Relationships of Carbohydrate and Nitrogen Content with Strawberry Transplant Vigor and Fruiting Pattern in Annual Production Systems

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ABSTRACT

In strawberry (*Fragaria* x *ananassa* Duch.), fruit production systems based on leafless, bare-root transplants, successful plant establishment is dependent on crown/root reserves for the formation of new feeder roots and new leaves. Successful stand establishment, early fruiting, and sustained high productivity in strawberry have been correlated with total nonstructural carbohydrate (TNC) reserves. However, nitrogen (N) reserves have largely been overlooked. The importance of root carbon and N has been highlighted in studies focused on growth of perennial plants, where apparently growth and fruiting in spring are determined primarily by N reserves. In temperate fruit trees, protein would be the main form of N storage and the predominant storage amino acid would be arginine. This could be the case of strawberries, which share many of the general characteristics of temperate fruit trees. In this frame, the concept that confers a primary role to TNC over any other reserve nutrient in strawberry needs to be reconsidered. The N cycling process in strawberries remains largely unknown; however, emerging research lines suggest a key function of N in early fruit production of fresh-dug strawberry transplants, questioning the importance of TNC as the unique storage compounds involved in plant vigor.

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INTRODUCTION

All highly productive strawberry (*Fragaria x ananassa* Duch.) regions of the world utilize annual planting systems, in which plantations are completely renewed each autumn using freshly dug transplants. Due to use of annual plantings, nursery transplant production and quality are important considerations, and highly specialized strawberry transplant nurseries have been developed to supply quality transplants worldwide. The concept of quality involves trueness to type of the cultivar, plant maturity, transplant size, extent of physical damage, and phytosanitary condition. Due to the high cost of annual planting, fruit growers require transplants physiologically balanced at the time of digging, medium to large size and free of physical damage and pests and diseases (Roudeillac and Veschambre 1987; Galletta and Bringhurst 1990; Faedi and Baruzzi 2003).

Strawberry short-day cultivars go through several developmental stages (Guttridge 1969; Taylor 2002; Darnell *et al.* 2003). In a model suggested by Durner and Poling (1988), axillary buds differentiate into stolons (runners) when exposed to long photoperiods, axillary buds form branch crowns when the photoperiod decreases, and floral induction takes place when plants are exposed to very short days.

Because of this developmental sequence, commercial runner plant nurseries often are located at relatively high latitudes (HL > 40° N lat.) and/or at high elevations (HE). High-latitude sites have longer photoperiods than low latitude sites in summer and this enhances daily photosynthesis and runner plant production. High-elevation sites, as well, have lower summer temperatures than low elevation sites (Ruan *et al.* 2009). Thus, HL combined with HE, ensures runner plant exposure to decreasing temperatures and photoperiod in the nursery prior to digging in early/mid-autumn (Shaw 2004).

Strawberry transplants are exposed to several stresses between the time of nursery digging and after planting in the fruiting field. These stresses affect plant vigor and can cause economic losses to strawberry growers, either by death of plants (shortly after planting) or reduced vigor and decreased productivity over an entire season (Larson and Shaw 2002).

In California, the largest strawberry transplant producer in the world, plant leaves are mechanically mowed immediately prior to digging the nursery. Plants are then dug using

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modified potato diggers which shake the plants to remove dirt from the roots. Crowns may be crushed and broken in the course of all this operation (Duval *et al.* 2003). These plants are immediately transported to trim sheds in large plastic bins, cooled to < 4°C, and then sorted and trimmed by hand to commercial standards (Galletta and Bringhurst 1990). Trimming involves removal of remaining leaves and petioles to 2.5–5.0 cm in length; some nurseries also prune roots to about 10 cm in length to achieve plant uniformity and facilitate planting (Larson 1998).

