. Sci.* 34:360-363.
- Darrow, G.M. and Waldo, G.F. 1932. Effect of fertilizers on plant growth, yield and decay of strawberries in North Carolina. *Proc. Amer. Soc. Hort. Sci.* 29:318-324.
- DeGomez, T.E., Martin, L.W. and Breen, P.J. 1986. Effect of nitrogen and pruning on primocane fruiting red raspberry 'Amity'. *HortScience* 21:441-442.
- Deng, X. and Woodward, F.I. 1998. The growth and yield responses of *Fragaria* × *ananassa* to elevated CO<sub>2</sub> and N supply. *Ann. Bot.* 81:67-71.
- Dennis, F.G., Lipecki, J. and Kiang, C. 1970. Effect of photoperiod and other factors upon flowering and runner development of three strawberry cultivars. *J. Amer. Soc. Hort. Sci.* 95:750-754.
- Desmet, E.M., Verbraeken, L. and Baets, W. 2009. Optimisation of nitrogen fertilization prior to and during flowering process on performance of short day strawberry 'Elsanta'. *Acta Hort.* 842:675-678.
- Dijkstra, J. and Scholtens, A. 1993. Growing early and late raspberries in containers. *Acta Hort.* 352:49-54.
- Durner, E.F. and Poling, E.B. 1987. Flower bud induction, initiation, differentiation, and development in the 'Earliglow' strawberry. *Sci. Hort.* 31:61-69.
- Durner, E.F. and Poling, E.B. 1988. Strawberry developmental responses to photoperiod and temperature: a review. *Adv. Straw. Prod.* 7:6-14.
- Durner, E.F., Barden, J.A., Himelrick, D.G. and Poling, E.B. 1984. Photoperiod and temperature effects on flower and runner development in day neutral, June bearing, and everbearing strawberries. *J. Amer. Soc. Hort. Sci.* 109:396-400.
- Fear, C.D. and Nonnecke, G.R. 1989. Soil mulches influence reproductive and vegetative growth of 'Fern' and 'Tristar' day-neutral strawberries. *HortScience* 6:912-913.
- Ferree, D.C. and Stang, E.J. 1988. Seasonal plant shading, growth, and fruiting in 'Earliglow' strawberry. *J. Amer. Soc. Hort. Sci.* 113:322-327.
- Freeman, J.A., Eaton, G.W., Baumann, T.E., Daubeney, H.A. and Dale, A. 1989. Primocane removal enhances yield components of raspberries. *J. Amer. Soc. Hort. Sci.* 114:6-9.
- Gast, K.L.B. and Pollard, J.E. 1991. Rowcovers enhance reproductive and vegetative yield components in strawberries. *HortScience* 26:1467-1469.
- Gough, R.E., Shutak, V.G. and Hauke, R.L. 1978. Growth and development of highbush blueberry. II. Reproductive growth, histological studies. *J. Amer. Soc. Hort. Sci.*

- 103:476-479.
- Guttridge, C.G. 1969. *Fragaria*. p.247-267. In: L.T. Evans (ed.), The Induction of Flowering. Cornell Univ. Press, Ithaca, NY.
- Guttridge, C.G. 1985. *Fragaria* × *ananassa*. p.16-33. In: A.H. Halevy (ed.), Handbook of Flowering. Vol. III. CRC Press, Boca Raton, Fla.
- Guttridge, C.G. and Thompson, P.A. 1963. The effects of gibberellins on growth and flowering of *Fragaria* and *Duchesna*. J. Exp. Bot. 15:631-646.
- Guttridge, C.G. and Wood, C.A. 1961. Defoliation of strawberry plants. Scottish Agr. 41:39-42.
- Hall, I.V. 1958. Some effects of light on native lowbush blueberries. Proc. Amer. Soc. Hort. Sci. 72:216-218.
- Hall, I.V., Craig, D.L. and Aalders, L.E. 1963. The effect of photoperiod on the growth and flowering of the highbush blueberry (*Vaccinium corymbosum* L.) Proc. Amer. Soc. Hort. Sci. 82:260-263.
- Hancock, J.F. 1999. Strawberries. CABI Publish., New York, NY.
- Hartmann, H.T. 1947. The influence of temperature on the photoperiodic response of several strawberry cultivars grown under controlled environment conditions. Proc. Amer. Soc. Hort. Sci. 50:243-245.
- Hartz, T.K., Baameur, A. and Holt, D.B. 1991. Carbon dioxide enrichment of high-value crops under tunnel culture. J. Amer. Soc. Hort. Sci. 116:970-973.
