Effects of Interacting Populations of *Alternaria solani*, *Verticillium dahliae*, and the Potato Leafhopper (*Empoasca fabae*) on Potato Yield

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ABSTRACT

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Yield reduction in potato caused by early blight (*Alternaria solani*), Verticillium wilt (*V. dahliae*), and potato leafhopper (*Empoasca fabae*) was studied on three cultivars, Russet Burbank, Norland, and Red Pontiac, in factorially arranged field experiments in 1983 and 1984. Early blight epidemics were initiated by inoculation, and the fungicide chlorothalonil was used to develop varying levels of disease. A Verticillium wilt treatment was introduced either by inoculating stems at flowering (1983) or by applying a conidial suspension to the seed piece (1984). Varying levels of potato leafhopper nymphs were developed by managing the natural population with insecticides. In 1983, main effects of cultivar, leafhopper, early blight, and Verticillium wilt on yield were significant ($P = 0.05$). In addition, cultivar × leafhopper, cultivar × early blight, leafhopper × early blight, and leafhopper × early blight × Verticillium wilt interactions were significant ($P = 0.05$). Maximum yield reduction averaged across cultivars by each pest alone was 54, 31, and 12% for leafhopper, early blight, and Verticillium wilt, respectively. Maximum yield loss by any combination of pests was 63%. Significant effects on yield in 1984 were cultivar, leafhopper, early blight, and cultivar × early blight ($P = 0.05$). Maximum yield reductions averaged across cultivar by early blight and leafhoppers alone were 18 and 15%, respectively. In combination, early blight and leafhoppers reduced yield a maximum of 26%. Cultivar × early blight interactions were related to greater yield losses on late-maturing cultivars (Russet Burbank and Red Pontiac) than on an early-maturing cultivar (Norland). Pest × pest interactions showed that yield losses by solitary pests were not additive. Differences in results between 1983 and 1984 were due to differences in the range of pest levels attained.

Additional key words: crop loss assessment.

Yield reductions caused by individual pests of potato (*Solanum tuberosum* L.) have been documented extensively (7,15,17,20,26,29), but much less is known about the combined effects of two or more pests on crop yield. Chiarappa et al (2) and Le Clerg (16) both noted the need for more investigations of possible interactions between organisms, because estimates of pest effects on yield for management or surveys are usually made under the assumption that each pest acts independently. Synergystic yield-loss relationships, however, have been found in the potato early-dying complex (23) and the potato virus S × potato virus X interaction (18).

In addition to synergistic interactions, there is evidence of another type of interaction between some pests of potato. Two previous multiple-pest/yield-loss studies identified negative (nonadditive) interactions between late blight (caused by *Phytophthora infestans* (Mont.) de Bary) and Colorado potato beetles (*Leptinotarsa decemlineata* (Say)) (14) and between early blight (caused by *Alternaria solani* (Ell. & Mart.) Jones & Grout) and Verticillium wilt (caused by *Verticillium dahliae* Kleb.) (8). These responses are termed negative interactions because, in an additive yield-loss model, each individual pest has a positive coefficient (i.e., increasing insect or disease levels are increasingly detrimental to the crop), whereas the pest × pest interaction term has a negative coefficient, reflecting the nonadditivity of the combined effects. This type of interaction is important because the expected benefit from control of one pest is dependent on the level of the other pest(s). For example, at one location in Colorado (8), significant yield increases from control of early blight with fungicides occurred only in plots that were also fumigated to control Verticillium wilt.

In Minnesota, three of the most important yield-reducing pests of potato are early blight (28), Verticillium wilt (27), and the potato leafhopper (*Empoasca fabae* (Harris))(1). These pests commonly occur within the same field, and all are most prevalent from midseason to late-season. The purpose of this study is to examine the effects of each of these pests alone and in combination on yield of three potato cultivars using factorially arranged field experiments.

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MATERIALS AND METHODS

Cultural practices. The experiments were done on a Waukegan silt-loam soil at the University of Minnesota, Rosemount Agricultural Experiment Station. Planting dates were 18 May 1983 and 24 May 1984. At planting, B-sized whole seed of cultivars Norland, Red Pontiac, and Russet Burbank were placed 30 cm apart in 1-m rows. Each cultivar was planted in units that measured 40 m by 64 rows (1983) or 48 rows (1984) wide. Every eight rows, alfalfa (*Medicago sativa* L. cv. Vernal) was interplanted in strips 5 m wide to enhance leafhopper pressures and to harbor predaceous insects that suppress aphid populations on the potatoes (1).

Fertilization consisted of 111-22-67 kg/ha NPK preplant. For weed control, the herbicides applied were *S*-ethyl dipropylthiocarbamate (5.9 kg a.i./ha preplant) and metribuzin (0.28 kg a.i./ha postemergence). The potatoes were hilled in early July both years.

Experimental design. The experiments were replicated three times with one unit of each cultivar per replicate. Treatments were arranged as a combination of two strip-plot designs (Fig. 1) (3). In the first strip-plot arrangement, leafhopper (L) treatments were stripped across cultivar (C) units in widths of eight (1984) or 16 rows (1983). Four levels of leafhopper treatments were used in 1983 and six in 1984. Within each cultivar × leafhopper subunit ($C_i \times L_j$) was a second strip-plot design of early blight (E) and Verticillium wilt (V) treatments (Fig. 1). Four levels of early blight were included in 1983 and three in 1984. Two levels of Verticillium wilt were established in both years.

