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# Growth Analysis of Field-grown Strawberry Genotypes Differing in Yield: I. The Matted Row System

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**Abstract.** Seven field-grown strawberry genotypes (*Fragaria* × *ananassa* Duch.) were grown in matted rows and harvested weekly from early spring until the end of harvest. An increase in plant dry weight through the season was due mainly to inflorescence and leaf development. Genotypes differed in the progression of the natural log of plant dry weight and leaf area over time, relative growth rate, absolute growth rate, leaf area ratio, and unit leaf rate. Genotypes differed in growth variables through the season, but only crown dry weight during the fruiting period was correlated with yield among genotypes. Total plant dry weight was not correlated with yield, indicating the importance of the percent dry matter partitioned to the inflorescence.

The continued interest in producing higher-yielding cultivars of many crops has stimulated interest in physiological factors contributing to final yield, and in the possibilities of selecting for these factors in breeding programs. Researchers have attempted to correlate yield of soybean (1), cotton (12), and tall fescue (13) genotypes with various growth characteristics. Growth pattern and yield of strawberry are dependent on the amount of dry matter formed and its distribution to the various plant organs. Various plant characteristics in strawberry have been found to be associated with yield (11). Olsen et al. (9) described the seasonal growth pattern of a strawberry genotype. However, it is not known whether strawberry genotypes differ in growth patterns. Also, differences among genotypes in growth during fruiting may be related to yield.

The purpose of this study was to determine a) whether strawberry genotypes differ in growth patterns when grown in matted rows and b) whether yield among genotypes is correlated with growth characteristics during fruiting.

## Materials and Methods

Seven genotypes were selected because of observed differences in growth pattern and yield. Plants were set 4 May 1984 on a Typic Hapludalf (Fox sandy loam) at the Cambridge Research Station, Univ. of Guelph at a distance of 0.45 m apart within the row and 1.2 m between rows in a completely randomized design. Water was supplied by trickle irrigation and plants were grown according to standard commercial practices. Plants were deblossomed in 1984 and the runners were trained to form a matted row 0.45 m wide. From 9 to 30 May 1985, four plants per genotype were dug each week. Nine plants per genotype per week were dug from 5 to 26 June 1985. These were randomly selected from within the matted row. Care was taken not to damage the remaining plants in the matted row.

Roots were not included in the analysis. All plants were separated into crowns, inflorescences (including fruit, if present), petioles, and leaf laminae. Leaf area was determined using a LI-3000 Area Meter (Lambda Instruments, Lincoln, Neb.) fitted with a LI-3050A transparent belt accessory. All plant parts were oven-dried to a constant weight at 70°C. Specific leaf weight (SLW) was calculated for each plant by dividing total leaf dry weight by total leaf area.

Yield data for each genotype were obtained from 2-m sections of matted row arranged in a randomized complete bloc design with three blocks. Fruit were collected as they ripened and total yield per plot was calculated.

**Growth analysis.** Logarithmic transformations (natural log) of primary data (plant dry weight, leaf area, and inflorescence dry weight) were done to make the variance of the data more nearly homogeneous over time. The transformed data were fitted to the empirical functions:  $\ln W = f_w(T)$ ; and  $\ln L = f_L(T)$ ; where  $W$  is plant dry weight,  $L$  is leaf area per plant, and  $T$  is time (5). The regression equations that best fit the data were determined by analysis of variance (ANOVA) and chosen to balance statistical exactitude and biological realism. Fitted functions were used to calculate growth parameters as follows (5):

$$\text{Relative growth rate (RGR)} = \frac{1}{W} \cdot \frac{dW}{dT} = f_w'(T);$$

$$\text{Absolute growth rate (AGR)} = \frac{dW}{dT} = f_w'(T) \cdot \exp [f_w(T)];$$

$$\text{Leaf area ratio (LAR)} = L/W = \exp [f_L(T) - f_w(T)];$$

$$\text{Unit leaf rate (ULR)} = \frac{1}{L} \cdot \frac{dW}{dT} \\ = f_w'(T) \cdot \exp [f_w(T) - f_L(T)];$$

$$\text{RGR} = \text{ULR} \times \text{LAR}.$$

ULR is equivalent to the term net assimilation rate (NAR) used by some authors (5).

