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Differential response of early and intermediate flowering strawberry cultivars to nursery late-season nitrogen applications and digging date

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The response of 'Ventana', an early flowering cultivar, and 'Camarosa', an intermediate flowering cultivar, to nursery late-season nitrogen (N) applications and digging date were studied in strawberry (*Fragaria* x *ananassa* Duch). Two experiments were conducted. In the first experiment, runner plants dug on September 20 and October 11 from a high-latitude nursery in California, were established in growth chambers set at 25°/15ºC day/night temperature, 12-h photoperiod, and grown for 90 days. Compared to the first experiment, in the second experiment plants received extra N (foliar-applied) in the nursery in late summer, and runner plants were not grown in GC but in open field (Irvine, California). In the second experiment, runner plants were dug on Sept 20 and Oct 2. In both experiments, plants dug in September were exposed to ~100 chilling units (CU: hours ≤7.2°C) and plants dug in October were exposed to ~300 CU. As a result, October-dug plants had greater crown and root dry weight, and greater concentration of starch and total nonstructural carbohydrates (TNC) in leaves, crowns and roots, compared to September-dug plants. In control plants, from September to October, root TNC concentration increased in 'Camarosa' from ~6% to ~11%, and in 'Ventana' from ~14% to ~21%, and leaf N concentration ranged from 1.47 to 1.81% in 'Camarosa', and from 1.60 to 1.96% in 'Ventana'. Late-summer N applications increased plant N concentration and early-season yields. Late-summer nursery N applications reduced dead leaf biomass (DLB) and dead leaf area (DLA) in both cultivars, although 'Ventana' had lower DLB and DLA than 'Camarosa'. 'Ventana' had a greater leaf number and flowered earlier, and had greater early fruit production than 'Camarosa'. The genetic earliness of 'Ventana' would be correlated with the potential of the plant for accumulation of higher initial levels of leaf N and root TNC, and for having greater leaf longevity, compared to 'Camarosa'.

Key words: *Fragaria* x *ananassa* Duch., foliar urea, carbohydrates, chilling, plant maturity, early flowering cultivars.

INTRODUCTION

Successful plant establishment, early growth and early fruit production in strawberry (*Fragaria* x *ananassa* Duch.) have been related to total nonstructural carbohydrate (TNC) and nitrogen (N) reserves (Bringhurst et al., 1960;

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Larson, 1994; Kirschbaum et al., 2010a). Plants with high root TNC concentration rapidly generate feeder roots (Schupp and Hennion, 1997), providing resources for flower bud initiation (Long, 1935) and early fruit development (Nishizawa and Shishido, 1998).

In the northern hemisphere, N and TNC storage process in roots and crowns of strawberry plants starts in September with the onset of chilling temperatures, and these nutrients are remobilized for bud and new leaf development in spring, as reviewed by Kirschbaum et al. (2010b).

In previous experiments conducted in California, strawberry runner plants cv. 'Camarosa' dug from HL nurseries in early October had enhanced vigor and greater early season fruit production than runner plants dug 2-3 weeks earlier in September, as a result of longer exposures to nursery chilling and decreasing photoperiods (Kirschbaum, 2012). Thus, early season fruit production in 'Camarosa' was also successfully increased as a result of late-summer nursery foliar-N applications (Kirschbaum et al., 2010a). Nevertheless, it is uncertain if both environmental factors will induce the same response in other strawberry cultivars since in this species the genotype x environment interaction is strong. For instance, one study showed that in order to accumulate ~40 $mg.g^{-1}$ FW of starch, in Spain, 'Camarosa' needed 400 chilling hours or units (CU) while 'Pajaro' required 700 CU (Lopez et al., 2002). 'Ventana', a cultivar released by the University of California, is characterized by greater early season fruit production compared to 'Camarosa' (Shaw and Larson, 2002), becoming an feasible cultivar for studying the role of nursery chilling and TNC and N reserves in early season fruit production.

In California, high-latitude strawberry nursery managers usually terminate N applications by the beginning of August in an effort to reduce vegetative growth and "harden off" developing runner plants. This hardening off process was thought to increase TNC accumulation, and reduce susceptibility to disease and transplant stress (Kirschbaum et al., 2010b); however, in a previous study with 'Camarosa', which is intermediate cultivar, we found out that late season nursery N applications were beneficial for early fruit production (Kirschbaum et al., 2010a). In light of these findings, we would like to assess if this is also valid for other cultivars with a different production cycle such as 'Ventana', which is an early cultivar.

The objectives of this work were 1) to study the comparative growth and developmental responses of 'Ventana' and 'Camarosa' to progressive exposure to decreasing temperatures and photoperiods, 2) to compare the responses of the two cultivars to late summer N fertilizer applications and digging date in terms of tissue N and TNC partitioning, and 3) to relate the effects of initial tissue TNC and N contents of nursery plants to subsequent fruit production patterns in the fruiting field.

