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Relationship Between Achene Number, Achene Density, and Berry Fresh Weight in Strawberry

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Abstract. **Field-grown genotypes (*Fragaria* ×*ananassa* Duchesne) were studied in two seasons to determine the relationship of primary berry fresh weight to the total number of achenes per berry and the number of achenes/cm² of receptacle tissue. Within genotypes grown in matted rows (1985), berry fresh weight was correlated with the total number of achenes per berry. In the hill system (1986), berry weight was correlated with the number of achenes and the number of achenes/cm². Genotypic variation in berry weight in the matted row was related to the total number of achenes. In the hill system, there were no differences in the total number of achenes per berry between high- and low-yielding genotypes, but the highest-yielding genotype had fewer achenes/cm².**

Normal development of the strawberry receptacle is dependent on the release of hormone(s) from the fertilized ovules or achenes (5, 6). Thus, the potential weight of a berry is a function of the total number of achenes on the surface and the amount of receptacle developed per achene. The potential total number of achenes per berry is determined during flower bud initiation and is dependent on berry position on the inflorescence (3) and genotype and environment (11). The number of achenes per cm² (NA/C) of surface on ripe berries is a measure of berry development (1) and is dependent on the environment (10) and genotype (12). Thus, measurements of NA/C have been used to calculate percent shortfall in yield based on the smallest values of NA/C for a given genotype under optimal conditions (7, 10, 11).

The objectives of this study were to determine a) the relationship between primary berry weight and the total number of achenes per berry in genotypes varying in yield, b) whether the maximum berry expansion possible differs among genotypes, and c) whether differences in inflorescence structure could account for some of the variability in berry weight among genotypes.

Materials and Methods

1985. Two commercial cultivars, Redcoat and Veeglow, and two selections, 62E55 and 71M59, were chosen for their differences in yield. Planting occurred 4 May 1984 on a typic Hapludalf (Fox sandy loam) at the Cambridge Research Station, Univ. of Guelph. Plants were set 45 cm apart within the row with 1.2 m between rows in a randomized complete block design with three blocks. Water was supplied by trickle irrigation, and plants were grown according to standard commercial practices. Plants were deblossomed the first year and runners trained to form a matted row 45 cm wide. In 1985, prior to inflorescence emergence, 10 random plants per genotype were tagged for each replicate (a 2-m section of matted row). Berries were harvested when fully ripe, and uniformly developed primary berries were subsampled for achene counts. Only primary fruit were sampled to decrease variability as berry position influences both achene number and spacing (3).

Achene counts. The fresh weight was determined for each berry. The NA/C was obtained by averaging the number of achenes visible in a circular 1-cm² aperture held against the berry at two random locations (2). The berries then were frozen individually in labeled paper bags for subsequent counts of total number of achenes. The total number of achenes per berry was counted by slicing the berry into pieces and summing the number of achenes present on each part.

Peduncle/pedicel dimensions. Measurements of peduncle and pedicel dimensions were obtained for the four genotypes mentioned. The dimensions of all the inflorescences on each plant were averaged. Peduncle length was measured from the base of the inflorescence to the first branch using a ruler. The length of the pedicel was determined from the point at which it branched from the peduncle to the point of attachment of the primary berry. The midpoint diameter of each was measured with calipers (accurate to 0.01 mm).

1986. The genotypes 'Redcoat', 62E55, 83T6, and 132E57 were selected as they have been observed to differ in yield. Planting occurred 1 May 1985. Plants were set 30 cm apart within the row with 1.2 m between rows in a randomized complete block design with five blocks. Irrigation and fertilization occurred as in 1985. Plants were deblossomed the first year and maintained in the hill system by frequently removing runners. Total yield was obtained for each of nine plants per genotype per block. Five ripe primary berries were subsampled from each plant and the total number of achenes and NA/C was determined as mentioned previously.

Statistical analyses. Data were subjected to analysis of variance, and means were compared with Duncan's multiple range test. Correlation analyses were performed between berry fresh weight, the total number of achenes per berry, and the number of achenes/cm² (NA/C). Berry fresh weight was regressed on the total number of achenes per berry and NA/C for each genotype. In 1986, the data for each genotype were grouped according to the NA/C and separate regressions of berry weight on the number of achenes per berry were performed for each group (2).

Results and Discussion

In genotypes grown in matted rows (1985), a separate regression equation describing the relationship between berry fresh

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Table 1. Regression equations of primary berry fresh weight (B, in g) on the total number of achenes per berry (T) and the number of achenes/cm² of receptacle tissue (A) for four strawberry genotypes during the fruiting seasons of 1985 and 1986.

