Fitness of Metalaxyl-Sensitive and Metalaxyl-Resistant Isolates of *Phytophthora infestans* on Susceptible and Resistant Potato Cultivars

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ABSTRACT

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Intact leaflets and tuber disks of 14 cultivars of potato were inoculated with three metalaxyl-sensitive (MS) and three metalaxyl-resistant (MR) isolates of *Phytophthora infestans* in the absence of metalaxyl. Infection frequency, lesion area, sporulation capacity in leaflets, and sporulation capacity in tuber disks were recorded at 4, 6, 7, and 7 days after inoculation, respectively. Infection frequency varied among cultivars and among fungal isolates. Cara was significantly ($P < 0.05$) less susceptible to leaflet infection induced by either metalaxyl-sensitive (MS) or metalaxyl-resistant (MR) isolates compared with the other cultivars tested. Lesion area varied significantly among cultivars and between MS and MR isolates. MR isolates produced significantly ($P < 0.05$) larger lesions than MS isolates in nine cultivars. Lesions were restricted in the other five cultivars (Draga, Cara, Dunja, Tarzan, and Timata) regardless of the isolates used for inoculation. Sporulation in leaflets varied significantly among cultivars and in two cultivars among fungal isolates. Dunja, Tarzan, and Timata allowed for no fungal sporulation in leaflets, whereas in the other 11 cultivars sporulation ranged between about 100 and 26,000 sporangia per square centimeter of leaflet lesion. In Spunta and Atica, MS isolates sporulated significantly better ($P < 0.05$) than MR isolates. Sporulation on tuber disks varied among cultivars and among fungal isolates. It was lowest in Avondale, Cara, and Timata and highest in Tarzan. Tuber disks of four cultivars (Atica, Liseta, Cara, and Dunja) supported significantly higher sporulation of MS compared to MR isolates of the fungus. Sporulation in leaflets and tuber disks was poorly correlated, while infection frequency was correlated ($r = 0.56$) with sporulation in leaflets. The MR group of isolates had a significantly higher compound fitness index compared with the MS group of isolates in foliage of the potato cultivars tested. This higher fitness, however, did not render the foliage resistance of some cultivars ineffective.

Late blight is the most destructive disease of potato in Israel. Since metalaxyl-resistant isolates of *Phytophthora infestans* were detected in the country in 1982 (1) disease outbreaks became more frequent and more severe. Resistant isolates have been detected in fields not treated with phenylamide-containing fungicides and on different cultivars, indicating a higher fitness of the resistant isolates in the absence of a positive selection pressure. Of 48, 39, and 73 field isolates we have collected from various locations and cultivars of potato in the country during 1986, 1987, and 1988—40, 26, and 42, respectively, were highly resistant to metalaxyl (profusely sporulated on tuber disks inoculated in the presence of 100 mg of metalaxyl per liter).

In a previous paper (2) we reported on a comparative examination of some fitness components of metalaxyl-sensitive (MS) and metalaxyl-resistant (MR) populations of *P. infestans* on potato (cv. Alpha) foliage. It was shown (2) that lesion areas induced in intact leaflets by MR isolates were significantly larger than those induced by MS isolates, and that no significant differences were recorded among the two populations in infection frequency or sporulation capacity. Epidemics induced in walk-in plastic tunnels were significantly more severe with MR than with MS isolates. In other papers we showed that MR isolates were more competitive than MS isolates in mixed MR and MS inoculations in growth chambers (4) and epidemics in plastic tunnels (5).

The aim of the present study was to examine four fitness parameters of MS and MR isolates of *P. infestans* on susceptible and resistant potato cultivars with the hope to explain the persistance

of metalaxyl-resistant isolates in Israel and improve management strategies. A prediction was made as to the behavior of the two fungal populations on late blight-susceptible potato crops in Israel.

MATERIALS AND METHODS

Plant material. Experiments were conducted with 14 potato (*Solanum tuberosum* L.) cultivars. Tubers of Clauster were imported from France; Dunja, from West Germany; Avondale and Cara, from Ireland; and tubers of the other 10 cultivars, from the Netherlands. Plants were grown in the greenhouse (19–28 C) from certified potato tubers in 1.5-L pots containing sandy loam, one tuber per pot. Plants were fertilized twice a week with 1% N:P:K (20:20:20) solution. Plants were used for inoculation at 6–7 wk after planting when they had three to five shoots per pot with nine to 10 compound leaves per shoot. Experiments with tuber disks were conducted with either certified tubers (imported from Europe and used immediately or after being stored at 8 C for 1 and 2.5 mo), or with uncertified tubers, produced locally, and used at 3 mo after harvest.

