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Research article

Plant architecture of 'Albion' strawberry (*Fragaria* × *ananassa* Duch.) is not influenced by light source during conditioning

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Abstract: Architectural analysis describes the position and fate (vegetative or floral) of plant meristems to account for differences in meristem sensitivity to stimuli depending on developmental stage and position on the plant. To provide further insight into the flowering responses of long-day strawberries to nitrogen (N), photoperiod and light source, 'Albion' strawberry plants were conditioned with 100 or 800 ppm N under ND (natural daylength) or LD (long days, natural days plus 24-hr supplementary illumination provided by either 60- or 7-watt incandescent bulbs) and greenhouse growth was evaluated for a total of 10 weeks following conditioning. After greenhouse forcing, plants were dissected and their floral architecture evaluated. Additional plants were established in early July in off-season plasticulture production where fruit, crown and stolon production were evaluated. Both light sources were equally effective in eliciting long-day photoperiod responses. No photoperiod effect on floral precocity, leaf, crown, or runner production was observed during greenhouse forcing. Plants under ND tended to produce more inflorescences during the first 5 weeks while LD enhanced inflorescence and flower production during the last 3 weeks of forcing. In dissected plants, maximum floral initiation was observed in plants receiving elevated N under LD. LD inhibited branch crown formation, but had no effect on the number of vegetative, floral or stolon producing axillary meristems regardless of N treatment. LD conditioning enhanced early yield (through 4 September). Field stolon and branch crown formation was supressed in plants receiving low N with LD conditioning. Stolon and branch crown inhibition by LD conditioning was not observed with elevated N. Growth data combined with architectural mapping of meristems allows more conclusive statements regarding treatment effects on specific stages of floral physiology (i.e. induction, initiation, differentiation and development) compared to more generalized conclusions obtained with growth data alone. The separation of direct and indirect effects on floral

physiology is possible with floral architectural analysis.

Keywords: *Fragaria* × *ananassa* Duch.; flowering; greenhouse production; season extension; precocity; floral initiation; floral differentiation; floral architecture

Abbreviations: ND: natural daylength; LD: 24-hr incandescent illumination; N: nitrogen

1. Introduction

'Albion' is a high quality, productive long-day strawberry which has performed well in off season production trials in New Jersey, USA using plants conditioned with long days and elevated nitrogen prior to field establishment [1,2]. Van Delm et al. [3,4] demonstrated that greenhouse production using long-day cultivars such as 'Capri', 'Charlotte' and 'Portola' could be enhanced by subjecting plants to cyclic lighting with 100-watt incandescent lamps to stimulate long-day flowering during forcing. Similarly, Hamano et al. [5] reported enhanced flowering in long-day cultivars using 24-hr lighting with 60-watt incandescent lamps.

Strings of incandescent lights (Lind Equipment TLS-100CG14 Contractor-grade stringlight, A-19 socket, 60 watt bulbs, 30 m length, sockets spaced 3 m apart, Lind Equipement, Markham, Ontario, Canada) are effective for conditioning plants but they are relatively expensive ($10 USD, January 2018 per m^2). Much less expensive alternative strings (C9 socket, 7 watt bulbs, spaced 0.3 m apart (Novelty Lights, Inc., Centennial, CO)) are available ($3 USD, January 2018 per m^2). Lower cost lights would be particularly useful in implementing long-day, cyclic lighting strategies to enhance fruiting in field or high tunnel production similar to those suggested for greenhouse production [3,4]. It is not known whether or not the less expensive, lower wattage strings are effective in eliciting the long day response needed for flowering.

Photoperiod is the major trigger for flower initiation in strawberry [6]. Flowering is generally enhanced if N fertilization is briefly increased after plants have been exposed to the photoperiod signal for initiation for a short time (~1 week) [7–9]. If it is applied before, at the beginning of or too long after initiation, N inhibits flowering [7,10] and reduces yield [7]. Durner [1,2,11–13] demonstrated that flowering of the long-day cultivars 'Elan', 'Tarpan', 'Gasana' and 'Albion' could be enhanced with 4 weeks of elevated N if applied beginning the second week of a 5-week exposure to long days. Cultivars responded similarly and rapidly (within 4 weeks after the commencement of treatment) to long days and elevated N with increased rate (enhanced precocity) and intensity (enhanced inflorescence and flower number) of flowering. Off-season productivity of 'Albion' in a plasticulture system was enhanced with such conditioning [1,2].

Inflorescence and floral counts over time are often used to detect cultural or environmental effects on flowering and productivity. Floral architecture models (also known as flower mapping) describe the position and fate (vegetative or floral) of buds on a plant [14–16] to account for differential stimuli sensitivity of each meristem on a plant depending on specific stage of development and position on the plant [15,17]. Some meristems will respond to stimuli while others will not. Each meristem is evaluated via dissection under a stereoscope and identified as a vegetative or floral bud, a stolon or a branch crown with either a vegetative or floral apex. The floral status can

be described with a more complex rating scale from 0 (vegetative) to 9 (completely floral) if desired based on the purpose of the research [18]. Floral architectural analysis has the advantage over growth data evaluations in that it allows a much more complete assessment of plant responses to environmental factors with respect to meristem fate.

This study was designed to evaluate the effectiveness of a low cost light source for long-day conditioning of 'Albion' for off-season production.

