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Flowering of kiwifruit (*Actinidia deliciosa*) is reduced by long photoperiods

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Abstract Mature kiwifruit (*Actinidia deliciosa* 'Hayward') vines grown under standard orchard management were exposed to 16-h photoperiods from the longest day in summer until after leaf fall in autumn. Photoperiod extension was achieved with tungsten halogen lamps that produced 2–8 μmols m^{-2} s^{-1} photosynthetically active radiation. Long day treatments did not affect fruit dry matter or fruit weight at harvest during the growing season that the treatments were applied or during the following growing season. However, flowering was reduced by 22% during the spring following treatment application. As this reduction in flowering was not accompanied by a decrease in budbreak, the long day effect is not consistent with a delay in the onset of winter chilling. It is suggested therefore, that the observed reduction in flowering may be because of a diminution of floral evocation.

Keywords winter chilling; floral evocation; floral commitment; flowering; *Actinidia*

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INTRODUCTION

Flower development in kiwifruit (*Actinidia deliciosa* (A. Chev.) C.F. Liang et A.R. Ferguson 'Hayward') is spread over two growing seasons, as is seen in citrus (Lord & Eckard 1985), grape (Pratt 1971), and olive (Hartmann 1951). In kiwifruit, shortly after budbreak in the first growing season, the first axillary buds (first-order buds) are initiated on developing shoots. Second-order meristems then develop in the axils of the budscales and leaf primordia of these buds (Snowball 1995; Walton at al. 1997). The most basal of meristems differentiate second-order buds (termed basal buds by Brundell (1975a)) and the rest remain as meristems until the beginning of the second growing season. Consequently, no floral structures can be seen in dormant kiwifruit buds during winter. During spring of the second growing season, the meristems located in the basal nodes of the first-order buds tend to differentiate inflorescences and those in the distal nodes tend to differentiate new second-order buds (Walton & Fowke 1993). The relatively long period between floral evocation and flower differentiation may render kiwifruit more susceptible to reversion (Tooke et al. 2005) and/or flower abortion. Good descriptions of kiwifruit flower differentiation can be found in Brundell (1975b) and Polito & Grant (1984). The second-order buds initiated during the spring of the second growing season are analogous to the first-order buds initiated during the first growing season, thereby reiterating the cycle of growth and development.

Given the temporal separation between second-order meristem initiation and flower differentiation, there has been some effort directed towards determining when kiwifruit meristems undergo evocation (or floral commitment). Sequential shoot-defoliation experiments have been used by several groups to address this question (Davison 1974; Snelgar & Manson 1992; Snowball 1996). However, shoot-defoliation experiments not only remove the source of the inductive signal but also the source of photosynthate and therefore the results should

be considered tentative. None the less, using this methodology evocation is generally accepted to occur during the first growing season of bud development. Davison (1974) suggested evocation starts in late summer and continues through until autumn, though the data of Snelgar & Manson (1992) indicate that the meristems contained within the older, more developed first-order buds undergo evocation earlier, at the beginning of summer. Snowball (1996) giving more weight to the effect of the loss of carbohydrate postulated that evocation may not occur until immediately before flower differentiation in the spring of the second growing season. Shoot shading experiments have also been used to determine the timing of evocation in kiwifruit (Fabbri et al. 1992), and that work supports the timing put forward by Davison (1974). More recent work, based on morphological development (Walton et al. 1997) and floral homeotic gene expression studies (Walton et al. 2001), supports the concept that first-order kiwifruit buds undergo evocation early in their development, starting in late spring of the first growing season.

Evocation appears to occur progressively along each shoot, from the base to the apex, near the time the subtending leaf ceases expansion (Snelgar & Manson 1992). Consequently, when experimental treatments such as defoliation are applied early in the growing season, the reduction in flowering is greater on the distal portions of canes (Snelgar & Manson 1992).

Photoperiod has been shown to play an important role in floral induction in many species (Vince-Prue 1975). The type of response can vary widely between species; some are induced by long photoperiods, others by short photoperiods and still others are day neutral. Day length has been shown to be perceived by the leaves, although floral development occurs in the shoot or bud meristems. Recently, significant advances have been made on elucidating the genetic mechanisms that confer photoperiodic control of flowering and has been recently reviewed by Corbesier & Coupland (2005).

It is clear that kiwifruit require a period of low temperatures during winter dormancy to achieve adequate flowering in the following spring (McPherson et al. 2001). In warm climates, where winter chilling is poor, vine yields are limited by low flower numbers (Allan et al. 1999). However, the factors that control the onset of dormancy during autumn, the accumulation of chilling during winter, and the release from dormancy during spring are poorly understood.

