

SUSCEPTIBILITY OF CEREALS TO ORGANOCHLORINE PESTICIDES

Sher Akbar* and Lyndon J. Rogers

*Department of Biochemistry and Agricultural Biochemistry,
The University College of Wales, Aberystwyth, Dyfed, SY23 3DD, Wales, UK*

(Received September 8, 1985; revised May 21, 1986)

The results of surveys of a number of cereal types for susceptibility to the organochlorine pesticides 1, 1, 1-trichloro-2, 2-bis (*p*-chlorophenyl) ethane ('DDT') and toxaphene are presented. Different genes appear to be implicated in the responses to the two pesticides, though their biochemical mode of action is similar.

Key words: DDT; Toxaphene; Photosynthetic Electron Flow.

INTRODUCTION

Following prolonged exposure, certain weed species have developed resistance to the herbicides used for their control. The first instances recorded were of increased tolerance to 2, 4-D, but resistant biotypes of thirty-four weed species have now been recorded; resistance in most cases has been to triazines but in a few cases to paraquat and terbuthryne [1]. Tolerance, i.e. decreased sensitivity but not resistance, to a wider range of herbicides has been shown in a further sixteen species.

There have also been reports that a few crop species show susceptibility to pesticides other than herbicides. Varietal differences to DDT (1, 1, 1-trichloro-2, 2-bis (*p*-chlorophenyl) ethane) have been reported for *Hordeum* spp. (barley) [2], *Secale* spp. (rye) [3] and *Triticum* spp. (wheat) [4], and to toxaphene (camphechlor) for *Avena* spp. (oats) [5]. Toxaphene is a complex mixture of more than 200 constituents with an average elemental composition of $C_{10}H_{10}Cl_8$. In all these susceptibility is the dominant character and can be attributed to a single major gene. In these surveys susceptibility was diagnosed from the chlorosis or discolouration of leaves which developed within a week of the foliar application of the pesticide. In susceptible barley the biochemical mode of action of DDT has been shown to be an inhibition of photosynthetic electron flow and concomitant formation of ATP [6]. These lead to a decreased CO_2 assimilation but sugars accumulate in treated leaves because translocation, an energy-dependent process, is inhibited [7]. The bioche-

mical response of rye to DDT [8, 9] and of oats to toxaphene [10, 11] is similar. Using inhibition of photosynthetic electron flow as an index of susceptibility we have looked at the response to the two pesticides of a range of varieties of five cereals.

MATERIALS AND METHOD

Plant material. Except for maize, surveys were based on seed samples supplied from the US Department of Agriculture Small Grain Collection, and represented a wide distribution in terms of country of origin, and for some cereals also of species. Some commercial UK varieties were included. The maize varieties used were a selection from the Maize and Millet Research Station, Pirsabak, Pakistan.

Test of susceptibility. Seedlings were sprayed at the two-to-three leaf stage with a 0.25% (w/v) emulsion of technical DDT in 0.1% (v/v) Tween 60:acetone (9:1 by vol.) or a 1.2% (w/v) solution of toxaphene in 0.1% (v/v) Tween 60. Seedlings used as controls were treated with 0.1% (v/v) Tween 60:acetone (9:1 by vol.) or 1.0% (v/v) xylene in 0.1% (v/v) Tween 60, respectively. Two days after treatment, and before any chlorosis was evident, leaves were harvested, chloroplasts isolated, and rates of dichlorophenolindophenol and ferricyanide photoreductions determined by methods described elsewhere [6].

RESULTS

Varieties where chloroplasts from treated plants showed an inhibition of photosynthetic electron flow of 40% or more were classed as susceptible. One or two seedlings were kept to confirm susceptibility from the chlorosis

*Department of Agricultural Chemistry, NWFP Agricultural University, Peshawar, Pakistan.

Table 1. Susceptibility of oats to DDT and toxaphene.

