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Strawberry Growth and Development in an Annual Plasticulture System

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Abstract. **The growth and development of three strawberry cultivars commonly grown in a plasticulture system were documented. Strawberry plants were harvested monthly and divided by roots, crown, leaves, flowers, and fruit and then dried in an oven. The dry matter production and resource allocation proceeded along a predictable pattern of development. The establishment phase was characterized by an active period of growth of root, crown and leaves in the fall. Through the winter, the plants underwent slow growth, ending in a transition period in the late winter/early spring when resources were allocated to both vegetative and reproductive growth. In the spring, all plant parts received significantly increased allocation of, or redistribution of, resources. Cultivars of California origin, 'Chandler' and 'Camarosa', displayed similar trends in yield, dry matter production, seasonal resource allocation, and growth analysis variables throughout the season. 'Sweet Charlie', a cultivar from Florida, showed lower dry matter accumulation and relative growth rate in the spring, higher harvest index and lower yield than the California cultivars.**

Strawberries are produced on ≈10603 ha in the eastern United States (Hokanson and Finn, 2000). In North Carolina, strawberry production has changed dramatically with the introduction of the plasticulture system. In 1996–97 there were ≈960 ha in strawberries in North Carolina, with the majority of this acreage in plasticulture (Hokanson and Finn, 2000). This level of production ranked North Carolina fourth behind California, Florida, and Oregon (NCDA&CS, 1999). Increased production, higher quality fruit, better disease and weed control, decreased labor costs, and more efficient water usage stimulated the use of plasticulture on >80% of North Carolina's strawberry acreage (Garwood, 1998; Poling, 1993).

The matted row system was for decades the predominant cultural system outside of California and Florida and much is known about the growth and development of strawberries in this system (Darrow, 1966; May et al., 1994; Pritts and Handley, 1998). However, very little research has been conducted on the growth and development of the strawberry in the southeastern United States (SEUS) plasticulture system. Plasticulture and matted row production systems are very different. In the matted row system, transplants are set in the spring, and crowns develop throughout the summer giving rise to runner plants that fill in the beds. Fruit is first harvested in the second year and plants are typically left in the ground for several seasons. In contrast, in the annual plasticulture system, transplants are set at high densities in fall, and harvest occurs ≈6 months after planting. Plants are removed from the field shortly after the final fruit harvest.

The major plasticulture strawberry cultivars in the SEUS are Chandler, Camarosa, and Sweet Charlie. 'Chandler' is most frequently planted due to its phenotypic stability; long harvest period, adequate cold tolerance, early maturity, flavor, color, and high yield potential (Poling, 1993). 'Camarosa', a recently introduced California cultivar, is becoming increasingly popular because it has firmer flesh, which allows transit of berries to more distant marketplaces. 'Sweet Charlie', an early ripening cultivar from Florida, enables growers to find a production niche early in the season when crop value is at its highest.

General plant adaptation and fruit characteristics of the cultivars used in SEUS plasticulture systems have been documented (Ballington, 1997; Ballington et al., 1998, Poling 1993; Poling and Monks 1994). What has not been reported is how strawberry plants allocate their resources throughout the growing season. In addition, the phenology, or onset and duration of phases of plant part development, have not been well documented under this system. This information could be used to develop more efficient crop management strategies.

The overall objective of this study was to develop a baseline of data on strawberry plant growth and development in an annual plasticulture system. We wanted to compile a detailed description including dry weight accumulation, allocation of resources, and physiological performance of the whole strawberry plant over a growing season. Our specific objectives were to: 1) document changes in dry matter accumulation and allocation; 2) chronicle phases of plant phenology; and 3) conduct extensive growth analysis of the three cultivars most commonly grown in North Carolina.

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Materials and Methods

Field experiments were conducted during the 1997–98 growing season. The experimental site was located at the Tidewater Research Station, Plymouth, N.C. (USDA Hardiness Zone 7b, latitude: –76.65, longitude: 35.87). The soil was a Megget fine sandy loam. 'Camarosa', 'Chandler', and 'Sweet Charlie' plants with leaves attached were obtained bare-root from an Ontario, Canada, nursery. A randomized complete block design was used with four replications. Plants were set in 0.76-m wide fumigated beds, with 1.52 m between the centers of each bed. Plants were set on 17 Oct. 1997. Plots were single beds 7.6 m, with double rows of plants staggered 0.3 m apart. Each plot contained 50 plants, with the center 30 plants being designated for fresh fruit harvest. The remaining 20 plants were allotted to whole plant harvest. Standard cultural programs were followed according to North Carolina recommended practices (Poling and Monks, 1994).

