culinary use of the fruits. Preliminary (unpublished) data show that tasters can distinguish fruits that differ in ripeness by 0.5 OD, and that such fruits make pies or tarts that differ in consistency and taste. Furthermore, blends of unripe green and red fruits (classed as VL in ACY) and overripe fruits (classed as H in ACY) might be pureed and used in cooked products. Consequently, more data are needed to establish classifications of ripeness and firmness that indicate fruit quality and potential uses, including uses for fruits not ripe enough, too ripe, or too soft to be useful in the fresh market but useful as processed products.

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# Inheritance of Fruit Detachment in Strawberry[1]

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*Abstract*. Diallel crosses were used to determine the inheritance patterns for capping percentage, capping force, and pedicel breaking force in *Fragaria* × *ananassa* Duch. cultivars. The diallel crosses were evaluated with the Jinks-Haymen formulae and these results were compared with the phenotypic evaluation of the parent cultivars. Capping percentage, capping force, and pedicel breaking force are different genetic traits but they were significantly correlated with each other. The pattern of inheritance for each trait was controlled by both additive and dominant genes. The overall direction of dominance for the respective traits was for higher capping percentage, lower capping force and lower pedicel breaking force. 'Gorella' exhibited extreme overdominance for low capping force. Because of the large environmental influence on these traits, progeny tests such as diallel crosses provide a better evaluation of the genetic potential of a cultivar than its phenotypic performance.

An effective method of mechanically harvesting strawberries is necessary to stabilize the strawberry industry in the United States (4, 9). Various systems of mechanical harvest are currently being proposed and tested (2, 4, 8, 9). Harvest mechanization of other fruits and vegetables has often required the consideration of plant traits that previously were of little importance. Capping and pedicel breaking may be such traits for the strawberry. Typically, in hand harvest the fruit caps or the pedicel breaks. These two areas of separation are comparable to the two abscission areas reported for cherries (6), though the strawberry fruit does not naturally abscise. Capping is defined as the removal of the fruit from the plant with the calyx remaining attached to the plant, and pedicel breaking occurs when the fruit stem breaks, leaving the calyx attached to the fruit.

The commercial strawberry (*Fragaria* × *ananassa* Duch.) is an octaploid with x = 7; 2N = 56 chromosomes (7), but it often behaves genetically as an amphidiploid (11, 12). Strawberry cultivars are asexually propagated. Though they often behave as amphidiploids, they are not homozygous and genetic ratios are frequently complex.

The purpose of this study was to determine the pattern of inheritance for capping and for pedicel breaking so that these characters could be more quickly incorporated into commercial cultivars.

## Materials and Methods

Based on literature reports (7) and personal observations, we separated strawberry cultivars into 4 classes for capping ease. Two cultivars in each classification were selected for use as parents for the diallel analysis. The capping classification used and the cultivars selected were: easy; ('Juspa' and 'Gorella'), good; ('Tennessee Beauty' and 'Fresno'), average; ('Blakemore' and 'Albritton') and difficult; ('Surecrop' and MD-US 3082).

All research was conducted at the University of Arkansas Main Experiment Station, Fayetteville. The 8 cultivars were crossed in all possible combinations in the winter of 1969–1970 and the reciprocals were combined. In addition, 'Juspa' and 'Surecrop' were selfed. The fruit was collected when mature and the seeds extracted with a laboratory blender, air dried, and planted in flats containing a mixture of ½ peat and ½ sand. The seedlings upon emergence were

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transplanted into 6-cm peat pots containing greenhouse soil and grown in a lathhouse. After 6 weeks the seedlings were transplanted into a field in seedling squares (11), and the plants were watered, cultivated as needed to promote good growth, and herbicide was applied to control weeds.

The field design was a randomized complete block with 5 replications. Each replicate was composed of 15 seedling squares from each of the 30 seedling populations and 3 squares from each of the 8 asexually propagated parent cultivars making a total of 2370 plants evaluated in the experiment. The planting was inspected daily during the harvest season of 1971. When the primary fruits appeared ripe in a seedling square, 10 primary fruits were evaluated for capping and pedicel breaking with the "capometer", an instrument developed for this purpose (5). The force in g required for capping or pedicel breaking, whichever occurred first, was recorded for each fruit and a mean calculated for each seedling square.

