Foliar Sensitivity of Soybeans from Early Maturity Groups to Ozone and Inheritance of Injury Response

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ABSTRACT

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Soybean genotypes of maturity groups 00, 0, and I were evaluated in 1982 and 1983 for foliar sensitivity to ambient ozone (O_3). PI 153.283 and PI 153.284 were sensitive to O_3, showing 25–50% foliar stippling and premature defoliation. Nineteen of the 35 genotypes evaluated for 2 yr were tolerant to O_3, showing little or no visible injury. PI 189.907 and PI 153.317 showed no visible injury in the field both years despite frequent O_3 episodes in 1983. Crosses were made between two O_3-tolerant (PI 189.907 and PI 153.317) and one O_3-sensitive (PI 153.283) genotype. Parental, F_1, F_2, and backcross populations were exposed to 0.30 ppm O_3 for 4 hr in a greenhouse fumigation chamber. Injury response distributions were not significantly different within O_3-tolerant parents, reciprocal F_1 populations, and F_2 populations. F_1 plants were intermediate in injury response compared with the parents. Injury response distribution in the F_2 was nonnormal and exhibited three peaks. Foliar sensitivity to O_3 appears to be qualitatively inherited in these genotypes, and a possible genetic model is discussed.

Ozone (O_3) is a widespread phytotoxic air pollutant that is known to injure soybean (*Glycine max* (L.) Merr.) foliage (11,21). Visible O_3 injury is evident as chlorotic or necrotic flecking on adaxial leaf surfaces, bifacial necrosis, and premature defoliation of cotyledonary, unifoliolate, and trifoliolate leaves (11,21). Such symptoms appear when plants are exposed to high (acute) O_3 concentrations (0.20–0.70 ppm) for a short time (few hours). Similar symptoms and growth and/or yield reductions can occur when plants are exposed to low (chronic) O_3 concentrations (0.06–0.15 ppm) over longer periods (several weeks) (9,10). Phytotoxic O_3 episodes may occur often in soybean-growing areas because of long-distance transport of the pollutant and its precursors from urban to rural sites (14,16).

Variability in O_3 injury response among cultivars of soybeans has been observed. Tingey et al (22) exposed 14 cultivars representing different maturity classes to 0.30 and 0.70 ppm O_3 for 1.5 hr and found marked differences in cultivar responses. Miller et al (17) evaluated 21 genotypes of maturity groups II–VII for injury responses to 0.50 ppm O_3 for 2 hr and noted some variability, particularly with two plant introductions. Heagle (7,8) reported that sensitivity rankings of four genotypes differed depending on O_3 dose and type of injury response measured. Rankings within a response type measured were, however, fairly stable for the range of chronic and acute O_3 doses tested.

Breeding for resistance or tolerance to air pollutants offers a feasible approach to minimizing damage to crops. Injury response to O_3 is known to be a heritable trait in onion (5), potato (3,4), corn (2), bean (15), tall fescue (13), petunia (6), and tobacco (1,12,19). Little is known about O_3 sensitivity in soybean genotypes from early maturity groups, and no information regarding the inheritance of O_3 injury response in soybeans is available. This report focuses on the foliar sensitivity of several soybean

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genotypes from early maturity groups to ambient O_3. The inheritance of injury response to O_3 fumigations in a greenhouse chamber was also investigated to determine the usefulness of O_3 tolerance in these lines to soybean breeders.