Genotype	Regression equation[z]	SE[y] a	SE[y] T	SE[y] A	SE[y] TA	R^2 (%)
	Matted row–1985					
62E55	B = 5.471 + 0.054T − 0.475A	1.344	0.002	0.064	---	89.0
Redcoat	B = 4.455 + 0.0541 − 0.038A	0.996	0.003	0.049	---	86.0
71M59	B = 3.767 + 0.057T − 0.384A	1.212	0.002	0.059	---	90.4
Veeglow	B = 1.106 + 0.051T − 0.203A	0.776	0.002	0.038	---	93.8
	Hill system–1986					
62E55	B = 7.520 + 0.049T − 0.717A	0.754	0.001	0.044	---	86.5
Redcoat	B = −9.344 + 0.105T + 0.580A − 0.004TA	2.034	0.009	0.155	0.001	88.9
83T6	B = −3.793 + 0.062T + 0.083A − 0.001TA	3.775	0.009	0.228	0.001	78.9
132E57	B = 6.089 + 0.024T − 0.395A + 0.0004TA	1.448	0.004	0.070	0.0002	89.1

[z]All regression equations were significant at $P \leq 0.0001$. For all genotypes in 1985 and 62E55 in 1986, the A x T interaction was not significant ($P \leq 0.05$).
[y]Standard errors of a: the intercept; T: the total number of achenes per berry; A: the number of achenes/cm²; and TA: the interaction of T and A.

Table 2. Correlation coefficients between primary berry fresh weight, the total number of achenes per berry (T), and the number of achenes/cm² (NA/C) for four strawberry genotypes in 1985 and 1986.

Genotype	N		Berry fresh wt (g)	NA/C
		Matted row–1985		
62E55	66	NA/C	−0.1001	
		T	0.8897***[z]	0.2300
Redcoat	64	NA/C	−0.0518	
		T	0.8506***	0.3468**
71M59	68	NA/C	−0.1787	
		T	0.9172***	0.0779
Veeglow	63	NA/C	0.2334	
		T	0.9528***	0.4109***
		Hill system–1986		
62E55	209	NA/C	−0.2729***	
		T	0.8326***	0.1633*
Redcoat	219	NA/C	−0.1827**	
		T	0.9112***	0.0175
83T6	192	NA/C	−0.1481*	
		T	0.8214***	0.2090**
132E57	202	NA/C	0.1786*	
		T	0.9018***	0.4668**

*,**,***Significant $P \leq 0.05$, 0.01, and 0.001, respectively.

weight and the total number of achenes and the NA/C had to be fit for each genotype (Table 1). In all of these genotypes, primary berry fresh weight was highly correlated with the total number of achenes per berry but not with NA/C (Table 2). Also, in 'Redcoat' and 'Veeglow', berries with a large number of achenes had a higher NA/C than those with low achene number (Table 2). In the hill system (1986), berry fresh weight among genotypes was related to both the NA/C and the number of achenes per berry (Table 1). In 'Redcoat', 83T6, and 132E57 there was a significant interaction between the NA/C and the number of achenes per berry (Table 1). Berry fresh weight was correlated with the number of achenes per berry and the NA/C in all genotypes in 1986 (Table 2). In 62E55, 'Redcoat', and 83T6, berries with a large fresh weight had fewer achenes per cm² than did those with low fresh weight. However, in 132E57, there was a positive correlation between the NA/C and berry weight. Berries with a large total number of achenes tended to have a large NA/C in 62E55, 83T6, and 132E57 (Table 2).

The genotypes differed in yield, mean berry fresh weight, number of achenes/cm², and total number of achenes per berry when grown in matted rows in 1985 and in the hill system in 1986 (Table 3). In the matted row, the highest-yielding genotype, 62E55, had a greater number of achenes per berry than the other three genotypes, but did not have the lowest NA/C (Table 3). Thus, in the matted row, genotypic variation in berry weight and, perhaps, yield were more dependent on total number of achenes per berry than the NA/C. Moore et al. (4) found that large-fruited clones had more achenes per berry and produced more receptacle tissue per achene than small-fruited clones. However, Olsen et al. (7) found that differences in berry weight of two genotypes could not be accounted for by differences in the total number of achenes per berry. In the present study, the amount of receptacle tissue developed per achene appeared to be related to berry fresh weight among genotypes (Table 3). In the hill system, 62E55 had heavier berries than the lowest yielder, 132E57; yet, there was no significant difference in the number of achenes per primary berry (Table 3). However, 62E55 had a greater amount of berry expansion than 132E57, as evidenced by fewer NA/C and greater amounts of receptacle tissue developed per achene (Table 3). Perhaps, in 132E57, the achenes released less hormone, resulting in less receptacle tissue development per achene than in other lines. In 1986, 'Redcoat' and 62E55 plants were grown in the hill system and not in matted rows. Rainfall and temperature during the summer months were very similar between the two years. Thus, reduced inter-plant competition in the hill system may have resulted in the improved berry size, as evidenced by fewer NA/C (Table 3). The genotype 62E55 had more achenes/berry in 1986 than in 1985, suggesting that the growing system may influence flower bud differentiation in this genotype.

