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Research article

Programmed flowering of the F1 long-day strawberry cultivar 'Elan' with nitrogen and daylength manipulation

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Abstract: Consumer demand for locally grown, high quality strawberries is increasing even though California, Florida and Mexico provide a year-round source of strawberries for the world market. In most of the US, locally grown strawberries are only available for a short time in late spring from seasonal fruiting short-day cultivars thus off-season strawberry production is an attractive option for growers. Seed propagated hybrids such as 'Elan' are becoming more widely available and offer an alternative to often low yielding cultivars used for off-season production. To determine whether or not 'Elan' could be programmed to flower with photoperiod or nitrogen, seedlings were fertilized with either 100 or 800 ppm nitrogen for 4 weeks in September beginning one week after exposure to either short days, the natural photoperiod, or long days, the natural photoperiod supplemented with 24 hours of incandescent radiation. Plants were then greenhouse forced under both photoperiods and floral phenology evaluated. Elevated nitrogen during floral initiation in September enhanced and accelerated flowering and plants receiving elevated nitrogen during initiation under long days flowered more than any other treatment. To determine whether or not flowering could be enhanced a second time in the same plants, another 4 week period of elevated nitrogen was provided in December and plant phenology evaluated through mid-January. Elevated nitrogen (800 ppm) in December enhanced December and January flowering. Seedlings were conditioned with elevated nitrogen for a third time in late spring then field planted (early summer) on raised beds with white or black plastic mulch. Elevated nitrogen in late spring enhanced yield in field production. No effects of mulch color, initiation photoperiod or interaction of considered factors were detected. Flowering differences detected in greenhouse studies translated into differences observed in the production field suggesting programmed fruiting with elevated fertilization under field or greenhouse conditions would be feasible.

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

Abbreviations:

ND: natural daylength;
24LD: natural daylength supplemented with 24 h incandescent radiation (Phillips Duramax Soft White A19 60 watt) suspended 0.3 m above the plant canopy;
N: nitrogen

1. Introduction

Consumer demand for locally grown, high quality strawberries has steadily increased even though California, Florida and Mexico provide a nearly year-round source of relatively inexpensive strawberries for the world produce market [1]. In most of the US temperate zone locally grown strawberries are available for a short time in late spring from seasonal fruiting, short-day cultivars. This makes off-season strawberry production in temperate regions of the US attractive to growers.

The local strawberry season can be extended by forcing an early spring crop [2,3], extending production in the fall under high tunnels with day-neutral or conditioned short-day cultivars [4-6], or forcing during the winter months with day-neutral or conditioned short-day cultivars [7]. Although numerous attempts at off-season forcing have been reported [7-11] commercial success in North America is extremely limited even though profitable off-season production is common in Europe and Japan [12-14]. In all off-season production scenarios, preparation of plant material prior to forcing is critical to success [12,14].

Strawberry plugs [15] are often used for season extension in the US [2-7] and they may be conditioned by photoperiod or temperature to enhance fruiting [7,16]. Vegetatively propagated plug plants may carry over photoperiod and temperature effects on flowering and runner production from mother plants [17]. In addition, plugs may become root-bound [10] and their productivity can vary depending on distance in order from the mother plant [10,18,19]. Plugs may be infected with viruses [20,21] or disease inoculum [22] and it is often difficult to secure plugs of desired cultivars [4].

Seed propagated long-day (day neutral) F1 strawberry hybrids have become increasingly popular in Europe, Asia and Russia [23-31] and seeds of these hybrids are becoming increasingly available to growers. Seed propagated cultivars have potential advantages over vegetatively propagated plug plants. Seeds are free of soil-borne diseases, are easily shipped and stored and are easily adapted to mechanized production of transplants. There are no special cultural methods or equipment needed for production and cultivars are widely adapted to many production systems [25]. Unfortunately, limited research has evaluated their potential for North American production. The cultivars ‘Milan’ and ‘Elan’ (both F1 hybrids, ABZ Seeds, The Netherlands) were evaluated in field trials alongside vegetatively propagated day-neutral cultivars including ‘Albion’ and ‘Seascape’ in Ontario. Both seed-propagated cultivars tended to produce moderate yields, however fruit was fairly small [32]. Initial trials by ABZ Seeds [26] indicated that F1 hybrids are best suited for greenhouse production and the main advantage of seed propagated F1 hybrids would be in forced culture [23]. Under greenhouse conditions, yields of numbered F1 selections averaged about 1500 grams per plant (7.5 $kg \cdot m^{-2}$) over four months [26].