Fungal isolates. Three MS and three MR isolates of *P. infestans* collected from the three major potato production areas in the country were used for inoculations: MS1, MS2, MS3, MR1, MR2, and MR3. Details on the isolates are given in Table 1.

Fitness components. The following fitness components were comparatively measured in MS and MR isolates: 1) infection frequency = proportion of leaflets infected out of those inoculated; 2) lesion area = areas of lesions produced at 6 days postinoculation in intact leaflets; 3) sporulation capacity in leaflets = number of sporangia produced per square centimeter of lesion in intact leaflets at 7 days postinoculation; 4) sporulation capacity in tuber disks = number of sporangia produced per square centimeter of tuber disk surface at 7 days postinoculation.

Assessment of fitness components. Fitness components were assessed according to Tooley et al (8) and Kadish and Cohen (2). Three experiments were performed with intact plants and four with tuber disks. The same three MS and three MR isolates and the same 14 potato cultivars were used in all experiments. With intact plants, three plants per isolate per cultivar (totaling 252 plants per experiment) were used in each experiment with 30 leaflets (mostly subterminal) inoculated in each plant. Full details on the techniques used for assessing infection frequency, lesion areas, and sporulation capacity in foliar lesions were given before (2). With tubers, 20 disks (0.8 cm diameter, 3 mm thick) were inoculated per isolate per cultivar in each experiment. Disks were each inoculated with a 10-μl sporangial suspension droplet containing 1,200 $\pm$ 100 sporangia per milliliter, and incubated at 20 C in the dark. Our previous experience has shown that five to 10 sporangia per droplet per tuber disk were required to produce infection/sporulation in 90% of the disks inoculated (3). At 7 days after inoculation sporangia produced were removed by shaking the disks in 20 ml of water and sporangial yield mea-

TABLE 1. Details on the origin, susceptibility to metalaxyl, mating type, and virulence factors of the isolates of *Phytophthora infestans* used in this study

Isolate[a]	Site	County	Collection date	Mating type	Virulence factors[b]	Metalaxyl resistance MIC[c]
MS1	Bet-Kama	Northern Negev	1983	A2	1,3,4,7,(8)	1
MS2	Nir-Eliyahu	Central coast	1984	A2	1,3,4,7,8,10	1
MS3	Sufa	Western Negev	1986	A1	1,3,4,7,8	1
MR1	Gvuloth	Western Negev	1984	A2	1,3,4,7,8,10	>1,000
MR2	Bror-Hayil	Northern Negev	1985	A2	1,3,4,7,8,10	>1,000
MR3	Mishmereth	Central coast	1986	A2	1,3,4,7,8	>1,000

[a] Designation according to Kadish and Cohen (2).
[b] Determined with leaves of *Solanum tuberosum* differentials carrying one of the following single resistance genes: R1, R2, R3, R4, R7, R8, R9, and R10 (Kadish and Cohen, *unpublished*). MS1 exhibited poor sporulation on R8.
[c] MIC = minimal inhibitory concentration: dosage of metalaxyl (μg a.i. per milliliter) required to totally suppress infection/sporulation of the fungus in tuber disks of cv. Alpha (2).

TABLE 2. Infection frequency of metalaxyl-sentitive (MS) and metalaxyl-resistant (MR) field isolates of *Phytophthora infestans* to leaflets of 14 potato cultivars at 18–20 C (4 days)

	Mean proportion leaflets infected[w]						
Cultivar	MS1	MS2	MS3	MR1	MR2	MR3	Mean (cultivar)[x]
Spunta	0.80	0.87	0.87	0.70	0.88	0.79	0.81 b
Alpha	0.74	0.84	0.83	0.68	0.84	0.77	0.78 b
Clauster	0.70	0.71	0.91	0.69	0.85	0.87	0.78 b
Atica	0.54	0.52	0.50	0.51	0.59	0.74	0.57 c
Nicola	0.94	0.85	0.97	0.81	0.84	1.00	0.89 a
Avondale	0.77	0.73	0.81	0.57	0.75	0.77	0.73 b
Mondial	0.56	0.69	0.58	0.60	0.67	0.63	0.61 c
Liseta	0.50	0.54	0.67	0.40	0.61	0.55	0.54 cde
Desiree	0.67	0.80	0.74	0.63	0.78	0.73	0.72 b
Draga	0.50	0.62	0.51	0.57	0.54	0.50	0.52 de
Cara	0.37	0.27	0.36	0.36	0.46	0.33	0.36 f
Dunja	0.56	0.53	0.57	0.76	0.63	0.67	0.62 c
Tarzan	0.80	0.82	0.70	0.73	0.91	0.90	0.80 b
Timata	0.63	0.40	0.46	0.37	0.45	0.54	0.47 e
Mean (isolate)[y]	0.65 AB	0.65 AB	0.67 A	0.59 B	0.69 A	0.70 A	
Mean (group)[z]	...	0.65	...	...	0.66	...	