Variety No.	Name	Response to DDT						Response to toxaphene						Reaction	
		DCPIP reduced		Fe(CN) ₆ ³⁻ reduced		% Inhibition	Reaction	DCPIP reduced		Fe(CN) ₆ ³⁻ reduced		% Inhibition	Reaction		
		UT	T	UT	T			UT	T	UT	T				
PI 203450		129	121	6	142	144	(-1)	R	103	44	57	114	50	56	S
" 219574	Gentry HS 14160	113	119	(-6)	128	134	(-5)	R	127	78	38	133	84	37	S
" 234842	—	101	97	4	127	102	19	R	97	27	72	114	35	69	S
" 266827	—	133	133	0	139	144	(-4)	R	120	55	54	131	60	54	S
" 287314	Kleiner Nackhafer	108	107	1	128	124	3	R	—	—	—	—	—	—	—
" 355005	—	123	116	6	139	133	4	R	107	67	37	116	74	36	S
" 361866	—	112	109	3	124	127	(-2)	R	90	33	63	99	40	59	S
" 361912	—	99	104	(-5)	124	131	(-6)	R	109	45	58	126	54	57	S
CI 797	Algerian	95	106	(-12)	137	133	3	R	115	45	61	129	58	55	S
" 1191	Banner	131	146	(-11)	145	135	6	R	103	50	51	115	55	52	S
" 1667	Silensia	96	109	(-14)	130	116	10	R	105	47	55	117	55	54	S
" 2824	Illinois Hull-less	99	106	(-7)	127	116	8	R	96	40	58	107	51	52	S
" 3422	New Nortex	—	—	—	—	—	—	—	92	61	33	134	112	16	I
" 3816	—	84	95	(-13)	118	116	2	R	—	—	—	—	—	—	—
" 4121	—	83	97	(-17)	91	91	0	R	—	—	—	—	—	—	—
" 5198	Koelz W 9478	96	102	(-6)	108	111	(-3)	R	111	50	55	120	55	54	S
" 8025	Moregrain	—	—	—	—	—	—	—	90	65	27	118	108	8	I
" 9023	CD 3994	93	96	(-3)	107	105	2	R	108	63	41	124	78	37	S
—	Blyth	—	—	—	—	—	—	—	137	62	55	163	78	52	S
—	Fyne	—	—	—	—	—	—	—	102	46	55	130	62	52	S
—	Leanda	—	—	—	—	—	—	—	124	60	51	143	72	49	S
—	Maris Oberon	—	—	—	—	—	—	—	106	61	42	124	78	37	S
—	Maris Tabard	—	—	—	—	—	—	—	116	60	48	131	73	44	S
—	Orlando	—	—	—	—	—	—	—	118	68	42	133	80	40	S
—	Pinto	—	—	—	—	—	—	—	107	65	39	121	76	37	S
—	Saladine	—	—	—	—	—	—	—	105	56	46	116	68	41	S
—	Trafalgar	—	—	—	—	—	—	—	109	61	44	123	72	41	S

Rates for chloroplasts from untreated (UT) and treated (T) seedlings are given as μmol acceptor reduced/hr/mg chlorophyll. S, susceptible; I, intermediate reaction; R, resistant. Variety number is that in the US Department of Agriculture Small Grains Collection.

which developed subsequently. Resistance was concluded if rates of photoreduction for chloroplasts from treated and untreated plants were within 15%. However, some varieties showed an intermediate response where the photosynthetic reaction was inhibited by 20 to 30%. The data from the surveys are shown in Tables 1-5.

DISCUSSION

For oats (Table 1) the survey included representatives from *A. fatua*, *A. nuda*, *A. sativa* and *A. strigosa*. All the varieties were resistant to DDT and agreements in photoreduction rates between chloroplasts from treated and untreated seedlings were particularly good. In contrast, all the varieties were susceptible to toxaphene, except for

Moregrain and New Nortex which gave an intermediate response. Possibly, toxaphene may have caused some generalised membrane damage unrelated to the gene effect, since in greenhouse trials in an earlier survey [5] these two varieties were classed as resistant. Supplies of seeds were insufficient to permit additional tests.