In many species, the onset of dormancy is controlled by the decrease in photoperiod during autumn, although leaf fall is more often controlled by temperature (Vince-Prue 1975). Species with a wide latitudinal distribution often show ecotypic variation to photoperiod so that the critical daylength for the induction of dormancy can vary with the environment from where the plants originate (Vince-Prue 1975). Northern populations of *Picea abies* are known to be more sensitive to photoperiod than southern populations (Qamaruddin et al. 1995). When moved to high latitudes, ecotypes from low latitudes tend to continue growing late in the season and consequently are more prone to frost damage. However, for many commonly grown fruit trees, including apple and pear, the onset of dormancy appears to be insensitive to daylength (Vince-Prue 1975).

Photoperiod may also affect chilling accumulation during winter. Erez et al. (1968) showed that decreasing the amount of light during winter chilling of peach increased subsequent budbreak of vegetative shoots. Reducing either the photoperiod, or the light intensity during the photoperiod, were both effective. Freeman & Martin (1981) extended this work by showing that low levels of light during chilling also enhanced floral budbreak in peach.

There is some evidence that kiwifruit respond to photoperiod. Lu & Rieger (1990) reported that short photoperiods enhance cold acclimation of *A. deliciosa*, and Lionakis & Schwabe (1984) reported that growing cuttings of *A. deliciosa* 'Bruno' (formerly *A. chinensis* 'Bruno') under 16-h rather

Table 1 Fruit quality and yield attributes at harvest in 2001. "Long day" (LD) treated vines were exposed to a 16-h photoperiod from 16 December 2000 to 6 July 2001. Fruit firmness, soluble solids concentration (SSC), and dry matter (DM) were assessed on eight fruit per vine on 5 June 2001. Fresh weight (FW) and the number of fruit were assessed using all of the remaining fruit, which were harvested on 6 June 2001. (NS, not significant.)

	FW (g)	Fruit/m^2	Flesh firmness (kgf)	SSC (%)	DM (%)
Control	108	48	6.4	9.2	15.5
LD	104	54	6.4	9.1	15.4
$P = 0.05$	NS	NS	NS	NS	NS

than 8-h days generally increased shoot elongation and stem diameter while reducing the starch and sucrose content of the shoots.

Of more interest is a preliminary field trial where flowering in kiwifruit was reduced in plants grown under continuous light from midsummer until leaf drop (E. F. Walton & P. J. Fowke unpubl. data). Fluorescent lights reduced the number of floral shoots by 13% and the number of flowers per shoot by 22%, but incandescent lights had a greater effect and reduced the number of floral shoots by 43% and the number of flowers per shoot by 36%. These preliminary observations, coupled with our understanding of flower development in kiwifruit, prompted the current work to determine whether photoperiod does affect flowering in kiwifruit.

MATERIALS AND METHODS

The experiment was carried out on the HortResearch orchard at Te Puke, Bay of Plenty, New Zealand (39°49′S, 176°19′E). The vines used were mature (>10 years old) 'Hayward' kiwifruit vines trained on a pergola trellis and planted in single rows. Rows were 4.3 m apart and vines were spaced at 5.6 m within rows. Every second vine in the row was used as a guard vine, to ensure that control vines were at least 5.6 m from the nearest lights. Control or "long day" (LD) treatments were then randomly allocated to a total of eight vines, i.e., four vines per treatment.

Two 500 W Philips ZF tungsten halogen lamps, housed in rainproof aluminium housings, were mounted on poles above each of the four LD vines. The lamps were positioned 3 m apart and 2.4 m above the vine canopy. Tests carried out in the laboratory with a single lamp showed that positioning the rectangular lamp 2.4 m above the ground gave an even light distribution of 2–8 μmols m^{-2} s^{-1} photosynthetically active radiation (PAR) over an area c. 2.5 m by 3.6 m. PAR was measured using quantum sensor (Licor 190SB, Lincoln, Nebraska, United States). The shape of the reflector housing resulted in PAR dropping abruptly outside the immediately illuminated area. Consequently, PAR from the lamp was not detectable c. 5 m from the lamp. Simulation studies using contour plots for two lamps suggested that a PAR level of 4–20 μmol m^{-2} s^{-1} over an area 6 m × 3.6 m could be obtained with two 500 W lamps spaced 3 m apart and 2.4 m above the canopy. Light levels below 0.25% of full sunlight (5 μmol m^{-2} s^{-1}), are known to be effective in delaying the onset of dormancy in other deciduous species (Vince-Prue 1975). Tinus (1995) reported that an oscillating light at intensities as low as 0.5 μmol m^{-2} s^{-1} prevented bud dormancy in *Picea pungens*, whereas Whitman et. al. (1998) found that threshold values for flowering of *Campanula* and *Coreopsis* ranged from <0.05 to 0.4 μmol m^{-2} s^{-1}.