[w] Results represent means from three experiments with 30 leaflets inoculated per cultivar per isolate in each experiment.
[x] Waller-Duncan k-ratio t-test ($k = 100$) for comparing means of all six isolates on each cultivar. Means followed by the same letter are not significantly different at 5% probability level.
[y] Waller-Duncan k-ratio t-test ($k = 100$) for comparing means of each isolate on all 14 cultivars. Means followed by the same letter are not significantly different at 5% probability level.
[z] Mean infection frequency of the MS isolates is not significantly different from that of the MR isolates (F value = 0.07; $P > F = 0.7942$).

sured using a hemacytometer (four counts).

Statistical analyses. Analysis of variance (ANOVA, 6) was performed for each fitness component with each isolate to compare cultivars; with each cultivar to compare isolates (Tables 2–5); and, with cultivar × isolate to establish interactions (Table 8). The Waller-Duncan k-ratio t-test ($k = 100$) was used (6) for mean separation of cultivars or isolates in cases where the overall F test for a fitness component was significant (Tables 2–5). Escapes in Table 4 (leaflets that were inoculated but on which no lesions developed) were handled using the GLM procedure (6). A statistical comparison of isolates nested within each group (three experiments with three isolates in a group) was performed (Table 7) to determine the variation within and between the MS and MR groups for each fitness component on each cultivar. $P > t$ values are given (Table 7) for normal t-test values. Pearson's correlation coefficients (r) between fitness components were performed for all six isolates and all fourteen cultivars using the CORR procedure (6).

RESULTS

The two groups of isolates exhibited a large variation for fitness components (Tables 2–7). Isolates within each group differed significantly ($P < 0.05$) in infection frequency, lesion area, sporulation capacity in leaflets, compound fitness index in foliage, and sporulation capacity in tuber disks (Tables 2–7). Results from all 14 cultivars used showed that the MR group of isolates differed significantly ($F = 76.51$, $P > F = 0.0001$) from the MS group

TABLE 3. Area of late blight lesions induced in leaflets of 14 potato cultivars by metalaxyl-sensitive (MS) and metalaxyl-resistant (MR) field isolates of *Phytophthora infestans* at 20 C (7 days)

	Mean lesion area (mm^2)[w]						
Cultivar	MS1	MS2	MS3	MR1	MR2	MR3	Mean (cultivar)[x]
Spunta	141.2	155.1	118.5	554.8	495.7	545.7	335.2 cd
Alpha	153.0	104.9	103.3	638.5	509.7	583.0	348.7 cd
Clauster	157.9	125.2	113.6	583.4	277.6	654.1	318.6 d
Atica	167.3	88.7	120.4	326.2	303.7	545.6	258.6 e
Nicola	207.7	191.5	164.0	676.8	529.3	556.5	387.7 b
Avondale	207.0	113.2	135.6	667.1	478.8	313.1	320.7 d
Mondial	296.9	282.5	270.5	856.1	709.8	821.2	539.5 a
Liseta	176.3	231.6	141.5	666.0	480.3	500.4	366.0 bc
Desiree	90.2	27.4	46.4	156.5	217.4	153.2	115.2 f
Draga	15.6	8.5	5.8	8.8	61.4	7.3	17.9 g
Cara	20.3	26.2	9.4	26.9	12.9	38.3	22.4 g
Dunja	5.5	7.0	7.1	11.6	5.2	6.0	7.1 g
Tarzan	5.5	5.0	5.0	5.7	5.0	5.6	5.3 g
Timata	22.1	11.0	16.5	12.8	13.8	15.6	15.3 g
Mean (isolate)[y]	119.0 D	97.6 E	90.7 E	370.8 A	293.5 C	339.0 B	
Mean (group)[z]		102.4			334.4		

[w] Data represent means from three experiments with 30 leaflets inoculated per cultivar per isolate in each experiment.
[x] Waller-Duncan k-ratio t-test ($k = 100$) for comparing means of all six isolates on each cultivar. Means followed by the same letter are not significantly different at 5% probability level.
[y] Waller-Duncan k-ratio t-test ($k = 100$) for comparing means of each isolate on all 14 cultivars. Means followed by the same letter are not significantly different at 5% probability level.
[z] Mean lesion area of the MR isolates is significantly larger than that of the MS isolates (F value = 76.51; $P > F = 0.0001$).