- Heide, O. 1977. Photoperiod and temperature interactions in growth and flowering of strawberry. Physiol. Plant. 40:21-26.
- Heiberg, N., Lunde, R., Nes, A. and Hageberg, B. 2008. Long cane production of red raspberry plants and effect of cold storage. Acta Hort. 777:225-229.
- Hicklenton, P., Forney, C. and Domytrak, C. 2003. Use of row covers and post harvest storage techniques to alter maturity and marketing period for highbush blueberries. Acta Hort. 626:287-295.
- Hytönen, T., Mouhu, K., Koivu, I., Elomaa, P. and Junttila, O. 2008. Prohexadione-calcium enhances the cropping potential and yield of strawberry. Eur. J. Hort. Sci. 73:210-215.
- Ito, H. and Saito, T. 1962. Studies on the flower formation in the strawberry plants. I. Effects of temperature and photoperiod on the flower formation. Tahoku J. Agric. Res. 13:191-203.
- Keep, E. 1961. Autumn-fruiting in raspberries. J. Hort. Sci. 36:174-185.
- Krewer, G., Cline, B. and NeSmith, D.S. 2007. Southeast regional blueberry horticulture and growth regulator guide. The Southern Region Small Fruits Consortium. <http://www.smallfruits.org/SmallFruitsRegGuide>.
- Kronenberg, H.G. and Wasenaar, L.M. 1972. Dormancy and chilling requirement of strawberry varieties for early forcing. Euphytica 21:454-459.
- Latet, G., Meesters, P. and Bries, J. 2002. The influence of different nitrogen (N) sources on the yield and leaching in open field strawberry production. Acta Hort. 567:455-458.
- Le Mière, P., Hadley, P., Darby, J. and Battey, N.H. 1996. The effect of temperature and photoperiod on the rate of flower initiation and the onset of dormancy in the strawberry (*Fragaria* × *ananassa* Duch.). J. Hort. Sci. 71:361-371.
- Le Mière, P., Hadley, P., Darby, J. and Battey, N.H. 1998. The effect of thermal environment, planting date and crown size on growth, development and yield of *Fragaria* × *ananassa* Duch. cv. Elsanta. J. Hort. Sci. & Biotech. 73:786-795.
- Lieten, P. 2002. The effect of nutrition prior to and during flower differentiation on phyllody and plant performance of short day strawberry Elsanta. Acta Hort. 567:345-348.
- Lobos, G.A., Retamales, J.B., del Pozo, A., Hancock, J.F. and Flore, J.A. 2009. Physiological response of *Vaccinium corymbosum* 'Elliott' to shading nets in Michigan. Acta Hort. 810:465-470.
- Lockshin, L.S. and Elfving, D.C. 1981. Flowering response of 'Heritage' red raspberry to

- temperature and nitrogen. HortScience 16:527-528.
- Long, J.H. 1939. The use of certain nutrient elements at the time of flower formation in the strawberry. Proc. Amer. Soc. Hort. Sci. 37:157-168.
- Lopez-Medina, J. and Moore, J.N. 1999. Chilling enhances cane elongation and flowering in primocane-fruiting blackberries. HortScience 34:638-640.
- Lopez-Medina, J., Moore, J.N. and Kim, K.-S. 1999. Flower bud initiation in primocane-fruiting blackberry germplasm. HortScience 34:132-136.
- McGregor, G.R. 1987. Daminozide affects growth and yield of 'Heritage' red raspberry. HortScience 22:38-40.
- Meesters, P. and Pitsioudis, A. 1999. Extension of the harvest period of raspberries in Belgium (moderate maritime climate). Acta Hort. 505:419-421.
- Mingeau, M., Perrier, C. and Ameglio, T. 2001. Evidence of drought-sensitive periods from flowering to maturity on highbush blueberry. Sci. Hort. 89:23-40.
- Mochizuki, M.J., Daugovish, O., Ahumada, M.H., Ashkan, S. and Lovatt, C.J. 2010. Carbon dioxide enrichment may increase yield of field-grown red raspberry under high tunnels. HortTech. 20:213-219.
- Mochizuki, T., Yoshida, Y., Yanagi, T., Okimura, M., Yamasaki, A. and Takahashi, H. 2009. Forcing culture of strawberry in Japan - production technology and cultivars. Acta Hort. 842:107-109.
- Mori, T. 1998. Effect of temperature during flower bud formation on achene number and fresh weight of strawberries. J. Jap. Soc. Hort. Sci. 67:396-399.
