

Genetic analysis of pungency and soluble solids in long-storage onions *

Philipp W. Simon

Vegetable Crops Research Unit, Agricultural Research Service, U.S. Department of Agriculture, Department of Horticulture, University of Wisconsin-Madison, Madison, WI 53706 USA

Received 26 June 1994; accepted 12 December 1994

Key words: *Allium cepa*, diallel, flavor, generation means analysis, pyruvate

Summary

Pungency and soluble solids are important quality attributes of onion. An eight-parent diallel over two years indicated a preponderance of additive genetic variation for both attributes. Variation among years was significant for pungency but not solids. No reciprocal cross differences were noted for pungency or solids. Generation means analysis for four crosses over two years had a good fit with a simple additive-dominance model to explain the inheritance of both traits in most cases. Both diallel and generation means analyses demonstrated some dominance for low pungency. Broad sense heritability estimates averaged 0.64 for pungency and 0.83 for soluble solids. Selection was effective for increasing and decreasing pungency in derivatives of five crosses. Pungency and soluble solids were correlated among parental inbreds and hybrids but not within F_3 's. The additive control and heritability suggest that onion pungency and soluble solids can be effectively and independently selected.

Introduction

The pungent flavor of onions is the primary attribute accounting for their widespread popularity. The biochemical development of pungent onion flavor from derivatives of cysteine has been studied extensively but few studies have examined the genetic basis of pungency. Warid (1952) concluded that the heritability for onion pungency was 0.71 from parent-offspring regression. Owen (1961) estimated that relatively few genes are involved in onion pungency based upon several segregating populations. Pal & Singh (1988) determined that additive gene action had more of an effect on pungency than dominance in an 8-cultivar diallel. Lin et al. (1995) evaluated a 9-inbred diallel where additive gene action was also more important than dominance for both pungency and soluble solids whereas generation means analysis of three crosses usually indicated an acceptable fit with a simple additive-dominance model and heritability of 0.4–0.8 for these attributes.

Soluble carbohydrates contribute to onion sweetness and, because they account for most of the soluble

or dissolved solids, they are a major factor in onion processing quality. McCollum (1968) and Kadam & Nwasike (1986) estimated the heritability of solids in several onion populations to be 0.6 to 0.8. To better understand the genetics of onion qualities this study evaluated pungency as estimated by pyruvate and soluble solids in an eight-inbred onion diallel for two years and in a 4-parent subset of this diallel for one or two more years. Generation means analyses were performed for 4 crosses over two years and the response to selection was evaluated for onion pungency and solids in 3 generations beyond the F_1 for 5 onion crosses.

Materials and methods

Eight male-fertile long-storage USDA onion inbreds developed for Northern U.S. production were intercrossed in all combinations including reciprocals, in 1981. Inbreds were selected for this experiment because of their range in pungency and soluble solids (Table 1). In 1983, using a 4-parent subset of this 8-parent diallel, F_2 populations were generated by self-pollinating individual F_1 bulbs and BC_1 popula-

* The U.S. Government right to retain a non-exclusive, royalty free licence in and to any copyright is acknowledged.

Table 1. Mean pungency and soluble solids of eight onion inbred parents

Inbred	Pungency (micromoles pyruvate/gfw)				Soluble solids (refractive index)		
	1982	1986	1988	1991	1982	1986	1991
B8155	4.2a ^z	7.0a	5.9a	7.3a	7.0a	7.9a	7.7a
B2399	6.2b	6.7a	6.5a	8.4a	9.1b	9.8d	9.0b
B1834	11.0d	14.3c	18.0c	14.9c	16.7e	15.2f	15.8e
B4535	15.3e	16.2d	16.6c	15.2c	11.0d	9.8d	10.4cd
B826 ^y	9.6c	13.8c	11.1b	14.3c	10.2cd	9.6cd	10.3cd
B611-1 ^y	4.0a	9.2b	5.8a	9.2a	9.7bc	10.9e	9.9c
B5718 ^y	9.0c	13.1c	10.0b	12.0b	10.7d	10.3de	11.0d
B9161 ^y	4.3a	6.8a	6.1a	7.7a	9.0b	8.9bc	9.0b
LSD 0.05	1.09	1.33	1.82	1.96	0.94	0.77	0.87

^z Values in a column followed by the same letter are not significantly different at the 5% level, Duncan's multiple range test.