The smallest experimental unit ($C_i \times L_j \times E_k \times V_m$, denoted as "plot" in further discussion) measured four rows wide by either 16.8 m (1983) or 12.2 m (1984). The 1983 experiment had 96 plots per replicate arranged in a 3 × 4 × 4 × 2 factorial, and the 1984 experiment had 108 plots per replicate (3 × 6 × 3 × 2 factorial). Yields were taken on the middle two rows of each plot in late September after the crop had totally senesced (1983) or a hard freeze had occurred (1984).

Introduction and management of pest levels. Development of pest levels was done either by introducing a pest by inoculation to specific levels or by spraying levels with pesticides to suppress pest populations. For leafhoppers, all levels were obtained by applying insecticides in varying rates targeted at the natural population. Levels of early blight were achieved by spraying fungicide on certain levels or inoculating other levels to initiate epidemics. Verticillium wilt levels were obtained by inoculation.

To manage leafhopper levels in 1983, the insecticide methoxychlor was applied to levels 1, 2, and 3 at rates of 2.02, 0.34, and 0.056 kg a.i./ha, respectively. Level 4 was an untreated control. Application dates were 8 and 19 July and 8 and 18 August. In 1984, methamidophos (0.56 kg a.i./ha) was applied to border rows of treatment level 1. Methoxychlor applied at 1.23, 0.41, and 0.13 kg a.i./ha constituted levels 2, 3, and 4, respectively. Level 5 was treated with pirimicarb (0.28 kg a.i./ha), and level 6 was an untreated control. Application dates in 1984 were 7 and 20 July and 2, 13, and 28 August. All insecticides were applied using a boom sprayer with three drop nozzles per row operating at 1,724 kPa and delivering 935 L/ha.

Early blight inoculum was prepared by growing cultures of *A. solani* on Difco potato-dextrose agar (PDAS) containing streptomycin (100 mg/L) for 10–12 days at room temperature in the dark. On inoculation dates, the cultures were pureed with water in a blender for 15–20 sec, strained through cheesecloth, and diluted to a concentration of 2.5 cultures per liter. The inoculum suspension was applied with a hand-held sprayer to early blight levels 3 and 4 in 1983 and level 3 in 1984 at a rate of about 0.75 L/plot. Inoculation dates in 1983 were 15, 16, and 18 July for level 4, and 3 and 15 August for level 3. Inoculation dates in 1984 were 14, 18, and 26 July and 2 August. All inoculations were made near or at dusk.

The fungicide chlorothalonil was used to control early blight on levels 1 and 2. Fungicide was applied at 1.17 kg a.i./ha in 1983 and 1.75 kg a.i./ha in 1984 using a boom sprayer with four nozzles per row (two overhead and two drop) operating at 689.4 kPa and delivering 608 L/ha. Level 1 was treated weekly until harvest, beginning 6 July 1983 and 25 July 1984. Level 2 was treated 6 and 21 July and 26 August 1983 and 10 August 1984.

For Verticillium wilt, inoculum was prepared by growing *V. dahliae* for 5–7 days on PDAS at room temperature in the dark. In 1983, conidia were washed off the plates with distilled water and adjusted to 1×10^7 spores per milliliter with a hemacytometer. Cultures in 1984 were pureed with water in a blender for 15–20 sec, strained through cheescloth, and adjusted to 1×10^7 spores per milliliter.

Potato stems in the high level of Verticillium wilt (level 2) were inoculated at flowering in 1983. Norland was inoculated first (5–7 July), followed by Red Pontiac (8–12 July) and Russet Burbank (12–14 July). Automatic dispensing syringes (Cornwall Continuous Pipette, Becton, Dickinson, & Co., Rutherford, NJ 07070) fitted with 18-gauge needles were used for the inoculations. About 0.05–0.10 ml of inoculum was injected once into one of the three main vascular strands of each stem 2–4 cm above the soil surface. Only the middle two rows of each plot were inoculated. The control treatment (level 1) was injected in a similar manner with distilled water.

To inoculate the level 2 Verticillium wilt treatment in 1984, the seed pieces were sprayed until runoff with hand-held sprayers just before they dropped from the planter into the seed furrow. Level 1 was an untreated control.

Treatment evaluation. To determine the degree and range of insect or disease intensity and effects on the host, weekly visual ratings were made beginning in late July or early August and continuing until harvest. For a particular pest, evaluations were made on each cultivar and each treatment level of the pest in the plots with lowest levels of the other pests. For example, early blight was evaluated on plots in the following set: $C_i \times L_1 \times E_k \times V_1$ (where L_1 and V_1 are the low levels of leafhoppers and Verticillium wilt, respectively).

Ratings taken were percent defoliation and percent early blight severity and hopperburn severity on the remaining foliage. Percent defoliation included foliage lost because of the effects of the pests as well as through natural senescence. Standard area diagrams published by Granovsky and Peterson (6) were used as an aid in making the assessments for early blight and hopperburn. Chlorotic leaves (prevalent in plots with Verticillium wilt [9]) were grouped in the defoliated class. Three ratings were taken in each plot on each date.

Leafhopper treatments were also evaluated by counting the potato leafhopper nymphs on 30 midplant leaves destructively sampled from each $C_i \times L_j$ subunit. Nymphs were sampled because they are more injurious to potatoes than are adults (26) and because they show essentially no interplot movement (13). In 1983, eight 30-leaf counts per $C_i \times L_j$ subunit were taken on 25 July and 12 August. In 1984, one count per $C_i \times L_j$ subunit was made on 3 and 15 August.

