



Research article

Enhanced flowering of the F1 long-day strawberry cultivars ‘Tarpan’ and ‘Gasana’ with nitrogen and daylength management

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Abstract: Interest in sustainable self-sufficiency, particularly when considering produce has increased. Strawberries, especially particularly the seed propagated, long-day, F1 hybrids such as ‘Tarpan’ and ‘Gasana’, fit self-sufficient, sustainable production models well. They provide aesthetic as well as culinary benefits producing colorful, attractive blossoms and flavorful fruit. To determine if ‘Tarpan’ and ‘Gasana’ flowering would respond to photoperiod and nitrogen, seedlings were fertilized with 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. Photoperiod and N fertility during floral initiation in September affected subsequent flowering of both cultivars. The response was rapid with significant differences observed 4 weeks after the commencement of treatment. Both cultivars responded with increased rate (enhanced precocity) and intensity (enhanced inflorescence/flower number) of flowering with elevated N. In ‘Gasana’ elevated N accelerated flowering by 2–3 weeks. There was a slight acceleration of flowering in lower N plants with long-day forcing, however, elevated N was much more effective in accelerating flowering than long-day forcing. In ‘Tarpan’, long-day forcing and elevated N were equally effective in accelerating flowering. Inflorescence production per plant or crown and the number of flowers per plant were enhanced with elevated N in both cultivars. Long-day forcing stimulated the number of inflorescences produced per crown in both cultivars. The number of flowers per plant in ‘Tarpan’ was also enhanced by long-day initiation or forcing. Elevated N, short-day initiation or long-day forcing enhanced the number of flowers per inflorescence in ‘Gasana’. Elevated N under long-day initiation or under short-day initiation when followed by long-day forcing enhanced the number of flowers per inflorescence in ‘Tarpan’.

Keywords: *Fragaria* × *ananassa* Duch; flowering, greenhouse production; season extension; precocity; floral initiation; floral differentiation; ornamental strawberries

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

Interest in sustainable self-reliance has increased markedly over the past decade. Home-grown and locally grown produce is often preferred over imported produce or produce that has been shipped a long distance. Strawberries fit self-sufficient, sustainable production models well. In most of the US temperate zone locally grown strawberries are available for only a short time in late spring from seasonal fruiting, short-day cultivars, making off-season strawberry production particularly attractive to both growers and consumers wishing to become more self-reliant.

Vegetatively propagated day neutral cultivars such as ‘Seascape’ and ‘Selva’ have been recommended for season-long production, especially on a small scale [1]. However, the flowering response of day neutral cultivars is temperamental [2-4] at best. Though attempts at season-long forcing have been reported [5-9], success in North America is extremely limited even though profitable off-season production is common in Europe and Japan [10-12]. In all off-season/season-long production scenarios, preparation of plant material prior to forcing is critical to success [10,12]. Strawberry plugs [13] are often used for season extension in the US [5,14-18] and they may be conditioned by photoperiod or temperature to enhance fruiting [5,19]. Unfortunately, vegetatively propagated plug plants have a number of problems associated with their use [20]. They may carry photoperiod and temperature effects on flowering and runner production from mother plants, they may become root-bound and their productivity can vary depending on distance in order from the mother plant. In addition they may be infected with viruses or disease inoculum and it is often difficult to secure plugs of desired cultivars.

New seed propagated long-day strawberry cultivars provide opportunities for season-long production as both ornamental and culinary crops. Most F1 seed propagated hybrids have attractively colored flowers [1,21,22] followed by medium to large fruit with excellent culinary qualities [23]. A combination of different cultivars makes an attractive display of white (‘Elan’), pink (‘Gasana’) and red (‘Tarpan’) flowers followed by an abundance of tasty fruit which provides a multipurpose horticultural crop. A single pot with one plant each could make an attractive gift presentation which could be grown and programmed to flower for specific seasonal uses including Fall and Winter holidays such as Thanksgiving, Chanukah, Kwanza, Christmas and New Years, followed by spring holidays such as Valentine’s Day, Mother’s Day and Easter.