^y in 1982, 1986 diallels, but not 1988, 1991 diallels.

Table 2. Model ANOVA for pyruvate and soluble solids in an 8-parent onion diallel

	Source	df	SS	MS	F	P
Pyruvate	Year	1	1305.6	1305.6	1088.1	<0.01
	Rep (Year)	6	7.4	1.2	0.5	0.83
	Genotype	63	3104.7	49.3	7.3	<0.01
	Y × G	63	431.1	6.8	2.6	<0.01
	Error	378	975.3	2.6		
Solids	Year	1	0.3	0.3	3.0	0.89
	Rep (Year)	6	0.6	0.1	2.0	0.67
	Genotype	63	1254.9	19.9	24.9	<0.01
	Y × G	63	53.2	0.8	15.3	<0.01
	Error	378	19.3	0.1		

tions were produced by emasculating recurrent inbred umbels and crossing them with pollen of the F₁ hybrids. F₃ and F₃M seed was produced in 1985 and 1987, by self-pollinating and sib-mating 2 to 4 selected bulbs, respectively. Seed was produced in Madison, Wisconsin, using bulbs produced the previous year.

Bulbs were produced by direct-seeding in April on muck soil in Palmyra, Wisconsin. The experimental design was a randomized complete block with four replications. Five individual bulbs were sample in each replicate for all generations except at F₂ where 20–24 bulbs were sampled in each replicate. Bulbs were harvested in September when leaves had senesced and stored at 4–8° C after curing at ambient temperatures two to four weeks. Pungency and solids were evaluated between November 20 and January 3.

Pungency was measured by the pyruvate method (Schwimmer & Weston, 1961) whereas soluble solids was measured as refractive index (Mann & Hoyle, 1945) using an Abbe refractometer. Pungency and solids samples used were obtained from individual bulbs at their equator with a 6 to 8 mm cork borer. Central and outermost scales were removed from plugs thus obtained and samples were immediately comminuted for pungency evaluation or placed in polyethylene bags and frozen (-20° C) for solids evaluation (1–3 months later).

The complete 8 × 8 diallel was evaluated for pungency and solids in 1982 and 1986. A 4 × 4 subset of this diallel was evaluated for pungency in 1988 and 1991 and for solids in 1991 only. F₂'s and BC₁'s were

Table 3. Diallel analysis of variance of eight onion inbreds, their hybrids and reciprocals for pyruvate and soluble solids over two years

	Source	df	SS	MS	F	P
Pyruvate	GCA	7	2829.2	404.2	59.4	< 0.01
	SCA	28	244.6	8.7	1.3	0.91
	Recip	28	39.7	1.4	0.2	0.98
	Yr × GCA	7	134.1	19.2	7.3	< 0.01
	Yr × SCA	28	264.6	9.5	3.6	< 0.01
	YR × Recip	28	16.5	0.6	0.2	0.99
	Error	378	990.9	2.6	–	–
Soluble Solids	GCA	7	1223.6	174.8	218.5	< 0.01
	SCA	28	19.3	0.7	0.9	0.93
	Recip	28	12.1	0.4	0.5	0.97
	Yr × GCA	7	26.5	3.8	68.6	× 0.01
	YR × SCA	28	20.1	0.7	13.0	< 0.01
	YR × Recip	28	6.6	0.2	4.3	< 0.01
	Error	378	20.8	0.06	–	–

also evaluated in 1986 and 1991. F₃ and F₃M generations were evaluated in 1988.

Selection was exercised in the development of the F₂, F₃, and F₃M generations. For each family, the bulbs with highest and lowest pungency were self-pollinated to generate F₂'s whereas for subsequent generations 2 or 3 individual bulbs (for F₃ generation) or groups of 2–4 bulbs (for F₃M generation) were used.