Whole plants were harvested every 4–6 weeks. At each whole-plant harvest date, four plants of each cultivar were harvested, including all belowground plant parts. Roots were washed over a fine mesh sieve to separate soil from roots. Plants were then divided by roots, crowns, leaves (including petioles), flowers, and fruit. At each whole plant harvest, the number of crowns per plant was recorded. Leaf area of fresh leaves was determined with a LI-COR LI-3200 leaf area meter (LI-COR, Lincoln, Neb.). All plant parts were bagged separately, and placed in a drying oven (Fisher Scientific, Pittsburgh) at 70 °C for 10 d.

Growth analysis of relative growth rate (RGR), specific leaf area (SLA), leaf area ratio (LAR), and harvest index (HI) were calculated from recorded total yield, leaf areas, and dry weights of sacrificed plant parts. These indices of plant growth were defined by the following equations:

$$RGR = dW/dt\ (1/W) \qquad [d^{-1}]$$

$$LAR = A/W \qquad [m^2 \cdot g^{-1}]$$

$$SLA = A/W_L \qquad [m^2 \cdot g^{-1}]$$

$$HI = (\text{Fruit dry weight} / \text{plant dry weight})\ (100)$$

where W is individual plant dry weight in grams, t is time, A is leaf area (m^2), and W_L is plant leaf biomass (dry weight) in grams (Chiarello et al., 1989).

Harvest index estimates were calculated two ways. The first calculation included the whole plant dry weight (roots, crowns, leaves, flowers, and fruit). The second calculation included only above ground dry weights (for simplicity defined here as leaves, flowers, and fruit). Whole plant dry weights were taken from the average of April, May, and June whole plant data. Fruit dry weight was calculated from the average total dry weight of fully ripe fruit from separate plots of the three cultivars.

Harvested fruit from each plot was separated into marketable and nonmarketable berries. Fruit was considered marketable if it was blemish free and weighed >10 g. Total yield per plant, marketable yield per plant and average fruit weight were calculated for all three cultivars. Fruit was harvested from plants in the center of the plots assigned to fruit harvest only.

To document the monthly allocation of biomass to each tissue, we divided the dry weight of each plant part by the total dry weight of the plant in that month (e.g., December root dry weight/December whole plant dry weight). To depict the phenology, or onset and duration of each individual plant part in the lifespan of the strawberry, we plotted the biomass allocated to each plant part as a percentage of its total weight over time (e.g., leaf dry weight December/ leaf dry weight October to June).

Significant differences in leaf area and dry weights among cultivars were detected through analysis of variance. Analysis of yield in response to factors of plant growth was done with a stepwise regression analysis.

The State Climate Office of North Carolina at North Carolina State Univ. provided climate data. Monthly temperatures were averaged over a 20-year period from 1979 through 1998. In addition, observed average maximum, minimum and mean temperatures were recorded for each month of the research.

Results

Differences in plant dry weights were detected among the three cultivars primarily in the spring (Table 1). 'Sweet Charlie' had a lower root dry weight in June, and leaf and flower dry weight in March and May. Large variations in individual plants may have been responsible for lack of significant variation in dry weight in several months, including fruit dry weight in April and May. 'Chandler' had greater leaf area than 'Sweet Charlie' in March and May.

Plant biomass allocation shifted dramatically throughout the period from October through June (Fig. 1). In October, at the time of planting, the majority of plant biomass (>65%) was leaves for all three cultivars. After planting, the allocation of biomass changed dramatically. In November, ≈5 weeks after planting, there was a shift in biomass to the root system. For each cultivar, over 65% of the biomass was concentrated in the root system. This general trend continued through December for all three cultivars. This was the period of time when there was an increase in number of crowns in 'Chandler' (Table 2). During January and February, all cultivars began to allocate a small amount of biomass to reproductive tissue (flowers), and root biomass diminished to between 45% to 60% for

Table 1. Dry weight (g) of roots, crown, leaves, flowers, and fruit and leaf area (LA) (cm^2) from October to June of the cultivars Chandler (Chan), Camarosa (Cam), and Sweet Charlie (SC).