The statistical procedures included Wr and Vr values calculated for the diallel crosses by the Haymen method (10). Wr is the covariance of the offspring of each parental array with the non-recurring parent. Vr is the variance of the offspring of each parent (1). The plotting of Wr and Vr gives a measure of the contribution of additive genes and dominant genes to total variation. The variation is expressed as $H_1/D$. When $H_1/D$ equals 1 there is complete dominance, less than 1 indicates both dominant and additive genes contribute to variance, and greater than 1 signifies overdominance. The sum of Wr + Vr values denotes the relative order of dominance for individual parents within the diallel crosses. The Jinks-Haymen formulae assume a simple underlying genetical system, especially diploid segregation (10). Though strawberries are octoploid, they often behave genetically as amphidiploids (11, 12), so this method of measuring genetic variation has validity.

## Results and Discussion

Capping percentage, capping force and pedicel breaking force were all significantly correlated with each other (Table 1). Capping force is an important part of capping, but it is not the only factor involved. The correlation between capping force and pedicel breaking force was in part the result of the procedures used. With our procedure the force was only determined for the weakest point of attachment. For example, if 200 g of force capped a fruit, all that is known about the pedicel is that it withstood 200 g of force without breaking. If it takes 800 g of force to break a pedicel we know it will require more force than this to cap, and also, a stronger pedicel is needed. The force differential between capping and pedicel breaking was relatively small in the cultivars tested (Table 2).

The means of each of the 2 selfed populations, 'Juspa' × self and 'Surecrop' × self, did not differ significantly from their parents for capping percentage, a usual test of homozygosity. This was not conclusive proof of homozygosity in this case, however, because of inbreeding depression.

*Capping percentage.* Capping percentage had a broad sense heritability of 43%. The parent clones were ranked by Duncan's multiple range test, and Wr + Vr values (Table 2, 3). The order of the Duncan multiple range test of actual values and the order of dominance determined by Wr + Vr values are not the same. This would be expected since over ½ of the phenotypic expression of the offspring was due to environment.

Table 1. Correlation coefficients between capping percentage, capping force, and pedicel breaking force in the strawberry.[z]

| Characters | r |
|---|---|
| Capping percentage and capping force | .2236** |
| Capping percentage and pedicel breaking force | −.1023** |
| Capping force and pedicel breaking force | .4095** |

** Significant at the 1% level.

[z] 1976 degrees of freedom.

Table 2. Parental means for capping percentage, capping force, and pedicel breaking force in strawberry.

| Parent | Capping % | Capping force g | Pedicel breaking force g |
|---|---|---|---|
| MD-US 3082 | 24ab[z] | 545abc | 517 |
| Surecrop | 34abc | 590abc | 497 |
| Albritton | 41abc | 665bc | 638 |
| Fresno | 46abcde | 632abc | 641 |
| Blakemore | 49bcde | 502ab | 391 |
| Gorella | 72def | 829c | 870 |
| Tennessee Beauty | 75ef | 750bc | 683 |
| Juspa | 83f | 615abc | 465 |
| parental $\bar{x}$ | 53 | 635 | 584 |
| progeny $\bar{x}$ | 52 | 631 | 585 |

[z] Mean separation within a column by Duncan's multiple range test, 5% level. Duncan's calculated for parents plus progeny; only the parental values are shown here.