In 1984, isolations for *V. dahliae* were made four times during the season. On each isolation date, 30 stems of each cultivar (10 from each replicate and all from different plants) were sampled from both treatment levels. The isolations were made from stem

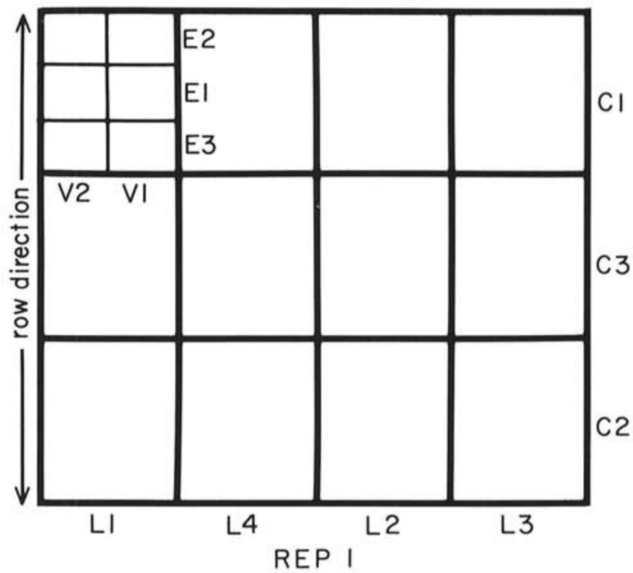

Fig. 1. An example of one replicate of the design used in the experiments. Leafhopper (L) treatments were stripped across cultivar (C) units. Both the L strips and the C units were randomized within each replicate. In the upper left is a second strip-plot design involving early blight (E) and Verticillium wilt (V). This arrangement was repeated with independent randomization within each $C_i \times L_j$ subunit.

TABLE 1. Potato leafhopper counts[w,x] on different treatment levels in 1983 and 1984

		Date			
		1983		1984	
Cultivar	Level	25 Jul	12 Aug	3 Aug	15 Aug
Norland	1	0.3 a	0.0 a[y]	3.0 abc	0.7 a
	2	6.3 b	2.7 a	2.3 abc	0.3 a
	3	43.7 d	54.7 b	3.7 abc	0.0 a
	4	91.3 e	*[z]	3.0 abc	1.7 ab
	5	–	–	7.7 bc	42.0 c
	6	–	–	13.7 c	29.7 c
Red Pontiac	1	1.7 a	0.0 a	0.3 ab	0.7 a
	2	9.7 b	3.3 a	1.7 ab	0.3 a
	3	44.3 d	52.3 b	0.0 a	0.3 a
	4	100.0 e	203.3 c	7.3 bc	4.3 b
	5	–	–	4.0 abc	35.3 c
	6	–	–	14.3 c	39.3 c
Russet Burbank	1	1.0 a	0.3 a	0.7 ab	0.7 a
	2	6.0 b	2.0 a	3.0 abc	0.0 a
	3	19.3 c	32.0 b	5.3 abc	0.0 a
	4	44.3 d	253.3 c	1.0 ab	1.0 a
	5	–	–	5.3 abc	8.0 c
	6	–	–	16.0 c	40.3 c

[w] Counts were made across all levels of early blight and Verticillium wilt and represent the number of leafhopper nymphs per 30 midplant leaves.
[x] Data were log-transformed [$\log(x+1)$] for analysis of variance.
[y] Means within a column followed by the same letter are not significantly different ($P = 0.05$) according to Duncan's multiple range test.
[z] Plants within this treatment level had completely senesced.

tissue 5–15 cm above the soil surface. Stems were surface-disinfected in 1% NaOCl for 1–2 min. After disinfection, a 2-cm segment was removed from the proximal end of each stem with a sterile knife. Each stem was squeezed with a sterile pliers near the cut surface and the expressed sap was streaked onto a modified ethanol-water agar (30). The plates were examined after 5–7 days for the presence of *V. dahliae* microsclerotia. In 1983, a similar attempt was made to isolate *V. dahliae* from potato stems using the dried stem grinding and plating technique outlined by Davis et al (4). However, the stems were beginning to senesce when the samples were taken and results of the assay were not interpretable because of high stem colonization by *Colletotrichum* spp.

TABLE 2. Areas[a] under percent hopperburn (AUHBC) and percent early blight (AUEBC) curves for three potato cultivars in 1983 and 1984

		AUHBC		AUEBC	
Cultivar	Level	1983	1984	1983	1984
Norland	1	11.3	0.2	9.7	6.6
	2	23.3	0.0	12.5	12.8
	3	56.3	0.4	13.5	15.8
	4	56.3	2.2	19.7	–
	5	–	24.3	–	–
	6	–	26.0	–	–
Russet Burbank	1	0.3	0.0	15.0	6.8
	2	17.1	0.0	20.1	12.1
	3	42.9	0.0	24.5	16.7
	4	41.9	0.7	29.2	–
	5	–	8.8	–	–
	6	–	13.0	–	–
Red Pontiac	1	9.9	0.0	17.4	8.5
	2	11.6	0.0	20.4	14.4
	3	38.8	0.0	19.1	23.7
	4	54.1	2.8	30.8	–
	5	–	17.6	–	–
	6	–	24.7	–	–
LSD (0.05)[b]		9.8	5.0	8.0	4.1

[a] The area under curves for each pest treatment was computed on plots with low levels of the other two pests.

[b] Fischer's protected least significant difference ($P = 0.05$) for means in the corresponding column.