Cultivar	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June
					Roots				
Chan	0.5	11.1	8.4	4.4	16	26.9	4.1	5.5	6.9
Cam	0.9	7.8	7.1	10.1	9.2	4.9	6.4	6.9	7
SC	0.4	3.6	2.6	5.5	6.6	16.5	3	3.7	1.9
LSD	NS	NS	NS	NS	NS	NS	NS	NS	4.1
					Crown				
Chan	0.3	1.1	1.3	1.3	2.9	5.8	4.7	7.8	11
Cam	0.3	0.7	0.7	1.5	1.9	2.6	6.3	8.3	13.8
SC	0.2	0.3	0.5	1.5	1.7	3.1	2.9	4.1	6.8
LSD	NS	NS	NS	NS	NS	2.4	NS	NS	NS
					Leaves				
Chan	1.6	2.8	3	4	6.1	17.4	33.7	32.9	41.8
Cam	1.5	1.8	1.7	4.1	5.7	17.4	34.6	31.7	40.2
SC	1.4	1.1	0.5	2.9	3.9	8	15.9	16.9	24.3
LSD	NS	NS	NS	NS	NS	6.6	NS	10.1	NS
					Flower				
Chan	---	---	---	0.6	1.2	5.9	6.9	8.1	3.8
Cam	---	---	---	0.8	1.5	3.2	4	5.5	2.9
SC	---	---	---	0.4	0.9	1.8	3.6	3.6	3.3
LSD	NA	NA	NA	NS	NS	3	NS	1.9	NS
					Fruit				
Chan	---	---	---	---	---	---	18.4	16.7	5.4
Cam	---	---	---	---	---	---	14	20.7	4.5
SC	---	---	---	---	---	---	5.4	8.9	1.6
LSD	NA	NA	NA	NA	NA	NA	NS	NS	NS
					LA				
Chan	179	291	280	367	578	2014	3868	3660	2450
Cam	172	194	155	365	538	849	3588	3349	3266
SC	182	135	50	263	359	822	1916	2042	3854
LSD	NS	NS	NS	NS	NS	803	NS	1336	NS

NA = Not applicable, NS = nonsignificant, where significant $P \leq 0.05$.

