PARASITIC POTENTIAL OF VERTICILLIUM ALBO-ATRUM FROM CULTIVATED AND UNCULTIVATED AREAS

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ABSTRACT

PARASITIC POTENTIAL OF VERTICILLIUM ALBO-ATRUM FROM CULTIVATED AND UNCULTIVATED AREAS

by Joseph A. Ignatoski

The origin of Verticillium albo-atrum on strawberry was investigated by conducting a survey of the host range and parasitic potentials of 13 isolates from cultivated crops and 7 from uncultivated areas on 20 different plants normally growing in these two areas.

All isolates were parasitic on each test plant with the exception of the peppermint isolate on violet. Isolates from the uncultivated areas were parasitic on cultivated strawberry and thus are potential pathogens.

Three isolates from soil in uncultivated areas and 4 isolates from crop plants in cultivated areas were similar in parasitic potential and host range, suggesting that the 4 isolates from the cultivated areas could have originated in an uncultivated area.

Some plants from both uncultivated and from cultivated areas were as susceptible to invasion by Verticillium isolates as susceptible cultivated plants and thus could serve as multiplication sites for the fungus.

PARASITIC POTENTIAL OF *VERTICILLIUM ALBO-ATRUM* FROM CULTIVATED AND UNCULTIVATED AREAS

By

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INTRODUCTION

The form genus Verticillium was established by Ness VonEsenbeck (19) in the year 1816. In 1879 a pathogenic form was observed on potato (Solanum tuberosum L.) by Reinke and Berthold (21) and given the species epithet of albo-atrum. Since this initial discovery of pathogenicity, numerous hosts for this organism have been reported (6).

A review of the literature from 1879-1928 was published by Rudolph in 1931 (22) including a host range which consisted of trees, shrubs and weeds as well as cultivated plants. This host range was determined by observing the death of the plant as a result of infection and hence was a measurement of pathogenicity. From experiments cited in this review and others 3, 29, 33) it can be concluded that Verticillium attacks and kills plants in many speices and families and that no one isolate is specific to one family or species to the exclusion of all others.

Others, however, have reported specificity (9). Verticillium isolates which were pathogenic on peppermint appeared to be pathogenic only on peppermint, (i.e. killing it), but parasitic on a number of hosts (i.e. present in the hosts tissue without the plant showing

The purpose of this study was to compare the host range and parasitic potential (average distance moved by each isolate above level of inoculation in each test plant) of Verticillium found in cultivated areas with those of isolates from uncultivated sites with the hope that the comparison would provide clues that would be useful in reconstructing the origin of this parasite on cultivated strawberry.

MATERIALS AND METHODS

Fungus Isolates: Twenty isolates of Verticillium were obtained for comparison, 13 from cultivated fields and 7 from uncultivated more natural plant arrays. Thirteen isolates of V. albo-atrum were obtained with sterile techniques from cultivated plants exhibiting symptoms of Verticillium wilt (Table 1). Aerial portions were surface sterilized with 50% Clorox (2.6% sodium hypochlorite) for 1 - 3 min, cut into 3 cm pieces with a sterile scalpel and plated on potato dextrose agar.

In addition seven isolates of V. albo-atrum, were obtained from borders of seven out of ten woodlots, in which wild strawberries were found. This was accomplished in two ways: (1) by isolation from aerial portions of plants as described above; and (2) by isolation from the soil in each woodlot by a modification of an alcohol-agar-streptomycin technique (16). A solution was prepared containing 95 ml sterile distilled water, 1 g of agar, 5 ml of absolute ethyl alcohol and 1000 ppm streptomycin or 0.25 ml of 10% lactic acid. To this solution 1 g of soil was added, swirled, and poured into 5 petri dishes. After 5 - 7 days the plates were examined for the presence of Verticillium.

Cultures were maintained by single spore transfer on potato-dextrose agar. Inoculum consisting of a

TABLE I.--Isolates of *Verticillium* from Michigan and their source.

Isolate No.	Type	Source	
		Uncultivated or Cultivated	Soil or Plant
1	M[a]	Uncultivated	Soil
2	M	Uncultivated	Soil
3	M	Uncultivated	Soil
4	M	Uncultivated	Soil
5	M	Uncultivated	Soil
6	M	Uncultivated	Strawberry *Fragaria virginana* L.
7	M	Uncultivated	Wild Rose *Rosa setigera* Michx.
8	M	Cultivated	Red raspberry *Rubus occidentalis* L.
9	M	Cultivated	Strawberry var. Surecrop
10	M	Cultivated	Strawberry var. Blakemore
11	M	Cultivated	Strawberry var. Midway
12	S[b]	Cultivated	Strawberry var. Midway
13	M	Cultivated	Strawberry var. Earlidawn
14	M	Cultivated	Strawberry var. Earlidawn
15	M	Cultivated	Strawberry var. Earlidawn
16	M	Cultivated	Strawberry var. Earlidawn
17	M	Cultivated	Strawberry var. Earlidawn
18	S	Cultivated	Peppermint *Mentha piperita* L.
19	DM[c]	Cultivated	Potato *Solanum tuberosum* L.
20	DM	Sub-culture of 19	Potato *Solanum tuberosum* L.

[a] M - Mycelial

[b] S - Sclerotial

[c] DM - Dark Mycelial

suspension of spores and mycelial fragments was prepared by homogenization of 10 day old cultures (which were prepared by mass spore transfer) with 100 ml sterile distilled water in a Waring Blendor.

Plants: The following three categories of plants were selected to classify the 20 isolates as to host range and parasitic potential. Those from the cultivated areas were Tomato var. Bonny Best, representing a susceptible solanaceous crop, cultivated strawberries, var. Earlidawn (very susceptible) and Robinson (tolerant), and five species of plants commonly found as weeds in cultivated strawberry fields (Table 2).

Plants from the uncultivated areas were 11 species commonly found in proximity to wild strawberries (F. virginiana L.) including wild strawberries and the Del Norte clone of F. chiloensis from California (Table 2).

Plants were maintained in the greenhouse. Strawberry plants from both uncultivated and cultivated sources were propagated with supplementary illumination for runner production. Isolations were attempted from runners and petioles of the mother plants to confirm that the daughter plants were free of Verticillium. These Verticillium-free daughter plants were then used for further propagation.

TABLE 2.--Plants Used to Determine Host Range and Parasitic Potential.

Plant No.	Family genus species	Origin	Common Name	Height at time of Inoc. (cm)
	Polygonaceae			
1	*Rumex crispus* L.	W[a]	Dock	21
	Amaranthaceae			
2	*Amaranthus retroflexis* L.	W	Pigweed	24
	Portulaceae			
3	*Portulaca oleracea* L.	W	Purslane	9
	Caryophyllaceae			
4	*Stellaria media* L.	W	Chickweed	12
5	*Lychnis alba* Mill.	W	White Cockle	12
	Ranunculaceae			
6	*Ranunculus abortivus* L.	P[b]	Meadow Rue	15
	Rosaceae			
7	*Fragaria chiloensis* L.	P	Wild Strawberry	6
8	*Fragaria virginiana* Duchesne clone 1	P	Wild Strawberry	12
9	*Fragaria virginiana* Duchesne clone 2	P	Wild Strawberry	12
10	*Fragaria virginiana* Duchesne clone 3	P	Wild Strawberry	15
11	*Fragaria* var. Earlidawn	C[c]	Cult. Strawberry	15
12	*Fragaria* var. Robinson	C	Cult. Strawberry	12
13	*Potentilla recta* L.	P	Potentilla	18
14	*Rosa setigera* Michx.	P	Wild Rose	15
	Leguminosae			
15	*Vicia angustifolia* Reichard	P	Vetch	50
	Violaceae			
16	*Viola* sp.	P	Violet	9
	Umbelliferae			
17	*Daucus carota* L.	P	Wild Carrot	15
	Solonaceae			
18	*Solanum dulcamara* L.	P	Nightshade	30
19	*Lycopersicum esculentum* Mill var. Bonny Best	C	Cult. Tomato	24
	Compositae			
	Teraxacum officinale Weber	P	Dandelion	15 17.5

a W - Weeds commonly found in cultivated strawberry fields

b P - Plants growing in proximity to wild strawberries and wild strawberries

c C - Cultivated plants

All other plants were propagated from seed collected in the field. Seeds which did not germinate promptly were placed between layers of moist, sterile vermiculite in wax milk cartons and stored at 3°C for three months. The cartons were then placed at room temperature and the seeds allowed to germinate. The seedlings were transplanted into sterile 4 inch pots containing sterile soil mixed with unsterile peat and sand (2:1:1).