Computation of areas under curves and statistical analyses. The following summary variables were computed from the original pest ratings: area under the proportion of defoliation curve (AUDEFC), area under the proportion of hopperburn curve (AUHBC), and area under the proportion of early blight curve (AUEBC). To account for effects of environment on host growth, the time scale used for the integrations was the temperature-dependent physiologic age (P-AGE) developed by Sands et al (24). Integrations were started on 15 July in both years, which was within 1 day of the first early blight inoculation and within 1 wk of when leafhopper nymphs were first found in the crop. Integrations were made as follows using the midpoint rule between observation dates: Area under curve =

$$\Sigma_{t=1}^{n}\ [Y_t + Y_{t-1}]/2 * [\text{P-AGE}_t - \text{P-AGE}_{t-1}],$$

where Y = variable rated (on a proportional scale), t = tth observation date, and n = total number of observations (which varied between cultivars because of differences in cultivar maturity). To facilitate interpretation of AUDEFC, within each cultivar, the AUDEFC value attained for each pest treatment level was divided by the AUDEFC value attained for plots with low levels of all three pests.

All statistical analyses, including analysis of variance, and mean separation were done using the *Statistical Package for the Social Sciences* (10,19). A significance value of $P = 0.05$ was used in all statistical tests.

RESULTS

Effect of treatments on pest levels. Levels of individual pest treatments were evaluated to determine degree and range of infestations that resulted from the management practices. In 1983, the methoxychlor treatments resulted in gradients of potato leafhoppers where, within each cultivar, all four nymph levels were significantly different from one another on the first sampling date, 25 July (Table 1). In addition, significant differences occurred between levels 2–4 on the remaining observation date, 12 August. In 1984, development of the maximum leafhopper population occurred later in the season than in 1983 (Table 1) and maximum nymph levels were only 16% (Russet Burbank) to 36% (Norland) of populations attained in 1983. On the 15 August 1984 sampling

TABLE 3. Ratios[a] of area under the percent defoliation curve (AUDEFC) for potato leafhopper, early blight, and Verticillium wilt treatments to a control treatment for three potato cultivars in 1983 and 1984

		Potato leafhopper		Early blight		Verticillium wilt	
Cultivar	Level	1983	1984	1983	1984	1983	1984
Norland	1	1.00	1.00	1.00	1.00	1.00	1.00
	2	1.01	1.17	1.12	1.16	1.27	1.14
	3	1.20	1.06	1.16	1.28	–	–
	4	1.43	1.16	1.69	–	–	–
	5	–	1.12	–	–	–	–
	6	–	1.29	–	–	–	–
Russet Burbank	1	1.00	1.00	1.00	1.00	1.00	1.00
	2	1.02	1.08	1.29	1.15	1.38	1.03
	3	1.16	1.12	1.41	1.29	–	–
	4	1.53	1.11	1.82	–	–	–
	5	–	1.00	–	–	–	–
	6	–	1.00	–	–	–	–
Red Pontiac	1	1.00	1.00	1.00	1.00	1.00	1.00
	2	0.97	1.13	1.23	1.19	1.35	1.16
	3	1.13	1.16	1.44	1.42	–	–
	4	2.33	1.08	2.26	–	–	–
	5	–	1.10	–	–	–	–
	6	–	1.10	–	–	–	–
LSD (0.05)[b]		0.41	0.14	0.19	0.10	0.28	0.08

[a] The ratio of AUDEFC for each pest treatment was computed on plots with low levels of the other two pests. Values of the ratios give a relative measure of the magnitude of effects on the host attained each year.

[b] Fischer's protected least significant difference ($P = 0.05$) for means in the corresponding column.

date, nymph counts were significantly greater on levels 5 and 6 than on levels 1–4 (Table 1).

As with counts of nymphs, significant differences in hopperburn and defoliation occurred between leafhopper levels within cultivars in both years (Tables 2 and 3); however, differences in leafhopper-induced defoliation were not as frequent as differences in hopperburn. Both years, the highest percentage of hopperburn occurred on Norland and the least on Russet Burbank.

Significant differences in early blight severity and early blight-induced defoliation occurred in all three cultivars in 1983 and 1984 (Tables 2 and 3). From midseason to late-season, defoliation was the major effect of the disease, resulting in differences of 10–60% across levels within a cultivar. Conversely, the range in early blight severities rarely exceeded 10% until late in the season, when overall percent defoliation was also high.

Significant differences in percent defoliation across Verticillium wilt levels within a cultivar occurred both years (Table 3). Toward the end of the 1983 season, nearly every stem in the inoculated level of cultivars Russet Burbank and Norland showed advanced early dying disease symptoms (22) whereas early dying disease symptoms were rare in the uninoculated level. For Red Pontiac, early dying symptoms were not as pronounced, but there was a consistent trend toward greater defoliation in the inoculated level (Table 3).

TABLE 4. Percent recovery[a] of *Verticillium dahliae* from two Verticillium wilt levels in the 1984 experiment

Cultivar	Level	Date: 4 Aug	11 Aug	17 Aug	11 Sept
Norland	1	6.7	16.7	13.3	*[b]
	2	16.7	33.3	40.0	*
Red Pontiac	1	0.0	6.7	6.7	26.7
	2	6.7	50.0	30.0	46.7
Russet Burbank	1	6.7	0.0	16.7	10.0
	2	23.3	20.0	60.0	53.3
LSD 0.05[c]		17.3	16.3	36.3	29.8

[a] Isolations were made from 10 stems of each level per cultivar per relicate.
[b] Plants in this treatment level had completely senesced.
[c] Fischer's protected least significant difference ($P = 0.05$) for means in the corresponding column.

In 1984, differences in defoliation resulting from inoculation with *V. dahliae* were less than in 1983 (Table 3), and advanced early dying symptoms rarely developed in either treatment level. Recovery of *V. dahliae* by isolation (with one exception) never exceeded 50% in the inoculated level (Table 4). Although there were some significant differences in recovery between levels within cultivars, background recovery of *V. dahliae* from uninoculated plots reduced the range between levels (Table 4).