Besides their ornamental and culinary uses, seed propagated cultivars have possible advantages over vegetatively propagated plug plants. Seeds are free of soil-borne diseases, are simply shipped and stored and are adapted to mechanized transplant production. There are no special cultural or equipment requirements needed for production and cultivars are widely adapted to different production systems [22]. Trials by ABZ Seeds [24] indicated that F1 hybrids are best suited for greenhouse production and the main advantage of seed propagated F1 hybrids would be in forced culture [21].

Photoperiod and temperature regulate flowering in strawberry and their effects have been studied extensively [25]. Mineral nutrition affects productivity in strawberry [26] but reports on its effects during floral induction are limited [25]. Sonstebly et al. [27] reported increased flowering associated with elevated nitrogen (N) during short day conditioning of the short-day cultivar 'Korona'. Flowering was enhanced when N fertilization was increased after the initiation process had begun [27-29] but N applied before, at the beginning of or too long after initiation, inhibited flowering [27,30] and reduced yield [27]. Lieten [31] had previously observed enhanced flowering of 'Elsanta' in plants when fertilization was applied during but not before natural floral induction. Sonstebly and Heide [32,33] published extensive reports on the flowering physiology of the F1 seed-propagated cultivar 'Elan'. They determined that 'Elan' is a qualitative long-day plant [33] at high temperatures (>27 °C) with a critical photoperiod of 15 h [32]. 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 [33].

Durner [20] demonstrated that flowering of the F1 long-day cultivar 'Elan' could be programmed by nitrogen and daylength manipulation. Elevated nitrogen (800 ppm N for 4 weeks) during floral initiation in September enhanced and accelerated flowering in October and November. A second elevation in N (800 ppm N for 4 weeks) in December enhanced December and January flowering. Seedlings that were conditioned with elevated nitrogen a third time in late spring and field planted in early summer exhibited enhanced yield.

This study was designed to investigate whether flowering of seedlings of the F1, seed-propagated cultivars 'Gasana' and 'Tarpan' could be enhanced by manipulating N nutrition and photoperiod during floral initiation as previously observed in the cultivar 'Elan' [20].

2. Materials and Method

Seeds of the F1 hybrid cultivars 'Tarpan' and 'Gasana' 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 5 inch 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.

Beginning 09 September 2014, single crowned plants with 4 fully expanded leaves were placed under natural daylength (ND) or natural daylength supplemented with 24 h incandescent radiation (Phillips Duramax Soft White A19 60 watt) suspended 0.3 M above the plant canopy (24LD). After 1 week plants were fertilized weekly for four consecutive weeks with Sea-Plus liquid fish and seaweed (3% available N, 2% available P₂O₅, 2% available K₂O) (Living Acres, New Sharon, ME) 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 vs

24LD) arranged in a randomized complete block replicated 3 times. Sub-plots were N level and sub-sub plots were forcing photoperiod (24LD vs 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 (weeks) after the start of conditioning (09 September) until the first inflorescence appeared.

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. [34] 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 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 before plants were transferred to their respective forcing photoperiod (10/16) and 6 weeks after concluding September N treatment (12/3). The two cultivars were analyzed separately.

3. Results

3.1. 'Gasana'

3.1.1. Evaluation immediately after treatment

Elevated N during floral initiation in September significantly enhanced the number of leaves, branch crowns and inflorescences per plant as well as the number of leaves and inflorescences per branch crown (Table 1). Branch crown number was also enhanced by exposure to ND compared to 24LD during initiation. No interactions of photoperiod with N were detected after 4 weeks of treatment for any measured variable and no runners were produced during this period.

3.1.2. Precocity

A significant interaction between September N and initiation photoperiod was detected for precocity (Table 2). Elevated N fertility accelerated flowering regardless of initiation photoperiod. The effect was more pronounced when elevated N was administered under ND (+3.0 weeks) compared to 24LD (+2.1 weeks). In addition, an effect of initiation photoperiod was only observed in plants receiving 100ppm N during initiation; plants flowered approximately one week earlier under

24LD initiation photoperiod compared to ND. There was no observed effect of initiation photoperiod in plants receiving 800 ppm N.