For diallel analysis, crosses were considered fixed effects. Griffing's (1956) Method 1, Model 1 procedure was used for analysis. Since year effects are random and genotype effects are fixed, year × GCA, year × SCA, and year × reciprocal interactions were used to test significance of GCA, SCA and reciprocal effects, respectively, when these interactions were significant. Significance of heterosis effects (F₁ deviation) was measured by comparison of (F₁-midparent) to $(3 \times \text{error mean square}/\text{number of replicates})^{1/2}$ whereas significance of backcross deviation was measured by comparison of (BC-midparent) to $(10 \times \text{error mean square}/16r)^{1/2}$.

A weighted generation mean analysis was calculated for each cross for each year (Mather & Jinks, 1977). Genetic parameters were estimated with least squares regression (Rowe & Alexander, 1980). Broad sense heritability was estimated by the method of Mahmud & Kramer (1951) where $H^2 = (VF_2 - VE)/VF_2$; $VE = (VP_1 + VP_2 + VF_1)/3$.

Table 4. General combining ability for onion pyruvate and solids of onion inbred parents used in a diallel cross

	Pyruvate		Solids	
	8 × 8	4 × 4	8 × 8	4 × 4
B8155	-1.71	-2.12	-1.26	-1.61
B2399	-1.60	-1.84	-0.62	-0.88
B1834	1.48	1.19	2.66	2.64
B4535	3.05	2.77	-0.09	-0.16
B826	0.87		-0.15	
B611-1	-1.53		0.01	
B5718	0.70		0.15	
B9161	-1.24		-0.69	

SE ($g_i - g_j$) = 0.71 (pyruvate, 4 × 4), 0.76 (pyruvate, 8 × 8), 0.09 (solids, 4 × 4), 0.11 (solids, 8 × 8).

Results and discussion

Inbred variation

Pyruvate and solids content varied widely among the eight onion inbreds evaluated (Table 1). Pyruvate concentration was more variable between years than was soluble solids but rankings among inbreds were roughly the same each year. Lin et al. (1995) found similar levels of variation among inbreds for these two attributes in one year. B8155 was lowest in pyruvate

Table 5. Generation means, standard deviations, estimates of gene effects, and deviations from midparent values for pyruvate in four onion crosses over two years

	B8155 × B2399		B8155 × B1834		B8155 × B4535		B1834 × B4535	
	1986	1991	1986	1991	1986	1991	1986	1991
Generation ^z :								
P ₁	7.0	7.3	7.0	7.3	7.0	7.3	14.3	14.9
	± 1.2	± 0.8	± 1.2	± 0.8	± 1.2	± 0.8	± 2.2	± 1.1
P ₂	6.7	8.5	14.3	14.9	16.2	16.2	16.2	16.2
	± 2.2	± 1.0	± 2.2	± 1.1	± 2.6	± 1.5	± 2.6	± 1.5
F ₁	6.9	7.0	11.0	10.7	10.3	10.9	15.0	15.1
	± 0.8	± 0.8	± 2.7	± 0.8	± 2.2	± 0.6	± 2.5	± 0.5
F ₂	7.4	7.4	12.0	12.4	10.7	11.9	14.4	14.3
	± 2.8	± 2.6	± 1.8	± 1.2	± 3.3	± 3.0	± 3.0	± 2.9
BC ₁	6.9	7.3	8.7	9.1	8.1	8.3	14.0	14.8
	± 1.7	± 1.5	± 1.5	± 1.1	± 0.9	± 2.4	± 4.4	± 3.9
BC ₂	7.1	7.4	12.4	13.3	12.4	13.8	15.7	15.3
	± 8.4	± 2.2	± 2.5	± 1.3	± 1.9	± 3.6	± 3.1	± 3.7
Statistic								
m	6.9**	7.9**	10.8**	11.3**	11.4**	11.8**	15.2**	15.5**
	± 1.1	± 0.6	± 1.2	± 0.6	± 1.6	± 1.3	± 1.6	± 0.9
d	0.1	-0.6	-3.8*	-3.9*	-4.5*	-4.5*	-1.0	-0.6
	± 1.1	± 0.7	± 1.1	± 0.6	± 1.2	± 0.8	± 1.6	± 0.9
h	-0.1	-0.9	-0.5	-0.3	-1.7	-0.9	-0.4	-0.4
	± 1.4	± 1.0	± 2.4	± 1.0	± 2.2	± 1.0	± 2.4	± 1.0
χ ²	0.1	0.1	0.4	1.4	0.2	1.2	0.7	0.2
Deviation								
F ₁	-13.5**	-1.6	-23.7**	-5.0*	-10.2**	-17.7**	-14.4**	0
BC ₁	-0.1	-0.2	-0.3	0.1	-0.6	-0.8	-0.7	-0.2
BC ₂	0.3	-0.4	0.4	0.5	-0.9*	0.3	0.1	0.4