Effect of pest levels on yield. Analysis of variance was done on total yield from each plot (Table 5). In 1983, main effects of cultivar, leafhopper, early blight, and Verticillium wilt were significant. In addition, cultivar × leafhopper, cultivar × early blight, leafhopper × early blight, and leafhopper × early blight × Verticillium wilt interactions were significant. The average yield across cultivars on plots with low levels of all pests was 20.4 t/ha (Fig. 2). Maximum yield reductions caused by each pest individually averaged across cultivars were 11.0 (53.8%), 6.3 (30.7%), and 2.5 (12.3%) t/ha for leafhopper, early blight, and Verticillium wilt, respectively (Fig. 2). Maximum yield reduction by any combination of the pests was 12.8 (62.8%) t/ha (Fig. 2).

In 1984, significant effects were cultivar, leafhopper, early blight, and cultivar × early blight. Yield averaged across cultivars on plots with low levels of all pests was 40.4 t/ha. Maximum yield reductions averaged across cultivars by either leafhopper or early blight individually were 6.1 (15.0%) and 7.3 (18.1%) t/ha, respectively (Fig. 3). For a combination of leafhopper and early blight, the maximum reduction was 10.5 t/ha (25.9%) (Fig. 3).

For Norland, the range of yield reduction by early blight in both years was smaller than for either Russet Burbank or Red Pontiac (Fig. 4). Similarly, the range in yield reduction across leafhopper levels was smallest in Norland both years (Fig. 5), although the cultivar × leafhopper interaction was not significant in 1984. In 1983, the highest yielding leafhopper level in Norland was level 1, whereas level 2 yield was greatest in Russet Burbank and Red Pontiac (Fig. 5).

Yield loss attributable to a single pest was greatest when other pests were at low levels. For example, at low levels of leafhopper and early blight in 1983, the yield difference between Verticillium wilt levels was 2.6 t/ha (Fig. 2). However, at higher levels of early blight, the difference between Verticillium wilt levels declined to

TABLE 5. Analysis of variance of total yield (t/ha) from three potato cultivars subjected to various combinations of potato leafhoppers, early blight, and Verticillium wilt

Source of variation	1983 df	1983 Mean square	1983 Variance ratio[a]	1984 df	1984 Mean square	1984 Variance ratio
Block	2	116.99		2	243.58	
Cultivar (C)	2	211.90	9.25*[b]	2	965.19	11.72*
Error 1	4	22.90		4	82.36	
Leafhopper (L)	3	957.55	143.80**	5	274.57	6.71**
Error 2	6	6.66		10	40.91	
C × L	6	20.22	3.21*	10	26.27	1.49
Error 3	12	6.30		20	17.62	
Early blight (E)	3	173.05	64.12**	2	614.98	35.81**
C × E	6	8.86	3.28**	4	103.15	6.01**
L × E	9	9.50	3.52**	10	10.13	0.59
C × L × E	18	2.53	0.94	20	10.08	0.59
Error 4	72	2.70		72	17.17	
Verticillium wilt	1	47.17	10.64**	1	12.56	0.52
C × V	2	7.50	1.69	2	10.22	0.43
L × V	3	8.90	2.01	5	8.98	0.36
C × L × V	6	4.66	1.05	10	13.61	0.57
Error 5	24	4.43		36	23.92	
E × V	3	1.69	1.91	2	7.46	0.90
C × E × V	6	0.54	0.62	4	9.74	1.17
L × E × V	9	2.18	2.47*	10	9.19	1.10
C × L × E × V	18	0.57	0.65	20	5.94	0.80
Error 6	72	0.88		72	8.32	

[a] The ratio of the mean square of a particular source of variation to the appropriate mean square error.
[b] * = Significant at $P = 0.05$ and ** = significant at $P = 0.01$.

