Laboratory Versus Field Response of Potato Genotypes to Oxidant Stress

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ABSTRACT

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Foliar resistance of 26 potato (*Solanum tuberosum*) cultivars and genotypes from a seven-parent diallel to oxidant stress was assessed after exposure either to 774 $\mu g/m^3$ ozone for 3 hr under laboratory conditions at University Park, PA, or to ambient oxidants at New Brunswick, NJ. Controlled ozone exposures provided a reliable method for identifying resistance to oxidant stress that would be effective over a range of field environments. Genotypes that were relatively susceptible to ozone in laboratory tests often appeared resistant to oxidant injury in the field, but genotypes susceptible to oxidant stress in the field were also susceptible in the laboratory. The mode of inheritance of resistance to ozone, as indicated by the relative importance of general and specific combining ability in the diallel analysis, varied among laboratory and field experiments.

Additional key words: air pollution, genetics

Speckle leaf is a foliar disorder of potato (*Solanum tuberosum* L.) frequently associated with ozone (O_3) and oxidant air pollutants in general (2,8,9,14). These abiotic stresses can reduce both yield and quality of potato tubers (8,13). The differential response of potato cultivars to ambient oxidants (2,7–9,11,14,15) and controlled O_3 exposures (3,8,12) has been reported. We have recently investigated the mode of inheritance of resistance to O_3 in potato (5). In our genetic studies, relatively small, container-grown plants were produced in the greenhouse and exposed to single, short-term, relatively high-level O_3 fumigations in a controlled-environment chamber. The conditions of this relatively artificial method may be contrasted with those in the field, where plants receive repeated exposures to a mixture of atmospheric constituents, including O_3, under a wide range of environmental conditions. Air pollution exposures may occur at different stages of plant development during the growing season. The objectives of this study were: 1) to determine the reliability of predicting the resistance of potato genotypes to oxidant stress in the field based on their response to O_3 in controlled exposures, and 2) to assess the value of genetic information from laboratory studies of resistance to O_3 in determining the most effective selection methods for improving the resistance of potatoes to oxidant stress in the field.

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MATERIALS AND METHODS

Cultivar studies. Twenty-six relatively early-maturing commercial potato clones were evaluated for resistance to O_3 in both laboratory and field experiments. Tubers of each cultivar were obtained from the Beltsville Agricultural Research Center, Beltsville, MD, in 1978 and were increased in the field during the 1978 and 1979 growing seasons. After each increase, tubers were placed in cold storage at 4 C and 90% relative humidity (RH) until bud dormancy was broken and then held at 16 C and 90% RH for 3 wk before planting. During the second week of storage at 16 C, seed pieces were prepared with a 2.5-cm melon scoop and allowed to suberize for 4–6 days. Seed pieces were then treated with an 8% fungicide dust (zinc ion-maneb complex) at 10 mg/g and were retained in the 16 C storage chamber until planting.

Laboratory experiments. One seed piece from each clone was planted in each of 40 replicates in a randomized complete block design on 10 March and 5 July 1980. Seed pieces were planted 2.5 cm deep in plastic pots (6 × 6 × 6 cm) containing Redi-earth (W. R. Grace & Co., Cambridge, MA), a peat-vermiculite mix (1:1, v/v), with the addition of 1.6 kg/m^3 Osmocote (Sierra Chemical Co., Newark, CA), controlled-release fertilizer (14-6.1-11.6, NPK).

All plants were grown in a greenhouse maintained at 34 ± 10 C and 42 ± 27% RH during the day and 21 ± 10 C and 67 ± 32% RH at night, as monitored by hygrothermographs (Wm. Lambrecht AG., Goettingen, West Germany). Supplemental lighting was provided by 86% input wattage of 215W, cool-white fluorescent and 14% 40W incandescent lighting suspended 80 cm above the medium surface. The supplemental irradiance at the medium level was 50 ± 20 $\mu E\ s^{-1}m^{-2}$ as measured by an LI-185A light meter (Lambda Instruments Corp., Lincoln, NE). A 16-hr photoperiod was maintained.

