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Research article

Fall nitrogen enhances spring nitrogen enhanced flowering in the long day strawberry cultivar 'Elan'

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Abstract: Architectural analysis describes the position and fate (vegetative or floral) of plant meristems to account for differences in their 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, 'Elan' seedlings were fertilized in mid-October, overwintered in a greenhouse, then dissected the following March and their floral architecture evaluated. Additional plants from fall N treatments were placed under ND and fertilized weekly for four weeks with 100, 400, 800 or 1200 ppm N during greenhouse-forcing under ND and growth monitored until June. Plants were dissected after forcing and their floral architecture evaluated. Fall fertilized plants were significantly more floral than non-fertilized controls before forcing. Some axillary buds of fertilized plants formed floral branch crowns but there were no floral branch crowns on non-fertilized plants. Precocity was not affected by fall N and 400, 800 or 1200 ppm spring N were equally effective in accelerating flowering (+1 week) compared to 100 ppm spring N. Fall N enhanced the number of inflorescences and flowers produced by the primary crown. Spring N enhanced flowering of branch crowns and the total numbers of inflorescences and flowers per plant. Inflorescence production was a qualitative response to N while flower production was quantitative. Architectural models of post-forcing dissected plants provided additional insight. All 100 ppm spring N terminal meristems were floral while 400 and 800 ppm spring N meristems were less floral. All terminal meristems of plants receiving 100 ppm fall N before 1200 ppm spring N were floral but meristems from plants that did not receive fall N before 1200 ppm spring N were much less floral. Branch crown formation was enhanced with elevated (400, 800 or 1200 ppm) spring N and prior fall N enhanced their floral nature.

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

Abbreviations: ND: natural daylength; N: nitrogen

1. Introduction

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 [1-3] followed by medium to large fruit with excellent culinary qualities [4]. In addition, seeds of these cultivars are free from soil borne diseases, are easily shipped and stored and are adapted to mechanization [5], all characteristics that are advantages over vegetatively propagated cultivars often utilized in US attempts at season-long production.

Photoperiod and temperature regulate flowering in strawberry and their effects have been reported extensively [6]. Flowering responses to photoperiod in particular are used to categorize cultivars as short day, long day or day neutral [6,7]. The responses to photoperiod and temperature are often complex and sometimes erratic, thus categorization into specific types might be best replaced with a continuum from single to continuous cropping [8]. Seed-propagated, F1 hybrids such as 'Elan', 'Gasana' and 'Tarpan' are fairly predictable in their flowering behavior which can be regulated with photoperiod [9,10] and nitrogen fertilization [5,11]. Sonsteby and Heide [9,10] published extensive reports on the flowering physiology of the F1 seed-propagated cultivar 'Elan' which they determined was a qualitative long day plant [10] at high temperatures (> 27 °C) with a critical photoperiod of 15 hrs. [9]. They further 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 [10].

Reports on mineral nutrition effects during floral induction are limited [6]. In general, flowering is enhanced when N fertilization is increased after the initiation process begins [12-14] but N applied before, at the beginning of or too long after initiation, inhibits flowering [12,15] and reduces yield [12]. Limited N before induction often reduces vegetative growth and promotes flower induction, initiation and differentiation [16-20]. Plants with limited N seem to be more sensitive to inductive conditions [17,21,22] and initiation takes place rapidly when such plants are exposed to inductive conditions [5]. However, if N levels remain low during initiation and differentiation, inflorescences may abort [23], differentiation may be reduced [5,24] or plants may revert to vegetative growth [25]. If N is well supplied before floral induction, plants tend to be less sensitive to floral inducing stimuli [21], flower induction is significantly reduced and stolon and shoot growth are stimulated [22,23,25]. In addition, initiation may be inhibited and differentiation of previously initiated inflorescences may be delayed [21,26,27].

Durner [5] 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.

In a second study, Durner [11] verified that two other seed-propagated F1 hybrid cultivars, 'Tarpan' and 'Gasana' responded similarly to N application. Both cultivars responded rapidly (within

4 weeks after the commencement of treatment) to long days and elevated N with increased rate (enhanced precocity) and intensity (enhanced inflorescence/flower number) of flowering. In 'Gasana' elevated N accelerated flowering by 2–3 weeks and 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 and flower production were enhanced with elevated N in both cultivars.