Table 3. Comparison of actual values with expected values for an additive inheritance model for fruit capping percentage in strawberry.[z]

| Parents | F[y] | B | S | G | M | J | T | Wr + Vr[x] |
|---|---|---|---|---|---|---|---|---|
| Fresno | | | | | | | | 1.65 |
| Blakemore | * | | | | | | | 2.27 |
| Surecrop | * | * | | | | | | 2.30 |
| Gorella | * | −1 | * | | | | | 2.72 |
| MD-US 3082 | * | * | * | * | | | | 2.80 |
| Juspa | * | * | * | −1 | * | | | 3.05 |
| Tennessee Beauty | * | * | * | −1 | * | * | | 3.55 |
| Albritton | +1 | * | * | * | +1 | +1 | +1 | 3.84 |

[z] Actual values are reported as * if within ± one $\sigma$ of expected or the number of $\sigma$ that the value differs. Standard deviation was ±1.5 fruit. Parents arranged by Wr + Vr order of dominance from most to least.

[y] Cultivars first letter only, same order as vertical column.

[x] Wr + Vr – The lower the value the greater the dominance.

The lack of discrete classes within progenies and also between progenies indicates multigenic control of capping percentage. The $H_1/D$ value of 0.78 (Fig. 1) suggests that both additive genes and dominant genes were operative in controlling capping percentage. The grand mean of the $F_1$'s was almost the same as the grand mean of the parent clones (Table 2) and most means of individual progenies did not deviate more than 1 standard deviation from the expected mean for additive gene action.

The relative importance of additive genes and dominant genes can be determined for some parent clones by analysis of their offspring performance. For example, 'Gorella' and 'Albritton' progenies differed significantly from the expected means (Table 3). 'Gorella' phenotypically and genotypically was an intermediate parent. The means of 3 crosses out of 7 in which 'Gorella' was a parent was more than 1 standard deviation less than the expected mean. 'Gorella' was the only cultivar used in which 'Howard 17' was not in the ancestry. Possibly 'Gorella' has different genes regulating capping than the other parent clones. Of the dominant genes expressed in the diallel, 'Albritton' had the fewest and phenotypically was a below average capper but in 4 of the 7 crosses in which 'Albritton' was 1 parent the progeny means exceeded the expected mean for additive action by more than 1 standard deviation. This suggests that 'Albritton's capping ability is the result of additive gene action and, in the progeny, dominant genes for high capping percentage are contributed by the other parent. Of the dominant genes controlling capping percentage, expressed in the diallel, 'Fresno' had the most (Fig. 1). However, except when crossed with 'Albritton', the actual mean equalled the expected mean for additive variance (Table 3). The additive gene hypothesis is supported by the Wr, Vr graph (Fig. 1) which shows the parents were near the midpoint for dominance. Since the parents differed significantly in phenotype and genotype, yet none was near either the dominant or recessive extremes, additive variance was the major contributor in the test. Though 'Juspa' selfed and 'Surecrop' selfed did not differ significantly from their parents, their standard deviations were about the same as the other $F_1$'s, also suggesting additive gene action.

*Capping force.* Capping force data were obtained only for the fruit that capped, which varied from 150 fruits for the progeny with the lowest capping percentage to over 600 fruits for the highest capping progeny. The broad sense heritability for capping force was 18%. This indicates that capping force was greatly affected by environment. The comparison of Wr and Vr scores and the ranking by Duncan's multiple range test also demonstrates the marked interaction of genotype and environment (Table 2, 4).

The $H_1/D$ value of .77 (Fig. 2) indicates that capping force was controlled by a combination of additive genes and dominant genes. The relative importance of additive and dominant genes could be identified for some parents through the analysis of their progeny. The 2 selfed populations revealed the multitude of genes involved and heterozygosity of the parents for capping force. Of the dominant genes expressed in the diallel, 'Juspa' had over 75% and 'Surecrop' had approximately 50% (Fig. 2). The standard deviations were 199 for 'Juspa' selfed and 329 for 'Surecrop' selfed as compared with the tests' overall standard deviation of 238. The smaller deviation of 'Juspa' selfed and the Wr, Vr graph (Fig. 2) suggest that 'Juspa' is almost homozygous for the dominant genes that influence capping force which were expressed in the diallel. Yet the additive genes in 'Juspa' had more effect on the progeny in the diallel cross than the dominant genes. For example, 5 of the 7 'Juspa' progenies deviated by less than 1 standard deviation from the expected mean for additive variance and in the 2 that deviated more than 1 standard deviation the parents had exhibited overdominance in other crosses (Table 4).