MATERIALS AND METHODS

Nursery experiments

Nursery treatments were applied in a commercial runner plant propagation nurseries near Dorris (41°58'N, 121°55'W, 1292 m elevation), California. Cold-stored mother plants were used as nursery stock. In 2003, 'Camarosa' plants were established on 45-cm-in-row plant spacing and 'Ventana' on a 40-cm-in-row plant spacing on Apr 4. In 2004, 'Camarosa' and 'Ventana' planting dates were Apr 14 and 18, respectively. Water was supplied by drip irrigation. Plants were grown with standard commercial nursery management, including application of 224 kg N/ha, applied preplant (March) and through the drip irrigation system (May through the first week of August). In the 2004 experiments, N was applied foliarly in late summer. The N formulation was UAN 32 (1% concentration), and it was applied on Sep 6, Sep 13 and Sep 20, 2004 at rates of ~27 kg N/ha each. Second-daughter plants (D2, the 2nd runner plants that develop in a series from stolons of the mother plant) were randomly harvested on Sep 20 and Oct 11, 2003, while first-daughter (D1) and D2 plants were harvested on Sept 20 and Oct 2, 2004. In 2004, plants dug on Sep-20 received two applications of foliar N of 27 kg N/ha each, and plants dug on Oct-2 received three applications of 27 kg N/ha each. Ten plants of each daughter order and nursery N treatment were cold stored at 1°C for 3-4 days, washed thoroughly, dissected into leaflets, petioles, crown and root tissues, and dried at 65°C for 4 days. For all plants, crown diameter was determined prior to drying. In 2004, after drying and dry mass (DM) determination, plants were analyzed for soluble and non-soluble total nonstructural carbohydrates, and total N. The analytical procedure for TNC consisted of enzymatic starch hydrolysis with amyloglucosidase, followed by high performance liquid chromatography (HPLC) for analysis of sugars (Smith, 1969). Total N analysis was performed with a Carlo Erba (Italy) elemental analyzer.

Growth chamber experiments

Bare-root 'Camarosa' and 'Ventana' D2 plants, consisting of leaves, crowns and roots were harvested from a HL nursery near Dorris, California on Sept 20 and Oct 11, 2003, and leaves were removed from all the plants after digging. Plants were planted in rectangular pots 13x13x15 cm (long:wide:deep) filled with "Sunshine mix" (Sun Gro Horticulture Inc., Canada) potting media, which consisted of sphagnum peat moss, perlite, dolomite limestone and gypsum. A teaspoon of controlled-release fertilizer (22-7-10 "Agriform", Grace-Sierra Horticultural Products Co., USA) was applied to each pot at time of planting. Plants were placed in controlled environment chambers, where temperature and photoperiod were set at 25/15ºC day/night and 12 h, respectively. Plants were watered every 2-3 days. Flower emergence date and weight of harvested ripe fruit were progressively recorded for 90 days, when plants were removed from the growth chambers, dissected into component tissues (reproductive, petiols, leaflets, crown, root and fruit) and oven-dried at 65°C for 4 days. Crown diameter, leaf area, and the number of leaves, flowers and fruits (per plant) were measured prior to drying.

Fruiting field experiments

Bare-root D1 and D2 'Camarosa' and 'Ventana' plants consisting of leaves, crowns and roots were harvested from the nursery on Sept 20 and Oct 2, 2004, cold stored at 1°C for 3-4 days and planted in experimental plots at the University of California's South Coast Research and Extension Center, Irvine (33°39'N, 117°41'W). Preplant soil fumigation was applied using a (wt:wt) mixture of 2

Table 1. Cumulative chilling units (CU) corresponding to each plant sampling date in Dorris (California), 2003 and 2004.

Sampling date	Cumulative chilling units (hours at T≤7.2°C)
2003	
20 Sept	116
11 Oct	308
2004	
17 Sept	132
01 Oct	295

methyl bromide : 1 chloropicrin at a rate of 392 $kg.ha^{-1}$. Plants were established in offset 4-row beds 162 cm wide x 40 cm high using a 40-cm in-row plant spacing (61,250 plants/ha). Each plot consisted of 10 plants of a unique daughter order (D1 and D2), digging date and N treatment. The experimental setup was a completely randomized design with 3 replications. All plots were maintained according to recommendations for California commercial winter plantings (Welch, 1989). Fruit were harvested weekly from Dec 21, 2004 to Apr 11, 2005, using commercial fruit maturity standards. Fruit yields were determined for each plot on a per-plant basis. Canopy diameter as well as leaf and flower numbers were determined prior to fruiting on 11 Nov 2004. Data were subjected to analysis of variance and means were separated using SAS (SAS Institute, 2003).

RESULTS

Accumulated CU in Dorris were very similar in the 2003 and 2004 nursery seasons (Table 1).

First experiment series

Digging date had a significant effect on leaflet, crown and total plant DM (Table 2). In general, a delayed nursery digging date resulted in greater leaf, petiole, crown, root and total plant DM of ‘Ventana’ for both D1 and D2 plants. In ‘Camarosa’ the response was similar to ‘Ventana’ except later-dug D1 plants, which had less leaflet and petiole DM than early-dug D1 plants resulting in decreased plant DM. ‘Ventana’ plants had a significantly larger root biomass and crown diameter than ‘Camarosa’ plants. Daughter plant order affected plant DM, crown diameter, leaf number and leaf area (LA) (Tables 2 and 3). First daughter plants were larger than D2 plants in both cultivars. Digging date did not significantly affect crown diameter, number of leaves or leaf area (LA).

In growth chamber experiments, a delay in nursery digging (Table 4) resulted in reduced time to flowering. Cultivar also influenced the time from planting to flowering with ‘Ventana’ flowering earlier than ‘Camarosa’ (Table 4). After a 90-day growth period, ‘Camarosa’ and ‘Ventana’ plants dug in October had greater flower number, fruit number, fruit fresh weight, fruit DM and reproductive DM compared to plants dug in September (Table 5). Reproductive DM included the whole fruit cluster (pedicel, peduncles, and flowers and fruits at different developmental stages). In general, vegetative traits such as crown diameter, crown DM, leaf number, petiole DM, leaflet DM, LA and root DM were not significantly influenced by digging date. The root:shoot DM ratio was reduced in the plants from the later digging date. After a 90-day growth period, plants dug in October had larger biomass than September-dug plants. Leaf number, fresh fruit weight and fruit DM were significantly greater ($p=0.01$, $p=0.01$ and $p=0.05$, respectively) in ‘Ventana’ than in ‘Camarosa’ (data not shown).