While inflorescence and floral counts over time are effective in detecting cultural or environmental effects on flowering and potential productivity, floral architectural analysis has advantages over count data evaluations. Floral architecture models describe the position and fate (vegetative or floral) of buds on a plant [28-30] to account for differences in sensitivity to different stimuli of each meristem on a plant depending on specific stage of development and position of each meristem on the plant [29,31]. Evaluating the status of each individual meristem allows observation of the differential ability of meristems in different physiological phases and relative positions on the plant to respond to environmental signals; some meristems will respond 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 [32].

This study was designed to investigate the flowering response and floral architecture of long day 'Elan' seedlings to nitrogen rate during spring greenhouse forcing and whether or not the response was affected by nitrogen fertilization in the fall prior to forcing.

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 22 May 2015. After seven days they were moved to the greenhouse at ambient (24/18 °C day/night) temperatures and allowed to grow for 2 weeks. On 04 June 2015 seedlings were transplanted into Fafard Organic Mix (FOF-30) (Sun Gro Horticulture, Agawam, MA) in 38 cell plug trays (Johnny's Selected Seeds, Albion ME.). Seedlings were watered as needed and fertilized biweekly in July and August with Sea-Plus liquid fish and seaweed (3% available N, 2% available P_2O_5, 2% available K_2O) (Living Acres, New Sharon, ME) diluted with water to provide 100 ppm N. Beginning in mid-October 2015, half of the seedlings were fertilized with Sea-Plus diluted to 100 ppm N once a week for 4 weeks. Plants were held over the winter in the greenhouse under the natural photoperiod at a temperature of (24/18 °C day/night) and watered as needed. All seedlings were transplanted to 5 inch plastic pots into FOF-30 mix on 9 March 2016 and allowed to grow under ambient greenhouse conditions for 3 weeks. On 31 March 2016 twelve each of 0 and 100 ppm N October-fertilized seedlings were dissected under a stereoscope and evaluated for: the number of leaves per main crown, the number of leaf primordia in the terminal bud, the status of the terminal (vegetative or floral) and axillary (vegetative, stolon, branch crown (vegetative or floral)) buds and stage of floral development (0 = domed meristem, 1 = primary flower discernable, 2 = secondary flowers discernable, 3 = tertiary flowers discernable) for all inflorescences observed. Nodes were numbered from 1 to n, where 1 was the axil of the first true leaf and n was the axil of the most recently fully expanded leaf.

Beginning 31 March 2016, single crowned plants with 4 fully expanded leaves were placed

under natural daylength (ND) and fertilized weekly for four consecutive weeks with Sea-Plus diluted with water to provide 100, 400, 800 or 1200 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 bi-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 ND. Plants were arranged in a split plot design in the greenhouse with main plot of fall N treatment (0 or 100 ppm N) arranged in a randomized complete block replicated 12 times. Sub-plots were spring N treatment (100, 400, 800 or 1200 ppm N). The experimental unit was a single plant.

Observations of plant growth and development in the greenhouse were made at weekly intervals from 31 March until 1 June 2016. 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 spring treatment (31 March) until the first inflorescence appeared. Ten plants from each treatment combination (a total of 80 plants) were dissected under a stereoscope immediately at the end of the greenhouse forcing phase of the experiment. Plants were evaluated for number of leaves, number of nodes, status of axillary buds (vegetative (leaf), stolon, or branch crown (vegetative or floral)) and number of flowers/flower initials visible on each inflorescence. The status (vegetative or floral) of the terminal bud of the main crown as well as any branch crown was also evaluated.

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. [33] 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 observations made on 1 June 2016 and for plants dissected on 31 March and 2 June 2016.

3. Results

3.1. Architectural characterization via dissections 31 March 2016

Fall N fertilization altered the architecture of seedlings determined via dissection of overwintered plants the following March (Table 1, Figure 1). Fertilized plants had one additional leaf and were significantly more floral compared to non-fertilized controls. Some axillary buds of fertilized plants had formed branch crowns (some were floral) while there were no branch crowns in non-fertilized plants (Table 1). Sixty percent of the terminal buds of fertilized seedlings were floral with an average floral stage just past initial visibility of the king primordia.

Table 1. Architectural characterization of 'Elan' strawberry seedlings on 31 March prior to spring N fertilization but after fall N fertilization and overwintering in a greenhouse under natural daylength and ambient temperature (24/18 °C day/night).