MATERIALS AND METHODS

Soybean plant introductions (PIs) and U.S./Canadian cultivars were obtained from the USDA soybean germ plasm collection (Department of Agronomy, University of Illinois). One hundred thirty-three genotypes of maturity groups 00, 0, and I were selected to represent different geographic sources. Plants of each genotype were grown for seed increase and evaluation of foliar O_3 sensitivity at a site containing Hadley fine sandy loam (Typic Udifluvents). Ground limestone at 2,241 kg/ha and 0-44-83 kg/ha NPK granular fertilizer were incorporated into the soil before planting. One row of each genotype was machine planted (50 seeds per genotype) on 29 May 1982. *Rhizobium japonicum* (soybean inoculant, Nitrogen Co., Clearwater, FL) was added to the furrow via a granular applicator mounted on double-disc opening planters. Row width was 75 cm and seeds were spaced 10 cm apart. Weeds were controlled with a preemergence application of 1.7 kg a.i./ha alachlor and 0.85 kg a.i./ha linuron and by hand-weeding late in the season. O_3 concentrations were monitored and continuously recorded in Amherst, MA, throughout the summer with a Dasibi model 1003AH UV spectrophotometric O_3 analyzer calibrated with an AID model 565 O_3 generator.

Plants were evaluated for O_3 injury by assessing severity of visible foliar injury symptoms on two dates, 21 July and 23 August. Each plant was examined, and oxidant stipple (flecking) was quantified by the following injury index: 0 = no visible symptoms, 1 = <25% leaves stippled, 2 = ≥25–<50% leaves stippled, 3 = ≥50–<75% leaves stippled, 4 = ≥75–100% leaves stippled. Mean injury indices were calculated over both evaluation dates for each genotype. Forty-one genotypes classified as tolerant or sensitive to ambient O_3 were chosen for further evaluation.

The 41 selected genotypes were grown again in 1983 at a site containing Hinkly loamy sand (Typic Udorthents). Ground limestone at 1,120 kg/ha and granular fertilizer at 39-39-39 kg/ha NPK were incorporated into the soil before planting. The site was divided into three blocks, each containing a 2-m single-row plot of each of the 41 genotypes. Row width was 1.22 m and seeds were spaced 10 cm apart. Seeds were treated with inoculant before hand planting on 2 June. Weeds were manually removed throughout the growing season, and irrigation was applied overhead as needed to prevent moisture stress. Ambient O_3 concentrations were recorded as previously described. Plants were evaluated for O_3 sensitivity by the previously described injury index on two dates, 14 July and 14 August. Mean injury indices were calculated over blocks and dates for each genotype.

Three genotypes were selected for use in genetic analysis of O_3 injury response based on foliar reactions observed in 1982 and 1983. Reciprocal crosses were made between PI 153.283 (O_3-sensitive) and PI 153.317 (O_3-tolerant) or PI 189.907 (O_3-tolerant) in the field in 1983. Genetic markers in the O_3-sensitive genotype were white flower color and green hypocotyl pigment and in the two O_3-tolerant genotypes, purple flower color and purple hypocotyl pigment (18). F_1 and parental populations were grown in the field in 1984, and marked F_1 plants were used to produce F_2 seed. Pollen from marked F_1 plants was backcrossed to the O_3-sensitive parent.

A greenhouse screening procedure was developed to test the populations for injury response to an acute O_3 exposure. Two Plexiglas chambers (48 × 46 × 81 cm) with a 6.3-cm-diameter port in each were used. The bottomless chambers were seated in sand-filled galvanized metal trays. The two chambers were connected with 6.3-cm-diameter vacuum tubing attached to each port. O_3 was generated in one chamber with a variable-output Wellsbach O_3 generator and was force-ventilated into the exposure chamber with a 5.08-cm shaded pole blower. O_3 was monitored in the exposure chamber through a Teflon probe attached to the Dasibi O_3 analyzer. The system allowed ±0.02 ppm control over O_3 concentration in the exposure chamber. Additional lighting was supplied during fumigations with a General Electric 400 HID lamp suspended 1.5 m above the exposure chamber. Sand was saturated with water before use, and relative humidity was >90% during fumigations. Temperature during fumigations ranged from 27 to 30 C.