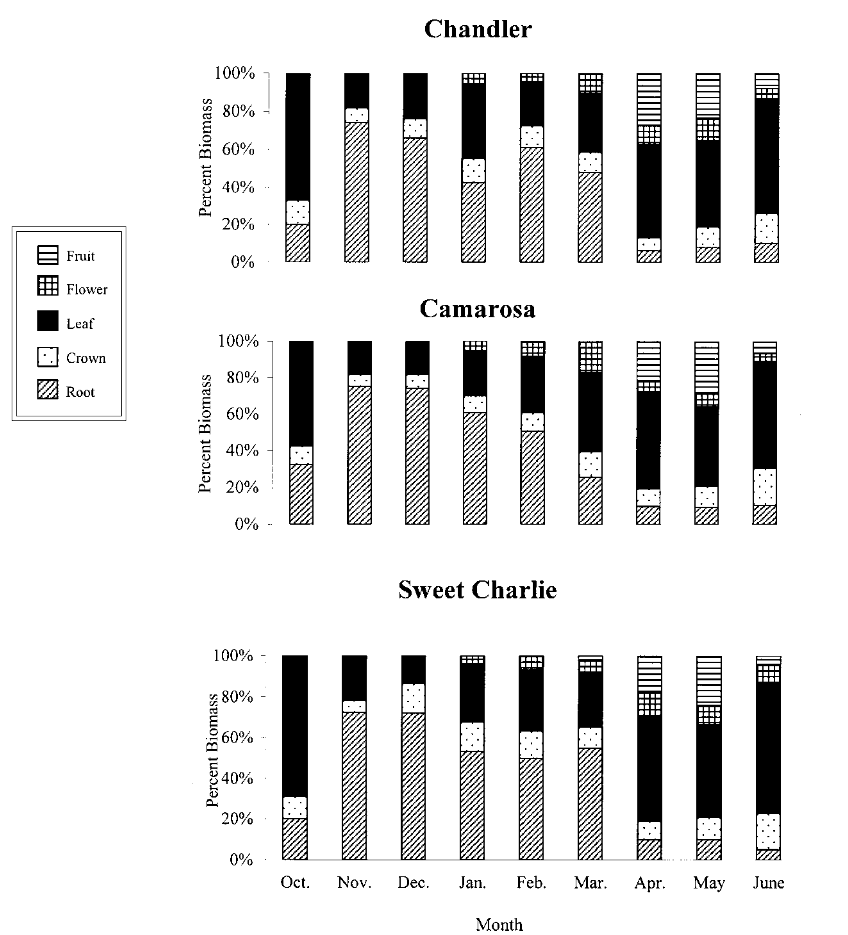

Fig. 1. Percent biomass of fruit, flower, leaf, crown, and root, at monthly intervals of three strawberry cultivars.

Table 2. Number of crowns per plant from October to June of three strawberry cultivars.

Date	Chandler	Camarosa	Sweet Charlie
Oct.	1	1	1
Nov.	2	1	1
Dec.	2	1	1
Jan.	2	2	2
Feb.	5	3	2
Mar.	7	6	3
Apr.	6	6	3
May	8	7	3
June	7	6	3

all cultivars. Leaf dry weight and area increased for all three cultivars from the previous months during this period of time (Table 1). In March, about 5% to 10% of strawberry plant biomass was allocated to flowers, and crown dry weight increased for all three cultivars (Table 1) even though the proportion of crown biomass to the whole plant did not change dramatically over previous months (Fig. 1).

The most dramatic shift in strawberry plant biomass allocation occurred in April when up to 35% of the biomass was in flowers and fruit (Fig. 1). There was also a surge in allocation to leaves at this time in all cultivars, and a concomitant decline in root biomass. This pattern of biomass allocation persisted in the month of May for all three cultivars, when the plants were in the peak fruit production. In June, allocation of biomass to flowers and fruits was lower than in the previous month. Leaf biomass comprised the largest proportion of whole plant dry weight in the last month of this study.

In general, similar patterns of plant phenology for all plant parts were observed for all three cultivars. Fig. 2 depicts this relation for 'Chandler'. Roots had two periods of growth, in the fall following transplanting (November and December) and just prior to fruiting in the spring (February and March). Crown growth was steady through the fall and generally increased from February through June. Although leaves comprised a major proportion of whole plant biomass at planting, they produced the largest increase in their total biomass in the months prior to and during fruiting (March through June). Flowers, although present in January and February, made their largest contribution in March through June. Fruit biomass contribution was greatest during April and May.

Relative growth rates were uniform from October through March for all cultivars (Table 3). In April, the RGR for 'Sweet Charlie' was significantly reduced during peak production compared with the other two cultivars. Leaf area ratio and SLA were similar for all cultivars throughout the growing season (Table 3). However, all cultivars displayed fluctuations in LAR and SLA as the season progressed. For example, LAR was very high at planting, decreased for the next few months, and then gradually increased as the plant prepared for flowering and fruiting. A similar trend was seen with SLA, levels decreased after planting and remained low through the winter and increased in the spring.

'Chandler' and 'Camarosa' had the highest and 'Sweet Charlie' had the lowest total yield and marketable yields (Table 4). 'Sweet Charlie' and 'Chandler' had comparable fruit weights. 'Sweet Charlie' had the highest HI with or without below ground plant parts (Table 5). Step-wise regression showed no correlation between leaf, crown, or root biomass and yield (data not shown).

Average maximum, minimum, and mean temperatures for the duration of this experiment were close to the 20 year averages (Table 6), although, in our study, maximum, minimum, and mean temperatures were slightly lower in November and December and higher in January and February.

Discussion

The three strawberry cultivars that we evaluated displayed very similar growth and development patterns throughout most of the growing season. In the fall, the strawberry plants allocated their resources to roots, crowns, and leaves. This was the establishment period when plants acclimated to their new environment and begun collection of photosynthates prior to the winter season. This establishment period was followed by two months of slow growth of these same plant parts in December and January. During February through March, there was a gradual shift of resources to vegetative and reproductive plant parts. In the spring months (April to May), new resources were either directly allocated to or remobilized from other plant parts to facilitate reproductive growth. This shift in relative biomass was in contrast to those found by May et al. (1994). They found that the relative proportion of biomass of each plant part remained constant throughout the growing season in the establishment year of a matted row system.