2. **Materials and methods**

2.1. Experiment one—greenhouse evaluation of conditioning light source

Dormant cold-stored crowns of the long-day cultivar 'Albion' were obtained from a commercial nursery (Nourse Farms, Inc., South Deerfield, MA, USA). Roots were trimmed to 2.5 cm in length and crowns planted in 20.3 × 14.3 cm (diameter × height) round azalea pots (3.3 L volume) into Fafard Organic Mix (FOF-30) (Sun Gro Horticulture, Agawam, MA) on 11 May 2017. On the same day, 12 of these plants were placed under each of three photoperiods in a greenhouse at 24/18 ^{o}C day/night temperatures. Plant density on the greenhouse bench was 5 plants·m^{-2}. The three photoperiods were (1) natural daylength [14:30 on May 19 maximum 15:00 on June 21 and 14:30 on 24 July], (2) long days with 60 watt bulbs (LD, natural daylength supplemented with 24-hr incandescent radiation (Phillips Duramax Soft White A19 60 watt, 1000-hr life) suspended 15 cm above the plant canopy, 2 bulbs m^{-2}) and (3) long days with 7 watt bulbs (LD7W, natural daylength supplemented with 24-hr incandescent radiation (C9, 7 watt bulbs, 3000-hr life (Novelty Lights, Inc., Centennial, CO) suspended 15 cm above the plant canopy, 6 bulbs m^{-2}). The red: Far-red light ratios for ND, LD using 60-watt bulbs and LD using 7-watt bulbs, measured using a Field Scout Red/Far Red Meter (Spectrum Technologies, Aurora, IL, USA) at canopy level were 1.01, 1.04 and 1.02, respectively. On 17 May 2017 all plants were trimmed to one crown then fertilized weekly for 4 consecutive weeks with Scotts Miracle grow water soluble fertilizer (24% available N, 8% available P_2O_5, 16% available K_2O) (Marysville, Ohio) diluted with water to provide either 100 or 800 ppm·N. Each time plants received 100 mL of solution which was more than sufficient to saturate the soil. Six plants under each photoperiod received 100 ppm·N and six received 800 ppm·N. Following the 4 week fertility treatment plants were maintained under their respective photoperiods and evaluated weekly until 24 July 2017 for the number of fully expanded leaves, stolons, branch crowns, inflorescences and flowers produced per plant. Stolons were removed as they appeared. The number of flowers per inflorescence was calculated as the total number of flowers per plant divided by the number of inflorescences per plant. Initiation was evaluated via inflorescence counts, differentiation via flowers per inflorescence and development via precocity. Precocity was estimated as the length of time (weeks) after the start of treatment (11 May) until the first, second and third inflorescence appeared. Floral growth responses were adjusted for differences in vegetative crown growth by floral parameters to a per-crown basis. All plants were dissected under a stereoscope when the experiment was terminated on 24 July 2017 to evaluate floral architecture. Plants were evaluated for number of leaves, number of nodes, status of axillary buds (vegetative (leaf), stolon, floral (2 nodes with floral terminal) or branch crown (3 or more nodes, vegetative or floral terminal)) and number of flowers/flower initials visible on each inflorescence. Only axillary buds with 3 or more nodes were considered branch crowns. The status (vegetative or floral) of the terminal bud of the main crown

was also evaluated. Initiation was evaluated as the main crown terminal meristem status (floral or vegetative) and differentiation via main crown terminal meristem floral stage (number of individual flowers discernible per meristem). Similar evaluation of branch crown meristems was performed separately.

All 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. Aligned rank transformations (ART) were performed as suggested by Wobbrock et al. [19] using the ARTool program (http://depts.washington.edu/aimgroup/proj/art/). ART data were analyzed using an analysis of variance using the GLM procedure of SAS (SAS Institute, Cary, NC). Detected differences among photoperiod treatments were evaluated with 2 single df planned contrasts, one to compare photoperiod (ND versus LD and LD7W combined) and the other to compare light source (LD versus LD7W) using CONTRAST statements in the GLM procedure. Differences between nitrogen treatments were separated with Fisher's Protected LSD. Results are presented for cumulative values for observations made on 31 May 2017, 30 June 2017, 24 July 2017 and dissected plants. Data for interim observation dates are presented for completeness in tables, however, only results for the previously listed dates are presented for clarity and to avoid redundancy. Data for branch crown meristem dissection data were severely unbalanced since none of the plants given low N under LD7W formed branch crowns. Branch crown meristem data was therefore analysed comparing only two photoperiod levels (ND vs LD) rather than three. N main effects and interactions with photoperiod were also considered in the branch crown meristem analysis.

2.2. Experiment two—field production

Dormant cold-stored crowns of the long-day cultivar 'Albion' were obtained from a commercial nursery (Nourse Farms, Inc., South Deerfield, MA, USA). Roots were trimmed to 2.5 cm in length and crowns planted in 7.6 cm square pots (320 cm^3 volume) into Fafard Organic Mix (FOF-30) (Sun Gro Horticulture, Agawam, MA) on 12 May 2017 and allowed to grow under ambient greenhouse (natural daylength 24/18 ^oC day/night temperatures) conditions for 3 weeks. Beginning 02 June 2017, plugs were conditioned with photoperiod and N as described above for 5 weeks. On 9 June 2017 all plants were trimmed to one crown. Following conditioning (3 July 2017)) plants were established in a plasticulture field planting at Rutgers Horticultural Research Farm 3 in New Brunswick, NJ. Plants were set on raised beds (20 cm high × 90 cm wide) covered with white on black (1 mil)) plastic mulch with the white side exposed. There were two staggered rows per bed with 30 cm between rows and 38 cm between plants in the row. Irrigation was provided as needed via drip tape (10 mil Medium Weight 5/8 "AquaTraxx Drip Tape, 12" spacing, Flow rate 0.45, The Toro Company, Bloomington, MN) placed in the center of the bed underneath the plastic mulch.

The experimental design was a split plot with the main plot of photoperiod arranged in a randomized complete block with 10 replicates. The sub-plots were levels of nitrogen. Experimental units were single plants.

Ripe fruit were harvested, counted and weighed from individual plants on each of the following dates: 8/17, 8/23, 8/30, 9/4, 9/12, 9/18, 9/21, 9/25, 9/29, 10/3, 10/7, 10/11, 10/17, 10/23, 10/31 and 11/06. Yield data were combined to create 3 cumulative totals (yield through 4 September, 3 October and 6 November, subsequently identified as August, September and October) for fruit weight and number. Average fruit size was estimated by dividing total yield by total fruit number for individual plants.