**Analyses of means.** To make the data more homogenous over time, the season was separated into two growing periods, fruit-filling (flowering to first pick) and fruiting (first pick to end of harvest). Mean values for all measured variables were calculated for both periods. Data were analyzed by ANOVA and means compared with Duncan's multiple range test. Correlation analyses were performed between mean values for all variables dur-

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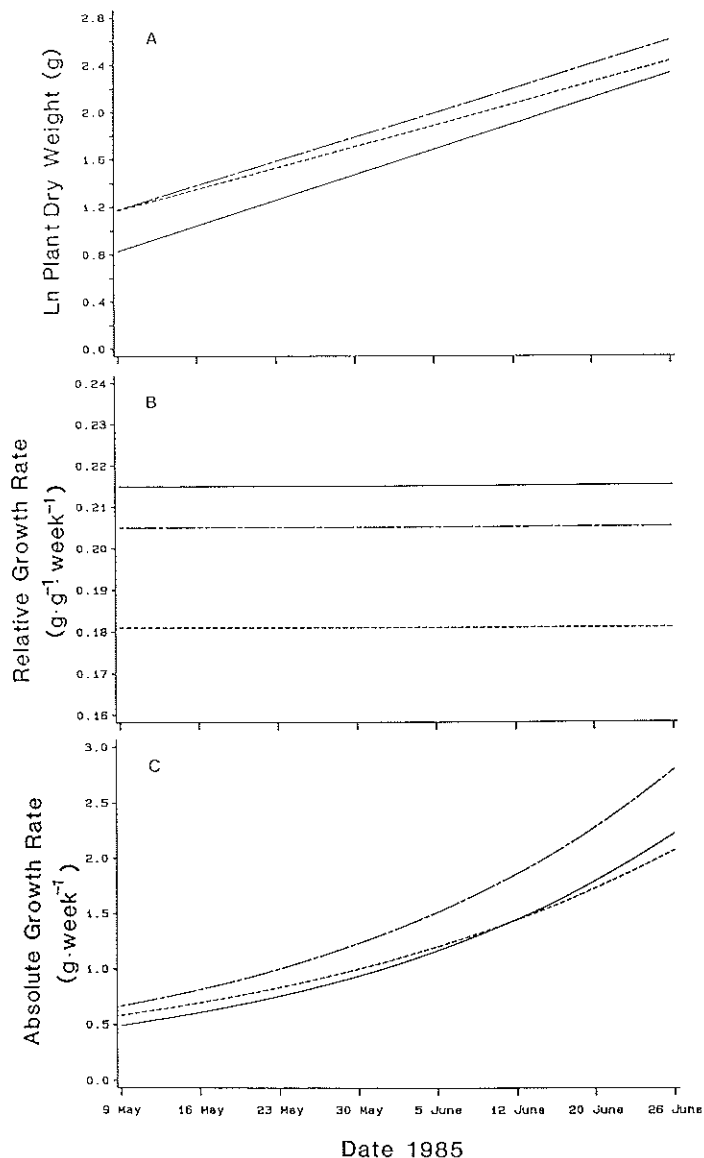


Fig. 1 Growth parameters of 62E55, 83T6, and 132E57. (A) The natural logarithm of plant dry weight. (B) Relative growth rate. (C) Absolute growth rate. 62E55 (—); 83T6 (---); 132E57 (····).