For barley (Table 2) the occurrence of susceptibility to DDT is well documented and this was confirmed in the present survey. Some two-thirds of the varieties, including representatives of *H. deficiens*, *H. distichon*, *H. irragulare* and *H. vulgare*, were susceptible. For this cereal there was a striking correlation between susceptibility to DDT and reaction to toxaphene. Nine varieties were susceptible to both, and there was no susceptible-resistant pairing for response to the two pesticides. Were it not for the differ-

Table 2. Susceptibility of barley to DDT and toxaphene

Variety No.	Name	Response to DDT						Response to toxaphene							
		DCPIP reduced		Fe(CN) ₆ ³⁻ reduced		Reaction	DCPIP reduced		Fe(CN) ₆ ³⁻ reduced		Reaction				
		UT	T	% Inhibition	UT		T	% Inhibition	UT	T		% Inhibition			
PI 361052	Ymer	69	76	(-10)	92	107	(-16)	R	85	60	29	91	68	25	I
" 282576	—	75	49	34	81	46	43	S	—	—	—	—	—	—	—
" 235639	—	64	33	48	102	59	42	S	—	—	—	—	—	—	—
" 361678	DN-32	—	—	—	—	—	—	—	69	36	48	74	42	43	S
CI 6140	Danne 13	70	33	53	101	46	54	S	84	41	51	84	65	29	S
" 2229	Nudideficiens	64	40	37	99	45	54	S	86	24	72	101	33	67	S
" 11474	—	79	50	36	91	46	49	S	102	41	59	105	77	26	S
" 10251	—	87	38	56	101	43	57	S	71	37	48	65	44	32	S
" 7269	Anodium	—	—	—	—	—	—	—	68	31	51	64	38	40	S
" 10566	—	61	69	(-13)	94	92	2	R	89	60	32	86	64	25	I
" 12687	Krasnyj Dar	89	52	41	97	60	38	S	79	24	69	58	44	24	S
" 7783	—	—	—	—	—	—	—	—	96	82	14	113	98	13	R
" 12019	—	71	37	47	74	44	40	S	81	37	54	120	77	35	S
" 12982	Isaria Nova	65	25	61	91	44	61	S	75	25	66	85	62	27	S
" 6010	—	67	36	46	88	62	30	S	85	27	68	89	44	50	S
" 15239	OAC WB 58-27	45	25	45	61	33	45	S	77	17	77	69	13	81	S
" 15004	Iris	51	35	31	65	46	29	I	84	19	77	68	31	54	S

Rates for chloroplasts from untreated (UT) and treated (T) seedlings are given as μmol acceptor reduced/hr/mg chlorophyll. S, susceptible; I, intermediate reaction; R, resistant. Variety number is that in the US Department of Agriculture Small Grains Collection.

ent response to the pesticides in oats, the results for barley might suggest that the same gene was involved in the responses to both DDT and toxaphene, since their biochemical modes of action are very similar. The survey data for oats seem to rule this possibility out, though genes with similar roles in chloroplast membrane assembly could be responsible for the DDT and toxaphene response.

Previous tests have suggested that susceptibility to DDT in rye [3] and wheat [4] is widespread, but this was not borne out by the biochemical assay. In the rye varieties (Table 3) mainly *S. cereale* but including *S. segetale*, only three varieties were clearly susceptible, while for wheat (Table 4) no variety could be classed as susceptible and only two gave an intermediate response. In the greenhouse trials [4] only seven wheat varieties out of forty tested were resistant but *T. aestivum* varieties, which made up a third of the survey, were classed as moderately susceptible. Of the commercial durum wheat varieties included in that survey three were resistant and all but one of the remaining six varieties proved to be mixed populations for reaction to DDT. In the earlier trials with rye [3] a susceptible response was the development of a chlorosis following two treatments with DDT. Mixed reaction, but

with susceptible plants predominating, was common. For this cereal, two varieties were also included in the present survey. Lovaspatonai was susceptible in both, our and the earlier tests, but seeds supplied as Rheidol gave plants which were resistant from the biochemical assay, whereas seedlings were predominantly susceptible in the earlier greenhouse trials.