Photoperiod and temperature are the most important environmental signals for regulating flowering in strawberry and their effects have been studied extensively [33]. Sonsteby and Heide [34,35] published extensive reports on the flowering physiology of the F1 seed-propagated cultivar 'Elan'. They reported that 'Elan' is a qualitative long-day plant [35] at high temperatures (> 27 °C) with a critical photoperiod of 15 hrs. [34]. They also proposed that all recurrent flowering (RF) cultivars (traditionally called everbearers, day-neutrals and remontants) are qualitative long-day plants at high temperatures (27 °C), quantitative long-day plants at intermediate temperatures (between 10 and 27 °C) and day-neutral at temperatures below 10 °C [35].

Mineral nutrition is known to affect productivity in strawberry [36] but reports on its effects during floral induction are limited [33]. Sonsteby et al. [37] reported increased flowering associated with elevated N during short day conditioning of the short-day cultivar 'Korona'. N fertilization interactions with photoperiod on floral initiation in strawberry are critically dependent on timing of application. Flowering is enhanced when N fertilization is increased after the initiation process has begun [37-39] but N applied before, at the beginning of or too long after initiation, inhibits flowering [37,40] and reduces yield [37]. Lieten [41] had previously observed enhanced flowering of 'Elsanta' in plants when fertilization was applied during but not before natural floral induction.

This study was initiated to investigate whether flowering and fruiting of seedlings of the F1, seed-propagated cultivar 'Elan' could be programmed by manipulating N nutrition and photoperiod during floral initiation.

2. Materials and Methods

Seeds of the F1 hybrid cultivar 'Elan' were purchased from Johnny's Selected Seeds (Albion, ME), sown in vermiculite and germinated at 20 °C beginning 05 May 2014. After seven days, many radicles were visible and the seed trays were moved to the greenhouse at ambient (24/18 °C day/night) temperatures and allowed to grow for 4 weeks. On 05 June 2014 seedlings were transplanted into Fafard Organic Mix (FOF-30) (Sun Gro Horticulture, Agawam, MA) in 50 cell plug trays (Johnny's Selected Seeds, Albion ME.) then transplanted to 12.7 cm plastic pots into FOF-30 mix 4 weeks later. Seedlings grew an additional 8 weeks before commencement of treatments. Seedlings were watered twice daily as needed and fertilized with 100 ppm N Sea-Plus liquid fish and seaweed (3-2-2) (Living Acres, New Sharon, ME) biweekly.

Beginning 09 September 2014, single crowned plants with 4 fully expanded leaves were placed under ND or 24LD. After 1 week plants were fertilized weekly for four consecutive weeks with Sea-Plus diluted with water to provide 100 or 800 ppm N. Each plant received 100 mL of solution which was more than sufficient to saturate the media. Following the 4-week fertility treatment, all plants were fertilized weekly with Sea-Plus diluted with water to provide 100 ppm N. Immediately after conclusion of the N treatment, plants were forced in the greenhouse under either 24LD or ND. Plants were arranged in a split-split plot design in the greenhouse with main plot of photoperiod (ND versus 24LD) arranged in a randomized complete block replicated 3 times. Sub-plots were N level and sub-sub plots were forcing photoperiod (24LD versus ND). The experimental unit was 4 single plants.

Observations of plant growth and development in the greenhouse were made at weekly intervals beginning 24 September 2014. The following data were collected: the number of fully expanded leaves, the number of runners, the number of branch crowns, the number of inflorescences and the total number of flowers produced per plant. The number of flowers per inflorescence was calculated as the total number of flowers per plant/the number of inflorescences per plant. Initiation was evaluated via

inflorescence counts, differentiation via flowers per inflorescence and development via precocity. Floral growth responses were adjusted for differences in vegetative crown growth by calculating the number of inflorescences produced per crown. Precocity was estimated as the length of time after the start of conditioning (09 September) until the first inflorescence appeared.