Fall N (ppm)	Leaves per crown	Leaf primordia per crown	Branch crown inflorescences per plant	Branch crown floral stage	Terminal inflorescences per primary crown	Terminal floral stage
0	4.7 b[z]	3.0 a	0 b	0 b	0.2 b	0.3 b
100	5.8 a	2.9 a	0.3 a	0.8 a	0.6 a	1.3 a

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

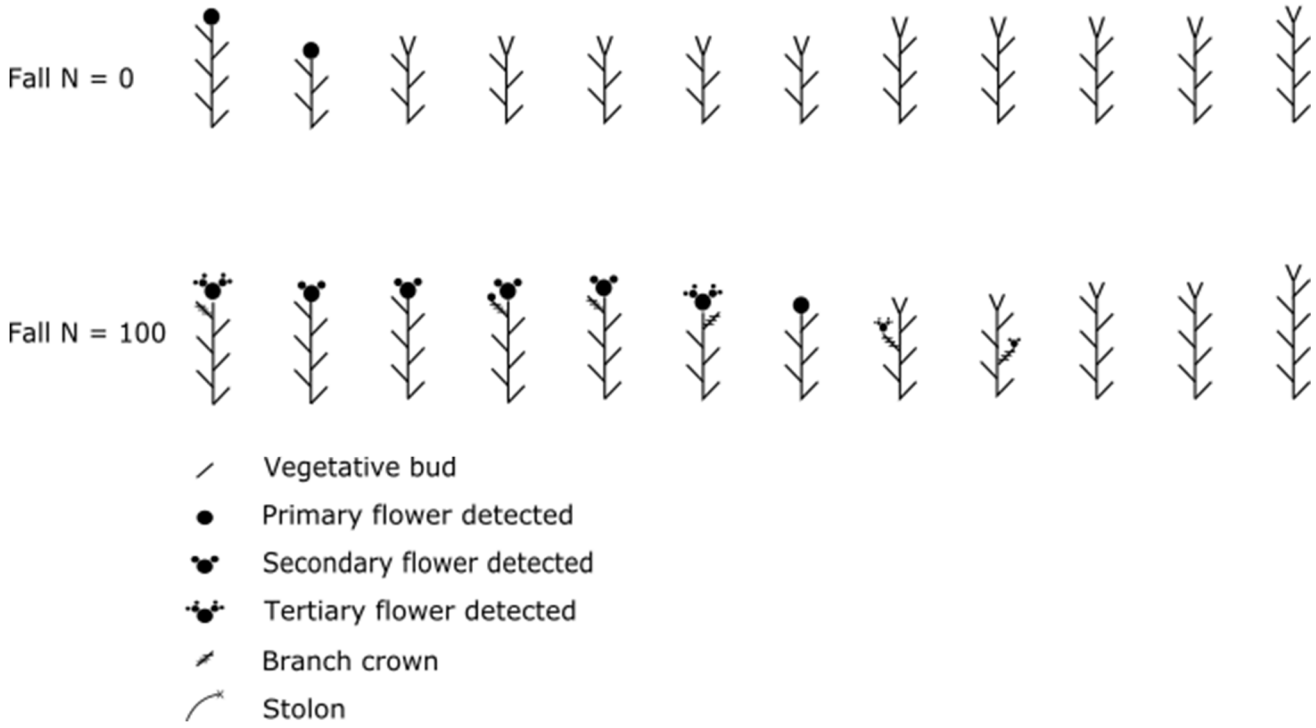

Figure 1. Architectural characterization of 'Elan' strawberry seedlings on 31 March prior to spring N fertilization but after fall N fertilization and overwintering in a greenhouse under natural daylength and ambient temperature (24/18 °C day/night).

Table 2. Influence of spring N fertility on 'Elan' strawberry precocity during greenhouse forcing estimated 9 weeks after the start of the experiment.

Spring N (ppm)	*Precocity (weeks to flower)*
100	5.5 a[Z]
400	4.4 b
800	4.4 b
1200	4.3 b

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

3.2. Precocity

Precocity during spring greenhouse forcing was not affected by fall N fertilization. Spring N levels of 400, 800 or 1200 ppm N were equally effective in accelerating flowering by approximately 1 week compared to 100 ppm N (Table 2).

3.3. Growth 6 weeks after treatment

3.3.1. Fall fertilization main effect

Fall N fertilization slightly enhanced the number of inflorescences and flowers per main crown (Table 3).

Table 3. Effect of fall N fertilization on the number of inflorescences and flowers per main crown for 'Elan' strawberry seedlings on 6 June following spring N fertilization and forcing in a greenhouse under natural daylength and ambient temperature (24/18 °C day/night).