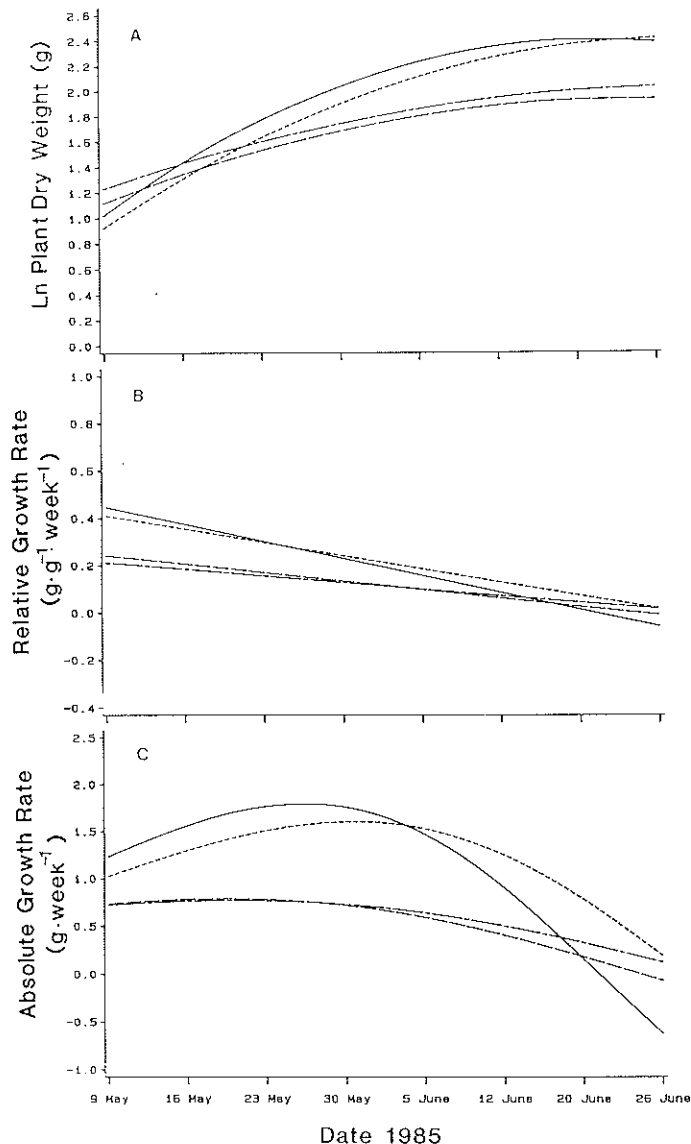


Fig. 2 Growth parameters of 'Redcoat', 'Veestar', 94L12, and 71M59. (A) The natural logarithm of plant dry weight (B) Relative growth rate. (C) Absolute growth rate. 'Redcoat' (---); 'Veestar' (····); 94L12 (—); 71M59 (— · —).

ing the fruit-filling and fruiting periods and yield among genotypes.

### Results

Total plant dry weight increased dramatically from 9 May to 26 June 1985. The increase in dry weight was mainly due to inflorescence and leaf development during the season. Crown dry weight remained relatively constant (data not shown).

A separate regression equation of the natural log (ln) of plant dry weight on time was determined for each genotype. The genotypes separated into two groups. A linear equation described the change in the ln plant dry weight with time for 62E55, 83T6, and 132E57 (Fig. 1A). Genotype 132E57 had the lowest ln plant dry weight throughout the season (Fig. 1A). For genotypes 94L12, 71M59, 'Redcoat', and 'Veestar' a quadratic equation best fit the data (Fig. 2A). 'Veestar' and 71M59

had lower plant dry weights than 'Redcoat' and 94L12 during fruit-filling and fruiting (Fig. 2A).

Genotypes 132E57, 62E55, and 83T6 had a constant relative growth rate (RGR) throughout the season. 132E57 had the greatest RGR at  $0.215 \text{ g} \cdot \text{g}^{-1}$  per week and 83T6 had the lowest RGR of  $0.181 \text{ g} \cdot \text{g}^{-1}$  per week (Fig. 1B). The absolute growth rate (AGR) of these three genotypes increased exponentially over the season (Fig. 1C).

In 'Redcoat', 94L12, 71M59, and 'Veestar', the RGR showed linear declines from 9 May to 26 June (Fig. 2B). At the beginning of the season, 'Redcoat' and 94L12 had double the RGR of 'Veestar' and 71M59. However, the decline in RGR was more rapid in 'Redcoat' and 94L12. Thus, all four genotypes had near-zero relative growth rates at the end of harvest (Fig. 2B). All four genotypes showed curvilinear declines in AGR during the season (Fig. 2C). The AGR of 94L12 and 'Redcoat' was initially high near  $1.1 \text{ g/week}$ , then peaked on 30 May and

