Inheritance in Sweet Corn for Resistance to Acute Ozone Injury[1]

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Abstract. A high degree of inheritance for resistance and susceptibility in sweet corn (*Zea mays* L.) to acute ozone leaf injury under field conditions was shown during 2 and 3 generations of breeding with 3 series of cultivars. Crosses of highly susceptible × resistant inbreds gave notably susceptible F_1's. F_2 families segregated quantitatively but extremes were sometimes recovered. Distribution in F_2 was skewed toward low injury. Resistant X resistant crosses gave almost fully resistant F_1's and F_2's. A study involving a second series of inbreds also showed a close relationship between susceptibility in a parent and in its derived F_1's. Three generations of selection and inbreeding, beginning with a segregating population, resulted in near fixation in resistant sublines but showed continued segregation in progenies from susceptible selections.

Sweet corn is one of many crop plants that can show leaf injury in the field due to ozone (8). Susceptible and resistant cultivars are known, and in the Los Angeles Basin of southern California some F_1 hybrids have repeatedly sustained acute damage during the last several years (1, 3). Certain inbreds have transmitted different levels of susceptibility to their hybrids (3). Other greenhouse and field studies have shown significant reductions in yield due to oxidants in the cvs. Golden Midget (6) and Jubilee (11).

Sweet corn is especially suited for ozone injury studies because the leaves of susceptible cultivars rapidly show prominent areas of collapsed tissue under conditions of high ozone and high temperature. Different areas of a leaf become susceptible over an extended period of time, and successively younger leaves become reactive as plant growth and flowering proceed. In the Riverside area, cultivar reactions have been highly consistent from year to year. More subtle, non-acute leaf injury, evidenced by premature chlorosis and senescence, has also often been reported after ozone exposure (3, 6, 11).

At Riverside, breeding and selection among various groups of cultivars were carried out from 1970 through 1973, with evaluation for acute injury under natural field conditions. Evidence for a high degree of inheritance for this characteristic is presented here.

Materials and Methods

Inbreds used in this study included NK6604, NK6942, and NK7428 loaned by Northrup, King, and Co.; 349/RS and 11 others loaned by Joseph Harris Co.; 81-1 and 471-U6 obtained through the USDA and Purdue University; Od-3 and WQ9A from the USDA Regional Vegetable Breeding Laboratory, Charleston, SC; and CA-0333 developed at Riverside from a P39A background. The 1970 F_3 segregating family of Table 3 was from a cross of P39A with an Inversion 2a stock from the Maize Genetics Stock Center, University of Illinois. It did not carry the inversion, but was segregating from the *su*, gene.

Individual field families in all years were single 15-m rows with plants 30 cm apart. Inbreds of Table 1 were grown at 2 planting dates in each of 3 years; F_1 and F_2 families of Table 2 were replicated twice at a single planting date each. Plants were scored for ozone leaf injury 4 or 5 times after they were 5 weeks old, and 1 to 2 days following high oxidant levels (20-40 pphm for 2 hours or more) accompanied by maximum temperatures of 95°F or higher. These conditions regularly produced severe new acute injury on susceptible cultivars. Injury grades were 1 (no visible injury) to 9 (very severe tissue collapse on large leaf areas) as previously described (3). Grades listed in tables represent cumulative injury at fresh market maturity. Resistant, intermediate, and susceptible classes (R, I, and S) represent grades 1-2, 3-5, and 6-9, respectively.

Results

Of 9 parent inbreds grown in the field, during 3 summers, 5 were resistant, 2 were intermediate, and 2 were very susceptible (Table 1). All were consistent in their reactions, the resistant ones showing only trace injury and the susceptibles suffering severe damage each year. Three commercial F_1 hybrids with widely different reactions to ozone were also grown each summer. In agreement with an earlier study (2) 'Bonanza' was consistently R, 'Gold Winner' was I, and 'Monarch Advance' was S.