On 04 December 2014, each experimental unit (4 plants) was subdivided to provide a second fertility treatment consisting of either 100 or 800 ppm N for 4 weeks. The experimental design was reconfigured for statistical analysis to a split-split-split plot design in the greenhouse with main plot of September photoperiod (N versus 24LD) arranged in a randomized complete block replicated 3 times. Sub-plots were September N level and sub-sub plots were forcing photoperiod (plants remained in the forcing photoperiod to which they had been assigned after the September N treatment). Sub-sub-sub plots were secondary N treatment. The experimental unit was 2 single plants. Observations on plant growth and development were made as previously described. In addition, the numbers of leaves, inflorescences and flowers produced from 4 December through 15 January were calculated to evaluate N influence on new growth.

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. [42] using the ARTool program (http://depts.washington.edu/aimgroup/proj/art/). This procedure allows for analyzing data from a factorial treatment structure using ranks rather than raw data, alleviating the non-normality problem and allowing for tests of interactive effects. Most procedures using ranks (non-parametric) test for main effects only. ART data were analyzed using an analysis of variance (ANOVA) using the ANOVA procedure of SAS (SAS Institute, Cary, NC). Detected differences among photoperiod or nitrogen treatments were separated with Fisher's Protected LSD. Data are presented for plants immediately after 4 weeks of September N treatment, 6 weeks after concluding September N treatment and 2 weeks after concluding December N treatment.

To determine whether or not photoperiod or N fertility conditioning in the greenhouse would enhance flowering under field conditions, seedlings from the aforementioned greenhouse experiments were allowed to grow under ambient conditions in the greenhouse from 15 Jan 2015 until 21 April 2015. During this time, plants were fertilized with 100 ppm N biweekly. Plants were watered twice daily as needed. Beginning 21 April 2015, half of the plants were placed under ND while the others were placed under 24LD. After 1 week half of the plants under each photoperiod were fertilized weekly for four weeks with 100 ppm N and the other half with 800 ppm N. Each plant received 100 mL of solution. On 10 June, plants were transplanted to the field on raised beds with either black or white on black plastic mulch (white side exposed) with drip irrigation. The field experimental design was a split-plot with mulch color as main plot replicated 8 times in a randomized complete block design. Sub-plot was a factorial combination of photoperiod (ND versus 24LD) and N (100 versus 800 ppm N) arranged as completely random 2 plant experimental units within main plots. Fruit were harvested, weighed and counted on 28 July, 30 July, 5 and 12 August. Due to labor constraints, harvests were not continued. However, the 4 harvests conducted were sufficient to reveal treatment differences on flowering. Yield data was analyzed via an ANOVA and means separated with Fisher's Protected LSD when appropriate.

A timeline of experimental activity is presented in Table 1 and an ANOVA table with sources of variation, degrees of freedom and errors used for testing is presented in Table 2.

Table 1. Activity timeline for 'Elan' seedlings.

Date	Activity
05 May 2014	Seeds sown in vermiculite and germinated at 20 C
12 May 2014	Seed trays moved to the greenhouse at ambient (24/18 C day/night) temperatures.
05 June 2014	Seedlings transplanted into 50 cell plug trays
03 July 2014	Seedlings transplanted to 12.7 cm plastic pots.
09 September 2014	Single crowned plants with 4 fully expanded leaves placed under ND or 24LD.
16 September 2014	Plants fertilized weekly for four consecutive weeks with 100 or 800 ppm N.
24 September 2014	Weekly observations of plant growth and development start.
14 October 2014	Photoperiodic forcing treatment under either 24LD or ND started.
04 December 2014	Second fertility treatment of either 100 or 800 ppm N for 4 weeks started. Weekly observations discontinued.
15 January 2015	Greenhouse component completed.
15 Jan 2015–21 April 2015	Plants continue to grow under ambient greenhouse conditions. Fertilized biweekly with 100 ppm N.
21 April 2015	Half of the plants placed under ND while the other half placed under 24LD
28 April 2015	Half of the plants under each photoperiod fertilized weekly for 4 weeks with 100 ppm N and the other half with 800 ppm N.
10 June 2015	Plants transplanted to the field.
28 July 2015–12 August 2015	Fruit harvested, weighed and counted.