About 3 wk after planting and 11 hr before O_3 exposure, plants were transferred to a controlled-environment exposure chamber (16) maintained at 21 ± 1 C and 70 ± 2% RH. A 16-hr photoperiod, coincident with the greenhouse lighting schedule, was maintained in the chamber. Chamber irradiance of 255 ± 30 $\mu E\ s^{-1}m^{-2}$, measured as described earlier, was provided by cool-white fluorescent tubes held 163 cm above the medium surface. Plants were exposed to 774 $\mu g/m^3$ (0.40 ppm) O_3 for 3 hr beginning during the fourth hour of the photoperiod. This dosage was selected because it produced maximum variation in the severity of foliar necrosis among cultivars in preliminary experiments. Ozone was generated by passing oxygen through an OREC O3V1 ozonator (Ozone Research and Equipment Corp., Phoenix, AZ) and was monitored with a Dasibi 1003AH O_3 monitor (Dasibi Environmental Corp., Glendale, CA). Plants were returned to the greenhouse during the last hour of the photoperiod.

Four runs, designated Lab-1 through Lab-4, each containing 20 plants of each cultivar, were exposed to O_3 on 2 and 4 April and 20 and 21 July 1980, respectively. Plants were evaluated for foliar injury 72 hr after each O_3 exposure period. The susceptibility of each plant to O_3 was determined by identifying the most severely injured leaf and visually estimating, within 10% intervals, the leaf area exhibiting necrosis.

Field experiments. Twenty-five seed pieces of each clone were planted in each of six replicates in a randomized complete block design on 24 April 1979

and 16 May 1980 at the Rutgers University Vegetable Research Farm, New Brunswick, NJ. Single-row plots of 81 × 732 cm were used, with plants spaced approximately 30.5 cm apart within rows. The soil was a Sassafras sandy loam fertilized with band applications of ammonium nitrate at 202 kg/ha on 13 June 1979 and 16 June 1980. In addition, 2,242 kg/ha of pulverized, dolomitic limestone and 1,569 kg/ha 5-4.4-4.2, NPK fertilizer were broadcast and disked in on 10 April 1980.

At planting, a systemic insecticide, aldicarb, was applied to the soil at 3.36 kg a.i./ha. Additional insect control was supplied by foliar applications of fenvalerate at 126 g a.i./ha on 10 May, 18 and 28 June, 1 August 1979, and 13 July and 17 August 1980. Preemergence applications of alachlor and linuron at 1.68 kg a.i./ha and 0.56 kg a.i./ha, respectively, were used for weed control in both years.

Five field evaluations designated 79-1, 79-2, 80-1, 80-2, and 80-3 were conducted on 12 June and 20 July 1979 and 3 and 22 July and 11 August 1980, respectively. Air monitoring data for New Brunswick, NJ, collected with a Bendix 5513340 chemiluminescent O_3 analyzer (Bendix Corp., Lewisburg, WV) indicated hourly O_3 levels in excess of 0.08 ppm for 7, 19, 24, 52, and 15 hr during the 7 days immediately preceding the 79-1, 79-2, 80-1, 80-2, and 80-3 evaluations, respectively. The 26 plots of each replicate were each rated on the basis of the symptom severity most frequently observed. In 1979, plants within plots were evaluated by visually estimating the percent leaf area exhibiting injury for either the most severely injured leaf (79-1) or the entire plant (79-2), using the Horsfall-Barratt scale (10). In 1980, plants were evaluated by the same assessment techniques employed in the laboratory experiments.

Diallel studies. Parent clones were selected from among the 26 cultivars based on their qualitative response to 677 $\mu g/m^3$ (0.35 ppm) O_3 for 3 hr in preliminary experiments. We initially identified Superior, Chieftain, and Norchip as resistant to O_3; Monona, Norland, and Haig as intermediate; and Cherokee as susceptible to O_3. These seven clones were self-pollinated and crossed in all possible combinations, yielding a complete 7 × 7 diallel with seven S_1 and 42 F_1 families.

In the summer of 1979, seedlings were transplanted into the field and tubers were harvested separately from plants of each S_1 and F_1 family and from each parent clone. Tuber and seed piece storage conditions and seed piece preparation procedures were identical to those used for the cultivar evaluations.

Laboratory experiment. One seed piece from a different member of each S_1 and F_1 family and from each parent clone was planted in single replicates of a randomized complete block design on 13 April 1980. Cultural practices, greenhouse and exposure chamber conditions, and O_3 exposure and injury assessment procedures were the same as those employed in the cultivar evaluation studies. One run, containing nine replicates of the diallel, was exposed to O_3 on 3 May 1980.