- Neocleous, D., Papadopoulos, I. and Vasilakakis, M. 2005. Growing red raspberry in soilless culture under different chilling treatments for early summer production. Small Fruits Rev. 4:37-48.
- Nishiyama, M. and Kanahama, K. 2000. Effect of temperature and photoperiod on the development of inflorescences in everbearing strawberry (*Fragaria × ananassa* Duch.) plants. Acta Hort. 514:261-267.
- Nonnecke, G.R. and Taber, H.G. 1989. Effects of row cover on vegetative and reproductive growth of 'Heritage' red raspberry. Acta Hort. 262:391-394.
- Norvell, D.J. and Moore, J.N. 1982. An evaluation of chilling models for estimating rest requirements of highbush blueberries. J. Amer. Soc. Hort. Sci. 107:54-56.
- Ogden, A.B. and van Iersel, M.W. 2009. Southern highbush blueberry production in high tunnels: temperatures, development, yield, and fruit quality during the establishment years. HortScience 44:1850-1856.
- Oliveira, P.B., Lopes da Fonseca, L. and Monteiro, A.A. 1994. Influence of summer pruning on winter production of primocane fruiting red raspberries under protected cultivation in mild winter climates. Acta Hort. 357:295-302.
- Oliveira, P.B., Lopes da Fonseca, L. and Monteiro, A.A. 2001. Combining different growth techniques for all-year-round red raspberry production in Portugal. Acta Hort. 585:545-553.
- Oliveria, P.B., Oliveria, C.M. and Monteiro, A.A. 2004. Pruning date and cane density affect primocane development and yield of 'Autumn Bliss' red raspberry. HortScience 39:520-524.
- Oliveira, P.B., Oliveira, C.M., Lopes da Fonseca, L. and Monteiro, A.A. 1996. Off-season production of primocane-fruiting red raspberry using summer pruning and polyethylene tunnels. HortScience 31:805-807.
- Oliveira, P.B., Oliveira, C.M., Machado, P.V., Lopes da Fonseca, L. and Monteiro, A.A. 1998. Improving off-season production of primocane-fruiting red raspberry by altering summer-pruning intensity. HortScience 33:31-33.
- Opstad, N. and Sønsteby, A. 2008. Flowering and fruit development in strawberry in a field experiment with two fertilizer strategies. Acta Agric. Scand. Section B: Soil Plant Sci. 58:297-304.
- Palencia, P., Martinez, F., Medina, J.J., Vazquez, E., Flores, F. and Lopez-Medina, J. 2009. Effects of climate change on strawberry production. Acta Hort. 838:51-53.
- Pitsioudis, A., Latet, G. and Meesters, P. 2002. Out of season production of raspberries.

- Acta Hort. 585:555-560.
- Pitsioudis, F., Odeurs, W. and Meesters, P. 2009. Early and late production of raspberries, blackberries, and red currants. Acta Hort. 838:33-37.
- Pritts, M., Hanson, E., Fiola, J. and Kelly, M.J. 1992. Rowcovers accelerate fruiting and increase productivity in primocane-fruiting red raspberries. HortTech. 2:46-51.
- Pritts, M.P., Langhans, R.W., Whitlow, T.H., Kelly, M.J. and Roberts, A. 1999. Winter raspberry production in greenhouses. HortTech. 9:13-15.
- Pritts, M.P., Worden, K.A. and Eames-Sheavly, M. 1989. Rowcover material and time of application and removal affect ripening and yield of strawberries. J. Amer. Soc. Hort. Sci. 114:531-536.
- Reeder, R.K., Obreza, T.A. and Darnell, R.L. 1998. Establishment of a nondormant blueberry (*Vaccinium corymbosum* hybrid) production system in a warm winter climate. J. Hort. Sci. 73:655-663.
- Renquist, A.R., Breen, P.J. and Martin, L.W. 1982. Effect of polyethylene mulch and summer irrigation regimes on subsequent flowering and fruiting of 'Olympus' strawberry. J. Amer. Soc. Hort. Sci. 107:373-376.
- Robertson, M. 1957. Further investigations of flower-bud development in the genus *Rubus*. J. Hort. Sci. 32:265-273.
- Serçe, S. and Hancock, J.F. 2005. Inheritance of day-neutrality in octoploid species of *Fragaria*. J. Amer. Soc. Hort. Sci. 130:580-584.
