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Full Length Research Paper

Accumulation pattern of total nonstructural carbohydrate in strawberry runner plants and its influence on plant growth and fruit production

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The pattern of total nonstructural carbohydrate (TNC) accumulation in strawberry (*Fragaria ananassa* Duch.) nursery runner plants, cv. 'Camarosa', was determined for three growing seasons. Plant growth and fruit production patterns were also evaluated. The experiments were carried out on plants propagated in high latitude (41°50' N) and high elevation (1292 m) nurseries in Siskiyou County, California. Plants were sampled beginning in late summer through early autumn and analyzed for dry mass (DM) and TNC. Plants from different digging dates were established in growth chambers (GC) at UC Davis or fruit evaluation plots in Irvine, California. In the nursery, TNC concentration in storage tissues increased steadily from the second week of September to the third week of October, and crown and root TNC concentration was positively correlated with the accumulation of chilling units (hours ≤7.2°C). The root TNC concentration consistently increased from 6 to 10% DM from mid-September to the first week of October. Transplant growth and fruiting pattern were affected by digging date. Overall, the roots were more sensitive to chilling in terms of TNC accumulation, than the crowns. Therefore, roots would be the appropriate organ for assessing TNC status and potential digging dates of strawberry nursery runner plants early in the fall.

Key words: Transplant, carbohydrate, chilling, growth analysis.

INTRODUCTION

Winter strawberry (*Fragaria ananassa* Duch.) production systems in mild climates rely on fresh-dug, bare-root runner plants, which are exposed to several stresses between the time of nursery digging and plant establishment in the fruiting field. Variable temperature exposure during the processes of plant harvest, postharvest handling and planting may contribute to deterioration of plant quality due to respiration. It has been reported that plants consumed glucose reserves at rates of 4.7, 24.3 and 49.2 mg.day^{-1} per plant when they were exposed to 1, 13 and 20°C, respectively (Dickmann and Blanke, 2000). This can be exacerbated by exposure to high temperature stress in the fruiting field at the time of planting, thus affecting plant establishment and fruit production (Dradi et al., 1999).

Starch is the prevailing non-soluble, nonstructural carbohydrate, and glucose, fructose and sucrose are the predominant soluble nonstructural carbohydrates in roots and crowns of strawberry plants (Bringhurst et al., 1960; Macias-Rodriguez et al., 2002). Starch accumulation in roots is influenced by temperature; moreover, total non-structural carbohydrate (TNC) concentration in strawberry roots increases with chilling hour accumulation (Bringhurst et al., 1960; Dradi et al., 1996; Freeman and Pepin, 1971; Hicklenton and Reekie, 2000; Le Miere et al., 1996; Lieten, 1997). For this reason, runner plants for early fall plantings in mild climates are mostly propagated in nurseries located at high latitude (HL) and/or high elevation (HE) sites (Shaw, 2004), where chilling exposure starts the last weeks of summer.

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Abbreviations: TNC, Total nonstructural carbohydrate; **DM,** dry mass; **GC,** growth chambers.

Meanwhile, there is limited information on how initial plant TNC content influences the fruiting pattern in mild climate regions (example southern California, central Florida, and northern Argentina), where strawberry crops are established early in the fall and first harvests are expected to occur just 6 weeks later. Hence, this study focused on California strawberry runner plants propagated in HE/HL nurseries. The objectives were to determine the effects of chilling on TNC accumulation and partition-ing in strawberry plants, and its influence on plant growth and fruiting pattern in winter production systems.

MATERIALS AND METHODS

In 1998, short-day 'Camarosa' strawberry plants were grown in a HL/HE nursery in the Butte Valley, California (41.89° N latitude, 121.98° W longitude; 1293 m). Mother plants were planted with 112 cm between rows and 40 cm between plants within the row (22,250 plants/ha) on April 15th and grown under conventional cultivation procedures. Water was supplied by sprinkle irrigation. Fertilization consisted of 225 kg $N.ha^{-1}$, 282 kg $P_2O_5.ha^{-1}$, and 296 kg $K_2O.ha^{-1}$. Other nutrients were applied at minor rates according to standard fertilization practices for nurseries in the region. A group of the 5 first and second daughter plants (the first and second consecutive plants developed from the stolons of the mother plants) were randomly dug at September 10th and October 1st. Field temperatures were recorded with a CR21 Micrologger (Campbell Scientific Inc., UT). Chilling units (CU) were computed as the sum of hours at temperatures ≤7.2°C.