In rye the twenty varieties tested showed a spread of reaction to toxaphene falling about equally into the three categories; there was a good fit to the three groups and not a continuum of response. However, in oats there was no evidence to suggest widespread sensitivity to toxaphene and only one variety could be classed as susceptible.

Though the survey of maize (Table 5) was less extensive, there was no clear case of sensitivity to DDT, but two varieties were sensitive to toxaphene. Varieties showing susceptibility to toxaphene were thus found in all five cereal types with oat and barley varieties being usually susceptible, and rye showing a wide range of response. Under the conditions of testing used, susceptibility to DDT was widespread in barley and also occurred in rye but wheat varieties, predominantly *T. aestivum*, were resistant. This species was moderately susceptible in greenhouse

Table 3. Susceptibility of rye to DDT and toxaphene.

Variety No.	Name	Response to DDT						Response to toxaphene						Reaction	
		DCPIP reduced		Fe(CN) ₆ ³⁻ reduced		Reaction	DCPIP reduced		Fe(CN) ₆ ³⁻ reduced		Reaction				
		UT	T	% Inhibition	UT		T	% Inhibition	UT	T		% Inhibition	UT		T
	Rheidol	74	78	(-5)	95	102	(-7)	R	65	56	14	92	88	4	R
	Rhayader	95	88	7	106	105	1	R	99	71	28	132	98	26	I
	Greenfold	78	67	14	92	80	13	R	87	46	47	70	41	41	S
	Lovaspatonai	93	53	44	106	61	42	S	—	—	—	—	—	—	—
PI 168199	Harlan JR	—	—	—	—	—	—	—	87	44	49	98	48	51	S
" 235536	Grand Crouelle	46	52	(-13)	63	66	(-5)	R	87	49	43	92	57	38	S
" 240675	Centeno de la Estam Zuela	46	43	7	51	52	(-2)	R	91	40	56	98	51	47	S
" 267102	Perevaya	70	56	20	76	63	17	R	89	48	46	106	66	37	S
" 272338	1-3-127	58	59	(-2)	70	68	3	R	110	55	50	123	58	52	S
" 284842	Nemelorsrag	55	57	(-4)	79	87	(-10)	R	99	71	28	93	68	26	I
" 326284	K 5836	51	56	(-10)	72	76	(-6)	R	95	72	24	97	78	19	I
" 344516	Hungarian Giant	96	42	56	92	39	57	S	—	—	—	—	—	—	—
" 357067	TK15576-67	64	50	22	86	56	35	S	61	44	28	81	57	29	I
CI 3	Adams	73	70	4	77	79	(-2)	R	70	45	35	72	47	34	S
" 5	Balbo	47	46	2	65	58	10	R	—	—	—	—	—	—	—
" 17	Gator	75	79	(-5)	83	82	1	R	72	40	44	114	63	44	S
" 32	Von Lochow	61	44	28	71	55	22	I	—	—	—	—	—	—	—
" 80	Kirszkajh	63	66	(-5)	81	76	7	R	64	49	23	101	80	20	I
" 84	Tetraploid Vilmorin	67	68	(-1)	74	74	0	R	75	53	29	112	83	26	I
" 102	5-SC-12	82	76	7	89	86	4	R	85	62	27	110	82	25	I
" 106	Irlanda	64	66	(-3)	78	79	(-1)	R	87	83	5	127	121	5	R
" 109	Korean	77	69	11	81	79	2	R	85	77	9	90	84	6	R
" 110	Korea 1	100	82	18	91	86	6	R	79	67	15	100	89	11	R
" 169	Vita-Graze	52	55	(-6)	59	65	(-10)	R	86	81	6	114	108	5	R

Rates for chloroplasts from untreated (UT) and treated (T) seedlings are given as μmol acceptor reduced/hr/mg chlorophyll. S, susceptible; I, intermediate reaction; R, resistant. Variety number is that in the US Department of Agriculture Small Grains Collection.

trials [4] with different varieties. The data from these surveys, including that from an earlier survey of a different range of barley varieties [6], are summarised in Table 6.

