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The effects of *Alternaria solani* and *Verticillium dahliae* on potatoes growing in Israel

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Summary

The effects of two major fungal diseases of potatoes growing in hot climates, early blight (*Alternaria solani*) and Verticillium wilt (*Verticillium dahliae*), were investigated in field trials. Large populations of clones were grown in the Negev, Israel in the Spring and Autumn seasons of three years, 1983, 1984 and 1985. Although symptoms of the diseases were seen in both seasons they were less severe in the Autumn. The effects of *A. solani* on yield, when expressed as percent of the control plot yield were also less in the Autumn than the Spring. With *V. dahliae,* however, the proportional effect on yield was greater in the Autumn. The decreases in yield associated with the two diseases were examined in terms of losses to the grower. The advantages of breeding for resistance/tolerance to these diseases were clear, emphasising the need for suitable screening techniques.

Introduction

Verticillium wilt and early blight, caused by *Verticillium dahliae* and *Alternaria solani* respectively, are major fungal pathogens of irrigated potato crops grown in hot climates (Harrison & Venette, 1970; Douglas & Pavek, 1972; Krikun & Orion, 1979; Nachmias & Krikun, 1985).

V. dahliae, a soil-borne pathogen, is capable of surviving in field soil for many years as microsclerotia. Following their germination, the hyphae penetrate the roots (Schnathorst, 1982) and colonise the vascular system (Robinson et al., 1957; Perry & Evert, 1983, 1984) causing two major symptoms; stunting and unilateral chlorosis (followed by necrosis and wilt) in the foliage (Isaac & Harrison, 1968). Previous studies on the effect of *V. dahliae* infection on yield have been made on only a few cultivars and have not taken into account the severity of the disease or yearly and seasonal variation.

A. solani is an air-borne pathogen whose dark, multicellular spores are dispersed by wind and rain splash. The fungus penetrates wounded leaves, causing typical symptoms of dark concentric rings. Its occurrence is widespread but its importance in reducing tuber yield has not been clarified (Rotem, 1981).

Resistance and tolerance to Verticillium wilt of several potato cultivars has been

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reported by Davis et al. (1983) and Nachmias et al. (1985). Although some cultivars are more tolerant than others, the disease is usually controlled by soil fumigation (Harrison, 1974; Krikun & Orion, 1979). There have been few reports of early blight resistance or tolerance (Frank et al., 1979) and there are no cultivars suitable for the Negev or areas of similar climate; the disease is controlled mainly by applying high doses of fungicides and managing irrigation treatment (Holley et al., 1985).

In the study reported here, a large population of diverse potato germplasm was used in field trials to evaluate the relative importance of *V. dahliae* and *A. solani* infection over several years, their seasonal effects on yield and to assess the need for resistant/tolerant cultivars. It should be noted that *A. solani* can also cause symptoms in the tubers, black dry rot after storage, but only from infections that occur at harvest via mechanical damage. In this study the tubers were hand lifted to avoid this problem. The study therefore concentrates on foliage and yield characters although further losses due to development of symptoms in store and loss of quality might add weight to the case for the production of resistant/tolerant cultivars.

Materials and methods

The site and its climate. Field trials were carried out at Gilat Regional Experiment Station (30° 40'E, 31° 20'N) in the northern Negev, Israel in 1983, 1984 and 1985. The climate is arid-Mediterranean with mild winters and hot, rainless summers. The soil is loessial, silt loam with an average of 50 % organic matter and a pH of between 7.8 and 8.1. There are two seasons for potato growing; 1) Spring – potatoes are planted in the second half of February and harvested in June and 2) Autumn – planting is in late August and harvesting is in January. These seasons have a similar overall mean temperature and daylength but their patterns differ within each season. Fig. 1 illustrates the mean weekly temperatures for 1983 and shows that in Spring temperature increases during the growing season while in Autumn it progressively decreases.

The potato clones. The clones used included a large range of genotypes maintained by the Scottish Crop Research Institute (SCRI) and represented cultivars, breeders' clones, Neo-tuberosum clones (Glendinning, 1976) and clones from an improved diploid population (Carroll, 1982). The number in any year or season varied from 395 in Spring 1983 to 81 in Spring and Autumn 1985. Although the composition of the population differed, even at its minimum it can be considered as a representative sample of potato germplasm. Twelve clones were present on all occasions but no trial was grown in the Autumn season of 1983–84.

The trial management. Husbandry was in accordance with local practice. The trials were irrigated by a sprinkle system to 700–800 mm of water. Fertilizers were incorporated into the soil before planting and additional amounts supplied via the irrigation system. Pest and disease management reduced the development of unintentional infections.