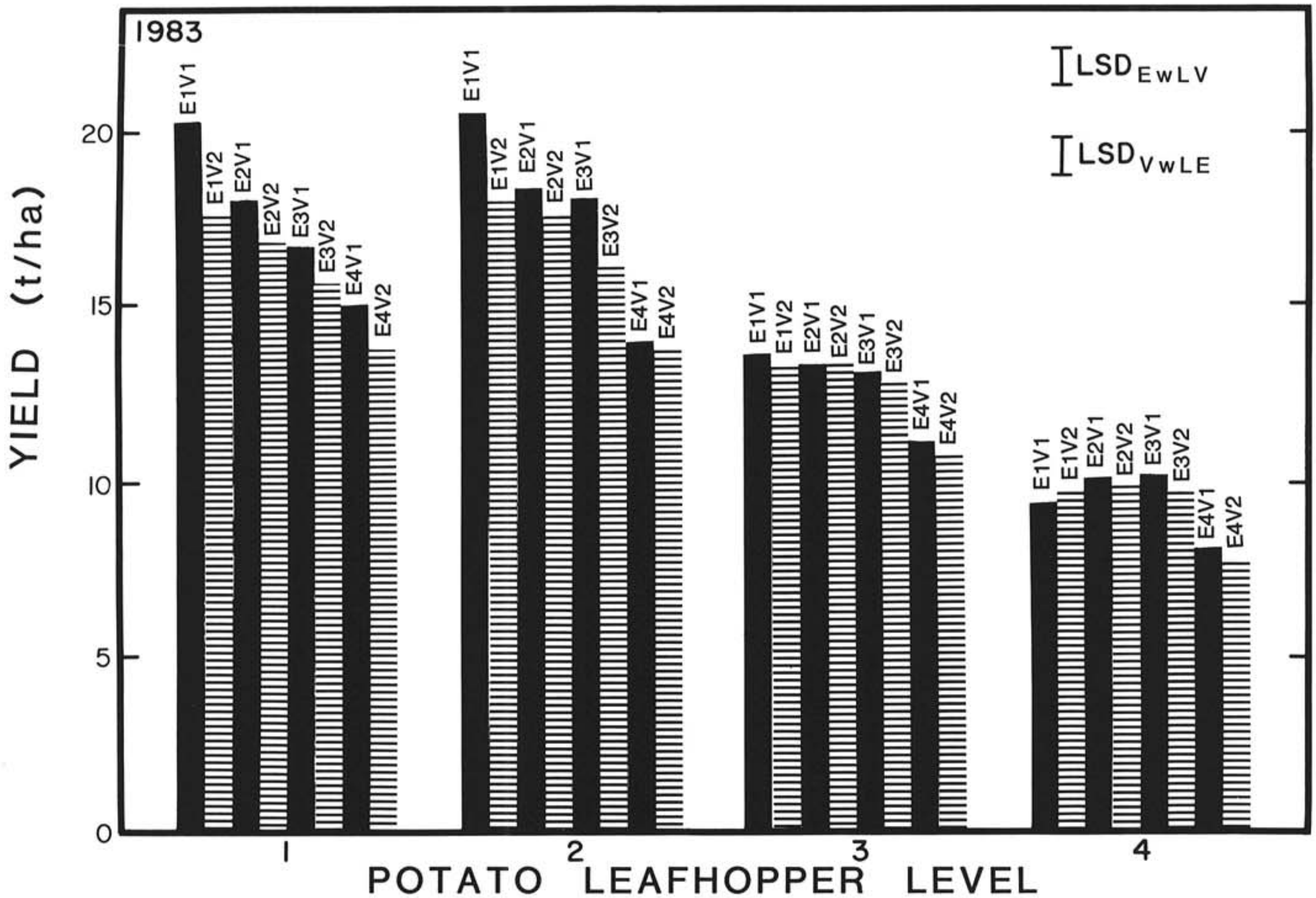

Fig. 2. Potato yields in 1983 averaged across cultivars for early blight (E) and Verticillium wilt (V) subplots within potato leafhopper levels. Bars in the upper right are the least significant differences (LSD) ($P = 0.05$) for early blight means within a leafhopper and Verticillium wilt level (EwLV) and for Verticillium wilt means within a leafhopper and early blight level (VwLE).

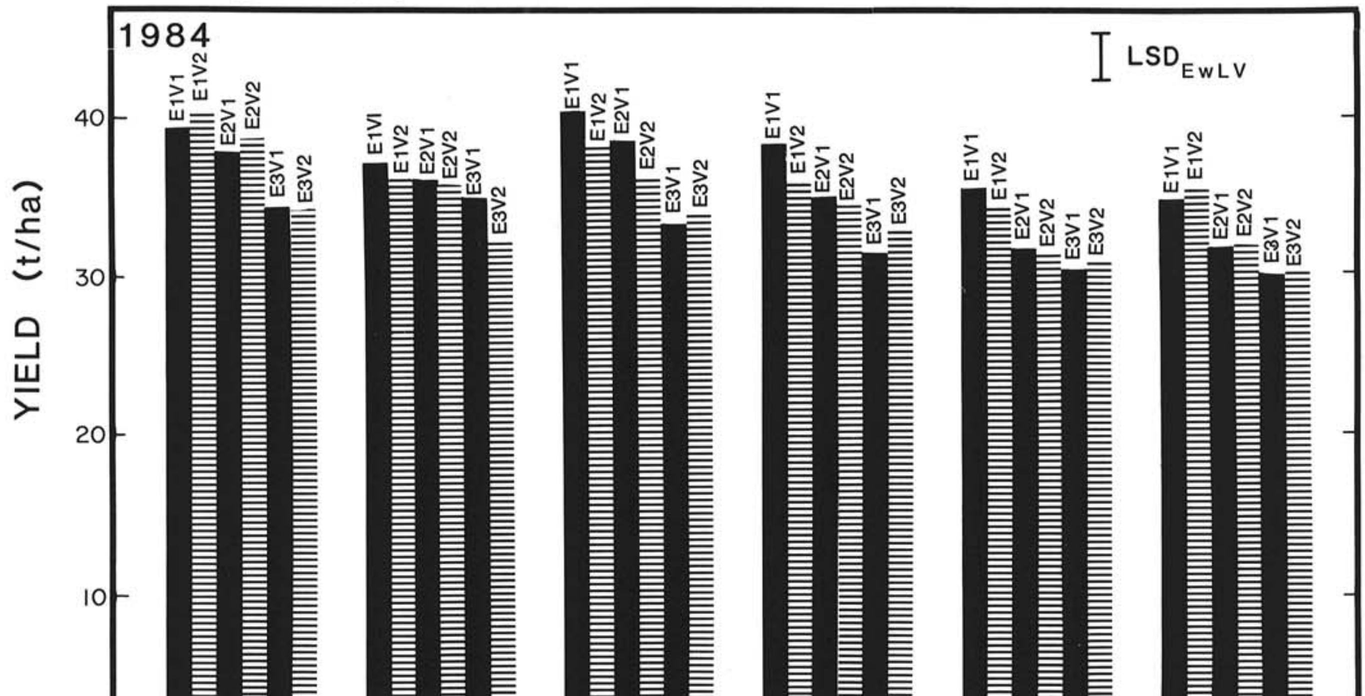

Fig. 3. Potato yields in 1984 averaged across cultivars for early blight (E) and Verticillium wilt (V) subplots within potato leafhopper levels. The bar in the upper right is the least significant difference (LSD) ($P = 0.05$) for early blight means within a leafhopper and Verticillium wilt level (EwLV). Differences between Verticillium wilt means within a leafhopper and early blight level were not significant.