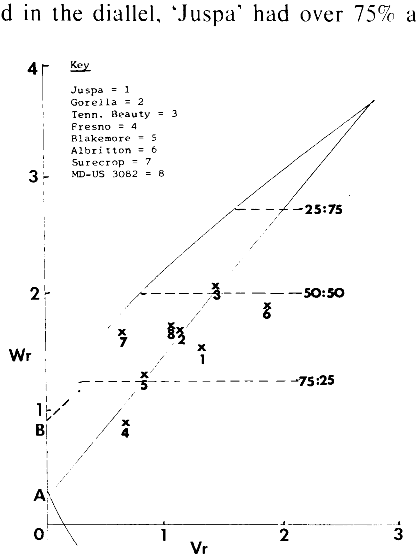

Fig. 1. (Vr, Wr) graph for capping percentage. The points lie near a straight line of unit slope inside the limiting parabola $Wr^2 = 4.556$. The 3 points of division and the ends of the line correspond to parents with 100%, 75%, 50%, 25%, and 0% dominants (reading up from the bottom). AB/OB estimates H1/D = .78.

Table 4. Comparison of actual values with expected values for an additive inheritance model for capping force in strawberry.[z]

| Parents | J[y] | B | T | A | S | F | G | Wr + Vr[x] |
|---|---|---|---|---|---|---|---|---|
| Juspa | | | | | | | | 2,025 |
| Blakemore | * | | | | | | | 4,775 |
| Tennessee Beauty | * | * | | | | | | 5,130 |
| Albritton | −1 | * | * | | | | | 6,483 |
| Surecrop | * | −1 | * | * | | | | 7,926 |
| Fresno | * | * | * | * | * | | | 9,823 |
| Gorella | −1 | * | −3 | * | * | * | | 11,924 |
| MD-US 3082 | * | +1 | +1 | +1 | * | +1 | +1 | 14,489 |

[z] Actual values are reported as * if within ± one $\sigma$ of expected or the number of $\sigma$ that the value differs. Standard deviation was ± 86 g. For each trait parents arranged by Wr, Vr, order of dominance from most to least.

[y] Cultivars first letter only, same order as vertical column.

[x] Wr + Vr – The lower the value within a column the greater the dominance.

MD-US 3082 contained more recessive genes for capping force than any other parent (Fig. 2), yet in 5 crosses out of 7, its $F_1$'s had a higher than expected mean by more than 1 standard deviation. MD-US 3082's low capping force is due to its large number of additive genes for low capping force.

'Gorella' and 'Tennessee Beauty' varied greatest from the Wr, Vr line of best fit and both showed overdominance for low capping force (Fig. 2). The mean of the $F_1$ between 'Gorella' and 'Tennessee Beauty' was more than 3 standard deviations below the expected mean for additive gene action (Table 4). This indicates either epistasis or that both cultivars have dominant genes for capping force at different loci.

*Pedicel Breaking Force.* The Wr, Vr values met the test for statistical validity, however, the cultivars do not match a line of best fit (Fig. 3). MD-US 3082, 'Surecrop', 'Fresno', and 'Blakemore' were clustered near the limiting parabola suggesting additive gene action. The others were scattered over the graph. Except for 'Gorella', the Wr + Vr values were also very close indicating little if any difference in relative dominance (Table 5). Most of cultivar's differences are due to additive gene action. Though the breaking force inheritance seems to be primarily additive, some cultivars have dominant genes with the direction of dominance towards low breaking force. 'Gorella' has the most recessive genes and its breaking force is far higher than any of the others (Tables 2, 5).