Table 1. Influence of September N and photoperiod during floral initiation on ‘Gasana’ strawberry leaf, crown and inflorescence production measured immediately after 4 weeks of N treatment.

<i>September N (ppm)</i>	Leaves per plant	Crowns per plant	Inflorescences per plant	Leaves per Crown	Inflorescences per crown
100	9.4 b ^z	2.0 b	0.4 b	5.1 b	0.3 b
800	16.4 a	3.0 a	1.8 a	5.7 a	0.6 a
<i>Initiation photoperiod</i>	Crowns per Plant				
ND	2.7 a				
24LD	2.3 b				

^zMean separation within column by Fisher’s Protected LSD, 0.05 level.

Table 2. Influence of September N fertility and photoperiod during floral initiation on ‘Gasana’ strawberry precocity (weeks after start of conditioning) estimated 10 weeks after the start of the experiment.

	<i>September N (ppm)</i>	
<i>Initiation photoperiod</i>	100	800
ND	6.1 a ^z	3.1 a
24LD	5.4 b	3.3 a

^zMean separation within column by Fisher’s Protected LSD, 0.05 level.

3.1.3. Evaluation 6 weeks after completion of treatments

The effects of September N fertilization during flower initiation on leaf, crown, and flower production were clearly observed 6 weeks after treatments were completed (Table 3). Elevated September N significantly enhanced the number of leaves, crowns and flowers per plant. More flowers were produced per inflorescence in plants subjected to ND (5.6) compared to 24LD (4.9) during initiation in September. A significant interaction between N fertilization during initiation and forcing photoperiod was observed in the number of flowers per inflorescence. More flowers were produced per inflorescence in plants forced under either photoperiod after receiving 800 ppm N during initiation (Table 3). In plants receiving 100 ppm N during floral initiation, fewer flowers per inflorescence were produced when forced under ND compared to 24LD. There was no difference due to forcing photoperiod in plants given 800 ppm N during initiation.

Fewer crowns were produced per plant when they were forced under 24LD compared to ND (3.1 and 3.5 crowns per plant, respectively). There was no significant treatment effect on leaves per crown (mean = 7.2) and no runners were produced during this period.

A significant interaction among initiation photoperiod, N fertilization during initiation and forcing photoperiod was detected for the number of inflorescences produced per plant or crown. There was no effect of N fertilization or forcing photoperiod for plants subjected to initiation under ND; plants produced an average of 3.0 inflorescences per plant and 1.0 inflorescence per crown.

Elevated N fertilization during floral initiation under 24LD stimulated inflorescence production per plant especially when plants were forced under ND conditions (Table 4). There was no difference in inflorescence production per plant between ND vs 24LD forcing for plants given 800 ppm N during initiation, however, inflorescence production per plant for those given 100 ppm N was slightly greater when forced under 24LD compared to ND. Elevated N during initiation or 24LD during forcing stimulated the number of inflorescences produced per crown (1.0 inflorescence per crown) compared to 100 ppm N followed by forcing under ND (0.6 inflorescences per crown) (Table 4).

Table 3. Influence of September N, photoperiod during floral initiation and photoperiod during greenhouse forcing on ‘Gasana’ strawberry leaf, crown and flower production per plant, and flower production per inflorescence after 6 weeks of greenhouse forcing following treatment.

	<i>September N (ppm)</i>	
	100	800
Leaves per plant	18.0 b ^Z	28.6 a
Crowns per plant	2.8 b	3.9 a
Flowers per plant	8.3 b	23.4 a
	Flowers per inflorescence	
	<i>Forcing photoperiod</i>	
<i>September N (ppm)</i>	ND	24LD
100	2.9 b	4.1 a
800	7.5 a	6.4 a

^ZMean separation within row by Fisher’s Protected LSD, 0.05 level.

Table 4. Influence of September N and photoperiod during greenhouse forcing on ‘Gasana’ strawberry inflorescence production per plant and crown after 6 weeks of greenhouse forcing following treatment for plants exposed to 24LD during floral initiation in September.