0.96 t/ha (on $L_1 E_3$) and 1.2 t/ha (on $L_1 E_4$) (Fig. 2). Similarly, for early blight treatments at low levels of leafhopper and Verticillium wilt, the difference between levels 1 and 4 was 5.2 t/ha, but if the high level of Verticillium wilt was also present, the difference between early blight levels 1 and 4 was reduced to 3.9 t/ha (Fig. 2).

In 1983 plots with high numbers of leafhopper nymphs (levels 3 and 4), yield differences between Verticillium wilt levels within the same early blight level were not significant (Fig. 2). Also, within these same leafhopper levels, yield differences between early blight levels 1–3 did not differ from one another; however, the highest early blight level (level 4) was significantly less than the other three levels (Fig. 2).

DISCUSSION

The strip-plot design used in this experiment was chosen because this type of design tends to provide higher precision on treatment interactions while sacrificing some precision on main effects (3). Also, because of larger plot sizes, strip-plot designs greatly facilitate the planting and spraying operations and tend to reduce effects of interplot interference (11). A disadvantage of this design is the large number of error terms (six), which complicates comparisons between levels within and between treatments.

A problem with this type of experiment, not resolved, is separation of effects of pesticides from effects of pests. For this reason, disease epidemics and insect populations were documented extensively, and we used only nonsystemic pesticides with no documented effects on host growth. However, on the basis of yields attained for Russet Burbank and Red Pontiac on leafhopper levels 1 and 2 in 1983 (Fig. 5), we believe the high rate of methoxychlor used on level 1 may have had a detrimental effect on plant yield.

An objective of this study was to obtain a wide range of relatively realistic insect infestations and disease epidemics across treatment levels. In this regard, only the inoculation of early blight level 4 in 1983 initially damaged the crop more than was expected because of extremely favorable conditions for infection immediately after inoculation. This level was more like an epidemic with an earlier onset date. For Verticillium wilt, the 1983 stem inoculation, although artificial, resulted in a pattern of disease progression similar to natural epidemics. Timing of the inoculation at flowering corresponds to when *V. dahliae* is usually first recovered under natural conditions.

The wide difference between average yields on plots with low levels of all pests in 1983 (20.4 t/ha) and 1984 (40.4 t/ha) exemplifies the different growing conditions in the two seasons. In 1983, weather during July and August was warmer (mean temperature = 24.4 C) and drier (2.59 mm of rain per day) than in 1984 (mean temperature = 22.2 C and 4.47 mm of rain per day). Recent research in Ohio by Rowe et al (23) suggests that yield reductions by early dying disease are greater in seasons with high heat stress. In this experiment, aside from differences in inoculation method, heat stress may partially explain why potato early dying symptoms developed in 1983 but not in 1984 even though recovery of *V. dahliae* from stems of the inoculated level averaged 40% over the first two sampling dates in August (Table 4).

Reports in the literature state that short-season cultivars are generally more susceptible to both hopperburn (25) and early blight (5). This was evident in this experiment, where in both years, the maximum percentage of hopperburn and the relative rates of

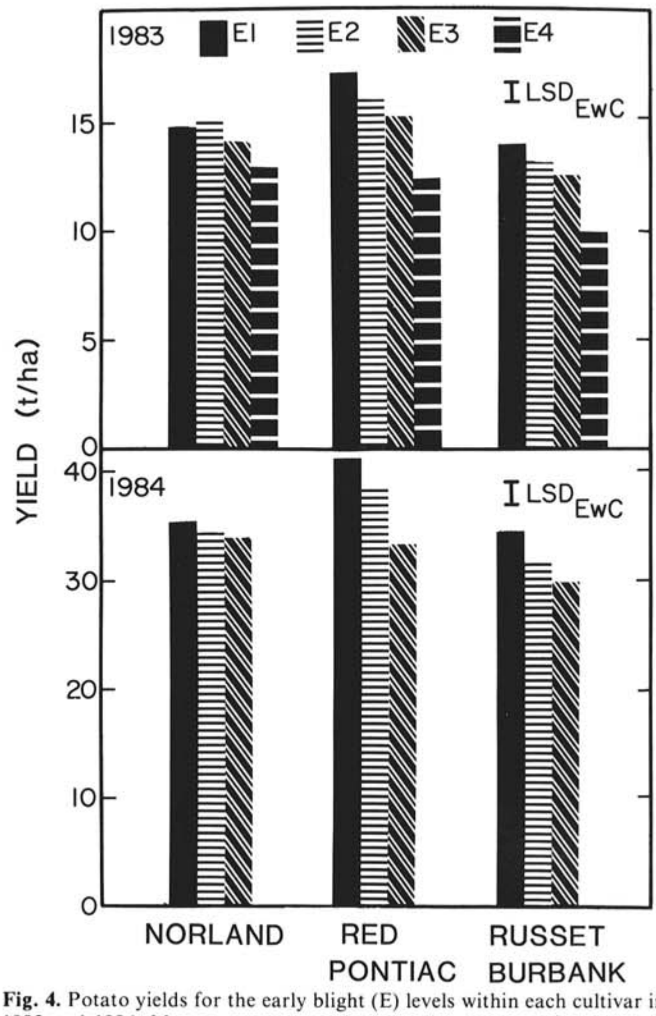

Fig. 4. Potato yields for the early blight (E) levels within each cultivar in 1983 and 1984. Means were averaged across the potato leafhopper and Verticillium wilt levels. Bars in the upper right corners of each histogram are the least significant differences (LSD) ($P = 0.05$) for the early blight means within a cultivar (EwC).