Fall N (ppm)	Main crown inflorescences	Flowers per main crown
0	1.1 b[z]	7.2 b
100	1.5 a	8.9 a

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

3.3.2. Spring fertilization main effect

Spring N fertilization significantly enhanced the number of leaves per main crown, the total number of leaves per plant, the proportion of branch crowns with an inflorescence, the total number of branch crown inflorescences per plant, the total number of inflorescences per plant, the number of flowers per main crown, the number of flowers on branch crowns, and the total number of flowers per plant (Table 4). Enhancement was achieved equally with 400, 800 or 1200 ppm N for all but the number of flowers per main crown. The number of flowers per main crown increased with increasing N rate.

3.3.3. Fall × spring fertilization interaction

An interaction between fall and spring N fertilization was detected for branch crown leaf formation, the number of branch crowns per plant and the number of runners per plant (Table 5). More leaves were produced on branch crowns of plants receiving 400 or greater ppm spring N compared to 100 ppm spring N. Plants that received 100 ppm fall N did not produce branch crowns the following spring when provided only 100 ppm spring N. Plants receiving 400, 800 or 1200 ppm spring N produced on average 1.8 (400 and 1200 ppm N) or 2.4 (800 ppm N) branch crowns per plant (Table 5). Branch crown production was enhanced with elevated spring N (400 to 1200 ppm N) compared to 100 ppm spring N in plants not receiving fall N.

No runners were produced by plants receiving 100 ppm spring N with or without fall N (Table 5). Few plants receiving 100 ppm fall N produced runners even with 400, 800 or 1200 ppm spring N. Plants that did not receive fall N responded to 800 and 1200 ppm spring N with enhanced runner production (Table 5).

Table 4. Effect of spring N fertilization on the number of leaves per main crown, total number of leaves produced per plant, the proportion of branch crowns with an inflorescence, the total number of branch crown inflorescences per plant, the total number of inflorescences per plant, the number of flowers per main crown, flowers per branch crown and total flowers per plant of 'Elan' strawberry seedlings following forcing in a greenhouse under natural daylength and ambient temperature (24/18 °C day/night).

Spring N (ppm)	Leaves per main crown	Total leaves per plant	Proportion of branch crowns with an inflorescence	Total branch crown inflorescences per plant	Total inflorescences per plant	Flowers per main crown
100	10.3 b[Z]	11.3 b	0.0 b[z]	0.0 b	1.3 b	5.9 c
400	11.3 a	17.1 a	0.3 a	0.5 a	1.9 a	8.1 b
800	11.7 a	18.7 a	0.2 a	0.4 a	1.8 a	8.4 ab
1200	11.8 a	18.2 a	0.4 a	0.7 a	2.0 a	9.8 a
	Flowers on branch crowns	Total flowers per plant				
100	0.0 b	5.9 b				
400	1.7 a	9.8 a				
800	1.1 a	9.5 a				
1200	1.8 a	11.6 a				

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

Table 5. The number of leaves produced by each branch crown, the number of branch crowns per plant and the number of runners per plant for 'Elan' strawberry after fall N fertilization, overwintering in a greenhouse under natural daylength and ambient temperature (24/18 °C day/night) followed by spring N fertilization and forcing in a greenhouse under natural daylength and ambient temperature (24/18 °C day/night).

	Fall N (ppm)	
	0	100
Spring N (ppm)	*Leaves per branch crown*	
100	1.8 b[Z]	0.1 c
400	3.7 a	2.4 b
800	3.2 a	3.2 a
1200	3.8 a	3.1 ab
	Branch crowns per plant	
100	0.8 b	0.1 c
400	1.9 a	1.8 b
800	1.8 a	2.4 a
1200	1.9 a	1.8 b
	Runners per plant	
100	0.0 b	0.0 b
400	0.8 b	0.2 ab
800	2.0 a	0.3 ab
1200	1.7 a	0.5 a

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

3.4. Architecture determined via dissections 6 weeks after treatment

3.4.1. Fall fertilization main effect

Fall N enhanced the total number of nodes as well as the number of floral nodes per plant determined via dissection following spring N fertilization and forcing in a greenhouse (Table 6).

Table 6. Effect of fall N fertilization on the total number nodes and the number of floral nodes per primary crown of 'Elan' strawberry seedlings determined via dissection following spring N fertilization and forcing in a greenhouse under natural daylength and ambient temperature (24/18 °C day/night) for 6 weeks.

