13. Kotowski, F. 1926. Temperature relations to germination of vegetable seed. *Proc. Amer. Soc. Hort. Sci.* 23:176-184.
14. Obendorf, R. L. and P. R. Hobbs. 1970. Effect of seed moisture on temperature sensitivity during imbibition of soybean. *Crop Sci.* 10:563-566.
15. Phillips, J. C. and V. E. Youngman. 1971. Effect of initial seed moisture content on emergence and yield of grain sorghum. *Crop Sci.* 11:354-357.
16. Pollock, B. M. 1969. Imbibition temperature sensitivity of lima bean seeds controlled by initial seed moisture. *Plant Physiol.* 44:907-911.
17. ________, E. E. Roos, and J. R. Manalo. 1969. Vigor of garden bean seeds and seedlings influenced by initial seed moisture, substrate oxygen, and imbibition temperature. *J. Amer. Soc. Hort. Sci.* 94:577-584.
18. ________ and V. K. Toole. 1966. Imbibition period as the critical temperature sensitive stage in germination of lima bean seeds. *Plant Physiol.* 41:221-229.
19. Toole, V. K., R. E. Wester, and E. H. Toole. 1951. Relative germination response of some lima bean varieties to low temperatures in sterilized and unsterilized soil. *Proc. Amer. Soc. Hort. Sci.* 58:153-159.
20. Winston, P. W. and D. H. Bates. 1960. Saturated solutions for the control of humidity in biological research. *Ecology* 41:232-237.

J. Amer. Soc. Hort. Sci. 101(3):324–329. 1976.

A Ten-parent Diallel Cross to Evaluate Inbred Line Performance and Combining Ability in Onions[1]

George L. Hosfield[2], Grant Vest[3], and C. E. Peterson[2,4]
Agricultural Research Service, North Central Region, U.S. Department of Agriculture, Madison, WI 53706

Additional index words. genetic variance, environmental stability, genotype x environmental interaction, relic heterozygosity, composite population, gene pools, population improvement, gene fixation

Abstract. **The diallel cross technique was used to evaluate the performance of onion (*Allium cepa* L.) inbred lines in F_1 combinations and to estimate combining ability of several traits. All possible crosses, including reciprocals, among 10 inbred lines of diverse origin and known horticultural performance were tested at 3 locations in 1973. Cytoplasmic male-sterility was used to insure that all seed from maternal plants was hybrid. Cross variances were highly significant for all traits at all locations. General combining ability effects accounted for most of these differences. Specific combining ability effects were significant at all locations for yield, weight/bulb, firmness, and percent of storage loss. In all instances variance components of general combining ability were larger than those of specific combining ability. Specific rankings of the best and poorest lines for the traits measured according to the effects of their general combining ability were not identical at each location, but the same inbreds were generally in the same positive or negative grouping. Inbreds M728 and M2399 transmitted substantial yield and bulb weight to their progeny, while Ia163 consistently depressed these traits in the F_1's. These results confirm the contribution that inbreds M728, M2399, and Ia163 make to a hybrid. Significant mean squares for reciprocal effects were apparent at all locations for only yield and maturity. Maternal effects per se influenced reciprocal variation, but were, generally, less important than nonmaternal reciprocal causes.**

Early breeding work in onions demonstrated that the loss of vigor with successive generations of inbreeding was restored after hybridization, and that F_1's from crosses of inbred lines were more uniform than parental populations in size, shape, color of bulbs, and other traits (12). The discovery of cytoplasmic-genic male sterility in onions by Jones and Clarke (11) enabled hybridization to be accomplished with ease and made practical the commercial production of hybrid seed. The improved yield, storage quality, bulb uniformity, and maturity of F_1 hybrids resulted in their prompt commercial acceptance.

The development of large numbers of high quality male-sterile and male-fertile inbred pairs was slow because onions are biennial. With the few lines available, breeders tested hybrid combinations empirically. They developed inbreds that were vigorous, good keepers, and attractive and tested them in the most promising combinations. Thus, as a consequence of three decades of hybrid onion breeding with relatively small numbers of high-performing inbreds, breeders have made observations and conclusions as to the contribution these lines made in hybrid combinations. Today, with an ever-increasing inventory of high-quality inbreds available, onion breeders must develop a more sophisticated and efficient approach to selecting and testing parents that will produce superior hybrid varieties.

A diallel crossing system can be used to evaluate systematically inbred performance in F_1 combinations. This technique also provides an analytical tool to estimate the combining ability (15) of the traits under selection and to evaluate the selection potential of individual crosses. Superior-performing crosses will produce segregates that are also highly productive (10).

We undertook the present investigation to obtain quantitative genetic information resulting from diallel crosses in onions, and to consider its implications for future onion breeding programs.