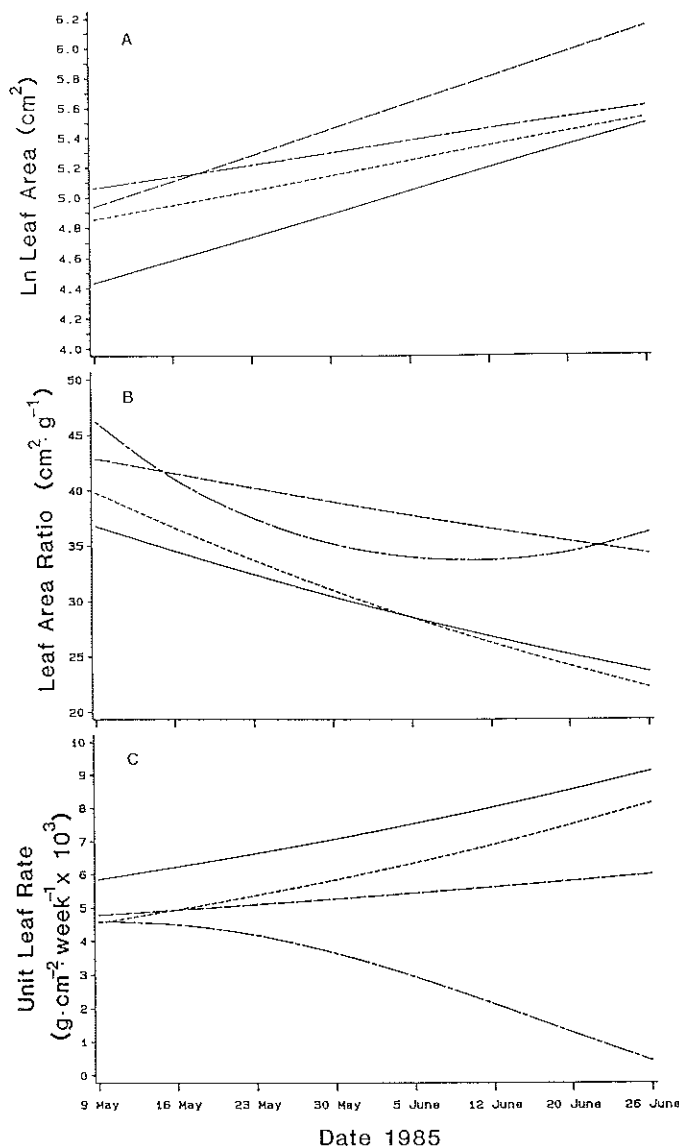


Fig. 3. Growth parameters of 62E55, 83T6, 132E57, and 71M59. (A) The natural logarithm of leaf area. (B) Leaf area ratio. (C) Unit leaf rate. 62E55 (---); 71M59 (—); 83T6 (·····); 132E57 (-·-·-).

rapidly declined to 0.2 g/week in 'Redcoat' and to negative values in 94L12 at the end of harvest. The AGR of both 71M59 and 'Veestar' was relatively low and decreased only slightly in comparison (Fig. 2C).

The genotypes also separated into two groups with regard to the development of leaf area with time. The ln leaf area of 62E55, 71M59, 83T6, and 132E57 increased linearly with time (Fig. 3A). Leaf area development was most rapid in 62E55 (Fig. 3A). During the fruit-filling period, 62E55, 71M59, and 83T6 had a greater leaf area than 132E57 (Table 1). However, during fruiting, 62E55 had a larger leaf area than the other three genotypes. This was in part due to a greater number of leaves, but mainly to a larger average leaf area (Table 1). The natural log of leaf area as a function of time showed a quadratic phase of growth in 'Redcoat', 94L12, and 'Veestar' (Fig. 4A). Leaf area in 'Redcoat' and 94L12 increased rapidly and reached high values during fruit-filling compared to 'Veestar'. In 94L12, there was drop in leaf area after 12 June (Fig. 4A; Table 1).

The ratio of leaf area to plant weight, LAR, varied among genotypes (Figs. 3B and 4B). The LAR of 'Veestar', 132E57, 83T6, and 62E55 declined through the season. In 62E55, LAR declined from an initial value of 43 cm<sup>2</sup>·g<sup>-1</sup> to 34 cm<sup>2</sup>·g<sup>-1</sup> after 7 weeks, a value higher than the LAR of all other genotypes except 71M59 (Figs. 3B and 4B).