Seeds of each population were treated with inoculant and were sown in 10.2-cm pots filled with steam-pasteurized potting medium (1:1:1, soil:sand:peat, limed to pH 6.5–7.0) at one seed per pot. Thirty-five pots were planted each day over a 3-wk period because chamber size permitted only 30 pots per fumigation. Nine pots each day were seeded with the three parental lines (three each); the rest were sown with seeds of the other populations selected at random. Fumigations were conducted from 0930 to 1330 hours EST at 0.30 ± 0.02 ppm O_3. Plants were grown in the greenhouse at 21–32 C and fumigated when the first trifoliolate leaf was fully expanded (about 21 days after planting) (8,21). Two plants of each O_3-tolerant parent and four plants of the O_3-sensitive parent were included in all fumigations. Plants were returned to the greenhouse benches after fumigation and evaluated for O_3 injury symptoms 48 hr later. O_3 injury was determined by estimating the percent leaf area necrosis for each of the two unifoliolate leaves and the three leaflets of the first trifoliolate leaf. A mean value for the three leaves per plant was calculated, and population distributions for leaf injury classes were constructed. Fumigation uniformity over dates was tested by analysis of variance of the absolute injury response for the eight parents included in each fumigation. Injury response distributions were tested for normality with a one-sample Kolmgorov-Smirnov (KS) and for homogeneity between populations using a two-sample KS test (20).

RESULTS

Seasonal O_3 concentrations are reported as weekly O_3 hours above 0.06 ppm (0700-1900 hr EST) (Table 1) and episode frequency distributions are described. Of the 124 total O_3 hours above 0.06 ppm in 1982, 79.8% were from 0.06 to 0.08 ppm, 16.1% from 0.08 to 0.10 ppm, 3.2% from 0.10 to 0.12 ppm, and 0.8% from 0.12 to 0.14 ppm. Ambient O_3 concentrations were higher in 1983

Table 1. Weekly (0700–1900 hours EST) ozone hours above 0.06 ppm recorded in 1982 and 1983

1982		1983	
Week ending	O_3 hours ≥0.06 ppm	Week ending	O_3 hours ≥0.06 ppm
7 June	0	...	...
14 June	6	15 June	24
21 June	4	22 June	29
28 June	12	29 June	30
5 July	2	6 July	42
12 July	24	13 July	21
19 July	21	20 July	27
26 July	5	27 July	22
2 August	8	3 August	60
9 August	29	10 August	29
16 August	5	17 August	21
23 August	4	24 August	32
30 August	1	31 August	35
6 September	3	...	...

Table 2. Soybean genotypes from early maturity groups sensitive to ambient O_3

Genotype	Source	Maturity group	Injury index[a] 1982	Injury index[a] 1983
Harly	USA/Canada	I	0.8	0.4
Hardome	USA/Canada	0	0.5	0.4
Mandarin Ottowa	USA/Canada	0	0.6	0.6
Soysota	USA/Canada	I	0.6	1.0
Traverse	USA/Canada	0	0.1	0.5
FC 30.233	Canada	I	0.1	0.2
FC 30.683	Canada	I	0.1	0.5
PI 63.271	Manchuria	I	0.1	0.3
PI 68.474-2	Manchuria	I	0.2	0.5
PI 84.668	Korea	I	0.2	0.3
PI 153.214	Belgium	I–	0.3	0.6
PI 153.283	Belgium	I–	1.4	1.6
PI 153.284	Belgium	0	1.4	1.6
PI 189.875	France	00	0.3	0.3
PI 232.902	Hungary	0	0.2	0.5
PI 248.404	Yugoslavia	0	0.1	0.3

[a] Mean values of 50 plants in 1982 and three replicates of 25 plants each in 1983 evaluated on two dates per year. Injury index (0–4): 0 = no visible injury and 4 = ⩾75–100% leaves injured.