In strawberry fruit production systems based on leafless, bare-root transplants, successful plant establishment is dependent on crown/root reserves for the formation of new feeder roots and new leaves. Once autotrophic function of the plant is reestablished, plant reserves become less important. Furthermore, the first inflorescence, which may be initiated in the nursery (Long 1939), constitutes a major energy-demanding sink. Indeed, the growth of the first fruits might depend on the total nonstructural carbohydrates (TNC) status of the transplant (Nishizawa and Shishido 1998). If winter fruit production is a goal, the development of marketable fruit from the first truss is highly desirable. Yet, as winter production is carried out in warm regions, transplants must also cope with heat stress. In southern California, ambient temperatures at the time transplants are set in the fruiting field (early October) are often >30°C, and soil temperatures can be 40°C or greater.

Successful stand establishment, early fruiting, and sustained high productivity in strawberry have been correlated with TNC reserves (Bringhurst *et al.* 1960; Larson 1994; Kirschbaum *et al.* 1998) but the influence of plant tissue nitrogen reserves in runner plant vigor and reproduction also is not well understood in strawberry. Studies on other temperate fruit crops of the *Rosaceae* family suggest that spring growth and fruiting are primarily determined by N reserves rather than by TNC reserves (Cheng and Raba 2003). On the other hand, some researchers consider N as an "uncontrollable factor" in strawberry because they were not able to establish a correlation between plant N status and plant vigor and fruiting pattern (Raynal-Lacroix *et al.* 1999). Emerging research lines suggest a major role of tissue N concentration in early fruit production of fresh-dug strawberry transplants, questioning the importance of TNC as the unique storage compounds involved in plant vigor (Kirschbaum *et al.* 2010).

THE BROAD PICTURE

Temperate climate plants exhibit seasonal patterns of allocation and utilization of non-structural carbohydrates (mainly starch, sucrose, glucose and fructose) and N that are in synchrony with phenological phases and physiological processes. A typical physiological process in these plants is the partitioning of nutrients to storage organs (mainly stems and roots) when they are exposed to decreasing temperatures and photoperiods (autumn), as an adaptive strategy for surviving cold winters, and for resuming growth the following spring (Ino *et al.* 2003; Wong *et al.* 2003).

In sugar maple (*Acer saccharum* Marsh.), starch is the major TNC accumulated in stems and roots in late summer and early fall (Wong *et al.* 2003). During the cold season, starch hydrolysis releases soluble sugars that may play a role in cold tolerance (Wong *et al.* 2003), or be used for winter respiration (Ino *et al.* 2003). In spring, vegetative growth relies on stored TNC as has been shown for walnut (*Juglans regia* L.) trees and the evergreen shrub *Daphniphyllum macropodium* (Ino *et al.* 2003; Lacointe *et al.* 2004). The involvement of N reserves as source of nutrients to sustain early season growth has been also demonstrated in studies with fall applied N to persimmon trees (*Diospyros kaki* cv. 'Fuyu') and to walnut trees, where redistribution of storage N to the new growth prevailed over seasonal N-sources during the spring flush of growth (Deng *et al.* 1989; Kim *et al.* 2009).

The importance of root carbon and N reserves has been highlighted in studies focused on spring regrowth of perennial grasses and Mediterranean tree species whose foliage had been physically damaged in the fall (El Omari *et al.* 2003; Dhont *et al.* 2004). In alfalfa, defoliation reduces taproot TNC concentration (Graber *et al.* 1927), and low concentrations of TNC are associated with poor winter survival and reduced spring regrowth (Reynolds 1971). In addition to starch reserves, amino acids and soluble proteins are also reduced in alfalfa by fall harvests, with negative effects on root dry weight and spring regrowth (Dhont *et al.* 2004).

Studies analyzing the contribution of N and TNC root reserves to growth and resprouting of holm-oak (*Quercus ilex* L.) trees indicate that N-deprived plants used N from root reserves to support a growth rate similar to that of non-deprived plants (El Omari *et al.* 2003). However, N-deprived plants lost their resprouting capacity in spite of a high TNC accumulation and N resupply to the soil. After the supply of N was restored to N-deprived plants, this nutrient mainly accumulated in underground organs, limiting the above-ground growth. Resprouting plants first remobilized N stored in roots, and thereafter took it up from the nutrient solution. Similarly, early shoot and root growth of newly-planted apple trees in Canada were supported by N remobilized from woody tissue rather than by applied N. Demand for root-supplied N was low until 11 weeks after planting, when a rapid development of roots >1 mm in diameter occurred (Neilsen *et al.* 2001).