Subsequently, the plants were washed with tap water to remove soil particles, and dissected into leaves, crown and root. Leaf area was recorded (LI-3000, LI-COR Biosciences, NE) and all tissues were dried for 96 h at 65°C. After taking dry weights, tissues were ground with a Wiley mini mill (Thomas Scientific, NJ) to pass a 40-mesh screen and subjected to TNC analysis (Smith, 1969). The analytical procedure consisted of enzymatic starch hydrolysis with amyloglucosidase, followed by high performance liquid chromatography (HPLC) for analysis of sugars. In 2002, the experimental procedure was basically the same as that followed in 1998, except that planting date was April 20, and digging dates were August 8th, September 9th, September 18th and October 7th. On August 8, the 2nd daughter plants were too small to be analyzed and therefore were not sampled. The same procedures were followed in 2004, except that the planting date was April 14th, drip irrigation was used, and digging dates were September 17th and October 1st.

Following the nursery season, experiments were conducted to evaluate the effect of digging date and plant TNC concentration on transplant vigor in 1998 and 2004. Nursery runner plants harvested at September 10th and October 1st were grown in growth chambers in 1998 and in the field in 2004. In 1998, the 1st daughter plants were immediately transplanted to a growth chamber where day/night temperatures, photoperiod and RH were set at 22°C / 12°C, 11 h and 75%, respectively. Plants were planted in rectangular pots 13 × 13 × 15 cm (length: width: depth) pots filled with "Sunshine mix" (Sun Gro Horticulture Inc., Canada) potting mix, which consisted of Canadian sphagnum peat moss, perlite, dolomite limestone and gypsum. A teaspoon of slow release fertilizer (22-7-10 Agriform, Grace-Sierra Horticultural Products Co., USA) was applied to each pot at planting. Plants were watered every 2 to 3 days. Stolons and flower trusses that emerged during the growth chamber experiment were removed throughout the 6-week growing period. Plants were then harvested and dried as previously described. The effect of digging date on plant vigor was evaluated in terms of plant dry mass.

'Camarosa' daughter plants (daughter 1 = D1, and daughter 2 = D2) harvested on 20th September and 2nd October, 2004 were cold-stored at 1°C and planted in experimental plots for fruit production evaluation at the University of California's South Coast Research and Extension Center, Irvine, CA (33°39'N, 117°41'W) on the 24th of September and 5th of October (Figure 1). Preplant soil fumigation was applied using a (weight: weight) mixture of 2 methyl bromide: 1 chloropicrin at a rate of 392 $kg.ha^{-1}$. Plants were established in diagonal quadruple rows on 162 cm wide × 40 cm high beds using a 36-cm in-row plant spacing (72,884 plants/ha). Each plot consisted of 10 plants of each daughter order (D1 and D2). The experimental setup was a completely randomized design with 3 replications. All plots were maintained according to recommendations for California commercial winter plantings (Strand, 1994). The fruits were harvested weekly using commercial fruit maturity standards. Fruit production was recorded until plants from each planting date accumulated 715 growing degree days (GDD). GDD were calculated by subtracting 10°C from the daily mean temperature that was obtained by dividing the sum of the daily maximum and minimum temperatures by 2 (Himelrick and Galletta, 1990). Fruit yields were determined for each plot on a per-plant basis. Data were subjected to analysis of variance and means were separated using SAS (SAS Institute, 2003).