The ULR of 'Redcoat', 94L12, 71M59, and 'Veestar' decreased through the season to values near zero or negative after 7 weeks (Fig. 4C). The ULR of 132E57 and 83T6 increased to  $9 \times 10^{-3}$  and  $8 \times 10^{-3}$  g·cm<sup>-2</sup> per week, respectively, at the end of harvest. In 62E55 the ULR remained relatively constant throughout the sampling period (Fig. 3C).

The specific leaf weight (SLW) of 71M59 tended to be greater than that of the other genotypes during both the fruit-filling and fruiting periods. Genotype 132E57 also had a high SLW during the fruiting period (Table 1).

The ln inflorescence dry weight increased linearly with time for all genotypes. During the fruit-filling period, 71M59 and 132E57 had a smaller inflorescence or truss dry weight than the other genotypes. This was mainly due to fewer trusses per plant rather than a smaller average truss weight (Table 2). 'Veestar' and 71M59 had the smallest truss dry weight during the fruiting period. The truss weight of 132E57 increased 242%, a substantial increase relative to the next greatest increase of 134% in 83T6 and the smallest increase of 18% in 'Veestar' (Table 1).

**Partitioning of dry matter.** Genotypes differed in the amount of dry matter partitioned to the various plant organs (Table 2). During the fruit-filling period, 71M59 and 'Veestar' partitioned the greatest amount of the dry matter produced to the crown. In 'Redcoat', crown dry weight accounted for only 9% of the total plant dry weight. 71M59 partitioned the smallest percentage of dry matter to the inflorescence and the greatest to the leaves, compared to the other genotypes (Table 2). During fruiting, the percent dry matter partitioned to the crown decreased in all genotypes, except 62E55 and 71M59, compared to the fruit-filling period. The percentage partitioned to the inflorescence increased in all genotypes except 62E55. Less dry matter was partitioned to the leaves during fruiting than during fruit-filling in all genotypes except 62E55 and 'Redcoat' (Table 2). The percentage of truss dry weight ranged from 39% to 63% among genotypes (Table 2).

**Correlation analyses.** Yield per section of matted row among genotypes was correlated only with average crown dry weight during the fruiting period (Table 3). The number of inflorescences during the fruit-filling period was significantly correlated with the number of crowns, crown dry weight, and leaf area per plant. Yield per section of matted row was not correlated with growth variables measured during fruit-filling.

## Discussion

There were differences among genotypes in the progression of ln plant dry weight with time. Plant dry weight appeared to have reached maximum values at the end of fruit harvest in 'Redcoat', 94L12, 'Veestar', and 71M59 (Fig. 2A). This was evidenced by a decline in RGR throughout the season (Fig. 2B). In 62E55, 83T6, and 132E57, plant dry weight had not yet reached maximum values at the end of the fruiting season (Fig. 1B). A constant RGR during the first fruiting season was also observed by Olsen et al. (9). The constant RGR of 62E55, 132E57, and 83T6 may indicate that these genotypes had less interplant competition for water, nutrients, and/or light within the matted row. Within these three genotypes, 132E57 had the greatest RGR and 83T6 the lowest. Genotypes differed in RGR

Table 1. Mean values per plant of growth variables during the fruit-filling (30 May–12 June 1985) and fruiting (12–26 June 1985) periods for seven strawberry genotypes.

Genotype	Crown no.	Crown dry wt (g)	Leaf no.	Leaf dry wt (g)	Leaf area (cm <sup>2</sup> )	SLW (mg·cm <sup>-2</sup> )	Truss no.	Truss dry wt (g)
<i>Fruit-filling period (N = 14)<sup>a</sup></i>								
94L12	1.6 a <sup>z</sup>	0.99 a	8.5 a	3.3 a	377 a	8.6 ab	3.7 a	2.61 a
62E55	1.5 a	0.62 bc	5.9 b	2.0 b	243 b	8.3 ab	2.8 b	2.47 a
83T6	1.1 b	0.57 bc	4.8 bc	1.9 bc	235 b	7.7 b	2.4 bc	2.48 a
71M59	1.0 b	0.65 bc	3.7 cd	2.1 b	223 b	9.5 a	1.6 d	1.40 b
Redcoat	1.5 a	0.62 bc	5.9 b	2.2 b	298 b	7.5 b	2.6 b	2.95 a
Veestar	1.6 a	0.73 b	5.9 b	1.7 bc	216 bc	8.0 b	2.8 b	2.45 a
132E57	1.1 b	0.45 c	3.1 d	1.2 c	143 c	8.3 ab	2.0 cd	1.32 b
<i>Fruiting period (N = 27)<sup>a</sup></i>								
94L12	1.5 b <sup>z</sup>	0.97 b	6.3 a	2.4 bc	338 b	6.9 c	2.6 ab	5.57 ab
62E55	1.9 a	1.26 a	6.6 a	3.4 a	450 a	7.6 abc	2.1 cd	4.27 b
83T6	1.3 bc	0.69 cd	5.3 b	1.7 de	232 c	7.3 bc	2.7 ab	5.81 a
71M59	1.1 c	0.80 c	4.4 b	2.2 cd	259 c	8.4 a	1.8 d	2.85 c
Redcoat	1.5 b	0.78 c	7.1 a	2.9 ab	389 ab	7.3 bc	2.8 a	4.52 ab
Veestar	1.2 c	0.58 d	5.0 b	1.6 e	215 c	7.1 c	2.4 bc	2.89 c
132E57	1.3 bc	0.62 cd	5.1 b	1.8 cde	224 c	8.0 ab	2.6 ab	4.52 ab