Table 3. Soybean genotypes from early maturity groups tolerant to ambient O_3

Genotype	Source	Maturity group	Injury index[a] 1982	Injury index[a] 1983
Hidatsa	USA/Canada	00	0.0	0.0
Goldsoy	USA/Canada	0	0.0	0.0
Manchuria	USA/Canada	I	0.0	0.1
Ogeman	USA/Canada	00	0.0	0.2
Ontario	USA/Canada	I	0.0	0.1
Norchief	USA/Canada	0	0.0	0.1
Morsoy	USA/Canada	00	0.0	0.2
Sioux	USA/Canada	00	0.0	0.1
Wisconsin Black	USA/Canada	I	0.0	0.0
PI 89.001	Manchuria	0	0.0	0.0
PI 96.152	Korea	I	0.1	0.0
PI 153.317	France	0	0.0	0.0
PI 181.532	Japan	I	0.1	0.0
PI 189.907	France	I–	0.0	0.0
PI 189.939	France	0	0.0	0.1
PI 189.940	France	00	0.0	0.0
PI 227.326	Japan	0	0.0	0.1
PI 232.997	Germany	00	0.0	0.0
PI 238.921	Czechoslovakia	0	0.0	0.1

[a] Mean values of 50 plants in 1982 and three replicates of 25 plants each in 1983 evaluated on two dates per year. Injury index (0–4): 0 = no visible injury and 4 = ⩾75–100% leaves injured.

Table 4. Foliar injury response of parental, F_1, F_2, and backcross populations to 0.30 ppm O_3 for 4 hr in a greenhouse chamber

Population	No. of plants	Leaf area necrosis[a] (%)	Variance
Parental			
PI 153.283 (O_3-sensitive)	53	55.7	146.2
PI 153.317 (O_3-tolerant)	26	16.9	180.5
PI 189.907 (O_3-tolerant)	21	13.2	27.6
Combined O_3-tolerant	47	15.3	113.5
F_1			
PI 153.317 × PI 153.283	5	31.5	44.0
PI 153.283 × PI 153.317	13	40.0	253.1
PI 189.907 × PI 153.283	1	30.3	···
PI 153.283 × PI 189.907	4	26.6	28.1
Combined F_1	23	35.4	180.8
F_2			
PI 153.283 × PI 189.907	53	28.4	376.2
PI 153.283 × PI 153.317	74	32.7	267.8
Combined F_2	127	30.9	314.9
Backcross:			
BC_1 (PI 153.283 × F_1)	9	39.2	50.4

[a] Mean values of two unifoliolate leaves and three leaflets of the first trifoliolate leaf per plant 48 hr after fumigation.

(Table 1). Of the 372 total O_3 hours above 0.06 ppm in 1983, 52.9% were from 0.06 to 0.08 ppm, 25.8% from 0.08 to 0.10 ppm, 6.9% from 0.10 to 0.12 ppm, 7.5% from 0.12 to 0.14 ppm, 5.9% from 0.14 to 0.16 ppm, and 0.8% from 0.16 to 0.18 ppm.

Variability in foliar injury response to O_3 was observed among genotypes grown in 1982 and those evaluated again in 1983. Visible foliar symptoms consisting of flecking or stippling of adaxial leaf surfaces first appeared on lower leaves (unifoliolate followed by lower trifoliolate leaves). Injury was generally more severe in 1983 than in 1982. Unifoliolate and early trifoliolate leaves of O_3-sensitive genotypes were so severely injured in 1983 that bifacial necrosis spread over entire leaf surfaces and premature leaf abscission occurred. Visible injury severity for genotypes evaluated both years reflected O_3 levels recorded. Those genotypes responding similarly in 1982 and 1983 were classified into two groups. PI 153.283 and PI 153.284 were highly sensitive, with 25–50% foliar injury (Table 2). Five cultivars and nine PIs were less sensitive, with 5–25% leaves damaged (Table 2). Nine cultivars and 10 PIs showed little (<5%) or no visible injury despite frequent O_3 episodes occurring in 1983 (Table 3). Four PIs including PI 189.907 and PI 153.317 showed no foliar injury in 1982 and 1983 (Table 3).