RESULTS AND DISCUSSION

Nursery temperatures and chilling

The daily minimum and maximum average temperatures during the fall plant sampling periods followed similar patterns in the three nursery seasons of this study. However, in 2002 there were daily freezes early and late in the season, and the minimum temperatures in those weeks were much lower than in the equivalent weeks of 1998 and 2004. The minimum and maximum average temperatures were -0.9 and 25°C in 1998, -2.1 and 20.7°C in 2002, and -0.8 and 18.8°C in 2004. The onset of chilling temperatures varied among seasons (Figure 2). The first days with chilling temperatures were 11-September-1998, 1-September-2002 and 31-August-2004. For this reason, the cumulative CUs corresponding to the same calendar dates were different for each year (Table 1). However, besides the time gap between the three studied nursery seasons, the overall rates of CU accumulation were very similar among them (Figure 2). Indeed, the slopes of the adjusted regression lines for the three seasons were virtually equal (Figure 2). This shows that the three years were comparable and provided relevant information to this study.

Several studies in different regions reported that the onset of chilling temperatures and accumulation of chilling hours varies among seasons as consequences of climatic variations that typically occur every year (Hicklenton and Reekie, 2000; Lopez et al., 2002; Palha et al., 2002). Nursery runner plants dug in October were exposed to more chilling and accumulated more TNC in roots and crown than plants dug in August - September, similar to 'Elsanta' plants in France (Raynal-Lacroix et al., 1999; Robert et al., 1999). In HE nurseries in Portugal (Palha et al., 2002), root starch concentration in

Figure 1. Experimental plots for fruit production evaluation at the University of California's South Coast Research and Extension Centre, Irvine, CA.

'Chandler' increased with CU accumulation as follows (in %DM): 8.7 (107 CU), 13 (188 CU), 18.9 (244 CU) and 22.8 (536 CU). These observations are consistent with the hypothesis that TNC accumulation in storage tissues in strawberries is correlated with cumulative cold (chilling) exposure. However, each cultivar has a different chilling need.

Nursery plant growth

The daughter plant order affected total plant DM, where D1 plants were larger than D2 plants (Table 2). The whole plant DM increased from the earliest to the latest sampling date in 'Camarosa' D1 in 2002 and in D1 and D2 plants in 2004. The observed DM increase was consistent with previous works conducted with short day cultivars in Missouri and Japan, where plant DM increased from 3.05 g/plant, in August, to 10.83 g/plant, in October (Long and Murneek, 1937; Nishizawa et al., 1998). Except for 1998, where differences were not statistically significant, crown and root DM of D1 and D2 plants increased between extreme sampling dates (Table 2). Since the California winter strawberry production system requires fresh-dug runner plants without leaves (Strand, 1994), root and crown biomass play a fundamental role in plant establishment and early fruit production. The rate of DM increase was higher in roots than in crowns, especially in 2002 and 2004 (Table 2). Root DM values and accumulation rates followed patterns analogous to previous studies. For example, Long and Murneek (1937) observed that the root DM of a short-day cultivar grown in Missouri increased from 0.70 g/plant in August to 3.30 g/plant in November. In Japan, Nishizawa et al. (1998) also recorded similar values in the short-day cultivar 'Donner': 1.5 g/plant in September and 4.4 g/plant in October. Root growth during September - October might be attributed to the normal development of the roots as well as an increased allocation of reserve nutrients to this organ (Long and Murneek, 1937).

In addition, the leaf area (LA) was much greater in 2002 than in the other two seasons. D1 plants had greater LA than D2 plants (Table 3). The values were within previously reported ranges (Long and Murneek, 1937) but were in contrast with petiole DM, which increased from the first to the last sampling dates, and varied consistently between plant orders (Table 2).