^z mean ± s.d.; mean statistics and deviations denoted *, ** are significantly different from 0 at 5%, 1% level, respectively.

and solids each year. B9161, B2399, and usually B611-1 were low as well, while B5718 and B826 were usually intermediate for both attributes. B4535 and B1834 were high for both attributes with B1834 being especially high in solids.

Diallel analyses

Significant genotype effects and genotype × year interactions were found for pyruvate and solids in the 8-parent diallel over two years (Table 2). As noted for parental inbreds, year effects were much larger for pyruvates than for solids. Year effects were highly significant for pyruvate but insignificant for solids. The four-parent diallel over 3 years for solids and 4 years for pungency was also analyzed and the same trends were found (data not presented).

General combining ability contributed significantly to genetic variation for pyruvate and solids (Table 3). SCA was not important. Lin et al. (1995) found relatively greater GCA effects for solids and less for pyruvate. Reciprocal effects were insignificant for both pyruvate and soluble solids. Interactions of GCA, SCA, and reciprocal effects with year were significant for solids. Year by reciprocal interactions were insignificant for pyruvate but significant interactions of GCA and SCA with year were noted. Analysis of the 4-parent diallel over 3 or 4 years (for solids and pyruvate, respectively) was also performed and trends were comparable in all regards to those for the 8-parent diallel over two years (data not presented). The relative contribution of inbred parents to pyruvate and soluble solids was estimated by comparison of GCA effects (Table 4). Parents with low pyruvate and solids levels had highly significant negative GCA effects whereas those with

Table 6. Generation means, standard deviations, estimates of gene effects, and deviations from midparent values for soluble solids in four onion crosses over two years

	B8155 × B2399		B8155 × B1834		B8155 × B4535		B1834 × B4535	
	1986	1991	1986	1991	1986	1991	1986	1991
Generation								
P ₁	7.9	7.7	7.9	7.7	7.9	7.7	15.2	15.8
	± 0.6	± 0.3	± 0.6	± 0.3	± 0.6	± 0.3	± 0.9	± 0.6
P ₂	9.8	9.0	15.2	15.8	9.8	10.4	9.8	10.4
	± 0.5	± 0.6	± 0.9	± 0.7	± 0.5	± 0.9	± 0.4	± 0.9
F ₁	8.7	8.1	12.2	12.2	9.3	8.7	12.8	13.8
	± 0.6	± 0.3	± 0.1	± 0.8	± 0.4	± 0.6	± 0.3	± 0.6
F ₂	8.8	8.4	11.9	12.0	9.0	8.9	13.5	14.4
	± 0.9	± 0.9	± 2.5	± 2.2	± 1.0	± 1.2	± 3.2	± 4.9
BC ₁	6.4	7.2	10.3	11.6	6.3	8.4	14.1	15.0
	± 1.0	± 1.3	± 1.7	± 1.5	± 0.6	± 1.3	± 3.0	± 2.8
BC ₂	7.4	7.8	14.0	14.5	9.6	9.7	11.3	11.9
	± 0.8	± 1.3	± 2.0	± 1.8	± 0.7	± 1.4	± 2.1	± 3.1
Statistic								
m	8.5**	8.3**	11.6**	11.3**	8.5**	9.1**	12.5**	13.1**
	± 0.4	± 0.3	± 0.6	± 0.3	± 0.4	± 0.5	± 0.6	± 0.6
d	-0.9*	-0.7*	-3.7*	-4.1*	-1.4*	-1.4*	2.7*	2.7*
	± 0.4	± 0.3	± 0.6	± 0.3	± 0.4	± 0.5	± 0.6	± 0.6
h	-0.5*	-0.3*	0.6*	0.5	0.7*	-0.3	0.3	0.7
	± 0.8	± 0.5	± 0.6	± 0.7	± 0.5	± 0.8	± 0.8	± 0.8
χ ²	8.0*	1.2	0.4	1.1	10.2*	0.3	0.6	0.1
Deviation								
F ₁	-1.1	0	1.7	2.5	3.3	-3.3	6.9*	-0.7
BC ₁	0.3	-0.7	0.3	1.7*	-2.3**	0.2	0.1	0.2
BC ₂	0.2	-0.8*	0.3	0.5	0.1	0.2	0	-0.2