Second experiment series

A delay in digging date resulted in significantly increased crown and root biomass for both cultivars and for both daughter plant orders (Table 6). In general, ‘Ventana’ had greater crown DM than ‘Camarosa’, but ‘Camarosa’ had greater root DM.

Late-summer foliar N applications did not affect leaf, crown, root, or plant biomass, crown diameter and LA, but resulted in increased leaf number (Table 7) and decreased dead leaf DM, dead LA (DLA) and DLA:LA ratio at the time of nursery digging (Table 8). First daughter plants had greater dead leaf DM and DLA than D2 plants. ‘Camarosa’ had greater dead leaf DM, DLA and DLA:LA ratio than ‘Ventana’. In control plants, dead leaf DM, DLA and DLA:LA ratio were greater in October than in September; however, N-treated plants generally did not increase dead leaf DM, DLA and DLA:LA ratio from September to October.

In general, a delay in nursery digging date resulted in significantly greater crown diameter and leaf number, but had no effect on LA (Table 7). ‘Ventana’ had greater crown diameter ($p=0.0337$), leaf number ($p=0.0112$) and LA ($p=0.0812$) than ‘Camarosa’. There was a significant effect of daughter order on crown diameter with D1 plants having larger crowns than D2 plants.

Table 2. Effects of digging date on dry mass distribution in daughter 1 (D1) and daughter 2 (D2) strawberry ('Camarosa' and 'Ventana') plants dug from HL nurseries near Dorris (California), 2003.

Cultivar	Daughter	Plant dry mass (g)		Leaflet dry mass (g)		Petiole dry Mass (g)		Crown dry mass (g)		Root dry mass (g)	
		20 Sep	11 Oct	20 Sep	11 Oct	20 Sep	11 Oct	20 Sep	11 Oct	20 Sep	11 Oct
Camarosa	D1	7.35[1]	6.61	3.93	3.34	1.84	1.61	0.41	0.46	1.17	1.20
	D2	2.65	3.16	1.25	1.50	0.60	0.78	0.18	0.21	0.63	0.46
Ventana	D1	4.74	9.24	2.20	4.71	1.11	1.86	0.23	0.60	1.19	2.08
	D2	3.94	5.02	2.12	2.67	0.88	1.07	0.14	0.32	0.80	0.96
						Pr> F					
Digging date (Dd)		*		**		*ns*		**		*ns*	
Cultivar(C)		*ns*		*ns*		*ns*		*ns*		*	
Daughter(D)		**		**		**		**		**	
DdxC		*		*		*ns*		**		*ns*	
DdxD		*ns*		*ns*		*ns*		*ns*		*ns*	
CxD		*ns*		*ns*		*ns*		*ns*		*ns*	
DdxCxD		*ns*		*		*ns*		*ns*		*ns*	

[1]Analysis of variance: *, ** and ns, significant at $p < 0.05$, 0.01 and non-significant, respectively.

Compared with controls, late-season N applications significantly enhanced N concentrations in leaves (Table 9), crowns (Table 10) and roots (Table 11), and, in general, decreased starch and TNC concentrations in leaves, crowns and roots. Crown tissue glucose concentration decreased as a result of N applications in seven out of eight mean comparisons; however, glucose in other tissues, as well as fructose and sucrose in general, did not show a defined trend in response to N applications.

Digging date had a significant effect on N concentration in leaves (Tables 9), generally decreasing from September to October in all tissues. However, for N-treated plants, little or no decrease in N was observed. Thus, the process of reduction of N concentrations observed in crowns and roots of control plants was reversed by late-summer N applications (Tables 10 and 11).

'Ventana' had greater concentrations of root glucose, fructose and sucrose, and greater concentrations of starch and TNC than 'Camarosa' (Table 11), while plants of 'Camarosa' maintained higher concentrations of starch in leaves than plants of 'Ventana' (Table 9).

In fruit evaluation plots, plants that had received late-summer N applications in the nursery had increased canopy diameters and leaf and flower numbers (Table 12), and increased early season yields (to 21 Feb) compared with control plants (Table 13). However, nursery late-summer N applications did not significantly affect total season fruit production. For 'Ventana' plants treated with foliar N in the nursery, early season marketable yields increased by 3 and 41% compared to controls, for plants planted on Sept 24 and Oct 5, respectively. Plants dug in September started to produce fruit on Dec 21, 2004 and had greater early season fruit production in terms of yield and fruit number compared to October plantings, which commenced fruit production on Jan 4, 2005. 'Ventana' outyielded 'Camarosa' in early season fruit production and had greater marketable yield, mean fruit weight, marketable fruit number and better appearance.

Table 3. Effects of nursery digging date on crown diameter, number of leaves and leaf area of daughter 1 (D1) and daughter 2 (D2) strawberry ('Camarosa' and 'Ventana') plants dug from HL nurseries near Dorris (California), 2003.

Cultivar	Daughter	Crown diameter (mm)		Number of leaves/plant		Leaf area (cm^2)	
		20 Sept	11 Oct	20 Sept	11 Oct	20 Sept	11 Oct
Camarosa	D1	14.8[1]	15.6	7.0	5.9	631	607
	D2	13.3	11.2	4.7	4.2	343	299
Ventana	D1	16.2	17.8	6.1	6.7	712	772
	D2	12.4	13.2	4.3	4.8	333	420
				P>F			
Digging date (Dd)		*ns*		*ns*		*ns*	
Cultivar(C)		*		*ns*		*ns*	
Daughter(D)		**		**		**	
DdxC		*ns*		*		*ns*	
DdxD		*ns*		*ns*		*ns*	
CxD		*ns*		*ns*		*ns*	
DdxCxD		*ns*		*ns*		*ns*	

[1]Analysis of variance: *, ** and ns, significant at p < 0.05, 0.01 and non-significant, respectively.