TNC concentration and partitioning

Crowns generally had higher initial TNC concentration than roots. TNC concentration in crowns and roots

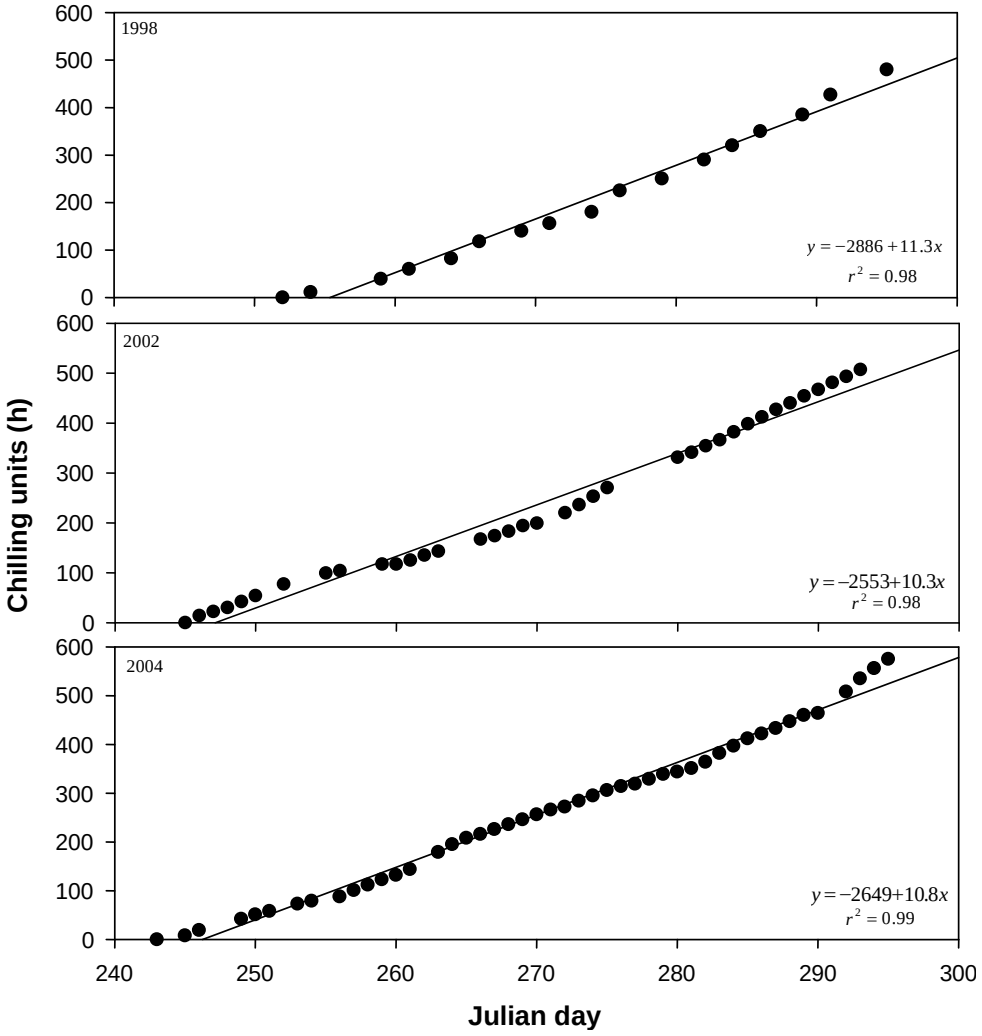

Figure 2. Chilling units accumulation in the Butte Valley (Siskiyou County), California, in 1998, 2002 and 2004.

Table 1. Cumulative chilling units (CU) at Butte Valley (41.89° N lat., 121.98° W long., 1293 m elevation, Siskiyou County, California).

Date	Cumulative Chilling units (hour) (T≤7.2°C)
1998	
10 September	0
01 October	180
22 October	480
2002	
08 August	0
09 September	77
18 September	125
07 October	331
2004	
17 September	132
01 October	295

Table 2. Dry mass partitioning of daughter 1 (D1) and daughter 2 (D2) strawberry ('Camarosa') plants dug from California high-latitude/high-elevation nurseries in 1998, 2002 and 2004.