Inoculation: Once the plants had reached the desired stage of growth (Table 2), four plants of each species or clone were inoculated with each isolate and ten plants were used as uninoculated controls. Plants were inoculated by washing the roots free of soil and dipping them into a suspension of spores and mycelial fragments up to a point 7 cm below ground line. The plants were then placed in sterile pots and then the soil added to avoid contaminating the roots above the level of inoculation.

Isolation: After 28 days the plants were uprooted and soil removed with running water. The root systems were completely immersed in 10% Clorox for 3 minutes to eliminate shallow, superficial infections and to destroy any remaining inoculum. Aerial portions were immersed in 50% Clorox for 1 - 3 minutes, depending on their thickness, and then cut into successive 3 cm sections. The first sections consisted of 2 cm of the inoculated area and 1 cm above (Fig. 1). Sections were placed into

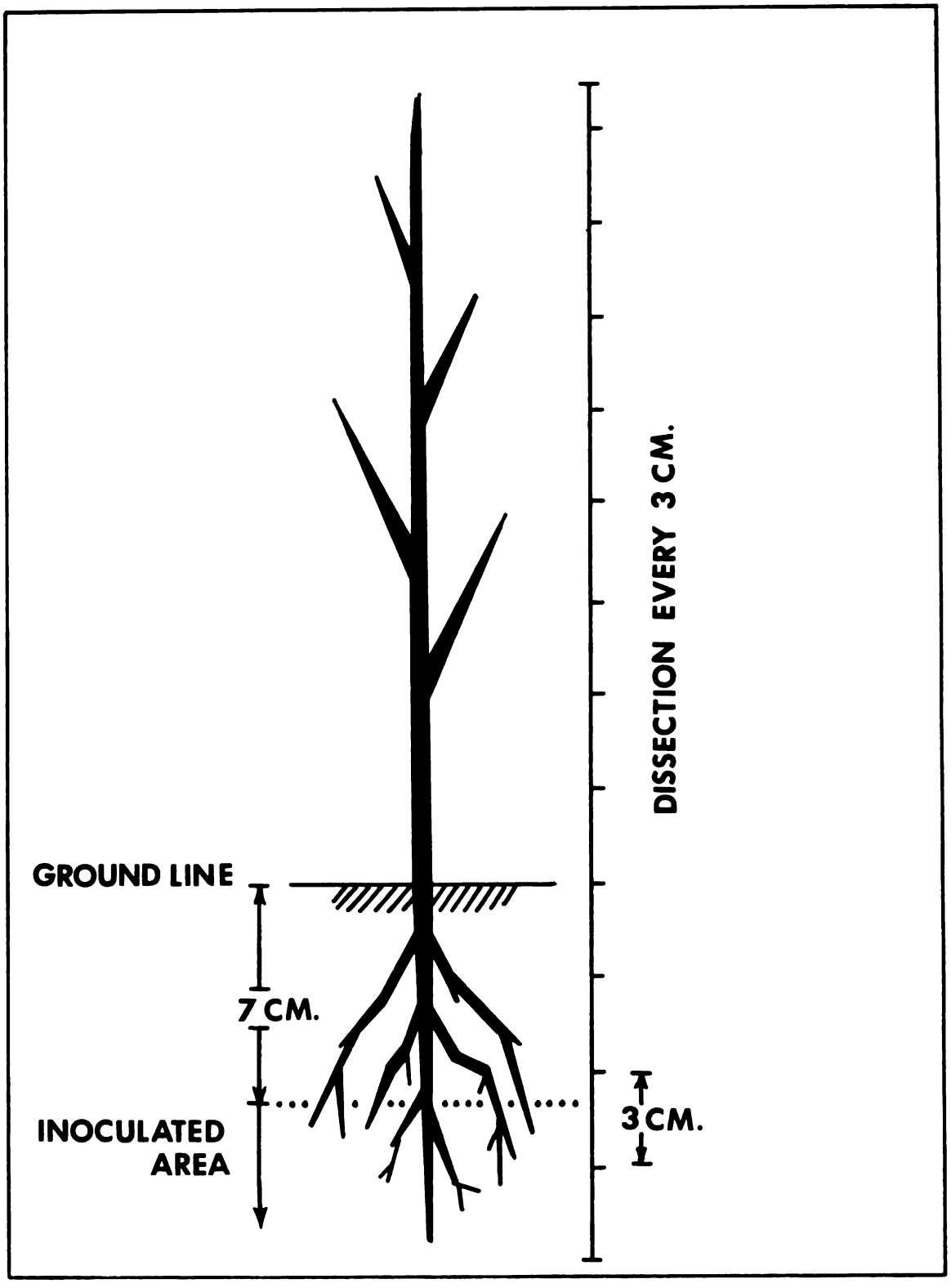

Figure 1.--Dissection of plants for isolation.

a petri dish of 1% water agar containing 250 ppm terramycin. After 10-14 days the presence of Verticillium was determined. Similar procedures were followed for each of the 10 control plants.

Table 3.--Average distance (cm) 20 isolates of V. albo-atrum moved upward from level of inoculation in 20 test plants. (Average for 4 replications. Ground line is at 6 cm). Coding of plants corresponds to Table 1; Coding of isolates corresponds to Table 2. The least significant differences between means was calculated according to the Tukey method for multiple comparisons: $d_{.05} = 1.84$; $d_{.01} = 2.03$.