Table 4. Effects of planting date and cultivar on the time elapsed from planting to flowering of strawberry ('Camarosa' and 'Ventana') plants dug from HL nurseries near Dorris (California) on Sept 20 and Oct 11, 2003, and established in growth chambers (on Sept 24 and Oct 15, 2003.

Source of variation	Time from planting to flowering (d)	*P>F*
Planting date		
24 Sept	58.34[1]	**
15 Oct	47.20	
Cultivar		
Camarosa	53.69	*
Ventana	50.68	

[1]Analysis of variance: * and **, significant at p < 0.05 and 0.01, respectively.

Table 5. Effects of digging date and cultivar on growth and development of runner plants dug from a HL nursery near Dorris (California) and grown in growth chambers for 90 days (2003).

Variable	Camarosa			Ventana		
	20 Sept		11 Oct	20 Sept		11 Oct
Crown Diameter (mm)	13.2[1]	*ns*	12.8	13.8	*ns*	14.1
LA (cm^2)	466	*ns*	494	568	*ns*	638
Leaves/plant	7.8	*ns*	8.3	10.3	*ns*	12.0
Flowers/plant (FL)	4.2	*ns*	5.7	1.7	*	4.7
Fruits/plant (FR)	3.0	**	5.2	3.7	*ns*	3.3
FL+FR	7.2	*	10.8	5.3	*	8.0
Whole Plant DM (g)	6.3	**	8.5	7.7	**	10.7
Reproductive DM (g)	1.4	**	3.1	1.9	**	4.4
Petiols DM (g)	0.67	*ns*	0.84	0.80	*ns*	0.77
Leaflets DM (g)	2.6	*ns*	2.8	3.0	*ns*	3.4
Crown DM (g)	0.26	**	0.40	0.37	*ns*	0.44

Table 5. Cont.

Root DM (g)	1.5	*ns*	1.4	1.7	*ns*	1.6
Fruit FW (g)	5.6	**	26.8	16.4	**	42.8
Fruit DM (g)	0.6	**	2.4	1.3	**	3.6
Root:Shoot DM ratio	0.30	**	0.18	0.28	**	0.18

[1]Analysis of variance: *, ** and ns, significant at $p < 0.05$, 0.01 and non-significant, respectively.

DISCUSSION

Late-season nursery N applications increased early-season fruit production for strawberry plants dug from a HL nursery and planted in fruit evaluation plots in southern California. These results support the concept that early strawberry fruit production is enhanced by increasing N fertilization near the end of the nursery runner propagation period (Kirschbaum et al., 2010a), but cultivar and digging date can alter the response. In a previous report, October-dug 'Camarosa' plants treated in late-summer with foliar N in the nursery had, on average, 22% greater early season yields than control plants (Kirschbaum et al., 2010a). In the present study, 'Camarosa' treated with late-season foliar N had 12 and 22% greater yield compared to controls for plants dug on Sept 20 and Oct 2, respectively. 'Ventana' plants treated with late-season foliar-applied N had 7% and 36% greater early-season marketable yields compared with controls for plants dug on Sept 20 and Oct 2, respectively.

Fruit number per plant increased with nursery foliar-N treatments and this increase accounted for the greater early yields obtained from N-treated plants as average fruit weight was not affected by nursery N treatment. Whole-season yields were not altered significantly by N treatments. Consistent with previous work (Kirschbaum et al., 2010a), this research indicates that late-summer applied N accelerates plant growth and development resulting in greater early yields without affecting plant yield potential, since whole-season yields were not influenced by N treatments.

Concerns about late season N fertilization in strawberries have been related to the development of excessive foliage, increased susceptibility to pathogens, fruit softening, delayed flowering and ripening, and lower yields (Albregts and Howard, 1987; Daugaard, 2003; Hancock, 1999; May and Pritts, 1990; Miner et al., 1997; Tanaka et al., 2002; Yamasaki et al., 2002). However, in our experiments, we did not observe any of these symptoms and fruit quality attributes such as mean fruit weight, appearance and firmness were not altered significantly by N treatments.

Increased plant vigor due to greater initial runner plant biomass may explain the occurrence of greater early season yields, but we did not observe significant effects of late-season N applications on runner plant biomass or LA. Although N-treated runner plants had less dead leaf DM and leaf area (DLA), and decreased DLA:LA ratios than control plants, it would seem that the contribution to LA of the greater number of senescent leaves due to N application was not significant. The fact that 'Ventana' had significantly less dead leaf DM and DLA as well as a lower DLA:LA ratio than 'Camarosa' may indicate that 'Ventana' leaf longevity is greater than that of 'Camarosa'. Similarly, late-summer N applications might have resulted in increased leaf longevity and a decreased rate of leaf senescence, as has been observed in other species (Erley et al., 2002).

Late-season N applications had a significant effect on plant N and TNC concentration and partitioning, but cultivar and digging date modified these responses. Late-season N applications significantly enhanced N concentration in leaves, crowns and roots, and, in most cases, decreased starch and TNC concentrations in the same organs, which is consistent with previous findings of our research group (Kirschbaum et al., 2010a). Other authors have reported similar results in other temperate fruit crops, proposing that a portion of the carbon from TNC is incorporated into storage amino acids (arginine) and storage proteins, decreasing the carbon stored as starch, glucose and fructose (Bi et al., 2004; Cheng et al., 2004). This may be also the case of strawberries and would explain the decrease in TNC we observed in strawberry plants receiving late-season N.