In each year and season three areas were used, a Control area which was kept disease free, a Verticillium area into which *V. dahliae* had been introduced, and an Alternaria area which was artificially infected during the growing season with *A. solani* spores. The control area was prepared by soil fumigation (Krikun & Orion, 1979) and during the growing season it was kept as disease free as possible.

The infestation of the Verticillium area was achieved by evenly spreading dry potato haulms, carrying microsclerotia of *V. dahliae*, on the soil surface and then ploughing these into the soil. The area was subsequently used to grow potatoes for two or three years to build up a dense inoculum before it was used. The inoculum density, when assessed each year by plating air dried soil on Peg XT agar (Nicot & Bonse, 1987), was consistently between 50–90 microsclerotia per g of soil. The level of the nematode *Pratylenchus thorneii* was only about 20 nematodes per 100 g of soil.

The Alternaria area was maintained prior to the trials as disease free as was the Control but during the growing season of the trial the foliage was sprayed with *A. solani* spores prepared by growing cultures of *A. solani* on tomato agar (10 % tomato juice and 2 % agar at a pH of 7.6, Bashi & Rotem, 1975). The cultures were exposed to sunlight for 10 minutes every 24 hours but otherwise incubated in darkness at 27 °C. After five days concentric rings of spores were evident. The cultures were then blended in distilled water and immediately sprayed onto the foliage in the field which had been wetted by sprinkle irrigation for the previous hour. A spore suspension of 100 000 spores ml^{-1} was used at the rate of 10 l for every 1000 m^2 of the trial area. The spraying was carried out 45 days after planting and repeated every 10 days.

Characters scored. Specific symptoms of Verticillium wilt, were assessed 90 and 110 days after planting on a 0–5 scale: 0, no symptoms; 1, trace of symptoms; 2, 30 % of leaves infected; 3, 50 % of leaves infected; 4, >75 % leaves infected; and 5, plant dead. For early blight, symptoms were recorded every 10 to 14 days starting 60 to 70 days after planting. The percentage of leaf area infected was assessed by eye and then the early blight score estimated as the increase in percentage leaf area infected over a 14 day period at the time of maximal disease increase (generally between 75 and 95 days after planting).

The plants were defoliated 110 days after planting, the plots were machine dug and the tubers manually collected into net bags. The tubers were graded by hand into marketable (over 60 g) and chats (less than 60 g) fractions whose weights were recorded. The yields were converted to kg per plant.

Trial designs. The experimental layout in each year and season consisted of randomised complete blocks with the same randomisation being imposed on each of the three areas i.e. Control, Verticillium and Alternaria. In 1983 there were three categories of plants grown, differentiated by the numbers of tubers planted. The 'A' clones were grown in two replicate five-tuber plots, the 'B' clones were grown as a one replicate five-tuber plot and the 'C' clones as a one replicate three-tuber plot, in each treatment. In 1984 there were also three categories, but the 'A' clones were four replicate eight-tuber plots, the 'B' two replicate eight-tuber plots and the 'C' was one replicate three-tuber plot. The plot sizes and numbers of replicates in 1985 were the same as those in 1984 but no 'C' material was grown.

Results

The results for the early blight and Verticillium wilt symptoms, and the marketable (ware) yields from the Control, Alternaria and Verticillium plots given in Table 1 are the overall mean of the clones present in each year and season. The variances between clones indicate the variation in expression of the characters in the population. The in-

Table 1. Means ($\bar{x}$) and between clone variances (V_x) for the clones present in each of the three years. In two of the years the clones were grown in two seasons; Spring and Autumn. The characters recorded were: early blight score (maximum change in leaf area infected in a 14 day period), Verticillium wilt score (0 – 5 scale, 0 = no infection, 4 = >75 % infection and 5 = dead plant) and ware (= marketable) yield, measured as the weight of tubers >60 g in kg per plant.

		Spring				Autumn		
		1983	1984	1985	mean	1984	1985	mean
Number of clones		395	240	81		102	81	
Disease scores								
Early blight	$\bar{x}$	55.52	64.68	56.11	58.66	42.86	48.37	45.30
	V_x	698.54	463.97	367.50		581.29	393.21	
Verticillium wilt	$\bar{x}$	3.64	3.44	2.64	3.46	2.64	2.47	2.56
	V_x	0.90	1.10	0.89		0.35	0.43	
Marketable yield								
Control plot	$\bar{x}$	1.00	1.01	0.92	0.99	0.72	0.63	0.68
	V_x	0.13	0.24	0.42		0.02	0.21	
Alternaria plot	$\bar{x}$	0.78	0.77	0.71	0.77	0.67	0.59	0.63
	V_x	0.09	0.12	0.25		0.02	0.18	
Verticillium plot	$\bar{x}$	0.74	0.63	0.49	0.67	0.36	0.39	0.37
	V_x	0.07	0.11	0.12		0.02	0.11	