Table 2. ANOVA table with sources of error, degrees of freedom (df) and errors used for testing main effects and interactions.

Source	Df	Testing error
Total	48	
Correction factor (μ)	1	
Block	2	
September photoperiod	1	A
Error a	2	
September Nitrogen	1	B
September Nitrogen X September photoperiod	1	B
Error b	4	
Forcing photoperiod	1	C
Forcing photoperiod X September Nitrogen	1	C
Forcing photoperiod X September photoperiod	1	C
Forcing photoperiod X September Nitrogen X September photoperiod	1	C

Error c	8	
Second Nitrogen treatment	1	D
Second Nitrogen treatment X September photoperiod	1	D
Second Nitrogen treatment X September Nitrogen	1	D
Second Nitrogen treatment X September Nitrogen X September photoperiod	1	D
Second Nitrogen treatment X Forcing photoperiod	1	D
Second Nitrogen treatment X Forcing photoperiod X September Nitrogen	1	D
Second Nitrogen treatment X Forcing photoperiod X September photoperiod	1	D
Second Nitrogen treatment X Forcing photoperiod X September Nitrogen X September photoperiod	1	D
Error d	16	

3. Results

3.1. Evaluation immediately after treatment

Elevated N during floral initiation in September significantly enhanced leaf, branch crown and inflorescence production (Table 3). Inflorescence production was also enhanced by exposure to 24LD compared to ND during initiation. No interactions of photoperiod with N were detected after 4 weeks of treatment for any measured variable. Plants did not runner during this period.

Table 3. Influence of September N and photoperiod during floral initiation on 'Elan' strawberry leaf, crown and inflorescence production measured immediately after 4 weeks of N treatment.

September N (ppm)	Leaves per plant	Crowns per plant	Inflorescences per plant
100	7.4 b[z]	1.5 b	0.1 b
800	10.8 a	2.2 a	0.4 a
Initiation photoperiod	Inflorescences per plant		
ND	0.1 b		
24LD	0.4 a		

[z]Mean separation within column by Fisher's Protected LSD, 0.05 level.

3.2. Precocity

A significant interaction between September N and initiation photoperiod was detected for precocity (Table 4). Elevated N fertility accelerated flowering regardless of initiation photoperiod. The effect was more pronounced when elevated N was administered under ND (+2.5 weeks) compared to 24LD (+1.7 weeks). A significant interaction between September N and forcing photoperiod was also detected. Plants given 100 ppm N during floral initiation flowered sooner when forced under 24LD compared to ND. Those given 800 ppm N during initiation flowered approximately 1.5 weeks sooner than those given 100 ppm N and were not affected by forcing photoperiod (Table 4).

Table 4. Influence of September N fertility and photoperiod during floral initiation on 'Elan' strawberry precocity (weeks after start of experiment) estimated 12 weeks after the start of the experiment.

	September N (ppm)	
Initiation photoperiod	100	800
Natural	7.5 a[Z]	5.0 b
24hr Incandescent	5.9 a	4.2 b
Forcing photoperiod	100	800
Natural	7.5 a[Y]	4.7 a
24hr Incandescent	6.0 b	4.5 a

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

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

3.3. Evaluation 6 weeks after completion of treatments

The effects of September N fertilization during flower initiation on leaf, crown, and flower production were clearly evident 6 weeks after treatments were completed (Table 5). Elevated September N significantly enhanced the number of leaves, crowns, runners and flowers per plant as well as the number of flowers per inflorescence. Plants produced an average of 1 inflorescence per crown and this value was not influenced by initiation photoperiod, September N, or forcing photoperiod. There was a significant interaction of initiation photoperiod with September N on the number of inflorescences per plant (Table 5). Plants receiving elevated N under 24LD during floral initiation produced an average of 3.2 inflorescences per plant compared to an average of 1.7 for the other three treatments. Forcing photoperiod did not have a significant effect on any of the parameters studied.

Table 5. Influence of September N and photoperiod during floral initiation on 'Elan' strawberry leaf, crown, inflorescence, flowers per plant and flowers per inflorescence after 6 weeks of greenhouse forcing following treatment.