	<i>September N</i>	
	100	800
<i>Forcing photoperiod</i>	Inflorescences per plant	
ND	1.7 b ^Z	3.4 a
24LD	2.6 b	3.4 a
	Inflorescences per crown	
ND	0.6 b	0.9 a
24LD	1.0 a	1.0 a

^ZMean separation within row by Fisher’s Protected LSD, 0.05 level.

3.2. ‘Tarpan’

3.2.1. Evaluation immediately after treatment

Elevated N during floral initiation in September significantly enhanced leaf, branch crown, runner and inflorescence production per plant and inflorescence production per crown (Table 5). No interactions of photoperiod with N were detected after 4 weeks of treatment for any measured

variable. Plants produced an average of 5.8 leaves per crown regardless of initiation photoperiod, N or forcing photoperiod treatment.

Table 5. Influence of September N during floral initiation on ‘Tarpan’ strawberry leaf, crown and inflorescence production measured immediately after 4 weeks of N treatment.

<i>September N (ppm)</i>	Leaves per plant	Crowns per plant	Runners per plant	Inflorescences per plant	Inflorescences per crown
100	10.4 b ^z	2.1 b	0.0 b	0.5 b	0.3 b
800	16.8 a	2.9 a	0.5 b	1.5 a	0.5 a

^zMean separation within column by Fisher’s Protected LSD, 0.05 level.

3.2.2. Precocity

A significant interaction between September N and initiation photoperiod was detected for precocity (Table 6). Plants exposed to 24LD or given 800 ppm N during initiation in September flowered sooner (+3.1 weeks) than those given 100 ppm N under ND.

Table 6. Influence of September N fertility and photoperiod during floral initiation on ‘Tarpan’ strawberry precocity (weeks after start of conditioning) estimated 10 weeks after the start of the experiment.

	<i>September N (ppm)</i>	
<i>Initiation photoperiod</i>	100	800
ND	6.7 a ^z	3.6 a
24LD	3.6 b	3.5 a

^zMean separation within column by Fisher’s Protected LSD, 0.05 level.

3.2.3. Evaluation 6 weeks after completion of treatments

An interaction between September N fertilization and forcing photoperiod was detected for the number of leaves produced per plant (Table 7). In plants given 800 ppm N, there was no effect of forcing photoperiod on leaf production per plant. In plants receiving 100 ppm N, fewer leaves were produced per plant under 24LD forcing compared to ND forcing. In general, elevated N enhanced leaf production, however the effect was not statistically significant under ND forcing.

A significant interaction of initiation photoperiod, N fertility and forcing photoperiod was detected for the number of crowns produced per plant (Table 8). Elevated N under the ND initiation photoperiod resulted in an average of one additional crown per plant compared to 100 ppm N regardless of forcing photoperiod (Table 8). Elevated N under the 24LD initiation photoperiod treatment had a similar stimulating effect, however a significant effect of forcing photoperiod on crown production was observed for plants receiving 100 ppm N under 24LD (Table 8); plants forced under 24LD produced fewer crowns per plant compared to those forced under ND.

A significant interaction of initiation photoperiod, N fertility and forcing photoperiod was detected for the number of runners produced per plant (Table 8). No runners were produced following exposure to 24LD in September. Following exposure to ND during September, only plants

receiving 800 ppm N followed by forcing under 24LD produced runners, and even then, runner production was limited (0.2 runners per plant).

Table 7. Influence of September N fertility and photoperiod during forcing on the number of leaves per plant ‘Tarpan’ strawberry measured 10 weeks after the start of the experiment.

	September N (ppm)	
	100	800
<i>Forcing photoperiod</i>	Leaves per plant	
ND	19.6 a ^Z	28.9 a
24LD	16.4 b	31.0 a

^ZMean separation within column by Fisher’s Protected LSD, 0.05 level.

Table 8. Influence of September initiation photoperiod, N fertility and photoperiod during forcing on the number of crowns and runners per plant ‘Tarpan’ strawberry measured 10 weeks after the start of the experiment.