Studies with CO_2 enrichment conducted by Cheng and Raba (2003) on Gala apple trees illustrate the interaction between carbon and N, as major reserve nutrients. Fall CO_2 enrichment significantly increased the total amount of reserve TNC. Soil N application in the fall significantly increased N content and the total amount of N accumulated in the tree, but reduced the concentration and total amount of reserve TNC. Fall CO_2 enrichment did not affect total leaf area, fruit number, or fruit yield the following year. Regardless of the current N supply, trees with high N but low TNC reserves had a larger total leaf area, higher fruit number, and total yield than trees with low N but high TNC reserves. They concluded that growth and fruiting of apple trees in spring are determined primarily by N reserves, not by TNC reserves.

The application of foliar urea and ammonium nitrate in the fall appears to be an efficient method of increasing N reserves. In autumn, foliar-applied N is rapidly absorbed by leaves, converted to amino acids, and translocated to bark and roots for storage in apple (Dong *et al.* 2002). The enzymatic GS/GOGAT pathway assimilates ammonium into glutamine and glutamate, which are rich in carbon. After this step, N is incorporated into other amino acids via transamination reactions (Taiz and Zeiger 1998). Consequently, part of the carbon from nonstructural carbohydrates is incorporated into amino acids and proteins, decreasing the carbon stored as starch, glucose and fructose (Cheng *et al.* 2004).

June-budded almond (*Prunus dulcis* (Mill) D.A. Webb) trees fertilized with different N rates showed that increasing N supply raises the concentration of amino acids and the proportion of N stored as amino acids. However, protein was still the main form of N storage. The predominant storage amino acid was arginine. A negative relationship was found between total amino acid and nonstructural carbohydrate concentrations, suggesting that carbohydrate is increasingly used for N assimilation as the supply of N increases (Bi *et al.* 2004).

A study on the effects of autumn foliar urea-N sprays on N absorption and partitioning in peach trees showed that leaves rapidly absorbed urea-N and transported it to perennial tree parts within 4-7 d after application. Of the urea-N translocated, most was recovered in roots (≥38%) following application in September or October. Urea-N applied in November, however, remained largely in the current year wood (45%). Foliar application of urea in September or October supplied the equivalent of about 20% of crop N

content (Rosecrance *et al*. 1998).

N-foliar application depleted TNC content by approximately 60% and those carbohydrates were recovered in proteins and free amino acids in grape vines (Xia and Cheng 2004). Cheng and Fuchigami (2002) observed a linear relationship between total N accumulated in apple trees during the previous season and the amount of reserve N remobilized for new shoot and leaf growth. Fall foliar application of N not only significantly increased N concentration in both shoots and spurs but also improved fruit number and yield (Dong and Fuchigami 2003).

Strawberries share many of the general characteristics discussed above with other plants; however, the specific interrelations between TNC and N storage remain elusive.

INVOLVEMENT OF INITIAL PLANT TOTAL NONSTRUCTURAL CARBOHYDRATES LEVELS IN VIGOR AND FRUITING PATTERN OF STRAWBERRY PLANTS

In the strawberry plant, the accumulation of carbohydrates in storage organs (crown and root) is a function of the interaction between plant and environment. Strawberry plants are sensitive to decreasing daylengths and temperatures (autumn), which trigger the process of nutrient storage. Starch is the prevailing non-soluble carbohydrate in roots and crowns (Greve 1936; Bringhurst *et al*. 1960; Nishizawa and Hori 1989), while glucose, fructose and sucrose are the predominant soluble carbohydrates in strawberry crowns (Macias-Rodriguez *et al*. 2002). Studies conducted in Canada and England found little starch accumulation in strawberry roots in August, intermediate quantities in October and large amounts in November (Mann 1930; Freeman and Pepin 1971). The storage process in roots begins in the parenchymatous tissues of the stele, and later there is a general accumulation in the cortex. By December, most parenchymatous cells are packed with starch granules (Mann 1930).