The origin of the genetic response in cereals to these pesticides is of interest. Until recently, DDT was one of the most widely used pesticides, and toxaphene continues to be used extensively in the USA. Both have long environmental persistence. However, cereal crops are unlikely to have met sufficiently repeated contacts with the pesticides to promote selection of resistant strains, and it is difficult to see how the possession of the gene could give a selective advantage to the crop. Possibly susceptibility to the pesticides, the dominant character, is through the possession of a gene coding for a component of the photosynthetic membrane which incidentally conveys susceptibility to DDT or toxaphene. A parallel would be the recent

recognition that resistance to triazines in some weeds has arisen through a change in a single amino acid residue in the so-called 32Kd herbicide-binding protein, which is a membrane component having a role in the Q_B region of the photosynthetic electron transport chain [12]. Recently, it has been shown that three residues in the 32Kd protein can be independently altered in weed biotypes to produce three distinct patterns of resistance to herbicides acting at this site [13], and plants with different levels of resistance to s-triazines display varying cross resistances to other herbicides. The genetic change to give a different response to a pesticide could therefore be of a single base in the gene; different responses to DDT and toxaphene in the various cereals, even though biochemical mode of action is similar for the two pesticides, might be due to separate changes in the structure of the binding site(s) of the same thylakoid polypeptide. A possible

Table 4. Susceptibility of wheat to DDT and toxaphene

Variety No.	Name	Response to DDT						Response to toxaphene							
		DCPIP reduced		Fe(CN) ₆ ³⁻ reduced		Reaction	DCPIP reduced		Fe(CN) ₆ ³⁻ reduced		Reaction				
		UT	T	% Inhibition	UT		T	% Inhibition	UT	T		% Inhibition			
PI 91673	4	64	63	2	87	85	2	R	79	75	5	87	75	13	R
" 134945	232	42	47	(-12)	54	50	8	R	60	56	7	88	79	10	R
" 168693	Noris	67	49	27	73	61	16	I	93	91	2	118	117	1	R
" 185932	11-888	78	81	(-4)	97	95	2	R	—	—	—	—	—	—	—
" 190932	2481	74	73	1	85	88	(-4)	R	65	70	(-8)	88	91	(-3)	R
" 234238	Idaho 1880 NRBA	75	74	1	87	94	(-8)	R	100	84	16	103	90	12	R
" 248990	—	76	62	18	83	64	23	I	81	35	56	107	52	51	S
" 272521	1-1-2715	69	71	(-2)	94	93	1	R	91	83	8	125	130	(-4)	R
" 282932	D-357-1	—	—	—	—	—	—	—	78	85	(-9)	91	94	(-3)	R
CI 3994	Kavarna ICM 325	57	63	(-10)	71	73	(-3)	R	64	60	6	82	79	4	R
" 10438	Love HH C50	68	71	(-4)	84	82	2	R	63	58	8	89	84	6	R
" 12470	Frontana	63	61	3	73	75	(-3)	R	85	67	21	106	95	10	R
" 13389	Taylor 16	52	62	(-19)	71	77	(-8)	R	75	66	12	83	75	9	R
" 15818	Heine C73	73	70	4	87	82	6	R	69	62	14	86	77	10	R
" —	Dirk	64	71	(-11)	93	86	7	R	68	69	(-1)	105	109	(-4)	R
" —	Chenab 70	80	82	(-2)	65	59	9	R	82	83	(-1)	69	63	8	R
" —	C 271	75	71	5	58	61	(-5)	R	78	65	16	55	45	18	R
" —	Sandal	92	86	6	80	84	(-5)	R	96	76	20	87	67	22	I
" —	Barani 70	72	79	(-10)	75	85	(-13)	R	77	70	9	86	69	19	R
" —	Pak 70	86	77	10	111	102	8	R	87	80	8	106	82	22	R
" —	Khyber 79	92	93	(-1)	87	92	(-6)	R	95	83	12	82	61	25	R
" —	Chenab 79	111	96	13	93	77	17	R	109	100	8	96	78	18	R
" —	SA 75	76	85	(-12)	103	105	(-2)	R	79	71	10	101	92	8	R
" —	C3	84	84	0	95	88	7	R	86	82	5	96	86	10	R