^z mean ± s.d.; mean statistics and deviations denoted *, ** are significantly different from 0 at 5%, 1% level, respectively.

high levels had highly significant positive GCA effects, as is expected with GCA so important to the overall analysis of variance. Relative effects noted in the 8-parent diallel over 2 years and four parent diallel over 3 or 4 years were fully comparable. Specific combining ability effects were insignificant for pyruvate and soluble solids, and trends were similar for comparable crosses in the 4-parent and 8-parent diallels.

High GCA estimates indicated a predominance of additive gene action for onion pungency and soluble solids. Reciprocal effects were minor for both traits as were year effects for soluble solids. Year effects were notable for pungency but trends among inbreds were similar. Therefore response to selection should still be high.

Generation mean analyses

Generation means analyses for 4 hybrid combinations over two years usually indicated a good fit with a simple additive-dominance model to explain the inheritance of pyruvate and soluble solids (Tables 5 and 6). Joint scaling tests yielded non-significant estimates for A, B, and C for all families for either attribute (data not presented). For pyruvate, estimates of the additive component (d) were significantly less than 0 for all crosses except the low × low pungency cross (B8155 × B2399) and the high × high pungency cross (B1834 × B4535). Estimates of the dominance component (h) were never significant but they were always negative. The F₁ deviation for pyruvate was usually significantly negative indicating a tendency for dominance of low pungency. BC deviation was significant for B8155/B4535 pungency in 1986.

Table 7. Broad sense heritability for pyruvate and soluble solids in 4 onion crosses over 2 years

Cross	Year	Pyruvate	Soluble Solids
B8155 × B2399	1986	58	87
B8155 × B2399	1991	89	74
B8155 × B1834	1986	56	93
B8155 × B1834	1991	44	91
B8155 × B4535	1986	61	61
B8155 × B4535	1991	88	70
B1834 × B4535	1986	34	95
B1834 × B4535	1991	85	97
average	both	64	83

For soluble solids, estimates of the additive component were significantly less than 0 for all crosses except B1834 × B4535 where they were significantly greater than 0. Greatest absolute values for (d) were noted for crosses involving the high solids parent, B1834. Dominance estimates were significant for three crosses including both years for B8155 × B4535. Deviation in F₁ and BC generations were generally insignificant.

The simple additive-dominance model was inadequate for B8155 × B4535 and B8155 × B2399 soluble solids in 1986 where the backcross to the lower solids parent, B8155, had lower soluble solids than other families in these experiments. These families were among the last to be sampled for soluble solids that spring and B8155 has significantly shorter dormancy than other inbreds used in this work so these families may have been beginning to break dormancy and consequently experiencing a reduction in soluble solids, although sprouting was not evident. The additive-dominance model fit for these families in 1991.

Frequency distributions of families used in GMA were widely dispersed, especially for pungency, and they generally failed to demonstrate clear evidence for discrete groups of segregants in F₂ and backcross generations. Backcrosses of the low × high pyruvate crosses, B8155 × B1834 and B8155 × B4535, to the high pyruvate parent may be an exception since they demonstrated weak bimodality. Transgressive segregants, especially in the high category, may support this.