In the present study, significant effects of cultivar on leaf N concentration were observed. In control plants, leaf N concentration of 'Camarosa' ranged from 1.47 to 1.81% and in 'Ventana' from 1.60 to 1.96 %, showing that nearly all control plants were N-deficient according to the standard sufficiency range for total N in strawberry leaf blades (2.0-2.8 % dry weight; Pritts and Handley, 1998). Late-season N applications resulted in leaf N concentrations in the sufficient range which apparently impacted plant vigor after plants were established in the fruiting field.

The results of this study are also consistent with the hypothesis than TNC accumulation in reserve organs of strawberry plants correlates CU accumulation and decreasing photoperiods (Kirschbaum et al., 2010b). Digging date affected TNC concentration in leaves, crowns and roots, and TNC concentration was greater on Oct 2 than on Sept 20 in all plant tissues. 'Camarosa' root TNC concentration increased from 6.17 to 10.90% in D1

Table 6. Effects of late season N application on dry mass partitioning of daughter 1 (D1) and daughter 2 (D2) strawberry ('Camarosa' and 'Ventana') plants dug from HL nurseries near Dorris (California), 2004.

Cultivar	Digging date	Daughter	Plant dry mass (g)		Leaflet dry mass (g)		Petiole dry mass (g)		Crown dry mass (g)		Root dry mass (g)	
			N0	N1	N0	N1	N0	N1	N0	N1	N0	N1
Camarosa	20 Sep	D1	9.05	8.47	4.20	4.41	2.97	2.55	0.65	0.54	1.23	0.98
		D2	5.87	4.30	2.91	2.08	1.67	1.30	0.41	0.31	0.88	0.69
	2 Oct	D1	9.35	8.72	4.33	4.00	2.97	2.70	0.78	0.69	1.29	1.32
		D2	6.91	7.42	3.43	3.73	1.73	1.92	0.47	0.53	1.27	1.25
Ventana	20 Sep	D1	7.31	8.07	3.42	4.36	2.41	2.47	0.72	0.52	0.76	0.72
		D2	5.86	6.48	3.18	3.55	1.57	1.70	0.42	0.41	0.69	0.82
	2 Oct	D1	9.33	9.21	4.28	4.68	3.08	2.80	0.79	0.76	1.18	0.99
		D2	8.89	7.68	4.94	3.72	2.33	2.25	0.64	0.64	0.97	1.08
							Pr> F					
Digging date (Dd)			**		*		**		**		*ns*	
Cultivar (C)			*ns*		*ns*		*ns*		*		*	
Daughter(D)			**		**		**		**		*	
Nitrogen (N)			*ns*		*ns*		*ns*		*ns*		*ns*	
DdxC			*		*ns*		*ns*		*ns*		**	
DdxD			*ns*		*ns*		*ns*		*ns*		*	
DdxN			*ns*		*ns*		*ns*		*ns*		*ns*	
CxD			**		*ns*		*ns*		*ns*		*ns*	
CxN			*ns*		*ns*		*ns*		*ns*		*ns*	
DxN			*ns*		*ns*		*ns*		*ns*		*	
DdxCxDxN			*ns*		*ns*		*ns*		*ns*		**	

[1]Analysis of variance: *, ** and ns, significant at $p < 0.05$, 0.01 and non-significant, respectively.

plants, and 'Ventana' root TNC concentration increased from 13.67 to 21.33%, for plants dug in September and October, respectively. This is in agreement with previous studies where 'Camarosa' TNC concentration increased from ~6 to ~10%, and 'Selva' (a day-neutral cultivar) from 4 to 14% (Kirschbaum et al., 2012), for September and October, respectively. According to our experimental results, 'Ventana' has the greatest levels of TNC among this group of cultivars and is the earliest.

Currently, recommended planting dates for 'Ventana' in southern California are around Oct 1 (Kirk Larson, personal communication). However, prior to Feb 21, 2004, 'Ventana' control plants, planted on Sept 24, produced ~50% more yield than Oct-5-planted plants. As reported previously (Baum, 2005), we also observed that early season fruit production and total season fruit production were greater in 'Ventana' than in 'Camarosa'. 'Ventana' also overcame 'Camarosa' in total season average fruit size, appearance and firmness.

The number of leaves and LA in the fall has been correlated with yield the following spring in biennial strawberry crops (Sproat and Darrow, 1935). We observed that plants receiving nursery

Table 7. Effects of late season N applications on crown diameter, number of leaves and leaf area of D1 and D2 strawberry ('Camarosa' and 'Ventana') plants dug from HL nurseries near Dorris (California), 2004.

Cultivar	Digging date	Daughter	Crown diameter (mm)		Number of leaves/plant		Leaf area (cm^2)	
			N0	N1	N0	N1	N0	N1
Camarosa	20 Sept	D1	15.4[1]	15.8	4.0	4.8	554	680
		D2	13.8	15.8	3.8	4.6	560	568
	2 Oct	D1	18.1	18.3	4.3	4.4	605	600
		D2	14.7	15.7	3.7	4.9	448	563
Ventana	20 Sept	D1	16.0	15.7	4.2	4.9	581	628
		D2	13.9	15.8	4.0	4.6	589	568
	2 Oct	D1	20.3	18.4	4.8	5.1	735	770
		D2	17.3	17.4	5.3	5.4	661	599
					Pr> F			
Digging date (Dd)			**		*		*ns*	
Cultivar (C)			*		*		*ns*	
Daughter(D)			**		*ns*		*ns*	
Nitrogen (N)			*ns*		**		*ns*	
DdxC			*ns*		*		*ns*	
DdxD			*ns*		*ns*		*ns*	
DdxN			*ns*		*ns*		*ns*	
CxD			*ns*		*ns*		*ns*	
CxN			*ns*		*ns*		*ns*	
DxN			*ns*		*ns*		*ns*	
DdxCxDxN			*ns*		*ns*		*ns*	

[1]Analysis of variance: *, ** and ns, significant at $p < 0.05$, 0.01 and non-significant, respectively.