Isolates	TEST PLANTS																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	Grand Ave. cm
1	9.0	10.5	3.0	3.0	12.0	6.0	3.0	0.7	4.5	4.5	8.3	6.75	4.5	7.5	1.5	4.5	4.5	1.5	4.5	3.7	5.2
2	3.0	5.3	3.0	6.8	10.5	12.8	5.25	2.3	2.3	6.0	9.8	6.8	6.8	7.5	2.3	3.0	4.5	4.5	6.0	3.8	5.6
3	6.0	17.3	3.0	2.3	9.0	6.0	6.8	2.3	3.8	7.5	10.5	6.8	9.0	8.3	4.5	6.0	3.0	5.3	6.8	5.3	6.5
4	7.5	12.8	3.0	3.8	3.8	6.8	8.3	4.5	6.0	6.0	11.3	4.5	4.5	7.5	0.8	6.0	3.0	4.5	7.5	6.8	5.9
5	6.8	17.3	3.0	0.8	6.8	3.8	6.0	6.0	2.3	1.5	12.0	7.5	6.8	9.0	5.3	4.5	3.8	5.3	6.0	6.8	6.0
6	6.8	21.0	2.3	6.0	3.0	6.0	6.0	4.5	6.8	5.3	8.3	9.0	5.3	7.5	10.5	3.8	6.0	4.5	6.0	6.8	6.8
7	4.5	8.3	3.0	0.8	8.3	6.0	8.3	0.8	2.3	5.3	9.0	6.0	3.0	9.0	7.5	0.8	3.8	3.3	6.8	2.3	4.9
8	5.3	19.5	7.5	3.0	9.8	3.8	7.5	6.8	6.0	3.8	16.5	6.8	6.0	8.3	7.5	8.3	5.3	3.8	6.8	6.0	7.4
9	7.5	9.0	3.8	5.3	4.5	11.3	9.0	6.8	4.5	3.8	10.5	6.8	11.3	7.5	6.0	5.3	5.3	3.8	6.8	8.3	6.8
10	7.5	22.5	3.8	6.0	9.0	6.8	4.5	3.0	2.3	3.0	12.0	10.5	12.8	7.5	7.5	3.0	3.8	4.5	6.8	4.5	7.0
11	6.0	16.5	6.0	0.8	4.5	7.5	5.3	0.8	6.0	5.3	14.3	8.3	6.0	7.5	4.5	14.3	4.5	4.5	6.0	4.5	6.6
12	9.0	24.8	12.0[a]	6.0	4.5	18.0	10.5	9.8	18.0	18.0	21.0	18.0	17.3	20.3	18.0	1.5	6.0	24.0	21.0	15.8	14.6
13	6.0	21.0	3.0	12.0	16.5	9.0	7.5	6.8	6.0	6.0	20.3	13.5	10.5	8.3	15.8	7.5	3.0	6.0	6.0	6.0	9.5
14	3.0	21.0	3.0	4.5	10.5	5.3	6.0	0.0	3.8	9.8	13.5	7.5	6.8	8.3	12.8	5.3	4.5	3.8	3.8	7.5	7.0
15	8.3	19.5	3.0	2.3	9.0	7.5	6.8	6.8	4.5	3.0	19.5	6.0	9.8	6.0	10.5	3.8	4.5	3.0	6.8	6.8	7.4
16	9.0	18.8	3.0	6.8	10.5	105.	5.3	6.0	6.8	10.5	12.8	11.3	4.5	9.8	9.0	11.3	4.5	1.5	8.3	3.8	8.2
17	6.8	12.0	4.5	5.3	10.5	6.0	7.5	7.5	6.8	3.0	10.5	8.3	4.5	8.3	2.3	3.8	3.0	3.8	4.5	2.3	6.0
18	6.0	25.5	12.0[a]	12.8	6.0	9.0	12.0	8.3	12.0	12.0	18.8	17.3	18.8	18.8	18.0	0.0	6.0	7.5	21.0	15.0	12.8
19	4.5	4.5	4.5	6.0	3.0	8.3	9.8	9.0	4.5	6.0	9.0	4.5	5.3	6.8	6.0	1.5	3.8	4.5	6.0	3.0	5.5
20	7.5	4.5	3.0	4.5	6.0	6.0	8.3	3.8	5.3	7.5	15.8	9.8	7.5	21.0	3.8	2.3	5.3	3.8	6.0	6.0	6.9
Grand Ave. cm	6.5	15.6	4.3	4.9	7.9	7.8	7.2	4.8	5.7	6.4	13.2	8.8	8.0	9.7	7.7	4.8	4.4	5.1	7.7	6.2	

[a]All plants were dead 28 days after inoculation.

RESULTS

V. albo-atrum was isolated from 7 of the 10 uncultivated areas; 5 isolates were directly from soil and one each from symptomless wild rose and symptomless wild strawberry (Table 1). Thirteen isolates were obtained from cultivated crops (Table 1). To determine whether or not there were differences between these isolates, 20 test plants (Table 2) were inoculated with each of the 20 isolates (Table 1) and the distance the isolates grew within the plant determined (Table 3). The distance an isolate grows in a particular host was considered a measurement of the parasitic potential of the parasite. All 20 isolates were parasitic to some degree on every test plant with the exception of the peppermint isolate on violet. Thus no host specificity was observed. Only purslane, when inoculated with isolate No. 12 from cultivated strawberry or No. 18 from peppermint, died before the end of 28 days. No Verticillium was recovered from any control plant. All 7 isolates from the uncultivated areas were parasitic on cultivated strawberry since each isolate grew above ground line (Table 3).

In order to compare the parasitic potentials of the 13 isolates obtained from cultivated areas with the 7 from

uncultivated areas, it was necessary to determine whether the isolates acted differently or similarly on different test plants. The parasitic potential of the isolates was measured by the distance grown above the level of inoculation for each isolate in every test plant. In order to compare the parasitic potentials on the 20 test plants, correlation coefficients were obtained for all 400 possible pairs of isolates. If the isolates from both areas formed two homogenous but distinct groups a large number of high positive and negative correlation coefficients would be obtained. A frequency distribution of these values would result in a bimodal curve. If the isolates from both areas are similar and form not two but one homogenous group, a normal unimodal frequency distribution of these values would be obtained.

The 400 correlation coefficients obtained (Fig. 2) ranged from -0.6 to +0.6 and had a unimodal frequency distribution which appeared to be normally distributed. Similar frequency distributions were obtained for correlation coefficients among isolates from cultivated areas and among these from uncultivated areas. Thus the isolates from both areas are not two distinct groups but are very similar and appear to be a part of the same population.

The parasitic potentials, or the average distance moved by the 20 isolates on each test plant, was skewed with the majority of isolates moving 5 to 8 cm (Fig. 3). The isolates

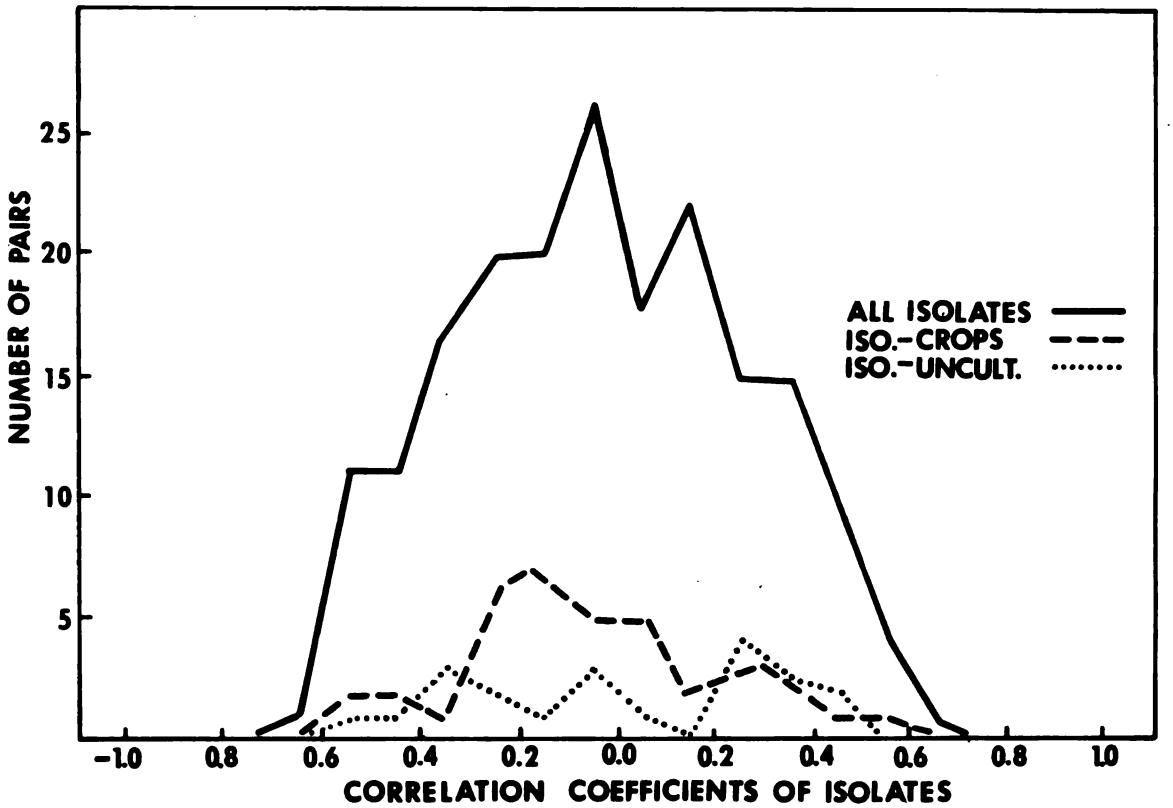

Figure 2.--Frequency distribution of correlation coefficients for all 400 possible pairs of 20 isolates when inoculated into 20 hosts and plotted in intervals of 0.1 for correlation coefficients.