Stolons were counted and removed on 8/17, 9/12 and 11/14. Plants were harvested and the number of crowns per plant determined on 14 November 2017.

All 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. Aligned rank transformations (ART) were performed as suggested by Wobbrock et al. [19] using the ARTool program (http://depts.washington.edu/aimgroup/proj/art/). ART data were analyzed using an analysis of variance using the GLM procedure of SAS (SAS Institute, Cary, NC). Detected differences among photoperiod treatments were evaluated with 2 single df contrasts, one to compare photoperiod (ND versus LD and LD7W combined) and the other to compare light source (LD versus LD7W) using CONTRAST statements in the GLM procedure. Differences between nitrogen treatments were separated with Fisher's Protected LSD. Data are presented for cumulative values previously described for August, September and October.

3. Results

3.1. Photoperiod, nitrogen and light source evaluation of greenhouse data

3.1.1. Precocity

No effects of photoperiod, nitrogen or light source were detected for precocity of the first inflorescence (Table 1). All plants flowered 3 weeks after the start of the experiment. Precocities of the second and third inflorescence were significantly affected by nitrogen but not photoperiod or light source and there was no interaction between photoperiod and nitrogen (Table 1). Elevated nitrogen during conditioning accelerated the production of both the second and third inflorescences (Table 2).

3.1.2. Crown and stolon production

No effects of photoperiod, nitrogen or light source were detected for crown or stolon production (Table 1). All plants produced an average of 1.8 and 3.9 crowns and stolons per plant, respectively.

3.1.3. Leaf production

A significant photoperiod X nitrogen interaction was detected on the third observation date (31 May, Table 1). Plants receiving 800 ppm N during conditioning had produced an average of 5.2 leaves per plant when conditioned with 60-watt bulbs compared to 6.3 leaves if conditioned with 7-watt bulbs (contrast $\alpha = 0.05$) and the contrast comparing ND with LD was not significant ($\alpha = 0.74$) (Table 3). No photoperiod effect was detected for plants receiving 100 ppm N during conditioning: Plants had produced an average of 5.9 leaves per plant (Table 3).

Table 1. F-test probabilities (α) for photoperiod and nitrogen conditioning main effects, photoperiod X nitrogen interactive effects, and contrasts of photoperiod effects on precocity, cumulative leaf, inflorescence and flower production per plant of 'Albion' strawberry grown in a greenhouse following conditioning in New Jersey, USA.

	Effect α				Contrast α
Variable/Month	Photoperiod	Nitrogen	Photoperiod X nitrogen	LD vs ND	60 watt vs 7 watt bulb
			Precocity		
First inflorescence	0.36	0.42	0.42	0.18	0.77
Second inflorescence	0.56	0.01	0.86	0.21	0.83
Third inflorescence	0.36	0.04	0.63	0.16	0.48
Total number of crowns	0.71	0.33	0.79	0.48	0.73
Total number of stolons	0.37	0.79	0.15	0.54	0.10
			Cumulative leaf production per plant		
19 May	0.89	0.50	0.32	0.82	0.57
26 May	0.60	0.49	0.26	0.95	0.26
31 May	0.51	0.87	0.04	0.85	0.13
7 June	0.60	0.90	0.22	0.35	0.69
16 June	0.46	0.25	0.23	0.82	0.30
23 June	0.49	0.18	0.35	0.60	0.31
30 June	0.36	0.07	0.61	0.92	0.18
6 July	0.87	0.19	0.67	0.97	0.64
12 July	0.97	0.10	0.58	0.73	0.99
19 July	0.45	0.03	0.51	0.27	0.74
			Cumulative inflorescence production per plant		
19 May	0.70	0.86	0.68	0.52	0.71
26 May	0.23	0.10	0.45	0.26	0.66
31 May	0.13	0.34	0.38	0.09	0.60
7 June	0.06	0.03	0.75	0.05	0.68
16 June	0.36	0.41	0.75	0.18	0.78
23 June	0.51	0.01	0.46	0.54	0.23
30 June	0.92	0.01	0.23	0.66	0.95
6 July	0.30	0.02	0.56	0.10	0.71
12 July	0.10	0.04	0.17	0.03	0.89
19 July	0.33	0.09	0.45	0.15	0.78
			Cumulative flower production per plant		
19 May	0.56	0.75	0.54	0.76	0.32
26 May	0.26	0.11	0.48	0.24	0.64
31 May	0.35	0.48	0.38	0.12	0.52
7 June	0.27	0.03	0.34	0.08	0.47
16 June	0.49	0.10	0.69	0.16	0.89
23 June	0.21	0.01	0.19	0.33	0.06
30 June	0.06	0.07	0.12	0.23	0.38
6 July	0.07	0.08	0.16	0.05	0.33
12 July	0.04	0.08	0.13	0.03	0.27
19 July	0.04	0.03	0.30	0.02	0.25

Table 2. Influence of N fertility and photoperiod on precocity of second and third inflorescences and inflorescence and leaf production during greenhouse forcing of 'Albion' strawberry.

Date	N (ppm)	
	100	800
	Precocity of second inflorescence	
	6.8 a[Z]	5.1 b
	Precocity of third inflorescence	
	8.3 a	7.5 b
	Cumulative leaf production per plant 19 July	
19 July	12.6 b	15.3 a
	Cumulative inflorescence production per plant	
07 June	0.61 b	1.17 a
23 June	1.33 b	2.11 a
30 June	1.83 b	2.72 a
6 July	2.39 b	3.17 a
12 July	2.89 b	3.89 a
	Cumulative flower production per plant	
07 June	2.1 b	4.6 a
23 June	5.4 b	8.6 a
19 July	17.1 b	21.5 a
	Cumulative inflorescence production Photoperiod	
Date	ND	LD
19 May	0.6 a	0.5 a
26 May	0.8 a	0.5 a
31 May	1.0 a	0.5 a
07 June	1.3 a	0.7 a
16 June	1.5 a	1.1 a
23 June	1.9 a	1.7 a
30 June	2.3 a	2.3 a
06 July	2.4 a	3.0 a
12 July	2.8 b	3.7 a
19 July	3.3 a	3.9 a

*Note: [Z] Mean separation within row by Fisher's Protected LSD, 0.05 level.