Field experiments. An additional seed piece of each parental, S_1, and F_1 genotype planted in the greenhouse was also planted with the cultivar evaluation plots in New Brunswick, NJ, on 16 May 1980. Nine replicates of a randomized complete block design were established in rows 81 cm apart with 30.5 cm between plants within rows. All cultural treatments applied to plots of the 1980 cultivar study were also used for plants of the diallel. The percent leaf area exhibiting necrosis was estimated for the most severely injured leaf of each plant on 3 and 22 July 1980 by the same method used in the laboratory. As a result of plant mortality, the data analysis was limited to eight replicates.

Genetic analysis. The diallel cross analyses of variance were similar to Gardner and Eberhart's Analysis III (6). The among hybrids sum of squares was partitioned into general combining ability (GCA), specific combining ability (SCA), maternal effects, and nonmaternal reciprocal differences. No method of separating additive, digenic, trigenic, and quadrigenic effects in an autotetraploid diallel could be determined when parents were a fixed set of clones (4). Heritability estimates were not made because the selection of parents violated an essential assumption for estimation of genetic variances (1).

RESULTS AND DISCUSSION

Cultivar studies. Considerable variation was observed among laboratory and field experiments in the relative response of cultivars (Table 1). With the possible exception of Cherokee, no clones consistently exhibited a high degree of

Table. 1. Mean oxidant injury (%) for 26 potato clones estimated in four laboratory and five field evaluations

	Laboratory evaluation				Field evaluation				
Clone	**Lab-1**	**Lab-2**	**Lab-3**	**Lab-4**	**79-1**	**79-2**	**80-1**	**80-2**	**80-3**
Alamo	38.5	27.5	33.5	36.5	23.4	7.0	23.3	15.0	23.3
Bake King	50.5	45.0	63.0	69.7	6.2	7.8	38.3	45.0	35.0
Blanca	16.0	26.5	11.5	13.5	10.9	7.0	8.3	15.0	28.3
Cherokee	60.5	58.5	57.5	49.5	32.3	10.9	60.0	73.3	66.7
Chieftain	4.7	9.0	10.5	8.2	4.3	7.8	0.8	6.7	5.0
Chippewa	13.0	17.7	12.5	10.5	1.2	2.3	5.8	25.0	16.7
Dazoc	30.5	45.3	12.0	25.5	1.2	7.0	20.0	15.0	13.3
Haig	35.0	38.0	19.5	18.5	3.9	20.3	28.3	36.7	26.7
Irish Cobbler	47.0	62.1	22.0	23.5	7.0	11.7	26.7	45.0	35.0
Manota	64.5	52.0	21.5	41.0	2.3	4.7	41.7	63.3	55.0
Mesaba	27.0	25.0	15.0	22.0	3.9	61.5	15.0	56.7	48.3
Monona	40.5	40.2	11.0	18.0	2.7	5.1	31.7	25.0	16.7
Norchip	13.0	7.2	9.0	15.5	3.5	6.2	2.5	5.8	0.8
Norgold Russet	9.0	9.2	10.5	8.0	1.2	2.3	0.0	0.8	0.0
Norland	35.5	39.5	33.5	39.5	7.8	54.2	28.3	56.7	56.7
Peconic	33.7	43.5	21.5	19.5	1.2	5.1	28.3	13.3	15.0
Pioneer	21.2	20.5	25.5	23.5	34.4	14.1	11.7	33.3	35.0
Pungo	25.0	18.5	7.0	10.5	6.2	5.1	11.7	13.3	6.7
Red LaSoda	26.5	20.5	32.5	19.5	6.2	6.6	16.7	8.3	5.0
Red Warba	29.0	42.5	19.5	37.0	1.8	53.1	23.3	56.7	65.0
Rushmore	60.8	50.4	16.0	23.0	3.5	7.8	16.7	45.0	35.0
Seminole	35.0	59.5	28.0	44.5	2.3	4.7	33.3	26.7	15.0
Superior	9.0	8.2	9.2	7.7	1.2	3.5	0.0	0.0	0.8
Triumph	27.7	21.2	12.0	13.5	1.2	6.2	10.0	45.0	35.0
Warba	39.5	38.0	18.5	22.0	2.5	41.7	28.3	60.0	55.0
Waseca	45.0	46.5	26.0	27.0	5.1	41.7	33.3	55.0	46.7
LSD (0.05)	11.4	11.9	7.8	9.9	5.3	7.7	10.2	8.5	8.0