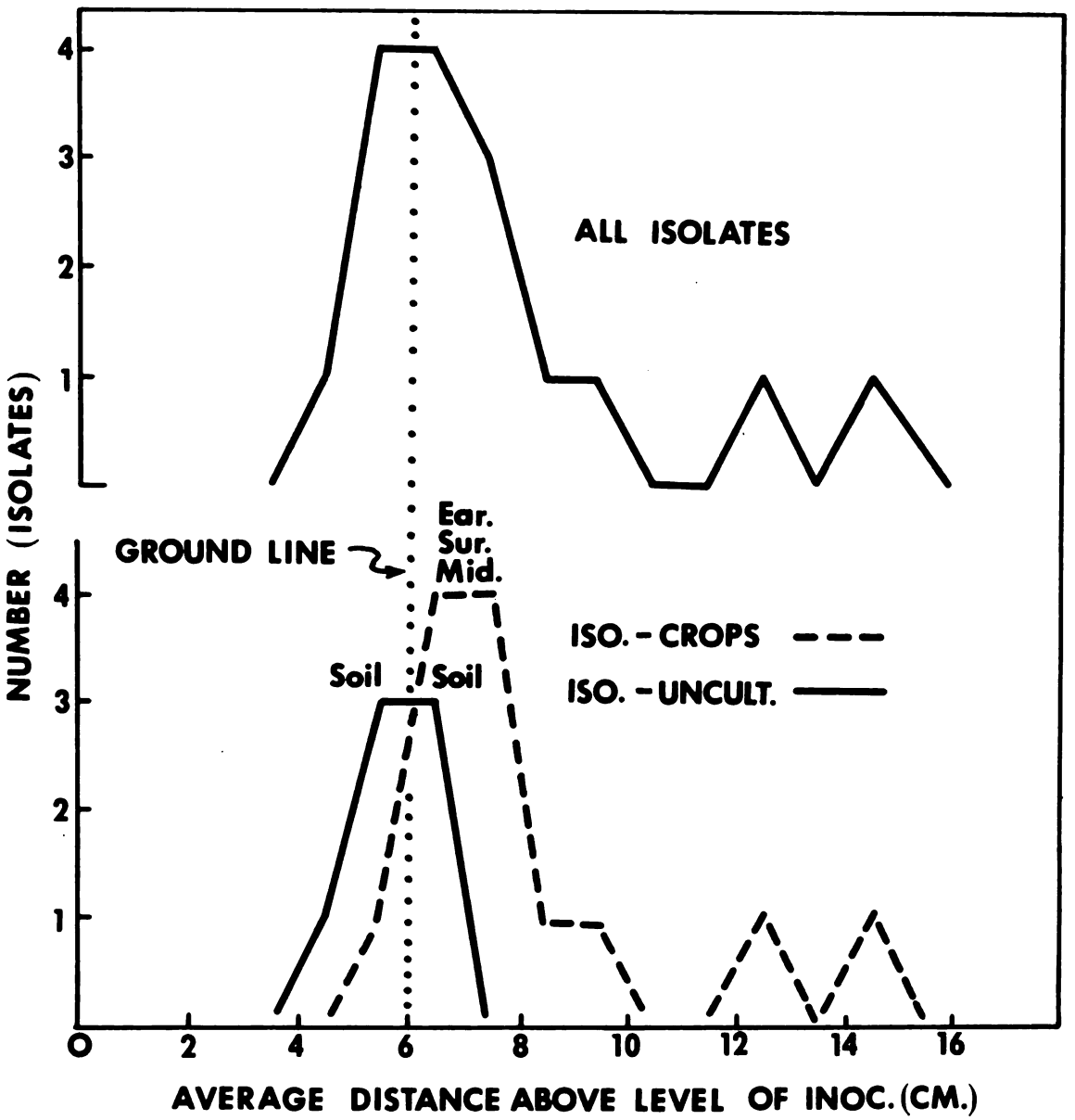

Figure 3.--Frequency distribution of parasitic potentials for 20 isolates as shown by the number of isolates plotted against (cm) from the cultivated crops--[Earlidawn (ear.) Surecrop (sur.) and Midway (Mid.) moving 6.0 to 6.8 cm] and from uncultivated areas-- [Two soil isolates moving 5.6 to 5.9 cm and one moving 6.5 cm] are significantly similar at the .05 level of probability for their correlation coefficients.

moving further than 12 cm were the two sclerotia formers. Similar distributions were obtained for isolates from both cultivated crops and uncultivated areas (Fig. 3). The points between 5 and 7 cm on the abscissa corresponding to the peaks on both curves are not significantly different at the .05 level of probability. There were high positive correlation coefficients (.05) in regards to similarity of distance grown above level of inoculation in each of the 20 test plants for 7 of 14 isolates that grew an average of 5-7 cm from the point of inoculation (3 isolates were from cultivated crops and 4 were from soil from the uncultivated sites). Thus these isolates are very similar in host range and parasitic potential.

On the basis of where the plants came from they can be grouped into 3 categories for comparison of parasitic potentials of 7 isolates from the uncultivated areas: (1) cultivated susceptible crops, (2) plants found growing in the proximity of wild strawberries, and (3) weeds commonly found in cultivated strawberry fields (Fig. 4). All 7 isolates were parasitic on the 1st category of plants with 6 isolates moving farther than 6 cm (ground line) from the level of inoculation. The same isolates when inoculated into the second and third category of plants formed two groups in regards to parasitic potential. In the first group, isolates did not grow above ground line (growing 3 to 4 cm) and in the other group the isolates

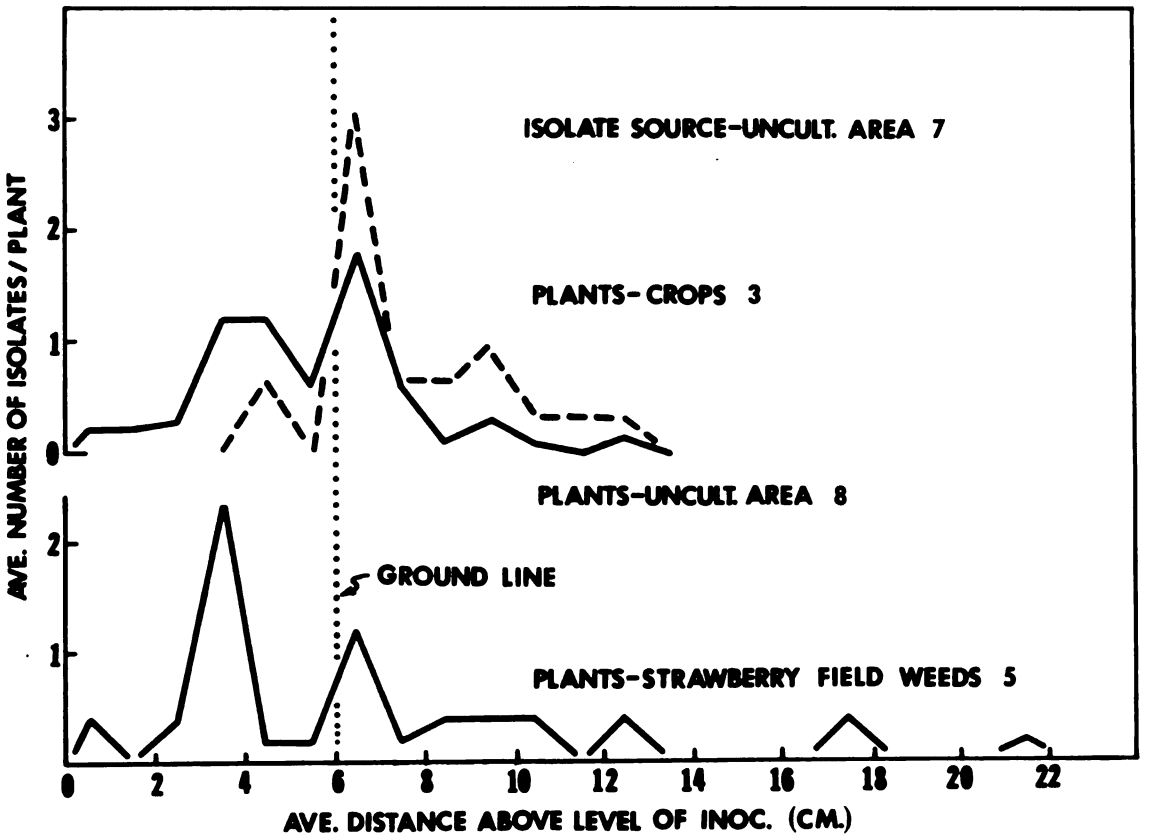

Figure 4.--Frequency distribution of parasitic potentials for 7 isolates from virgin areas as shown by the average number of these isolates per plant of each respective group plotted against the average distance they moved (cm) from the level of inoculation.

grew above ground line (6 cm) and were as parasitic as the 6 isolates were on susceptible crops. The same was observed for isolates from the cultivated crops (Fig. 5).