Rates for chloroplasts from untreated (UT) and treated (T) seedlings are given as μmol acceptor reduced/hr/mg chlorophyll. S, susceptible; I, intermediate reaction; R, resistant. Variety number is that in the US Department of Agriculture Small Grains Collection.

Table 5. Susceptibility of maize to DDT and toxaphene

Variety	Response to DDT						Response to toxaphene							
	DCPIP reduced		Fe(CN) ₆ ³⁻ reduced		Reaction	DCPIP reduced		Fe(CN) ₆ ³⁻ reduced		Reaction				
	UT	T	% Inhibition	UT		T	% Inhibition	UT	T		% Inhibition			
PR 7525	75	88	(-17)	104	122	(-17)	R	70	56	20	135	114	15	(R)
PR 7734	92	80	13	124	134	(-8)	R	60	43	28	113	84	25	I
PR 7930 (1)	93	88	5	98	102	(-4)	R	79	42	47	92	52	43	S
PR 7930 (2)	96	99	(-3)	117	123	(-5)	R	76	78	(-3)	104	102	2	R
Zia	88	86	2	115	108	6	R	52	35	32	102	62	39	S
Sarhad (W)	97	84	13	119	104	12	R	66	52	21	91	74	18	(R)
Sarhad (Y)	98	87	11	125	127	(-2)	R	65	58	10	95	88	7	R
Changez	78	72	8	93	88	5	R	52	44	15	91	80	12	R
Shaheen	82	60	26	99	83	16	(I)	66	57	13	96	88	8	R
New Shaheen	66	65	2	96	80	17	R	55	42	23	87	73	16	(R)

Rates for chloroplasts from untreated (UT) and treated (T) seedlings are given as μmol acceptor reduced/hr/mg chlorophyll. S, susceptible; I, intermediate reaction; R, resistant. Seeds were from the Maize and Millet Research Station, Pirsabak, Pakistan.

Table 6. Pesticide reaction of populations from cereals

	Varietal response to DDT			Varietal response to toxaphene		
	Susceptible	Intermediate reaction	Resistant	Susceptible	Intermediate reaction	Resistant
<i>Avena</i> spp.	0	0	16 (-1 ± 7.5)	22 (50 ± 9)	2 (21 ± 9.5)	0
<i>Hordeum</i> spp.	11 (46 ± 8.5)	1 (30)	2 (-9 ± 7)	12 (52 ± 18)	2 (25 ± 4)	1 (13)
	16 (56 ± 16)	0	8 (-2 ± 4)*			
<i>Secale</i> spp.	3 (44 ± 10)	1 (25)	19 (3 ± 8.5)	8 (45 ± 6)	7 (25 ± 3)	5 (10 ± 5)
<i>Triticum</i> spp.	0	2 (18 ± 4)	21 (-0.5 ± 8)	1 (54)	1 (21)	21 (8 ± 8)
<i>Zea mays</i>	0	1 (21)	9 (2 ± 9.5)	2 (40 ± 6)	1 (27)	7 (12.5 ± 7)