GMA indicated both onion pungency and soluble solids are quantitative traits but gene numbers for each may be fairly small and inheritance patterns fairly predictable with a simple genetic model.

Heritability and response to selection

Broad sense heritability estimates were usually high for pyruvate and soluble solids (Table 7). These estimates inappropriately treat genotypes as random effects, thus weakening their validity (Baker, 1978). To more accurately estimate heritability of onion pyruvate and soluble solids, a broader study of parent-offspring similarity is required but the estimates in this study are consistent with the GMA model.

To obtain an estimate of response to selection gain, two high pyruvate and two low pyruvate F₂ plants were self-pollinated in each of five crosses (Table 8). Soluble solids levels were not selected for but were evaluated in each generation. Selection for altered pyruvate content was effective in all crosses with differences in the high and low selections of approximately 10 μM/gfw in both a low × high cross (B8155 × B4535) and, interestingly, the high × high cross (B1834 × B4535). At the F₂, means tended to rise in the crosses with B8155 and drop in the (B1834 × B4535) progeny but they were generally similar in F₂, F₃, and F₃M. Since a limited longday onion germplasm base was used in developing populations for selection in these experiments, the identification of other favorable alleles from short-day and Spanish onion germplasm could be useful in the development of longday elite onions with improved quality. A strategy to identify such populations developed for corn (Dudley, 1987) could be useful for onion improvement.

It is often assumed that soluble solids and pungency are correlated (Lin et al., 1995; McCollum, 1968). Among diallel parents, hybrids, F₂ and BC generations this correlation was observed (Table 9). Soluble solids levels varied dramatically among F₃ F₃M, and in contrast to parental inbreds and earlier generations, pungency-solids correlations among F₃ and F₃M populations selected for pungency had very weak positive or sometimes negative correlation. This suggests the opportunity to select for soluble solids and pungency level with some independence.

Conclusions

Diallel and generation means analysis indicated relatively simply, predictable inheritance patterns, albeit quantitative, for onion pungency and soluble solids. Results were comparable to limited previous genetic studies on these traits. Additive genetic variance predominated but some dominance for low pungency

Table 8. Change in onion pungency in 5 onion crosses over 3 generations of selection

Cross	Selection	Generation Parental	F ₁	F ₂	F ₃	F ₃ M
8155 × 2399	High	6.5(2.3) ^z		8.1(2.6)	8.4(1.5)	10.7(0.6)
	Average ^y	6.2	6.1(1.1)	7.3	7.2	7.6
	Low	5.9(1.0)		6.6(2.6)	5.0(0.8)	4.4(0.8)
8155 × 1834	High	18.0(2.9)		14.4(1.9)	10.4(0.5)	5.2(0.3)
	Average	13.0	11.4(1.0)	12.5	12.2	
	Low	5.9(1.0)		10.5(1.2)	8.3(0.6)	
8155 × 4535	High	16.6(3.6)		14.4(3.4)	13.3(3.6)	14.9(2.4)
	Average	11.3	9.3(2.5)	11.9	10.8	15.4(1.9)
	Low	5.9(1.0)		9.4(2.4)	7.2(2.0)	15.8(1.9)
2399 × 1834	High	18.0(2.9)		16.7(2.2)	11.2(0.9)	16.8(0.9)
	Average	12.3	12.9(2.9)	13.0	12.7	14.9(2.4)
	Low	6.5(2.3)		9.2(1.8)	8.3(2.0)	15.4(1.9)
1834 × 4535	High	18.0(2.9)		18.1(2.9)	13.2(2.8)	15.8(1.9)
	Average	17.3	17.3(3.1)	14.3	14.2	16.8(0.9)
	Low	16.6(3.6)		10.5(2.8)	9.9(2.1)	16.8(0.9)
					11.6(1.9)	7.0(1.4)
					10.7(1.7)	8.6(2.0)
					10.1(1.1)	
					21.9(1.8)	
					11.6(1.9)	
					10.7(1.7)	
					7.7(1.6)	

^z Values are mean pungency (s.d.). ^y Average: midparent for parental generation, actual values for F₁, and average of high selections and low selections for F₂, F₃ and F₃M.

was evident. Both broad-sense heritability estimates and the distribution of segregants in F₂ and BC generations also suggested that selection for both traits should be effective and this was found to be true in F₃ and F₃M families selected for pungency. Interestingly, the strong positive correlation between pyruvate and soluble solids noted in parental inbreds and F₁ hybrids was greatly reduced within and among F₃ and F₃M families to suggest that it is possible to exercise selec-

tion for high solids, low pungency onion which would be of much interest for the fresh onion market.