Table 2. Pearson product-moment correlations among four laboratory and five field evaluations of resistance to oxidant stress in 26 potato clones[a]

	Laboratory evaluation				Field evaluation			
	Lab-1	Lab-2	Lab-3	Lab-4	79-1	79-2	80-1	80-2
Lab-2	0.85 **	...	...	...	...	...	...	...
Lab-3	0.57 **	0.49 *	...	...	...	...	...	...
Lab-4	0.68 **	0.66 **	0.87 **	...	...	...	...	...
Field 79-1	0.18	0.07	0.51 **	0.30	...	...	...	...
Field 79-2	0.11	0.16	0.08	0.19	−0.05	...	...	...
Field 80-1	0.87 **	0.87 **	0.70 **	0.78 **	0.22	0.20		...
Field 80-2	0.72 **	0.65 **	0.46 *	0.57 **	0.19	0.60 **	0.69 **	...
Field 80-3	0.63 **	0.59 **	0.45 *	0.56 **	0.29	0.66 **	0.64 **	0.95 **

[a] * = Significant at the 0.05 level; ** = significant at the 0.01 level.

susceptibility to O_3; however, cultivars Chieftain, Norgold Russet, and Superior were among the most resistant to O_3 in all experiments. The range of symptom severity and type observed was generally comparable in both laboratory and field evaluations. The clones most resistant to oxidant stress in each experiment exhibited between 0 and 11% injury, and the clones most susceptible to O_3 were in the range of 60–75% injury, with the exception of the first field evaluation made in 1979, where all clones exhibited less than 35% injury.

Differences among laboratory runs conducted at two dates, April (Lab-1 and Lab-2) and July (Lab-3 and Lab-4), between runs within dates, among clones, and clone × date and clone × run interactions were all highly significant ($P=0.01$). Although significant differences were detected among clones, those differences were inconsistent between dates and between runs within dates. Despite differences among runs, all laboratory evaluations were correlated significantly with one another (Table 2). As might be expected, high correlations were observed between Lab-1 and Lab-2, and between Lab-3 and Lab-4, ie, between runs within dates.

In both 1979 and 1980 field studies, highly significant variation ($P = 0.01$) among runs and among clones and a highly significant run × clone interaction were observed. The variation among field runs was comparable to that observed among laboratory runs. No significant correlations were observed between 79-2 and 80-1 or between 79-1 and any other field test (Table 2). All other correlations among field evaluations were highly significant.

When laboratory data were compared with field results from 1979, almost no significant correlations were observed (Table 2). Laboratory results were generally poor predictors of field performance in 1979. When laboratory data were compared with field results from 1980, however, significant correlations were observed among all comparisons. The field evaluation most highly correlated with the laboratory data was 80-1.

The consequences of laboratory screening and field selection for resistance to oxidant stress may be illustrated by considering the clone means in Table 1. Generally, those clones identified as resistant to O_3 in the laboratory were also resistant to oxidants in the field, but clones that appeared resistant to oxidant stress in one field evaluation were often relatively susceptible in other field tests. This trend was especially striking in the 79-1 field evaluation, where many of the clones were relatively resistant to oxidant stress (Table 1). The comparatively narrow range of the data from 79-1, noted earlier, may reflect the absence of sufficient injury to adequately separate the genotypes. The reliability of selection for resistance to oxidant stress in the field would clearly increase if evaluations were conducted in several environments or over more than one season. Laboratory screening reliably identified resistance to oxidant stress that was effective over a range of field environments.

Table 3. Mean squares from the analysis of variance and nonorthogonal comparisons for a seven-parent diallel evaluated for resistance to oxidant stress once in the laboratory and in the field on 3 July (Field 1) and 22 July (Field 2) 1980