In 1971 a series of crosses (Table 2) was made with resistant inbred NK6942 and susceptible NK6604, respectively, as common parents with other inbreds of Table 1. All of 3 R × R hybrids involving NK6942 showed low mean injury (grades 1-2) in both F_1 and F_2 and the range in F_2 was limited to grades 1-3. Comparable crosses involving NK6604 (group II) showed intermediate to severe injury in F_1 and statistically greater injury in F_2 than group I. Some F_2 plants were as severely injured as the susceptible grandparent (Fig. 1). I × S and S × S hybrids were severely injured in F_1; injury in F_2 often reached grade 9. Susceptible inbred Od-3, whose injury is not as severe as that of NK6604, was a parent in the S × R cross (group III) and the S × S (group IV). It appeared to contribute susceptibility to about the same degree as NK6604.

Selection and inbreeding were also carried out from a segregating family unrelated to the previous inbreds (Table 3). Two main sublines were established, from R and S plants. Selection for resistance consistently gave progenies with many R, a few I, and no strongly S plants, although uniformly resistant families were not obtained. Selection for susceptibility gave segregating families through 3 generations, including R, I, and S individuals and high proportions of injured plants. Selfing of an R phenotype within this subline in 1971 and 1972 produced high proportions of R offspring (families 729 and 738) while a sib of S × R produced many S offspring. Differences in

Table 1. Grades of acute leaf injury by ozone to 9 sweet corn inbreds in the field, during 3 summers.

Inbred line	Ozone reaction class[z]	Mean injury grades			
		1971	1972	1973	3-year
NK6942	R	1	1.5	1.5	1.3
81-1	R	1	1.5	1	1.2
WQ9A	R	1	1	1	1.0
471-U6	R	1.5	1	1	1.2
CA-0333	R	1.5	1.5	1	1.3
NK7428	I	3	3.5	2.5	3.0
349/RS	I	3	3	—	3.0
NK6604	S	8	9	8	8.3
Od-3	S	6	6.5	5.5	6.0

[z] R, resistant; I, intermediate; and S, susceptible, are cumulative grades 1-2, 3-5, and 6-9 respectively at market maturity; see Methods.

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Table 2. Ozone leaf injury grades of F_1 and F_2 families from crosses among inbreds of Table 1[z]

Inbreds crossed (1971)			Mean grade of F_1 (1972)	Grade of F_2 family (1973)		
Group	Identity	Ozone reaction class		Mean	Range	Group mean
I	81-1 × NK6942	R × R	2	1.3	1-3	1.23**
	WQ9A × NK6942	R × R	2	1.1	1-3	
	471-U6 × NK6942	R × R	1	1.3	1-3	
II	81-1 × NK6604	R × S	7	3.1	1-8	2.83**
	WQ9A × NK6604	R × S	4	2.7	1-6	
	471-U6 × NK6604	R × S	7	2.7	1-6	
III	Od-3 × NK6942	S × R	4	2.7	1-5	2.70
IV	NK7428 × NK6604	I × S	8	5.3	2-8	5.50**
	349/RS × NK6604	I × S	9	5.5	2-9	
	Od-3 × NK6604	S × S	8	5.7	3-9	

[z] Injury grades and classes as in Table 1.

** Asterisks indicate that the differences between group means II minus I, IV minus I, and IV minus II are significant at 1%.

Table 3. Effects of selection on ozone leaf injury to sweet corn in the field, during 3 generations[z]

1970 Segregating F_3 family	1971						1972						1973			
	Family number	Segregation R	I	S	Selected plants	Pollination	Family number	Segregation R	I	S	Selected plants	Pollination	Family number	Segregation R	I	S
Plant 1, reaction R, selfed	712	41	11	0	R, R	Sib	724	31	7	0	R	Self	731	45	5	0
					R	Self	725	40	4	0	R	Self	732	37	9	0
					R	Self	726	38	5	0	R, R	Sib	733	45	7	0
							Totals:	109	16	0			Totals:	127	21	0
Plants 3 and 8, reaction S, sibbed	713	17	10	28	S	Self	727	14	5	16	S	Self	734	7	10	22
											S	Self	735	12	15	16
											I, I	Sib	736	18	18	16
					S, R	Sib	728	3	10	24	S	Self	737	15	17	17
							Totals:	17	15	40			Totals:	52	60	71
					R	Self	729	25	9	4	R	Self	738	37	5	0

[z] Injury classes as in Table 1. P values for chi square (null hypothesis) were <0.005 for comparisons of total segregation ratios of R versus S selections within each year.

total segregation ratios between the 2 main sublines were significant beyond 0.005 each year by chi square tests.