---

[1] Received for publication December 19, 1975. Results of cooperation between the Agricultural Research Service, USDA, and Departments of Horticulture, University of Wisconsin, Madison, WI, 53706, and Michigan State University, East Lansing, MI, 48823. Research supported, in part, by the College of Agriculture and Life Sciences, University of Wisconsin.

[2] Research Geneticist and Research Horticulturist, NCR, ARS, USDA, respectively.

[3] Associate Professor of Horticulture, Michigan State University.

[4] The authors thank Dr. F. E. Moeller and Mr. Emmett Harp, ARS, USDA, North Central States bee research laboratory, Madison, WI, for supplying honeybees. Appreciation is extended to Dr. R. R. Smith, ARS, USDA, Dept. of Agronomy, Univ. of Wis., Madison, for statistical advice.

[5] Mention of a trade name, proprietary product, or specific equipment does not constitute a guarantee or warranty by the U.S. Department of Agriculture and does not imply its approval to the exclusion of other products that may be suitable.

[6] Nyquist, W. E. 1966. Diallel cross analysis of general, specific, maternal, and nonmaternal reciprocal effects. Unpublished mimeo for a computer program. Agronomy Department, Purdue University, Lafayette, Indiana 47907.

Materials and Methods

Ten inbred onion lines adapted to the muck soils of the northern Midwest were selected as parents. The lines Beltsville (B) 2264 and 2190; Iowa (Ia) 163; Michigan (M) 728, 1411, 2935, and 2399; Rochester Bronze (Rb) 101; and Wisconsin (W) 202 and 404 were chosen to provide a broad genetic base. These lines have been used for many years in various hybrids, and their performances in F_1 combinations have been evaluated.

Seed of the 90 crosses generated by this diallel were planted in 1973 in a randomized complete block with 4 replications near Palmyra and Randolph, Wisconsin, and East Lansing, Michigan. These locations differed in length of growing season, latitude, rainfall, temperature, and muck soil type. F_1 plants were grown in 3.66-m (12-ft) long single rows spaced 53 cm (21 inches) apart. Plants were thinned to 5.1 cm (2 inches) apart, and mature bulbs were harvested from the center 2.44 m (8 ft) of row. After harvesting and weighing for yield, a 25-bulb sample at each location was placed in storage for evaluations on keeping quality. Another 10-bulb sample from each plot was evaluated within 2 months after harvest for firmness and internal characteristics.

The following traits were measured: 1. maturity (no. of days from planting until 50% of the "tops" were down); 2. yield (total fresh wt of harvested bulbs in q/ha); 3. bulb wt (g/bulb); 4. firmness (average of 5 pressure readings per bulb with a Shore type "0-2" durometer[5] from a 10-bulb sample/replication); 5. rings/bulb (no. of complete circular rings per bulb); 6. no. of centers (no. of meristematic areas, growing points, surrounded by a complete circular ring); 7. ring thickness (radius of the complete rings divided by the no. of rings, in mm); 8. storage loss (% of original storage wt).

Plot means were calculated for all traits except maturity, yield, and storage loss, which are reported as plot totals. Analyses of variance were performed on data for each location. Percentage data for storage loss were transformed by the arcsin $\sqrt{X}$ transformation before any analyses were performed. Means and mean effects (effects of GCA) were transformed back to the original scale and are presented in tables as percent. Because the variation associated with crosses was significant for all traits at all three locations, analyses of combining ability were performed using the program of Nyquist[6]. In this program, the theory for combining ability formulas is the same as that of Griffing's Model 1, Method 3(6), but his analysis was extended to include the partition of F_1 reciprocal variation into maternal and nonmaternal sources according to Cockerham (1). In Griffing's Model 1 all effects are fixed, and the experimental material is the population about which inferences are made.

Estimates of variance components were calculated for each source of the combining-ability analyses of variance with appropriate algebraic manipulation of terms comprising the expected mean squares. The components in their general terms are presented as follows:

$$\text{variance component for general combining ability} = \frac{\Sigma g_i^2}{p-1}$$

$$\text{variance component for specific combining ability} = \frac{2}{p(p-3)} \sum_{i<j}\sum s_{ij}^2$$

$$\text{reciprocal variance component} = \frac{2}{p(p-1)} \sum_{i<j}\sum r^1{}_{ij}^2$$

$$\text{variance component for maternal effects} = \frac{\Sigma m_i^2}{p-1}$$

$$\text{variance component for nonmaternal reciprocal effects} = \frac{2}{p(p-2)} \sum_{i<j}\sum r_{ij}^2;$$

where g_i is the GCA effect of the i_{th} parent, s_{ij} is the SCA effect for the cross between the i_{th} and j_{th} parent, r^1 is the reciprocal effect involving the reciprocal crosses between the i_{th} and j_{th} parents, m_i is the sex effect of the i_{th} parent, r_{ij} is the nonmaternal reciprocal effect of the i_{th} and j_{th} parents, and p is the no. of parents which equals 10.