Many degrees of susceptibility (cm invasion above inoculation level) were observed between the 20 isolates and the 20 test plants, and these degrees of susceptibility appear to exhibit a normal distribution (Fig. 6.) The test plants formed two groups when the average distance all isolates moved in each test plant was compared (Fig. 7): (1) slightly susceptible, the isolates moving 3 to 4 cm, and 2) the moderately susceptible to very susceptible, the isolates moving farther than 6 cm or above ground line. The same was true for the plants from the uncultivated areas and for weeds from cultivated strawberry fields. Strawberry plants did not form a homogenous group but reacted from slightly to very susceptible. Earlidawn was the most susceptable (the 20 isolates moving an average of 13.2 cm) and Robinson was next (the 20 isolates moving an average of 8.8 cm).

When the test plants are compared as to the distance each of the 20 isolates moved, four groups are obtained: (1) variable (Fig. 8 a and b) resistant (Fig. 9, purslane etc.), (3) slightly resistant (Fig. 9, chickweed etc.), and (4) susceptible (Fig. 9, strawberry var. Earlidawn etc.).

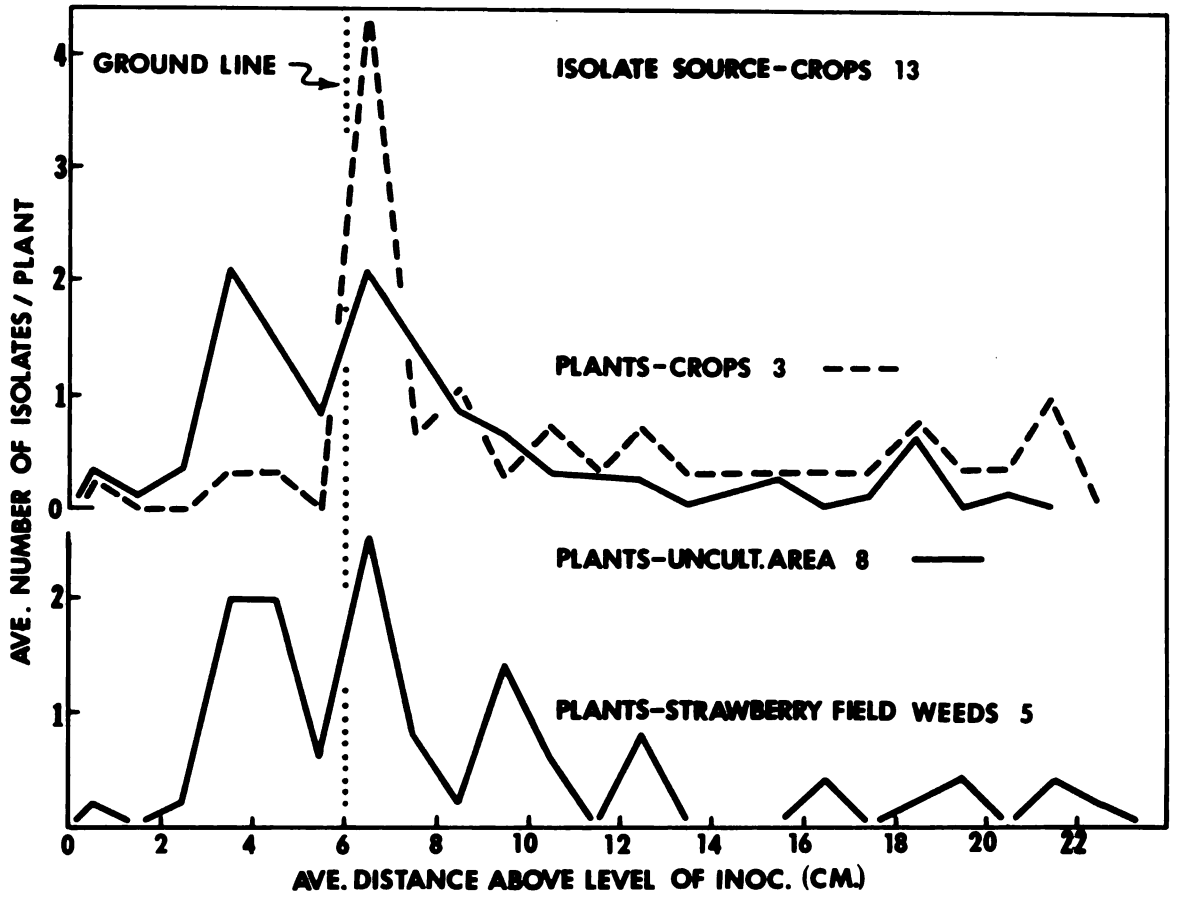

Figure 5.--Frequency distribution of parasitic potentials for 13 isolates from cultivated crops as shown by the average number of these isolates per plant of each respective group plotted against the average distance they moved (cm) from the level of inoculation.

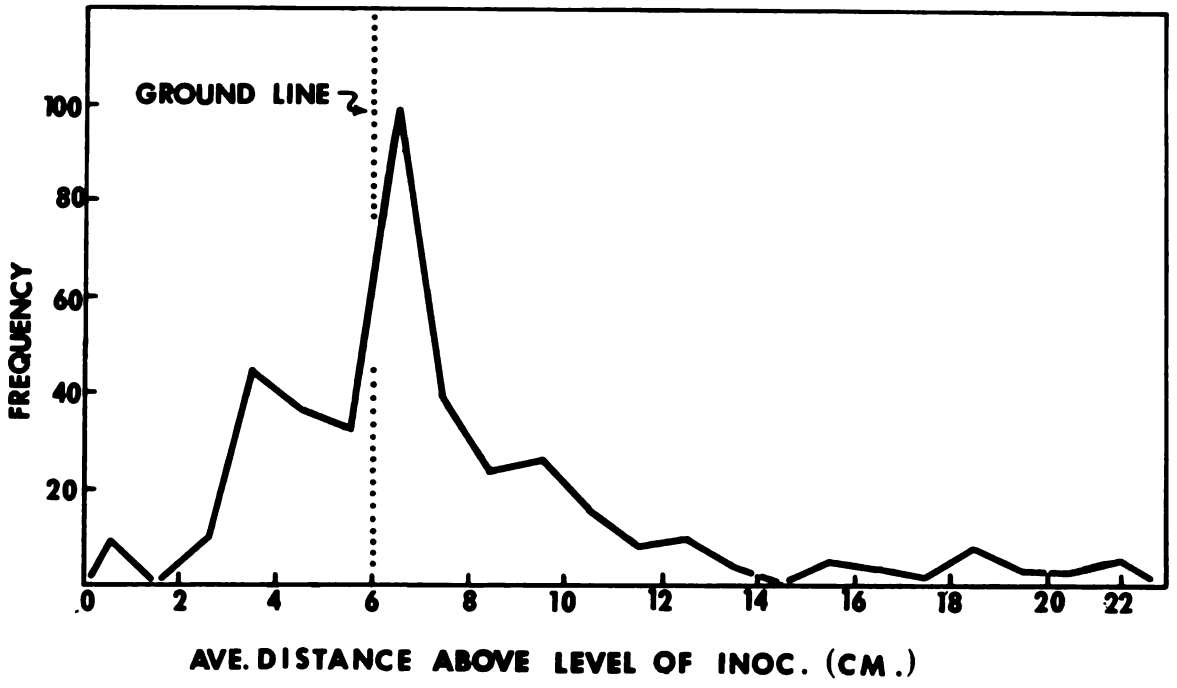

Figure 6.--Frequency distribution of 400 host-parasite (isolate) combinations shown by the frequency of these combinations plotted against the average distance moved (cm) by the fungus from the level of inoculation.