Eleven greenhouse fumigations were conducted for the genetic analysis and were uniform, with absolute injury response of the eight parents included in each fumigation as a measure. Fumigation date effect on absolute parental injury was not significant ($P = 0.05$), as mean leaf area necrosis values ranged from 31.7 to 39.4%. PI lines selected as parents based on injury response in the field responded similarly to 0.30 ppm O_3 in the greenhouse. O_3-tolerant PI 153.317 and PI 189.907 had mean leaf area necrosis values of 16.9 and 13.2%, respectively (Table 4). Leaf injury distributions for the two O_3-tolerant parents were not significantly different ($P = 0.05$) by a two-sample KS test, and the data were pooled (Fig. 1). O_3-sensitive PI 153.283 had a mean of 55.7% leaf area injury (Table 4) and an injury response distribution with only slight overlap with the tolerant response type (Fig. 1). F_1 populations were intermediate in response compared with parental types and had mean injury values ranging from 26.6 to 40% (Table 4). Injury response distributions of reciprocal F_1 populations PI 153.317 × PI 153.283 and PI 153.283 × PI 153.317 were homogeneous ($P = 0.05$, KS test). F_1 injury response distributions for crosses involving either O_3-tolerant parent and PI 153.283 did not differ significantly ($P = 0.05$, KS test), and F_1 data were pooled (Fig. 1).

F_2 populations derived from PI

153.283 × PI 153.317 and PI 153.283 × PI 189.907 had mean leaf area injury values of 28.4 and 32.7%, respectively (Table 3). Injury response distributions for the two F_2 populations were homogeneous ($P = 0.05$, KS test) and were pooled. The pooled F_2 injury distribution was nonnormal and exhibited three peaks separated at 15 and 35% leaf area necrosis (Fig. 1). O_3-tolerant, O_3-sensitive, and F_1 (intermediate) response types were recovered in the F_2. Arc-sine [square root] transformation of leaf area necrosis values, recommended for percentage data (20), failed to normalize the F_2 distribution. The backcross population was intermediate and skewed toward sensitivity compared to the parents (Table 4).

DISCUSSION

Although variability in injury response to ambient O_3 was observed among the soybean genotypes evaluated, only two of the 35 genotypes evaluated for 2 yr were highly sensitive in the field. Most genotypes were O_3-tolerant and five did not show any visible foliar injury during 1982 or 1983. Soybean genotypes from early maturity groups appear to be generally field tolerant to oxidant pollutants when measured by foliar sensitivity. O_3 was the only oxidant measured in this study, and other pollutants such as peroxyacetyl nitrate and nitrogen oxides may have contributed to leaf damage in the field.

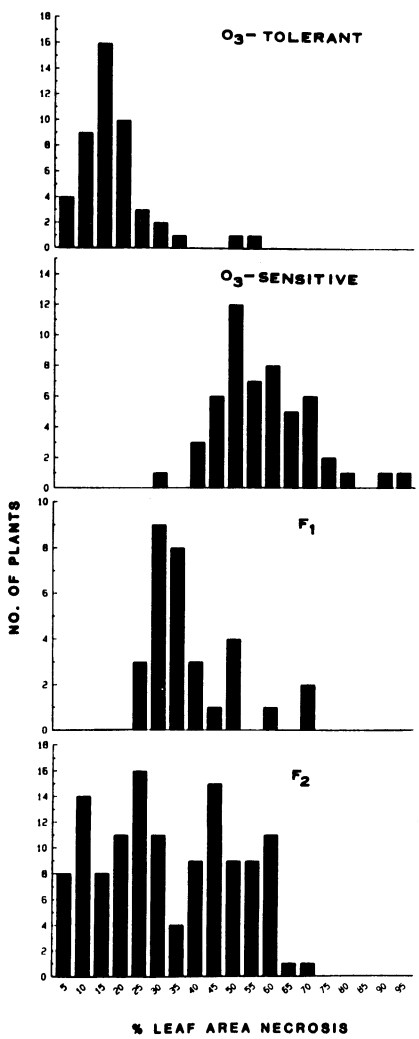

Fig. 1. Injury response distribution of parental, F_1, and F_2 populations to 0.30 ppm of O_3 for 4 hr in a greenhouse fumigation chamber.