Table 8. Effects of late season N applications on dead leaf dry mass, dead leaf area and DLA:LA DM ratio of D1 and D2 strawberry ('Camarosa' and 'Ventana') plants dug from HL nurseries near Dorris (California), 2004.

Cultivar	Daughter	Dead leaf DM (g)		Dead LA (DLA) (cm^2)		DLA/LA (%)	
		N0	N1	N0	N1	N0	N1
				September			
Camarosa	D1	1.53[1]	0.73	172	82	21.5	9.9
	D2	0.54	0.33	73	45	13.5	9.6
Ventana	D1	0.58	0.14	59	14	9.0	2.6
	D2	0.29	0.26	27	24	4.6	4.3
				Pr> F			
Cultivar (C)		**		**		**	
Daughter(D)		**		*		*ns*	
Nitrogen (N)		**		**		*	
CxD		*		*ns*		*ns*	
CxN		*ns*		*ns*		*ns*	
DxN		*ns*		*ns*		*ns*	
CxDxN		*ns*		*ns*		*ns*	

Table 8. Cont.

				October			
Camarosa	D1	1.62	0.73	195	78	23.6	11.1
	D2	0.90	0.45	136	59	23.2	9.4
Ventana	D1	1.07	0.21	110	23	13.8	2.8
	D2	0.39	0.15	48	18	6.2	2.8
				Pr> F			
Cultivar (C)		**		**		**	
Daughter(D)		**		*		*ns*	
Nitrogen (N)		**		**		**	
CxD		*ns*		*ns*		*ns*	
CxN		*ns*		*ns*		*ns*	
DxN		*		*ns*		*ns*	
CxDxN		*ns*		*ns*		*ns*	

[1]Analysis of variance: *, ** and ns, significant at $p < 0.05$, 0.01 and non-significant, respectively.

N had a greater leaf number at the time of digging, resulting in larger canopy diameter and greater flower numbers after planting. By Nov 11, September-dug plants also had greater canopy diameter and leaf number than October-dug plants. Similarly, by 11 Nov, 'Ventana' had greater root DM, crown diameter, leaf number and LA at the time of digging than 'Camarosa', and also greater leaf number after planting. These correlations may partially explain the high early- season yields obtained by N-treated, September-dug, 'Ventana' plants.

In contrast to field experiments, growth chamber experiments allowed the evaluation of plant vigor and early season yield potential under environmental conditions that did not change from one digging date to another. Nursery runner plants harvested from a HL nursery in 2003 accumulated ~100 h of chilling when dug on Sept 20 and ~300 h when dug on Oct 11. The observed reduction in time to flowering for October-dug plants compared to September-dug plants could be due to an extended exposure to chilling temperatures, shorter photoperiods, and larger initial plant biomass. In general, after a 90-day growth period, plants dug on 11 Oct had greater fruit and flower numbers, fruit weight (fresh and dry), reproductive dry weight and whole plant dry weight than plants dug on 20 Sept and this was consistent for both cultivars.

Our observations of 'Ventana' plants flowering earlier and having greater fresh fruit weight and fruit DM than those of 'Camarosa' agree with the hypotheses that chilling stimulates the development and emergence of previously-differentiated inflorescences and that chilling sensitivity varies among cultivars (Larson, 1994). 'Ventana' seems to have a lower chilling requirement than 'Camarosa'.

Since the California winter strawberry production system relies on fresh-dug runner plants without leaves (Galletta and Bringhurst, 1990), root and crown biomass play a fundamental role in plant establishment and early fruit production. Plants dug at the later dates each season had more crown and root DM than plants dug earlier. Root DM values and accumulation rates followed patterns analogous to previous studies (Kirschbaum et al., 2012; Long and Murneek, 1937; Nishizawa et al., 1998). Increased root DM during Sept-Oct could be attributed to an increased allocation of reserve nutrients to this organ (Bringhurst et al., 1960; Larson, 1994; Long and Murneek, 1937).

Previous work indicated that TNC concentration in strawberry runner plants is positively correlated with exposure to cold temperatures and short photoperiods (Kirschbaum et al., 2010b and 2012; Ruan et al., 2009) and that TNC concentration is negatively correlated with N applications (Kirschbaum et al., 2010a).

Our results support these previous observations and provide evidence for cultivar differences in regard to the effects of chilling on TNC and N accumulation and partitioning, TNC and N dynamics and TNC-N interactions.

Our results support the hypothesis that N reserves are major resources for fall-dug runner plant regrowth after transplanting. Nitrogen reserves have largely been overlooked as having a major role in strawberry transplant establishment and early fruit development in annual production systems (Kirschbaum et al., 2010b). Although details of the N cycling process in strawberries remains to be elucidated, our results indicate that late-season N applications allow plants to remain actively growing during the period of flower differentiation (Hancock, 1999; Long, 1939; Strik and Proctor, 1988), in addition to enhancing mobilization of N to crowns and roots, and with positive effects on early season flowering and fruiting.

Table 9. Effects of late-season N applications on the concentration of N and carbohydrates in leaflets of daughter 1 (D1) and 2 (D2) strawberry plants ('Camarosa' and 'Ventana').