		September N (ppm)	
		100	800
<i>Initiation photoperiod</i>	<i>Forcing photoperiod</i>	Crowns per plant	
ND	ND	2.8 a ^Z	3.8 a
	24LD	2.3 a	3.7 a
24LD	ND	2.8 a	3.5 a
	24LD	1.9 b	3.8 a
<i>Initiation photoperiod</i>	<i>Forcing photoperiod</i>	Runners per plant	
ND	ND	0.0 a ^Y	0.0 a
	24LD	0.0 b	0.2 a
24LD	ND	0.0 a	0.0 a
	24LD	0.0 a	0.0 a

^ZMean separation within column by Fisher’s Protected LSD, 0.05 level.

^YMean separation within row by Fisher’s Protected LSD, 0.05 level.

Inflorescence production per plant was enhanced with 800 ppm N administered during September floral initiation (Table 9).

The number of flowers produced per plant was enhanced by a 24LD photoperiod during initiation, 800 ppm N during September or 24LD during forcing (Table 9).

Leaf production per crown was enhanced by exposure to ND or 800 ppm N in September or 24LD during forcing (Table 9).

A significant main effect of initiation photoperiod was detected for inflorescence production per crown (Table 9). Initiation under 24LD enhanced inflorescence production per crown by 0.5 inflorescences per crown compared to initiation under ND (Table 9).

An interaction between forcing photoperiod and N fertility during September was also detected for the number of inflorescences produced per crown (Table 10). Plants exposed to 24LD or given 800 ppm N during initiation in September produced significantly more inflorescences per crown than plants exposed to ND and given 100 ppm N.

Table 9. Influence of September N, photoperiod during floral initiation and photoperiod during greenhouse forcing on ‘Tarpan’ strawberry inflorescence production per crown after 6 weeks of greenhouse forcing following treatment.

	<i>September N (ppm)</i>	
	100	800
Inflorescences per plant	3.1 b	5.3 a
Flowers per plant	11.0 b	27.0 a
Leaves per crown	7.8 b	8.5 a
	<i>Initiation photoperiod</i>	
	ND	24LD
Flowers per plant	15.0 b ^Z	22.2 a
Leaves per crown	8.6 a	7.6 b
Inflorescences per crown	1.2 b	1.7 a
	<i>Forcing photoperiod</i>	
	ND	24LD
Flowers per plant	16.3 b	21.0 a
Leaves per crown	7.8 b	8.4 a

^ZMean separation within row by Fisher’s Protected LSD, 0.05 level.

Table 10. Influence of September N fertility and photoperiod during forcing on the number of inflorescences produced per crown in ‘Tarpan’ strawberry measured 10 weeks after the start of the experiment.

	<i>September N (ppm)</i>	
	100	800
<i>Forcing photoperiod</i>	Inflorescences per crown	
ND	1.0 b ^Z	1.4 a
24LD	1.8 a	1.6 a

^ZMean separation within column by Fisher’s Protected LSD, 0.05 level.

Table 11. Influence of September initiation photoperiod, N fertility and photoperiod during forcing on the number of crowns, runners per plant and flowers per inflorescence in ‘Tarpan’ strawberry measured 10 weeks after the start of the experiment.

		<i>September N (ppm)</i>	
		100	800
<i>Initiation photoperiod</i>	<i>Forcing photoperiod</i>	Flowers per inflorescence	
ND	ND	3.6 a ^Z	4.1 a
	24LD	3.5 b	5.9 a
24LD	ND	3.4 b	5.3 a
	24LD	3.8 b	5.1 a

^ZMean separation within row by Fisher’s Protected LSD, 0.05 level.

An interaction among initiation photoperiod, September N fertilization and forcing photoperiod

was detected for the number of flowers per inflorescence (Table 11). No effect of N fertilization was observed in plants subjected to initiation under ND followed by forcing under ND. Elevated N enhanced the number of flowers per inflorescence in all other treatments.

4. Discussion

Photoperiod and N fertility during floral initiation in September clearly affected flowering from October to December of both 'Gasana' and 'Tarpan'. The response to elevated N or photoperiod was rapid in both cultivars with statistically significant differences observed 4 weeks after the commencement of treatments. Similar quick responses to N and photoperiod were reported for 'Elan' [20].