Starch accumulation in roots is more likely influenced by temperature rather than by photoperiod (Le Miere *et al*. 1996). TNC accumulation in storage tissues is sensitive to exposure to cold temperatures, as measured in roots and crowns of 'Sweet Charlie' runner plants. 'Sweet Charlie' plants propagated in Quebec had increased TNC content compared to plants propagated in Florida. September average maximum and minimum temperatures were 19.4 and 10.6°C in Quebec, and 31.7 and 22.7°C in Tampa. In Quebec, photoperiods decreased from 13:17 h (September 1) to 11:43 h (October 1), and in Tampa from 12:43 h to 11:53 h (Kirschbaum *et al*. 1998). Consequently, both nurseries had similar photoperiodic conditions and very different temperature regime in September. Strawberry plants ('Elsanta') exposed to 15°C accumulated similar content of root starch regardless the photoperiod was 9 or 13 h (Le Miere *et al*. 1996). This together suggests that TNC accumulation in roots is likely to be controlled by temperature rather than by photoperiod; however other studies consider photoperiod more important than temperature (Maas 1986).

Chilling is quantified by the summation of chilling units. One chilling unit (CU) is one hour of exposure to temperatures ≤7°C. California and Florida cultivars are considered low-chill cultivars compared to European cultivars according to Bigey (2002), who included 'Camarosa' and 'Sweet Charlie', two cultivars from California and Florida, respectively, in the lowest chilling requirement group (<700 CU). Cultivars have a specific chilling requirement associated with the accumulation of specific amounts of TNC. For instance, in order to accumulate ~40 mg.g^{-1} FW of starch, in Spain, 'Camarosa' needed 400 CU while 'Pajaro' required 700 CU (Lopez *et al*. 2002). The roots of the Canadian cultivars 'Veestar', 'Bounty' and 'Kent' stored 10% DW of starch after 40, 110 and 200 CU, respectively (Hicklenton and Reekie 1998).

Hicklenton and Reekie (2000) proposed that CU have a "minor role" as an indicator for the optimum digging date

for intended for cold-storage and dug between November 7 and 21 in Nova Scotia, Canada. However, by that date in Nova Scotia, plants had accumulated maximum amounts of reserve TNC. This is not the case of fresh plants dug early in autumn, where reserve TNC might play a role on transplant quality.

Successful long term cold storage of runner plants, stand establishment, early fruiting, and high productivity in strawberry have been related to TNC reserves. Root TNC appears to play a role in maintaining plant quality during cold storage of 'Frigo' plants (Bringhurst *et al*. 1960; Worthington 1969; Lieten 1997). 'Lassen' and 'Shasta' plants dug from low elevation northern California nurseries before November 15 had little or no starch, poor storage ability, poor survival after planting, and lacked vigor. In contrast, plants dug after December 1 had 75% greater starch reserves, were suitable for long-term storage, and had satisfactory vigor after transplanting (Bringhurst *et al*. 1960). 'Elsanta' plants dug in The Netherlands before November 21 had lower root DW, starch and sucrose concentration, and subsequent less fruit production and vigor than plants dug on January 25, where chilling units were 87 and 890, respectively (Lieten 1997).

Total nonstructural carbohydrate reserves drop during cold storage due to plant respiration. During a 6-month cold-storage period (-2°C), respiration rates of dormant strawberry plant roots ranged from 4.2 to 8.3 mg CO_2 kg^{-1} h^{-1} FW and total sugars decreased by 33% (Worthington 1969). Root respiration in the fall can reach values in the range of 36-72 mg CO_2 kg^{-1} h^{-1} FW depending on root temperature (Blanke 1995). The role of nonstructural carbohydrate reserves is crucial for long term storage since plant respiration consumes NC during the storage period. Total nonstructural carbohydrate reserves could provide transplants a carbon buffer to meet respiratory and/or growth demands until the photosynthetic apparatus be regenerated (Kobe *et al*. 2010). Therefore, carbohydrate content has to be large enough to provide for both root respiration during prolonged cold storage periods and plant establishment and survival in the fruiting field. Indeed, due to root respiration after planting, 'Frigo' 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).