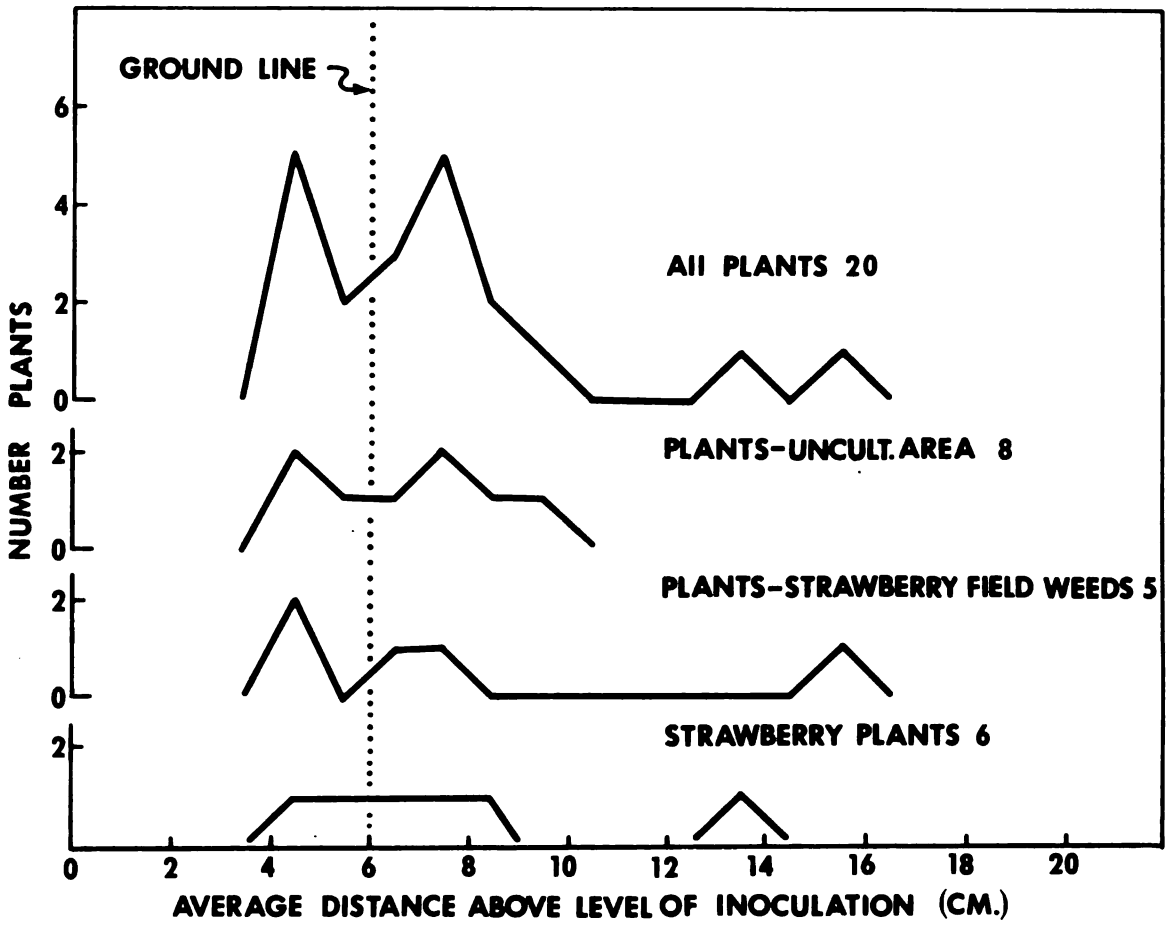

Figure 7.--Frequency distribution of test plants as shown by the number of test plants in each respective group plotted against the average distance moved (cm) by 20 isolates in 4 replications.

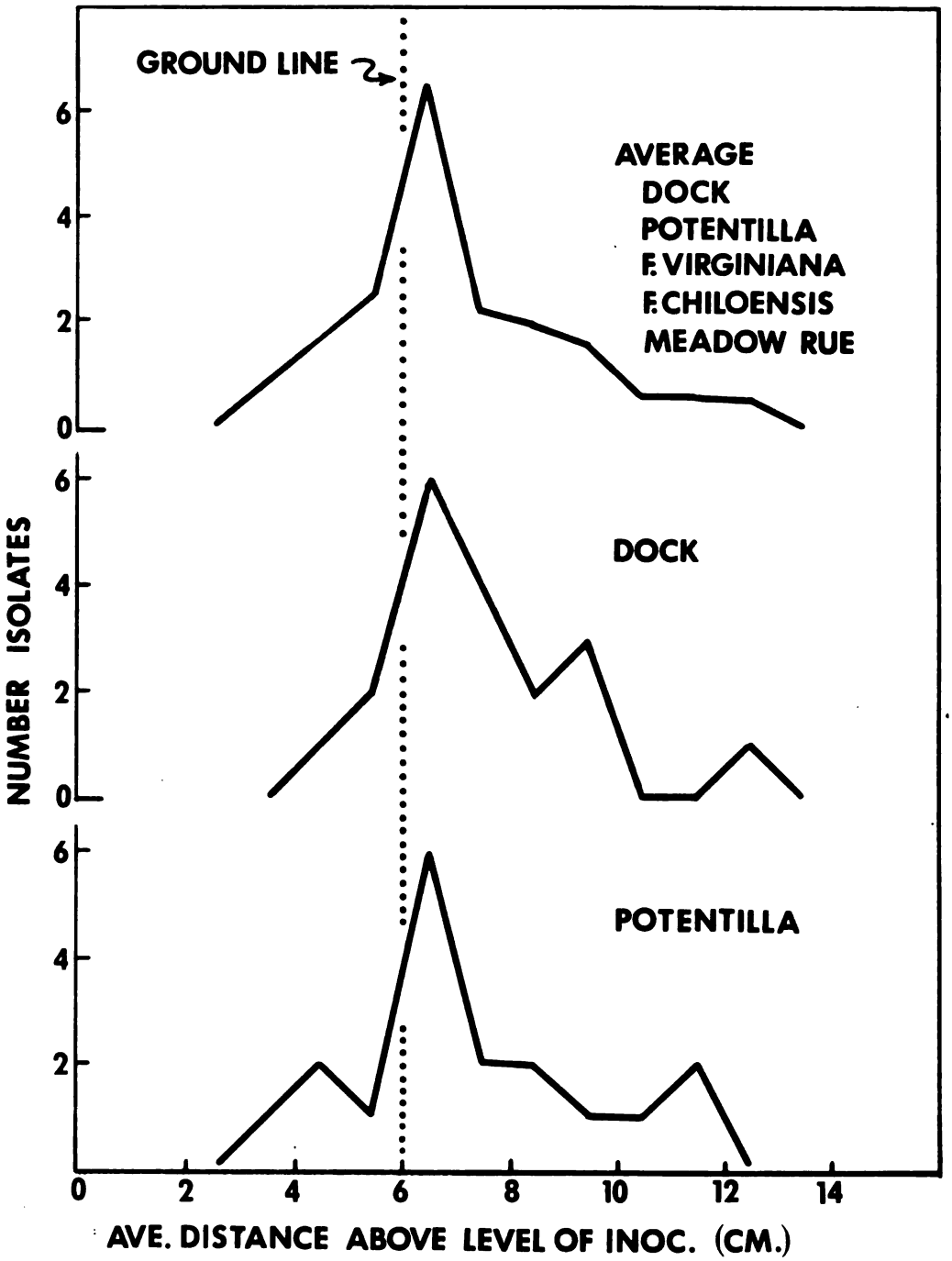

Figure 8a.--Frequency distribution of the 20 isolates on Dock, Potentilla, F. virginiana etc., as shown by the average distance they moved (cm) from the level of inoculation.