Results

Experiment means, their standard errors, and coefficients of variability (CV) are presented for each trait at each location (Table 1). Because information of this kind is limited, these results will serve as a point of reference for future onion experiments. Error mean squares from the separate analyses of variance were not homogeneous (Table 2) as determined by Bartlett's procedure described in Snedecor (14).

Cross mean squares were statistically significant for all traits at the three locations (Table 2). These genotypic differences were further investigated by analyses for combining ability, in which cross variation was partitioned into general combining ability (GCA), specific combining ability (SCA), and reciprocal effects. Variation from reciprocal effects was further broken down into maternal and nonmaternal causes. The GCA was highly significant for all traits at East Lansing and for 5 and 7 characters at Palmyra and Randolph, respectively. No SCA differences were significant for ring thickness, rings/bulb, and centers/bulb at Palmyra, but the mean squares for these traits were significant at Randolph. No SCA differences among crosses were significant for maturity at Randolph, but differences were noted for this trait at Palmyra. These observations suggest that the environment strongly affects the SCA of some traits. Differences among crosses for reciprocal effects at all 3 locations were apparent only for yield and maturity (Table 2). Reciprocal effect mean squares for the other 6 traits varied from location to location with respect to significance patterns. Maternal effect mean squares were always significant for yield, maturity, ring

Table 1. Means, standard errors, and coefficients of variation for yield, maturity, bulb traits, and storage performance of onion, measured on progeny of a ten-parent diallel evaluated at 3 locations, 1973.

	Palmyra			Randolph			East Lansing		
Character	General mean	Standard error	CV (%)	General mean	Standard error	CV (%)	General mean	Standard error	CV (%)
1. Yield (q/ha)	388	30.1	11.0	531	33.6	9.0	407	56.9	19.8
2. Maturity (days)	109	2.7	3.5	111	1.8	2.3	122	0.7	0.8
3. Bulb wt (g)	86.2	9.1	12.5	136.1	9.1	9.6	113.4	13.6	16.3
4. Rings/bulb (no.)[z]	5.5	0.4	9.6	5.1	0.3	8.2	5.2	0.4	9.4
5. Ring thickness (mm)	3.3	0.2	7.3	3.3	0.2	6.9	–	–	–
6. Firmness (scale)[z,y]	81.5	1.0	1.6	82.5	0.7	1.1	83.7	0.8	1.1
7. Centers/bulb (no.)[z]	1.7	0.1	11.4	1.9	0.1	5.7	1.8	0.2	10.5
8. Storage loss (%)[z]	84.9	6.2	10.4	62.9	6.8	15.3	19.8	4.3	26.8

[z] Data based on 3 replications at East Lansing.

[y] Durometer units on a scale from 0 to 100; firmer onions have the larger numbers.

Table 2. Mean squares from analyses of variance and combining ability analyses of variance of 8 quantitative traits of onion measured on progeny of a 10-parent diallel at 3 locations, 1973.

Location and source of variation	Yield and related characters				Quality characters			
	Yield (q/ha)	Maturity (days)	Bulb wt (g)	Rings/ bulb (no.)	Ring thickness (mm)	Firmness[y] (scale)	Centers/ bulb (no.)	Storage loss (%)
Palmyra								
Reps	22,391	223.7	412	0.72	1.98	110.0	0.49	1,912
Crosses	24,642**	80.3**	742**	1.23**	0.27**	7.3**	0.10**	586**
GCA	150,827**	492.5**	4,844**	8.43**	1.92**	48.5**	0.59**	4,579**
SCA	14,400**	49.2**	309**	0.37	0.07	4.0**	0.05	142**
Reciprocal	7,371**	22.1*	247**	0.46**	0.08	1.7	0.04	132**
Maternal	8,434**	44.5**	144	0.36	0.10	2.1	0.03	271**
Nonmaternal	7,105**	16.5	268**	0.48**	0.08	1.6	0.04	98
Error	3,621	14.9	124	0.28	0.06	1.8	0.04	77
Randolph								
Reps	31,278	128.6	2,061	0.02	0.37	122.1	0.06	8,450
Crosses	52,307**	36.3**	2,226**	1.53**	0.25**	3.5**	0.03**	687**
GCA	385,499**	266.3**	16,737**	12.32**	1.65**	22.4**	0.15**	5,300**
SCA	15,710**	6.0	515**	0.55**	0.09*	1.4**	0.03**	247**
Reciprocal	14,137**	13.9**	660**	0.14	0.09**	1.2*	0.02	106
Maternal	16,280**	21.8**	371**	0.22	0.13*	2.0**	0.01	89
Nonmaternal	13,601**	12.0**	721**	0.13	0.08*	1.1	0.02	111
Error	4,519	6.6	165	0.17	0.05	0.9	0.01	93
East Lansing[z]								
Reps	452,397	494.9	20,096	0.08	–	1.4	0.11	86
Crosses	44,962**	172.4**	2,346**	1.53**	–	4.3**	0.14**	232**
GCA	246,268**	1,199.3**	17,273**	11.50**	–	23.8**	0.80**	1,607**
SCA	26,466**	74.3**	907**	0.52**	–	1.4*	0.08**	153**
Reciprocal	19,087*	43.3**	515	0.31	–	2.8**	0.06*	19
Maternal	29,500*	75.8**	474	0.43	–	10.6**	0.13**	14
Nonmaternal	16,483	35.2**	515	0.28	–	0.8	0.04	20
Error	12,950	0.9	350	0.24	–	0.9	0.04	28