By depicting the phenological development of the various tissue, we elucidated the strawberry plants effort to allocate resources

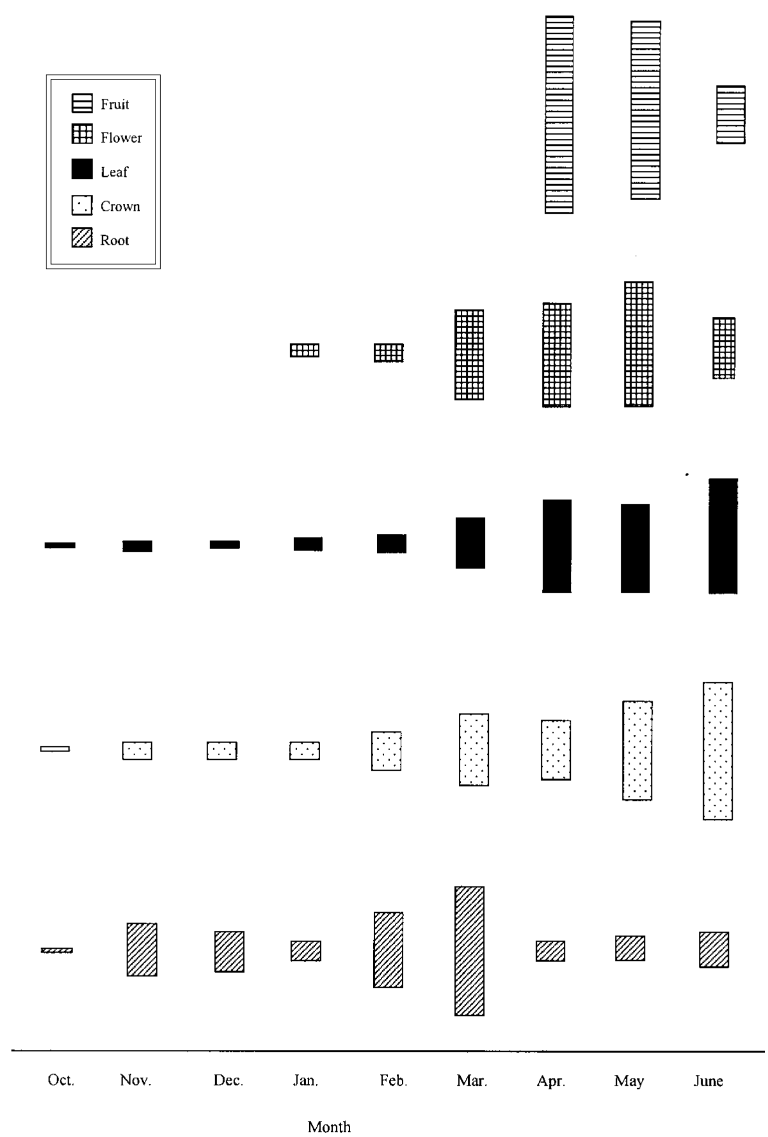

Fig. 2. Diagram showing the relationship between plant part biomass from October through June for the cultivar Chandler, the height of the bars indicates the percent of biomass allocation of that plant part in any one month as a portion of its total allocation over time; the higher the bar, the more biomass allocated during that month.

Table 3. Relative growth rate (RGR) (d^{-1}), leaf area ratio (LAR) ($m^2 \cdot g^{-1}$), and specific leaf area (SLA) ($m^2 \cdot g^{-1}$) from October to June of the cultivars Chandler (Chan), Camarosa (Cam) and Sweet Charlie (SC).