Sampling date	Plant dry mass (g)		Leaflet dry mass (g)		Petiole dry mass (g)		Crown dry mass (g)		Root dry mass (g)	
	D1	D2	D1	D2	D1	D2	D1	D2	D1	D2
1998										
10 September	12.0[1]	11.09	5.70	5.02	3.25	2.84	0.91	0.68	2.16	2.53
01 October	12.8	11.60	6.65	5.40	3.52	3.10	0.81	0.76	1.83	2.37
2002										
08 August	7.57	-	5.50	-	1.68	-	0.15	-	0.24	-
09 September	14.79	6.84	9.34	4.17	3.36	1.57	0.39	0.21	1.71	0.89
07 October	15.08	6.29	9.17	3.12	3.23	1.39	0.59	0.29	2.09	1.49
2004										
17 September	8.05	6.43	3.89	3.36	2.44	1.64	0.62	0.42	0.74	0.75
01 October	10.00	7.72	4.06	3.40	2.77	1.81	0.71	0.51	1.32	1.32
Probability					**Pr > F**					
1998										
Date	***		***		ns		***		ns	
Daughter	***		***		***		***		ns	
Date × Daughter	ns		ns		ns		ns		ns	
2002										
Date	***		*		***		***		***	
Daughter	***		***		***		***		***	
Date × Daughter	ns		ns		ns		*		ns	
2004										
Date	***		ns		ns		*		***	
Daughter	***		ns		***		***		ns	
Date × Daughter	ns		ns		ns		ns		ns	

[1]Analysis of variance: *, *** and ns, significant at $p < 0.05$, 0.001 and non significant, respectively.

increased rapidly from September to October (Table 4). The correlation between chilling and TNC accumulation was stronger in roots than in crowns (Figure 3). 'Camarosa' reached a TNC concentration of 9 - 12% (90-120 mg g^{-1} DM) by the first week of October, when conventionally most of the runners of this cultivar are dug for commercial strawberry production in southern California (Strand, 1994). Even though the time that elapsed between each year (1988, 2002 and 2004) was different, TNC accumulation data fit well in the adjusted trend line (Figure 3). Again,

Table 3. Crown diameter and leaf area of daughter 1 (D1) and daughter 2 (D2) strawberry ('Camarosa') plants dug from high-latitude/high-elevation nurseries in 1998, 2002 and 2004.

Sampling date	Crown diameter (mm)		Leaf area (cm^2)	
1998	**D1**	**D2**	**D1**	**D2**
10 September	10.5[1]	8.5	427	231
01 October	10.6	8.4	642	311
2002				
08 August	-	-	-	-
09 September	15.7	13.3	1327	664
07 October	14.5	13.5	1025	465
2004				
17 September	15.6	14.8	616	564
01 October	18.2	15.2	602	505
Probability		**Pr > F**		
1998				
Date	ns		***	
Daughter	***		***	
Date × Daughter	ns		ns	
2002				
Date	ns		ns	
Daughter	*		**	
Date × Daughter	ns		ns	
2004				
Date	**		ns	
Daughter	***		ns	
Date × Daughter	ns		ns	

[1]Analysis of variance: *, **, *** and ns, significant at $p < 0.05$, 0.01, 0.001 and non significant, respectively.

Table 4. Effects of digging date on chilling exposure, and on crown and root total non-structural carbohydrate (TNC) concentration of 'Camarosa' daughter 1 and 2 (D1 and D2) plants dug from high-latitude/high-elevation nurseries in 1998, 2002 and 2004.

Sampling date	Cumulative hilling units (hours at T≤7.2°C)	TNC Concentration (% DM)					
		Crown		Root		Leaflet	
		D1	D2	D1	D2	D1	D2
1998							
10 September	0	6.05[1]	6.09	3.41	4.46	-	-
01 October	180	6.87	7.24	9.97	8.57	-	-
22 October	480	11.52	9.65	16.86	16.74	-	-
2002							
08 August	0	9.56	-	5.17	-	11.73	-
09 September	77	9.37	9.36	4.78	5.17	8.13	8.53
18 September	125	9.80	9.73	5.45	6.87	6.73	5.90
07 October	331	14.07	10.75	9.83	12.28	9.83	6.70
2004							
17 September	132	8.13	8.08	5.85	5.67	5.57	6.07

Table 4. Continued.