*,**Significant at the 5% (*) and 1% (**) probability level.

[z] Rings per bulb and quality character data based on 3 replications.

[y] Durometer units on a scale from 0 to 100; firmer onions have the larger numbers.

thickness, firmness, centers/bulb, and storage loss when reciprocal effect F-tests showed significance for these traits (Table 2).

The GCA variance components were always larger than SCA components (Table 3). Thus, additive gene effects of the inbred lines were more important than their nonadditive effects in determining performance in crosses. In most cases, maternal variance components were smaller than nonmaternal reciprocal components. This suggests that for most traits evaluated, nonmaternal reciprocal effects contributed more to the total genetic variance than maternal effects.

Although specific rankings of the best and poorest lines according to their GCA effects were not exactly the same at each location, the same inbreds were generally in the same positive or negative grouping (Table 4). The only exception was inbred M728, which had a –0.34 value for bulb firmness when grown at Palmyra and a +0.57 for this trait when grown at East Lansing. Inbreds M728 and M2399 exhibited significant favorable GCA effects for yield and bulb weight at all locations, but Ia163 consistently depressed the performance of its F_1's for these traits at each environment.

Discussion

Utility in breeding. Our results substantiate the conclusions previously noted as to the contribution these onion lines make to hybrids. Breeders have observed that M2399 and Ia163 are good and poor general combiners, respectively, for yield. When one considers the GCA effect for this trait averaged across locations, M2399 was the highest and Ia163 the lowest yielder, respectively, of the 10 inbreds we evaluated. The Wisconsin inbreds, 202 and 404, are relatively firm onions. Based on their high positive CGA effect for firmness, these inbreds can be expected to transmit this quality to F_1's. Negative GCA effects for some traits (Table 4) are of interest because some lines can subtract from the general mean of a particular character. Some breeding programs are concentrating efforts to develop onion hybrids that are early maturing, single centered, and good keepers. Lines exhibiting significant negative GCA effects for maturity, centers/bulb, and storage loss should be noted and could possibly be utilized in such an onion selection program.

Genetic variance. Because GCA and SCA can be interpreted in terms of additive and nonadditive genetic variance, respectively, the partitioning of cross variation into these components gives a description of the genetic situation in a set of lines (8). The type of genetic variance in the reference population indicates the type of breeding scheme that will maximize trait improvement – the kind of material to select and those traits that capitalize on the heterotic effects of hybridization. Although most of the differences noted among crosses for all characters were due to genes with primarily additive effects, the small but significant amounts on non-additive variance present cannot be overlooked. For yield, maturity, and storage loss, non-additive variance is ample for use in specific hybrid combinations.

Environmental influences. Comparisons of the average performance in individual lines (Table 4) indicate that the stability of a line to environmental differences can be assessed. Inbreds M728 and M2399 demonstrated clear-cut superiority to other lines for transmitting to their F_1's across environments a high yield and a high performance level of some of the other traits. On the other hand, Ia163 was a poor combiner for yield at all three locations. Other lines performed well in hybrid combinations at one location but not another. Hybrids with

Table 3. Variance components and their standard deviations for yield, maturity, bulb traits, and keeping quality of onion, estimated at 3 locations from a 10-parent diallel, 1973.