The progeny means that deviated from those expected for additive gene action had either MD-US 3082 or 'Tennessee Beauty' as 1 parent

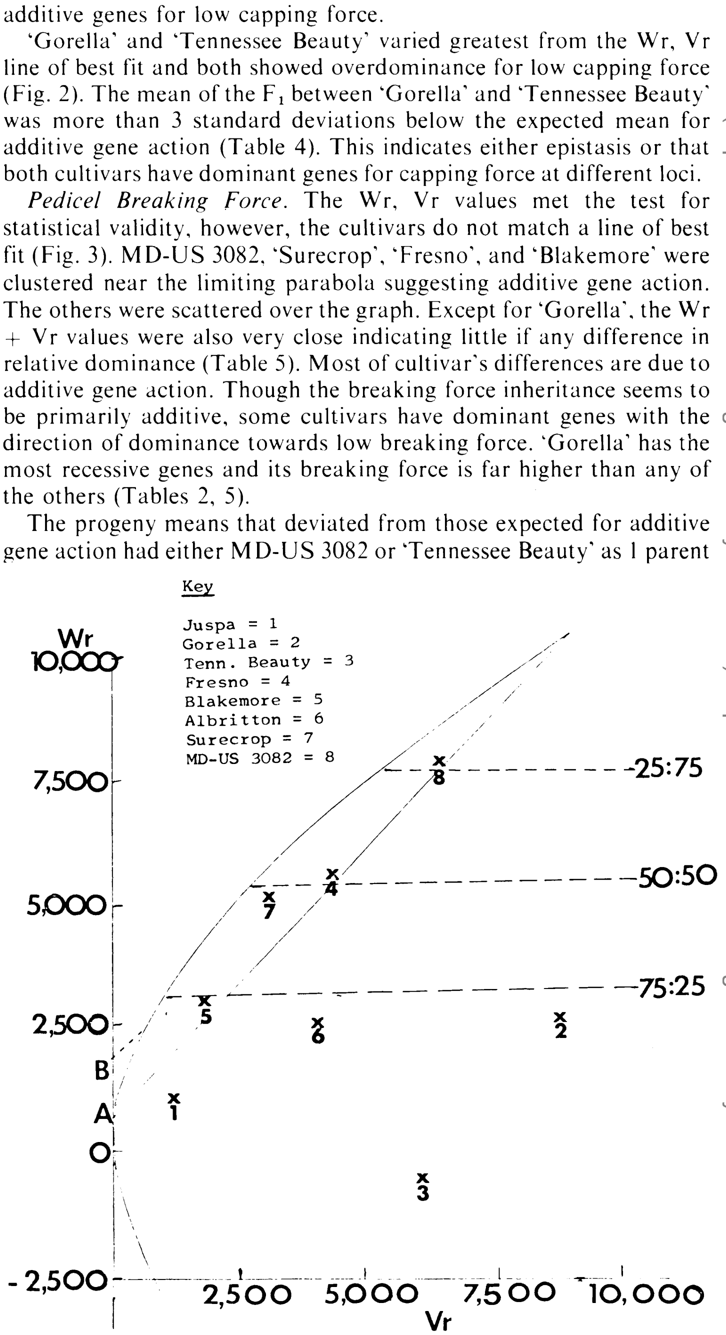

Fig. 2. (Vr, Wr) graph for capping force. The points lie near a straight line of unit slope (except for cultivar 2) inside the limiting parabola $Wr^2 = 11{,}387$ Vr. Three points of division and the ends of the line correspond to parents with 100%, 75%, 50%, 25% and 0% dominants (reading up from the bottom). AB/OB estimates H1/D = .77.