Reserve TNC has been considered relevant to plant vigor and fruiting pattern because plants with increased root nonstructural carbohydrate concentration rapidly generate more feeder roots (Schupp and Hennion 1997), providing resources for flower bud initiation (Long 1935) and early fruit development (Nishizawa and Shishido 1998). The reliance of strawberry plants on root reserves for increasing root mass has been proposed by Mann (1930), who periodically dissected roots and shoots of strawberry plants and detected a depletion of nonstructural carbohydrate after each period of vigorous root growth. Root reserves are considered a primary factor of vigor by commercial nurseries which dig plants early in fall for use in annual fruit production systems. Provided that most of the runner plants for annual planting systems are defoliated before digging, the energy supply for successful stand establishment and initial growth comes exclusively from stored reserves. Studies conducted on 'Camarosa' in Mexico (Macias-Rodriguez *et al*. 2002), and on 'Toyonaka' in Japan (Nishizawa 1995), indicated that root NC decreased rapidly during the first three weeks after planting, suggesting that stored carbohydrates in strawberry crowns and roots are consumed during early phases of plant growth.

There is limited information on how initial plant TNC reserve influences fruiting patterns in warm, subtropical regions, where plantations are established early in the fall, and winter fruit production is very desirable. Runner plants of 'Sweet Charlie' propagated in Canada had higher initial concentration of root starch (+142%) than plants propagated in Florida, and had higher early season (+500%) and total (+30%) yields when planted in Central Florida in early

October (Kirschbaum *et al*. 1998).

Initial TNC concentration and content in roots and crowns were correlated positively with the accumulation of chilling hours (h≤7.2°C) and increased from mid-September to early-October, according to studies conducted in HL/HE nurseries located northern California (42° North latitude). Crown and root biomasses, early growth and early-season fruit production were enhanced in October-dug plants compared to September-dug plants. Root TNCs were more sensitive to chilling-hour accumulation than crown TNCs. Root TNC concentration (expressed in % of dry mass, DM) consistently increased from 4 to 14, 6 to 11, and 14 to 21 in 'Selva', 'Camarosa' and 'Ventana', respectively, suggesting a genotype-related response (Kirschbaum 2005). A similar pattern was noted with older California varieties but dug in late autumn, although only starch content was measured, and with a qualitative method based on the number of parenchymatous root cortex cells filled with starch (Bringhurst *et al*. 1960).

Standardization of plant reserve status is complex because the reserve status is strongly related to genotype, nursery location and the particular temperature regime of each year. Chemical characterization of strawberry runner plants is an emerging demand and is increasingly gaining attention worldwide. A better characterization of the plant material would improve agronomic practices and profits, as well as the current levels of confidence between nurseries and fruit growers.

NITROGEN RESERVES IN STRAWBERRY RUNNER PLANTS: A WORLD TO BE EXPLORED

Nitrogen is the major nutrient element utilized by strawberry (Albregts and Howard 1980), and it is essential during early growth, bud differentiation, and flowering. However, excess N nutrition can result in excessive foliage, increased susceptibility to pathogens, fruit softening and late ripening (May and Pritts 1990; Nam *et al*. 2006). Historically, commercial nurseries have reduced N applications by mid-summer to "harden plants off" by reducing vegetative growth. This hardening is thought to result in increased carbohydrate accumulation and reduced susceptibility to disease and transplant stress (K. Larson, pers. comm.).

A large fraction of plant N is localized in the leaves of *Fragaria chiloensis* (L.) Duch., one of the parents of the cultivated species *F*. x *ananassa*. As much as 70-80% of applied N is allocated to the foliage, increasing Rubisco content of the leaves and suggesting that excess of leaf N might be stored in the form of Rubisco (Moon *et al*. 1990). Although leaf N is translocated to storage tissues such as crowns and roots at late summer and during the fall (Kirschbaum 2005), as much as 50 kg.ha^{-1} of remaining leaf N might be removed from the crop when leaves of mother and runner plants are mowed in the nursery prior to plant harvest (Strik *et al*. 2004).