Character	Component				Nonmaternal reciprocal
	GCA	SCA	Reciprocal	Maternal	
Palmyra					
1. Yield (q/ha)	2,300 ± 990	1,347 ± 386	469 ± 177	60.2 ± 44.7	435 ± 190
2. Maturity (days)	7.5 ± 3.6	4.3 ± 1.5	0.905 ± 0.6	0.371 ± 0.26	0.204 ± 0.51
3. Bulb wt (g)	82.5 ± 0.0	20.6 ± 0.0	20.6 ± 0.0	0.00 ± 731	20.6 ± 0.0
3. Rings/bulb (no.)	0.127 ± 0.1	0.011 ± 0.25	0.022 ± 0.01	0.001 ± 0.002	0.025 ± 0.01
5. Ring thickness (mm)	0.029 ± 0.01	0.002 ± 0.06	0.003 ± 0.002	0.0005 ± 0.0006	0.003 ± 0.003
6. Firmness (scale)	0.730 ± 0.4	0.267 ± 1.5	−0.008 ± 0.05	0.004 ± 0.01	−0.020 ± 0.05
7. Centers/bulb (no.)	0.009 ± 0.004	0.002 ± 0.02	−0.0002 ± 0.001	−0.0001 ± 0.0002	0.000 ± 0.001
8. Storage loss (%)	70.3 ± 33.7	8.1 ± 4.3	6.9 ± 3.6	2.4 ± 1.6	2.5 ± 3.0
Randolph					
1. Yield (q/ha)	5,953 ± 2,529	1.399 ± 421	1,202 ± 335	147 ± 86	1,135 ± 360
2. Maturity (days)	4.1 ± 2.0	−0.076 ± 0.19	0.913 ± 0.387	0.190 ± 0.13	0.67 ± 0.36
3. Bulb wt (g)	268 ± 0.3	41.2 ± 0.0	61.8 ± 0.0	0.00 ± 0.00	61.8 ± 0.1
4. Rings/bulb (no.)	0.190 ± 0.091	0.047 ± 0.016	−0.004 ± 0.004	0.0006 ± 0.001	−0.006 ± 0.005
5. Ring thickness (mm)	0.025 ± 0.012	0.005 ± 0.003	0.005 ± 0.002	0.001 ± 0.001	0.004 ± 0.003
6. Firmness (scale)	0.337 ± 0.165	0.070 ± 0.04	0.046 ± 0.034	0.014 ± 0.012	0.023 ± 0.03
7. Centers/bulb (no.)	0.002 ± 0.001	0.002 ± 0.001	0.0004 ± 0.0004	−0.0001 ± 0.01	0.001 ± 0.001
8. Storage loss (%)	81.4 ± 38.9	19.3 ± 7.4	1.7 ± 3.0	−0.1 ± 1.7	2.3 ± 3.4
East Lansing					
1. Yield (q/ha)	3,646 ± 1,616	1,690 ± 717	767 ± 466	207 ± 156	442 ± 451
2. Maturity (days)	18.7 ± 8.8	9.2 ± 2.2	5.3 ± 1.1	0.94 ± 0.45	4.3 ± 1.0
3. Bulb wt (g)	268 ± 0.3	61.8 ± 0.1	20.6 ± 0.0	0.00 ± 0.00	20.6 ± 0.1
4. Rings/bulb (no.)^z	0.24 ± 0.11	0.048 ± 0.062	0.012 ± 0.012	0.003 ± 0.003	0.008 ± 0.01
5. Ring thickness (mm)	--	--	--	--	--
6. Firmness (scale)^z	0.48 ± 0.23	0.088 ± 0.057	0.32 ± 0.10	0.16 ± 0.08	−0.01 ± 0.03
7. Centers/bulb (no.)^z	0.016 ± 0.008	0.008 ± 0.003	0.003 ± 0.002	0.002 ± 0.001	0.000 ± 0.002
8. Storage loss (%)^z	32.9 ± 15.7	20.7 ± 6.1	−1.5 ± 0.8	−0.24 ± 0.12	−1.3 ± 0.9

^{z}Data based on 3 replications.

W202 as a parent exhibited higher-than-average yields at Randolph, but low yields at Palmyra and East Lansing. Randolph is the northernmost location and generally has the shortest growing season. Moreover, W202 was selected at a location near Randolph; thus, this line probably represents an inbred that would combine well with others only in this specific environment. On the other hand, the environmental adaptability of RB101 was unpredictable. It was also selected near Randolph, but its performance in hybrid combination for yield was superior only at East Lansing. Experiments designed to evaluate the magnitude of genotype × environmental interactions are in order because the ability of the breeder to correctly evaluate horticultural performance of cultivars over wide areas and future years is essential to onion hybrid development. Moreover, the value of an inbred that combines well only under special conditions (e.g. yielding ability of W202 at Randolph) is dependent on the predictability of those conditions (2).

CV's associated with the 8 traits studied were acceptable for the 3 locations. However, at East Lansing, yield and storage loss had CV's that were 2 and 2½ times as large, respectively, as the average of the Wisconsin locations. This suggests that areas with diverse environments such as Wisconsin and Michigan, may be too variable for comparative tests on yield and keeping quality in onions. This possibility indicates that the breeder should be cautious: if onion hybrids are being considered for a general area, component lines should be tested under a wide range of environments early in their development.