Table 3. Significance level (α) for number of leaves per plant produced by 'Albion' strawberry during greenhouse forcing as affected by photoperiod and nitrogen conditioning.

	Nitrogen (ppm)	
Factor	100	800
	Cumulative leaves per plant on 31 May	
Photoperiod	0.49	0.07
Contrast 1		
Natural daylength vs long day	0.26	0.74
Contrast 2		
24-hr long-day,60 vs 7 watt bulbs	0.17	0.05

A significant nitrogen main effect on cumulative leaf production per plant was detected on the final (tenth) (19 July) observation date (Table 1). Plants receiving 800 ppm N during conditioning produced and average of 2.7 additional leaves per plant compared to plants receiving 100 ppm N during conditioning (Table 2). No effects of photoperiod, nitrogen or light source were detected for cumulative leaf production on all other dates (Table 1).

3.1.4. Inflorescence production

A significant nitrogen effect was detected for cumulative inflorescence production per plant on 5 observation dates (7, 23 and 30 June; 6 and 12 July) (Table 1). Plants that received 800 ppm N during conditioning produced significantly more inflorescences per plant than those that received 100 ppm N (Table 2). A significant overall photoperiod effect was not detected for inflorescence production per plant on any observation date (Table 1), however the contrast comparing ND to LD for 12 July was significant (Table 1). Plants under LD produced more inflorescences than those under ND (3.7 vs 2.8 inflorescences per plant, respectively). There was a tendency for enhanced inflorescence production under ND during the first 6weeks (Table 2), however the effect was not significant. A reversal in the trend began in week 8 and total inflorescence production on 12 July was significantly greater under LD compared to ND (Table 1, 2). The enhancement was not significant on the final observation date.

3.1.5. Flower production

Plants conditioned under LD had a greater cumulative number of flowers per plant on the last three observation dates 6, 12 and 19 July (Tables 1 and 4).

Table 4. Photoperiod effect on cumulative number of flowers per plant produced by 'Albion' strawberry during greenhouse forcing.

Contrast	α	Cumulative flowers per plant	
		6 July	
		ND	LD
ND vs LD	0.05	11.2	15.3
		60-watt	7-watt
LD, 60 vs 7 watt bulbs	0.33	14.2	16.4
		12 July	
		ND	LD
ND vs LD	0.03	13.9	19.5
		60-watt	7-watt
LD, 60 vs 7 watt bulbs	0.27	18.0	21.0
		19 July	
		ND	LD
ND vs LD	0.02	15.8	21.0
		60-watt	7-watt
LD, 60 vs 7 watt bulbs	0.25	19.7	22.4

A significant effect of nitrogen on cumulative flower production per plant was detected on 7 and 23 June and 19 July (Table 1). Elevated nitrogen during conditioning significantly enhanced flower production on all three dates (Table 2).

3.2. Photoperiod, nitrogen and light source evaluation of dissection data

3.2.1. Architectural characterization of greenhouse plant dissections

An architectural model of plants dissected after forcing is presented in Figure 1. The model provides a visual representation of meristem status for all meristems on the plant at the time of dissection. Statistical analysis reveals whether or not the visually perceived differences are significant or not (Table 5).

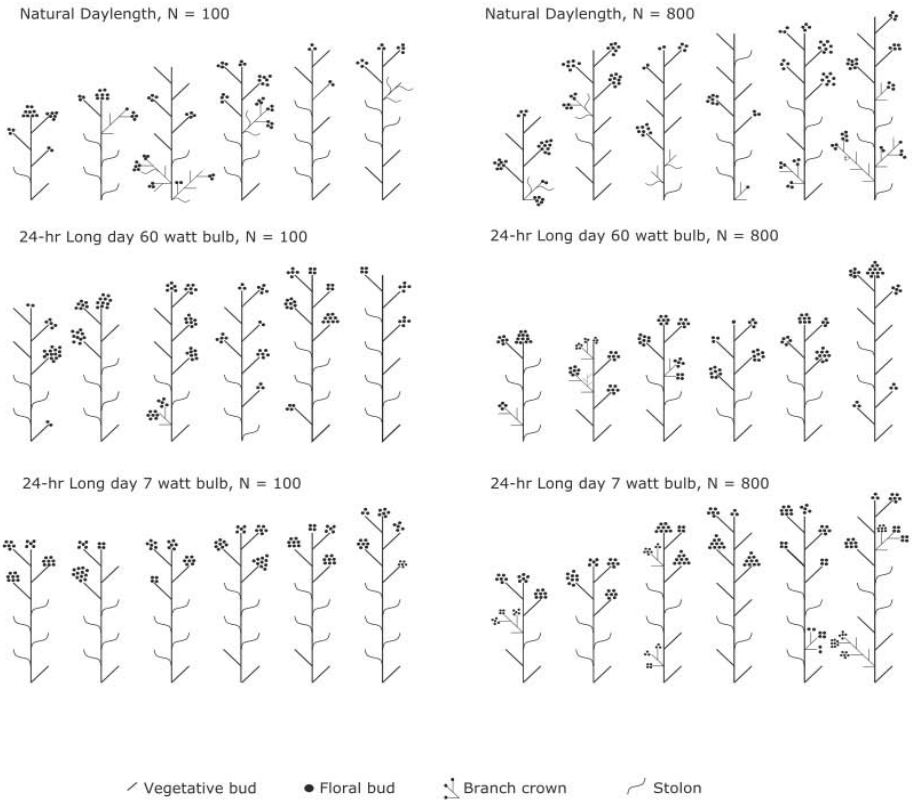

Figure 1. Architectural characterization of ‘Albion’ strawberry crowns on 24 July after greenhouse forcing following conditioning with nitrogen and photoperiod. Lack of symbol at terminal meristem indicates a vegetative meristem.