A single time switch was used to operate all eight lamps so that both evening and morning light was extended. Lamps were turned on 0.5 h before sunset, off at 2000 h, on at 0400 h, and off 0.5 h after sunrise. This gave LD vines 16-h photoperiods, which is the longest natural daylength experienced at this site. The LD photoperiod was imposed from 16 December to 6 July and consequently those vines were not exposed to any shortening of photoperiod from midsummer until after leaf fall in winter. Sixteen-hour photoperiods were longer than vines would experience in their natural habitat in China (latitude 25°–35°). All vines were sprayed with 6% (w/v) copper sulphate solution to induce leaf drop on 19 June 2001 and with hydrogen cyanamide (3% a.i.) on 22 August 2000 and 6 August 2001 to induce budbreak.

Operation of the lamps was monitored from 21 February onwards by installing a single PAR sensor (Palmer 1987) above each vine. The sensors were scanned at 60-s intervals by a Campbell CR10 data logger that recorded average light levels every 900 s.

Table 2 Budbreak and flowering characteristics of canes in spring 2001. "Apical" refers to the first nine winter buds on each cane, and "Basal" refers to buds 10–18. "Long day" (LD) treated vines were exposed to a 16-h photoperiod from 16 December 2000 to 6 July 2001. (NS, not significant.)

	Budbreak (%)		Floral shoots (%)		Flowers/shoot		Flowers/bud	
	Apical	Basal	Apical	Basal	Apical	Basal	Apical	Basal
Control	54	49	85	91	3.3	3.5	1.6	1.6
LD	61	46	75	72	2.6	2.8	1.4	1.1
$P = 0.05$	NS	NS	NS	0.03	0.00	0.01	NS	0.04

The logger was programmed to trigger an alarm the following day if the PAR levels fell below 4 μmol m^{-2} s^{-1} while the lights were on. The equipment functioned reliably during most of the experiment. Three of the eight bulbs failed during the experiment and these were replaced within 3 days of failing. Two vines had one night without light supplementation because a fuse burnt out (19 January 2001), and all vines had one night without lights on 7 April 2001 as a result of a programming error.

Fruit characteristics were measured before harvest by destructively sampling eight fruit from each vine. Fruit were selected as being a "typical" size for the vines, and c. 1 m along the leader from the trunk, and 1 m out from the leader as described by (Hopkirk et al. 1986). The fresh weight, dry matter content, and soluble solids concentration of each fruit was recorded using standard methods Snelgar & Hopkirk (1988). Flesh firmness was measured on both sides of each fruit using a hand held penetrometer, after a 1 mm slice of skin had been removed.

At harvest, all of the fruit on each vine were picked and individual fruit weights were recorded on an electronic grader.

In spring 2001, budbreak was monitored on six canes on each vine, twice weekly. A bud was recorded as broken if it had reached the "BB" stage, as defined by Brundell (1975a). The time course of budbreak was analysed using the total population of buds on the 24 canes for each treatment. A cumulative normal curve was fitted by least-squares to the cumulative count of burst buds. The estimated mean time of budbreak corresponded to the time when the fitted curve reached 50% budbreak. Total budbreak and number of flowers were recorded on 12 canes per vine during late October, when flower buds were c. 3–8 mm in diameter. The number of winter buds on each cane was also recorded. All buds, including the flat ones near the base of each cane, were included in these tallies.

RESULTS AND DISCUSSION

The LD treatment did not appear to affect vegetative growth during the treatment period. However, quantitative measurements were not made, so it is possible that changes in shoot growth similar to those reported by Lionakis & Schwabe (1984) could have occurred. Applied LDs did not affect fruit size, fruit firmness, soluble solids concentration, or dry matter content at harvest (Table 1). This is not surprising as the PAR levels used for LD were less than 0.5% of full sunlight so it is unlikely that total photosynthetic gain would have been measurably affected. For both control and LD vines, leaf fall in the block was c. 50% complete by 19 June.