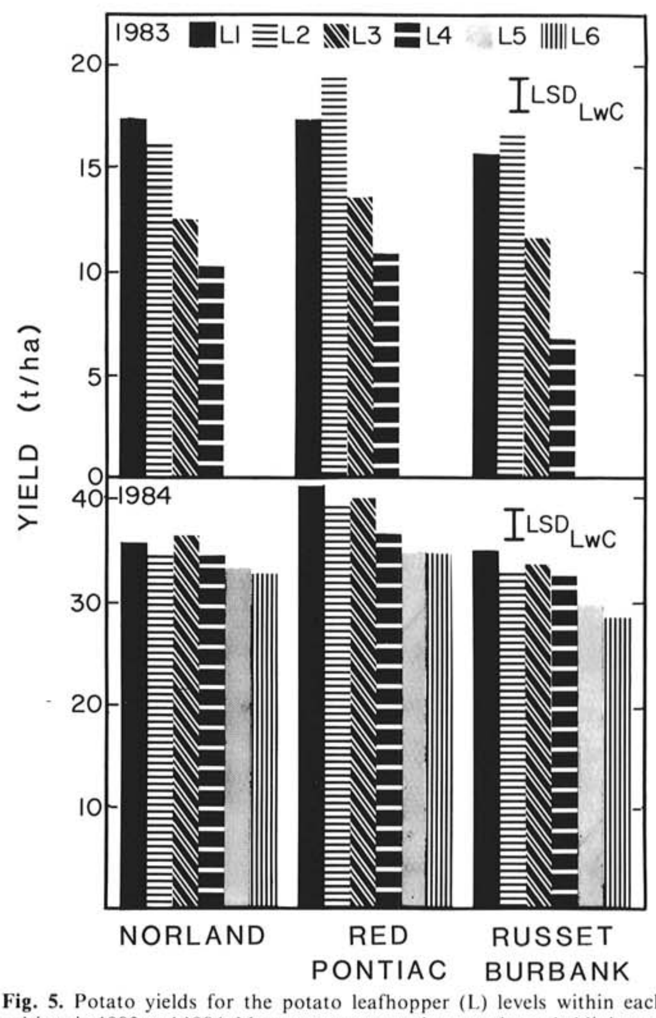

Fig. 5. Potato yields for the potato leafhopper (L) levels within each cultivar in 1983 and 1984. Means were averaged across the early blight and Verticillium wilt levels. Bars in the upper right corners of each histogram are the least significant differences (LSD) ($P = 0.05$) for the leafhopper means within a cultivar (LwC).

early blight development were greatest on Norland, the earliest maturing cultivar. However, the range of yield reduction caused by both leafhoppers and early blight was smaller on Norland than on Russet Burbank and Red Pontiac (both later maturing cultivars) (Figs. 4 and 5). A possible explanation for smaller yield reductions on Norland is that this cultivar benefited from its relatively high tuber-bulking rate (12) and shorter exposure to the pests.

Leafhopper × early blight and leafhopper × early blight × Verticillium wilt interactions in 1983 resulted from the nonadditivity of yield loss. To illustrate, if maximum yield reductions caused by individual populations of leafhoppers (54%), early blight (31%), and Verticillium wilt (12%) were additive, the yield loss total would approach 100%. In contrast, the observed maximum yield loss by any combination of the pests was only 63%. As Harrison (8) noted, these interactions are important because the expected amount of crop loss from one pest is dependent on the level(s) of second and/or third pests. For example, on 1983 leafhopper level 3, yield reductions from Verticillium wilt and early blight were negligible (Fig. 2), but as the level of leafhopper control increased, so did the amount of yield loss attributable to the two diseases. Alternatively, the interactions can be viewed in terms of benefits received from control. On the low leafhopper levels in 1983 (levels 1 and 2), the degree of Verticillium wilt in the inoculated level reduced the benefits of early blight control compared with that in the uninoculated Verticillium wilt level (Fig. 2).

There may not be a physiological explanation for why the leafhopper × early blight × Verticillium wilt interaction was significant in 1983 but not the leafhopper × Verticillium wilt or the early blight × Verticillium wilt interactions (Table 5), because if analysis of variance is repeated on the 1983 data without inclusion of any of the plots from the high leafhopper levels (levels 3 or 4), then the early blight × Verticillium wilt interaction is highly significant ($P = 0.01$) and the three-way interaction is no longer significant ($P = 0.05$).

The presence of pest × pest interactions in 1983 but not in 1984 is probably due to differences in the range of pest levels attained. In 1984, for all three pests, the ranges between the high and low defoliation ratios were smaller than in 1983 (Table 3). Therefore, it is reasonable to conclude that the negative pest × pest interactions found in this study will probably be detectable only when ranges of infestation levels for two or more pests are high.

Pest × pest interactions like those found in this study are probably mediated through the host and relate to competition between pests to use plant foliage and/or to reductions in plant vigor (8). For interactions of this type, Padwick (21) proposed a model for estimating yield loss from combined pest populations: Percent yield loss =

$$\{100 - [(100 - P_1)(100 - P_2) \ldots (100 - P_n)]/100^{n-1}\},$$

where P_1, P_2, . . . P_n are percent yield losses caused by solitary populations of each of the n pests. This model assumes that the only interaction between the pests is competition for the plant's resources, and with respect to yield, this means that one pest cannot affect or influence what other pests have already damaged. If this model is applied using the maximum yield losses found in this study for individual populations of each pest, the expected maximum yield loss from combined populations is 72%. This value is less than summed maximum yield losses caused by individual populations of each pest but greater than the 63% maximum yield loss that was actually measured. This hypothesis that negative interactions result from competition between pest populations will be explored more thoroughly in a subsequent paper.

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