<sup>a</sup>Means followed by the same letter within columns and period are not significantly different ( $P \leq 0.05$ ), Duncan's multiple range test.

Table 2. Percent of total plant dry weight partitioned to the various plant parts during the fruit-filling (30 May–12 June 1985) and fruiting (12–26 June) period for seven strawberry genotypes.

Genotype	Dry wt (%)			
	Crown	Petiole	Leaf <sup>a</sup>	Inflorescence
<i>Fruit-filling period (N = 14)<sup>a</sup></i>				
94L12	11 abc	19 a	38 ab	32 bc
62E55	11 abc	13 d	34 bc	42 a
83T6	10 bc	14 cd	32 c	45 a
71M59	13 a	17 abc	42 a	28 c
Redcoat	9 c	16 abcd	32 c	43 a
Veestar	13 a	14 bcd	31 c	42 a
132E57	12 ab	18 ab	32 c	36 ab
<i>Fruiting period (N = 27)<sup>a</sup></i>				
94L12	10 bc	12 cd	24 bc	54 b
62E55	12 a	17 a	32 a	39 d
83T6	8 c	9 d	20 c	63 a
71M59	12 a	14 bc	32 a	42 cd
Redcoat	9 c	15 ab	30 a	46 cd
Veestar	10 ab	12 c	28 ab	49 bc
132E57	9 c	12 cd	23 c	57 ab

<sup>a</sup>Leaf dry weight included leaf laminae only.

<sup>a</sup>Means followed by the same letter within columns and period are not significantly different ( $P \leq 0.05$ ), Duncan's multiple range test.

in soybean (1) and poplar (3). The AGR of 'Redcoat' and 94L12 peaked during the fruit-filling period and then decreased during fruit harvest (Fig. 2C). However, the AGR of 62E55, 132E57, and 83T6 increased throughout the season (Fig. 1C). Olsen et al. (9) also found that plant AGR increased throughout the season.

Leaf area development was most rapid in 62E55, 'Redcoat', and 94L12 (Figs. 3A and 4A). These genotypes had the greatest leaf area per plant during the fruit-filling period (Table 1). However, in 94L12 the leaf area per plant decreased during fruiting (Fig. 4A, Table 1). This was probably due to both a temporary cessation of leaf emergence and senescence of older leaves. In

'Redcoat', leaf area development slowed at the end of the fruiting season (Fig. 4A). This represented the effects of fruiting on leaf development, as has been shown in other studies (6, 7). Leaf area expansion did not decrease in 62E55, which had the greatest leaf area per plant during the fruiting period (Fig. 3A, Table 1). Thus, 62E55 may have had higher whole plant photosynthesis during fruiting than other genotypes.