Table 9. Simple phenotypic correlations for pungency and solids in populations of onion

Populations	Year			
	1	2	3	4
Diallel parents	0.54**	0.48**	0.88**	0.75**
Diallel hybrids	0.47**	0.31*	0.89**	0.67**
Among F ₂ 's and BC ₁ 's		0.66**		0.61**
Among F ₃ 's			0.26	
Among F ₃ M's			0.28	
Within selected F ₂ 's & F ₃ 's:				
(8155 × 2399) (low)	F ₂		0.34	
	F ₃		-0.16	
(8155 × 1834) (low)	F ₂		0.40*	
	F ₃		0.32*	
(8155 × 4535) (high)	F ₂		0.20	
	F ₃		-0.27*	
(1834 × 4353) (low)	F ₂		-0.22	
	F ₃		-0.39*	
(1834 × 4353) (low)	F ₂		0.18	
	F ₃		-0.16	
(1834 × 4353) (high)	F ₂		0.44*	
	F ₃		0.29*	
(1834 × 4353) (high)	F ₂		0.30*	
	F ₃		0.04	

*, ** – Significant probability at 5%, 1% levels, respectively.

References

- Baker, R.J., 1978. Issues in diallel analysis. *Crop Sci.* 18: 533–536.
- Dudley, J.W., 1987. Modification of methods for identifying populations to be used for improving parents of elite single crosses. *Crop Sci.* 27: 940–943.
- Griffing, B., 1956. Concept of general and specific combining ability in relation to diallel crossing systems. *Aust. J. Biol. Sci.* 9: 463–493.
- Kadams, A.M. & C.C. Nwasike, 1986. Heritability and correlation studies of some vegetative traits in Nigerian local white onion. *Plant Breeding* 97: 232–236.
- Lin, M.-W., J.F. Watson, & J.R. Baggett, 1995. Inheritance of soluble solids and pyruvic acid content of bulb onions. *J. Amer. Soc. Hort. Sci.* 120: 119–122.
- Mahmud, I. & H.H. Kramer, 1951. Segregation for yield, height, and maturity following a soybean cross. *Agron. J.* 43: 605–609.
- Mann, L.K. & B.J. Hoyle, 1945. Use of the refractometer for selection onion bulbs high in dry matter for breeding. *Proc. Amer. Soc. Hort. Sci.* 46: 285–292.
- Mather, K. & J.C. Jinks, 1977. Introduction to biometrical genetics. Cornell University Press, Ithaca, New York.
- McCollum, G.D., 1968. Heritability and genetic correlation of soluble solids, bulb size and shape in white Sweet Spanish onion. *Can. J. Genet. Cytol.* 10: 508–514.
- Owen, E.W., 1961. The inheritance of dry matter in onion bulbs. M.S. Thesis, Univ. Idaho, Moscow, Idaho. 35 p.
- Pal, N. & N. Singh, 1988. Analysis of genetic architecture of pungency (pyruvic acid) in onion. *Plant Breeding Abstract* 1988: 379.
- Rowe, K.E. & W.L. Alexander, 1980. Computations for estimating the genetic parameters in joint-scale tests. *Crop Sci.* 20: 109–110.
- Schwimmer, S. & W.J. Weston, 1961. Enzymatic development of pyruvic acid in onion as a measure of pungency. *J. Agr. Food Chem.* 9: 301–304.
- Warid, W.A., 1952. Inheritance studies in the onion. Ph.D. Thesis, Louisiana State University, Louisiana. 221 p.