	Laboratory experiment		Field experiments		
				Mean square[a]	
Source of variation	df	Mean square[a]	df	Field 1	Field 2
Total	501		447		
Replicates	8	0.3494 **	7	0.0754 **	0.1524 **
Treatments	55	0.1868 **	55	0.0394 **	0.0912 **
Clones	6	0.2714 **	6	0.0553 **	0.1892 **
Selfs	6	0.4714 **	6	0.1338 **	0.2845 **
Clones vs. selfs	1	0.3889 **	1	0.0604 **	0.0751
Hybrids	41	0.1308 **	41	0.0236 **	0.0502 **
General combining ability	6	0.4496 **	6	0.0784 **	0.0863 **
Specific combining ability	14	0.0869 **	14	0.0122	0.0571 **
Maternal effects	6	0.1317 **	6	0.0301 **	0.0614 *
Nonmaternal reciprocal	15	0.0437	15	0.0097	0.0248
Hybrids vs. (clones & selfs)	1	0.0675	1	0.0017	0.0386
Error	440	0.0379	385	0.0087	0.0247
		Nonorthogonal comparisons			
Clones vs. hybrids	1	0.3655 **	1	0.0368 *	0.0009
Selfs vs. hybrids	1	0.0449	1	0.0169	0.1075*

[a] * = Significant at the 0.05 level; ** = significant at the 0.01 level.

Diallel studies. Variation among parental, among S_1, and among F_1 genotypes of the diallel was highly significant in the laboratory run (Table 3). Highly significant differences were also observed for the independent comparison between clones and selfs and the nonorthogonal comparison between clones and hybrids. GCA, SCA, and maternal effects were highly significant, but reciprocal differences not associated with maternal effects were not significant. We obtained similar results when data from the laboratory run were pooled with data from three other laboratory runs, each containing additional genotypes from families of the same diallel (5). Data from four runs of a second seven-parent diallel also exhibited GCA and SCA effects that were highly significant; however, neither maternal nor nonmaternal reciprocal effects were significant (5).

Significant variation ($P = 0.05$) between the two field evaluation dates and significant data × replicate, date × clone, and date × self interactions prompted the use of separate analyses for each date. Data for both 3 July (Field 1) and 22 July (Field 2) evaluations exhibited highly significant differences among clones, among selfs, and among hybrids (Table 3). GCA and maternal effects were also significant at both dates. These results were similar in significance to those obtained in the laboratory study.

Table 4. Proportion of the sum of squares due to variation among hybrids attributable to general and specific combining ability, maternal effects, and nonmaternal reciprocal differences for a seven-parent diallel evaluated for resistance to oxidant stress once in the laboratory and in the field on 3 July (Field 1) and 22 July (Field 2) 1980

Source of variation	Proportion of hybrids sum of squares (%)		
	Laboratory	Field 1	Field 2
General combining ability	50.3	48.6	25.2
Specific combining ability	22.7	17.7	38.8
Maternal effects	14.8	18.6	17.9
Nonmaternal reciprocal	12.2	15.1	18.1

SCA, however, was significant in Field 2 only. Comparisons among clones and selfs and among clones and hybrids were significant for Field 1. Only the nonorthogonal comparison among selfs and hybrids was significant for Field 2 (Table 3).

Comparison of the relative contributions of GCA, SCA, maternal, and residual reciprocal effects to the total variation among hybrids for the laboratory and field runs is presented in Table 4. In the laboratory and in Field 1, GCA accounted for the largest portion of the variation among hybrids; however, SCA was the most important component in Field 2. Maternal and reciprocal differences not associated with maternal effects were relatively constant among experiments. The pooled results of four laboratory runs of the same diallel, reported previously (5), indicated substantially greater hybrid variability attributable to GCA than that observed in the one run reported here. We believe that the difference among runs was more a function of sampling variation than any real run effect.

The laboratory and Field 1 evaluations of the diallel exhibited a strikingly similar mode of inheritance. This similarity may be associated with the observation that the field plants were relatively small at the time the Field 1 data were collected and thus were more physiologically comparable to plants tested in the laboratory than plants evaluated in a later run. Correlations observed among results from the cultivar evaluations exhibited a similar trend (Table 2). The field run most highly correlated with laboratory results was 80-1, which, together with Field 1, was evaluated on 3 July 1980. Clearly, physiological age is only one of many environmental factors that may have contributed to the observed variation between field dates. Resistance of plants to oxidants early in the growing season may be of particular interest, however, because it has been hypothesized that oxidant stress has a greater impact on yield reduction during the period of rapid tuber development than at a later date (B. B. Clarke and E. Brennan, *unpublished*).

The severe selection pressure provided by controlled O_3 exposures reliably reduced the number of genotypes to be evaluated in field trials. Elimination of phenotypes susceptible to O_3 in the laboratory, followed by field selection for resistance to oxidant stress over a number of environments or years, would be an effective method for selecting useful germ plasm in a potato breeding program where resistance to O_3 is a primary objective.

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