Data in italics show the mean ± s.d. for inhibition of the Hill reaction in chloroplasts from treated compared to untreated seedlings. Experiments were with two Hill acceptors and *n* is twice the number of varieties. *Data for 24 varieties of *Hordeum* spp. from an earlier study (Owen *et al.*, 1975). Where the reaction of one or two varieties differed to the majority and seed supplies permitted the responses were confirmed by further experiments. The averaged % inhibitions were used in statistical analyses.

candidate would be the 41 Kd polypeptide associated with the photosystem 2 reaction centre since phenolic herbicides, in addition to their action at the DCMU site, act at this further site on the donor side of photosystem 2 [14]. DDT [6, 8] and toxaphene [10] also act on the donor side of this photosystem in addition to a site in the intermediate electron transport chain linking photosystem 2 to photosystem 1.

Amongst cereals examples of selective resistance to herbicides are now known. Chlorfenprop-methyl kills *A. fatua* at dose levels which have no effect on *A. sativa* or *A. sterilis*, while in *T. aestivum* some varieties are tolerant of levels of chlortoluron to which other varieties are susceptible. Increased tolerance to triallate, though not total resistance, was found in *A. fatua* after repeated treatment with the pesticide over many years. There can also be a natural intraspecific variation where some varieties in a species show lower susceptibility than usual but without this being a response to selection pressure from herbicide application [15]. The mechanisms of differential tolerance can be morphological, physiological or biochemical [16].

There is every reason to believe that other genes conferring resistance to pesticides exist in cereals and other crops, and these should in principle be transferable to susceptible commercial varieties or new varieties. This would give the potential for protection of crops from agricultural chemicals used against their pests, whether insect, fungus or weed.

Acknowledgement. One of the authors (S.A.) is grateful to the Government of Pakistan for a Postgraduate scholarship during the time this work was carried out. We thank the Crops Research Division, US Department of

Agriculture, Beltsville, Maryland, USA, for seed samples, and FBC Limited, Chesterford Park Research Station, Saffron Walden, Essex, UK, for toxaphene.

REFERENCES

1. K.J. Murphy, *Biologist*, **30**, 211 (1983).
2. G.A. Weibe and J.D. Hayes, *Agron. J.*, **52**, 685 (1960).
3. J.M. Jones and J.D. Hayes, *Pl. Path.*, **16**, 139 (1967).
4. L.W. Briggles, *Crop Sci.*, **4**, 457 (1964).
5. J.H. Gardenhire and M.E. McDaniel, *Crop Sci.*, **10**, 299 (1970).
6. W.J. Owen, L.J. Rogers and J.D. Hayes, *J. Exp. Bot.*, **26**, 692 (1975).
7. M.E. Delaney, W.J. Owen and L.J. Rogers, *J. Exp. Bot.*, **28**, 1153 (1977).
8. S. Akbar and L.J. Rogers, *Phytochem.*, **24**, 2785 (1985).
9. S. Akbar and L.J. Rogers, *Phytochem.* **24**, 2791 (1985).
10. S. Akbar and L.J. Rogers, *Phytochem.* in press (1986).
11. S. Akbar and L.J. Rogers, *Phytochem.* in press (1986).
12. J. Hirschbert, A. Bleecker, D.J. Kyle, L. McIntosh and C.J. Arntzen, *Z. Naturforsch.*, **39c**, 412 (1984).
13. M. Erickson, M. Rahire, J-D. Rochaix, and L. Mets, *Science*, **228**, 204 (1985).
14. P. Mathis and A.W. Rutherford, *Biochim. Biophys. Acta*, **767**, 217 (1984).
15. J.J. Sexsmith, *Weed Sci.*, **12**, 19 (1964).
16. K.I.N. Jensen, *Herbicide Resistance in Plants*, in H. LeBaron and J. Gressel (eds.) (Wiley, N.Y., 1982), p. 133.