	September N (ppm)	
	100	800
Leaves per plant	14.2 b[Z]	21.9 a
Crowns per plant	1.9 b	3.0 a
Runners per plant	0.1 b	0.8 a
Flowers per plant	5.8 b	13.3 a
Flowers per inflorescence	3.5 b	6.1 .a
	Inflorescences per plant	
	September N (ppm)	
Initiation photoperiod	100	800
ND	1.7 b[Z]	1.4 b
24LD	1.9 b	3.2 a

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

3.4. New plant growth in December and January during and after second Nitrogen elevation

Leaf growth in December and January was enhanced by September N (6.8 and 4.3 new leaves per plant for 800 and 100 ppm September N, respectively), ND forcing (6.2 versus 4.8 new leaves per plant for ND versus 24LD forcing photoperiod, respectively) or December N (6.5 and 4.5 new leaves per plant for 800 versus 100 ppm December N, respectively). The number of new leaves produced per crown was 2.2 and was not affected by initiation photoperiod, September N, forcing photoperiod, December N or any interaction of these variables.

New branch crown production in December and January was enhanced by forcing under ND (0.4 new crowns per plant) compared to forcing under 24LD (0.2 new crowns per plant).

A significant interaction between September initiation photoperiod and September N was detected for inflorescence production in December and January (Table 6). Elevated September N under both initiation photoperiods enhanced new inflorescence production in December and January with elevated nitrogen under 24LD inducing greater enhancement than under ND.

Table 6. Influence of initiation and forcing photoperiod and elevated September N on new inflorescence production in December and January of 'Elan' strawberry 6 weeks after the start of December fertilization.

	September N	
Initiation photoperiod	100	800
ND	1.2 b[Z]	2.2 a
24LD	1.1 b	2.6 a
Forcing photoperiod		
ND	1.0 b[Z]	1.8 a
24LD	1.3 b	3.2 a

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

Elevated September N enhanced new inflorescence production in December and January under both forcing photoperiods (Table 6) and the enhancement was greater under 24LD compared to ND forcing.

Elevated December N enhanced new inflorescence production (2.3 new inflorescences per plant in December and January) compared to 100 ppm N (1.2 new inflorescences in December and January). New inflorescence production per crown in December and January was significantly enhanced by elevated September N (0.8 and 0.5 new inflorescences per crown for 800 and 100 ppm N, respectively), forcing photoperiod (0.9 and 0.5 new inflorescences per crown for 24LD and ND forcing photoperiods, respectively) and elevated December N (0.9 and 0.5 new inflorescences per crown for 800 and 100 ppm N in December, respectively).

New flower production per plant was enhanced with elevated September N (10.7 versus 4.3 new flowers per plant for 800 and 100 ppm September N, respectively) or elevated December N (10.1 versus 4.9 new flowers per plant for 800 and 100 ppm December N, respectively). New flower production per inflorescence was enhanced when elevated December N followed 100 ppm N in September (4.4 versus 2.9 new flowers per inflorescence for 800 and 100 ppm December N, respectively) but no effect of December N was observed when it followed elevated September N (4.5 new flowers per inflorescence).

3.5. Total plant growth through mid-January

A significant interaction between September N fertility and forcing photoperiod was detected for leaf production. Plants given 100 ppm N in September produced an average of 18.1 leaves per plant regardless of forcing photoperiod. Plants given 800 ppm N produced significantly more leaves under ND (29.5 leaves per plant) compared to those forced under 24LD (24.6 leaves per plant). Elevated December N slightly enhanced total leaf production (23.9 and 21.3 leaves per plant for 800 and 100 ppm N, respectively).

A significant interaction among initiation photoperiod, September N and forcing photoperiod on branch crown production was detected. Following floral initiation under 24LD, plants had an average of 2.6 branch crowns regardless of September N fertility or forcing photoperiod. Following floral initiation under ND, plants fertilized with 100 ppm N during initiation had an average of 2.1 branch crowns. Those fertilized with 800 ppm N produced 3.8 branch crowns per plant under ND forcing and 2.8 crowns per plant under 24LD forcing conditions.