Fall N (ppm)	Total number of nodes	Number of floral nodes
0	11.4 b[z]	1.8 b
100	12.3 a	2.3 a

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

3.4.2. Spring fertilization main effect

The total number of nodes per plant increased with N fertilization up to 800 ppm spring N (Table 7). One or two additional nodes were formed on plants receiving 400, 800 or 1200 ppm spring N compared to plants receiving 100 ppm spring N. Spring N stimulated branch crown formation.

Table 7. Effect of spring N fertilization on the total number of nodes and the number of branch crowns of 'Elan' strawberry seedlings determined via dissection following spring N fertilization and forcing in a greenhouse under natural daylength and ambient temperature (24/18 °C day/night) for 6 weeks.

Spring N (ppm)	Total number of nodes	Number of branch crowns
100	10.9 c[z]	0.5 b
400	11.8 bc	1.9 a
800	12.7 a	2.0 a
1200	12.2 ab	2.0 a

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

Table 8. Influence of fall and spring N fertility on the number of runners per plant for 'Elan' strawberry seedlings following spring fertilization then forcing in a greenhouse under natural daylength and ambient temperature (24/18 °C day/night) for 6 weeks.

	Fall nitrogen (ppm)	
	0	100
Spring nitrogen (ppm)	*Number of runners*	
100	0.0 b[Z]	0.0 a
400	0.3 b	0.2 a
800	2.1 a	0.3 a
1200	1.8 a	0.8 a

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

3.4.3. Fall × spring fertilization interaction

Only plants receiving 800 or 1200 ppm spring N following 0 ppm fall N formed runners (Table 8). Plants receiving 100 ppm fall N did not produce runners regardless of spring N fertilization.

3.5. Architectural models for plants dissected after forcing

3.5.1. Terminal meristems

Architectural models of plants dissected after forcing are presented in Figures 2, 3 and 4. Figure 2 is presented for completeness and represents architectural models for each plant dissected indicating location and status of each bud. Figure 3 models only terminal meristems and collectively presents the location and status of the 10 terminal meristems dissected for each treatment combination. Figure 4 models the location and status of the axillary meristems of dissected plants and collectively presents the results.

In plants minimally fertilized (100 ppm N) in the spring, no terminal meristems were vegetative regardless of fall fertilization treatment (Figures 2 and 3). All terminal meristems of 100 ppm spring N were floral, presenting at least secondary flower initials and many with tertiary flower initials (17 of 20 plants) (Figure 3). Terminal meristems of plants fertilized with 400 ppm spring N were less developed florally with 9 of 20 meristems having tertiary floral initials, 7 of 20 meristems having secondary initials and 1 of 20 having only a primary initial. Three meristems were vegetative. Terminal meristems of plants fertilized with 800 ppm spring N were a bit more florally developed than those receiving 400 ppm spring N with 13 of 20 meristems having tertiary floral initials, 4 of 20 meristems having secondary initials and 1 of 20 having only a primary initial. Two meristems were vegetative. A significant difference was observed with the terminal meristem models of plants receiving 1200 ppm spring N when comparing those receiving 0 versus 100 ppm fall N (Figure 3). All terminal meristems of plants receiving 100 ppm fall N were floral with tertiary initials present in all samples. Plants not receiving fall N were much less developed with 4 of 20 meristems having tertiary floral initials and 5 of 20 meristems having secondary initials. One meristem was vegetative.

3.5.2. Axillary meristems

The fate of axillary meristems previously described for growth data was reflected in the architectural model developed for dissected plants. Spring N fertilization of 400, 800 or 1200 ppm N enhanced branch crown formation (Table 5) as previously noted. The architectural model of axillary meristem fate revealed that while 400, 800 and 1200 ppm spring N were similar in total number of meristems forming branch crowns (Table 5, Figure 4) for both 0 and 100 ppm fall N, the fates of the branch crown terminal meristems were more floral in plants receiving 100 ppm fall N (52 of 60 (86.7%) branch crown terminal meristems were floral) compared to those not receiving fall N (41 of 55 (74.5%) branch crown terminal meristems were floral). The stage of floral development for branch crown terminal meristems of 400, 800 and 1200 ppm spring N was consistent when comparing 0 and 100 ppm fall N (32 and 36 % with secondary initials and 68 and 64% with tertiary initials, respectively).