In 1972, 12 inbreds loaned by Joseph Harris Co. were classified for field injury: 9 were R, 1 was I, and 2 were S. In 1973, 22 of their F_1 hybrids were evaluated. Not all possible crosses were made but injury relationships between inbreds and hybrids were similar to those of Table 2. R × R crosses produced nearly all R hybrids, while R × S gave nearly all I and S. The S × S cross produced an S hybrid. This was a line cross between 2 genetically similar inbreds, with normal and restored T-sterile cytoplasm, respectively. The similar injury grades of these 2 inbreds, and of other hybrids involving them, suggest that sensitivity to ozone was not dependent on the cytoplasmic difference.

Discussion and Conclusions

This study shows a high degree of inheritance for ozone leaf injury in F_1 and later generations. When either parent was susceptible there was susceptibility in F_1, which suggests additivity or incomplete dominance of genes for the character. In F_2's from selfing, mean grades of families were clearly related to their F_1's and extremes of the grandparents were often recovered. However, mean F_2 grades were lower than might be expected, and some low-injury phenotypes appeared even from S × S and I × S grandparents. Very few plants with injury arose from R × R grandparents. The selection experiment of Table 3 showed a similar pattern, with resistance nearly fully fixed in 2 or 3 generations while susceptibility continued to segregate. This also suggests incomplete dominance for susceptibility. Engle and Gabelman (5) reported dominant genetic resistance to ozone in onion, correlated with stomatal closure. Howell et al. (9) found that in alfalfa, greenhouse selection over a period of years produced more resistant types.

In the present study, microclimate variations as in shading and soil moisture no doubt caused some phenotypic fluctuations among plants, but F_2 genetic segregation for plant vigor, growth rate, leaf quality, and quality of root systems may have been more important. Vigorous, fast-growing plants are often more susceptible to ozone injury, and segregates with inferior growth could have reduced mean F_2 injury grades. The number of genes involved is not known, but may be small. The genes must affect biochemical and physical processes which result in the visible symptoms. Cellular characters which have been correlated with ozone damage include levels of soluble sugars and amino acids (12) changes in chloroplasts, reactions of fatty acids and sulphydryl groups, and ionic changes. Ionic unbalance across cell membranes, resulting in disruption of cell metabolism, has been emphasized by Heath et al. (7).

Leaf age is recognized as a factor in several plants. In corn the relation of developmental age to acute tissue collapse among and within leaves was critical, and the correlation with high temperature was great (3). The role of stomatal closure was described in onion (5) and tobacco (4, 10) but it hardly accounts for the total differences between susceptible and resistant cultivars in sweet corn.

Yield reduction has occurred in sweet corn due to ozone injury (6, 11). Further data at Riverside in 1974 (C. R. Thompson and G. Kats, personal communication) showed that continuous exposure to ambient air containing ozone caused severe reduction in ear wt and kernel number in susceptible 'Monarch Advance', but only slight reduction

Fig. 1. Sister F_2 plants from the cross 81-1 (resistant) × NK6604 (susceptible) showing highly susceptible segregate (left) and resistant segregate (right), in the field. Picture shows cumulative ozone damage after several episodes of high pollution and high temperature.

in resistant 'Bonanza'. Both acute and chronic leaf injury were visible in 'Monarch Advance'.