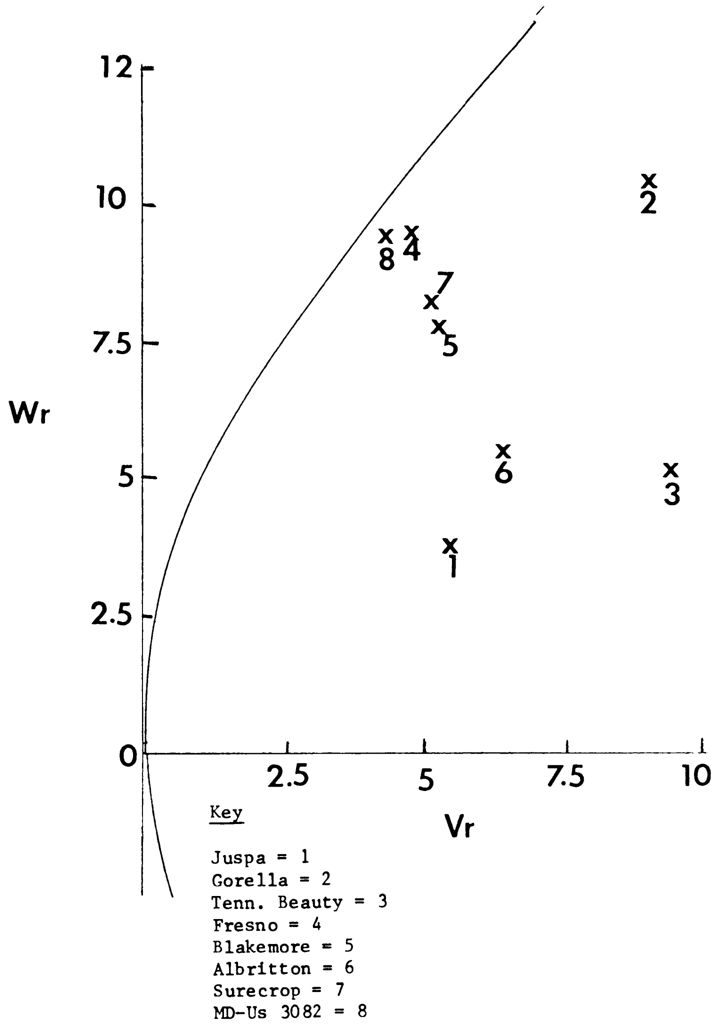

Fig. 3. (Vr, Wr) graph for pedicel breaking force. The majority of points are grouped near the limiting parabola $Wr^2 = 23{,}032$ Vr. The majority of points indicate a typical no dominance situation.

Table 5. Comparison of actual values with expected values for an additive inheritance model for pedicel breaking force in strawberry.[z]

| Parents | J[y] | B | A | M | S | F | T | Wr + Vr[x] |
|---|---|---|---|---|---|---|---|---|
| Juspa | | | | | | | | 9,170 |
| Blakemore | * | | | | | | | 10,447 |
| Albritton | * | * | | | | | | 12,246 |
| MD-US 3082 | +1 | +1 | * | | | | | 12,255 |
| Surecrop | * | * | * | +1 | | | | 12,323 |
| Fresno | * | * | * | * | * | | | 13,620 |
| Tennessee Beauty | –1 | * | –1 | * | * | * | | 14,541 |
| Gorella | * | * | * | * | * | * | –1 | 19,706 |

[z] Actual values are reported as * if within ± one $\sigma$ of expected or the number of $\sigma$ that the value differs. Standard deviation was ± 103 g. For each trait parents arranged by Wr, Vr, order of dominance from most to least.

[y] Cultivars first letter only, same order as vertical column.

[x] Wr + Vr – The lower the value within a column the greater the dominance.

(Table 5). The Wr, Vr graph (Fig. 3) depicts MD-US 3082 as a parent with primarily additive gene action. Thus any dominant genes contributed by other parents had maximum expressivity. The Wr, Vr graph (Fig. 3) indicates, as do the progeny means (Table 5), that 'Tennessee Beauty' exhibited overdominance for low pedicel breaking force.

The order of dominance for capping force and pedicel breaking force was remarkably similar (Tables 4, 5). Capping force and pedicel breaking force were significantly correlated and the inheritance in each case was apparently complex. In both cases the overall direction of dominance was towards lower required force.

Our results indicated that all cultivars were heterozygous and the characters were controlled by many genes. Each of the characters was highly influenced by envirioment. Therefore, mating the best phenotypes will not always result in the most rapid breeding progress. Baker (3) reported similar conclusions. Because the phenotype results from an interaction of genotype and environment, and since the genetic factors are not fixed, the use of Wr, Vr values or general combining ability scores to identify promising parents has considerable merit.

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