Abbott et al. (2) found that 66% of 'Redgauntlet' berries had eight or fewer NA/C. In this study, <1% of 62E55, 'Redcoat', 83T6, and 132E57 berries had eight, nine, 11, and 13 NA/C, respectively. Each of these values was the smallest observed for the corresponding genotype grown in the hill system. Thus, the mean number of achenes/cm² was very high compared to pre-

Table 3. Mean values for yield/plant, berry weight, number of achenes/cm², total number of achenes/berry, and weight of receptacle tissue developed per achene for strawberry genotypes studied in 1985 and 1986.

Genotype	Yield (g/plant)	N[z]	Primary berry wt (g)	NA/C[y]	Total no. of achenes	Tissue per achene (mg)
			Matted row–1985			
62E55	136.74 a[x]	66	11.74 a	20.5 a	293.5 a	40 b
Redcoat	109.38 b	64	8.89 b	20.6 a	225.1 b	39 b
71M59	74.67 c	68	10.56 a	18.8 c	244.3 b	43 a
Veeglow	77.50 c	63	8.54 b	22.3 b	236.0 b	36 c
			Hill system–1986			
62E55	737.3 a	209	13.9 a	14.7 c	346.7 b	40 b
Redcoat	662.8 a	219	10.6 c	13.3 d	233.8 c	45 a
83T6	651.1 a	192	12.6 b	17.5 b	396.1 a	32 c
132E57	257.0 b	202	8.9 d	20.6 a	337.8 b	26 d

[z]Number of primary berries subsampled.
[y]Number of achenes/cm².
[x]Means within columns and years separated by Duncan's multiple range test, $P = 5\%$.

vious studies (2, 4, 7). This difference probably was due to both genotypic and environmental differences between previous studies and this study. When the genotypes 'Veeglow' and 62E55 were grown in the greenhouse, the NA/C was similar to that found in the field (data not shown). Therefore, it seems unrealistic to calculate percent shortfall in yield using eight NA/C as an indication of potential berry expansion in these genotypes. Thus, although NA/C was affected by the growing system or the year (Table 3), the minimum NA/C attainable was also genotype-dependent. The lowest yielder, 132E57, had the greatest NA/C. In this study, a separate equation relating berry fresh weight to the total number of achenes and the NA/C was required for each genotype (Table 1). Therefore, to calculate shortfall in yield based on NA/C for a particular genotype (7, 9–11), the maximum berry expansion possible would have to be determined.

The data for 1986 were grouped according to the NA/C, and a separate regression of berry weight on total number of achenes was computed for each group (2). Abbott and Webb (1) devised the general formula: Berry fresh weight (g) = (total no. achenes − C) F/(no. of achenes per cm²), relating to uniformly developed berries. The value C is an adjustment thought to account for the nonspherical shape of the berries, and F is the specific weight to receptacle surface area ratio ($g \cdot cm^{-2}$). Both C and F may be cultivar-dependent (11). The parameters C, F, and S (the slope of the regression of berry fresh weight on the total number of achenes per berry) were calculated to determine whether the formula described by Abbott and Webb (1) relating these variables to each other was applicable for the genotypes in this study.

In 62E55, S decreased as the achene density per cm² increased (Table 4). Abbott et al. (2) showed a similar trend in 'Redgauntlet' and 'Cambridge Vigour'. In 132E57, 83T6, and 'Redcoat', S was relatively constant among different achene spacings (Table 4). According to Abbott et al. (2), if achene spacing is a factor determining berry weight, then small-fruited cultivars should have lower values of S than large-fruited cultivars. Among the four genotypes studied, there was a 1.6-fold range in mean berry weight; yet, there was no relationship between S and mean berry weight.