Cultivar	Digging date	Daughter	Nitrogen (% DM)		Glucose (% DM)		Fructose (% DM)		Sucrose (% DM)		Starch (% DM)		TNC (% DM)	
			N0	N1	N0	N1	N0	N1	N0	N1	N0	N1	N0	N1
Camarosa	20 Sep	D1	1.74	2.26	1.7	2.0	1.8	2.2	0.7	0.6	1.3	1.1	5.6	5.6
		D2	1.81	2.46	1.6	1.3	1.7	1.4	1.9	0.6	2.7	1.0	7.9	4.2
	2 Oct	D1	1.68	2.81	1.4	1.8	1.0	1.1	3.2	3.6	2.0	1.1	7.6	7.2
		D2	1.47	1.95	2.1	1.9	1.6	1.3	3.8	3.3	2.4	2.5	10.0	8.3
Ventana	20 Sep	D1	1.65	2.06	2.1	2.7	1.5	2.0	2.1	1.6	1.4	0.7	7.3	6.7
		D2	1.96	2.11	2.5	1.9	1.9	1.3	1.8	3.4	0.8	0.5	6.7	6.6
	2 Oct	D1	1.60	1.94	2.7	1.5	2.0	1.0	3.9	2.6	1.7	1.3	10.7	6.7
		D2	1.65	2.13	2.0	1.8	1.4	1.3	4.7	3.0	1.6	0.8	10.0	6.7
								Pr> F						
Cultivar (C)			*		**		*ns*		*		**		*ns*	
Digging date (Dd)			**		*ns*		**		**		**		**	
Daughter(D)			*ns*		*ns*		*ns*		*ns*		*ns*		*ns*	
Nitrogen (N)			**		*ns*		*ns*		*ns*		**		**	
CxDd			*ns*		*ns*		*ns*		*		*ns*		*ns*	
CxD			**		*ns*		*ns*		*ns*		**		*ns*	
CxN			**		*ns*		*ns*		*ns*		*ns*		*ns*	
DdxD			**		*ns*		*ns*		*ns*		*ns*		*ns*	
DdxN			**		*ns*		*ns*		*ns*		*ns*		*ns*	
DxN			*ns*		*ns*		*ns*		*ns*		*ns*		*ns*	
CxDdxDxN			**		**		*ns*		*ns*		*		*ns*	

[1]Analysis of variance: *, ** and ns, significant at $p < 0.05$, 0.01 and non-significant, respectively.

Table 10. Effects of late-season N applications on the concentration of N and carbohydrates in crowns of daughter 1 (D1) and 2 (D2) strawberry plants ('Camarosa' and 'Ventana').

Cultivar	Digging date	Daughter	Nitrogen (% DM)		Glucose (% DM)		Fructose (% DM)		Sucrose (% DM)		Starch (% DM)		TNC (% DM)	
			N0	N1	N0	N1	N0	N1	N0	N1	N0	N1	N0	N1
Camarosa	20 Sep	D1	0.85	1.31	1.6	2.5	1.1	2.0	3.5	1.4	2.8	1.7	9.1	7.2

Table 10. Cont.

		D2	0.82	0.80	1.7	1.5	1.4	1.0	2.5	3.7	2.9	1.6	8.4	7.7
	2 Oct	D1	0.80	1.80	1.8	1.3	2.0	2.3	3.0	1.4	2.8	2.4	9.6	7.3
		D2	0.69	1.11	2.3	2.0	2.1	2.3	0.8	1.1	4.8	3.4	9.9	8.8
Ventana	20 Sep	D1	1.13	1.27	1.9	1.2	1.9	1.4	0.8	0.6	1.8	2.3	6.7	5.7
		D2	1.13	1.14	1.5	1.4	1.7	1.7	1.0	1.1	0.6	1.1	4.3	5.4
	2 Oct	D1	0.93	1.40	1.6	1.1	1.7	1.4	1.7	1.2	2.8	2.4	8.2	6.3
		D2	0.94	1.45	2.0	1.1	2.4	1.3	1.3	1.1	2.8	2.2	9.2	6.0
								Pr> F						
Cultivar (C)			*		**		*ns*		**		**		**	
Digging date (Dd)			*ns*		*ns*		**		*		**		**	
Daughter(D)			*		*ns*		*ns*		*ns*		*ns*		*ns*	
Nitrogen (N)			**		*		*ns*		*		*		**	
CxDd			*ns*		*ns*		**		**		*ns*		*ns*	
CxD			*		*ns*		*ns*		*ns*		**		*ns*	
CxN			*ns*		*		**		*ns*		*		*ns*	
DdxD			*ns*		**		*ns*		**		*		*ns*	
DdxN			**		*		*ns*		**		*ns*		*	
DxN			*		*ns*		*ns*		**		*ns*		*ns*	
CxDdxDxN			*ns*		*ns*		*ns*		**		*ns*		*ns*	

[1]Analysis of variance: *, ** and ns, significant at p < 0.05, 0.01 and non-significant, respectively.

Table 11. Effects of late-season N applications on the concentration of N and carbohydrates in roots of daughter 1 (D1) and 2 (D2) strawberry plants (‘Camarosa’ and ‘Ventana’).

Cultivar	Digging date	Daughter	Nitrogen (% DM)		Glucose (% DM)		Fructose (% DM)		Sucrose (% DM)		Starch (% DM)		TNC (% DM)	
			N0	N1	N0	N1	N0	N1	N0	N1	N0	N1	N0	N1
Camarosa	**20 Sep**	**D1**	1.06	1.44	1.20	0.90	0.70	0.50	1.60	1.73	2.70	2.33	6.17	5.53
		D2	0.96	1.59	0.90	1.40	0.43	0.77	1.13	1.90	2.37	2.50	4.80	6.53
	2 Oct	**D1**	0.86	2.02	1.73	1.03	0.90	0.70	3.10	2.10	3.17	4.63	8.87	8.47
		D2	0.75	1.01	1.00	0.87	0.50	0.37	2.20	1.77	7.27	3.77	10.90	6.83
Ventana	**20 Sep**	**D1**	1.00	1.24	1.87	1.53	0.90	0.80	3.03	2.77	7.07	5.30	13.67	10.67
		D2	1.00	1.04	1.73	1.87	0.73	0.73	3.23	4.10	2.67	4.77	8.33	12.00
	2 Oct	**D1**	0.90	1.31	1.73	1.37	0.97	1.00	3.27	3.33	7.60	5.33	14.33	11.67
		D2	0.77	1.33	1.90	1.87	0.97	1.10	6.10	3.83	10.97	4.73	21.33	12.17

Table 11. Cont.