Nitrogen deficiency symptoms typically consist of yellowish-green foliage, but in severe cases, tips of older leaflets become red, and the color progressively spreads inward until the entire leaflet turns red-orange (Hancock 1999). The sufficiency ranges for leaf blade total N found in the literature are variable but quite similar. Pritts and Handley (1998) proposed 1.9, 2.0-2.8 and 4.0% (on dry weight basis) for "deficient below", "sufficient" and "excess", respectively. Ulrich *et al*. (1980) suggested 2.0-2.8, 2.8 and >3.0% as "deficiency symptoms", "tentative critical concentration" and "no deficiency symptoms", respectively. Yoshida *et al*. (1997) concluded that critical values of leaflet total N are around 2.8%.

Total nonstructural carbohydrate and N translocation to storage tissues occurs simultaneously in the fall. Research conducted in Canada (Gagnon *et al*. 1990) indicates that there is a high correlation between cold tolerance acquisition and accumulation of TNC and N in roots, suggesting that both TNC and N concentrations increase concurrently with decreasing temperatures. Strawberry plants exhibit seasonal fluctuations in N content, with peak levels in November (northern hemisphere) when nearly 80% of the total N is in the leaves. After the peak, due to yellowing and dying, leaf N decreases to ~1% in late autumn and winter. Simultaneously, N content increases in roots (mainly) and crowns, which serve as N storage organs in winter. Early in spring, N stored in root and crown tissues provide for buds and new leaves development (Mann 1930; Long and Murneek 1937).

Strawberry genotype can have a significant impact on plant N status. Different *Fragaria* species and varieties can have different-sized root systems (Darrow 1966), which can affect the ability of the plant to extract water and nutrients from the soil. Also, the roots of some varieties have the ability of remaining active even under low soil temperatures. 'Tioga' roots remained active longer in the fall and became active earlier in the spring compared to 'Shasta' and 'Tufts', in California (Ulrich *et al*. 1980). These authors used the term "foraging power" to classify cultivars in terms of their relative yield response to applied N: 'Tufts' > 'Tioga' > 'Shasta'. Furthermore, Neuweiler (1997) suggested that the new cultivars have greater N use efficiency than older ones.

Strawberry genotypes with higher leaf N content have increased photosynthetic capacity. In studies conducted with various *F. chiloensis* accessions, clone 'CA11' accumulated more N than clone 'RCP37'. In general, 'CA11' allocated more N to leaves, resulting in increased photosynthetic rates. As a result of greater N accumulation in leaves, 'CA11' plants had greater CO_2 assimilation, total Rubisco activity, dry weight, and leaves and crowns than 'RCP37', as N treatment increased from 0 to 200 mg.L^{-1} (Moon *et al*. 1990). Similar differences were found between *F. chiloensis* and *F*. x *ananassa*, where the first species had higher leaf CO_2 assimilation rate and higher leaf N than the second species, mostly in the form of Rubisco (Fallahi *et al*. 2000).

Managing rates and timing of N fertilization in strawberry nurseries is crucial for controlling nursery productivity, both in terms of number of runner plants per unit area and in terms of runner plant quality. However, the optimum N fertilization rate varies widely among experiments. Runner plants of 'Aliso' fertilized with 80, 320 and 640 kg.ha^{-1} of N (as $(NH_4)_2SO_4$) in the nursery (Israel) were planted in fruiting fields in October and grown for a complete season under three N fertilizer rates (150, 300 y 450 kg.ha^{-1}). Biomass, runner plant size and runner plant N content were reduced with the lowest N rat, but plants receiving 320 kg.ha^{-1} of N in the nursery outyielded all other treatments for fruit production, regardless of the N fertilization applied in the fruiting field. The authors of this work (Rodgers *et al*. 1985) concluded that N fertilization in the nursery is more essential than later field applications.

Nursery plants of 'Redcoat' fertilized with nutrient solutions of different N concentrations (2, 20, 70 and 120 ppm) responded positively to N fertilization. At harvest, in September, more runners, runner plants and leaf N were attained with the highest N-concentration in the nutrient solution (Blatt and Crouse 1970).