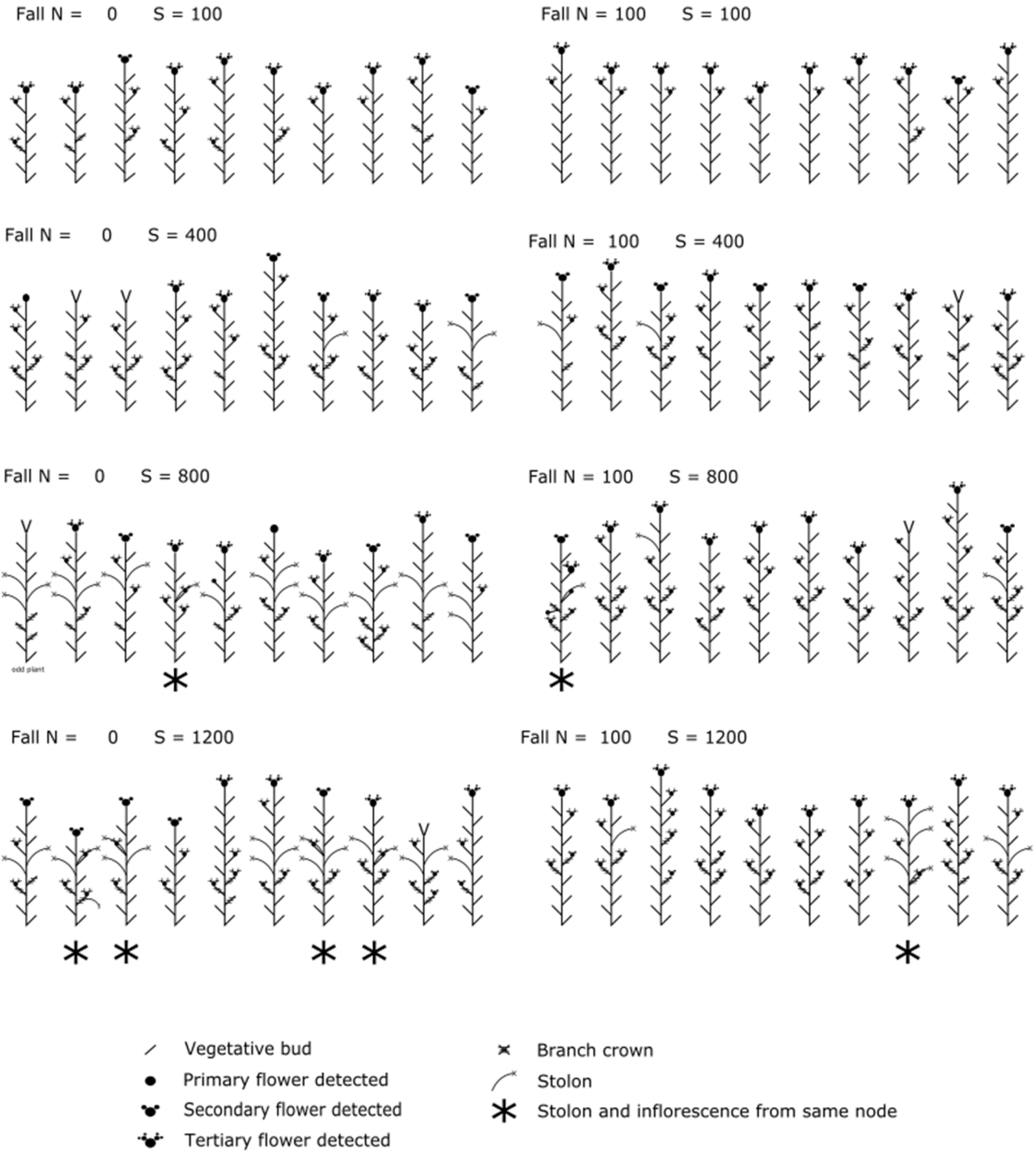

Figure 2. Architectural characterization of 'Elan' strawberry seedlings on 6 June after spring N fertilization and greenhouse forcing following October N fertilization and overwintering in a greenhouse under natural daylength and ambient temperature (24/18 °C day/night).

Figure 3. Terminal meristem architectural model of 'Elan' strawberry seedlings on 6 June after spring N fertilization and greenhouse forcing following October N fertilization and overwintering in a greenhouse under natural daylength and ambient temperature (24/18 °C day/night). Numbers indicate node.