	Pr> F					
Cultivar (C)	**	**	**	**	**	**
Digging date (Dd)	*ns*	*ns*	**	**	**	**
Daughter(D)	**	*ns*	*	*ns*	*ns*	*ns*
Nitrogen (N)	**	*ns*	*ns*	*ns*	**	**
CxDd	*ns*	*ns*	*	*ns*	*ns*	*ns*
CxD	*	*	*ns*	**	*ns*	*ns*
CxN	**	*ns*	*ns*	*ns*	*ns*	*ns*
DdxD	**	*ns*	*ns*	*ns*	**	**
DdxN	**	*ns*	*ns*	**	**	**
DxN	*ns*	**	*	*ns*	*ns*	*ns*
CxDdxDxN	**	*ns*	**	*ns*	**	**

[1]Analysis of variance: *, ** and ns, significant at p < 0.05, 0.01 and non-significant, respectively.

Table 12. Effects of late season N applications on canopy diameter, number of leaves and number of flowers (to Nov 11, 2004) of strawberry ('Camarosa' and 'Ventana') plants dug from HL nurseries near Dorris (California) and planted in Irvine (California). Daughter plants 1 and 2 were combined for the analysis of variance.

Cultivar	Digging date	Canopy diameter (cm)		Number of leaves/plant		Number of flowers/plant	
		N0	N1	N0	N1	N0	N1
Camarosa	**20 Sept**	24.55[1]	25.43	5.42	6.90	3.30	3.61
	2 Oct	18.54	18.99	4.06	4.41	1.46	2.33
Ventana	**20 Sept**	23.70	26.19	5.88	6.35	2.81	3.67
	2 Oct	17.41	19.55	4.76	5.00	1.41	2.58
				Pr>F			
Nitrogen (N)		**		**		**	
Digging date(Dd)		**		**		**	
Cultivar (C)		*ns*		**		*ns*	
NxDd		*ns*		**		*ns*	
NxC		*		*		*ns*	
DdxC		*ns*		**		*ns*	
NxDdxC		*ns*		*		*ns*	

[1]Analysis of variance: *, ** and ns, significant at p < 0.05, 0.01 and non-significant, respectively.

Table 13. Effects of nursery late-season N applications on early-season and whole-season yields of strawberry runner plants dug from HL nurseries near Dorris (California), 2004. Fruit production plots were established in Irvine (California). D1 and D2 were combined for ANOVA.

Cultivar	Nitrogen	Total yield (g/plant)		Marketable yield (g/plant)		Average fruit weight (g)		Marketable fruits/plant		Appearance		Firmness	
		20 Sep	2 Oct	20 Sep	2 Oct	20 Sep	2 Oct	20 Sep	2 Oct	20 Sep	2 Oct	20 Sep	2 Oct
Early season (Dec-Feb 21)													
Camarosa	**N0**	203	142	126	98	33.1	32.2	3.8	3.1	2.8	3.1	4.0	3.8
	N1	228	173	144	109	32.0	32.0	6.1	3.9	2.8	2.9	3.9	3.8
Ventana	**N0**	267	201	200	138	33.5	35.7	4.5	3.4	3.8	3.6	4.0	3.9
	N1	287	275	206	195	34.1	34.0	6.0	5.8	3.8	3.9	3.9	3.9
							Pr> F						
Nitrogen (N)		**		**		ns		**		ns		ns	
Digging date(D)		**		**		ns		**		ns		ns	
Cultivar (C)		**		**		ns		**		**		ns	
NxD		ns		ns		ns		ns		ns		ns	
NxC		ns		ns		ns		ns		*		ns	
DxC		ns		ns		ns		ns		ns		ns	
NxDxC		ns		*		ns		*		*		ns	
Total season (Dec-Apr 11)													
Camarosa	**N0**	1023	848	677	586	29.9	29.6	22.7	19.9	2.6	2.7	3.7	3.7
	N1	1044	904	673	615	28.7	29.8	23.4	20.7	2.6	2.8	3.6	3.7
Ventana	**N0**	1049	833	778	608	30.8	32.2	25.3	18.9	3.8	3.7	3.8	3.8
	N1	1015	889	736	667	30.8	30.9	24.0	21.6	3.8	3.9	3.8	3.8
							Pr> F						
Nitrogen (N)		*ns*		*ns*		*ns*		*ns*		*ns*		*ns*	
Digging date(D)		**		**		*ns*		**		*ns*		*ns*	
Cultivar (C)		*ns*		**		**		*ns*		**		**	
NxD		*ns*		*ns*		*ns*		*ns*		*ns*		*ns*	
NxC		*ns*		*ns*		*ns*		*ns*		*ns*		*ns*	
DxC		*ns*		*ns*		*ns*		*ns*		*ns*		*ns*	
NxDxC		*ns*		*ns*		*ns*		*ns*		*ns*		*ns*	

[1]Analysis of variance: *, ** and ns, significant at $p < 0.05$, 0.01 and non-significant, respectively.

Conflict of Interest

The authors have not declared any conflict of interest.

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