Literature Cited

1. Cameron, J. W. 1974. Patterns of inheritance of susceptibility in sweet corn to acute ozone injury under field conditions. *HortScience* 9(3) Section 2:279. Abstr.
2. ———, H. Johnson, Jr., O. C. Taylor, and H. W. Otto. 1970. Differential susceptibility of sweet corn hybrids to field injury by air pollution. *HortScience* 5(4): 217–219.
3. ———, and O. C. Taylor. 1973. Injury to sweet corn inbreds and hybrids by air pollutants in the field and by ozone treatments in the greenhouse. *J. Evniron. Quality* 2:387–389.
4. Dean, C. E. 1972. Stomate density and size as related to ozone-induced weather fleck in tobacco. *Crop. Sci.* 12:547–548.
5. Engle, R. L., and W. H. Gabelman. 1966. Inheritance and mechanism for resistance to ozone damage in onion, *Allium cepa* L. *Proc. Amer. Soc. Hort. Sci.* 89:423–430.
6. Heagle, A. S., D. E. Body, and E. K. Pounds. 1972. Effect of ozone on yield of sweet corn. *Phytopathology* 62:683–687.
7. Heath, R. L., P. Chimiklis, and P. Frederick. 1974. The role of potassium and lipids in ozone injury to plant membranes. Article 3, *In:* Air Pollution Effects on Plant Growth. Dugger, M. ed. Amer. Chem. Soc., Symposium Series 3, Washington, DC.
8. Hill, A. C., H. E. Heggestad, and S. N. Linszon. 1970. Ozone. p. B1–B22, *In:* Recognition of Air Pollution Injury to Vegetation: A Pictorial Atlas. Jacobson, J. S., and A. C. Hill, eds. Air Pollution Control Assoc., Pittsburgh, PA.
9. Howell, R. K., T. W. Devine, and C. H. Hanson. 1971. Resistance of selected alfalfa strains to ozone. *Crop Sci.* 11:114–115.
10. Lee, T. T. 1964. Sugar content and stomatal width as related to ozone injury in tobacco leaves. *Can. J. Bot.* 43:677–685.
11. Oshima, R. J. 1973. Effect of ozone on a commercial sweet corn variety. *Plant Disease Rep.* 57:719–723.
12. Ting, I. P., and S. K. Mukerji. 1971. Leaf ontogeny as a factor in susceptibility to ozone: amino acid and carbohydrate changes during expansion. *Amer. J. Bot.* 58:497–504.

Response of Mung Bean [*Vigna radiata* (L.) Wilczek Var. *radiata*] and Soybean [*Glycine max* (L.) Merr.] to Increasing Plant Density[1, 2]

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Abstract. The performance of the mung bean cultivar Thai Green Oil was compared with the soybean cutivar Hsih-Hsih over a range of 12 plant densities from 10,000 to 800,000 plants/ha. Increasing plant density was positively related to yield and plant height and negatively related with significant reductions in flowering, yield per plant and plant branching. The higher yield potential of soybeans at high plant densities, relative to mung bean, was attributed to differences in the production of the number of flowers per plant and, subsequently, the number of pods per plant. This relationship can be applied to breeding and selecting improved mung bean cultivars.

The Asian Vegetable Research and Development Center has initiated a mung bean (*Vigna radiata* (L.) Wilczek var. *radiata*) improvement program with the specific objective of elevating the yield potential of this nutritionally important Asian crop. One approach considered is to increase yield by increasing plant density.

It has long been known that the response of the soybean (*Glycine max* (L.) Merr.) to plant density varies among cultivars (3, 4). The application of this relationship has been hindered by crop management restrictions which require interrow tillage for weed control. Donovan et al. (1), recognizing the application of newly available chemical weed control methods, investigated this application, and reported increased soybean yield from closely drilled soybean stands.

In general, commercial yield levels of most bean species in Southeastern Asia are low and rarely exceed one metric ton/ha. Commercial soybean yields in Southern Taiwan are distinctly higher, commonly exceeding 2 and sometimes even 2.5 metric tons/ha. This difference is attributed to the development of an intense crop management system for soybeans following lowland paddy rice. One striking aspect of this crop management system is the relatively higher soybean seeding rates, ranging from 320,000 to 640,000 seeds/ha.

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