The X intercept of the regression of berry weight on the total number of achenes/berry (C) varied both among achene spacings within a genotype and among genotypes (Table 4). Webb et al. (9) found C to be relatively constant over different values of NA/C within a particular cultivar, but different among cultivars. C may also be affected by the environment (11).

The parameter F did not appear to be genotype-dependent (Table 4). However, Webb et al. (9, 11) suggested that F may be affected by the cultivar and the environment. They also suggested that F may be a factor determined during flower bud initiation, but this seems unlikely in this study as F varied with the spacing of the achenes for each genotype. Thus, the formula devised by Abbott and Webb (1) cannot be applied to the genotypes in this study, as F was not constant.

Within the matted row, there were no significant differences in mean peduncle or pedicel diameter among the four genotypes, but the highest yielders, 62E55 and 'Redcoat', had significantly longer peduncles and pedicels than the others (data not shown). Webb (8) found a linear relationship between berry fresh weight and pedicel diameter for several genotypes, with large berries having long and wide pedicels. He suggested that primary berries had a potential size advantage over secondary berries due to a reduced average length of the conducting system. Among the genotypes in this study, however, those with shorter peduncles and pedicels did not have the largest average primary berry weight. Differences in the sizing of berries among genotypes may be related to the amount of photosynthates partitioned to the truss.

Within genotypes, berry weight was related to the total number of achenes per berry and the NA/C. Differences in the sizing of berries and, perhaps, yield among genotypes were related to the total number of achenes when grown in the matted row (1985) and the NA/C when grown in the hill system (1986). Differences in the maximum berry expansion possible among genotypes was perhaps due to differences in the amount of hormone released from the achenes, but may also reflect differences in the amount of photoassimilates partitioned to the developing truss. The data suggested that selecting for a high total number of achenes per berry and a low number of achenes/cm² in genotypes may lead to a greater berry weight and perhaps yield.

Table 4. Data from the regressions of primary berry fresh weight on the total number of achenes per berry grouped according to the number of achenes/cm² of berry surface for genotypes studied in 1986.

Berry no.[z]	NA/C[y]	S[x]	C[w]	SE[v]	R^2 (%)	F[u]
		62E55				
9	≤10	0.053 ± 0.007	−10	1.53	90	---
26	11 or 12	0.051 ± 0.004	18	2.06	86	0.58
84	13 or 14	0.051 ± 0.002	62	1.98	84	0.69
47	15 or 16	0.049 ± 0.004	82	1.61	73	0.76
26	17 or 18	0.045 ± 0.002	86	1.29	94	0.79
12	19 or 20	0.041 ± 0.004	80	1.14	93	0.80
5	≥21	0.039 ± 0.020	80	2.62	55	---
		Redcoat				
20	≤10	0.074 ± 0.006	61	1.36	91	---
70	11 or 12	0.058 ± 0.002	39	1.26	93	0.67
82	13 or 14	0.046 ± 0.002	15	1.22	85	0.62
33	15 or 16	0.057 ± 0.003	66	1.04	93	0.88
14	≥17	0.030 ± 0.006	−86	1.19	70	---
		83T6				
11	≤13	0.049 ± 0.004	71	1.31	93	---
42	14 or 15	0.046 ± 0.003	81	2.15	87	0.66
55	16 or 17	0.034 ± 0.003	24	1.97	70	0.56
47	18 or 19	0.033 ± 0.004	34	2.02	65	0.62
18	20 or 21	0.037 ± 0.004	86	1.72	82	0.76
19	≥22	0.034 ± 0.005	103	1.44	75	---
		132E57				
14	≤15	0.033 ± 0.003	6	0.75	91	---
28	16 or 17	0.035 ± 0.003	50	0.96	80	0.57
48	18 or 19	0.028 ± 0.002	14	1.06	85	0.53
45	20 or 21	0.031 ± 0.002	56	0.96	90	0.64
31	22 or 23	0.032 ± 0.002	74	1.22	91	0.73
13	24 or 25	0.032 ± 0.002	94	0.85	94	0.78
12	26 or 27	0.039 ± 0.005	155	2.21	88	1.03
11	≥28	0.030 ± 0.003	131	0.90	93	---

[z]The number of berries in the sample.
[y]The number of achenes/cm².
[x]The slope of the line of berry fresh weight on the total number of achenes/berry ± SE.
[w]The X intercept of the regression of berry fresh weight on the total number of achenes/berry.
[v]The standard error of estimation (g) for the regression equation of berry weight on the total number of achenes.
[w]The number of achenes/cm² × S ($g \cdot cm^{-2}$).

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