The greenhouse screening test was effective in the separation of O_3-tolerant and O_3-sensitive parents used in the genetic analysis whose selection was based on response to ambient O_3. O_3-tolerant parents that showed no foliar injury symptoms in the field tests did respond to the 4-hr 0.30 ppm O_3 exposure with foliar necrosis (13.2–16.9%); however, injury response distributions were homogeneous, enabling the data to be pooled. Injury response of the sensitive parent was higher (55.7%), and the response distribution had little overlap with the tolerant type.

Inheritance of foliar O_3 tolerance appeared to be the same for both tolerant parents (PI 153.317 and PI 189.907), because injury response distributions were homogeneous within both tolerant parents, reciprocal F_1 populations, and F_2 populations. F_1 plants were intermediate in response compared with parental types, indicating that simple dominance was not in effect. Injury response in the F_2 was not normally distributed but formed three peaks in which tolerant parental, intermediate F_1, and sensitive parental types were represented. A quantitative model does not explain this type of segregation pattern. A possible explanation is that a few genes control injury response and partial dominance and gene interaction are involved in expression. One model that fits the observed segregation pattern is a two-gene model with complete dominance at one locus and partial dominance and epistasis at the other. The second gene in this model would be epistatic to the first in the homozygous recessive condition. Based upon parental and F_1 reactions and on the three peaks observed in the F_2, tolerant ($\leq 15\%$), intermediate (> 15–$\leq 35\%$), and sensitive ($> 35\%$) classes could be defined. The F_2 distribution fit a 3 tolerant:6 intermediate:7 sensitive ratio (chi-square = 2.28, $P = 0.25$–0.50). Assuming the sensitive parents to be homozygous recessive at gene pair 1 and homozygous dominant at gene pair 2, a backcross with the completely heterozygous F_1 would give an expected 0 tolerant:1 intermediate:3 sensitive ratio. The backcross distribution fit this ratio (chi-square = 0.33, $P = 0.80$–0.90), lending some further support for this two-gene model. The genotype of the tolerant parents would be homozygous dominant at gene pair 1 and homozygous recessive at gene pair 2 in order to produce the heterozygous F_1. Progeny testing of the respective F_3 families, not permitted by time and space restraints in this study, is needed for definitive evidence in support of this model.

Plants were fumigated in the greenhouse when the first trifoliolate leaf was fully expanded, an immature stage of plant development. Plant age has been shown by others to influence O_3 sensitivity. Heagle and Letchworth (10) reported different rankings of four soybean cultivars for foliar injury response to 0.10 ppm O_3 in open-top field chambers when plant age and exposure time varied. DeVos et al (4) showed that inheritance of O_3 sensitivity in potato varied over time, and plant age was one possible explanation for the differences observed. Plants were fumigated in this study at a time of maximum leaf sensitivity (21) and at a stage of plant development highly sensitive to O_3 based on our field observations. The influence of plant age on inheritance to O_3 sensitivity in soybean warrants attention, however, if results presented here are to be extrapolated to include older plant response.

This is the first report demonstrating heritability of foliar O_3 tolerance in soybeans, and results presented indicate a qualitative mechanism. O_3 tolerance in bean (15) and onion (5) is qualitatively inherited by a few genes and one gene, respectively. Inheritance of this trait in tobacco (1,12,19), tall fescue (13), sweet corn (2), petunia (6), and potato (3,4) are quantitative, with additive genes conferring tolerance. O_3 tolerance is a heritable trait in all reports to date, although the type appears to be crop specific. Breeding for O_3 tolerance in a sensitive soybean line should be feasible by hybridization and selection.

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