	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June
					RGR				
Chan	---	7.8	1.2	–0.7	21.3	81.9	125.4	289.1	200.2
Cam	---	4.7	0	4.6	2.5	0.6	100.7	421.7	392.7
SC	---	1	–0.3	3.6	3.7	26.5	–35	–10.9	–44
LSD	NA	NS	NS	NS	NS	NS	112.4	225.1	133.6
					LAR				
Chan	70.2	21.2	20.9	36.7	22.3	41.4	55.5	35.5	25.5
Cam	71.6	24.3	19.1	24.6	33	44.4	54.4	27.2	25
SC	84.1	25.6	14.1	28.5	32	37.5	45	34.5	29.1
LSD	NS	NS	NS	NS	NS	NS	NS	NS	NS
					SLA				
Chan	107.8	108	95.7	89.4	93.7	114.5	116.8	110.9	77
Cam	120.1	110	93.3	86.3	94.3	98.9	104.2	104.7	121
SC	122.3	110	98.4	92.6	92.4	102.9	105	121.2	105.3
LSD	NS	NS	NS	NS	NS	NS	NS	NS	NS

NA = Not applicable, NS = nonsignificant, where significant $P \leq 0.05$.

Table 4. Yield parameters of strawberry cultivars.

Cultivar	Total yield/plant (g)	Marketable yield/plant (g)	Avg berry wt (g)
Chandler	589.3	492.4	19.8
Camarosa	550.2	477.4	23.3
Sweet Charlie	321.8	286.3	20.3
LSD[z]	85.3	41.6	2.3

[z]Significant at $P \leq 0.05$

in the fall and especially in the spring (Fig. 2). Strawberry plants put forth an enormous output of reproductive effort in the spring in terms of fruit production as evidenced by HI's of 24 to 34. The root and crown systems were the only plant parts that displayed any appreciable growth prior to spring and these levels diminished just as the plants started to produce flowers and fruit. Previous research has shown that when strawberry plants were labeled with $^{14}CO_2$ in the fall, the plants utilized root carbohydrate reserves for early growth of flowers and leaves (Nishizawa et al. 1998). Furthermore, Biela et al. (1999) have shown that optimal vegetative and reproductive growth occurred when root zone temperatures were between 17 and 29 °C. These observations suggest that establishment of a good root system and initial crowns in the fall are very important determinants of plant yield. Optimizing growing conditions in the fall and late winter to minimize stress to the developing plants would help to ensure that the plant would achieve their maximum yield potential.

Strawberries grown in the plasticulture system in North Carolina are categorized as June-bearing, which initiate flower buds under short days (Darrow, 1966; Durner, 1988). In North Carolina, environmental conditions enable strawberries to have two periods of floral initiation. These periods are in the fall and spring. These two periods of optimal temperatures for floral initiation and differentiation may be at least in part the reason for the success of the plasticulture system in the SEUS. Although microscopic determination of floral initiation was not conducted, crown number and dry weight data indicated that the plants were allocating resources to the crowns in the fall and again in the spring.

The documentation of strawberry dry weights, allocation of resources, and charting of plant phenological phases has provided us with valuable information about strawberry crop ecology. However, whole plant growth analysis has enabled us to elucidate specific details of strawberry physiological adaptation. Although the growth analysis calculations used in this study were less sophisticated than other approaches (Chiarello et al., 1989), they do provide fundamental information about observed differences in growth. Relative growth rate is a fundamental measure of dry matter production, and can, therefore, be used to compare the performance of cultivars under the same growing conditions. In this study, the RGR of the three cultivars were statistically similar until the end of the season when 'Sweet Charlie' had a significantly lower RGR than the other two cultivars. Ironically, 'Sweet Charlie' also had the highest HI of the three cultivars. Calculation of HI takes into consideration the fruit to total biomass ratio, and is therefore a measure of reproductive efficiency. High HI values for 'Sweet Charlie' and lower RGR demonstrated that even though this cultivar yielded less fruit per plant, and produced less total and reproductive dry matter over time, it was more efficient in allocating its resources to fruit production.

Quantitative similarities in the two plant growth analysis variables SLA and LAR throughout the season indicated that leaves of the strawberry cultivars examined in this study have very similar inherent physiological potentials. Specific leaf area, the ratio of leaf area to leaf mass, is an important index of leaf structure. It is largely a function of leaf thickness and the amount of structural plant parts in leaves (Chiarello et al., 1989). Although there were no differences among cultivars over the growing season, the uniform rise or decline in leaf SLA among the three cultivars indicates that they all respond similarly as their external climate changes over the growing season. Differences in leaf anatomy in response to various environments have been observed in wild strawberry. Plants growing in low light or shade had developed thinner mesophyll areas than leaves grown under higher light conditions (Chabot and Chabot, 1977; Chabot et al., 1979). Lower SLA values in December and January indicate that the plants had thicker leaves. Thicker leaves are often associated with high light conditions (Chabot and Chabot, 1977; Chabot et al., 1979; Fitter and Hay, 1987). Butler (1999) identified four distinct flushes of leaves in this system: 1) leaves present at transplanting; leaves that emerged

Table 5. Harvest index for three strawberry cultivars.