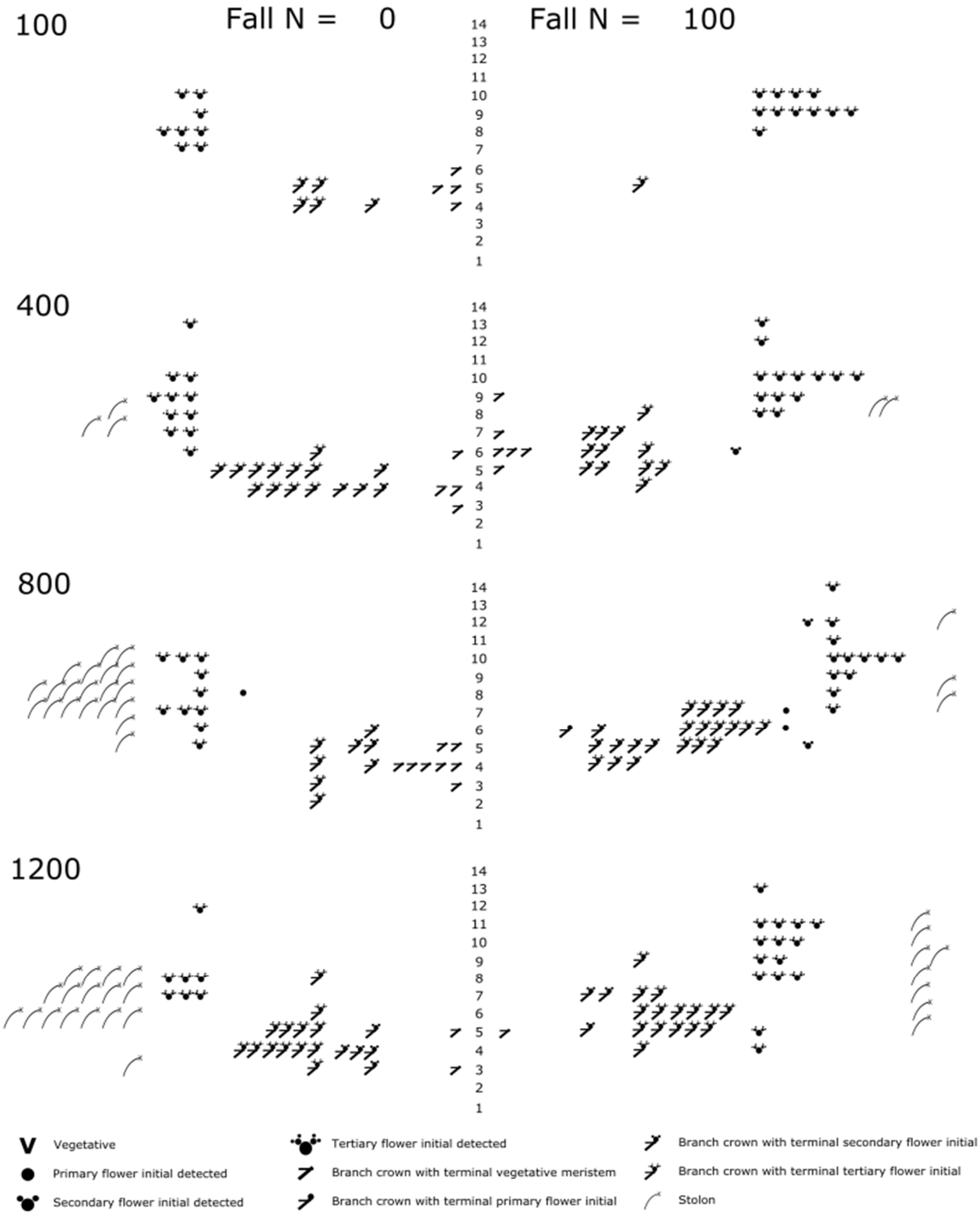

Figure 4. Axillary meristem architectural characterization of 'Elan' strawberry seedlings on 6 June after spring N fertilization and greenhouse forcing following October N fertilization and overwintering in a greenhouse under natural daylength and ambient temperature (24/18 °C day/night). Number indicates node.

4. Discussion

Fall N fertilization altered the architecture of 'Elan' seedlings by increasing node and leaf production and enhancing the floral nature of the seedlings (Table 1). These slight alterations were elicited by a relatively low level (100 ppm) of N and were observed nearly 6 months after treatment. Even so, the observation that a low level of N can elicit changes in the architecture of seedlings 6 months after application reiterates the importance of N fertility management in general and emphasizes that even slight alterations in fertility (0 vs 100 ppm, for example) can lead to changes in plant growth and development that are observed much later in the production cycle. Durner [34] reported a long term effect of photoperiod and temperature conditioning on 'Sweet Charlie' growth and flowering, so it is not surprising that other growth signals (N) would have a similar effect.