crease in *A. solani* infection is higher in the Spring, having a mean of 59 %, than in the Autumn, at 45 %. Nevertheless, in both seasons there was clearly considerable disease development. The pattern for the Verticillium wilt symptoms was similar but with less severe symptoms in the Autumn. Ware yields were lower in the Autumn than in the Spring season in all three areas. In the Spring the yields in the Control area ranged from 1.00 to 0.92, while in the Autumn they were 0.72 to 0.63. Although the plants included diploid clones, breeders' clones (many of which had not been selected to grow in hot climates), as well as commercial cultivars, the yields were comparable with those of adapted cultivars grown in this region giving about 1.5 kg per plant (Levy et al., 1986). The yields of the Verticillium and Alternaria plots were consistently lower than those of the Controls.

Although the number of clones present in different years and seasons varied (Table 1), this change in the population is unlikely to have any major effects on the results because of the large minimum sample size, 81 clones. To judge this directly, the results are given in Table 2, for the means of the same characters based on the 12 clones which were present on every occasion. Examination of Table 2 shows the same main features as Table 1. However, as the means are based on fewer observations they will be subject to a greater degree of error variation.

The effects of the two diseases on ware yield from all clones, are presented in Table 3 both as the differences in yield, within each year and season, between the disease and Control plots and as percentages of the Control. In Spring, infection with *A. solani* decreased the yield per plant by an average of 0.22 kg (22 %), while in Autumn it was only 0.05 kg, (7 %). Thus the disease symptoms are reduced in the Autumn (Table 1)

Table 2. Means ($\bar{x}$) averaged over 12 clones present on all occasions. The characters are as given in Table 1.

		Spring				Autumn		
		1983	1984	1985	mean	1984	1985	mean
Disease scores								
Early blight	$\bar{x}$	63.33	57.77	53.02	58.04	55.83	49.10	52.46
Verticillium wilt	$\bar{x}$	3.81	3.24	2.85	3.30	2.69	2.46	2.57
Marketable yield								
Control plot	$\bar{x}$	1.05	0.84	0.88	0.92	0.51	0.65	0.58
Alternaria plot	$\bar{x}$	0.85	0.61	0.72	0.73	0.50	0.53	0.51
Verticillium plot	$\bar{x}$	0.74	0.50	0.51	0.58	0.25	0.40	0.32

Table 3. The ware yields (in kg/plant), averaged over clones, in the Alternaria and Verticillium plots in comparison to those in the disease-free Control plots.

	Spring				Autumn		
	1983	1984	1985	mean	1984	1985	mean
Alternaria ware – Control ware	-0.22	-0.24	-0.21	-0.22	-0.05	-0.04	-0.05
%Alternaria ware/Control ware	78.0	76.0	77.2	77.8	93.1	93.6	93.3
Verticillium ware – Control ware	-0.26	-0.38	-0.43	-0.32	-0.36	-0.24	-0.31
%Verticillium ware/Control ware	74.0	62.0	53.3	67.7	50.0	61.9	54.4

Table 4. The ware yields (in kg/plant), averaged over the 12 clones that were present on every occasion, in the Alternaria and Verticillium plots in comparison to the disease free Control plots.

	Spring				Autumn		
	1983	1984	1985	mean	1984	1985	mean
Alternaria ware – Control ware	-0.20	-0.23	-0.16	-0.19	-0.01	-0.12	-0.07
%Alternaria ware/Control ware	80.9	72.6	81.8	79.3	98.0	81.5	87.9
Verticillium ware – Control ware	-0.31	-0.34	-0.37	-0.34	-0.26	-0.25	-0.26
%Verticillium ware/Control ware	70.5	59.5	58.0	63.0	49.0	61.5	55.2

while the seasonal effect on yield is even more apparent. The effects of *V. dahliae* on yield are clear in Table 3; the decrease is about the same in the two seasons, with a mean of 0.3 kg per plant, but because the Control yield is lower in the Autumn this represents a larger percentage decrease i.e. in Spring of 32 % while in Autumn of 46 %. Thus *V. dahliae* produces a significant decrease in yield in both seasons, but it has its greatest effect in Autumn even though the symptom expression is then less. The results (Table 4) for the 12 clones present in all years and seasons, confirm the relationships exhibited by the larger population.