Both cultivars responded with an increase in rate (enhanced precocity) and intensity (enhanced inflorescence number) of flowering with elevated September N. The response to September N application under different initiation photoperiods varied with cultivar. In 'Gasana' the response to N was similar under both initiation photoperiods with elevated September N accelerating flowering by 3 weeks when given during ND and by 2 weeks when given during 24LD. With the lower N rate there was a slight acceleration in flowering in response to long-day exposure (+0.7 weeks). In 'Tarpan' there was a 3.1-week acceleration in flowering with 800 ppm N given during initiation under ND while there was no acceleration in flowering due to elevated N when given during 24LD initiation: both 100 ppm N and 800 ppm N flowering in approximately 3.5 weeks. Thus in 'Tarpan' 24LD initiation and 800 ppm N were equally effective in accelerating flowering. In 'Gasana', elevated September N was much more effective in accelerating flowering compared to 24LD initiation. A significant interaction between September N and initiation photoperiod was previously reported for precocity in the LD cultivar 'Elan' [20]. Elevated N fertility accelerated flowering regardless of initiation photoperiod, however, the effect was more pronounced when elevated N was administered under ND compared to 24LD. While a significant interaction between September N and forcing photoperiod on precocity was reported for 'Elan' [20], no such interaction was detected for either cultivar in this present study. Precocity responses to N fertilization during floral initiation must consider cultivar as well as initiation and forcing photoperiods. In this study, enhanced N fertility significantly accelerated flowering as previously reported for the long-day cultivars 'Elan' [20] and 'Charlotte' [37], and a number of short-day cultivars [27,30,35].

Direct treatment effects on floral initiation in strawberry can be separated from indirect effects of altered vegetative growth by considering inflorescence production on a per-crown rather than on a per-plant basis [20]. Elevated N during September floral initiation in both 'Gasana' and 'Tarpan' in the present study directly enhanced floral formation and was not simply a response to greater overall growth with extra N since when the number of inflorescences per plant was adjusted for crown production, nearly twice as many inflorescences per crown were produced with elevated September N. Similar responses to N were reported for 'Elan' [20]. This study as well as the one reported for 'Elan' [20] clearly illustrate that flowering is easily manipulated by altering photoperiod and N fertility, suggesting that programmed flowering for targeted holiday ornamental as well as fruit production of F1 seedling cultivars is feasible. In addition, these results confirm that the effects of elevated N are quantitative. Enhanced flowering due to elevated N with or without photoperiod manipulation appears to be a general response of F1 long-day cultivars.

The longer term floral responses, that is those observed 6 weeks after the end of initiation and N treatment, varied with cultivar depending on parameter evaluated. For example, in 'Gasana'

subjected to ND during floral initiation, enhanced N did not stimulate inflorescence production per plant or crown. However, in plants induced under 24LD, inflorescence production per plant and crown was stimulated by elevated N during induction. In the cultivar 'Tarpan', inflorescence production per plant or crown was enhanced with elevated N administered during September floral initiation or by initiation under 24LD.

Both cultivars exhibited different responses to N and photoperiod (initiation and forcing) with respect to differentiation measured as flower production per inflorescence. In 'Tarpan', no effect of N fertilization was observed in plants subjected to initiation under ND followed by forcing under ND. Elevated N enhanced the number of flowers per inflorescence in all other treatments. In 'Gasana', more flowers were produced per inflorescence in plants subjected to ND or elevated N during initiation. In plants given 800 ppm N, no effect of forcing photoperiod was observed with respect to differentiation. Elevated (800 ppm) N in September triggers some aspect of the flowering pathway that results in enhanced differentiation [20]. Thus in the present study no effect of forcing photoperiod was detected when plants had adequate (800 ppm) N during initiation. However, in plants receiving limited N (100 ppm N), fewer flowers per inflorescence were produced with continued exposure to short days (ND forcing). This is not surprising since low N levels during initiation and differentiation cause inflorescence abortion [38], and reduced differentiation [11].