- Shaw, D.V. 2003. Heterogeneity of segregation ratios from selfed progenies demonstrate polygenic inheritance for day neutrality in strawberry (*Fragaria* × *ananassa* Duch.). J. Amer. Soc. Hort. Sci. 128:504-507.
- Snir, I. 1983. Chemical dormancy breaking of red raspberry. HortScience 18:710-713.
- Sønsteby, A. and Heide, O.M. 2006a. Dormancy relations and flowering of the strawberry cultivars Korona and Elsanta as influenced by photoperiod and temperature. Sci. Hort. 110:57-67.
- Sønsteby, A. and Heide, O.M. 2006b. Out-of-season strawberry production in Norway: yield responses of cv *Korona* to photoperiod preconditioning treatment. Acta Hort 708:371-374.
- Sønsteby, A. and Heide, O.M. 2007. Long-day control of flowering in everbearing strawberries. J. Hort. Sci. & Biotech. 82:875-884.
- Sønsteby, A. and Heide, O.M. 2008. Environmental control of growth and flowering of *Rubus idaeus* L. cv. Glen Ample. Sci. Hort. 117:249-256.
- Sønsteby, A. and Heide, O.M. 2009a. Effects of photoperiod and temperature on growth and flowering in the annual (primocane) fruiting raspberry (*Rubus idaeus* L.) cultivar 'Polka'. J. Hort. Sci. & Biotech. 84:439-446.
- Sønsteby, A. and Heide, O.M. 2009b. Long-day flowering response of everbearing strawberries. Acta Hort. 842:777-780.
- Sønsteby, A. and Heide, O.M. 2009c. Temperature limitations for flowering in strawberry and raspberry. Acta Hort 838:93-97.
- Sønsteby, A., Myrheim, U., Heiberg, N. and Heide, O.M. 2009a. Production of high yielding red raspberry long canes in a northern climate. Sci. Hort. 121:289-297.
- Sønsteby, A., Opstad, N., Myrheim, U. and Heide, O.M. 2009b. Interaction of short day and timing of nitrogen fertilization on growth and flowering of 'Korona' strawberry (*Fragaria* × *ananassa* Duch.). Sci. Hort. 123:204-209.
- Spann, T.M., Williamson, J.G. and Darnell, R.L. 2003. Photoperiodic effects on vegetative and reproduction growth of *Vaccinium darrowi* and *V. corymbosum* interspecific hybrids. HortScience 38:192-195.
- Spann, T.M., Williamson, J.G. and Darnell, R.L. 2004. Photoperiod and temperature effects on growth and carbohydrate storage in southern highbush blueberry interspecific hybrid. J. Amer. Soc. Hort. Sci. 129:294-298.
- Swain, P.A.W. and Darnell, R.L. 2002. Production systems influence source limitations to growth in 'Sharpblue' southern highbush blueberry. J. Amer. Soc. Hort. Sci. 127:409-414.



- Strik, B.C. 1985. Flower bud initiation in strawberry cultivars. *Fruit Var. J.* 39:5-9.
- Strik, B. and Buller, G. 2005. The impact of early cropping on subsequent growth and yield of highbush blueberry in the establishment years at two planting densities is cultivar dependant. *HortScience* 40:1998-2001.
- Strik, B.C. and Proctor, J.T.A. 1988a. The importance of growth during flower bud differentiation to maximizing yield in strawberry genotypes. *Fruit Var. J.* 42:45-48.
- Strik, B.C. and Proctor, J.T.A. 1988b. The relationship between achene number, achene density and berry fresh weight in strawberry. *J. Amer. Soc. Hort. Sci.* 113:620-623.
- Strik, B.C. and Thompson, E. 2009. Primocane-fruiting blackberries - Potential for extending harvest season and production regions. *HortScience* 44:23-24.
- Strik, B., Buller, G. and Hellman, E. 2003. Pruning severity affects yield, berry weight, and picking efficiency of highbush blueberry. *HortScience* 38:196-199.
- Strik, B., Buller, G. and Righetti, T. 2004. Influence of rate, timing and method of nitrogen fertilizer application on uptake and use of fertilizer nitrogen, growth, and yield of June-bearing strawberry. *J. Amer. Soc. Hort. Sci.* 129:165-174.
- Strik, B., Cahn, H., Bell, N., Cortell, J. and Mann, J. 1996. What we've learned about 'Marion' blackberry-potential alternative production systems. *Proc. Ore. Hort. Soc.* 87:131-136.
- Strik, B.C., Clark, J.R., Finn, C.E. and Bañados, P. 2007. Worldwide production of blackberries, 1995 to 2005 and predictions for growth. *HortTech.* 17:205-213.