LAR (4) varied among genotypes (Figs. 3B and 4B). The decrease in LAR in 62E55, 132E57, 83T6, and 'Veestar' could be attributed to the increase in the partitioning of dry matter to the inflorescence and a smaller-proportion partitioning of dry matter to the leaves (Table 2). It appeared that the larger the difference in percent leaf dry weight between the fruit-filling and fruiting periods, the greater the drop in LAR (Table 2; Figs. 3B and 4B). In 71M59, the slight increase in LAR at the end of the fruiting season may have been an indirect result of a small truss dry weight (Table 1). Differences in specific leaf weight (SLW) among genotypes were found in soybean (1, 2) and pea (8). In this study, genotypes differed in SLW during the fruit-filling and fruiting periods (Table 1). However, 71M59 tended to have the greatest SLW and, thus, a low SLW, or thinner leaves, could not have accounted for an increase in LAR in this genotype.

Genotypes have been found to differ in LAR (1, 3). Buttery and Buzzell (1) suggested that, in plants with a low LAR, the leaves have a larger sink for their photosynthetic products than do leaves of plants with a high LAR. Thus, a low LAR may favor high photosynthesis.

ULR depicts changes in dry weight that are the net result of photosynthesis, respiration, and mineral uptake (4). Differences in ULR among genotypes were found in soybean (1), poplar (3), and in this study. The decrease in ULR of 'Redcoat', 'Veestar', 94L12, and 71M59 during the fruiting season may have been due to the shading of lower leaves within the canopy, leading to a decrease in whole plant photosynthesis and thus decreased rates of dry matter production. In 132E57, 83T6, and 62E55, the ULR increased during the season (Figs. 3C and 4C).

In soybean, ULR was highly correlated with SLW and in-

Table 3. Correlation coefficients between mean values of various growth variables during the fruit-filling (30 May–12 June 1985) and fruiting (12–26 June 1985) periods, and yield per 2-m section of matted row (kg/plot) among genotypes. Correlation coefficients for the fruit-filling period are in bold.

	Crowns		Leaf area	Plant dry wt.	Trusses		
	Number	Dry wt.			Number	Dry wt.	Yield
Number of crowns		<b>0.63</b>	<b>0.60</b>	<b>0.69</b>	<b>0.85*</b>	<b>0.76*</b>	<b>0.32</b>
Crown dry weight	0.85*		<b>0.84*</b>	<b>0.83*</b>	<b>0.78*</b>	<b>0.44</b>	<b>0.65</b>
Leaf area	0.90**	0.87*		<b>0.98***</b>	<b>0.77*</b>	<b>0.69</b>	<b>0.66</b>
Plant dry weight	0.85*	0.77*	0.82*		<b>0.80*</b>	<b>0.80*</b>	<b>0.62</b>
Number of trusses	0.07	-0.36	-0.06	0.22		<b>0.73</b>	<b>0.60</b>
Truss dry weight	0.37	0.18	0.19	0.68	0.68		<b>0.26</b>
Yield	0.57	0.82*	0.56	0.62	-0.25	0.39	

\*\*\*, \*\* Significant at  $P \leq 0.05$ ,  $P \leq 0.01$ , or  $P \leq 0.001$ , respectively. N = 7.

Table 4. Fruit yield data for seven strawberry genotypes, 1985. Values are mean  $\pm$  SE.

Genotype	Yield per plot (kg)
94L12	7.2 $\pm$ 0.3
62E55	6.4 $\pm$ 0.9
83T6	4.4 $\pm$ 0.3
71M59	4.5 $\pm$ 0.2
Redcoat	3.2 $\pm$ 0.0
Veestar	3.1 $\pm$ 0.7
132E57	2.9 $\pm$ 0.1