Yielding ability. This study showed the ways some inbreds might transmit yielding ability to their F_1's. For instance, the high average yield across locations associated with M2399 was a result of bulb wt (Table 4). This, in turn, was influenced by the ability of M2399 to effectively transmit increased rings and ring thickness to its progeny. Combinations with M2399 matured later than did hybrids for most other lines. Thus, in average or long-season localities the later-maturing F_1 combinations of M2399 are able to utilize the longer season, which results in increased yields. Conversely, Ia163 depressed yield and bulb wt in its hybrids. This response was most likely due to the earliness Ia163 transmits to its F_1's.

Hybrids with M728 were late maturing and had high bulb wt and yields, but this inbred appears to transmit its yielding ability differently than M2399 does. While M2399 adds thick rings to its hybrids, M728 transmits thin rings; M728 transmits a higher degree of firmness than does M2399. This suggests that M728 may have a higher dry-matter content that is passed on to its hybrids. Although we have no direct evidence to support this, McCollum (13) has reported small but statistically significant positive phenotypic correlations between dry matter and bulb wt for some onion types. It is tempting to speculate that F_1 combinations with M2399 attain their bulb size and high yields by taking up more water late in the season than do hybrids with M728.

Reciprocal differences. The presence of reciprocal and maternal effects indicates that the choice of a parent to be used as either a pollen or seed parent might affect the performance of an F_1. Although reciprocal variation was inconsistent from location to location for most traits, variants between inbred components (male-sterile and male-fertile counterparts) are important for yield and maturity. Causes of reciprocal effects and their possible utilization in hybrid onion production warrants further investigation.

While reciprocal and maternal differences are generally absent in most plant species, these effects could arise in onions because of relic heterozygosity present in an essentially homozygous seed (nonrecurrent) parent after its development by backcrossing. Although both components of an inbred are virtually identical according to backcross theory and their coefficient of relationship (16), it is doubtful that by backcrossing one can recover the complete genotype of the recurrent (male-fertile) parent. Reports in the literature for other plant

Table 4. Estimates of general combining ability effects for 8 quantitative traits measured on F_1 progeny of a 10-parent onion diallel cross grown at 3 locations, 1973.

Location & inbred parent	Yield and related characters					Quality characters		
	Yield (q/ha)	Maturity (days)	Bulb wt (g)	Rings/ bulb (no.)	Ring thickness (mm)	Firmness[z] (scale)	Centers/ bulb (no.)	Storage loss (%)
Palmyra								
B2264	−8.6	−3.0	−5.0	0.12	−0.12	0.02	0.06	9.8
Ia163	−11.0	−5.4	−4.4	−0.02	0.12	0.37	−0.08	11.3
M728	26.1	2.6	8.9	−0.09	−0.02	−0.34	0.06	−2.3
Rb101	−1.7	1.6	−0.6	−0.76	−0.09	−0.60	0.15	10.4
M1411	−36.4	−0.9	−7.5	−0.22	−0.32	1.21	0.08	−2.5
B2190	21.3	−0.8	6.4	−0.11	0.03	0.06	0.05	2.5
M2935	−30.1	3.5	0.4	0.26	−0.11	−0.02	−0.04	−14.1
M2399	76.3	2.8	17.9	0.36	0.31	−1.95	−0.12	−7.5
W202	−1.0	−0.4	−5.9	0.56	0.09	0.35	−0.16	−6.2
W404	−34.9	0.1	−10.2	−0.09	0.11	0.91	0.00	−1.4
SE[y]	±7.5	±0.7	±1.9	±0.09	±0.04	±0.24	±0.04	±1.6
Randolph								
B2264	−36.8	−1.7	−13.2	−0.14	−0.11	0.03	0.01	7.4
Ia163	−75.4	−3.9	−21.4	−0.34	0.09	0.41	−0.06	5.8
M728	48.4	2.8	20.7	0.09	−0.07	0.11	0.04	−7.6
Rb101	−7.7	−1.2	−4.9	−0.60	−0.04	−0.88	0.03	17.1
M1411	−11.0	−0.7	−2.3	−0.40	−0.28	0.40	0.08	−0.2
B2190	−14.8	0.7	1.2	−0.29	0.05	−0.08	0.04	2.7
M2935	−19.7	2.2	4.2	0.38	−0.16	0.31	−0.04	−14.5
M2399	115.3	2.1	29.9	0.49	0.23	−1.23	−0.02	−6.0
W202	43.6	−0.1	3.9	0.78	0.18	0.40	−0.07	−7.1
W404	−41.8	−0.2	−18.2	0.01	0.11	0.51	−0.01	2.4
SE	±8.4	±0.5	±2.3	±0.07	±0.04	±0.17	±0.02	±1.7
East Lansing[x]								
B2264	−24.7	−4.3	−13.2	−0.08	–	0.35	0.03	2.7
Ia163	−81.1	−10.0	−26.3	−0.15	–	0.70	−0.15	9.9
M728	30.4	1.9	13.3	−0.06	–	0.57	0.08	−6.7
Rb101	63.5	2.4	7.6	−0.81	–	−0.64	0.17	6.9
M1411	−7.3	0.9	1.1	−0.48	–	0.28	0.21	−1.1
B2190	−9.8	−1.0	−2.0	−0.10	–	−0.25	0.01	3.5
M2935	−2.7	4.9	14.4	0.43	–	−0.45	0.00	−6.0
M2399	66.3	3.0	28.8	0.59	–	−1.46	−0.09	−5.4
W202	−16.0	−0.1	−10.5	0.82	–	0.11	−0.20	−4.8
W404	−18.7	2.5	−13.3	−0.16	–	0.79	−0.05	1.0
SE	±14.2	±0.2	±3.3	±0.10	–	±0.19	±0.04	±1.1