TABLE 4. Sporulation capacity of metalaxyl-sensitive (MS) and metalaxyl-resistant (MR) field isolates of *Phytophthora infestans* in leaflet lesions of 14 potato cultivars at 7 days after inoculation at 20 C

	Mean $\times 10^3$ sporangia per square centimeter of lesion[w]						
Cultivar	MS1	MS2	MS3	MR1	MR2	MR3	Mean (cultivar)[x]
Spunta	18.8	31.3	28.8	4.0	28.3	12.4	20.6 a
Alpha	13.4	19.8	24.9	7.7	26.5	8.4	16.8 b
Clauster	14.7	13.8	11.1	7.2	19.1	13.3	13.2 c
Atica	13.3	15.1	21.6	1.4	17.7	8.5	12.9 cd
Nicola	8.2	13.6	16.7	4.6	14.5	12.1	11.6 ed
Avondale	11.6	12.1	10.3	2.6	14.9	11.8	10.5 e
Mondial	2.9	1.9	4.5	0.6	6.9	1.2	3.0 f
Liseta	0.1	1.9	3.3	1.1	4.1	2.3	2.1 fg
Desiree	5.0	0.5	1.2	0.8	2.1	0.1	1.6 g
Draga	0	0.1	0.3	0	0.2	0.2	0.1 h
Cara	0	0.3	0.1	0.1	0.04	0.1	0.1 h
Dunja	0	0	0	0	0	0	0 h
Tarzan	0	0	0	0	0	0	0 h
Timata	0	0	0	0	0	0	0 h
Mean (isolate)[y]	6.3 C	7.9 B	8.8 A	2.2 E	9.6 A	5.0 D	
Mean (group)[z]		7.7			5.6		

[w] Data represent means from three experiments with 10–25 leaflets per cultivar per isolate in each experiment.
[x] Waller-Duncan k-ratio t-test ($k = 100$) for comparing means of all six isolates on each cultivar. Means followed by the same letter are not significantly different at 5% probability level.
[y] Waller-Duncan k-ratio t-test ($k = 100$) for comparing means of each isolate on all 14 cultivars. Means followed by the same letter are not significantly different at 5% probability level.
[z] Mean sporulation capacity in leaflets of the MS isolates is not significantly different from that of the MR isolates (F value = 3.87; $P > F = 0.0504$).

of isolates in mean lesion size (Table 3) and mean compound fitness index ($F = 19.76$, $P > F = 0.0001$, Table 6) but not in mean infection frequency (Table 2) or mean sporulation capacity in leaflets (Table 4). Mean sporulation capacity in tuber disks (Table 5) was significantly larger for the MS compared to the MR isolates.

The 14 cultivars exhibited a large variation in susceptibility to the pathogen. Pooled data from all isolates showed that cultivars differed significantly ($P < 0.05$) for infection frequency (Table 2), lesion area (Table 3), sporulation capacity in foliage (Table 4), compound fitness index in foliage (Table 6), and sporulation capacity in tubers (Tables 5).

Contrast estimates (not shown) computed for each fitness components with each cultivar revealed (Table 7) that the MR isolates produced significantly ($P = 0.0001$–0.0004) larger lesions than the MS isolates in nine cultivars. In the other five cultivars, namely: Draga, Cara, Dunja, Tarzan, and Timata (Table 3) both the MS and the MR isolates failed to produce lesions larger than 26 mm^2. The MR isolates, however, did not differ significantly (at 5% level) from the MS isolates in infection frequency (Table 7). Sporulation capacity in leaflets was significantly larger for the MS compared to the MR isolates in two cultivars (Spunta and Atica) while sporulation capacity in tuber disks was significantly larger for MS compared with the MR isolates in four cultivars (Atica, Liseta, Cara, and Dunja) (Table 7). Both the MR and the MS isolates failed to sporulate in leaflets of the cultivars Dunja, Tarzan, and Timata (Table 7). The overall fitness (CFI, compound fitness index; infection frequency × lesion area × sporulation capacity in leaflets) of the MR isolates was significantly larger ($P < 0.05$) than the overall fitness of the MS