Studies conducted across three nursery seasons in France with 'Darselect', 'Gariguette' and 'Elsanta', showed that root N content in the fall increased along with the rate of N inputs in the nursery in summer. Nursery runner plants were harvested in December/January ('Frigo' plants), cold-stored for six months and then planted in fruiting fields (Verpont 2003). The results were partially consistent with those of Rodgers's *et al*. (1985) work. However, no fertilizer effect on TNC reserves, plant establishment or yield was found. Kreusel and Lenz (1996), in Germany, observed reductions in TNC contents in roots of runner plants when the rate of N applied in the nursery was raised from 40 to 80 kg.ha^{-1} in late August.

Key enzymes in N metabolism such as nitrate reductase (NR) and glutamine synthetase (GS) are localized in strawberry leaves and roots (Claussen and Lenz 1999) as in most of the plants. Plants take N in the form of NO_3^- or NH_4^+.

Nitrate is first reduced to NO_2^- by NR in the cytoplasm of leaf mesophyll cells and root epidermal and cortical cells and then transported into plastids (chloroplasts in leaves, leucoplasts in roots), where it is reduced to NH_4^+ in a reaction mediated by nitrite reductase. The enzymatic GS/GOGAT pathway assimilates NH_4^+ into glutamine and glutamate, which are rich in carbon. After this step, N is incorporated into other amino acids via transamination reactions (Taiz and Zeiger 1998).

Acuña-Maldonado and Pritts (2008) showed that foliar urea applied in fall increased total plant N content and size, decreased TNC concentration, and also decreased yield in strawberry plants grown under a multiannual growing systems in New York State. Nevertheless, a study conducted by Kirschbaum *et al.* (2010) with transplants grown in California HL/HE nurseries, suggests that late-season nursery N applications enhance early yields, increase the number of early marketable fruits, do not affect total season yields or fruit quality, and result in greater N concentration in leaves, crowns and roots. In the same study, runner plants with leaf N concentration within the sufficiency range (1.9-2.8% of dry mass) produced the highest early yields. Total nonstructural carbohydrate concentrations decreased in most of the N-treated plants. Apparently, foliar N application in summer stimulates plant vegetative growth during the period of flower differentiation, enhance N mobilization to crown and root and accelerate flower development, contributing to the advancement of fruit production (Sønsteby *et al.* 2009). Increasing N reserves with late summer foliar N applications is one strategy that HL/HE nurseries can use to efficiently enhance vigor and early yields in transplants with foliar nitrogen levels below the sufficiency range.

Carrillo-Mendoza *et al.* (2005) applied foliar urea and sucrose in late summer and early fall to obtain more vigorous mature daughter plants with higher reserve content in Mexico. The interaction urea × sucrose was significant for root and crown dry biomass. Foliar urea increased the content of total reducing sugars in the crown (19%). Nitrogen content in root and stem increased with urea, but decreased with sucrose. The treatments did not affect photosynthetic rate, starch accumulation, earliness of flowering, nor fruit yield of the daughter plants. Probably, in spite of the increase of TNC and N in roots and crowns, the pool of these reserve nutrients was not enough to improve transplant vigor.

CONCLUDING REMARKS

In general, nonstructural carbohydrates are thought to play a major role in determining plant vigor but the optimal content of TNC required for plant survival and optimal yield performance has not been determined. Nitrogen reserves have largely been overlooked as having a major role in plant establishment and early fruit development. High plant N concentrations in nursery transplants are often considered deleterious due to increased disease susceptibility and poor performance and survival after transplant (Strand 1994).

The N cycling process in strawberries remains largely unknown as are the amino acids and proteins that constitute the major N reservoirs in storage tissues of strawberry plants. Questions related to N management in nurseries and fruiting fields, regarding to rates, methods of application (soil, irrigation, foliar) and timing remain to be answered from a practical standpoint.

Nitrogen reserves are significant resources for fall-dug runner plant regrowth after planting. The concept that confers a primary role to TNC over any other reserve nutrient needs to be reconsidered. The accumulation of N in reserve tissue has been known for a long time but it in the practice has been virtually ignored in major strawberry transplant producing regions of the world. The way that nonstructural carbohydrates and nitrogen interact in storage organs and how this interaction influences plant vigor remains elusive.

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