The generalized immediate vegetative response was an increase in leaf production and branch crown formation in both cultivars and an increase in runner production in 'Tarpan' with elevated September N. No runners were produced by 'Gasana' during this period. In 'Gasana' branch crown formation was enhanced by exposure to ND compared to 24LD during initiation and no effect of initiation photoperiod was detected for branch crown formation for 'Tarpan'. These results generally agree with previous reports that when N availability is low before induction, vegetative growth is often reduced [12,36,40-42]. Sonstebly et al. [27] reported no effect of N on crown number while Durner [20] reported enhanced crown production with elevated September N or ND forcing in 'Elan'. Crown branching is usually a short-day response [25,39] thus more crowns per plant would be expected under ND forcing.

The longer term vegetative responses, that is those observed 6 weeks after the end of initiation and N treatment, varied with cultivar depending on parameter evaluated. Elevated September N significantly enhanced the number of leaves in both 'Gasana' and 'Tarpan'. In addition, 'Tarpan' plants receiving low N in September produced fewer leaves under 24LD compared to ND forcing conditions. This observation on leaf production coupled with the observation of greater inflorescence production under low N 24LD conditions suggests that at least in 'Tarpan', inflorescences rather than leaves are favored under these conditions. Elevated September N significantly enhanced the number of crowns in both cultivars. In 'Gasana', fewer crowns were produced per plant when they were forced under 24LD compared to ND. In 'Tarpan', plants receiving 100 ppm N under 24LD then forced under 24LD produced fewer crowns per plant compared to those forced under ND. Crown branching is usually a short-day response [25,39] thus fewer crowns per plant would be expected under 24LD forcing. In 'Gasana', no significant treatment effect on leaves per crown was detected. In 'Tarpan', leaf production per crown was enhanced by exposure to ND or 800 ppm N in September or 24LD during forcing. In 'Gasana', no runners were produced during this period. In 'Tarpan', no runners were produced following exposure to 24LD in September. Following exposure to ND during September, only plants receiving 800 ppm N followed by forcing under 24LD produced runners, and even then, runner production was limited (0.2 runners per plant). 'Tarpan' appears to be more

sensitive to N and photoperiod than ‘Gasana’ since there were several instances where ‘Tarpan’ responded to treatment when ‘Gasana’ did not, i.e. runner production and leaf production per crown.

While this study did not investigate the timing of treatment application with respect to floral responses, it is important to reiterate the importance of treatment timing for altering flowering in strawberry. Limited N before induction often reduces vegetative growth and promotes flower induction, initiation and differentiation [12,31,40-42]. Plants with limited N seem to be more sensitive to inductive conditions [31,46,48] and initiation takes place rapidly when such plants are exposed to inductive conditions [20]. However, if N levels remain low during initiation and differentiation, inflorescences may abort [49], differentiation may be reduced [11,20] or plants may revert to vegetative growth [50]. If N is well supplied before floral induction, plants tend to be less sensitive to the floral inducing stimuli [46], flower induction is significantly reduced and stolon and shoot growth are stimulated [48-50]. Initiation may be inhibited and differentiation of previously initiated inflorescences may be delayed [43,46,51].

Prior to subjecting plants to photoperiod treatments to induce flowering, a limited N supply to the plants is warranted. This makes the plants more sensitive to the flower induction stimulus. However, since inflorescences may abort [45], differentiation may be reduced [11,20] or plants may become vegetative [46], once plants have been induced to flower and initiation is commencing, N levels must be increased to ensure normal differentiation. Enhanced N application should be commenced one week after induction has begun and not before then [27,29] 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 [20] followed by 4 weeks of elevated N (~1000 ppm N) then returned to lower rates thereafter for differentiation and development [20].

5. Conclusion

Photoperiod and N fertility during floral initiation in F1 seed-propagated long-day strawberries 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. While the responses to photoperiod and N varied with cultivar, the effects observed in this study were similar to those observed in a previous study for ‘Elan’ [20]. Long days can be used to induce floral initiation followed by elevated N for 4 weeks to enhance flowering. Photoperiod and N fertilization are viable tools for managing flowering in long-day strawberries.

Conflict of Interest

The author declares no conflicts of interest in this paper.

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