3.2.2. Evaluation of greenhouse plant dissection data

3.2.2.1. Main crown terminal bud status

A significant interaction of photoperiod and nitrogen fertilization was detected for the terminal bud status of the main crown (Figure 1, Table 5), Eighty-nine percent of the meristems of plants

receiving 100 ppm N were floral and there was no significant effect of photoperiod on the main crown terminal meristem status (Table 6). All plants receiving 800 ppm under LD were floral while only 50 percent of those under ND were floral, and the difference was significant (Table 6). No effect of light source was detected.

Table 5. F-test probabilities (α) for photoperiod and nitrogen main effects, photoperiod X nitrogen interactive effects, and contrasts for comparing photoperiod effects on dissection data of 'Albion' strawberry grown in a greenhouse following conditioning in New Jersey, USA.

Effect α				Contrast α	
Variable	Photoperiod	Nitrogen	Photoperiod X nitrogen	LD vs ND	60 watt vs 7 watt bulb
Terminal meristem status	0.06	0.01	0.04	0.02	0.48
Terminal meristem stage	0.08	0.92	0.12	0.03	0.72
% axillary vegetative	0.66	0.10	0.47	0.38	0.84
% axillary floral	0.55	0.93	0.33	0.37	0.54
% axillary stolons	0.37	0.01	0.50	0.20	0.60
% axillary branch crowns	0.07	0.04	0.84	0.02	0.80

Table 6. Main crown terminal bud status and % main crown axillary meristems producing stolons or branch crowns as determined at dissection for 'Albion' strawberry as affected by photoperiod and nitrogen conditioning.

	Nitrogen (ppm)	
Photoperiod	100	800
	Main crown terminal bud status (% floral)	
Natural daylength	83 a[Z]	50 b
24-hr, 60 watt bulbs	83 a	100 a
24-hr, 7 watt bulbs	100 a	100 a
Variable		
% axillary meristems producing stolons	41 a[Y]	28 b
% axillary meristems producing branch crowns	4 b	13 a
	Photoperiod	
	ND	LD
% axillary meristems producing branch crowns	14 a	6 b

*Note: [Z]Mean separation within column by Fisher's Protected LSD, 0.05 level.

[Y]Mean separation within row by Fisher's Protected LSD, 0.05 level.

3.2.2.2. Main crown terminal bud stage

Terminal meristems of plants grown under ND had fewer flower initials (3.0) compared to LD (5.5) and the difference was significant (Figure 1, Table 5). No effect of light source was detected.

3.2.2.3. Axillary bud status: Percentage vegetative

No effect of photoperiod, nitrogen or light source was detected for the % of axillary meristems on the main crown that were vegetative (24%) (Table 5).

3.2.2.4. Axillary bud status: Percentage floral

No effect of photoperiod, nitrogen or light source was detected for the % of axillary meristems on the main crown that were floral (34%) (Table 5).

3.2.2.5. Axillary bud status: Percentage stolons

Axillary meristems produced significantly fewer stolons in plants receiving 800 ppm N compared to those receiving 100 ppm N (Table 5, 6). No effect of light source was detected.

3.2.2.6. Axillary bud status: Percentage branch crowns

Significant nitrogen and photoperiod main effects on axillary meristem branch crown formation were detected (Table 5). More axillary meristems produced branch crowns in plants given 800 ppm N compared to those given 100 ppm N (Table 6). Fewer axillary buds formed branch crowns under LD compared ND (Table 6). No effect of light source was detected.

3.2.2.7. Branch crown terminal bud status

Neither photoperiod nor N affected branch crown terminal meristem status and there was no interaction between the two detected (Table 7).

Table 7. F-test probabilities (α) for photoperiod and nitrogen conditioning main effects and photoperiod X nitrogen interactions on branch crown dissection data of 'Albion' strawberry grown in a greenhouse following conditioning in New Jersey, USA.

	Effect α				
Variable	Photoperiod	Nitrogen	Photoperiod X nitrogen		
				Mean value	
Branch crown terminal meristem status	0.14	0.22	0.58	0.86	
% axillary vegetative	0.17	0.74	0.91	41	
				Photoperiod	
				ND	*LD*
Branch crown terminal meristem stage	0.01	0.51	0.13	2.1 b[Z]	4.8 a
% axillary stolons	0.04	0.58	0.70	37 a	0 b
				Nitrogen (ppm)	
				100	800
% axillary floral	0.10	0.02	0.99	36 b	41 a

*Note: [Z]Mean separation within row via Fisher's protected LSD, 0.05 level.

3.2.2.8. Branch crown terminal bud stage

Terminal meristems of branch crowns under LD were more floral than those under ND with 4.8 and 2.1 flowers per meristem, respectively (Table 7).

3.2.2.9. Branch crown axillary bud status: Percentage vegetative

No photoperiod, N or interaction between the two were detected for the percentage of branch crown axillary buds that were vegetative (41%) (Table 7).

3.2.2.10. Branch crown axillary bud status: Percentage floral

More axillary branch crown meristems were floral in plants given 800 compared to 100 ppm N (41 vs 36%, respectively, Table 7).

3.2.2.11. Branch crown axillary bud status: Percentage stolons

LD completely prevented stolon production by branch crown axillary meristems (Table 7).

3.3. Field plasticulture production trial

3.3.1. Precocity and yield

LD plants were more precocious, producing ripe fruit one week earlier (17 August) than ND plants (23 August) (Table 8). Early yield and fruit number (through 4 September) was enhanced by LD conditioning and light source did not influence productivity (Tables 8 and 9). Mid and late season yield and fruit number (through 3 October and 6 November, respectively) were enhanced by elevated N during conditioning. Cumulative average fruit size (g) on 3 October was slightly reduced by LD conditioning (Table 9) but was not affected by N or light source. Cumulative average fruit size was not affected by N, photoperiod or light source when estimated earlier or later in the season (September (12.5 g) or November (14 g)).