A significant September N X initiation photoperiod X forcing photoperiod X December N interaction was detected for the total number of inflorescences produced per plant (Table 7). N fertilization during initiation under ND had no effect on total inflorescence production, with plants producing an average of 3.4 inflorescences per plant (Table 7). The effect of N fertilization during 24LD initiation was quite pronounced. Plants given 800 ppm N during floral initiation under 24LD produced 3 more inflorescences per plant compared to those given 100 ppm N (Table 7). Plants forced under 24LD after floral initiation under 24LD produced 1.4 more inflorescences per plant compared to those forced under ND after 24LD September initiation. Forcing photoperiod after initiation under ND did not affect the total number of inflorescences per plant.

Elevated December N increased the total number of inflorescences produced per plant (Table 7). Plants given 800 ppm N in December produced significantly more inflorescences per plant than those given 100 ppm N. The quantitative effect of the added nitrogen was slightly greater for plants under 24LD compared to ND initiation (1.5 and 1 additional inflorescences per plant, respectively).

Table 7. Influence of photoperiod during floral initiation, forcing photoperiod and elevated September or December N on total inflorescence production per plant of 'Elan' strawberry.

	September N		*Forcing photoperiod*		*December N*	
Initiation photoperiod	100	800	ND	24LD	100	800
ND	2.8	4.0	2.9	3.9	2.9 b[Z]	3.9 a
24LD	2.4 b	5.4 a	3.2 b	4.6 a	3.2 b	4.7 a

[Z]Mean separation within row and treatment factor by Fisher's Protected LSD, 0.05 level. Lack of letters indicates not significant.

A significant September N X initiation photoperiod X forcing photoperiod X December N interaction was detected for the total number of inflorescences produced per crown (Table 8). After initiation under ND, plants forced under 24LD or given elevated N in December produced more inflorescences per branch crown (0.6 and 0.3 additional crowns per plant, respectively). Plants exposed to 24LD in September and fertilized with 100 ppm N produced an average of 1.3 inflorescences per crown regardless of forcing photoperiod. The number of inflorescences per crown produced after 800 ppm September N under 24LD initiation conditions varied with forcing photoperiod (Table 8). Plants

forced under ND produced an average of 1.4 inflorescences per crown. Inflorescences produced per crown under 24LD forcing after 800 ppm N during 24LD September initiation varied with December N treatment. Plants given 100 ppm N in December produced 1.5 inflorescences per crown while those given 800 ppm N in December produced 2.9 inflorescences per crown.

Table 8. Influence of photoperiod during floral initiation, forcing photoperiod and elevated September or December N on total inflorescence production per crown of 'Elan' strawberry.

Initiation photoperiod	*Forcing photoperiod*			
	ND		24LD	
ND	1.1 b[Z]		1.7 a	
	December N			
	100		800	
ND	1.2 b		1.5 a	
Initiation photoperiod	*September N*	*Forcing photoperiod*	*December N*	
			100	800
24LD	100	ND	1.3	
24LD	100	24LD		
24LD	800	ND	1.4	
24LD	800	24LD	1.5 b	2.9 a

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

The number of flowers per plant was influenced by September N, forcing photoperiod and December N, but not by initiation photoperiod. No significant interactions were detected. The numbers of flowers per plant were enhanced with elevated September or December N or under a 24LD forcing photoperiod (Table 9). The number of flowers per plant was directly related to the number of inflorescences per plant since the number of flowers per inflorescence was not affected by treatment (mean value of 4.0 flowers per inflorescence).

Table 9. Influence of forcing photoperiod and elevated September or December N on total flower production per plant of 'Elan' strawberry 6 weeks after the start of December fertilization.

	September N		*Forcing photoperiod*		*December N*	
	100	800	ND	24LD	100	800
Flowers per plant	6.5 b[Z]	12.9 a	8.3 b	11.1 a	6.9 b[Z]	12.5 a

[Z]Mean separation within row and treatment factor by Fisher's Protected LSD, 0.05 level.

3.6. Field experiment

Elevated late spring N led to enhanced yield in field production (Table 10). No effects of mulch color, initiation photoperiod or interaction of considered factors were detected. Totals presented are for 4 harvests over 2 weeks. Fruit was small, likely due to poor pollination during extremely hot weather (>35 °C max daily temperature). Data is included here to illustrate that differences detected in greenhouse based flowering studies with this cultivar translate into differences observed in the production field.