Fall N fertilization did not influence precocity. Spring N fertilization of 400, 800 or 1200 ppm N promoted precocity compared to 100 ppm spring N. The lack of an N rate effect at or above 400 ppm suggests that the precocity response to N is qualitative rather than quantitative. The enhancement with elevated N was modest (1.1 weeks earlier) when compared to the 2 to 3 week enhancement previously reported for 'Elan' [5] and 'Tarpan' and 'Gasana' [11]. Overall, N fertilization is effective in promoting the floral character in both long day [5,11,35] and short day cultivars [12,15,36].

In plants that received 100 ppm fall N, branch crown production was limited to plants receiving 400, 800 or 1200 ppm spring N; those provided 100 ppm N in the spring did not form branch crowns. Plants receiving no fall N produced approximately 1 branch crown per plant with 100 ppm N in the spring and 2 branch crowns with 400, 800 or 1200 ppm N. Sonsteby et al. [12] reported no effect of N on crown number while Durner reported enhanced crown production with elevated N in 'Elan' [5] and 'Tarpan' and 'Gasana' [11].

If plants received no N in the fall, they exhibited enhanced runner production with 400, 800 or 1200 ppm N in the spring. Plants that received 100 ppm N in the fall produced very few runners regardless of spring N fertilization. This is an important observation for propagators who rely on spring or summer runner production; even minimal (100 ppm) fall N fertilization can profoundly reduce runner production the following spring, at least in this long day cultivar.

The response to spring N appears to be qualitative with a threshold between 100 and 400 ppm N for all variables affected except for the number of flowers per primary crown, where the response appears to be quantitative.

Direct treatment effects on floral initiation in strawberry are separated from indirect effects of altered vegetative growth by considering inflorescence production on a per-crown rather than on a per-plant basis [5,11]. Elevated spring N directly enhanced floral formation (Table 4) and was not simply a response to greater general growth due to the N. Similar observations have been made for 'Elan' [5], 'Tarpan' and 'Gasana' [11]. Differentiation as measured by flower production was enhanced with either fall or spring N application. N triggers some aspect of the flowering pathway that results in enhanced differentiation [5] while low levels of N during initiation and differentiation cause inflorescence abortion [37], and reduced differentiation [24].

While low levels of N are often desired prior to floral induction to reduce vegetative growth and promote flower induction, initiation and differentiation [16-19,38-40], this study suggests that too little N (i.e., 0 ppm) can lead to reduced vegetative growth and may have a direct negative effect on inflorescence and flower production the following spring. It is difficult to ascertain whether the results observed in the 0 ppm N plants were a reflection of inhibited floral induction due to

extremely low (0 ppm) N levels or due to reduced initiation and differentiation following induction due to low N [5,22-24]. Induction has been measured via an increase in leaf primordia production [37]. Dissections prior to spring treatment indicated a reduced floral nature of both terminal and branch crown meristems in 0 ppm fall N compared to 100 ppm fall N plants (Table 1), yet both groups had a similar number of leaf primordia in the terminal bud. It seems that initiation rather than induction was curtailed in the 0 ppm N plants. If induction had been inhibited, one might expect fewer leaf primordia in non-induced plants. Since both groups had 3 leaf primordia per terminal bud but the 100 ppm N plants were microscopically significantly more floral (Table 1), induction had already likely occurred in both groups.

This study and others [5,11] clearly illustrate that flowering is easily manipulated by altering N fertility, particularly immediately prior to forcing suggesting that programmed flowering for targeted production of F1 seedling cultivars is feasible. This study also illustrates the effect of fall N fertility on spring responses to N. In addition, these results support the notion that enhanced flowering due to elevated N appears to be a general response of F1 long day cultivars [11].

5. Conclusion

N fertility of the F1 seed-propagated long day strawberry 'Elan' clearly affected flowering. The response to elevated spring N seemed to be qualitative for all variables eliciting a response except for floral differentiation which was quantitative. The responses observed in this study were similar to those observed in previous studies for 'Elan' [5] and 'Tarpan' and 'Gasana' [11]. Fall N application must be considered when assessing spring growth and flowering as even a low amount of N (100 ppm) can elicit responses such as an increase in the number of nodes per primary crown after greenhouse forcing the following spring as well as an increase in the number of inflorescences and flowers produced per crown during forcing. N fertilization is a viable tool for managing flowering in long day strawberries.

Conflict of interest

The author declares no conflicts of interest in this paper.

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