3.3.2. Stolon and crown production

A significant interaction between photoperiod and nitrogen during conditioning was observed for field production of both stolons and branch crowns (Tables 8 and 10). LD conditioning inhibited field production of stolons and branch crowns in plants receiving 100 ppm N during conditioning, (Table 10). In plants given 800 ppm N, no effect of photoperiod was detected (Table 10). No differences between LD light sources were detected for crown or stolon number (Table 8).

Table 8. F-test probabilities (α) for photoperiod and nitrogen main effects, photoperiod X nitrogen interactions, and photoperiod contrasts for cumulative yield (g), number of fruit per plant and average fruit size (g) of 'Albion' strawberry in an off-season plasticulture production system in New Jersey, USA. Tests for precocity, total crown number and total stolon production are also presented.

	Effect α			Contrast α	
Harvest Date	Photoperiod	Nitrogen	Photoperiod X nitrogen	LD vs ND	60 watt vs 7 watt bulb
			Effect on yield per plant		
4 September	0.06	0.31	0.92	0.04	0.24
3 October	0.54	0.03	0.33	0.36	0.58
6 November	0.80	0.04	0.07	0.87	0.53
			Effect on number of fruit per plant		
4 September	0.06	0.26	0.72	0.04	0.15
3 October	0.19	0.04	0.53	0.11	0.39
6 November	0.51	0.04	0.08	0.56	0.33
			Effect on average fruit size		
4 September	0.73	0.97	0.64	0.54	0.76
3 October	0.03	0.96	0.21	0.01	0.70
6 November	0.10	0.33	0.63	0.08	0.23
Variable	Photoperiod	Nitrogen	Photoperiod X nitrogen	LD vs ND	60 watt vs 7 watt bulb
Precocity	0.01	0.07	0.09	0.01	0.78
Total number of crowns	0.08	0.85	0.01	0.05	0.21
Total number of stolons	0.57	0.18	0.01	0.35	0.65

Table 9. Cumulative yield, number of fruit and average fruit size as affected by photoperiod and nitrogen of 'Albion' strawberry in an off-season plasticulture production system in New Jersey, USA.

	Conditioning photoperiod		Nitrogen (ppm)	
Harvest Date	Long-day	Natural daylength	100	800
		Cumulative yield per plant (g)		
4 September	94.9 a[z]	68.9 b	77.3 a	90.2 a
3 October	172.3 a	159.8 a	139.6 b	190.5 a
6 November	319.2 a	335.5 a	306.1 b	378.6 a
		Cumulative number of fruit per plant		
4 September	7.9 a	5.2 b	6.6 a	7.1 a
3 October	13.9 a	11.2 a	10.8 b	14.6 a
6 November	24.3 a	23.1 a	20.6 b	26.5 a
		Average fruit size (g)		
3 October	12.3 b	14.5 a	13.0 a	13.2 a

*Note: [z]Mean separation within row and treatment factor by Fisher's Protected LSD, 0.05 level.

Table 10. Number of branch crowns and stolons produced by 'Albion' strawberry as affected by photoperiod and nitrogen conditioning prior to field production in an off-season plasticulture production system in New Jersey, USA.

	Photoperiod	
Nitrogen (ppm)	Natural daylength	Long-day
	Crowns per plant	
100	9.0 a[z]	4.7 b
800	6.3 a	6.5 a
	Stolons per plant	
100	10.6 a	4.0 b
800	4.0 a	6.5 a

*Note: [z]Mean separation within row by Fisher's Protected LSD, α=0.05.

4. Discussion

Differences in the effects of photoperiod and nitrogen during conditioning on the floral ontogeny of strawberry were observed depending on the method of evaluation (greenhouse forcing, dissections, field productivity) highlighting the importance of using multiple methods, if possible, in determining treatment effects on flowering and fruiting in the strawberry. Even though the specific treatment effects on particular aspects of flowering or fruiting that were detected varied depending on evaluation method, general overall treatment effects were fairly consistent.

LD conditioning of long-day cultivars generally promotes a floral character in plants [11,12,20,21] which is ultimately reflected in enhanced yields [1–4]. In this study, flower production per plant was greater under LD compared to ND (Tables 1 and 4) and terminal meristems had more flower initials under LD compared to ND (Table 5). However, plants under ND rather than LD tended to produce more inflorescences during the first half of greenhouse forcing. This trend was reversed during the second half of forcing where more inflorescences were produced under LD. The lack of statistical significance on many of the observation dates may be due to the relatively small sample size (6 plants per treatment) in this study. In addition, if greenhouse forcing had continued beyond 10 weeks, more inflorescences would have likely been produced by plants under LD since when plants were dissected after 10 weeks in the greenhouse, LD had enhanced the floral nature of terminal meristems (dissection data), especially when N was elevated for conditioning (Table 6). Considering inflorescence and flower production with dissection data, LD generally enhanced the floral nature, similar to LD enhancement previously reported [1–7,11,12,20–22].

Plants that received 800 ppm N during conditioning produced significantly more inflorescences and flowers per plant than those that received 100 ppm N (Tables 2 and 4) similar to the floral enhancement with elevated N previously reported [1–3,7,10–13]. The synergistic enhancement of flowering by elevated N and LD previously reported [1] was observed in meristem dissections of greenhouse forced plants in this study. Plants receiving elevated N during conditioning required LD to maximize flower initiation as indicated by terminal meristem status (Figure 1, Tables 5 and 6); plants under ND had an average terminal meristem status of 0.50 while those under LD had a status of 1.00. Branch crown terminal meristems were more floral under LD and axillary meristems of

branch crowns were more floral with 800 ppm N compared to 100 ppm N. LD completely prevented stolon formation from branch crown axillary buds (Table 7).