Table 10. Influence of enhanced late spring N on summer field fruit production for 'Elan' strawberry.

Late spring fertility (ppm N)	Harvest weight (g·plant^{-1})	Number of fruit per plant
100	76 b^{Z}	18 b
800	94 a	26 a

^{Z}Mean separation within column by Fisher's Protected LSD, 0.05 level.

4. Discussion

Photoperiod and N fertility during floral initiation in September clearly affected flowering and the effects were still apparent four months later. A second elevation of N in December had a similar affect and in some instances was additive to the September N effect. Plants responded to a period of elevated N in April with enhanced flowering and fruiting when established outdoors in a commercial style production field. Plants were sensitive to N over a long period and responses similar to those observed in the greenhouse were seen in the field suggesting that programmed fruiting via N fertilization management is a viable strategy for both greenhouse and field production.

Programmed flowering of clonally propagated cultivars via N management has been successful in Europe and Japan and is most often combined with photoperiod treatment. Flowering in the short-day cultivar 'Korona' was accelerated and enhanced when fertility was elevated one week after photoperiodic induction began [37]. Fertilizing before induction reduced and delayed flowering. Greenhouse flowering in the short-day cultivars 'Korona', 'Polka' and 'Sonata' was significantly enhanced by increasing the temperature and fertility during floral induction [40]. Similarly, enhanced flowering of the short-day cultivars 'Polka', 'Sonata' and 'Korona' was achieved by a combination of enhanced fertilization and elevated temperature during induction [43]. Desmet et al. [38] reported an increase in yield and fruit number from an increase in N given after induction had started. This present study is the first documentation of enhanced flowering of a seed propagated F1 long-day cultivar with photoperiod and N conditioning.

Differences in timing and rate of N fertilization can result in amazingly different flower initiation, differentiation and development responses. When N is well supplied before induction, plants are less sensitive to floral inductive stimuli [44], flower induction is significantly reduced and stolon and shoot growth are stimulated [45-47]. Initiation may be totally inhibited and differentiation of previously initiated inflorescences may be delayed [41,47,48]. When N availability is low before induction, vegetative growth is often reduced and flower induction, initiation and differentiation promoted [14,17,41,49,50] because plants with low N availability seem to be more sensitive to inductive conditions [41,51,52]. Initiation can take place rapidly when such plants are exposed to inductive conditions, however if N levels remain low during initiation and differentiation, inflorescences may abort [53], differentiation may be reduced [13] or plants may revert to vegetative growth [54]. Thus once plants have been induced to flower and initiation is commencing, N levels must be increased to ensure normal differentiation. When N management is used as a tool for programmed flowering, enhanced N application should be commenced one week after photoperiod treatment to induce flowering has begun and not before then [37,39] as early application can significantly delay flower initiation. Ideally, N nutrition should be at a maintenance level (~ 100 ppm N) until after one week of induction [37] followed by 4 weeks of elevated N (~ 1000 ppm N) then returned to lower rates thereafter for differentiation and development.

The response to elevated N or photoperiod in the present study was rapid with statistically significant differences observed as early as 4 weeks after the commencement of treatment. The effects were long lasting as well with responses due to differences in September N observed 4 months later in January. Durner [55,56] previously reported that strawberry flowering responses to photoperiod and temperature conditioning may or may not be observed soon after treatments are completed [55] and were often observed months after the treatments had been initiated [56].

Enhanced flowering under both forcing photoperiods continued four months after nitrogen conditioning: plants with elevated September N and forced under ND produced 0.8 additional inflorescences per plant in December and January while those forced under 24LD produced 1.9 additional inflorescences. The main effect of elevated December N was even more striking: plants given 800ppm N in December produced 2.3 more new inflorescences per plant while those given 100 ppm N produced 1.2 new inflorescences. Durner [56] previously reported that the short day photoperiod conditioning enhancement of yield in the short-day cultivar 'Sweet Charlie' was observed 5 months after treatment. Floral initiation in induced plants of the short-day cultivar 'Korona' continued even under non-inductive conditions [57]. In the present study, elevated N in September, December and late spring might have enhanced the production of florigen which could lead to enhanced flowering (September and December treatments) or fruiting (late spring treatment). Van Delm et al. [58] observed that night interruption with incandescent light enhanced flower initiation and earlier fruiting for the second fruiting cycle of two long-day cultivars 'Charlotte' and 'Portola'. The effect was only observed in flowering of the second fruiting cycle and was gone by the third fruiting cycle. The lack of a prolonged effect of NI on floral initiation could be attributed to high temperature or crop overload signals that might deactivate the initiation set in motion by the NI.