In spring 2001, both control and LD treated vines reached 50% budbreak on 13 September, 38 days after hydrogen cyanamide had been applied. This is similar to the 40-day average reported by McPherson et al. (2001). The LD treatment did not affect the percentage budbreak, but it did significantly reduce both the percentage of shoots that produced flowers (% floral shoots), and the number of flowers on each floral shoot (Table 2). Although these reductions occurred on both the apical and basal portions of canes they were most pronounced on the basal portions. The combined effect of this was to reduce the overall mean number of flowers per winter bud by 22%. These reductions in flowering did not appear to be related to the slightly higher crop loads carried by LD vines in the previous season as the crop load at the June 2001 harvest was not a significant covariate for flowering in November 2001.

As a consequence of reduction in the number of flowers per bud, the vines exposed to LDs in 2001 carried 26% fewer fruit per square metre of canopy than control vines in 2002. These results are consistent with the unpublished data of E. F. Walton & P. J. Fowke. It is important to note, however, that the LD treatments had no significant effect on fruit size, vine yield, fruit firmness, soluble solids

Table 3 Fruit quality and yield attributes at harvest in 2002. "Long day" (LD) treated vines were exposed to a 16-h photoperiod from 16 December 2000 to 6 July 2001. Fruit firmness, soluble solids concentration (SSC), and dry matter (DM) were assessed on eight fruit per vine on 2 May 2002. Fresh weight (FW) and the number of fruit were assessed using all of the remaining fruit, which were harvested on 29 May 2002. (NS, not significant.)

	FW (g)	Fruit/m^2	Flesh firmness (kgf)	SSC (%)	DM (%)
Control	106	34	7.5	7.1	16.5
LD	110	25	7.4	7.2	16.7
$P = 0.05$	NS	NS	NS	NS	NS

concentration, or dry matter content at harvest during the following (2002) season (Table 3).

Did the LD treatments affect the accumulation of winter chilling?

The reductions in return bloom resulting from LDs could have been caused by changes in floral development during summer when evocation of the younger buds is thought to occur, or during winter, when low temperatures are thought to enhance flower production. Although the period when kiwifruit accumulate winter chilling is not well defined, McPherson et al. (2001) found that flower production is negatively correlated with average temperatures during May, June, and July. In the current work, the leaves remained on the vine for over half of this "winter" period and LD treatments were applied until well after leaf fall. Although applying hydrogen cyanamide to kiwifruit vines increases budbreak and flowering, it does not fully compensate for insufficient winter chilling, so flower production still decreases as mean winter temperatures increase (McPherson et al. 2001). Consequently, we would expect to see a reduction in both budbreak and flowering if the LD treatments delayed the onset of the accumulation of winter chilling (McPherson et al. 1994). Although the LD treatments resulted in a substantial reduction in flowering, the amount of budbreak was not affected and so the LD treatments do not appear to effect the accumulation of winter chilling in kiwifruit.

LD treatments may affect flower evocation

Floral evocation is generally thought to occur during the first growing season as first-order axillary buds develop, starting with the oldest, most mature buds (Snelgar & Manson 1992; Walton et al. 1997, 2001). During that time, there are a number of factors that can affect flowering in the following spring. As already stated, defoliating developing shoots early in their development reduces the proportion of floral shoots that develop the following spring. This is particularly near the tip of the canes, where leaves are latest to expand and become inductive. Defoliation also reduces the number of flowers borne on each floral shoot but it does not alter the percentage budbreak (Snelgar & Manson 1992). Training canes upwards at 60° during summer increases vegetative growth and reduces flowering (Snelgar & Manson 1990). Shading whole vines reduces the number of flowers on each shoot, but does not reduce budbreak (Snelgar et al. 1991). It is also possible to increase flowering by manipulating vines during summer. Girdling canes is thought to increase the amount of carbohydrates stored in the canes over winter, which results in a higher budbreak, and flowering in the following spring (Snelgar & Manson 1990).

Comparison of the data presented here with data from previous studies suggests that the reduction in flowering caused by continuous LDs is likely to be associated with a diminution of the evocation process, consistent with the preliminary study by E. F. Walton & P. J Fowke (unpubl. data). However, the relatively long duration of the LD treatments and the fact that flower development in kiwifruit is spread out over two growing seasons, means that we cannot be unequivocal about which part of the flower process is affected. Consequently, our hypothesis should be considered tentative until it can be validated by further, more targeted, experimental work.

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