While previous reports [1,2,11–13,20,21] suggested that increased flowering and fruiting of long-day cultivars could be obtained with either elevated N or LD during floral initiation, these results suggest that both are required for maximum transition of meristems to a floral nature. Others have previously suggested that elevated N before, at the beginning of or too late after initiation begins inhibits flowering [7,10]. Perhaps the elevated N shifts meristem sensitivity to photoperiod towards a more qualitative response (absolute photoperiod requirement for flower initiation) away from a more quantitative response (enhanced flower initiation with photoperiods closer to the critical photoperiod). In this study, if the elevated N shifted meristem sensitivity towards being more qualitative, LD would be required for maximum floral initiation. Plants receiving 100 ppm N may have had meristems which had a more quantitative than qualitative response, thus ND, which at the time were slightly over 14 hrs, were 'effective enough' to cause floral initiation in about 90% of the plants. In plants which had received 800 ppm N, meristem sensitivity had shifted to a more qualitative nature, thus 14 hr photoperiods were not as effective for floral initiation since only half the meristems under ND were floral while all of the meristems under LD were floral (Table 6).

Greenhouse evaluation indicated that elevated N enhanced precocity of the second and third inflorescence while field estimation of fruiting precocity indicated an enhancement with LD conditioning. N fertilization is generally effective in promoting the floral character in both long-day [3,11,12] and short-day cultivars [7,10,23]. When precocity specific effects of N have been observed, enhanced precocity has been in the 1 [13] to 3 [11,12] week range. While no photoperiod effects on floral precocity in the greenhouse were detected, LD plants were more precocious in the field and produced ripe fruit one week earlier (17 August) than plants conditioned under ND (23 August) (Table 8). Early yield and fruit number (through 4 September) was enhanced by LD conditioning which agrees with previous reports for 'Albion' [1,2]. Mid and late-season yield (October and November) was enhanced with elevated N during conditioning, reflecting the enhanced floral nature of the plants with elevated N detected in the greenhouse growth study and architectural analysis. Apparently early yield in this off-season system relies on the photoperiodic floral stimulus while enhanced later season yield is dependent on the elevated N during conditioning. The dissection data which revealed that the floral nature requires both LD and elevated N combined with the early and late season yield responses to photoperiod and N in the field suggests that LD are needed to trigger floral initiation and elevated N immediately after the trigger is needed to enhance continued flowering and fruiting later on. Even though plants were conditioned in June, the effects of the conditioning treatments were still apparent in November. These results support the idea previously illustrated [13,24] that photoperiod and N influence the fate of meristems long after plants are removed from conditioning treatments. The overall summary though is that LD and elevated N enhance field productivity, which agrees with enhanced floral productivity in greenhouse forcing and enhanced floral nature of dissections with LD and elevated N, supporting previous reports [1,2] of LD accelerated and enhanced yield of 'Albion' in an off-season system.

The fate of axillary meristems as affected by treatment was estimated with all three methods as well. Greenhouse forcing suggested that neither photoperiod nor N altered stolon or branch crown formation. However, with dissection, elevated N reduced the production of stolons (Table 6) in favour of promoting floral mersitems, especially in branch crown axillary buds. Branch crown axillary buds might respond to photoperiod and N more than axillary buds of the main crown since

those on the main crown may have already been programmed down a particular developmental road prior to planting since they were grown from dormant crowns. Branch crown axillary buds may be more sensitive to photoperiod and N thus more pliable in development since they were formed during the experiment (all plants trimmed to a single main crown at the beginning of the experiment). Dissections also suggested that LD inhibited branch crown formation by main crown axillary meristems and LD inhibited stolon production by branch crown axillary meristems.

In the field trial, no main effect of N was detected, however an interaction between photoperiod and N was detected. Fewer stolons and branch crowns were produced by plants receiving 100 ppm N under LD. No photoperiod effect was observed for plants given 800 ppm N (Table 10) perhaps because the elevated N induced floral formation. In plants receiving 100 ppm N during conditioning, long-day inhibition of stolon and branch crown formation was observed (Table 10) suggesting that more meristems were floral in the field when previously conditioned with LD or 800 ppm N which is reflected in increased yields with these treatments. It may not be long-day inhibition of branch crown and stolon development per se, but rather long-day promotion of the floral character. Sonsteby et al. [7] reported no effect of N on crown number while Durner reported enhanced crown production with elevated N in 'Elan' [11] and 'Tarpan' and 'Gasana' [12]. In the present greenhouse study, no effect of N on branch crown formation was detected, however, when plants were dissected, more axillary meristems had formed branch crowns that were given elevated N during conditioning. This agrees with earlier work of Durner [11,12]. In the present field study, no main effect of N was detected, however, there was an interaction of conditioning photoperiod with N fertilization. With limited N, plants conditioned under ND produced on average 3 more branches per plant compared to LD or ND with 800 ppm N (Table 10). Increased branch crown formation with low N under ND may reflect a tendency for axillary meristems to become floral quickly with elevated N or LD, thus fewer meristems become branch crowns under these conditions. The field evaluations suggest that lower N increases meristem sensitivity to photoperiod, not only for floral responses as previously reported [22,25,26] but also for the vegetative responses of stolon and branch crown production.

Light source did not affect plant growth in the greenhouse, the status of meristems at dissection or on field fruit, stolon or crown production. Both light sources were equally effective in eliciting a long-day response. The effect of light source on cumulative greenhouse leaf production detected on one observation date (31 May) for plants given 800 ppm N during conditioning (Table 3) did not manifest itself on any other date, thus it is doubtful that it was 'real', and was rather due to natural variability. Cyclic lighting may extend production of long-day cultivars [3,4]. Since no differences between the two light sources were detected for any parameter evaluated, it is reasonable to conclude that the low cost light strings would be effective in field or high tunnel cyclic lighting strategies to enhance fruiting. If such a lighting strategy was implemented, lighting expenses could be reduced by using the lower cost light strings.