TABLE 5. Sporulation capacity of metalaxyl-sensitive (MS) and metalaxyl-resistant (MR) field isolates of *Phytophthora infestans* in tuber disks of 14 potato cultivars at 20 C in the dark (7 days)

	Mean $\times 10^3$ sporangia per square centimeter of tuber tissue[w]						
Cultivar	MS1	MS2	MS3	MR1	MR2	MR3	Mean (cultivar)[x]
Spunta	132.5	140.3	125.6	92.0	162.4	113.2	127.7 bc
Alpha	135.2	212.5	190.0	54.3	134.8	213.0	156.6 ab
Clauster	46.5	45.5	34.0	17.5	47.8	25.3	36.1 efg
Atica	34.0	24.8	48.8	3.7	22.5	19.3	25.5 fg
Nicola	118.7	62.6	163.8	78.7	34.5	112.2	95.1 cd
Avondale	17.9	15.6	14.7	1.8	12.9	14.3	12.9 g
Mondial	81.9	72.2	100.7	86.0	54.7	52.9	74.7 de
Liseta	110.9	18.4	152.3	17.0	44.6	47.4	65.1 def
Desiree	52.4	31.3	39.6	22.5	38.6	68.5	42.2 efg
Draga	75.0	108.1	117.8	104.9	98.4	172.5	112.8 bcd
Cara	8.7	14.7	22.1	2.3	3.2	14.7	11.0 g
Dunja	75.9	75.9	97.1	45.1	38.2	93.4	70.9 def
Tarzan	78.2	151.8	203.8	96.6	149.0	417.7	182.9 a
Timata	15.2	6.0	4.6	1.8	3.7	15.2	7.8 g
Mean (isolate)[y]	69.2 BC	67.6 BC	89.2 A	43.2 D	59.2 CD	79.5 AB	
Mean (group)[z]		75.9			60.0		

[w] Data represent means from four experiments with 20 tuber disks per isolate in each experiment.
[x] Waller-Duncan k-ratio t-test ($k = 100$) for comparing means of all six isolates on each cultivar. Means followed by the same letter are not significantly different at 5% probability level.
[y] Waller-Duncan k-ratio t-test ($k = 100$) for comparing means of each isolate on all 14 cultivars. Means followed by the same letter are not significantly different at 5% probability level.
[z] Mean sporulation in tuber disks of the MS isolates is significantly different from that of the MR isolates (F value = 6.53; $P > F = 0.0108$).

TABLE 6. Compound fitness index of metalaxyl-sensitive (MS) and metalaxyl-resistant (MR) field isolates of *Phytophthora infestans* to leaflets of 14 potato cultivars in growth chambers

	CFI $\times 1000$[w]						
Cultivar	MS1	MS2	MS3	MR1	MR2	MR3	Mean (cultivar)[x]
Spunta	2,132	4,195	2,962	1,468	12,214	5,304	4,713 a
Alpha	1,526	1,755	2,127	3,349	11,398	3,809	3,994 b
Clauster	1,634	1,189	1,118	2,724	4,459	7,480	3,101 c
Atica	1,168	662	1,288	220	3,059	3,716	1,686 d
Nicola	1,566	2,211	2,648	2,473	6,369	6,765	3,672 bc
Avondale	1,812	1,026	1,166	982	5,292	2,817	2,183 d
Mondial	445	343	691	321	3,271	604	946 e
Liseta	9	220	313	271	1,219	631	444 ef
Desiree	300	11	35	78	351	6	130 f
Draga	0	0.6	0.7	0	4	0.06	1.1 f
Cara	0	1.0	0.7	1.0	0.3	1.0	1.1 f
Dunja	0	0	0	0	0	0	0 f
Tarzan	0	0	0	0	0	0	0 f
Timata	0	0	0	0	0	0	0 f
Mean (isolate)[y]	757 C	830 C	882 C	849 C	3,403 A	2,248 B	
Mean (group)[z]		823			2,159		

[w] Data represent means from three experiments described in Tables 2–4. CFI = Compound fitness index = infection frequency × lesion size × sporulation capacity in leaflets.
[x] Waller-Duncan k-ratio t-test ($k = 100$) for comparing means of all six isolates on each cultivar. Means followed by the same letter are not significantly different at 5% probability level.
[y] Waller-Duncan k-ratio t-test ($k = 100$) for comparing means of each isolate on all 14 cultivars. Means followed by the same letter are not significantly different at 5% probability level.
[z] Mean CFI for the MR isolates is significantly larger than that of the MS isoaltes (F value = 19.76; $P > F = 0.0001$).