Discussion

The symptoms of *A. solani* were more severe in the Spring than in the Autumn but in both seasons the percentage of leaf area infected was high. The scores, which represented the maximum change in percentage leaf area over a 14 day period, had a mean of 59 % and 45 % in Spring and Autumn respectively and were accompanied by respective decreases in yield of 22 % and 7 %. Thus the disease score and the effects on marketable yield are less in the Autumn than in the Spring but yield varies proportionally more than score. This may be a reflection of the different seasonal patterns of environmental conditions, for example, of temperature as shown in Figure 1. Such differences could be important, particularly during tuber bulking. Also, in Spring senescence is relatively slow, giving ample opportunity for *A. solani* to develop, while in Autumn it is often rapid since it is induced by adverse conditions such as storms.

V. dahliae symptoms were more extreme in the Spring than in the Autumn season (a mean of 3.5 compared with 2.6) while the effects on marketable yield were proportionally greater, yield being reduced by 33 % and 46 % respectively. This might appear paradoxical but may again reflect the effects of different climatic patterns in the two seasons. The factors involved are uncertain, but in the Spring growth is accompanied by increasing temperature (Fig. 1) and daylength which, with irrigation, leads to favourable growing conditions particularly during tuber bulking and the high yields actually obtained would support this view. In the Autumn, the temperature and day-

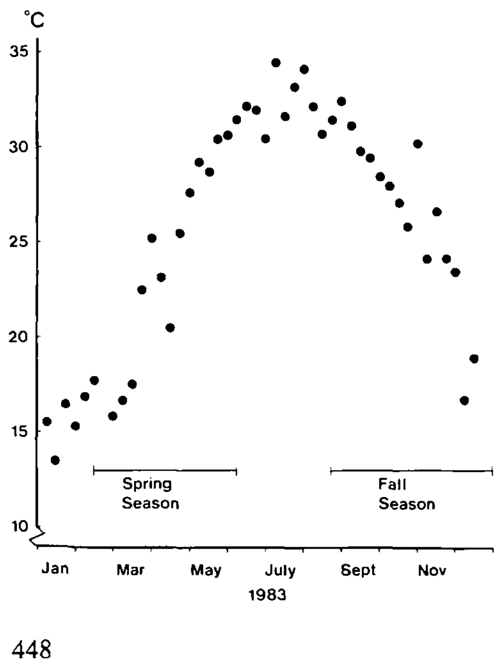

Fig. 1. The mean weekly temperatures at Gilat in the Negev in 1983.

length are decreasing continually, giving progressively less favourable conditions that lead to lower yields. If *V. dahliae* is not adversely affected by, for example, decreasing temperature, it would produce a more severe proportional effect on final ware yield.

Yield is decreased in Spring by 22 % with *A. solani* and 32 % with *V. dahliae*, both substantial losses. In the Negev a yield of 50 tonnes per hectare in spring can readily be achieved in commerce (Levy et al., 1986) so these decreases represent losses to the grower of 11 tonnes from *A. solani* and 16 tonnes from *V. dahliae* per hectare. In the Autumn season the decrease due to *A. solani* was 7 % while that for *V. dahliae* was 46 % and although the yields expected are lower than in the Spring (about 30 tonnes per hectare, Levy et al., 1986), the percentage reductions approximate 2 tonnes due to *A. solani* and nearly 14 tonnes to *V. dahliae*.

The cost of chemical control of these two diseases is high. *V. dahliae* is controlled by soil fumigation (Krikun & Orion, 1979); the chemicals together with the costs of application exceed $900 per hectare at 1987 prices. *A. solani* is usually controlled together with late blight (*Phytophthora infestans*) and so their costs are confounded. However, up to five sprays are applied each season, often by aircraft, and these are a substantial addition to the variable costs of production. In the absence of resistant/tolerant cultivars, chemical control of both of these diseases can be justified economically apart from, possibly, *A. solani* in the Autumn.

These economic considerations take no account of the ecological side-effects of the chemicals used, which are difficult to quantify, but they must be important long-term considerations. In addition, no allowance is made here for the technical difficulties in applying control measures. For example, it is difficult to fumigate soil if the field is sloping and in some countries sophisticated husbandry techniques are not available, especially where farms are small. Clearly, the best solution to minimise both adverse side-effects and potentially large losses of yield and profit must lie in the production of resistant, or at least tolerant, cultivars which require no additional technology for the grower. To achieve this, suitable screening techniques are required to allow the identification of resistant/tolerant clones and hence enable the selection of cultivars incorporating these characters together with those required commercially. The results show the benefits that might arise from the production of such cultivars.

The experiments reported here are part of a more extensive investigation into the possibilities of screening for resistance/tolerance to *A. solani* and *V. dahliae*.

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