The benefits of a field trial to estimate conditioning treatment effects on growth and productivity are obvious. The benefits of architectural analysis which includes laborious dissections may not be as evident. However, this paper clearly illustrates the advantages of including dissections in studies examining floral development in strawberry.

Inflorescence production during forcing is a measure of development rather than induction, initiation or differentiation [29]. In this experiment, LD or elevated N enhanced floral development (Tables 1 and 2). This supports other reports of enhanced floral development of long-day cultivars with elevated N or long-days [3,11,12]. Inflorescence counts provide a reasonable

measure of initiation, however, factors which may enhance initiation but not development may be missed without the additional information provided by dissections. In this study, the effects of photoperiod, N and lighting source on the number of inflorescences initiated as estimated by plant counts during forcing was variable depending on observation date. Only when plant count data is combined with the additional information afforded by dissections can a conclusive statement be made regarding the effects of various factors on initiation. In this study, count and dissection data suggested that long-days and elevated N both enhanced floral initiation in 'Albion'.

Flower counts during forcing provide a measure of differentiation but again, dissections provide information regarding the status of all meristems, not just those whose flowers have developed and become macroscopically visible. The terminal meristem bud stage provides an additional measure of factor effects on differentiation. In this study, there was a clear effect of elevated N enhancement of differentiation as measured by flower counts per plant (Table 2) and enhanced differentiation under LD compared to ND (Table 4). Flower counts per plant do not directly assess flower differentiation because increased flowers per plant may be due to increased inflorescences per plant. When adjusted to a flower per inflorescence basis, there are no differences among treatments (average of 3.5 flowers per inflorescence). The separation of direct and indirect factor effects on differentiation enhancement was made possible by floral architectural analysis. Dissection of the terminal meristem in this experiment revealed enhanced differentiation due to long-day conditioning, with no effect of elevated N.

Previous reports that N directly enhances floral formation and is not simply a response to greater general growth due to the N [13] relied on flower counts during forcing and not ratings of the dissected terminal meristem as in this study. Observations that differentiation as measured by flower production was enhanced with an elevated N application in other long-day cultivars [11,13] also relied on counts. Even so, greater flower numbers with growth counts supports the contention that elevated N stimulates floral development. This study indicates that differentiation per se is not enhanced by elevated N and that the greater number of flowers per plant is the result of a greater number of branch crowns and inflorescences per plant.

A previous report [13] suggested that responses to elevated N are qualitative with a threshold between 100 and 400 ppm N for all variables affected by N rate except for the number of flowers per primary crown, where the response appeared to be quantitative. These observations support the notion that elevated N directly enhances floral formation and is not simply a response to greater general growth due to the N. N triggers some aspect of the flowering pathway that results in enhanced differentiation [11] while low levels of N during initiation and differentiation cause inflorescence abortion [29], and reduced differentiation [30]. Low levels of N are desired prior to floral induction to reduce vegetative growth and promote flower induction, initiation and differentiation [22,28,31–35]. In addition, the fates of branch crown axillary meristems that likely formed during the experiment were influenced by photoperiod and N and the effect was observed long after conditioning. This provides additional evidence that the effect is systemic and not a transient effect of N or photoperiod effects on growth rate.

Growth data provides information on absolute numbers of stolons, branch crowns, etc. which vary from plant to plant while floral models provide an estimate of characteristics of the population of meristems, i.e. a % rather than an absolute number. Percentage values are stable regardless of absolute numbers and provide a better estimate of meristem fate. Field assessment of conditioning effects on branch crown and stolon formation confirms observations of dissection. Greenhouse

forcing likely does not reflect dissection data due to a much shorter growth period in the greenhouse (10 weeks) compared to more than 4 months in the field. If limited time and resources are available for greenhouse forcing, architectural analysis shows real benefits. If longer forcing is possible, such as field production, the extra effort of dissection must be compared to the extra effort of longer forcing.

This study supports others [11,12] that clearly illustrate that N fertilization is a viable tool for managing flowering in long day strawberries and that flowering is easily manipulated by altering N fertility and or photoperiod, particularly immediately prior to forcing. This study also illustrates that inexpensive, low wattage lights induce long-day responses similar to more expensive, higher wattage sources. This suggests that in-field cyclic lighting to promote extended fruiting of long-day cultivars is feasible.

5. Conclusion

Low cost 'holiday' light strings with C9, 7-watt clear bulbs are as effective as more expensive strings of A19, 60-watt soft white bulbs in effecting long-day photoperiod responses in the long-day cultivar 'Albion'. Photoperiod conditioning did not affect precocity of first, second or third inflorescence or leaf, crown, or stolon production. There was a tendency for plants under ND to produce more inflorescences during the first 5 weeks in the greenhouse while LD enhanced inflorescence production during the last 5 weeks of forcing. LD enhanced the number of flowers produced per plant. Plants receiving elevated N during conditioning required LD to maximize floral initiation as revealed via dissection of the main crown terminal meristem. Additionally, a greater number of flower initials were observed in dissections of plants grown under LD compared to ND. LD inhibited branch crown formation by axillary buds, but had no effect on the number of vegetative, floral or stolon producing axillary meristems. LD conditioning enhanced field plasticulture precocity, producing ripe fruit one week earlier than plants conditioned under natural daylengths and early yield (through 4 September) was enhanced by long-day conditioning. In field plasticulture, no effect of photoperiod was detected for stolon or branch crown production for plants given elevated N during conditioning. In plants not receiving elevated N during conditioning, long-day inhibition of stolon and branch crown formation was observed. Combining plant growth data with architectural mapping of meristems allows more conclusive statements regarding the effects of specific factors on specific stages of floral physiology (i.e. induction, initiation, differentiation and development) compared to more generalized conclusions obtained with growth data alone. The separation of direct and indirect factor effects on floral physiology are possible with floral architectural analysis.

Conflict of interest

The author declares no conflict of interest in this paper.

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