TABLE 7. Means, standard deviations of the means, and level of significance for difference between means of metalaxyl-sensitive (MS) and metalaxyl-resistant (MR) field populations of *Phytophthora infestans* for fitness components in growth chambers[a]

Cultivar	Infection frequency			Lesion area		
	MS	MR	$P > t$	MS	MR	$P > t$
Spunta	0.84 ± 0.05	0.77 ± 0.14	0.2088	138 ± 21	532 ± 77	0.0001
Alpha	0.80 ± 0.09	0.75 ± 0.10	0.3326	120 ± 25	577 ± 81	0.0001
Clauster	0.76 ± 0.12	0.78 ± 0.15	0.7390	132 ± 29	505 ± 184	0.0003
Atica	0.51 ± 0.06	0.62 ± 0.16	0.0854	125 ± 39	391 ± 142	0.0004
Avondale	0.76 ± 0.07	0.68 ± 0.13	0.1332	151 ± 50	489 ± 160	0.0002
Nicola	0.91 ± 0.10	0.87 ± 0.11	0.5195	187 ± 29	587 ± 84	0.0001
Mondial	0.58 ± 0.14	0.63 ± 0.10	0.4431	283 ± 66	795 ± 86	0.0001
Liseta	0.56 ± 0.11	0.51 ± 0.13	0.3394	183 ± 61	548 ± 120	0.0001
Desiree	0.73 ± 0.09	0.71 ± 0.09	0.5067	54 ± 30	175 ± 37	0.0001
Draga	0.52 ± 0.13	0.52 ± 0.12	0.9472	9 ± 4	25 ± 29	0.1500
Cara	0.33 ± 0.12	0.38 ± 0.17	0.4376	18 ± 15	26 ± 14	0.2945
Dunja	0.55 ± 0.13	0.68 ± 0.15	0.0596	6 ± 2	7 ± 4	0.4667
Tarzan	0.76 ± 0.17	0.84 ± 0.14	0.3020	5 ± 0	5 ± 1	0.4618
Timata	0.55 ± 0.19	0.44 ± 0.12	0.4805	16 ± 9	14 ± 7	0.5224
MSD	0.10	0.12		29	78	

[a] MSD = Minimum significant difference ($P = 0.05$) for comparing means of cultivars within each group of fungal isolates. Means represent values from three experiments with three isolates in each group. Infection frequency = proportion of leaflets infected out of those inoculated. Lesion area = the size of lesions in square millimeters. Sporulation leaflets = number of sporangia in thousands per square centimeter of lesion. Sporulation tubers = number of sporangia per square centimeter of tuber disk surface.

[b] Compound fitness index = infection frequency × lesion area × sporulation in leaflets.

isolates in the cultivars Alpha Clauster, Avondale, Nicola, and Liseta. It was larger for the MR than for the MS isolates, but not significantly different at 5% level in Spunta, Atica, Mondial, Desiree, Draga, and Cara (Table 7). For three cultivars (Dunja, Tarzan, and Timata) a value of CFI = 0 was obtained (Table 7) for either the MR or the MS isolates due to the failure of the pathogen to sporulate on their leaflets (Table 4).

Significant differences were recorded in cultivars' susceptibility to the blight regardless of the isolate used for inoculation. Cara was significantly ($P < 0.05$) less susceptible to infection compared with other cultivars (Tables 2 and 7). Cara, Timata, Draga, Tarzan, and Dunja were significantly less susceptible to fungal colonization in leaflets compared with the other cultivars (Tables 3 and 7). The fungus failed to sporulate in leaflets of Dunja, Tarzan, and Timata and produced significantly fewer sporangia ($P < 0.05$) in leaflets of Cara, Draga, Liseta, Desiree, and Mondial compared with the other six cultivars regardless of the isolate used for inoculation (Tables 4 and 7). Sporulation capacity in tuber disks was sparse in Timata, Cara, and Avondale, and abundant in Spunta, Alpha, Nicola, Draga, and Tarzan (Tables 5 and 7). Cultivars were divided into six groups (Table 6) according to the overall susceptibility of their foliage to the pathogen: Spunta was most susceptible to the pathogen because of the highest mean CFI value it produced (Table 6); Alpha, Nicola, Clauster, Atica, and Avondale were susceptible with a gradual decrease in mean CFI's; Mondial and Liseta were resistant; and Draga, Cara, Dunja, Tarzan, and Timata were highly resistant (Table 6).