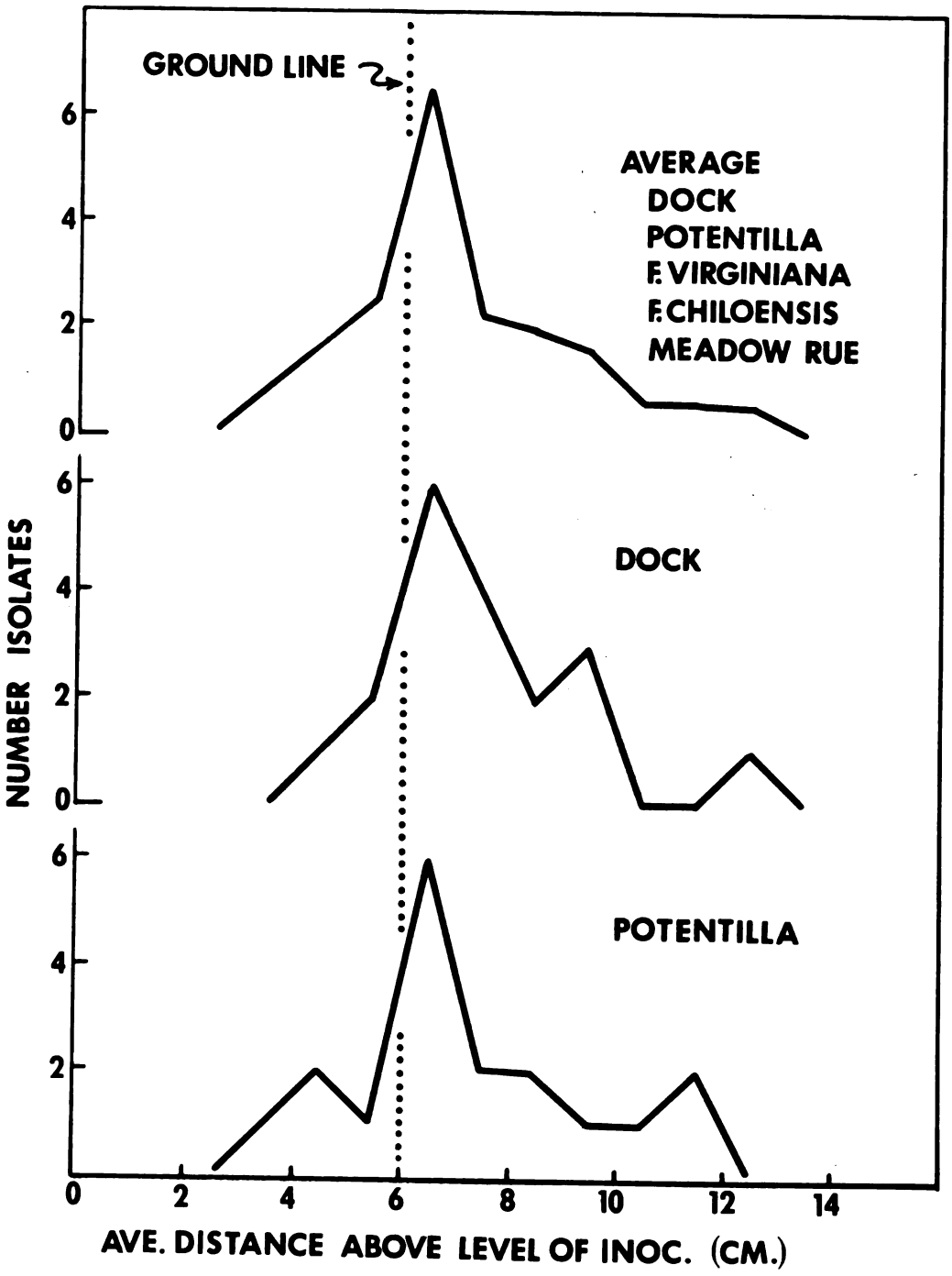

Figure 8b.--Frequency distribution of the 20 isolates on dock, potentilla, F. virginiana, etc., as shown by the average distance they moved (cm) from the level of inoculation.

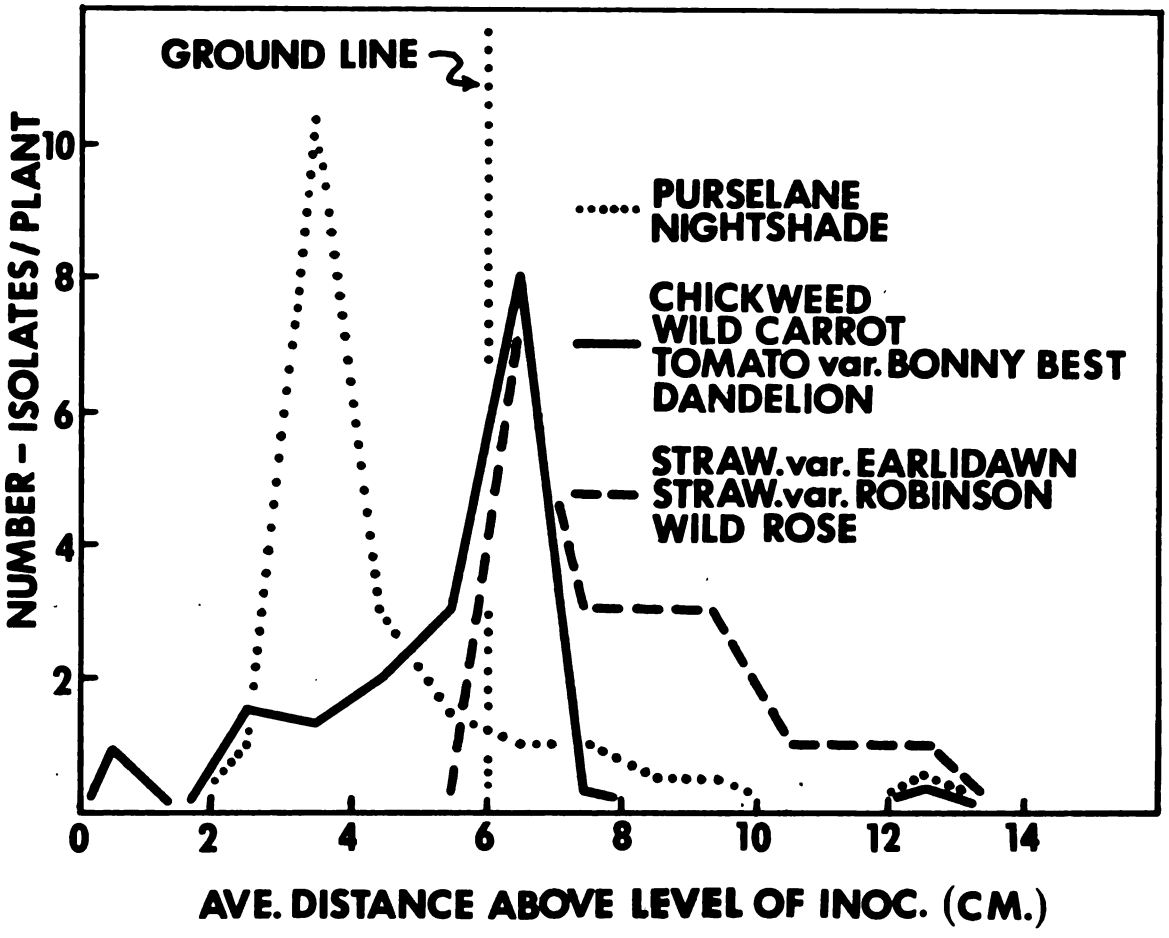

Figure 9.--Frequency distribution of the 20 isolates on these groups of plants, as shown by the average number of isolates per plant species of each respective group plotted against the average distance they moved (cm) from the level of inoculation.