- Strik, B., Clark, J.R., Finn, C. and Buller, G. 2008. Management of primocane-fruiting blackberry to maximize yield and extend the fruiting season. *Acta Hort.* 777:423-428.
- Strik, B., White, L., Bañados, M.P. and Calamar, A. 2006. Impact of management practices on blueberry shoot growth. *Proc. 10<sup>th</sup> North American Blueberry Research and Extension Worker's Conference*, Tifton, GA, June 4-8, 2006: p.123-129.
- Takeda, F. 1993. Chilling affects flowering of primocane-fruiting 'Heritage' red raspberry. *Acta Hort.* 352:247-252.
- Takeda, F., Glenn, D.M. and Stutte, G.W. 2008. Red light affects flowering under long days in a short-day strawberry cultivar. *HortScience* 43:2245-2247.
- Takeda, F., Strik, B., Peacock, D. and Clark, J.R. 2002a. Cultivar differences and the effect of winter temperature on flower bud development in blackberry. *J. Amer. Soc. Hort. Sci.* 127:495-501.
- Takeda, F., Strik, B., Peacock, D. and Clark, J.R. 2002b. Patterns of floral bud development in canes of erect and trailing blackberry. *J. Amer. Soc. Hort. Sci.* 128:3-7.
- Taylor, D.R. 2002. The physiology of flowering in strawberry. *Acta Hort* 567:245-251.
- Tehraniifar, A. and Battey, N.H. 1997. Comparison of the effects of GA<sub>3</sub> and chilling on vegetative vigour and fruit set in strawberry. *Acta Hort.* 439:627-631.
- Thompson, E., Strik, B.C., Finn, C.E., Zhao, Y. and Clark, J.R. 2009. High tunnel vs. open field: management of primocane-fruiting blackberry using pruning and tipping to increase yield and extend the fruiting season. *HortScience* 44:1581-1587.
- Vasilakakis, M.D., McCown, B.H. and Dana, M.H. 1980. Low temperature and flowering of primocane-fruiting red raspberry. *HortScience* 15:750-751.
- Verheul, M.J., Sønsteby, A. and Grimstad, S.O. 2007. Influences of day and night temperatures on flowering of *Fragaria* × *ananassa* Duch., cvs. Korona and Elsanta. *Sci. Hort.* 112:200-206.
- Vince-Prue, D. and Guttridge, C.G. 1973. Floral initiation in strawberry: spectral evidence for the regulation of flowering by long day inhibition. *Planta* 110:165-172.
- Williams, I.H. 1959. Effects of environment on *Rubus idaeus* L. IV. Flower initiation and development of the inflorescence. *J. Hort. Sci.* 34:219-228.
- Williams, I.H. 1960. Effects of environment on *Rubus idaeus* L. V. Dormancy and flowering of the mature shoot. *J. Hort. Sci.* 35:214-220.
- Williamson, J.F., Krewer, G., Maust, B.E. and Miller, E.P. 2002. Hydrogen cyanamide accelerates vegetative budbreak and shortens fruit development period of blueberry. *HortScience* 37:539-542.
- Williamson, B., Lawson, H.M., Woodford, J.A.T., Hargreaves, A.J., Wiseman, J.S. and

- Gordon, S.C. 1979. Vigour control, an integrated approach to cane, pest and disease management in red raspberry (*Rubus ideaus*). Ann. Appl. Biol. 92:359-368.
- Wood, C.A., Anderson, M.M. and Freeman, G.H. 1961. Studies of the cultivation of raspberries I. The effects of planting distances and of the winter tipping of canes. Hort. Res. 1:3-24.
- Yamasaki, A. and Yano, T. 2009. Effect of supplemental application of fertilizers on flower bud initiation and development of strawberry - possible role of nitrogen. Acta Hort. 842:765-768.
- Yamasaki, A., Yoneyama, T., Tanaka, F., Tanaka, K. and Nakashima, N. 2002. Tracer studies on the allocation of carbon and nitrogen during flower induction of strawberry plants as affected by the nitrogen level. Acta Hort. 567:349-352.
- Yáñez, P., Retamales, J.B., Lobos, G.A. and del Pozo, A. 2009. Light environment within mature rabbiteye blueberry canopies influences flower bud formation. Acta Hort. 810:471-473.
- Zhang, L., Strik, B.C. and Martin, L.W. 1992. Date of renovation affects fall and summer fruiting of June-bearing strawberry. Adv. Straw. Res. 11:47-50.