The direct effects of treatment on floral initiation in strawberry can be separated from indirect effects caused by altered vegetative growth by considering inflorescence production on a per crown rather than on a per plant basis. Enhanced initiation reflected in total inflorescences produced per crown from September through January was observed in plants exposed to 24LD throughout the experiment and provided elevated N in September and December. These plants produced nearly 3 inflorescences per crown compared to half that number for all other treatments and forcing combinations (Table 8). These results clearly illustrate that flowering is easily manipulated by altering photoperiod and N fertility, suggesting that programmed flowering for targeted fruit production of F1 seedling cultivars is feasible. In addition, these results show that the effects of 24LD and elevated N are quantitative.

Enhanced differentiation (flowers per inflorescence) due to elevated September N was apparent as early as 6 weeks after completion of treatments. Differentiation was enhanced with elevated N in December as well, but only when it followed 100 ppm N in September. No effect of December N was observed when it followed elevated September N. The elevated N in September triggers some aspect of the flowering pathway that results in enhanced differentiation (Table 5) and this enhancement is still observed in December and January. Additional N in December did not induce further enhancement. The enhanced September N enhanced differentiation since it was applied after induction had started [38].

Enhanced September N fertility significantly accelerated flowering by about 2 weeks. This is similar to results reported by Sonsteby et al. [37,40] where flowering was accelerated by a week with elevated N in several short-day cultivars. Le Miere et al. [43] reported that flowering was accelerated by a week with elevated N and temperature during induction. In this present study, exposure to 24LD accelerated flowering by about 2 weeks. This is similar to reports from van Delm et al. [58] where long

days simulated with night interruption of the long-day cultivar 'Charlotte' advanced cropping by 7 days and a slight enhancement was observed with 'Portola'.

While Sonsteby et al. [37] reported no effect of N on crown number, elevated N or forcing under ND enhanced the total number of crowns per plant in this study. New branch crown production in December and January was enhanced under ND compared to 24LD. Crown branching is often described as a short-day response [33,57] thus more crowns per plant would be expected under ND compared to 24LD.

Elevated N during floral initiation led to enhanced yield in field production. This response is not unusual since several researchers have reported increased yield following elevated N fertility during floral initiation [37,40]. In fact, enhanced N fertilization during initiation of short-day cultivars is used to create fruiting ready plugs for enhanced production in Norway [40]. In this present study, photoperiod during N fertilization of plugs being prepared for field production had no effect on flowering. This suggests that the daylength during conditioning under ND was sufficiently long (almost 15 hrs.) such that extending the daylength had no additive effect on floral initiation. Though production totals presented are for only 4 harvests over 2 weeks, the data illustrates that differences detected in greenhouse based flowering studies with this cultivar do translate into differences observed in the production field. The differences observed in the field establish that plants can be conditioned multiple times and elicit an enhanced flowering response each time. This lends credence to the possibility of programmed fruiting by altering fertility treatments under both field and greenhouse conditions.

5. Conclusion

Photoperiod and N fertility during floral initiation in September clearly affected flowering. The response to elevated N or photoperiod was rapid with statistically significant differences observed as early as 4 weeks after the commencement of treatment. The effects were long lasting as well with responses due to differences in September N observed 4 months later in January. A second elevation of N (in December) had a similar affect and in some instances was additive to the September N effect. The effects of treatment on floral initiation were direct since differences were detected on a per crown basis, which separates direct effects from indirect effects caused by altered vegetative growth. Plants responded to a period of elevated N in late spring with enhanced flowering and fruiting when established outdoors in a commercial style production field. Plants were sensitive to N over a long period and greenhouse observed responses translated to observations in the field which suggests that programmed fruiting via N management is a viable strategy for both greenhouse and field production.

Conflict of interest

The author declares no conflicts of interest in this paper.

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