01 October	295	8.48	9.37	8.67	8.87	7.43	9.15
Probability				**Pr > F**			
1998							
Date		***		***		-	
Daughter		ns		ns		-	
Date × Daughter		ns		ns		-	
2002							
Date		*		***		***	
Daughter		ns		ns		ns	
Date × Daughter		ns		ns		ns	
2004							
Date		*		***		***	
Daughter		ns		ns		ns	
Date × Daughter		ns		ns		ns	

[1]Analysis of variance: *, *** and ns, significant at $p < 0.05$, 0.001 and non significant, respectively.

this shows that the three years were comparable and provided relevant information to these experiments.

The rapid increase of root TNC in plants propagated in northern California nurseries (Table 4, Figure 3) as quantitatively described in this study has been previously described qualitatively by Bringhurst et al. (1960), who measured the accumulation of starch granules in the root cortex of strawberry plants. They reported that starch (the most abundant carbohydrate in root TNC) accumulated gradually in roots from October to late November. A comparable pattern of TNC accumulation in roots has been observed in strawberry plants grown in different regions such as Australia, Canada, Japan, Missouri and Portugal (Freeman and Pepin, 1971; Hicklenton and Reekie, 2000; Long, 1935; Long and Murneek, 1937; Menzel and Smith, 2012; Palha et al., 2002; Nishizawa et al., 1998). Our findings suggest that nursery chilling plays a key role in late-summer and early-fall accumulation of TNC in strawberry roots, and that the pattern of accumulation of TNC observed in northern California nursery plants is similar to those of other regions. The accumulation of reserve nutrients in storage tissues is apparently part of the plant acclimation process to enter dormancy and preserve carbohydrates to support flower development when weather conditions become more favorable for plant growth.

The role of the crown as a reserve organ is secondary compared to roots (Figure 3). Compared to roots, crowns have two constraints that limit their capacity as reserve organs; smaller biomass and lower rates of TNC accumulation. Our observations in 'Camarosa' are consistent with previous reports from USA (Missouri), France and Japan showing that other cultivars, such as 'Aroma', 'Elsanta' and 'Donner' accumulated TNC in the crown at a much lower rate than in roots, and maximum TNC content was significantly lower in crowns than in roots (Long and Murneek, 1937; Nishizawa et al., 1998; Raynal-Lacroix et al., 1999). These outcomes support the theory that crowns are less sensitive to chilling than roots in terms of capacity to accumulate TNC. Roots appear to have a stronger sink capacity than crowns and therefore attract more assimilate from leaves even though they are in the transport pathway between leaves and roots.

In general, an increase in TNC content in roots is concomitant with a decrease of TNC content in leaves (Hicklenton and Reekie, 2000). TNC concentration in leaf parenchyma storage cells increases in the fall and may peak anytime from middle October (Japan) to middle November (France), depending on the climate of the region where strawberry plants are grown (Nishizawa et al., 1998; Robert et al., 1999). The latitude of Siskiyou County (California) is intermediate between Japan and France latitudes and the process of TNC accumulation in leaves appeared to continue during our plant sampling periods. The data collected in the present research is within the range observed by Gast and Pollard (1989) in the short day cultivar 'Earliglow', in New Hampshire, who reported a range of TNC concentration in leaves from 4.8 % DM (Sept 6) to 13.1 % DM (Oct 21).

Plant vigor, growth and fruit production

In 1998, after a growth period of 6 weeks in growth chambers, plants dug in October had larger DM than plants dug in September, although differences were not significant (Table 5). In field plots, during the year 2004-2005 fruiting season, there were no significant differences