Analysis of variance (ANOVA) showed a significant interaction ($P > F = 0.0001$) between the potato cultivars and the fungal blight isolates for the effects on lesion size, sporulation in leaflets, and CFI but not for the effect on infection frequency (Table 8). Infection frequency was poorly correlated with lesion area but strongly correlated with sporulation capacity in leaflets for both MS and MR isolates (Table 9). Lesion area was significantly correlated with sporulation capacity in leaflets for the MR but not for the MS isolates. Poor correlations were found between sporulation capacity in leaflets and sporulation capacity in tubers (Table 9).

DISCUSSION

This study confirms earlier results obtained with the cultivar Alpha (2). We report here that MR isolates of the late blight fungus were fitter than MS isolates on all susceptible potato cultivars tested. This higher fitness was expressed in significantly larger lesions (×2.8–4.8) induced by MR compared with MS isolates in leaflets of these potato cultivars.

Sporulation capacity of MS and MR isolates in leaflets did not significantly differ, except for two cultivars on which the MS isolates sporulated better compared with the MR isolates. Nevertheless, total sporangial yield per lesion was (data not shown) significantly larger for the MR compared with MS isolates in all susceptible cultivars due to the much larger areas of lesions induced by the former isolates.

The tendency of MS isolates to vigorously sporulate was expressed also in tuber disks. In four cultivars MS isolates produced significantly more sporangia per unit tuber disk surface area compared with the MR isolates, while in the other 10 cultivars isolates of both populations did not differ significantly in sporangial yields.

The 14 cultivars used in this study were divided into several groups regarding susceptibility to late blight, depending on the fitness parameter used for grouping. Cara was relatively most resistant while Nicola was most susceptible to infection. The remaining 12 cultivars were moderately or highly susceptible to infection and more or less equally susceptible towards both the MS and MR fungal populations. The cultivars that strongly resisted lesion development were Draga, Cara, Dunja, Tarzan, and Timata. These five cultivars supported negligible (Draga and Cara) or no sporangial production (Dunja, Tarzan, and Timata) by the fungus. Draga, Dunja, and Tarzan were found highly resistant, whereas Cara, Avondale, and Tiamta were moderately resistant under field conditions (Grinberger and Cohen, *unpublished data*). Resistance to fungal colonization and sporulation was equally effective against the MS and the MR fungal isolates because isolates carried similar virulence factors. Draga and Dunja were reported (7) to carry unspecified major R genes for late blight resistance.

Tuber and foliage susceptibilities to *P. infestans* were not necessarily correlated (7). Under our conditions Desiree was moderately resistant against foliar and tuber disk attacks; Atica, moderately resistant in tubers but susceptible in foliage and Nicola, susceptible in both tissues. Only Cara and Timata were resistant in both the foliage and the tuber disks. Draga, Dunja, and Tarzan, which were resistant in foliage, were susceptible in tuber disks, while Avondale, which was susceptible in foliage, was resistant in tuber tissue. Avondale carries the R4 gene for resistance (7), which seems to be ineffective against foliar attack by the local isolates of the fungus. All six local isolates carry virulence factors 1, 3, 4, 7, and 8, with three carrying also virulence factor 10.

We concluded that the Israeli metalaxyl-resistant isolates of *P. infestans* tested here possess a higher fitness compared with the metalaxyl-sensitive isolates on the foliage of nine late blight-susceptible cultivars of potato. Five other cultivars were resistant

TABLE 7. (*continued from preceding page*)