[z] Durometer units on a scale from 0 to 100; firmer onions have the larger numbers.

[y] Standard error of the difference between two GCA effects.

[x] Rings per bulb and quality character data based on three replications.

species indicate that even small adhering segments of donor (nonrecurrent) parent chromosomes show marked effects on the phenotypes of these otherwise homozygous lines (5, 9).

Implications on hybrid breeding methodology. The development of new hybrids by random inbreeding is extremely inefficient; this problem is further augmented if no provision is made within the breeding program to produce improved populations as future gene pool sources (7). Population improvement should be given equal consideration with inbred development in any hybrid breeding program. Eberhart, Harrison, and Ogada (3) have outlined a comprehensive breeding system for *Zea mays* L. that provides an efficient method for population improvement in each cycle of selection while at the same time provides selected progenies for further inbreeding and testing. In its most general form, this procedure is a recurrent selection scheme practiced within a composite population.

Since both additive and nonadditive genetic variances were detected in the reference population we studied, and assuming this genetic situation is common in onions, selection methodology that most effectively uses both types of variance should be practiced. The comprehensive breeding scheme (3) could be modified to fit the pollen control situation in onions and adapted to effectively utilize both additive and nonadditive genetic variance. By using such a scheme, the onion breeder could follow a systematic and multi-step approach in his development of future hybrid varieties.

The selection of superior breeding material is the first phase of the comprehensive approach (3) to developing future onion hybrids. This would best be accomplished by compositing lines identified by a diallel crossing system as having the highest favorable general combining ability effects. Another consideration to be kept in mind is that the amount of heterosis following a cross between two particular lines depends on the square of the difference of gene frequency between lines (4). Therefore, crosses between genetically diverse parents generally exhibit more heterosis than crosses between more closely related strains. This suggests that it would be fruitful to simultaneously develop several breeding populations which are genetically diverse.

The second phase in the multi-step approach to producing new hybrids in onions is to improve the source populations themselves and at the same time develop lines which combine to produce superior progeny. During this stage of selection, the additive genetic variance present in the source population would be effectively utilized and the frequency of favorable genes would increase. Moreover, as each breeding population is improved, it will diverge from other populations with respect to gene frequencies of favorable alleles. Ultimately, as a major portion of these favorable genes become fixed and the additive genetic variance is exhausted, breeding procedures which utilize the nonadditive variance should be employed. This would be accomplished by isolating the best lines from each selection cycle and inbreeding further.

The final step in the hybrid onion program is to intercross high performing lines isolated from genetically diverse populations. The diallel crossing procedure would be effective to identify specific cross combinations that exhibit maximum heterosis.