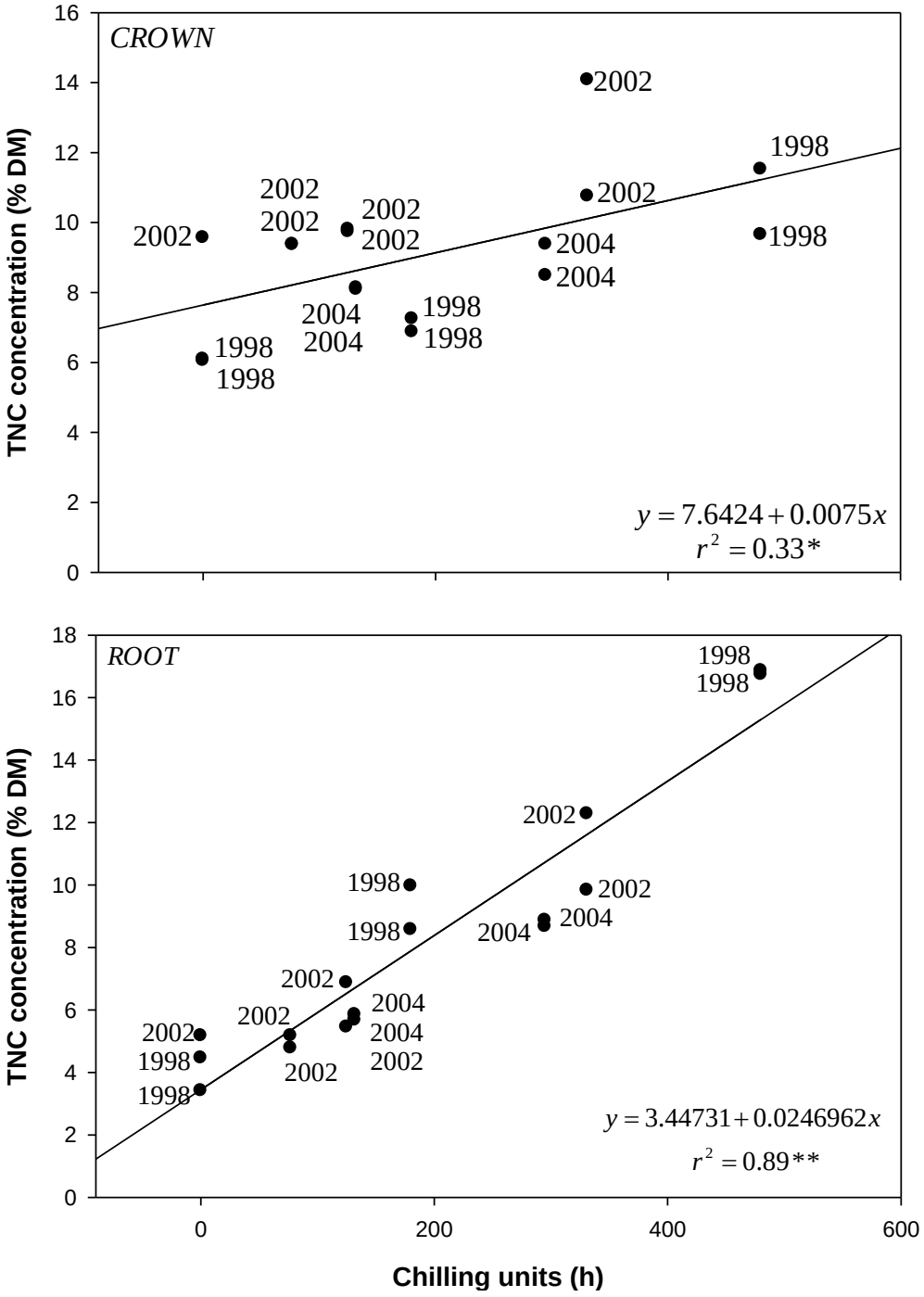

Figure 3. Effects of chilling on TNC concentration in crown and root of 'Camarosa' strawberry runner plants dug from HL/HE nurseries. Nursery seasons 1998, 2002 and 2004 were combined. * and ** indicate significance at P = 0.05 and 0.01, respectively.

between D1 and D2 plants in terms of total yield (p>0.8442), marketable yield (p>0.9521), number of fruit per plant (p>0.9818), average fruit weight (p>0.8736), fruit appearance (p>0.5867), and fruit firmness (p > 0.8541). Therefore, D1 and D2 plants were combined for analysis of variance. The plants dug in October had double amount of total and marketable yields and number of fruit per plant compared to September plants; however, September dug plants had larger average fruit size (weight) and fruit firmness (Table 6), which is coincident with previous reports.