Sporulation leaflets			Sporulation tubers			Compound fitness index[b] $\times 10^3$		
MS	MR	$P > t$	MS	MR	$P > t$	MS	MR	$P > t$
26.3 ± 6.8	14.9 ± 10.9	0.0194	132.7 ± 81.6	123.6 ± 103.3	0.6897	3,097 ± 1,049	6,329 ± 5,116	0.0976
19.3 ± 5.8	14.2 ± 9.9	0.2017	176.1 ± 145.3	134.0 ± 129.9	0.1765	1,803 ± 466	6,185 ± 4,528	0.0199
13.1 ± 2.1	13.2 ± 6.0	0.9925	41.7 ± 55.4	30.1 ± 41.0	0.2873	1,314 ± 340	4,888 ± 2,522	0.0027
16.7 ± 4.3	9.2 ± 8.0	0.0287	37.0 ± 39.3	15.2 ± 24.9	0.0036	1,039 ± 316	2,332 ± 2,230	0.1223
11.3 ± 1.3	9.7 ± 5.8	0.4422	16.2 ± 20.8	9.7 ± 15.6	0.1148	1,335 ± 499	3,031 ± 2,050	0.0394
12.8 ± 4.7	10.4 ± 4.6	0.2793	119.7 ± 136.7	75.1 ± 90.5	0.0850	2,142 ± 751	5,202 ± 2,229	0.0031
3.1 ± 1.3	2.9 ± 3.0	0.8144	85.9 ± 101.8	64.5 ± 75.9	0.2849	494 ± 171	1,399 ± 1,455	0.0998
1.8 ± 1.4	2.5 ± 1.4	0.2940	95.5 ± 131.9	34.8 ± 46.7	0.0093	181 ± 140	707 ± 513	0.0154
2.2 ± 2.1	1.0 ± 1.0	0.1336	41.9 ± 36.9	43.3 ± 41.8	0.8763	116 ± 141	145 ± 160	0.6839
0.1 ± 0.3	0.1 ± 0.2	0.8262	101.9 ± 113.2	119.3 ± 142.9	0.5757	0.4 ± 0.8	1.8 ± 2.7	0.1673
0.1 ± 0.2	0.08 ± 0.09	0.4054	15.1 ± 22.7	6.6 ± 15.1	0.0510	1.0 ± 1.4	1.2 ± 1.6	0.8168
0	0	...	85.9 ± 25.7	58.7 ± 29.0	0.0183	0	0	...
0	0	...	144.5 ± 10.9	220.9 ± 15.3	0.3676	0	0	...
0	0	...	8.6 ± 10.7	7.0 ± 14.1	0.6054	0	0	...
2.6	4.5		37.9	37.1		345	1924	

TABLE 8. Analysis of variance of effect of fungus isolates and potato cultivars on fitness components of *Phytophthora infestans* on potato foliage in intact plants in growth chambers

		Infection frequency		Lesion area		Sporulation leaflets		Compound fitness index	
Source	df	F	$P > F$	F	$P > F$	F	$P > F$	F	$P > F$
Model	83	5.70	0.0001	81.05	0.0001	50.44	0.0001	21.99	0.0001
Cultivar	13	29.16	0.0001	281.60	0.0001	237.27	0.0001	69.91	0.0001
Isolate	5	4.16	0.0014	336.96	0.0001	78.82	0.0001	64.93	0.0001
Cultivar × isolate	65	1.13	0.2668	21.26	0.0001	10.97	0.0001	9.1	0.0001
Error	168								
Total	251								

df = degrees of freedom; $P > F$ = Significance level of F-test. Number of observations in data set: 252. Compound fitness index = infection frequency × lesion area × sporulation capacity in leaflets.

TABLE 9. Correlation coefficients (and level of significance) between infection frequency, lesion area, sporulation capacity in leaflets, and sporulation capacity in tuber disks for 14 potato cultivars inoculated with metalaxyl-sensitive (MS) and metalaxyl-resistant (MR) isoaltes of *Phytophthora infestans* in growth chambers

Fitness component	LA[a]		SCL[b]		SCT[c]	
	MR	MS	MR	MS	MR	MS
IF[d]	0.3695 (0.1937)	0.3308 (0.2480)	0.5556 (0.0391)	0.5865 (0.0275)	0.5374 (0.0475)	0.5041 (0.066)
LA			0.6913 (0.0062)	0.4377 (0.1176)	0.0312 (0.9156)	0.1453 (0.6202)
SCL					0.1017 (0.7295)	0.3116 (0.2781)

[a] LA = Lesion area = lesion size in square millimeters.
[b] SCL = Sporulation capacity in leaflets = sporangia per square centimeter of lesion.
[c] SCT = Sporulation capacity in tuber disks = sporangia per square centimeter of tuber surface.
[d] IF = Infection frequency = proportion inoculated leaflets on which lesions developed.

against foliage attack of both fungal groups. Only two cultivars (Cara and Timata) were resistant against both foliar and tuber attacks.

The results explain the persistance of MR isolates of *P. infestans* and the severe outbreaks of MR-induced late blight epidemics on late blight-susceptible potato cultivars grown in Israel.

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