Literature Cited

1. Cockerham, C. C. 1963. Estimation of genetic variances. p. 53-94. *In* W. D. Hanson and H. F. Robinson (ed.) Statistical genetics and plant breeding. Nat. Acad. Sci. Nat. Res. Coun. Pub. 982.
2. Comstock, R. E. and R. H. Moll. Genotype-environment interactions. p. 164-196. *In* W. D. Hanson and H. F. Robinson (ed.) Statistical genetics and plant breeding. Nat. Acad. Sci. Res. Coun. Pub. 982.
3. Eberhart, S. A., M. N. Harrison, and F. Ogada. 1967. A comprehensive breeding system. *Zuchter* 37:169-174.
4. Falconer, D. S. 1960. Introduction to quantitative genetics. The Ronald Press Co., New York.
5. Fasoulas, A. C. and R. W. Allard. 1962. Nonallelic gene interactions in the inheritance of quantitative characters of barley. *Genetics* 47:899-907.
6. Griffing, B. 1956. Concept of general and specific combining ability in relation to diallel crossing systems. *Austral. J. Biol. Sci.* 9:463-493.
7. Hallauer, A. R. and S. A. Eberhart. 1970. Reciprocal full-sib selection. *Crop Sci.* 10:315-316.
8. Hayman, B. I. 1960. The theory and analysis of diallel crosses. III. *Genetics* 45:155-172.
9. Hosfield, G. L., J. A. Lee, and J. O. Rawlings. 1970. Agronomic properties associated with the glandless alleles in two varieties of upland cotton. *Crop Sci.* 10:392-395.
10. Johnson, L. P. V. 1963. Applications of the diallel-cross techniques to plant breeding. p. 561-570. *In* W. D. Hanson and H. F. Robinson (ed.) Statistical genetics and plant breeding. Nat. Acad. Sci. Nat. Res. Coun. Pub. 982.
11. Jones, H. A. and A. E. Clarke. 1943. Inheritance of male sterility in the onion and the production of hybrid seed. *Proc. Amer. Soc. Hort. Sci.* 43:189-194.
12. ———and G. N. Davis. 1944. Inbreeding and heterosis and their relation to the development of new varieties of onions. *U.S. Dept. Agr. Tech. Bul.* 874.
13. 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.
14. Snedecor, G.W. 1964. Statistical methods. Iowa State Univ. Press, Ames.
15. Sprague, G. F. and L. A. Tatum. 1942. General vs. specific combining ability in single crosses of corn. *J. Amer. Soc. Agron.* 34:923-932.
16. Wright, S. 1922. Coefficient of inbreeding and relationship. *Amer. Naturalist* 56:330-338.

J. Amer. Soc. Hort. Sci. 101(3):329–331. 1976.

Changes in Glycoalkaloid Content following Mechanical Injuries to Potato Tubers[1]

M. T. Wu and D. K. Salunkhe
Department of Nutrition and Food Sciences, Utah State University, Logan, UT 84322

Additional index words. Solanum tuberosum, glycoalkaloid, mechanical injuries

Abstract. **Mechanical injuries of tubers of potato (*Solanum tuberosum* L.) such as brushing, cutting, dropping, puncturing, and hammering greatly stimulated glycoalkaloid synthesis in both peel and flesh of tubers. The extent of glycoalkaloid formation depended on cultivar, type of mechanical injury, storage temperature, and duration of storage. High temperature storage stimulated more glycoalkaloid formation than that of low temperature. Most of the injury-stimulated glycoalkaloid formation occurred within 15 days after treatments. Mechanical injury caused by cutting of tubers resulted in the highest contents of glycoalkaloids both in flesh and peel.**

Considerable literature exists concerning cases of potato related poisoning in man and farm animals. The poisoning was attributed to the ingestion of large amounts of glycoalkaloids in the green tubers or sprouts. Glycoalkaloids which are potent cholinesterase inhibitors occur in potato tubers in various amounts depending upon the variety, stage of development, and environmental conditions. That an increased content of glycoalkaloids in tubers results from light exposures is well known (1, 2, 3, 4, 5, 7, 12, 13, 14). By removing slices of tissue parallel to the wounded surface of potato tubers at intervals after wounding, McKee (6) showed that solanine, one of the major glycoalkaloids, accumulated near a healed wound. Salunkhe et al. (9) reported that potato slices as used for French fries accumulated considerable contents of solanine after storage for 2 days. The higher the storage temperature, the more solanine accumulated. Light also stimulated the formation of solanine in potato slices (9). Little is known about the effects of mechanical injuries on glycoalkaloid content of potato tubers.

The present investigation was undertaken to determine the effect of mechanical injuries on the glycoalkaloid contents of potato tubers.

Materials and Methods

Three cultivars, 'Russet Burbank', 'Red Pontiac', and 'White Rose', were used in these experiments. Potato tubers with uniform size (150 ± 10 g) and shape and without any mechanical and pathological injuries were selected. Six treatments including control and five types of mechanical injuries on potato tubers were arranged in a randomized complete block design. There were three replications. There were two storage temperatures –4° and 21°C. Each replication consisted of 60 tubers. Five mechanical injury treatments included brushing, hammering, dropping, puncturing with a nail, and cutting. Brushing was accomplished by brushing the entire surface of the tubers with a steel brush to the depth of 1 mm. Hammering was done by hammering the entire surface of the tubers with a round tip hammer (7.06 cm^2) by a pressure of 1 kg/cm^2. Dropping was done by droppings of each tuber 6 times from a height of 2 m. Puncturing was done by punching a nail of 3 mm

---

[1] Received for publication July 27, 1975. This research was supported by Grant FD-00683-02 from the Office of Research Grants, Food and Drug Administration.