In Mexico, runner plants of 'Fresno', 'Tioga' and 'Aliso'

Table 5. Effects of digging date on growth of 'Camarosa' daughter 1 and 2 (D1 and D2) strawberry plants grown in growth chambers at day/night temperatures of 22°C/12°C and 11-h photoperiod for 6 weeks (1998).

Planting date	Plant DW (g)	
	D1	D2
10 September	6.6[1]	5.0
01 October	10.0	6.0
Probability	Pr >	
Date	ns	
Daughter	*	
Date × Daughter		

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

Table 6. Effects of digging date on the total and marketable yields, number of marketable fruit, average fruit size, fruit appearance, and fruit firmness of 'Camarosa' runner plants in Irvine, California.

Planting date	Yield (g/plant)		Number of	Fruit		
	Total	Marketable	Marketable fruit/plant	Weight (g)	Appearance	Firmness
24 September	78.9	66.2	2.0	33.0	3.3	4.0
05 October	157.5	116.8	4.6	25.7	3.0	3.8
Pr > F	***	***	***	***	*ns*	***

[1]Analysis of variance: *** and ns, significant at $p < 0.001$ and non significant, respectively.

with high initial root starch concentration (+45%) had higher yields (+62%) than plants with low root starch (Barrientos-Perez and Plancarte-Mendez, 1978). The runner plants of 'Sweet Charlie' propagated in Canada had higher initial concentration of root TNC (+142%) than plants propagated in Florida, and had higher early (+500%) and total (+30%) yields, when planted in Central Florida on the 3rd of October (Kirschbaum et al., 1998). Similarly, runners propagated at HE nurseries had greater whole plant and root dry weights, and TNC accumulation tended to be greater in runners from HE compared to low lands in Korea, due to chilling effects (Ruan et al., 2009). These findings suggest that chilling influences the accumulation of TNC in roots and crown, and that the TNC status of the runner plant has a significant impact on plant growth, development and fruit production. In fact, Durner and Poling (1987) suggested that chilling may promote floral differentiation and increased yield. Differential growth patterns of runner plants of equivalent size but originating in different nursery locations has been reported (Kirschbaum et al., 1998; Pirlak et al., 2002). The possible reasons why initial TNC content influences plant vigor and early fruiting pattern in strawberries have been suggested by Nishizawa et al. (1998) and Schupp and Henion (1998), who reported that TNC reserves accumulated during autumn, especially starch, which are used for supporting feeder root initiation and growth, initial leaf expansion and early flower development. Therefore, if the TNC pool is limited and part of the TNC are consumed by respiration (Dickmann and Blanke, 2000), less TNC is available for re-growth after transplanting. Furthermore, during spring re-growth in biennial crop systems, a 2-fold increase in respiration was measured by Brierley and Landon (1944), which is dependent on the TNC storage pool. Clearly, carbohydrate reserves are of vital importance in runner plants at digging time.

In summary, the results suggest that root TNC concentration is more sensitive to chilling hour accumulation than crown TNC concentration. Therefore, root sampling appears to be more appropriate than crown sampling for assessing the carbohydrate status of strawberry nursery runner plants early in the fall. Carbohydrate reserves accumulated in roots and crown of strawberry plants in late summer and early fall in the nursery were apparently utilized for supporting early growth of roots, newly developing leaves and inflorescences. Thus, the greater content of TNC in the roots appears to be a cause of increased early season fruit yield. The results obtained herein are useful for developing a plant maturity index and establishing minimum chilling exposures required to insure adequate quality of strawberry nursery runner plants. According to the data collected, the proposed minimum chilling exposure for high latitude California nurseries would be around 200 CU for 'Camarosa'. The proposed plant maturity index should take into considera-

tion other nutrients, especially nitrogen, as was shown in a previous report (Kirschbaum et al., 2010); both N and TNC in roots could be important for synthesizing storage amino acids or proteins, as it has been observed in temperate perennial trees. Meanwhile, further researches are needed to establish the relationships between TNC and mineral nutrients, and to determine cultural practices for improving reserve nutrient accumulation in storage tissues.

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