DISCUSSION

The similarity of 4 isolates from soil in uncultivated sites and 3 isolates from crop plants in cultivated areas with regards to host range and parasitic potential suggests that isolates from cultivated strawberry could have originated in formerly uncultivated areas and are indigenous to this area. The parasitic potentials of isolates from uncultivated areas on cultivated strawberry supports this.

Resistance to Verticillium wilt of strawberry has been found in wild strawberries of North and South America (20, 28, 30, 31) and presumably is the result of a prolonged interaction between host and parasite. This resistance also indicates that Verticillium is indigenous to this continent.

The susceptible wild rose, Potentilla and wild strawberries found in the uncultivated areas presumably could enable the fungus to persist and multiply in these uncultivated areas even in the absence of strawberry.

Similarly, weeds commonly found in cultivated strawberry fields as Pigweed, chickweed and white cockle may serve as hosts for multiplication of Verticillium (32). Verticillium is also reported to multiply in the rhizosphere and infect roots of susceptible or resistant peppermint, tomato and corn (10)(13). Thus good weed

control or crop alternation with non-multiplication hosts if possible would reduce the incidence of Verticillium wilt.

SUMMARY

The origin of Verticillium albo-atrum on strawberry was investigated by conducting a survey of the host range and parasitic potentials of 13 isolates from cultivated crops and 7 from uncultivated areas on 20 different plants normally growing in these two areas.

All isolates were parasitic on each test plant with the exception of the peppermint isolate on violet. Isolates from the uncultivated areas were parasitic on cultivated strawberry and thus are potential pathogens.

Three isolates from soil in uncultivated areas and 4 isolates from crop plants in cultivated areas were similar in parasitic potential and host range, suggesting that the 4 isolates from the cultivated areas could have originated in an uncultivated area.

Some plants from both uncultivated and from cultivated areas were as susceptible to invasion by Verticillium isolates as susceptible cultivated plants and thus could serve as multiplication sites for the fungus.

BIBLIOGRAPHY

1. Basu, P. K. 1961. *Verticillium* disease of strawberry. Canadian Journal of Botany 39:165-196.

2. Braun, A. J. 1951. *Verticillium* wilt now recognized as a destructive disease of strawberries in New York State. (Abstr.) Phytopathology 41:4.

3. Caroselli, N. E. 1961. *Verticillium* wilt of smoke bush. Plant Disease Reporter 45:24-25.

4. Cunningham, G. H. 1951. Plant disease investigations. 25th Annual Report New Zealand. Department of Scientific and Industrial Research. 1950-51:51-56.

5. Dobie, N. D., E. K. Vaughan, P. W. Miller and G. F. Waldo. 1958. New Facilities and procedures used for growing disease-free strawberry plants in Oregon. Plant Disease Reporter 42:1048-1050.

6. Engelhard, A. W. 1957. Host index of *Verticillium albo-atrum* Reinke & Berth (including *Verticillium dahliae* Kleb.) Plant Disease Reporter Supplement 224, pp. 24-49.

7. Fordyce, C. and R. J. Green. 1960. Studies of the Host specificity of *Verticillium albo-atrum* var. *menthae*. (Abstr.) Phytopathology 50:635.

8. Fulton, R. H. 1952. The disease problem with small fruits. Michigan State Horticulture Society Annual Report 1951:69-70.

9. Green, R. J. 1933. Studies on the host range of the *Verticillium* that causes wilt of *Mentha piperita* L.. Science 113:207-208.

10. Horner, C. E. 1954. Pathogenicity of *Verticillium* isolates to peppermint. Phytopathology 44:239-242.

11. Keyworth, W. G. and M. Bennett. 1951. *Verticillium* wilt of strawberry. Journal of Horticultural Science 26:304-316.

12. Lacy, M. L. and C. E. Horner. 1962. Reproduction of *Verticillium* in the rhizosphere and subsequent root infection of resistant and susceptible mint species. (Abstr.) Phytopathology 52:739.

13. Lacy, M. L. and C. E. Horner. Behavior of Verticillium dahlie in the rhizosphere and roots of host and non-host plants. In press.

14. Lacy, M. L. and C. E. Horner. Verticillium wilt of mint: interactions of inoculum density and host resistance. In press.

15. McKeen, W. E. and J. E. Bosher. 1955. Verticillium wilt of strawberry in British Columbia. Plant Disease Reporter 39:371-372.

16. Nadakavukaren, M. J. and C. E. Horner. 1959. An alcohol agar medium selective for determining Verticillium microsclerotia in soil. Phytopathology 49:527-528.

17. Nelson. R. 1947. Verticillium albo-atrum from M. piperita is specific to this host and closely related sp. of Mentha. (Abstr.) Phythopathology 37:17.

18. Nelson, R Verticillium wilt of peppermint. East Lansing, 1950. 259 p. (Michigan Agricultural Experiment Station Technical Bulletin No. 221).

19. Nees Von Esenbeck, C. G. 1816. Das System der Pilze and Schwamme. 329p. 46pl. Stahelschen Buchhandlung, Wurzburg.

20. Newton, W. and M. C. J. Van Adrichem. 1958. Resistance to Verticillium wilt in F_1 generations of Fragaria. Canadian Journal of Botany 36:297-299.

21. Reinke, J. and G. Berthold. 1879. Die Zersetzund der Kartoffél durch Pilze. Universitat Gottingen, Untersuchungen Botanisches Laboratorium 1:1-100. Berlin, Weigandt, Hempel, and Parey.

22. Rudolph, B. H. 1931. Verticillium hydromycosis. Hilgardia 5:197-353.

23. Sewell, G. W. F. and J. E. Wilson. 1958. Weed host of the progressive hopstrain of Verticillium albo-atrum Reinke and Berth. Report of the East Malling Research Station 1957, pp. 126-128.

24. Thomas, H. E. 1931. Verticillosis of strawberries. (Abstr.) Phytopathology 21:996.

25. Thomas, H. E. and E. V. Goldsmith. 1945. The Shasta, Sierra, Lassen, Tahoe and Donner strawberries. Bulletin of the California Agricultural Experiment Station 690.

26. Thomas, C. A. and R. E. Webb. 1956. Peppermint wilt induced by a Verticillium isolate from potato. (Abstr.) Phytopathology 46:238.

27. Torgenson, D. C. 1952. Observations of Verticillium wilt of geranium in Oregon. Plant Disease Reporter 36:51.

28. Van Aldrich, M. C. H. and W. R. Orchard. 1958. Verticillium wilt resistance in the progenies of Fragaria chiloensis from Chile. Plant Disease Reporter 42:1391-1393.

29. Van DenEnde, G. 1956. De reacties van verschillende waardplanten bij a antosting door Verticillium spp. (Abstr.) Tigdschrift over Plantenziekten 62:21 .

30. Varney, E. H., J. N. Moore and D. H. Scott. 1959. Field resistance of various strawberry varieties and selections to Verticillium Plant Disease Reporter 43:567-569.

31. Wilhelm, S. 1955. Verticillium wilt of the strawberry with special reference to resistance. Phytopathology 45:387-391.

32. Wilhelm, S. and H. E. Thomas. 1952. Solanum sacachoides, an important weed host to Verticillium albo-atrum. (Abstr.) Phytopathology 42:519-520.

33. Zimmer, D. E. 1964. Pathogenicity of Verticillium isolates to safflower. Plant Disease Reporter 48:456-457.