Cultivar	Harvest index (dry wt fruit/above ground plant dry wt)	Harvest index (dry wt fruit/total plant dry wt)
Chandler	32	25
Camarosa	31	24
Sweet Charlie	34	27

Table 6. Average maximum (Max), minimum (Min), and mean temperatures (°C) for Plymouth, N.C., from 1978–97, 1997, and 1998. Shaded areas represent time period of this experiment.

	1979–98 Averages			1997 Averages			1998 Averages		
Month	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean
Jan.	11.6	–0.3	5.6	12.8	1.1	7	14.6	3.7	9.2
Feb.	13.5	0.6	7	16.2	3.8	10	14.6	4.7	9.7
Mar.	18.1	3.9	11	20.8	6.8	13.8	18.5	6	12.2
Apr.	23.1	8.2	15.7	21.6	7.6	14.6	23.6	9.7	16.7
May	27.1	13.2	20.2	26.6	12.2	19.3	27.1	15.4	21.3
June	30.6	17.7	24.2	29.1	17	23	31.8	19.9	25.9
July	32.4	20.6	26.5	32.2	20.9	26.6	32.2	21.3	26.8
Aug.	31.3	19.5	25.4	31.1	18	24.6	31.9	21.1	26.5
Sep.	28.6	16.5	22.6	28.5	16.5	22.5	30.4	17.9	24.2
Oct.	23.8	10.2	16.9	24.1	10.3	17.2	24.3	10.5	17.4
Nov.	18.9	5.9	12.4	16.4	5.2	10.8	18.5	6.1	12.3
Dec.	14	1.7	7.8	12.7	2.2	7.4	18.5	5	9.8

in 2) November/December; 3) February; and 4) March and April. The November/ December leaves in this study were the thickest leaves. This flush of leaves had developed after transplanting when the plants were still relatively small, whole plant leaf area was low, and therefore competition for light was low.

Leaf area ratio is the ratio of leaf area to plant dry biomass, or the proportion of plant devoted to leaf material. It was highest at planting, and then dropped dramatically as the plant established itself in the fall and early winter. As the plant prepared for flowering and fruiting, LAR increased uniformly in all cultivars and then dropped off as fruit production peaked.

No significant correlations were observed between leaf area or leaf, root, or crown biomass and overall plant yield. Most likely cumulative effects of factors influenced plant productivity. In matted row systems, yield component analysis of strawberry genotypes uncovered a correlation between yield and vegetative variables (Hancock et al. 1984); however, in systems with less plant-to-plant competition (such as in an annual system), reproductive variables may have greater impact.

'Camarosa' and 'Chandler' had very similar patterns of growth and development for most of the season. 'Sweet Charlie' was in general similar to the other cultivars, however, when yield and vegetative growth differences appeared, 'Sweet Charlie' digressed from the other two cultivars. The different performance of the cultivars may be attributed to cultivar adaptation and genetic relatedness, although cultivar numbers were too low to make broad generalizations. The cultivars belong to two subgroups, California ('Camarosa' and 'Chandler'), and Florida ('Sweet Charlie') (Sjulin and Dale 1987). The plasticulture system in North Carolina was initiated with 'Chandler', so we postulate that 'Camarosa' would be easily substituted into this system, whereas 'Sweet Charlie' may not be as well adapted to this area and needs different management strategies, such as an earlier planting date.

In order to reach maximum strawberry productivity in the SEUS, it will be necessary to optimize environmental and cultural manipulations that aid in plant establishment and development, thus increasing the resources available for floral initiation in the fall and fruit development in the spring. This study provided data that described strawberry growth and development in a plasticulture system. This information will be used as a phenological baseline for developing more efficient plant management strategies.

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