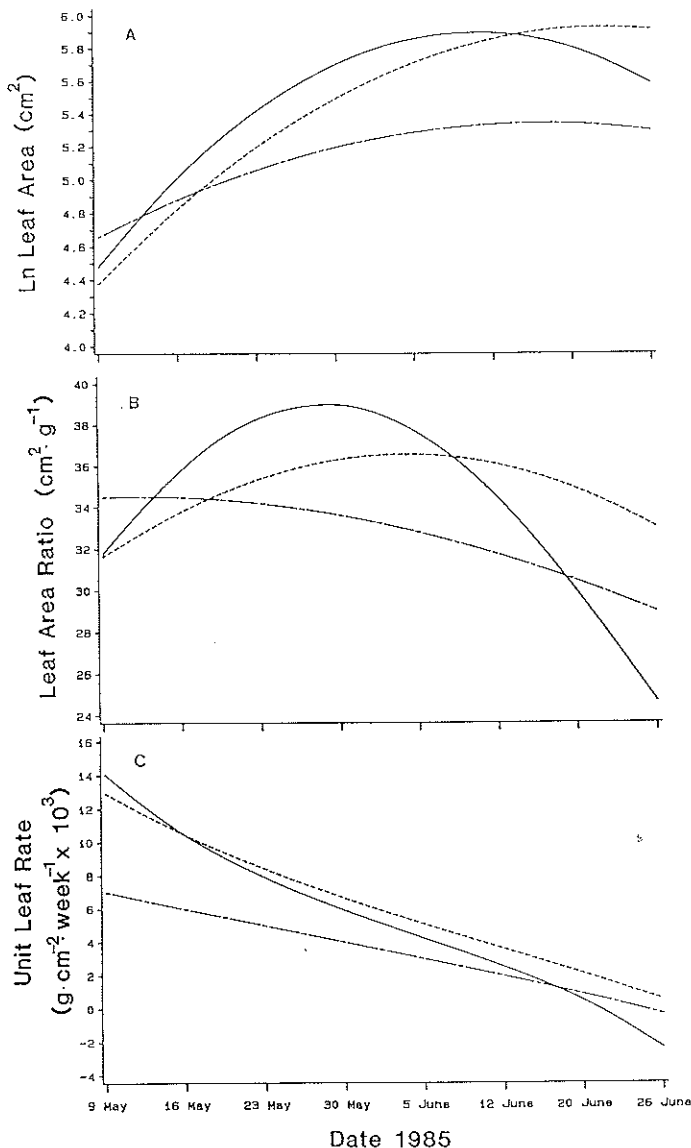


Fig. 4. Growth parameters of 'Redcoat', 'Veestar', and 94L12. (A) The natural logarithm of leaf area. (B) Leaf area ratio. (C) Unit leaf rate. 'Redcoat' (-----); 'Veestar' (— — —); 94L12 (———).

versely correlated with LAR (1). Thus, the authors suggested that SLW may be a useful characteristic for indirect selection of soybean yield. In this study, there was no direct relationship between SLW (Table 1) and LAR (Figs. 3B and 4B) or ULR (Figs. 3C and 4C).

The amount of dry matter partitioned to the inflorescence was not directly related to yield per plant (Tables 2 and 4). Despite a low yield, 132E57 partitioned a large percentage of total plant dry weight to the inflorescence (Table 2). In this genotype the inflorescence structure was large despite a small number of small fruit. 83T6 had a small supporting structure relative to 132E57 and had a greater yield (Table 4). Truss dry weight also increased linearly in the genotype OR-US4681 (9).

Yield per section of matted row among genotypes was correlated only with crown dry weight per plant during the fruiting period (Table 3). Yield per plant among strawberry genotypes was found correlated with crown dry weight, leaf area, and leaf dry weight during flower bud differentiation the fall prior to fruiting (10). Thus, the average crown dry weight per plant during fruiting was probably only correlated with yield as differences among genotypes were already established in the fall prior to or during flower bud differentiation. Total plant dry weight was not correlated with yield, indicating the importance of differences in the percent of dry matter partitioned to the harvested portion. The number of inflorescences was not correlated with yield among genotypes. Thus, genotypes such as 94L12, with relatively few trusses per plant, compensated for this by a greater number of berries per truss, a large average berry weight, a greater partitioning of assimilates to the inflorescence, or a greater photosynthesis per unit leaf area. Compensation between yield components of strawberry has been found before (9, 11). Strik and Proctor (11) found that yield within

strawberry genotypes was most associated with the number of berries per plant. Vegetative variables such as crown dry weight, leaf area, and number of trusses affected the number of berries per plant and, thus, indirectly yield (11).

In summary, when plants were grown in matted rows, there were differences among genotypes in the progression of ln plant dry weight and ln leaf area over time, RGR, AGR, LAR, and ULR. Only crown dry weight during the fruiting period was correlated with yield. The correlation coefficients of yield with crown dry weight, leaf area, plant dry weight, and the number of inflorescences during the fruit-filling period were high, indicating that if more genotypes had been studied these may have been significant. Yield among genotypes was not directly related to any single growth parameter (ULR, LAR, RGR, and AGR). In some genotypes, a high percent dry matter partitioned to the inflorescence compensated for a low RGR.

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